FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES

JOHANN WALCH (1725–1778)
NATURAL PHILOSOPHER, PROFESSOR OF THEOLOGY,
AND EARLIEST RESEARCHER ON TRILOBITES

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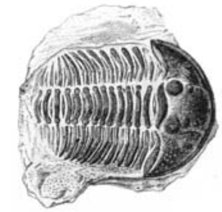

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FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES: INTRODUCTION

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As technical and general editor of this collection of these reports on the history of trilobite research, it is truly a delight to turn this collection over to the printer. Of course, it is relief to have finished checking everything from the correct use of n-dashes vs hyphens to whether or not current stratigraphic designations have been used in the manuscripts. But more importantly, this collection of fifteen papers is a significant contribution to the history of science, in general, and to the history of trilobite paleontology, in particular.

At the beginning of the 21st century, trilobite research has become perhaps the most dynamic subdiscipline of invertebrate paleontology. Research on the group ranges from its traditional systematic and biostratigraphic focus to applications in paleogeographic reconstructions and evolutionary theory.

The complexity, beauty, and mystery of trilobite fossils has long been appreciated by Paleolithic and pre-modern peoples (St. John and Peng [history of Chinese trilobite research]), This appreciation of trilobites is still reflected by the high prices that well-preserved and –prepared trilobites are sold for in the early and modern commercial fossil trade (see Mikulic and Kleussendorf). However, it is only with the "European Enlightenment" that trilobite fossils were first fit into interpretations of the "Scala naturae," although even Edward Lhwyd's first published illustrations of trilobites at the end of the 1600s only compared them to the forms of living organisms, but still somehow refused to admit their biological origin. The early 18th century saw their recognition as the remains of ancient life forms (St. John). By late in the 18th century, Johann Walch established that trilobites were most likely arthropods, and Khim and St. John's report helps flesh out an important "natural philosopher" known to most paleontologists merely as a "name" that coined the word "trilobite." For this reason, a portrait of Walch takes "pride of place" as the cover illustration of this bulletin.

For over a century, trilobite research was a small universe dominated by western and central Europeans (see Bruthansová *et al.)* and, later, North Americans, who took their craft to other continents. However, this scientific approach to the study of ancient life was quickly adopted by local scientists (Choi, Ghilardi and Simões; Jell, Peng [history of trilobite research in China and "biographies"]). Acute observations meant that the contributions of early synthesizers are still particularly pertinent to trilobite systematics (Bergström, Bruthansová *et al.*). The contributions of the gifted amateur, some of whom became renowned paleontologists (Brant and Davies) whether or not they had any formal training in geology or paleontology (see Yochelson), were important in the 19th century. The small world of paleontologic research and the important role of a very few men, yes, this was a male dominated pursuit then, and the New York State Museum (NYSM) in the 19th century, is seen in a number of these papers. Indeed, the young Walcott, then an NYSM employee visited Hartt (who first studied New Brunswick and Brazilian trilobites) in Saint John, New Brunswick, as well as members of the "Cincinnati School" at about the time he discovered the first incontrovertible evidence for arthropod limbs (papers by Yochelson, Ghilardi and Simões, Brandt and Davies). Walcott left the NYSM for the U.S. Geological Survey and made a major contribution to Chinese trilobite research and later, for better or for worse, hired Resser as the Survey's trilobite paleontologist (Yochelson and Sundberg reports), while John Mason Clarke, then Director of the NYSM, went to Brazil, and played an important role in documenting Devonian high latitude trilobites (Ghilardi and Simões).

Modern trilobite research is a more truly international science with the development of native-born national specialists on a number of continents (Ghilardi and Simões, Jell, Peng ["biographies"]), and an approach that includes the ethology and other aspects of the paleobiology of these arthropods (Babcock). The volume includes a contribution by Harry Whittington, one of the most important figures in modern trilobite research, and the supervisor of or model for many current trilobite researchers. Whittington ends this volume with the frank statement that, yes, we know so much about these extinct organisms, but we're also delighted that so many problems remain to be clarified about their higher-level phylogeny. At a time when the U.S.' public and media have again constructed a "controversy" between the reality of testable evolutionary science and a revealed belief system that includes creationism and "intelligent design," Whittington's short paper demonstrates the real satisfaction that can come from understanding the uncertainties about origins, but knowing that there are reality-based methods to resolve these uncertainties. If creationism and "intelligent design" ultimately

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prevail in the U.S. as the way to interpret our shared natural heritage, the contributions to this volume suggest that a scientific approach to understanding ancient life will continue to prevail in places like the Czech Republic, South Korean, Brazil, Australia, Britain, Sweden, and China.

The original concept for a volume on the history of trilobite research was D. Mikulic's. He and J. Kleussendorf solicited and brought the manuscripts together for publication and did preliminary editing. With a change in publishing venue, E. Landing completed the technical and line editing for this work's publication as a New York State Museum Bulletin.

ROLE OF MALFORMATIONS IN ELUCIDATING TRILOBITE PALEOBIOLOGY: A HISTORICAL SYNTHESIS

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ABSTRACT—Malformations of the exoskeletons of trilobites include injuries, teratological conditions, and pathological conditions. More than 1100 malformed specimens have been recognized since the 1840s, but until the late twentieth century, their paleobiological value was largely overlooked. In the early literature (mid-1800s to mid-1900s), malformed specimens were commonly treated as monstrosities or curiosities, and were described in the systematic literature along with specimens of normal morphology. A number of malformed specimens were not recognized as such when originally published, but this rarely led to erroneous conclusions about morphology. In at least one example, though, a species name was proposed for a single, malformed specimen.

Beginning in the 1880s, malformed specimens were occasionally treated outside of the purely systematic literature. From the 1950s–1990s, the number of papers on malformed trilobites rose dramatically. With the availability of a relatively large data set, interpretive work followed. Healed injuries have provided data on wound healing, configuration of the vital organs within the body, predator-prey relationships in the Paleozoic, and molting. Healed injuries due to sublethal predation have provided convincing evidence that predation played a significant role in metazoan evolution in the Early Paleozoic, and have provided the earliest known evidence for behavioral lateralization of some Paleozoic animals. Teratological conditions in trilobites have provided information about developmental patterns in the exoskeleton and, indirectly, about chromosomal plasticity. Pathological conditions in trilobites have provided information about some of the earliest putative examples of uncontrolled cellular growth, and how trilobites responded to attack by microorganisms and some boring organisms.

INTRODUCTION

The historical record relating to the study of malformations in trilobites is comparatively short. Recognition of trilobite malformations in the paleontological literature can be traced to the 1840s. However, few examples were published until the middle of the twentieth century. Apart from a report by Oehlert (1895) on approximately 800 specimens of the Ordovician trinucleid trilobite *Onnia pongerardi*, more than 90% of the trilobites documented with malformations have been published since 1950. By 1993, more than 300 malformed specimens, other than those of *O. pongerardi* reported by Oehlert (1895), were reported (Babcock, 1993a).

From modest beginnings as scientific curiosities or monstrosities (Portlock, 1843), malformations have emerged as an important source of paleobiological information on trilobites and associated Paleozoic organisms. They have provided insights into the physiology and behavior of animals that have had consequences across major taxonomic lines. Temporally, the impact of studies on trilobite malformations extends from animals of Cambrian age to modern forms. As summarized in this report, malformations have contributed to our understanding of wound response in trilobites. This has led to improved insights into morphological development, morphological plasticity, parasitic response, and molting. Malformations have provided important proxy information about the internal organization of trilobites, notably the locations of vital organs. Such information is rarely made available through by the fossilization of internal soft tissues. Finally, study of malformations has provided significant insights into the behavior of trilobites. Malformations have been a primary source of information concerning the importance of predation as a forcing factor in evolution. In particular, they record predator-prey interactions associated with skeletalization during the Cambrian explosion, and document further exoskeletal development associated with biological "arms races" during the Paleozoic (i.e., the Early and Middle Paleozoic Marine Revolutions). Malformations of trilobites provided key evidence for the early evolution of lateralized (left-right asymmetrical) nervous systems, and this has had important implications in other areas of the life sciences.

In this report, the published record of trilobite malformations is reviewed, as are the contributions to paleobiology that studies of trilobite malformations have afforded. An overview of the historical documentation of trilobite malformations is discussed first. Next, the types of injuries observed at the organismic level, the classification of malformations, and the origins of malformations at the cellular level, are discussed. Finally, the ways in which malformations helped to shape our understanding of trilobite paleobiology and the history of life are addressed.

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HISTORY OF STUDY

Reports of malformed trilobites from the nineteenth century are few in number, and it seems that no such specimens were published on prior to that time. During the 1800s, contributors to the literature on malformations included Portlock (1843), Owen (1852a, b), Walcott (1883), Hall and Clarke (1888), and Oehlert (1895). Illustrations from some of these early studies are reproduced in Fig. 1. In addition to studies on genuine abnormalities during the 1800s, Portlock (1843, p. 360, Pl. 21, fig. 5a; reproduced herein as Fig. 1B, 1C) and Peach (1894, p. 32, fig. 15) illustrated borings in trilobite exoskeletons. These examples of borings have been included in some previous discussions of malformations in trilobites (e.g., Størmer, 1931; Owen, 1985). However, they do not appear to qualify as true malformations because of the lack of definitive evidence for a cellular response in the living trilobites. These borings are only relevant to trilobite taphonomy (compare with borings showing cellular response to invasion; Conway Morris, 1981; Babcock, 1993a; Babcock and Peng, 2001).

Portlock (1843) seems to have provided the earliest report, including a description, of a malformed trilobite. Among the Carboniferous fossils in his "Report on the Geology of the County of Londonderry, and of Parts of Tyrone and Fermanagh," Portlock (1843, Pl. 11, fig. 4; reproduced herein as Fig. 1A; see Owens, 2000, fig. 2J) illustrated a pygidium of the phillipsiid *Phillipsia ornata* from Hook Head, County Wexford, Ireland, with three misshapen pleural ribs and interpleural furrows on the left side. In the accompanying description, Portlock (1843, p. 307) termed the specimen "a monstrosity, in which the upper side segments of one side have been singularly distorted."

Geological work conducted in frontier areas of America during the 1800s brought to light numerous fossils, many of them representing new taxa, and among the fossils described in early reports was at least one malformed trilobite. Owen (1852a, p. 574), in "Report of a Geological Survey of Wisconsin, Iowa, and Minnesota; and incidentally of a Portion of Nebraska Territory," described the new species *Dikelocephalus minnesotensis* from the Cambrian of Minnesota. In an accompanying volume, "Illustrations to the Geological Report of Wisconsin, Iowa, and Minnesota," Owen (1852b) illustrated several specimens assigned to *D. minnesotensis*. One of them (Owen, 1852b, Table I, fig. 1), a pygidium that Hughes (1994) later designated the lectotype of *D. minnesotensis*, shows malformed pleural ribs on the left side. The malformation, although quite clear in a photograph (Hughes, 1994, Pl. 11, fig. 18), is difficult to identify in Owen's (1852b) medal-ruled steel-plate engraving.

Walcott (1883; reprinted 1884) described a small right eye surrounded by a deformed area of the cephalon in a specimen from the Ordovician Trenton Limestone (presumably from New York) that he identified as *Illaenus crassicauda*. The specimen, from the collection of W. P. Rust of Trenton Falls, New York, was not illustrated, nor is its current location known. Walcott's (1883) report represented the first time that a malformed specimen was described apart from purely systematic or biostratigraphic work. The report also represents the first time that the cause of a malformation was hypothesized. Walcott (1883, p. 302) provided evidence that the abnormal eye was the result of an injury sustained during molting. In addition to his discussion of the malformed illaenid trilobite from the Trenton Limestone, Walcott (1883) mentioned other instances of malformation, and noted the frequency of malformation in trilobites. Walcott (1883, p. 302) stated that among the thousands of trilobites with eyes that he had examined, Rust's *I. crassicauda* specimen was the only one to show "any distortion or injury that occurred during the life of the animal." He also noted (Walcott, 1883, p. 302) that in "a few instances, the shell of the pygidium of *Asaphus platycephalus* has shown evidence of local fracture that appears to have occurred during the life of the animal, but these were very unsatisfactory."

Holm (1886, p. 92, Pl. 2, fig. 5a–c; numbered as 5a, 5b, 5d on the plate) described and illustrated a malformed cephalon of *Illaenus revaliensis* from the Silurian of Estonia. This report is notable, as it represents another early attempt to interpret the cause of a malformation. The right side of Holm's (1886, fig. 5a–c) specimen is of normal morphology, but the left side shows considerable deformity of the fixed and free cheeks, axial area, and posterior margin. The specimen has developed a doubling of the facial suture on the left side (which continues around the anterior of the glabella), a rearward displacement of the left eye, and an elongation of the left genal area. The second facial suture is incomplete, and probably was nonfunctional. Pits are developed along the left side of the glabella. The area of thoracic articulation is severely malformed on the left side, apparently because of an incomplete fusion of the first thoracic segment to the posterior cephalic margin. Holm (1886, p. 92) interpreted the origin of the malformation as damage initially suffered during molting, although disease may have exacerbated the deformity.

Hall and Clarke (1888), in Volume 7 of the landmark series "Palaeontology of New York," illustrated two malformed dalmanitid specimens of Devonian age. One specimen (Hall and Clarke, 1888, Pl. 13, fig. 6; reproduced herein as Fig. 1D) is a small pygidium of *Dalmanites* (*Coronura*) *aspectans* [*Coronura aspectans* of Harrington (1959) and Babcock (1997)] from Ohio with a "pathological deformity." Owen (1985) later suggested that the malformed pleural ribs on both sides of the *Coronura* pygidium were the result of larval injury or disease; he thought it unlikely that the abnormality was due to repair of an injury sustained late in life. A specimen referred to *Dalmanites* (*Cryphaeus*) *boothi*, var. *calliteles* by Hall and Clarke (1888, Pl. 16, fig. 22) [reproduced herein as Fig. 1E, upper left of slab; now *Bellacartwrightia jennyae* of Lieberman and Kloc (1997)] from New York shows a genal spine that was recognized as broken and healed prior to fossilization.

Oehlert (1895) reported that bifurcations along the genal spines of *Trinucleus pongerardi* [*Onnia pongerardi* of Owen (1985)] were quite common. These malformations occurred in 800 specimens that he studied from western France.

Few malformed trilobites were described during the first half of the twentieth century. About 20 such specimens appear in the literature from 1901 to 1950. These reports include those of Schmidt (1906), Burling (1917), Isberg (1917), Warburg (1925), Richter and Richter (1934), Saito (1934), Sun (1935), Lochman (1936, 1941), Westergård (1936), Kay (1937), Öpik (1937), Resser and Howell (1938), Resser (1939), Prantl (1947), and Sinclair (1947). Of these papers, only Burling (1917), Isberg (1917), Lochman (1941), and Sinclair (1947) were devoted to malformed trilobites; the other papers were monographic works that reported malformed specimens.

An olenellid cephalon, the holotype and only known

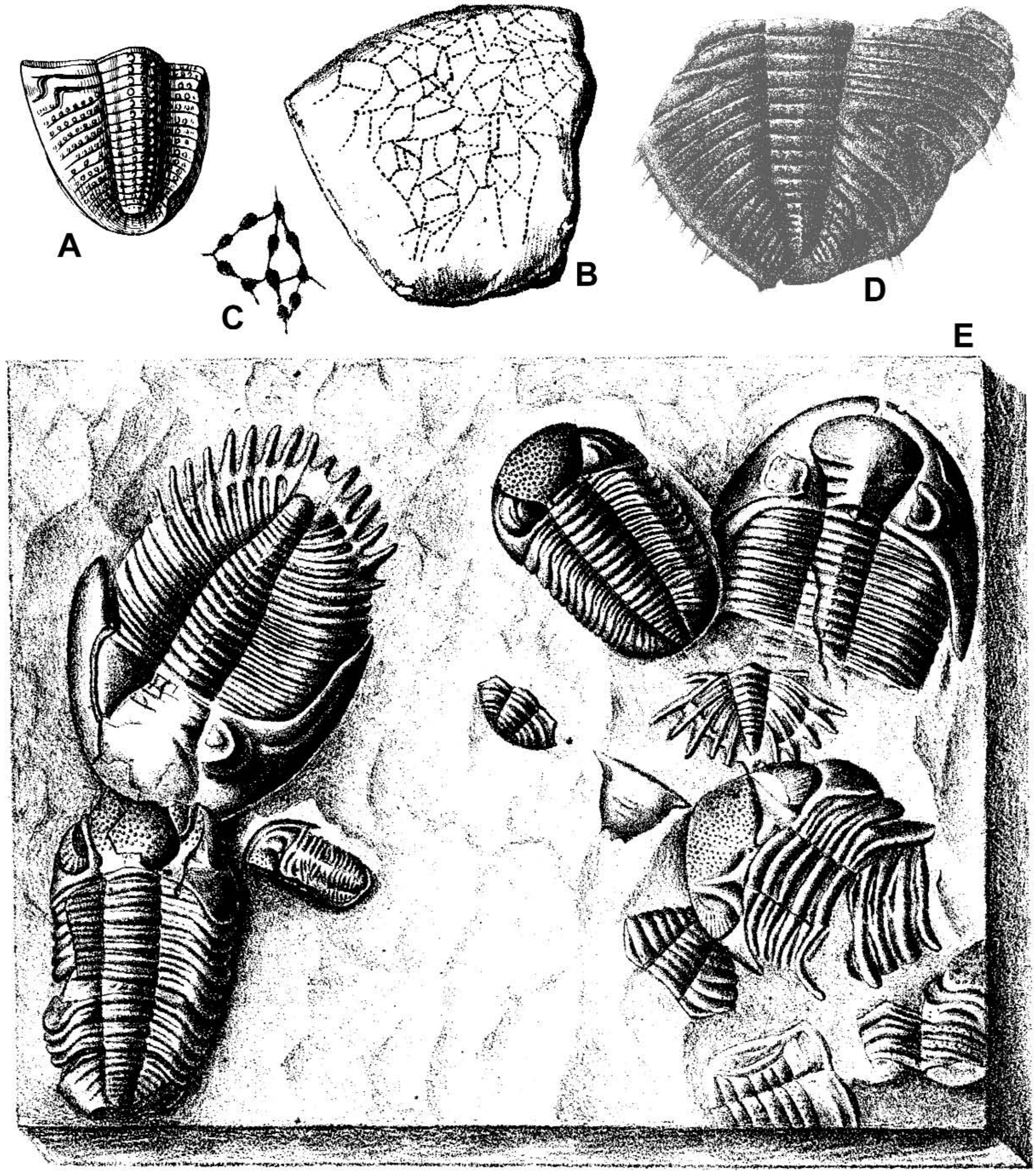

Fig. 1. Nineteenth century illustrations of malformed trilobites and postmortem borings. A, *Phillipsia ornate* pygidium with deformed pleural ribs and furrows on left side, illustrated by Portlock (1843, Pl. 11, fig. 4; reillustrated by Owens, 2000, fig. 2J); Ballysteen Formation (Carboniferous), Hook Head, County Wexford, Ireland; x1.5. B, C, Borings, *Entobia antiqua*, in exoskeleton of a trilobite, illustrated by Portlock (1843, Pl. 21, figs. 5a, 5b); Silurian, County Tyrone, Ireland; B, x1.5; C, enlargement of borings. D, *Coronura aspectans* pygidium with malformed pleural ribs on right and left sides and malformed margin on right, illustrated by Hall and Clarke (1888, Pl. 13, fig. 6) as *Dalmanites* (*Coronura*) *aspectans*; Columbus Limestone (Devonian), Columbus, Ohio; x1.5. E, *Bellacartwrightia jennyae* (upper left) with broken, healed, and regenerated right genal spine, illustrated by Hall and Clarke (1888, Pl. 16, fig. 22) as *Dalmanites* (*Cryphaeus*) *boothi*, var. *calliteles*); other specimens on slab are *B. jennyae*, *Eldredgeops rana*, and *Harpidella craspedota*; Ludlowville Formation, Centerfield Member (Devonian), Centerfield, New York; x1.5.

specimen, of *Olenellus peculiaris* Resser and Howell (1938, p. 223, Pl. 6, fig. 10; herein, Fig. 2E), was not recognized as a malformed specimen in its first description. The specimen from the Cambrian of Pennsylvania shows a large, asymmetrical, W-shaped healed injury and bases of two anomalous spines (broken in preparation prior to illustration by Resser and Howell, 1938) on the left side. The cephalon is on a small slab that is broken on the right side, which means that the shape of

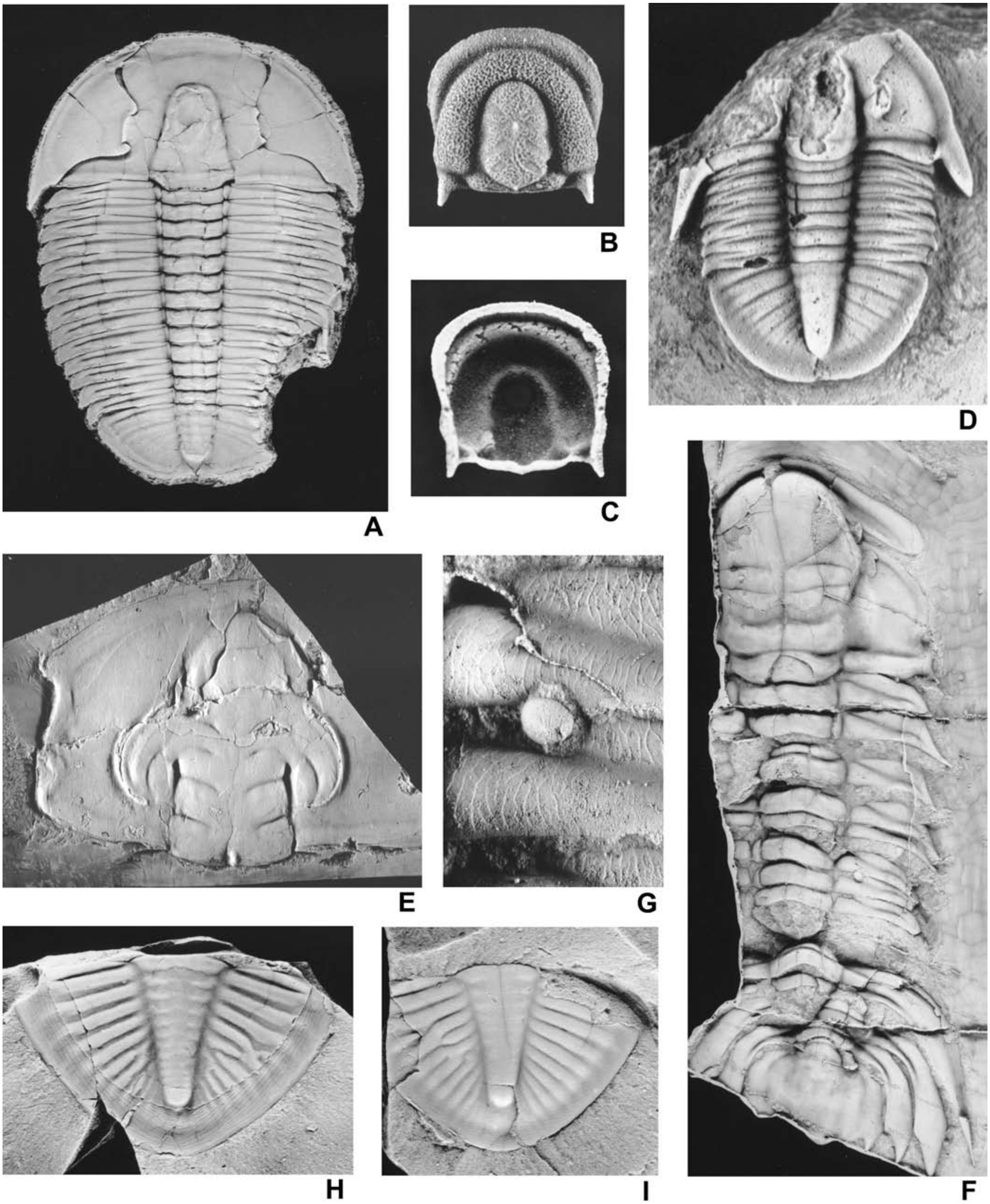
A
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Fig. 2. Examples of malformations in trilobites. A, *Elrathia kingii* with healed injury, a probable sublethal predation scar, on right posterior thorax and pygidium; an anomalous spine has developed at anterior of injured area; Wheeler Formation (Cambrian), House Range, Utah; x2.7; University of Kansas Museum of Invertebrate Paleontology, Lawrence, Kansas (KUMIP) 204773. B, C, *Arthrorhachis elspethi*, silicified cephalon with small boring to right posterior of axis in dorsal (B) and ventral (C) view; a small protruberance that has developed around the boring is evident on ventral side; Edinburg Limestone (Ordovician), near Strasburg Junction, Virginia; x15; KUMIP 204772. D, *Cedaria minor*, exoskeleton with injured and healed right genal area and regenerated genal spine; the injury is of uncertain origin; Weeks Formation (Cambrian), House Range, Utah; x3.5 KUMIP 259299. E, *Olenellus getzi* (holotype of *O. peculiarus* Resser and Howell, 1938), cephalon with large scar, inferred to be a sublethal predation scar, on left; bases of anomalous spines that were broken in preparation at anterior end and near middle of the injury; enlargement and deformation of exoskeleton present near margin of injured area; Kinzers Formation (Cambrian), near Rohrerstown, Pennsylvania; x1.1; United States National Museum (USNM) 90809. F, G, *Centropleura loveni*, latex cast of molt ensemble with tumor-like neoplasm in right posterior of thorax (F) and enlargement of the neoplasm and surrounding area (G); Kap Stanton Formation (Cambrian), J. P. Koch Fjord, Peary Land, North Greenland; F, x1.2; G, x8; Geologisk Museum, Copenhagen (MGUH) 21.083. H, *Pseudogygites latimarginatus* pygidium with abnormal, presumably teratological, pleural ribs on left and right; Whitby Formation (Ordovician), Bowmanville, Ontario; x2.2, Orton Geological Museum, The Ohio State University (OSU) 46321. I, *Pseudogygites latimarginatus* pygidium with abnormal, presumably teratological pleural ribs on left; Whitby Formation (Ordovician), Bowmanville, Ontario; x2.2, OSU 46396.

the undeformed genal area is not evident. Campbell (1969) recognized the specimen as an injured example of *Olenellus thompsoni*. Babcock (1993a, 2003) concurred with the view that it is an injured individual. Based on Lieberman's (1999) analyses, the specimen probably should be referred to *O. getzi*.

Beginning in the 1950s, there was a dramatic increase in the reporting of malformed trilobites. The number of specimens described between 1951 and 1960 (more than 20) nearly doubled the total number known to that time, exclusive of Oehlert (1895). Papers published during the 1950s include Ross (1951, 1957), Lamont (1952), Hupé (1953a, b), Westergård (1953), Prantl and Pribyl (1954), Snajdr (1956, 1958, 1960), Tjernvik (1956), Whittard (1956), Whittington (1956a, b), Cave (1957), Harrington and Leanza (1957), Öpik (1958), Palmer (1958, 1960), Harrington (1959), and Dean (1960). Most of the malformed trilobites illustrated in the 1950s are specimens included in monographic works that emphasize systematics or biostratigraphy. The rise in the amount of described material coincided with an increase in the number of specialists who worked on trilobites. This helps to explain the relative paucity of reports of trilobite malformations prior to the 1950s. Notable among the papers that documented trilobite malformations in the 1950s is Snajdr's (1956) paper, the first in a long series of his papers on malformed trilobites that appeared over the next 34 years (Snajdr, 1956, 1958, 1960, 1978a, b, 1979a, b, c, 1980, 1981a, b, 1990a, b).

Between 1961 and 1970, the number of malformed specimens (exclusive of Oehlert, 1895) nearly doubled again. Reports published during this interval recorded more than 40 malformed trilobites [Chernysheva (1961), Öpik (1961, 1967), Hessler (1962), Tripp (1962, 1967), Palmer (1965, 1968), Selwood (1965), Whittington (1966, 1968), Campbell (1967), Dean (1967), Erben (1967), Ormiston (1967), Rushton (1967), Whittington and Campbell (1967), Ingham (1968), Osmólska (1968, 1970), Robison and Pantoja-Alor (1968), Shaw (1968), Clarkson (1969), Hughes (1969), Pribyl and Vanek (1969), Schrank (1969), Alberti (1970), and Vanek (1970)]. Most occurrences of malformed trilobites documented during the 1960s were part of larger taxonomic monographs or biostratigraphic works.

A steady increase in the rate of publication on malformed trilobites occurred during the 1970s and 1980s. During this time, more than 60 papers were published that reported more than 110 malformed specimens. The proportion of those publications devoted specifically to malformations was about 30%, which represented a substantial increase over the proportion of papers devoted to malformations prior to that time [only about 10% of relevant papers published from 1843 to 1970 were devoted to malformations]. Papers published during the 1970s and 1980s that emphasized malformations include Pocock (1974), Shaw (1974), Hughes *et al*. (1975), Alpert and Moore (1975), Ludvigsen (1977a), Snajdr (1978a, b, 1979a, b, c, 1981b, 1985), Rudkin (1979, 1985), Owen (1980, 1983a, 1985), Tasch (1980), Vorwald (1982), Conway Morris and Jenkins (1985), and Babcock and Robison (1989a, b). Other 1970s and 1980s papers, primarily monographic in nature, that documented malformations include Chatterton (1971, 1980), Hahn and Hahn (1971), Hammann (1971), Hughes (1971), Kraft (1972), Lane (1971), Pribyl and Vanek (1973, 1986), Ingham (1974), Shaw (1974), Fortey (1975, 1980), Jell (1975, 1989), Chlupác (1977), Evitt and Tripp (1977), Ludvigsen (1977b, 1979a, b, c), Bergström and Levi-Setti (1978), Cowie and McNamara (1978), Henry (1980), Holloway (1980), Owen and Bruton (1980), Strusz (1980), Ludvigsen *in* Boucot (1981), Owen (1981, 1982, 1983b), Snajdr (1981a, b, 1987, 1990b), Hahn *et al*. (1982), Howells (1982), Owen and Harper (1982), Ludvigsen and Westrop (1983), Ramsköld (1983, 1984), Wandås (1984), Briggs and Whittington (1985b), Blaker (1988), and Zhang (1989).

The 1990s saw a reversal of this trend, with fewer than 30 malformed specimens described for the first time. Babcock (1993a) noted that at least 300 malformed trilobites, excluding the specimens known to Oehlert (1895), are present in collections. Of the known specimens, only about one-third had been illustrated by 1993. Publications between the years 1991 and 2000 that were devoted to malformations include Han and Zhang (1991), Babcock (1993a, b, 2000), Owen and Tilsley (1996), and Taylor (1996). Other 1990s publications with malformed trilobites include Robison (1991), Babcock (1994), Hughes (1994), Holloway (1996), Blaker and Peel (1997), St. John and Babcock (1997), Whittington (1997), Conway Morris (1998), Nedin (1999), Buchholz (2000), and Owens (2000).

During the writing of this report, I knew of seven publications containing malformed trilobites published or in preparation: Babcock and Peng (2001), Babcock and Zhang (2001), Lee *et al*. (2001), Jago and Haines (2002), Whiteley *et al*. (2002), Babcock (2003), and Babcock *et al*. (2003). Related discussions of malformations on trilobites, without illustrations, include Babcock (2000, 2002), and Babcock and Peel (2002).

By the 1980s, a sufficiently large number of malformed trilobites were known to permit detailed syntheses, and to permit breakthroughs in our understanding of trilobite paleobiology. For example, Owen (1985) observed a temporal pattern in the record of trilobite malformations, with the number of malformations broadly following a period-level diversity curve for the Paleozoic. Other current interpretations of the origins of malformations, their classification, and the types of information that malformations convey, are outlined below.

An interesting pattern emerging in the literature on trilobite malformations is that these reports occur overwhelmingly in the English-language literature of Europe and North America. This suggests that malformed trilobites elsewhere have been underreported. This seems to be true despite a concerted effort to search Chinese and Russian faunal atlases (with the help of some colleagues listed in the Acknowledgments), particularly those on Cambrian trilobites. While it is certain that some published occurrences of malformed trilobites have been overlooked, the number of such occurrences is unlikely to substantially alter the relative proportions noted herein. More than 93% of the reports on malformations cited in this review article (n = 166; see the References) were published in Europe (62.7%) or North America (30.7%). Papers published in Australia (3.6%) and Asia (3.0%) account for the remaining literature. English-language papers account for 84.9% of the papers cited herein on trilobite malformations, whereas German-language accounts account for 8.4%, Czech-language papers for 3.0%, French-language papers for 2.4%, and Chinese- and Russian-language papers each for 0.6%. Literature on malformations in languages other than English include: Holm (1886), Isberg (1917), Richter and Richter (1934), Öpik (1937), Schrank (1969), Alberti (1970), Hahn and Hahn (1971), Hammann (1971), Hahn *et al.* (1982), Buchholz (2000) in German; Prantl and Pribyl (1954), Snajdr (1958, 1960, 1979c), Pribyl and Vanek (1973) in Czech; Oehlert (1895), Hupé (1953a, b), Henry (1980) in French; Han and Zhang (1991) in Chinese; and Chernysheva (1961; p. 225, pl. 27, fig. 5) in Russian. Some crossover literature exists, such as Zhang (1989), who reported in English on a malformed specimen from Asia in a journal published in Europe; Lee *et al.* (2001), who reported on a malformed specimen from Asia in a journal published in North America; Saito (1934), Sun (1935), Babcock and Peng (2001), and Babcock and Zhang (2001), all of whom reported on malformed specimens from Asia in English-language literature published in Asia; and Harrington and Leanza (1957), who reported in English on a malformed specimen from South America in a paper published in North America. Some studies, notably Hupé (1953b), Harrington (1959), Tasch (1980), Owen (1985), Babcock (1993a), and Whittington (1997), assessed material from all known sources globally, yet these workers provided few citations to papers from outside Europe and North America. Frequency in the published record of trilobite malformations is partly due to the large number of journals published in Europe and North America, and the large number of English-language journals (particularly journals that postdate 1950 when reports of malformations began to increase dramatically).

Overall, more than 120 paleontologists have contributed to the literature on malformations. Most of these workers spent much of their professional lives working in Europe and North America or on islands (e.g., Greenland and Spitsbergen) politically associated with those continents. This suggests a monographic bias in favor of European and North American collections. It also suggests that considerable information on malformations remains untapped in collections from Asia, Australia, South America, Africa, and Antarctica.

CLASSIFICATION AND ORIGINS OF MALFORMATIONS

Frequency of malformation

Trilobites rank among the best sources of information about the spectrum of malformation in fossil animals. Although malformations are more common in fossil mollusks and perhaps some other invertebrates (see Kelley *et al.*, 2003), trilobites have served as an important source of information on injuries, pathological conditions, and teratological conditions. The number of malformed trilobites is proportionally quite low (see Walcott, 1883; Conway Morris and Jenkins, 1995; Jago and Haines, 2002). Based on my observations, the frequency of malformed trilobites in collections typically ranges up to 2%; in rare instances it exceeds 5%. This estimate, however, does not compensate for frequency differences that might result from examination of separated sclerites compared to articulated exoskeletons, molt ensembles compared to carcasses, stratigraphic occurrence, paleoecological context, differing susceptibilities to malformations among various taxonomic groups, monographic bias, or any other source of error. It is merely a rough approximation of the frequency of malformed specimens among all examined material. Snajdr (1985) observed that about 0.05% of encrinurine trilobites have abnormalities; this estimate is well within the normal frequency range.

Rarely, populations of trilobites include high frequencies of malformed specimens. In an extreme case, Oehlert (1895) reported that approximately 40% of Ordovician *Onnia* from France have malformed genal spines. Hughes (1969) reported another notable example; in Ordovician *Cnemidopyge* from Wales, 5% of *C. nuda*, and 28% of *C. bisecta* specimens show malformed pygidia. Hughes (1994) observed that an unequal spacing of the pleural furrows was common in *Dikelocephalus* from the Cambrian of the United States. Approximately 5% of pygidia that he illustrated show strongly malformed pleural ribs.

Malformation classification

Owen (1985) was the first to comprehensively survey trilobite malformations, and to employ a system for classifying them. Owen's (1985) work built upon, refined, and corrected a scattered literature on trilobite malformations. Prior to 1985, there was little consensus about the origin of malformations. Burling (1917), Lochman (1941), Sinclair (1947), Ludvigsen (1977a), Snajdr (1978a, b, 1979a, b, 1981b), Rudkin (1979), and Owen (1980, 1983a) provided important insights into the causes or repair history of most types of trilobite malformations.

According to Owen (1985), macroscopic trilobite malformations have three principal causes: 1), injuries, which resulted from physical breakage of the exoskeleton, followed by healing (cicatrization; Figs. 1E, 2A, D, E); 2), teratological conditions, which resulted from genetic or embryological malfunction (Figs. 1A?, 2H, I); and 3), pathological conditions, which resulted from disease or parasitic infection (Figs. 2B, C, F, G). Owen (1985) noted that not all of these malformations can be classified unambiguously. Some injuries in advanced stages of repair, for example, cannot be easily distinguished from teratologies if evidence of fracturing or callusing is lacking (Babcock *et al.*, 2003). Similarly, without evidence of swelling or boring, a local atrophy of the exoskeleton may be attributed to injury or teratological processes. Furthermore, some borings in organisms record predation (e.g., Carricker and Yochelson, 1968; Kelley and Hansen, 1993; Conway Morris and Bengtson, 1994; Kelley *et al.*, 2003), whereas others result from relationships that are parasitic (e.g., Conway Morris, 1981; Boucot, 1990) or symbiotic (e.g., Brett, 1978, 1985; Boucot, 1990).

Sublethal injuries in trilobites were likely the result of predaceous attack (Figs. 2A, E) or uncertain causes (mostly accidents; Figs. 1E, 2D). Owen (1985) noted that most injuries were probably sustained during molting or in the intermolt phase before hardening of the new exoskeleton, and that the features most susceptible to injury during molting were spines (Fig. 2D), bilamellar fringes, and narrow gaps between the dorsal exoskeleton and the doublure. Supporting evidence for the level of risk during molting was provided by a specimen of the Cambrian form *Ogygopsis* that evidently died during a failed attempt to shed its old exoskeleton (McNamara and Rudkin, 1984). Relatively minor injuries to the margins of sclerites, including some described by Dean (1960), Whittington (1968), Snajdr (1978a, 1979a), Ludvigsen (1979c), Owen (1983a, 1985), and Babcock (1993a), suggest molting injuries.

As distinguished by Babcock and Robison (1989a) and Babcock (1993a), lacerations incurred during predaceous attack 1) occur on areas of the exoskeleton not likely to have been injured accidently (such as spines, broad cephalic or pygidial borders, and areas that were operational in molting); 2) occur over a relatively extensive area of the body (often on two or more adjacent sclerites; Fig. 2A); and 3) are generally arcuate to triangular or asymmetrically W-shaped (not simple straight, slightly curved, or jagged breaks as might be expected from accidental damage; Figs. 2A, E).

Nedin (1999) noted an additional characteristic of some sublethal predation scars—their bilateral expression on the trilobite exoskeleton. Although relatively rare (Babcock, 2003), injuries to both sides of the exoskeleton, if they occurred at the same time (as indicated by the extent of repair during molt phases succeeding the injury), are strong evidence of sublethal attack by an organism with bilateral, rapacious limbs.

Sublethal malformations and healing

Babcock (1993a) integrated information from medical science (see Purtilo, 1978) with the study of trilobite malformations. In distinguishing between malformations at a macroscopic level and the cellular level, this work provided an enhanced understanding of the causes of macroscopic malformations in trilobites and other ancient organisms. The work also provided further support for Owen's (1985) classification scheme. Babcock (1993a) hypothesized that cells of living trilobites adapted to injury by four processes. These included: 1) compensatory hypertrophy, which occurred when cells were diseased or removed and the remaining cells compensated for the loss by increasing their mass; 2) hyperplasia, in which lost tissue was regenerated by new cellular growth by increased rate of mitosis; 3) atrophy, which involved extreme reduction in tissue size as a result of disease or decreased use, workload, blood supply, nutrition, or hormonal stimulation; and 4) metaplasia, which involved transformation of specialized cells into less specialized cells.

Compensatory hypertrophy is manifested in trilobites by enlargement around an injured or diseased area (e.g., Babcock, 1993a, 2003; Jago and Haines, 2002; Fig. 2A, D, E). Recognition of the onset of compensatory hypertrophy at the margin of a damaged exoskeleton provides a clear indication that the injury occurred during the life of an animal, and that the injury was sublethal.

Hyperplasia is manifested in trilobites by scarring (Figs. 1E, 2A, D, E), which is an important means of distinguishing sublethal injuries from lethal injuries (Babcock and Robison, 1989a; Babcock, 1993a, 2003; Pratt, 1998); regeneration of lost exoskeleton through successive molt stages (Tjernvik, 1956; Ludvigsen, 1977a; Rudkin, 1979; Owen, 1983a, 1985; Babcock, 1993a, 2003; herein, Figs. 2A, D, E); and growth of some neoplasms, which are gall-like swellings or tumors, through uncontrolled cellular proliferation (e.g., Snajdr, 1978a; Bergström and Levi-Setti, 1978; Babcock, 1993a, 1994; Fig. 2F, G).

Atrophy is manifested in trilobites by extreme reduction of a certain part of the body (e.g., Ludvigsen, 1979a, p. 77, fig. 56).

Metaplasia has not been unequivocally identified in trilobites, although the possibility exists that it has been involved in the growth of anomalous spines (Figs. 2A, E), particularly in response to injury (Babcock and Robison, 1989a; Babcock, 1993a, 2003; Jago and Haines, 2002). According to Babcock (1993a, 2003), however, it is more likely that anomalous spines are an expression of hyperplasia. Spines at the pleural tips, although abnormally elongated, are characteristic of the terminations of many pleurae, and therefore may not reflect cellular transformation, as required for metaplasia.

PALEOBIOLOGICAL INTERPRETATION OF MALFORMATIONS

Interpretive work on trilobite malformations remained rather limited in scope until the 1970s. Prior to 1970, the principal information available on causes of malformations in trilobites was contained in papers by Walcott (1883), Holm (1886), Burling (1917), Isberg (1917), Lochman (1941), and Sinclair (1947). From the 1950s to the 1990s, an increasing number of active trilobite specialists produced a large number of papers, and this led to a substantial increase in the reporting of malformed specimens. By the 1970s, the availability of large data sets and a burgeoning interest in the paleobiological information in the fossil record (e.g., Schopf, 1972; Raup and Stanley, 1978; Stanley, 1979; Erwin and Wing, 2000, and references therein) resulted in a general increase in interpretive work on fossils.

This trend became evident in the increased attention paid to the interpretation of malformations in trilobites (e.g., Vorwald, 1969, 1982; Alpert and Moore, 1975; Ludvigsen, 1977a; Snajdr, 1978a, b, 1979a, b, 1981b, 2000; Rudkin, 1979, 1985; Owen, 1980, 1983a, 1985; Briggs and Whittington, 1985b; Conway Morris and Jenkins, 1985; Babcock and Robison, 1989a, b; Han and Zhang, 1991; Babcock, 1993a, b, 2000, 2003; Nedin, 1999; Lee *et al.*, 2001; Babcock and Peng, 2001; Jago and Haines, 2002). In addition, Jago (1974), Babcock (1993a, 2003), and Pratt (1998) emphasized the paleobiological information content of broken, but not malformed, trilobites. Most such specimens either suffered breakage in lethal attacks, or were scavenged. Since the 1970s, trilobites have become an important source of paleobiological information, not just about the causes and expression of malformation in fossils, but also about larger paleoecological patterns and animal physiology. In the following sections, many of the salient contributions to paleobiological thought that have resulted from studies of malformations on trilobites are reviewed.

Wound response

Sublethal injuries in trilobites have provided some of the best information on wound response in the fossil record (see Kelley *et al.*, 2003). One of the earliest detailed investigations of wound response was Ludvigsen's (1977a). This report described a hypostome with crushed central body, which was healed by a thickening of the exoskeleton internally during the same intermolt interval in which the injury was sustained. Ludvigsen (1977a) hypothesized that this specimen illustrated an early phase of repair, and that further repair, including a masking-over of injured surfaces and regeneration of lost body parts, would have occurred through successive molt cycles. Later work [notably Rudkin (1979), Snajdr (1979a, b), Owen (1983a, 1985), and Conway Morris and Jenkins (1985)] supported Ludvigsen's (1977a) argument. Particularly convincing evidence of continued repair through a succession of molts was provided by descriptions of trinucleid trilobites with injuries to the wide fringe areas of the cephalon (Kay, 1937; Dean, 1960; Whittard, 1956; Whittington, 1968; Ingham, 1974; Hughes *et al.*, 1975; Owen, 1983a, 1985). Hessin (1988), in discussing a partially regenerated genal spine of an Ordovician *Ceraurus*, determined that trilobites regenerated lost body parts in a distoproximal direction, similar to the way that modern arthropods regenerate lost parts. Most preserved injuries on trilobites probably represent advanced stages of repair, and as noted by Owen (1985), many of these abnormalities resulted from the repair of injuries incurred during molting.

Malformations of macroscopic scale provide proxy evidence for cellular response to injury (see Needham, 1952; Purtilo, 1978), and in trilobites, the evidence is rather striking. Scattered reports that indirectly address cellular repair mechanisms appeared as early as the 1970s. Ludvigsen (1977a), Rudkin (1979), Snajdr (1979a, 1979b), and Owen (1983a, 1985) provided some of the most detailed descriptions of regeneration. Conway Morris and Jenkins (1985) noted the regenerative ability of trilobites, and commented on the remarkable tenacity of seriously wounded animals to cling to life. Additionally, Ludvigsen (1979a, p. 77, fig. 56) provided a probable example of an atrophied eye in a specimen of *Phacops* (now *Eldredgeops* according to Whiteley *et al.*, 2002). Babcock (1993a) first drew a connection between macroscopic malformations in trilobites and cellular-level injuries. Documentation of sublethally injured trilobites from the Early Cambrian (Conway Morris and Jenkins, 1985; Babcock, 1993a, 2003; Babcock and Peel, 2002) demonstrated that cellular repair mechanisms were in place by the beginning of the Phanerozoic, and it is likely that the mechanisms were likewise present in their arachnomorph sister taxa.

Disease, parasitic response, and symbiotic relationships

Evidence for disease, parasitic infection, and symbiotic relationships in trilobites comes from such pathological conditions as exoskeletal swellings, some types of borings, and possibly other types of deformation. Conway Morris (1981) summarized the fossil record of parasites, including the parasites of trilobites. Most cited evidence of parasitic infection in trilobites is in the form of gall-like or tumor-like swellings referred to as neoplasms (e.g., Snajdr, 1978a, b, 1981b; Conway Morris, 1981; Owen, 1985; Babcock, 1993a, 2003), although some borings by possible parasites also have been cited (Babcock and Peng, 2001; Fig. 2B, C).

Neoplasms (Fig. 2F, G) have been reported from a wide range of trilobites, but their origins remain uncertain. Some may be the result of parasitic infection (see Snajdr, 1978a), but others might be the result of cancerous or other types of uncontrolled tissue growth. Numerically, neoplasms are most commonly reported among Cambrian paradoxidids (Bergström and Levi-Setti, 1978; Snajdr, 1978a; Babcock, 1993a, 1994; herein, Fig. 2F, G), but they have been reported from Ordovician asaphids (Snajdr, 1979c; Owen, 1985), Ordovician cheirurids (Ludvigsen, 1979b; Ludvigsen *in* Boucot, 1981), Ordovician harpids (Snajdr, 1978b; Pribyl and Vanek, 1981), and Silurian and Devonian proetids (Snajdr, 1981b). Records of neoplasms among Cambrian trilobites (Bergström and Levi-Setti, 1978; Snajdr, 1978a; Babcock, 1993a, 1994) are among the oldest putative examples of uncontrolled (cancerous) cellular growth.

Borings developed in trilobite exoskeletons while the trilobites were alive, as well as in carcasses and molts. Exoskeletons bored during life provide information about the ability of trilobites to respond to certain parasites. The most convincing examples of parasitism in trilobites come from agnostoids that show evidence of tissue growth and exoskeletal deformation around small pits in the exoskeleton. Babcock (1993a) illustrated a boring that was sealed internally by a pearl-like protruberance (Fig. 2B, C). A similar specimen was described by Babcock and Peng (2001). Borings in agnostoids resemble those inferred to be nematode borings in foraminiferans (Sliter, 1971; but see Lipps, 1983, p. 357).

Some pits in trilobite exoskeletons may represent attachment sites of epizoans. Circular pits with slightly irregular margins that incompletely penetrate the exoskeletons of some Silurian *Calymene* specimens were referred to as "borings" (Whiteley *et al.*, 2002, fig. 2.15D-F). These shallow pits lack rims (characteristic of embedment) or other evidence of cellular response to injury, and it is unlikely that the pit-formers did much harm to the trilobite hosts as the pits do not penetrate deeply enough to affect the internal soft tissues. These features are similar to ones reported as *Tremichnus* from Silurian crinoids (Brett, 1985), which represent attachment sites of commensal epizoans (Brett, 1978; compare with epizoans on trilobites reported by Brandt, 1996).

Most reports of borings in trilobites (Portlock, 1843, p. 360, Pl. 21, fig. 5a; Peach, 1894, Pl. 32, fig. 15; Størmer, 1931, 1980; Bohlin, 1960; Lamont, 1975; Hughes, 1994) lack any suggestion of a cellular response to injury, and therefore seem to have occurred postmortem or postmolting (Dalingwater, 1975; Babcock, 1993a, 2003). Portlock (1843, p. 360; Pl. 21, figs. 5a, 5b; reproduced herein as Fig. 1B, C) erected the ichnospecies *Entobia antiqua* for borings in trilobite sclerites from the Silurian of County Tyrone, Ireland.

Owen (1985) suggested that scarred glabellas present in two previously illustrated trilobites might have resulted from parasitic infection. The specimens he referred to were a Cambrian *Centropleura* (Öpik, 1961) and an Ordovician *Megistaspis* (Ross, 1957).

Some authors [e.g., Schmidt (1906), Palmer (1965), Cowie and McNamara (1978) and Buchholz (2000)] have illustrated trilobites with rather deformed marginal areas associated with inferred healed injuries. In such cases as these, some deformation may have been due to infection associated with closing of the wounded areas. Alternative explanations for deformation of the type seen in these specimens are that they may be the result of 1) genetic or developmental malfunctions (Owen, 1985) or 2) stretching and tearing of tissue, including new soft exoskeleton, as described by Owen (1985, p. 256) in a discussion of a cranidium of a Cambrian *Elvinia* illustrated by Ludvigsen and Westrop (1983, Pl. 3, figs. 1, 2).

Predator-prey relationships and importance of predation in evolution

Sublethally injured trilobites and broken trilobite sclerites provide important information on predator-prey relationships that involved trilobites as prey. Burling (1917) illustrated an olenellid having a large, arcuate, healed injury, and was the first to document and interpret predation on a trilobite. Since that report, more than 180 other specimens with sublethal predation scars have been recorded (Babcock, 2003, and references therein). Papers dealing specifically with the issue of predation on trilobites are numerous. Perhaps the most notable are those that have dealt with predation by anomalocaridids or other arthropods from Cambrian fossil deposits with exceptional preservation (Lagerstätten, or so-called Burgess Shale-type deposits). Among the more influential contributions were those of Rudkin (1979, 1985), Bruton (1981), Vorwald (1982), Briggs and Whittington (1985b), Conway Morris and Jenkins (1985), Whittington and Briggs (1985), Babcock and Robison (1989a), Babcock (1993a, b), Hou *et al*. (1995), and Nedin (1999). Alpert and Moore (1975) suggested that sea anemones were predators of trilobites, but Babcock (1993a) questioned that interpretation. Cephalopods, fish, starfish, eurypterids, trilobites, and other animals have been implicated as predators of trilobites (e.g., Henry and Clarkson, 1974; Brett, 1977; Signor and Brett, 1984; Jell, 1989; Babcock, 1993a, b, 2003; Taylor, 1996; Davis *et al*., 2001), based partly on trilobite malformations, and partly on the fossil record of the inferred predators.

The calcified exoskeletons of trilobites evidently served as a deterrent to predation, but did not provide complete protection. Pratt (1998) provided strong evidence that large numbers of broken trilobite sclerites from certain strata, particularly strata with remains of inferred predators, are the result of successful predatory activity. Nedin (1999), drew on information from predation scars on trilobites and the probable functional morphology of Cambrian anomalocaridids, and developed a plausible scenario by which the sclerotized, but nonmineralized, mouthparts of anomalocaridids could bite through the trilobite exoskeleton by a rapid jerking motion of the head. Earlier, Hou *et al*. (1995) reasoned that a single bite by the chitinous mouthparts of an anomalocaridid against a calcite-reinforced trilobite exoskeleton would be relatively ineffective in producing lethal damage. The complicated action needed for an anomalocaridid to fatally wound a trilobite (Nedin, 1999) may explain, in part, the inferred inefficiency of anomalocaridids as predators by comparison with post-Cambrian predators (Babcock, 2003). The notion that the nonmineralized ventral surface of trilobites was susceptible to attack by animals has been discussed for more than a century (e.g., Pompeckj, 1892; Bergström, 1973; Clarkson and Henry, 1973; Speyer, 1980; Babcock and Speyer, 1987; Babcock, 2003). Babcock and Peng (2001) noted the possibility that small boring organisms could be successful predators of trilobites.

Beginning in the 1980s, predation scars on trilobites played a role in new ideas about predation as a forcing factor in early animal evolution. The importance of predation in evolution developed following Vermeij's (1977) description of a Mesozoic faunal revolution, and Signor and Brett's (1984) description of a Middle Paleozoic precursor to the Mesozoic marine revolution. Both of these rather protracted "events" involved an escalation that involved the evolution of increasingly efficient predatory mechanisms, followed by the evolution of predation-resistant morphologies in the prey. This escalation among predators and prey was a biological "arms race" (e.g., Vermeij, 1987; Kelley and Hansen, 1993). Thus, a rapidly expanding literature on predation among late Neoproterozoic and Early Paleozoic animals developed (e.g., Conway Morris, 1977; Rudkin, 1979; Snajdr, 1979a; Briggs and Whittington, 1985a, b; Fortey, 1985; Conway Morris and Robison, 1986; Runnegar, 1989, 1982, 1994; Grant, 1990; McMenamin and McMenamin, 1990; Robison, 1991; Bengtson and Zhao, 1992; Bengtson, 1994 and references therein; Conway Morris and Bengtson, 1994). Some of the most compelling evidence that predation pressure was a factor in the initial evolution of skeletons during the Neoproterozoic–Cambrian transition came from predation scars on early trilobites. Building on previous work on the functional morphology of anomalocaridid arthropods and the morphology of some sublethal predation scars (e.g., Vorwald, 1969, 1982; Briggs, 1979; Briggs and Whittington, 1985a, b; Whittington and Briggs, 1985), Conway Morris and Jenkins (1985), Babcock and Robison (1989a), and Babcock (1993a) extended the interpretation of a predator-prey relationship to anomalocaridids and Cambrian redlichiid and olenellid trilobites. Previously, much of the evidence on this inferred anomalocaridid-trilobite relationship was derived from Middle Cambrian strata (e.g., Vorwald, 1982; Briggs and Whittington, 1985b; Whittington and Briggs, 1985). Babcock (2003) summarized evidence that escalation (or a so-called "arms race") among predators and prey was underway by the first appearance of calcified trilobites, and continued into the Middle and Late Paleozoic. Escalation among predators and trilobite prey during the Early Paleozoic was portrayed as part of a biosphere-scale reorganization of marine ecosystems (Vermeij, 1995), and referred to as the Early Paleozoic Marine Revolution (Babcock, 2002, 2003). Recent recalibration of the Cambrian time scale (Grotzinger *et al*., 1995; Landing *et al*., 1998) and work on a global chronostratigraphy (e.g., Shergold, 1997; Geyer and Shergold, 2000; Peng and Babcock, 2001) provisionally place the first appearance of calcified trilobites at the beginning of the last half of the Cambrian. According to timescale standards in place prior to 2000, the first appearance of trilobites was considered Early Cambrian.

Increased understanding of the value of sublethal predation scars in documenting predator-prey relationships involving trilobites led to the realization that predation scars merely hint at Paleozoic predator-prey relationships because not all predators of trilobites were durophagous (Babcock, 2003). Such arthropod predators as *Leanchoilia* (Butterfield, 2002) and the naraoiids

(Whittington, 1977; Briggs and Whittington, 1985a; Vannier and Chen, 2002), which may have ripped into the nonmineralized tissues of trilobites or other animals rather than breaking calcified exoskeletons, probably left little preserved record of their feeding behavior. One implication of this conclusion, together with the interpretation that successful durophagy on trilobites tended to result in maceration of exoskeletal material (Babcock, 1993a, 2003; Pratt, 1998), is that the importance of predation in paleoecological and evolutionary studies has been underestimated. This is probably significant for the interpretation of metazoan life through the late Neoproterozoic and Cambrian prior to the advent of widespread skeletization when most predation can be expected to have left little or cryptic evidence.

Behavior, lateralization, and internal organization

Inference of predator-prey relationships involving trilobites has a history that dates at least to Pompeckj (1892), who postulated that enrollment in trilobites could be a response to predation (see review in Babcock, 2003). Snajdr (1979a) illustrated an Ordovician trinucleid trilobite with small, matching predation scars on marginal areas of the cephalon and pygidium that indicated an unsuccessful attack occurred while the animal was enrolled.

Direct, trace-fossil evidence of predation on trilobites dates to the recognition of sublethal predation scars (Burling, 1917). The record of predation scars includes numerous scattered reports, and has been reviewed by Babcock (2003), who noted that this literature suggests temporal changes in the dynamics of predator-trilobite relationships in the Paleozoic. A strong decline in the frequency of predation scars on trilobites occurred in the Furongian Epoch of the Cambrian, and this evidently coincided with the extinction of the anomalocaridids. Assuming that specimens retaining predation scars record unsuccessful attempts at predation and that low scar frequencies reflect highly successful predation, Babcock (2003) inferred that some Cambrian animals (notably anomalocaridids) were less efficient predators than their post-Cambrian counterparts (notably fish, cephalopods, and a variety of arthropods, including some trilobites).

Using large data sets of sublethal predation scars, Babcock and Robison (1989a) and Babcock (1993a, b, 2003) recognized a strong tendency for sublethal predation scars to be preserved on the pleural lobes, the posterior part of the body, and the right side of the body. Because trilobites with predation scars are the ones that survived attack, the occurrence of substantial injuries only on the pleural lobes was attributed to the presence of most of the vital organs within the axial lobe. In all likelihood, serious attacks on the nervous, circulatory, or alimentary organs in the axial area would have been fatal (Babcock and Robison, 1989a; Babcock, 1993a, 2003), and this would have resulted in the absence of these trilobites in the sample of sublethally injured specimens. A tendency for sublethal predation scars to be located posteriorly may reflect: 1) the tendency for predators to make first contact with the posterior half of the trilobite body or 2) the tendency for trilobites to escape if seized posteriorly rather than on the cephalon or anterior thorax.

Babcock and Robison (1989a, b) and Babcock (1993a, 2003) attributed lateral asymmetry in sublethal predation scars to a left-right behavioral asymmetry, or a behavioral lateralization, in trilobites, their predators, or trilobites and their predators. Behavioral lateralization in the earliest trilobites or their predators implies that animals possessed lateralized nervous systems by at least 521 Ma. This conclusion has an important influence on the interpretation of lateralized behavior across the animal kingdom, with implications for behavioral biology and ethology (e.g., Bradshaw, 1989; Bradshaw and Rogers, 1993).

Morphological development

Understanding of the morphological development of trilobites and their developmental rate has been enhanced by the study of malformations. Perhaps the most notable examples of specimens that have contributed developmental information involve teratology. A meraspis degree 0 of the Ordovician form *Apianurus* described by Whittington (1956b) has only one genal spine. This specimen was either broken during early ontogeny or exhibits a lateral asymmetry resulting from slightly different developmental rates of the right and left sides of the animal (Whittington, 1956b). A similar example from the early ontogeny of the Ordovician form *Sphaerocoryphe* was described by Shaw (1968). In early ontogeny, *Sphaerocoryphe goodnovi* had two profixigenal spines on each cheek, of which one was lost or atrophied during later ontogeny. A specimen described by Shaw (1968) retained two spines on one side, and one spine on the other side, and suggests lateral differences in developmental rate. Other species of *Sphaerocoryphe* retain two profixigenal spines throughout their ontogeny. A cranidium of the Cambrian form *Cernolimbus* described by Palmer (1965) has an abnormal, laterally asymmetrical expansion of the anterior border; whether this represents lateral differences in developmental rates is uncertain.

A number of workers have described abnormalities of the axial region of trilobites, and many of these examples were attributed to genetic or developmental malfunctions. Irregular development, or in some cases, effacement, of the lateral glabellar furrows can be one manifestation of teratology. Some of the best examples of effacement of furrows, exclusive of that considered to be part of the normal variation within species (e.g., Robison, 1994), were provided by Pribyl and Vanek (1973), Ludvigsen (1977b), Snajdr (1978a), Fortey (1980), and Owen (1985). Irregularly developed lateral glabellar lobes were illustrated by Hammann (1971) and Snajdr (1979a). In these latter two examples, left-right differences in furrow development may reflect a lateral asymmetry of developmental rates.

Numerous examples of abnormally developed segmentation or post-cephalic marginal spines have been described in trilobites, although the causes of malformation are not always certain. The first described abnormality in a trilobite (Portlock, 1843) involved malformed pleurae of the pygidium of a Carboniferous phillipsiid (see also Owens, 2000, fig. 2J). In many examples, fusion of segments, atrophy, or both fusion and atrophy occurred; these conditions commonly imply teratology.

Malformed thoracic or pygidial segments that may have resulted from teratological conditions were reported by Hall and Clarke (1888), Saito (1934), Westergård (1936), Harrington and Leanza (1957), Palmer (1958), Snajdr (1958, 1978a, 1981a, b, 2000), Hessler (1962), Tripp (1962), Campbell (1967), Rushton (1967), Hughes (1969), Chatterton (1971, 1980), Pocock (1974), Henningsmoen (1975), Bergström and Levi-Setti (1978), Henry (1980), Holloway (1980), Strusz (1980), Howells (1982), Owen (1985), Hughes (1994), Babcock (1993a; Fig. 2H, I), and Owen and Tilsley (1996). Thoracic segments that were fused with the anterior part of the pygidium, rather than being fully shed forward into the thorax from their locus of generation, were reported by Palmer (1960), Rushton (1967), Chatterton (1971), Evitt and Tripp (1977), Snajdr (1979b, 1981b), and Babcock (1993a).

Resser (1939) and Ross (1951; refigured by Owen, 1985) reported specimens with thoracic segments fused with the cephalon. In holaspid trilobites, fused segments could represent early cessation of the development of thoracic segments or partial release of extra segments. In either case, deviations from normal levels of growth hormones or minor genetic changes are the most likely root causes of malformation (Owen, 1985).

Cases involving the insertion of extra pleurae or axial rings in the pygidium have been reported by Hall and Clarke (1888), Jell (1975), Snajdr (1981a, b), Ramsköld (1983), and Owen (1985). Abnormally developed axial rings in the pygidium, some accompanied by abnormally developed pleural ribs, were reported by Tripp (1967), Ormiston (1967), Evitt and Tripp (1977), Snajdr (1981a, b), Hahn *et al.* (1982), Owen (1985), and Rudkin (1985). Jell's (1975) interpretation of an extra axial segment in the pygidium of some specimens of the Cambrian genus *Pagetia* is especially intriguing. The extra axial segment, Jell (1975) argued, was a male genital segment that in animals of non-parthenogenic generations, and appeared in response to environmental adversity. Some marginal spines of the pygidium that show results of teratological conditions or injury and repair were reported by Richter and Richter (1934), Whittington (1956), Erben (1967), Schrank (1969), Chatterton (1971), Lane (1971), and Owen (1985).

Some teratological conditions are quite common in certain taxa, and imply a reasonably high level of chromosomal plasticity or left-right asymmetry in developmental timing. One notable example is the high frequency of bifurcations (40%) along the genal spines of Ordovician *Onnia* from France, as reported by Oehlert (1895). Another example involves the frequency of malformed pygidia (5% to 28%) of Ordovician *Cnemidopyge* from Wales (Hughes, 1969). In a third example, malformed or subequally to unequally divided pleurae were reported by Hughes (1994) in the Cambrian species *Dikelocephalus minnesotensis* from the United States. Of 39 pygidia (including dorsal exoskeletons with pygidia) that Hughes (1994) illustrated, 5% show strongly malformed pleural ribs, and 23% show subequally or unequally divided pleurae. Hughes (1994, p. 18) also stated that subequal division of the pleurae is the most common condition in the species. In *D. minnesotensis*, unequal division of the pleurae reflects an enlarged propleural band, and results in a laterally asymmetrical disposition of the segments. In addition to variability in the shape or position of furrows, Hughes (1994, p. 17) noted that the combined number of pleural and interpleural furrows on the pygidium of *Dikelocephalus* varies between seven and ten, but the number of furrows is asymmetrically disposed between the right and left sides in some specimens. Variation in the lateral division of pleurae or furrows could result from lateral differences in the programmed rate of ontogenetic development, or chromosomal plasticity.

One of the most convincing cases of atrophy in a trilobite is in the left eye and genal area of a Devonian specimen of *Phacops* (now *Eldredgeops*) described by Ludvigsen (1979a). This reduction in the size of the gena and eye was attributed to injury (Ludvigsen, 1979a), but an otherwise normal morphology of the region indicates that developmental malfunction is a more likely cause (Owen, 1985). Owen's (1985) explanation accords well with Clarkson's (1969) observation of local fusion and reduction in the size (or even absence) of lenses in schizochroal eyes of the Devonian phacopine *Reedops*. Other cases involving irregular regeneration of eyes, putatively following injury, were reported by Walcott (1883), Isberg (1917), and Hupé (1953a).

Finally, an example of malformed reticulation in the pygidium of the Cambrian agnostoid *Glyptagnostus*, described by Öpik (1961), is possibly teratological. The specimen shows local swelling and local reduction of reticulation. Alternative explanations for the abnormality (Owen, 1985), are disease or parasitic infection.

Taphonomic information

Two aspects of trilobite taphonomy are germane to this review of malformations because events that occurred during life might be confused with those that occurred after death or molting. These include 1) postmortem or postecdysial borings and 2) lethal crushing of the exoskeleton. Portlock (1843, p. 360, Pl. 21, fig. 5a; Fig. 1B, C), Peach (1894, Pl. 32, fig. 15), Størmer (1931, 1980), Ruedemann and Howell (1944), Bohlin (1960), Lamont (1975), and Hughes (1994, Pl. 8, fig. 7) illustrated trilobites that appear to have been bored by small organisms. The borings in these examples were likely of postmortem or postecdysial remains (Dalingwater, 1975; Owen, 1985). Key evidence that the boring did not occur while the trilobites were alive is the absence of deformation indicative of cellular response to injury (compare with Fig. 2F, G). Similarly, a vermiform fossil associated with an *Olenellus* cephalon illustrated by Ruedemann and Howell (1944) is likely to be a taphonomic association because of the absence of any response in the tissue of the trilobite.

Lethal or postmortem breakage of the trilobite exoskeleton has received little attention, despite the common occurrence of broken sclerites. In some examples, broken trilobite sclerites occur within putative coprolites (Conway Morris and Robison, 1988; Babcock, 2003). Jago (1974), Babcock and Peel (2002), and Babcock (2003) discussed the postmortem disturbance of trilobite remains by scavengers, and Babcock (1993a, 2003) and Pratt (1998) discussed breakage of trilobite sclerites by predators.

SUMMARY

Exoskeletal malformations provide important information on the paleobiology of trilobites, and this information has had an impact on the interpretation of trilobites and on the physiology and behavior of Cambrian to modern animals. Over a span of 160 years, more than 1100 malformed trilobite specimens have been reported in more than 160 publications. Expression of injuries, teratological conditions, and pathological conditions of the exoskeleton reflects damage to soft tissues at the cellular and organismic levels. Injuries in trilobites have provided data on: 1) wound healing, which has had implications for understanding morphological development and plasticity, parasitic response, and molting; 2) configuration of the vital organs within the body; 3) predator-prey relationships and the active role that predation played in the evolution of Paleozoic animals, including information on the rise and modification of skeletons in biological "arms races;" and 4) lateralization of the nervous systems of early animals, which has implications for interpreting lateralization in all animals. Teratological conditions have provided information about developmental patterns and chromosomal plasticity. Pathological conditions have provided information about the way trilobites responded to infection, boring organisms, and uncontrolled cellular growth. The distribution of published reports suggests that abnormalities of trilobites from Asia, Australia, South America, Africa, and Antarctica have been underreported compared to those from Europe and North America. Thus, considerable, untapped information about trilobite malformations is likely to reside in collections from these areas.

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THE TRILOBITE WORLD OF J. W. DALMAN

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ABSTRACT—Although the author of only one major contribution on trilobites, J. W. Dalman (1827) made a lasting impression on the science of paleontology and the study of trilobites. More than half of the about 50 species known at the time were first described from his home country of Sweden, and many of them he published himself. His drawings are remarkably exact for his time, and his feeling for systematics was excellent, both at the level of species and at higher taxonomic levels. In fact, the genera and subgenera he recognized correspond to a great extent to modern trilobite orders. Many taxonomic names still in use were created by him, or are based on his names.

INTRODUCTION

Johan Wilhelm Dalman (Fig. 1) was born in 1787 at Hinseberg in Västmanland, Sweden, some 200 km west of Stockholm. Reyment (1980) provides a fuller account of his life. Dalman belonged to the nobility, and his father had been a student of Linnaeus. His studies at Lund and Uppsala universities included law, mining engineering, and medicine. In 1818, he became librarian of the Royal Swedish Academy of Sciences. He was also responsible for the zoological collections of the academy. These collections became the Swedish Museum of Natural History in 1820. Dalman was interested in insects and became a friend of C. Gyllenhaal and G. Marklin, who both collected trilobites. The Marklin collection, with several of Dalman's type specimens, is now in the University of Uppsala. Marklin was, at least on one occasion, paid by the Academy to collect fossils. Dalman was also a friend of Sven Nilsson, a famous zoologist and paleontologist.

Dalman had become a friend of Jöns Jacob Berzelius, a famous chemist who, among other accomplishments, was the first to realize the fundamental difference between organic and inorganic chemistry, and who precisely measured the atomic weights of about 50 elements. Berzelius became the Secretary General of the Royal Swedish Academy of Sciences in 1819, and, thus, was the supervisor in charge of Dalman. Berzelius was born in Östergötland, some 250 km south of Stockholm. It was to this area that Berzelius and Dalman made a trip in 1826, and collected Ordovician trilobites that are in the collections of the Swedish Museum of Natural History, and carry their labels.

Their collecting locality, some 15 km east of Motala, was named Husbyfjöl. This name has since been abandoned because it was poorly received — it means "toilet of the king's house" — and is now replaced on the maps by the more respectable name of "Västanå." The preserved labels have become scientifically important as they prove that a misunderstanding of one of Dalman's species has caused confusion in recent years. The first results of this collecting trip were soon published (Dalman, 1827). Dalman also described one trilobite in 1825. Afterwards, Dalman (1828a, b) published only a book on brachiopods and a review of new finds in 1828, the year that he passed away at an age of 41 years.

Fig. 1. Johan Wilhelm Dalman. Drawing used by Lea Ahlborn in 1860 for making a medallion; courtesy of the Royal Swedish Academy of Sciences.

DALMAN AND THE TRILOBITES

Dalman disliked the term "trilobite." As he noted in the general text (in Swedish; the descriptions are in Latin), his *Asaphus* (*Nileus*) *armadillo* is not trilobed, and so is not truly a trilobite. He therefore introduced the term "palaeades" for the trilobites.

FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES, Edited by Donald G. Mikulic, Illinois State Geological Survey, 615 East Peabody Drive, Champaign, Illinois 61820, Ed Landing, New York State Museum, The State Education Department, Albany, New York 12230, and Joanne Kluessendorf, Weis Earth Science Museum, University of Wisconsin-FoxValley, 1478 Midway Road, Menasha, Wisconsin 54952. New York State Museum Bulletin 507.

Needless to say, this name was never widely accepted.

Dalman's descriptions of trilobites are among the oldest in Scandinavia as they were published in 1825 and 1827. The years sometimes are given as 1824 and 1826, because the volumes cover the activities of the Royal Swedish Academy of Sciences for those years, but it is the year of printing that counts. Carolus Linnaeus (1759), or Carl von Linné, had much earlier described *Entomostracites paradoxus* α *expansus*. This is probably the species now known as *Asaphus expansus*, but the descriptions and illustrations of this and other trilobite species are so poor that they are now credited to Wahlenberg (1818, 1821), who redescribed them. These are among the first trilobites to be described.

Dalman (1827, p. 102) listed all trilobite species in the world that he considered recognizable. These included thirteen *Calymene* species, 20 of *Asaphus* with subgenera, two of *Ogygia*, five of *Olenus*, and one of *Battus*, for a total of 41 species. In addition, there were eight species for which the generic assignment was in doubt, making a total of 49. Of these, 28 were reported from Sweden, including the seventeen new species described by Dalman in 1827. This means that the number of species reported from outside Sweden was only 22. This fairly low number is surprising in the light of the literature on trilobites, which according to Dalman's (1827, p. 103–107, 288–292) list included no fewer than 53 titles.

Dalman complimented several of the descriptions with quite good illustrations. In the text, he mentioned an additional three species from Sweden, without listing or illustrating them. Because they can be identified, however, they were later recognized as Dalman's species, making a total of 30 Swedish species. These species are *Calymene*?/*Parapilekia speciosa* (Dalman, 1827, p. 74, 75) reported from Öland by Sven Nilsson, *Calymene*?/*Cyrtometopus clavifrons* (Dalman, 1827, p. 75) from Husbyfjöl in Östergötland, and *Illaenus centaurus* from Alböke in Öland (Dalman, 1827, p. 76). Dalman (1827, p. 74) stated in his Swedish general text that these were so poorly understood that he did not want to describe them, and only mentioned them with the intent of advising interested collectors.

Dalman's classification

Göran Wahlenberg (1818, 1821) had earlier published a number of trilobite species from Sweden under the generic name of *Entomostracites*. This was the name used by Linnaeus (1759) and also by Dalman (1825) when he described *Entomostracites actinurus* (now *Pliomera actinura*).

However, Dalman (1827) subsequently used a much more modern taxonomic and systematic approach. He recognized five genera and another three taxa which were treated as subgenera of *Asaphus*. These taxa were previously recognized by Brongniart (*in* Brongniart and Desmarest, 1822). Another genus, *Isotelus*, had been erected by DeKay (1824) based on his American species *Isotelus gigas*. Dalman judged *Isotelus* to be a synonym of *Asaphus* Brongniart, 1822. As *Isotelus* is an asaphid and because the concept of a trilobite genus at the time was similar to today's concept of an order, Dalman's judgment was very reasonable. *Isotelus* has since regained its status as a distinct genus.

Dalman (1827) ordered trilobite genera into divisions and sections as follows:

Palaeades [trilobites]

Sectio I Palaeades genuinae
- Divisio I Oculati
  - Genus I *Calymene* Brongniart, 1822
  - Genus II *Asaphus* Brongniart, 1822
- Divisio II Typhlini
  - Genus III *Ogygia* Brongniart *in* Desmarest (1817) (or the same name as used by Brongniart, 1822, now *Ogygites* Tromelin and Lebesconte, 1876)
  - Genus IV *Olenus* (synonymized with *Paradoxides* Brongniart, 1822)

Sectio II Battoides
- Genus V *Battus* (instead of the older *Agnostus* Brongniart, 1822)

The main divisions relied on the overall appearance of the body. The Battoides, or agnostids, have a head and tail of identical shape, and have no visible trace of eyes. The latter condition finds an interesting parallel in modern classifications, where a number of blind Cambrian trilobites, many of which are not interrelated, are lumped into the family Conocoryphidae (see Moore (ed.), 1959, and critique by Cotton, 2001, among others). Dalman's Battoides was monotypic, and the agnostids are still believed to be a phylogenetically uniform group.

The other main division is the "Palaeades genuinae." This is quite interesting: if they are the only true trilobites, it means that Dalman did not regard *Battus* (modern *Agnostus*) as a true trilobite. Since Dalman's time, agnostids have been regarded as true trilobites by most trilobite specialists. Recently, Dalman's contrarian view has been revived. This was made possible by Müller and Walossek's (1987) description of wonderfully preserved appendages of *Agnostus pisiformis*. Its appendages are remarkably different from appendages known from any trilobite or any other trilobite-like arthropod, and Walossek and Müller (1990) concluded that agnostids are probably more closely related to crustaceans than to trilobites. In all probability, the latter authors are correct in their conclusion — it is not difficult to recognize a trilobite-type of appendage. This, however, appears to be a conclusion that would disturb many specialists if it were really true, so agnostids are still generally treated as trilobites [as in the revised trilobite Treatise, Kaesler (1997)].

Dalman's "genuine" trilobites were described as having a semicircular head and a multisegmented body. He divided them into the Oculati and the Typhlini. The former had well devceloped eyes and could enroll. The latter had no eyes or, at least, no preserved eyes, and the body is preserved extended.

The Oculati are subdivided as follows, with modern counterparts named for Swedish forms:

Calymene	Calymenina: *Calymene*
	Cheirurina: *Cyrtometopus*, *Cybele*, *Pliomera*, *Parapilekia*, *Encrinurus*
	Phacopina: *Pterygometopus*
	Proetina: *Proetus*
Asaphus	
Asaphus (genuini)	
	Phacopina: *Dalmanitina* (*Mucronaspis*), *Dalmanites*
	Trinucleina: *Tretaspis*
	Asaphina: *Megistaspis*, *Ogygiocaris*, *Ptychopyge*, *Asaphus* (with *Isotelus*), *Niobe*
	Nileidae: *Symphysurus*
Asaphus (*Nileus*)	Nileidae: *Nileus*
Asaphus (*Illaenus*)	Illaenina: *Dysplanus*, *Illaenus*, *Eobronteus*
Asaphus (*Lichas*)	Lichina: *Lichas*
Asaphus (*Ampyx*)	Trinucleina: *Ampyx*
Asaphus?	"Conocoryphidae": *Bailiaspis*

The Typhlini are divided as follows, with modern counterparts named for Swedish forms:

Ogygia	Asaphina (no species reported from Sweden)
Olenus	Paradoxidacea: *Paradoxides*
	Olenacea: *Olenus*, *Peltura*, *Parabolina*

As can be seen, there are distinct similarities of Dalman's (1827) classification with that of the 1959 trilobite volume of the Treatise on Invertebrate Paleontology (Moore (ed.), 1959). Thus, calymenids, cheirurids, and phacopids are grouped, although some phacopids are placed among the asaphids. Dalman (1827) listed true asaphids under *Asaphus* genuini. He identified illaenids, lichids, and olenids as separate groups. Some unrelated taxa are found in some of these groups. Dalman's (1827) genera and 'subgenera' totaled nine, including the agnostids.

This tally compares well with the seven orders in the first edition of the trilobite 'Treatise' (Moore, 1959). Dalman had a 'waste-basket' group termed *Asaphus*, which consisted of an array of unrelated forms much in the way that the first 'Treatise' edition had the Ptychopariida, and the second 'Treatise' (Kaesler, 1997) added the Proetida.

Dalman's (1827) appreciation of systematics was very well developed. He saw clearly, in his genera and subgenera, the groupings which are now recognised as order-level taxa. Although there has been considerable addition and improvement below that level, I believe that not much improvement has been made at the order level. Indeed, few orders, if any, can be said with full certainty to be monophyletic.

It should be noted that Dalman (1827, p. 10–12) accepted the generic names created by Brongniart (1822) except for two. *Paradoxides* had grown to include other species in addition to Linnaeus' (1759) original form *Entomolithus paradoxus* (which is identical to Wahlenberg's (1818) *Entomostracites paradoxissimus*). As there was nothing "paradoxical" about the others, Dalman (1827) suggested the new name *Olenus* for *Paradoxides*. He added that Brongniart (1822) had earlier indicated that *Paradoxides* was an odd name. However, *Paradoxides* remains the valid name for a group of trilobites that includes *P. paradoxissimus* (Wahlenberg, 1818). Dalman's (1827) name *Olenus*, based on *Entomostracites gibbosus* Wahlenberg, 1818, is still valid. *Agnostus*, from the Greek word αγνειω or αγνοστος means 'unknown' according to Dalman's understanding of Greek, but could no longer be considered as unknown. Therefore Dalman (1827) gave it the name *Battus* from the name of a mythological being that was transformed into a black rock by the god Mercury.

Dalman as an observer

It appears from the Swedish text that Dalman (1827) was careful not to erect new species on material that he considered insufficiently preserved. It is also clear that, with few exceptions, he did not fall into the trap of assigning foreign names to Swedish fossils because the Swedish fossils somewhat resembled similar forms described outside of Sweden. In fact, many of the new species he described were based on the large collection that he and Berzelius brought together from the *Asaphus expansus* and *A. raniceps* Zones in the upper Lower Ordovician at Västanå (Husbyfjöl). No less than eight or nine of his sixteen new species had this origin. This fauna is now very well known, and there are some specimens identified as type specimens, whereas others still retain Dalman's and Berzelius' labels. Thus, there should be no doubt regarding the identification of Dalman's species. This is the general rule, but, as will be seen

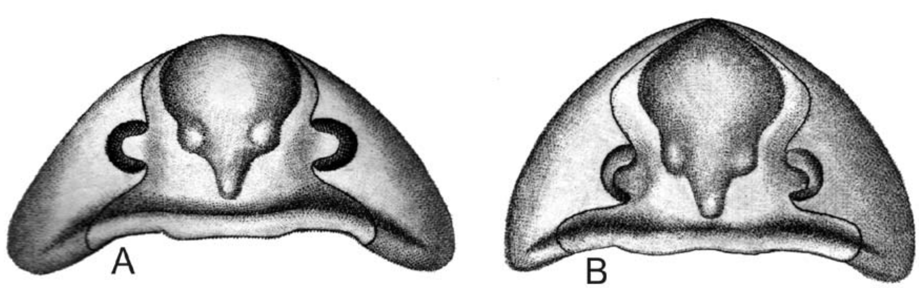

Fig. 2. Dalman's (1827) illustrations of *Asaphus expansus* (Wahlenberg, 1818) (Fig. 2A) and *A. raniceps* Dalman, 1927 (Fig. 2B). If Dalman's illustrations are life size, the former is 22 mm long along the midline, the latter 21 mm.

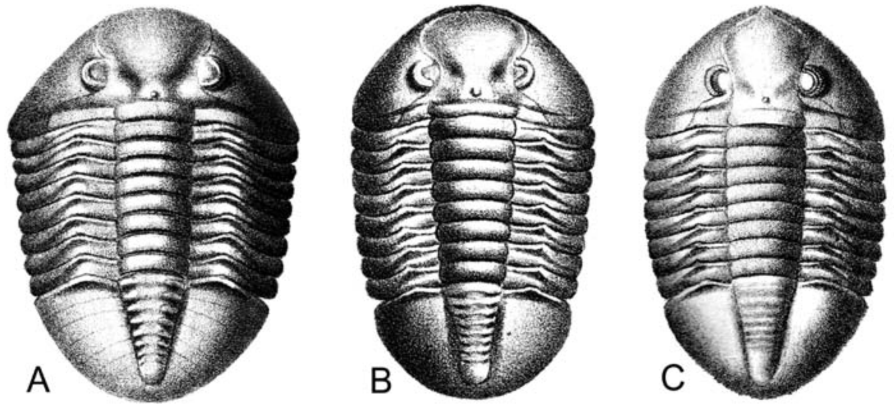

Fig. 3. Angelin's (1854) illustrations of *Asaphus expansus* (Wahlenberg, 1818) (Fig. 3A); *A. fallax* Angelin, 1854 (Fig. 3B); and *A. raniceps* Dalman, 1827 (Fig. 3C). *A. fallax* is seemingly somewhat intermediate in morphology between the two other species. A comparison with Dalman's illustrations reveals that *A. raniceps* of Angelin is identical to *A. raniceps* of Dalman. Angelin usually published at life size, which means that the specimens are 70, 60, and 74 mm long, respectively. This means that the first two specimens are large, whereas *A. raniceps* commonly reached a length of 100–110 mm.

below, it is not without exception.

Two closely related species from Västanå are *Asaphus expansus* (Wahlenberg, 1818) and *A. raniceps* Dalman, 1827. They are illustrated on Dalman's (1827) plate 3 as figures 3a–d and 4, respectively (Fig. 2). The latter has a characteristically more-pointed cephalon and sutures that reach the margin at the midline, not more laterally as in *A. expansus*. Angelin (1854, Pl. 28, figs. 1–1b, and 2–2c; see Fig. 3) illustrated the two species and added a third related form, *A. fallax* (see Angelin, 1854, Pl. 28, figs 1c, 3–3c). Angelin (1854) listed the latter as *Asaphus fallax* Dalman, referring to [Dalman's species in] "Mus. Holmiense" (i.e., the Swedish Museum of Natural History). Apparently, Dalman had labelled specimens with this name, and one such label is still preserved (Fig. 4). It is clear that Angelin studied and labelled the specimens available to Dalman, and there is no doubt in my mind that this was carefully and correctly done.

In 1905, Lamansky (1905) introduced an *Asaphus raniceps* Zone above the *Asaphus expansus* Zone. However, it has been repeatedly stated that *A. raniceps*, as described by Dalman (1827), and as understood by Angelin (1854), are two different species (Jaanusson, 1953, p. 394; Tjernvik and Johansson, 1980, p. 190, 194, Fig. 10A; Nielsen, 1995, p. 96; Bruton *et al.*, 1997, p. 108). This has forced us to tolerate the separate concepts of *A. raniceps* Dalman and of *A.* '*raniceps*' sensu Angelin [introduced by Jaanusson *in* Jaanusson and Mutvei (1953, p. 30)], and with a zone of *A.* '*raniceps*' where *A. raniceps* is supposedly not present. In summary, Jaanusson, Tjernvik, Johansson, Nielsen and Bruton *et al.* all agreed or accepted that Angelin had misunderstood Dalman's *A. raniceps*. This mistake resulted from both the somewhat schematic and inexact old illustrations and from the lack of modern studies of the material, as well as the variability of the species and its less than perfect preservation.

In addition to the specimens collected in Östergötland by Dalman and his eighteenth century colleagues, a large number of specimens were purchased in the 1990s from the collector Holger Pihl and, later on, from his widow. Altogether, the old and new collections from Östergötland in the Swedish Museum of Natural History now include many reasonably complete specimens [263 of *Asaphus expansus*, 83 of *A. fallax*, and 52 of *A. raniceps*]. A study of these (Bergström *et al.*, 2003) has concluded that Angelin was indeed right in his identification of Dalman's species. A problem that caused later confusion was that the type specimen of *A. fallax* has exceptionally strong glabellar muscle impressions, and this was taken to be the most reliable character of the species (see Nielsen, 1995, p. 80, 81, fig. 62). As a consequence, the species has been thought to be extremely rare, and other specimens of the same species have been regarded as specimens of *A. raniceps* (e.g., Nielsen, 1995, fig. 75a–d) or, quite commonly, *A. expansus* (Fig. 5). However, the strength of the muscle impressions varies between individuals in this species as well as in some related ones. For instance, Nielsen (1995, fig. 63A) illustrated a specimen of *A. lepidurus*

Fig. 4. One of Angelin's labels (above) for *Asaphus fallax* Angelin, 1854, associated with a label with Dalman's handwriting (below), which suggested this binomial name. This shows that Dalman had recognized the distinctness of this species although he did not publish on it.

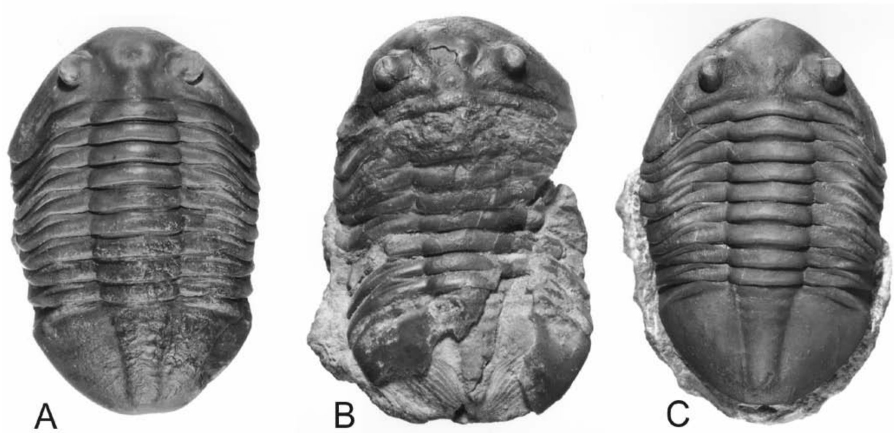

Fig. 5. Photographs of the three species of *Asaphus* discussed in the text. A, *A. expansus* (Wahlenberg, 1818), RM Ar 51076, from Husbyfjöl (= Västanå), length 71 mm. B, *A. fallax* Angelin, 1854, the type specimen, RM Ar 16575, from Husbyfjöl, length 62 mm. C, *A. raniceps* Dalman, 1827, a small specimen which still retains the occipital furrow, as in Dalman's illustration, RM Ar 55637, collected at Ljungsbro by H. Pihl, length 52 mm.

with similarly strong impressions, although this again is not typical of the species. It appears that twentieth century authors have not studied these collections as carefully as Dalman had.

SUMMARY

J. W. Dalman described a large proportion of the trilobites known during his lifetime. His drawings are exceptionally good for the period. In proposing new generic names, he provided one of the earliest frameworks for trilobite classification. In practice, the categories he recognized roughly correspond to orders and suborders currently in use. Dalman's contributions live on in the taxa named after him. These include the trilobites *Atractopyge dalmani* Owen and Tripp, 1988; *Bailiaspis dalmani* (Angelin, 1854); *Dalmanites* Barrande, 1852; *Dalmanitina* Reed, 1905; and the Dalmanitidae Vogdes, 1890. Also named for him are the brachiopods *Dalmanella* Hall and Clarke, 1892, and the Dalmanellidae Schuchert, 1913.

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APPENDIX—DALMAN'S TRILOBITES

Upper Paleozoic rocks are missing in Sweden, and the Swedish trilobites dealt with by Dalman are all from the Lower Paleozoic.

Plate/fig.	***Dalman's name***	***Modern name***
	Cambrian species	
VI: 2	*Asaphus*? *Sulzeri* (Schlotheim)	*Bailiaspis dalmani* (Angelin, 1854)
VI: 3	*Olenus Tessini* (Brongniart)	*Paradoxides paradoxissimus* (Wahlenberg, 1818)
VI: 4	*Olenus spinulosus*	*Parabolina spinulosa* (Wahlenberg, 1818)
—	*Olenus bucephalus* (Wahlenberg)	*Paradoxides* cf. *paradoxissimus* (Wahlenberg, 1818)
—	*Olenus gibbosus*	*Olenus gibbosus* (Wahlenberg, 1818)
—	*Olenus scarabaeoides*	*Peltura scarabaeoides* (Wahlenberg, 1818)
VI: 5a-d	*Battus pisiformis*	*Agnostus pisiformis* (Wahlenberg, 1818)
	Ordovician species	
I: 1a-c	*Calymene polytoma*	*Pliomera fischeri* Eichwald, 1825
I: 4a-d	*Calymene*? *bellatula*	*Cybele bellatula* (Dalman, 1827)
II: 1a-g	*Calymene sclerops*	*Pterygometopus sclerops* (Dalman, 1827)
—	*Calymene actinura*	*Pliomera actinura* (Dalman, 1825)
—	*Calymene*? *speciosa*	*Parapilekia speciosa* (Dalman, 1827)
—	*Calymene*? *clavifrons*	*Cyrtometopus clavifrons* (Dalman, 1827)
II: 3a-b	*Asaphus mucronatus*	*Dalmanitina* (*Mucronaspis*) *mucronata* (Dalman, 1827)
II: 5	*Asaphus extenuatus*	*Megistaspis* (*Megistaspidella*) *extenuata* (Wahlenberg, 1818)
II: 6	*Asaphus granulatus*	*Tretaspis granulatus* (Wahlenberg, 1818)
III: 1	*Asaphus dilatatus*	*Ogygiocaris dilatata* (Brünnich 1781)
III: 2	*Asaphus angustifrons*	*Ptychopyge angustifrons* (Dalman, 1827)
III: 3a-c	*Asaphus expansus*	*Asaphus expansus* (Wahlenberg, 1818)
III: 4	*Asaphus expansus* var. *raniceps*	*Asaphus raniceps* Dalman, 1827
IV: 1a-d	*Asaphus laeviceps*	*Niobella laeviceps* (Dalman, 1827)
IV: 2a-e	*Asaphus palpebrosus*	*Symphysurus palpebrosus* (Dalman, 1827)
IV: 3a-e	*Asaphus* (*Nileus*) *armadillo*	*Nileus armadillo* Dalman, 1827
V: 1a-c	*Asaphus* (*Illaenus*) *centrotus*	*Dysplanus centrotus* (Dalman, 1827)
V: 2a-f	*Asaphus* (*Illaenus*) *crassicauda*	*Illaenus crassicauda* (Wahlenberg, 1818)
V: 3a-c	*Asaphus* (*Ampyx*) *nasutus*	*Ampyx nasutus* Dalman, 1827
VI: 1	*Asaphus* (*Lichas*) *laciniatus*	*Lichas laciniatus* (Wahlenberg, 1818)
—	*Asaphus frontalis*	*Niobe frontalis* (Dalman, 1827)
—	*Asaphus* (*Illaenus*) *laticauda*	*Eobronteus laticauda* (Wahlenberg, 1818)
—	*Asaphus* (*Illaenus*?) *Centaurus*	*Illaenus centaurus* (Dalman, 1827)
	Silurian species (from Gotland and Britain?)	
I: 2	*Calymene Blumenbachii* (Brongn.)	(specimen possibly from Britain, Hisinger's collection)
p. 227	*Calymene B.* _ *tuberculosa*	*Calymene tuberculosa* Dalman, 1827
I: 3a-c	*Calymene B.* _ *pulchella*	"*Calymene blumenbachii pulchella* Dalman, 1827"
I: 5a-c	*Calymene concinna*	*Proetus concinnus* (Dalman, 1827)
II: 2a-b	*Calymene punctata*	*Encrinurus punctatus* (Wahlenberg, 1818)
II: 4	*Asaphus caudatus* (Brünnich)	*Dalmanites myops* (König, 1825)
III: 2a-c	*Asaphus angustifrons*	*Ptychopyge angustifrons* (Dalman, 1827)

DALMAN'S GENERA, AND GENERA BASED ON HIS SPECIES

Dalman erected five genus-level taxa (in addition to *Battus*, a junior synonym of *Agnostus*):

Dalman's genera	***type species***
Ampyx Dalman, 1827	*Asaphus* (*Ampyx*) *nasutus* Dalman, 1827
Illaenus Dalman, 1827	*Entomostracites crassicauda* Wahlenberg, 1818
Lichas Dalman, 1827	*Entomostracites laciniatus* Wahlenberg, 1818
Nileus Dalman, 1827	*Asaphus* (*Nileus*) *armadillo* Dalman, 1827
Olenus Dalman, 1827	*Entomostracites gibbosus* Wahlenberg, 1818

Several of his species are types of younger genera, as seen from the following list:

Genus level taxa in order of proposal	***Dalman's 1827 name***
Proetus Steininger, 1831	*Calymene concinna*
Dysplanus Burmeister, 1843	*Asaphus* (*Illaenus*) *centrotus*
Symphysurus Goldfuss, 1843	*Asaphus palpebrosus*
Cybele Lovén, 1846	*Calymene*? *bellatula*
Niobe Angelin, 1851	*Asaphus frontalis*
Cyrtometopus Angelin, 1854	*Calymene*? *clavifrons*
Ptychopyge Angelin, 1854	*Asaphus angustifrons*
Pterygometopus Fr. Schmidt, 1881	*Calymene sclerops*
Parapilekia Kobayashi, 1934	*Calymene*? *speciosa*
Megistaspis (*Megistaspidella*) Jaanusson, 1956	*Asaphus extenuatus*

TRILOBITES, CINCINNATI, AND THE "CINCINNATI SCHOOL OF PALEONTOLOGY"

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ABSTRACT—Trilobites from the abundantly fossiliferous, well-exposed strata of the Cincinnatian Series in its Cincinnati, Ohio, type area are ubiquitous in museum collections around the world. The excellent preservation and abundance of complete trilobites in Upper Ordovician lagerstätte from the series contribute to their popularity as subjects for paleontological research from classical taxonomy to the hydrodynamic properties of the trilobite exoskeleton. An equally well-preserved trilobite trace-fossil fauna from the type-Cincinnatian fueled the nascent study of ichnology in North America by demonstrating the value of trace fossils in understanding trilobite behavior.

Cincinnatian trilobites long have served as the inspiration for amateur and professional paleontologists. Members of the so-called "Cincinnati School of Paleontology" (including J. Locke, S. A. Miller, J. Mickleborough, F. B. Meek, A. F. Foerste, E. O. Ulrich, and R. S. Bassler) were the first to describe type-Cincinnatian trilobites. They established a tradition of scientific inquiry, and paved the way for the professional study of paleontology in the region. The impact of the geologists of the Cincinnati School was felt well beyond the type-Cincinnatian outcrop belt, and affected paleontologic and stratigraphic research in North America for well over a century.

INTRODUCTION

The type-Cincinnatian comprises approximately 212 meters (Sweet, 1979) of abundantly fossiliferous, interbedded mudrock and carbonate in the tri-state area of southwest Ohio, southeast Indiana, and north-central Kentucky. The regional structure, the Cincinnati Arch, and the lack of glacial cover allow exposures of this Late Ordovician lagerstätte in every ravine, streambed, road cut, and excavation. Natural and anthropogenic bedrock exposures abound, and many fossils weather out of the rock so that no specialized equipment or great physical exertion is required to amass a collection of museum-quality fossils of marine invertebrates. The abundance and exquisite preservation of the type-Cincinnatian fauna have made it a staple of museum and private collections around the world (see the internet pages of various natural history museums, including the Paleontologisk Museum of Oslo, Norway) and have spawned several generations of prominent paleontologists. In the first quarter-century of the Paleontological Society's existence, for example, one-fourth of its presidents had spent their formative years in the Cincinnati area (i.e., Schuchert, Ulrich, Foerste, Twenhofel, Cumings, Bassler; see *www.paleosoc.org*).

Trilobites were the most famous and first-studied group of the local fauna (Caster, 1982), and attracted the attention of world-renowned geologists. Charles Lyell, who toured the Ohio River valley during both his trips to North America (Lyell, 1845, 1849), was struck by the excellence of the fauna that was "so remarkably well preserved for so ancient a rock" (Lyell, 1845, p. 43) and the abundance of trilobites. He remarked that "No country is richer in fossils of this class than the United States" (Lyell, 1845, p. 45). He was particularly struck with the dimensions of local specimens of *Isotelus*, recording "the most perfect specimen being 8" long, and many large fragments of other individuals indicating a length of not less than 18 or 20 inches" (Lyell, 1849, p. 219, 220).

Lyell's hosts were local naturalists. Some of them, for example, John Locke and John Gould Anthony were amateur paleontologists, but amateur only in the sense that they had no formal training in paleontology. These enthusiasts were harbingers of an informal community dedicated to paleontological research in the type-Cincinnatian, a group that has become known as the "Cincinnati School of Paleontology."

In this report, we describe the impact of the Cincinnatian trilobite lagerstätte on paleontological research in North America, and use the historical development of the Cincinnati School of Paleontology as the temporal framework. We describe members of the Cincinnati School who authored works on trilobites, and we look at the years since the original "class" and the influence this "School" has had in shaping modern trilobite research.

Taxonomic note: In this paper, genus and species names are cited as used by the original author, and current taxonomic assignments are given in brackets [ ] following the original names.

THE CINCINNATI SCHOOL OF PALEONTOLOGY

Within the type-Cincinnatian outcrop belt, any interested person could aspire to paleontological proficiency, and for over

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a century many local residents achieved that goal. Among students of invertebrate paleontology in the nineteenth century, there were comparatively few professionals, but, rather, a large number of amateurs (Bassler, 1933). An amateur sometimes would metamorphose into a professional—first by independent publication of species descriptions or faunal lists, then, in some cases, by temporary work on a state survey, and finally, for a fortunate few, appointment to a permanent position on the national geological survey or in some museum or university (Bassler, 1933). One group of motivated amateur paleontological enthusiasts in the hinterland of Ohio became known as "The Cincinnati School of Paleontology."

K. E. Caster may have been the first to use the school metaphor in reference to these dedicated amateurs-turned-professionals. He cited "a veritable 'school' of American earth-scientists" (Caster, 1965, p. 167), and later used the term "Cincinnati 'School' of Paleontology" (Caster, 1982). However, the phenomenon was recognized even earlier by Becker (1938) and by Bassler (1947, p. iii), who termed this cohort the "Cincinnati geologists."

There is no single, definitive list of members of the Cincinnati School (but see Davis, 2001), nor have membership criteria been rigorously defined, but there are at least three elements to consider in such a definition. The first is geography; members should have a Cincinnati connection, each having lived some significant portion of life in the type-Cincinnatian outcrop area. The second is the time frame; most of the commonly listed members were active in the Cincinnati area in the second half of the nineteenth century. The third is professional status; the members at least started as amateurs. It would be misleading, however, to delineate membership strictly on geographic and temporal grounds. Important paleontologic work in the Cincinnati region began well before the mid-1800s, and extended through much of the twentieth century, and some of this research was done by workers who hailed from beyond the fringe of the type-Cincinnatian outcrop area. In some respects, the Cincinnati School is a frame of mind. Breadth-of-interest has been a leitmotiv. Most members were enthralled by fossils of a wide range of taxonomic groups, as opposed to being specialists on creatures in a single, narrow lineage. Therefore, we do not wish to impose rigorous criteria on defining the membership; we feel there is more information to be gained for our purpose by using broad criteria and giving first consideration for inclusion in this cohort to the impact of the workers on trilobite research. Thus, for example, John Locke, who was active well before the American Civil War, and August F. Foerste, who lived outside Cincinnati and was active mostly in the twentieth century, are included because of their important contributions to Cincinnatian trilobite research.

TRILOBITE RESEARCH AND THE CINCINNATI SCHOOL OF PALEONTOLOGY

John Locke (1792–1856)

Born in New Hampshire in 1792 and not moving to Cincinnati until 1822, John Locke (Fig. 3A) is credited as the first local amateur to become a professional geologist (Bassler, 1944). Locke was trained in medicine, was an astronomer, a teacher, a professor of chemistry, and, at least for a time, was Principal of the Cincinnati Female Academy (Bassler, 1945; Drake and Mansfield, 1827). He must have been an amazing fellow. Not only was he a geologist and teacher, but he was an inventor of scientific and surveying equipment, and was one of the first in Cincinnati to practice photography (Dexter, 1979; Gagel, 1998). In 1836, the Ohio Legislature created a committee to look into establishing a state geological survey, and Locke was appointed one of four members. The Survey was authorized the next year, and he was named one of five assistant geologists. His report on the southwest district of the State was the most extensive of the series, and he was the first person to recognize what is now called the Cincinnati Arch (Locke, 1838; Hansen and Collins, 1979). In subsequent surveys he established regional stratigraphic relationships. Accepting no salary, Locke offered his work free "to the service of our citizens" (Winchell, 1894, p. 345). John Locke was one of Lyell's hosts when he visited Cincinnati in the 1840s (Lyell, 1845).

Trilobite research.—Locke's most lasting contribution to trilobite paleontology was his description of *Isotelus maximus* Locke, 1838. He differentiated this species from the similar and earlier-named *I. megalops* Green, 1832 [= *I. gigas* Dekay, 1824] on the basis of its large size (53 cm (21 inches) vs. 13 cm (5 inches) for *I. megalops* (Locke, 1841, 1842, 1843a; Fig. 1). He feared his specimen might be "actually an overgrown *I. megalops* of Green" (Winchell, 1894, p. 345), but his species designation has stood the test of time. It is curious that Locke did not compare *I. maximus* with the type species of the genus, *I. gigas*, which had been described earlier than *I. megalops* (1824 vs. 1832). Perhaps Green's (1832*) Monograph of the Trilobites of North America* was more widely available than *the Annals of the Lyceum of Natural History of New York* in which Dekay's (1824) description appeared.

Locke (1838) mentioned *Isotelus maximus* in his survey of Ohio geology, and the name appeared again in a second-hand account of the discovery the large trilobite in the proceedings of the *Association of American Geologists* (= *American Journal of Science*) in 1841. When Locke's (1842) formal description appeared a year later, he attempted to alter the specific name of the species from *maximus* to *megistos* for aesthetic reasons. This emendation caused considerable confusion, as other workers treated the two species as separate entities (e.g., Foerste, 1919a, 1924). Foerste (1919a) noted that Locke had exercised considerable artistic license in the figure that accompanied the original description of *I. maximus*. As Locke (1838) explained, his drawing of the type specimen was based on a partial pygidium, and reconstructed and enlarged to twice its size, with a thorax and cehalon added, based on drawings of *I. megalops* Green. Locke (1842) based his formal description of *I. megistos* (a revision of his 1838 preliminary designation of *I. maximus*) on four specimens. The large, complete *Isotelus* in the accompanying illustration is the composite of Locke's 1838 *I. maximus* paper. Two of the additional specimens are represented by their pygidial outlines superimposed on the drawing of the large trilobite. Because Locke's (1842) suite of specimens came from different stratigraphic horizons and had slightly different pygidial outlines, Foerste (1910) advocated restricting *I. maximus* to forms from the younger Richmondian beds, and retaining *I. megistos* for *Isotelus* from the older Maysville/Corryville beds.

Just how many species of *Isotelus* are represented in the type Cincinnatian has not been resolved. Hu (1971) listed eight

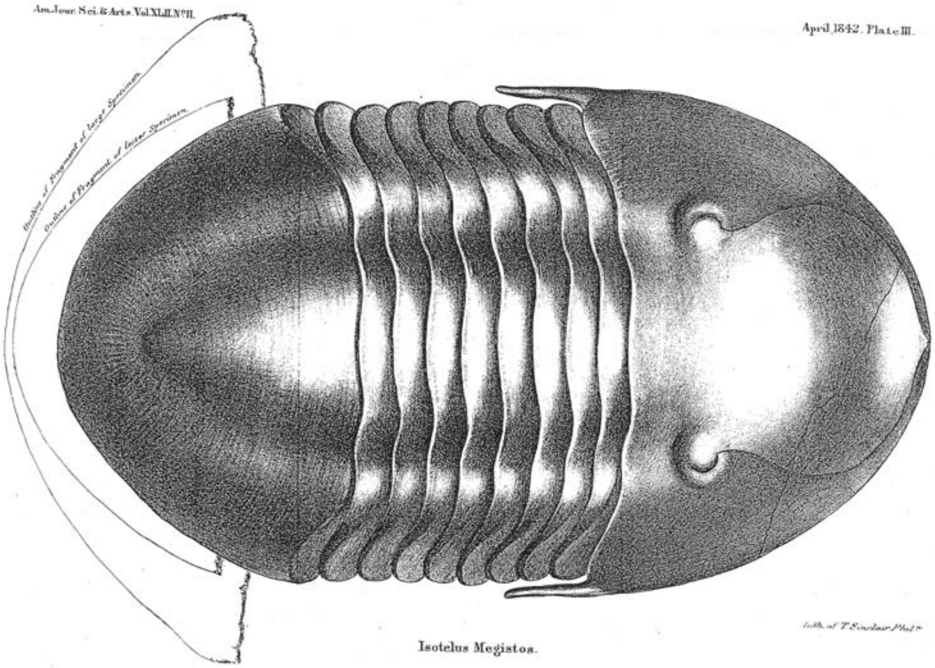

Fig. 1. Locke's (1842, pl. 3) *Isotelus* "*megistos*" [= *I. maximus*], reproduced here smaller than the 21-inch-long original drawing.

species that had been named from the Cincinnati area. Recent compendia list only *I. maximus* and *I gigas* (e.g., Babcock, 1996), but the morphologic variation evident in the genus (see discussions of Foerste, Ulrich, and Hu's species of *Isotelus*, below) suggest that the taxon is ripe for a systematic review.

Locke's *Ceraurus crosotus* (1843 b, c), a trilobite with a fringed cephalic border and tuberculate surface-texture, almost certainly should be placed in the genus *Acidaspis* Murchison, 1839. Locke's drawing of his most-complete specimen (Locke, 1843b; Fig. 2A) is a rather fanciful rendering of a trilobite with a most un-*Ceraurus*-like, anteriorily tapering glabella. His subsequent drawings of pygidia of this trilobite (Locke, 1843c; Fig. 2B herein) may be that of *Acidaspis* or *Primaspis*. The pygidia of these two trilobites differ primarily in the number of pygidial spines; the spines are evidently broken in the specimens figured by Locke, and make positive identification of these specimens unlikely. Meek (1873a) provisionally placed Locke's specimens in *Acidaspis*. Hughes and Cooper (1999) referred new specimens to *Primaspis crosotus* (Locke), presumably on the basic of cephalic characters, but the pygidial spines in the trilobites they illustrated were broken, rendering comparisons with Locke's (1843b) specimens of *C. crosotus* moot.

F. B. Meek (1817–1876)

Fielding Bradford Meek was born in Madison, Indiana, on the western edge of the type Cincinnatian outcrop belt. After failing in the mercantile business, he studied local fossils on his own, and attracted the attention of David Dale Owen, director of the federal geological survey office located in New Harmony, Indiana. As he organized the geological surveys of Iowa, Wisconsin, and Minnesota (1848–1849), Owen made Meek one of his assistants. Meek later joined James Hall in Albany, New York, as his assistant (1852–1858). During Summer 1853, Hall commissioned Meek and F. V. Hayden to explore the badlands of Nebraska. Meek's first paleontological publication, on Cretaceous fossils from Nebraska (Hall and Meek, 1856), grew out of this expedition.

Meek continued his association with Hayden for the rest of his life, and described the invertebrate fossils collected by Hayden during the latter's great western expeditions (e.g., Meek, 1873b). Meek was also informally connected with the other great geological surveys of the era, Clarence King's *Geological Survey of the 40^{th} Parallel* (Meek, 1870, 1877), John Wesley Powell's *Survey of the Rocky Mountain Region,* and Wheeler's *Survey West of the 100^{th} Meridian* (Meek, 1874). According to Bassler (1933), Meek was the outstanding paleontologist of these territorial surveys, although he officially was not connected with them (i.e., he did not have a salaried position), and preferred, according to one eulogist, to "command his own time and opportunities to do work in other inviting fields" (White, 1902, p. 79).

Meek left James Hall for Washington, D.C., and the Smithsonian Institution in 1858. The Castle (the original Smithsonian building) had recently been completed and was not yet fully occupied. Meek, a bachelor, took up residence in a tower room, where he lived and worked until his death in 1876 (White, 1902). Yochelson (1985) credits Meek, by benefit of his extensive federal survey experience, with establishing the tradition of geologic research within the fledgling National Museum.

Trilobite research.—As a professional geologist and paleontologist, Meek's reach extended well beyond the Cincinnatian. His association with the geological explorations of the western U.S. yielded numerous descriptions of Cambrian trilobites of the western interior. As an itinerant paleontologist for the emerging state geological surveys, Meek was able to "get in on the ground floor" in describing the fossil faunas. One of Meek's

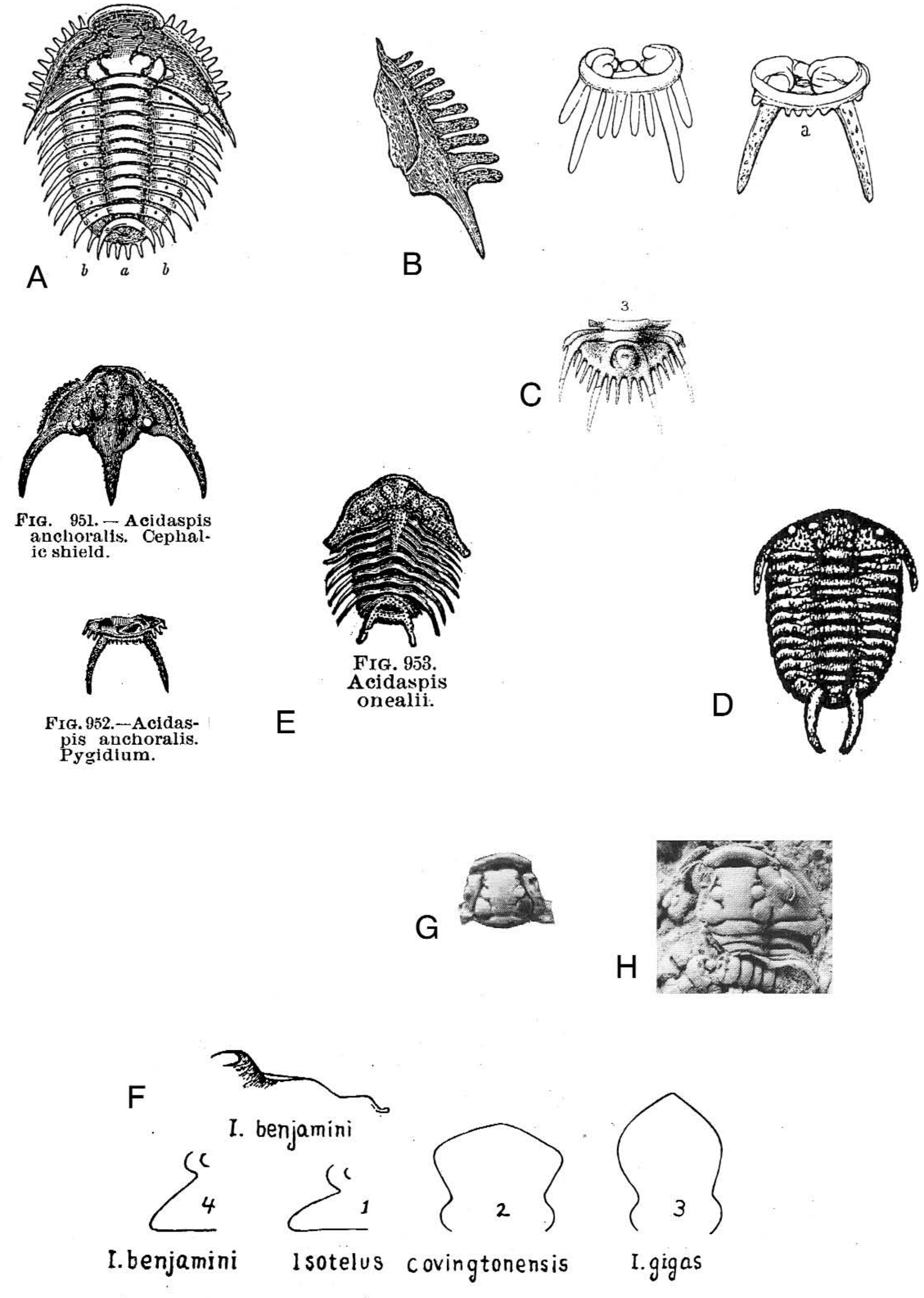

Fig. 2. Cincinnatian trilobites. A–G, Nineteenth Century illustrations by members of the Cincinnati School of Paleontology. All reproduced at approximately their original publication size. A, Locke's (1843a) *Ceraurus crosotus* [= *Acidaspis*]. B, Locke's (1843b) *Ceraurus crosotus* [=*Acidaspis*], right librigena and two pygidia. C, Meek's (1873a, pl. 4, fig. 3) *Acidaspis cincinnatiensis* (pygidium). E, Miller's (1889) *Acidaspis anchoralis* cephalon (top), pygidium (bottom), and *A. oneali.* D, Miller and Gurley's (1893, p. vii, fig. 80) *Ceraurus milleranus*. F, Ulrich's (1914) distinction between *Isotelus benjamini*, *I. covingtonensis*, and *I. gigas* based on differences in the outline and lateral profile of the glabella. G, Foerste's (1910, pl. 3, fig. 19) *Calymene abbreviata* [= *Gravicalymene abbreviata*]. H, Ross' (1979, pl. 3, fig. 12) *Gravicalymene truncatus* [= *Gravicalymene abbreviata*].

best-known survey works is an 1865 report on Illinois paleontology (Meek and Worthen, 1865a). Meek's association with Worthen was very productive, and between 1865 and 1877 Meek authored or co-authored with Worthen over 30 trilobite taxa (Table 1). Meek and Worthen were also among the first to describe the arthropods of the Mazon Creek lagerstätte (Meek, 1867a; Meek and Worthen, 1868b). They were the first to define a "Cincinnati Group" (= Cincinnatian Series) to embrace the Upper Ordovician eastern North America (Meek and Worthen, 1865b; Meek, 1867b).

Meek had a vexing predisposition to publish preliminary descriptions of new species without illustration. Most of these descriptions were published in the *Proceedings of the Philadelphia Academy of Science*, with assurance that full descriptions and illustrations would be published eventually (e.g., Meek, 1871). However, the elaboration and illustrations were not always forthcoming. In his compendium of North American fossils, Miller (1889) cited several of Meek's species as "not properly defined". These omissions created opportunity for restudy by later workers (see discussion of August Foerste, below).

Meek published numerous descriptions of Cincinnati fossils (e.g., Meek, 1873a), but placed a number of fossils into previously established taxa. Among trilobites, for example, Meek (1873a) placed the common local form of what was then referred

Table 1. F. B. Meek's trilobite descriptions.

Author(s)/Year	Original taxonomic designation	Status (reference#)*
Meek, 1861	*Crepicephalus oweni*	*Ptychoparia oweni* (4)
Meek and Worthen, 1865a	*Dalmania danae*	*Dalmanites danae* (1), (6)
"	*Lichas cucullus*	*Amphilichas cucullus* (4), (13)
"	*Phillipsia (Griffithides) portlocki*	(2); *Exochops portlocki* (5)
"	*Phillipsia (Griffithides?) sangamonensis*	(2); *Ameura sangamonensis* (5)
"	*Phillipsia (Griffithides) scitula*	(2); *Ditomopyge scitula* (5), (9), (10),(14)
"	*Proetus ellipticus*	(2); *Elliptophillipsia ellipticus* (8)
Meek, 1870	*Conocoryphe kingi*	*Elrathia kingi* (7), (11)
"	*Paradoxides ? nevadensis*	*Olenoides nevadensis* (6)
Meek and Worthen, 1870	*Asaphus (Isotelus) vigilans*	*Nileus vigilans* (4)
"	*Illaenus (Bumastus) graftonensis*	*Bumastus graftonensis* (4)
"	*Amphilichas cucullus cucullus*	(12)
"	*Phillipsia (Griffithides) bufo*	(2); *Griffithides bufo* (16)
"	*Phillipsia tuberculata*	(2), (8)
Meek, 1871	*Dalmanites ohioensis*	(2)
"	*Phillipsia stevensoni*	(2); *Kaskia stevensoni* (5)
"	*Proetus planimarginatus*	(2); *Dechenella planimarginatus* (13)
Meek, 1872	*Dalmanites carleyi*†	(2); *Pterygometopus carleyi* (4); *Achatella carleyi* (6), (9)
"	*Proetus spurlocki*†	(4); juvenile *Isotelus* (3)
Meek, 1873a	*Acidaspis cincinnatiensis*†	(2), (4), (14)
"	*Illaenus springfieldensis*	(4)
Meek, 1873b	*Agonostus bidens*	(2)
"	*A. maladensis*	"not properly defined" (2)
"	*Asaphus goniocercus*	questioned (2)
"	*Bathyurellus truncatus*	"not satisfactorily defined" (2)
"	*Bathyurellus wheeleri*	*Asaphiscus wheeleri* (2)
"	*Bathyurus serratus*	N.D.
"	*Conocoryphe gallatinensis*	*Ptychoparia oweni* (4)
"	*Bathyuriscus genus*	(7)
Meek, 1874	*Olenellus gilberti*	(15); *Elliptocephala gilberti* (2)
Meek, 1875	*Olenellus howelli*	*Elliptocephala howelli* (2)
"	*Phillipsia lodiensis*	*Australosutura lodiensis* (10), (14)

Notes:

*Key to references: (1) Meek and Worthen, 1868a (2) Miller, 1889 (3) Raymond and Barton, 1913 (4) Bassler, 1915 (5) Weller, 1936 (6) Delo, 1940 (7) Harrington, *et al.*, 1959 (8) Hessler, 1963 (9) Ludvigsen and Chatterton, 1982 (10) Brezinski, 1988 (11) Morris, 1988 (12) Thomas and Holloway, 1988 (13) Lieberman, 1994 (14) Babcock, 1996 (15) Lieberman, 1999 (16) Yale Invertebrate Paleontology Collections web-site 02/07/02 (http://www.yale.edu/ypmip) N.D. = no data.

†Type-Cincinnatian taxa.

to *Calymene* into the well-known *C. senaria* Conrad, 1841, a species originally described from the Upper Ordovician of New York State. It was not until August Foerste (see discussion, below) examined Meek's material that the ubiquitous Cincinnatian form of *Calymene* became *C. meeki* [= *Flexicalymene meeki* (Foerste, 1910)].

One of Meek's enduring trilobite taxonomic contributions was describing a species of the relatively rare Cincinnatian genus *Acidaspis*. *Acidaspis cincinnatiensis* Meek (1873a) is the only species of the genus from the type Cincinnatian to survive modern taxonomic scrutiny (Fig. 2C and Table 1; see discussion of S. A. Miller's *A. anchoralis* and *A. onealli*, below).

S. A. Miller (1837–1897)

Although a lawyer by training and vocation, Samuel Almond Miller (Fig. 3B) was a prolific writer. He even published his own scientific periodical, *The Cincinnati Quarterly Journal of Science*, which ran for eight numbers in 1874 and 1875. When the Cincinnati Society of Natural History commenced its own journal in 1878, it was rather similar to Miller's defunct one. This is hardly surprising, given the fact that he had been campaigning for the Society to publish its own journal (see, for example, Anonymous, 1875). Miller is probably best known for his compilations. His 1877 *The American Palaeozoic Fossils* was greatly expanded into the 1889 *North American Geology and Palaeontology for the Use of Amateurs, Students, and Scientists*. The latter, along with two supplements, was widely used by both amateur and professional fossil-enthusiasts, and Caster (1982, p. 25) has written, "It was probably the most used volume on American paleontology ever compiled…" The popularity of this volume made manifest the Cincinnati School tradition of creating bibliographies and indices of the local fauna.

Trilobite research.—Miller's (1889) compendium brought the whole of the Cincinnatian fauna to a wide audience, and his *Monograph of the Crustacea of the Cincinnati Group* (1874) focused on descriptions of the trilobites. Miller described a dozen trilobite species (Table 2). Of these, only *Ceraurus milleranus* Miller and Gurley, 1893, and *Encrinurus egani* Miller, 1880, survive today as widely recognized taxa (Fig. 2D). Miller named two species of the relatively rare Cincinnatian genus *Acidaspis* (Fig. 2E); however, recent compendia of the type Cincinnatian fauna (e.g., Davis, 1992; Babcock, 1996) recognized only *A. cincinnatiensis* Meek from the area.

Miller (1874) correctly interpreted slender, concentric "ichnolites" as the tracks of *Asaphus* [= *Isotelus*], and anticipated by almost a century Osgood's (1970) work on type Cincinnatian trilobite trace-fossils. Miller's interpretation is all the more impressive because the existence of trilobite appendages was not yet widely acknowledged (Mickleborough, 1883).

John Mickleborough

John Mickleborough is one of the less-well-known members of the Cincinnati School, and there seems to be little published biographical information about him. His 1883 paper listed him as holding a Ph.D. For seven years beginning about 1880, he was principal of the Cincinnati Normal School, a teacher-training establishment of the Cincinnati Board of Education. He then went on to become the headmaster of the Boy's High School in Brooklyn, New York (Venable, 1894; Lathrop, 1900). He was co-author of a type Cincinnatian fossil compendium (Mickleborough and Wetherby, 1878a, reprinted 1878b), and he was actively associated with the Cincinnati Society of Natural History from 1878 until at least 1883. In this capacity, he served as a member of a society committee on geological nomenclature (Miller, *et al.*, 1879).

Trilobite research.—Mickleborough's (1883) most significant contribution to trilobite research was his report that summarized what was known on the "Locomotory appendages of trilobites." Billings's (1870) discovery of appendages in *Asaphus* [= *Isotelus*] and Walcott's (1881) paper illustrating appendages in

Table 2. S. A. Miller's trilobite descriptions.

Author/Year	Original taxonomic designation	Status (reference #)*
Miller, 1875a	*Acidaspis O'Nealli*†	not recognized (9)
Miller, 1875b	*Acidaspis anchoralis*†	*A. cincinnatiensis* (5)
Miller, 1878	*Lichas harrisi*†	*Arctinurus harrisi* (3), (4) *Amphilichas harrisi* (5), (8)
Miller, 1880	*Encrinurus egani*	(3), (9)
Miller, 1889	*Ceraurus meekanus*†	*Ceraurinus icarus* (3); (7)
"	*Lichas faberi*†	*Amphilichas halli* (3)
Miller and Gurley, 1893	*Ceraurus milleranus*†	(1), (2), (3), (10)
"	*Illaenus danielsi*	(3)
"	*Lichas byrnesanus*	*Corydocephalus byrnesanus* (3); *Trochurus byrnesanus* (8)
"	*Lichas hanoverensis*	*Corydocephalus phlyctainoides* (3) *Trochurus hanoverensis* (8)
Miller, 1897	*Lichas paulianus*	*Corydocephalus wesenbergensis paulianus* (3)

Notes:

*Key to references: (1) Miller, 1889 (2) Raymond and Barton, 1913 (3) Bassler, 1915 (4) Foerste, 1917a (5) Foerste, 1917c (6) Whittington, 1956 (7) Ludvigsen, 1977 (8) Thomas and Holloway, 1988 (9) Gass, *et al.*, 1992 (10) Babcock, 1996.

†Type-Cincinnatian taxa.

Fig. 3. Cincinnati paleontologists described in this report. A, John Locke. B, S. A. Miller. C, Charles Schuchert. D, W. H. Twenhofel. E, Ray Bassler, E.O. Ulrich, and August Foerste (left to right), apparently at the U.S. National Museum. Fig. 3A from Winchell (1894); Figs. 3B–D courtesy of the Department of Geology, University of Cincinnati; Fig. 3E courtesy of the Dayton Society of Natural History's Boonshoft Museum, Dayton, Ohio.

Calymene [= *Flexicalymene*], *Ceraurus*, and *Acidaspis* were still recent, and Beecher's (1893) announcement of appendages in *Triarthrus* was yet to be made. Mickleborough (1883) discussed the reluctance with which these findings were greeted by many geologists. He cited Dana's (1875) geology textbook as an example of this intellectual inertia, "Trilobites differed [from modern crustaceans] in having no true legs" and that trilobites "probably often attached themselves to the rocks, like the shells called Limpets." [Twenty years later, after Beecher's (1893) description of appendages in *Triarthrus*, Dana (1895) revised this portion of his text.]

Mickleborough (1883) described a new specimen of a type Cincinnatian *Asaphus* [= *Isotelus*] with preserved appendages (see Babcock, 1996, fig. 8-2, 4). He characterized the anteriormost limb as chelate, although poor preservation of the specimen rendered this interpretation tenuous. Even so, Mickleborough's conclusion that trilobites were most closely related to chelicerates is interesting because of its congruence with modern interpretations of the relationships between trilobites and their nearest relations (e.g., Briggs and Fortey, 1989).

Nathaniel Southgate Shaler (1841–1906)

A native of Newport, Kentucky, across the Ohio River from Cincinnati, Nathaniel Southgate Shaler was born into comfortable circumstances. His father had attended Harvard and married into the Southgate family, an established Kentucky clan. Although he is not known for trilobite research, we mention Nathaniel Shaler as another Cincinnati paleontologist who reached lofty heights. The younger Shaler graduated from his father's alma mater, and studied under the great Louis Agassiz, an experience Shaler described at length in his autobiography (Shaler, 1909). Shaler was hired to teach at his alma mater, and he eventually took over Agassiz's duties when the latter reached retirement age. Among Shaler's achievements at Harvard was the establishment of a geology program (Wolff, 1908). His research interests continually evolved, and he published on topics from gravels for road beds to lunar topography (Wolff, 1908).

Trilobite research.—Shaler (1909) attributed his interest in paleontology to finding *Calymene* [= *Flexicalymene*] as a boy. His professional interests as an adult were broad and varied, but his association with another member of the Cincinnati School yielded descriptions of two new trilobite species descriptions (Shaler and Foreste, 1888; see Table 4).

E. O. Ulrich (1857–1944)

Edward Ulrich, as he was christened, was a native of Cincinnati. According to Bassler (1945, p. 332), Ulrich gave himself the middle name "Oscar" after the hero of a story he read as a youth. He attended Wallace and Baldwin College in Berea, Ohio, for a time and did a stint at medical school in Cincinnati. However, he did not have much use for formal education, because "he was taught too much that he didn't want and too little that he did" (Bassler, 1945, p. 333). What Ulrich wanted to study was the local fossil fauna. In 1877, his enthusiasm led to his being hired as Custodian of the Cincinnati Natural History Society's recently acquired building (Bassler, 1945). Early on, Ulrich became a mentor to several others of the Cincinnati School, and his home/paleontology studio became a Mecca to paleontology enthusiasts who visited the Cincinnati area. James Hall and August Foerste (discussed below) were frequent visitors. In 1878, 20-year-old Charles Schuchert brought Ulrich fossils for identification, beginning a friendship and a working relationship that lasted until James Hall, on a visit to Ulrich's studio, offered Schuchert a job in Albany. Schuchert moved east (eventually to his own distinguished career at Yale University, see below). Ray Bassler (also discussed below) was another early protégé of Ulrich.

Ulrich moved from his Newport studio in 1897 to take a position with the U.S. Geological Survey, where he worked until his official retirement in 1932 (Fig. 3E). Even after retirement Ulrich continued publishing as an honorary Associate in Paleontology at the Smithsonian, a title he had held since 1914 (see Yochelson, 1985, for an explanation of the interrelationship of USGS and Smithsonian appointments in paleontology). Ulrich served as President of the Paleontological Society in 1915. By the time of his retirement, he had been awarded a Ph.D. by Wallace and Baldwin College, which he had attended but from which he had never graduated.

Ulrich left a mixed legacy. His rise from modest circumstances to the top of his profession at a prestigious institution, without benefit of a college degree, inspires admiration. The route he took to reach that height, and some of the purposes to which he put his position and stature, however, are less commendable. His name is linked with several unsavory incidents in the history of North American paleontology. One episode involved fraud; Ulrich was a party, with N. H. Winchell, in falsifying the priority of brachiopod species names, and thus effectively stole these taxa from another worker (Weiss, 1997; Mikulic and Kluessendorf, 2001). In another, Ulrich, apparently out of professional jealousy and personal spite, attempted to wreak revenge on his former friend Charles Schuchert by backing an attempt to prevent Schuchert's election to the presidency of the Geological Society of America (Weiss, 1992; Weiss and White, 1998). Ulrich (1911) had proposed dramatic changes to North American Cambrian stratigraphy. Schuchert, Ulrich's long-time friend from their Cincinnati days, included Ulrich's proposed changes in the first edition of his historical geology textbook (Pirsson and Schuchert, 1915), and noted that these revisions were a work in progress. So great was Ulrich's investment of ego in this project, for which he hoped to be immortalized as an author of a geologic system—a là Sedgewick and Murchison (Weiss and White, 1998)—that the failure of Schuchert to embrace totally Ulrich's Ozarkian and Canadian systems marked the end of their friendship and precipitated the (unsuccessful) GSA election challenge. Other North American stratigraphers also had careers impeded by disagreements with Ulrich (Mikulic and Kluessendorf, 2001; Weiss, 2001). Ulrich stymied the development of North American Cambrian stratigraphy through "his authority, his disputative nature, and the tenacity with which he held his views" (Merk, 1985, p. 169). The most positive light in which Ulrich's legacy could be viewed is that he provoked "and I really mean provoked" (Raymond, 1944, p. 256) other researchers to examine their own work more closely than they otherwise might have done

Trilobite research.—Ulrich is best known for his studies of Cincinnatian bryozoans (Cuffey *et al*., 2002). However, by the end of his long career, he had published at least one paper on nearly every major invertebrate group, including annelids, sponges, and conodonts, as well as mollusks, brachiopods, ostracods, and trilobites (Bassler, 1945).

Table 3. E. O. Ulrich's trilobite descriptions to 1919.

Author/Year	Original taxonomic designation	Status (reference #)*
Ulrich, 1878	*Trinucleus bellulus*†	*Cryptolithus bellulus* (1), (3); *C. tessellatus* (9)
Ulrich, 1879	*Calymene nasuta*	*Calymenella nasuta* (1)
Ulrich, 1892	*Lichas (Hoplolichas) robbinsi*	*Amphilichas robbinsi* (1); *Probolichas robbinsi* (8)
"	*Lichas (Hoplolichas) bicornis*	*Amphilichas bicornis* (1), (8)
Ulrich, 1914	*Isotelus benjamini*†	(1); indistinguishable (4)
"	*Isotelus covingtonensis*†	(3); indistinguishable (4)
Ulrich, in Bassler, 1919	*Cryptolithus recurvus*†	(2); *C. bellulus* (3)

Notes:

*Key to references: (1) Bassler, 1915 (2) Foerste, 1924 (3) Whittington, 1941 (4) Hu, 1971 (5) Holloway, 1981 (6) Ludvigsen and Chatterton, 1982 (7) Ludvigsen and Tuffnell, 1983 (8) Thomas and Holloway, 1988 (9) Shaw and Lespérance, 1994.

†Type-Cincinnatian taxa.

Ulrich described at least a half-dozen trilobite species from the Cincinnati area (Table 3), but these taxa have not fared well under subsequent examination. Ulrich's distinction of his taxa *Isotelus benjamini* Ulrich, 1914 and *I. covingtonensis* Ulrich, 1914 from *I. gigas* was based on differences in the outline of the glabella (Fig. 2F). Hu (1971) judged this criterion to be ambiguous, and insufficient for species differentiation in *Isotelus*.

Ulrich (*in* Bassler, 1919) distinguished *Cryptolithus recurvus* from related species on the basis of a posteriorly recurved cephalic margin. Whittington (1941) concluded that the recurved margin in Ulrich's type specimen was an artifact of taphonomy rather than a real morphological character, and Whittington placed *C. recurvus* in synonomy with *C. bellulus*.

Bassler (1915) dispatched Ulrich's (1878) *Trinucleus bellulus* to *Cryptolithus*. Curiously, Ulrich did not compare *C. bellulus* to the well-established *C. tessellatus* Green, 1832; more recent workers (for example, Whittington, 1968; Hughes *et al*., 1975; and Shaw and Lespérance, 1994) consolidated *C. bellulus* within that species. Babcock (1996) recognized *C. tessellatus* as the only species of *Cryptolithus* from the Ohio Ordovician.

During his retirement, as an Associate in Paleontology at the Smithsonian, Ulrich was co-author with Charles Resser of three monographs on Cambrian trilobites (Ulrich and Resser, 1930, 1933, 1940). Ulrich's association with Resser does not enhance the former's reputation as a trilobite worker. Resser is regarded among Cambrian trilobite workers as "perhaps one of the worst paleontologists in North America" (Sundberg, 2000, p. 63; this volume) for obscuring the phylogeny and taxonomic diversity of Cambrian trilobites through his taxonomic profligacy. Resser's influence extended to at least one other paper by Ulrich (1930), a monograph on Appalachian telephinid trilobites, which listed 26 new species. Ulrich acknowledged that publication of this work, on which he had spent 25 years "but lacked the time to complete the manuscripts and illustrations," was made possible through the "gratefully accepted aid of Dr. C. E. Resser, who made most of the photographs and assisted otherwise in promoting the effort" (Ulrich, 1930, p. 1). In their first co-authored monograph, Ulrich and Resser (1930) named 25 new species of *Dikelocephalus.* Later workers criticized Ulrich and Resser's putative taxa as the result of oversplitting (Twenhofel, 1945; Raasch, 1951; Taylor and Halley, 1974; Westrop, 1986; Hughes, 1994). Ulrich had anticipated the criticism of oversplitting taxa. He justified his taxonomic fecundity on stratigraphic grounds, "if we are to get the utmost benefit from the fossils as stratigraphic and age indices it is absolutely essential to discriminate the species as closely as possible" (Ulrich, 1930, p. 10). His argument for splitting has not worn well. Quite the contrary, Raasch (1951, p. 137) blamed Ulrich and Resser's nomenclatural excess for "rendering the Dikelocephalidae useless for purposes either of biostratigraphy or phylogeny." In attempting to reconstruct the taxonomic basis for their species designation, Hughes (1994, p. 4) wrote, "almost any feature that showed morphological variation was automatically considered to be of taxonomic importance. The result was a large number of species descriptions based on minor and inconsistent differences between species." Labandeira and Hughes (1994) concluded, on the basis of a quantitative re-examination of Ulrich and Resser's type material, that all their supposed species actually comprise a single morphospecies. Hughes (1994) formally placed Ulrich and Resser's species of *Dikelocephalus* into the pre-existing *D. minnesotensis* Owen, 1852. Chatterton, *et al*. (1999) cited the large number of species in Ulrich's monograph as evidence that the genus is in need of revision.

A decade after the first Ulrich/Resser monographs were published, Delo (1940) listed himself as junior author to Ulrich on a dozen species of phacopid trilobites. Delo acknowledged Ulrich for allowing him to describe new material on which Ulrich had "previously begun investigation" (Delo, 1940, p. 1). Ulrich was 83 years old when Delo's monograph was published, and it is possible that Delo's sharing the species-authorship with Ulrich reflected the younger man's deference to this paleontological icon (and fellow Cincinnati-area native, see Becker, 1938) rather than Ulrich's participation in writing the species descriptions.

A year later, Whittington (1941, p. 21) acknowledged Ulrich for access to the latter's trilobites from Oklahoma, "on which he [Ulrich] had already placed manuscript names." Ulrich was designated the senior author on three genera that resulted from this arrangement, and Whittington named *Cryptolithoides ulrichi* in honor of his senior colleague.

Ulrich's connections with junior trilobite researchers willing to credit him with species co-authorship for providing specimens or in acknowledgment of his personal priority over the specimens and his collaboration with Resser, a known "splitter," combined to make Ulrich the most prolific describer of trilobites among the members of the Cincinnati School profiled herein. We tallied 150 trilobite species attributed to Ulrich and co-authors, 81 of which are described in a single paper (Ulrich and Resser, 1933) as compared to 34 trilobite species for Meek and 50 for Foerste. Yet, Ulrich's name is not primarily associated with trilobite research. This fact speaks volumes on the quality of Ulrich's trilobite species descriptions, especially those from his years as an Associate at the Smithsonian. For this reason, Table 3 is limited to a list of trilobites solely described by Ulrich, from his pre-Smithsonian, Cincinnati years.

Charles Schuchert (1858–1942)

Characterized by one eulogist as "one of the greatest paleontologists of his time" (Lull, 1943), Charles Schuchert started life as the child of German-immigrant parents of modest means who was smitten by the fossils of his native Cincinnati. Although he was not a trilobite specialist, we include Schuchert herein primarily because of his close association with other members of the Cincinnati School and his prominence in North American paleontology. Schuchert met Ulrich at a meeting of the Cincinnati Society of Natural History in 1878, and the two men became "inseparable companions" (Dunbar, 1942, p. 375). After the Schuchert family business was destroyed by fire in 1885, Schuchert moved in with Ulrich, and they worked together describing and illustrating fossils. Schuchert chose to concentrate on brachiopods and soon built a collection that caught the attention of the acquisitive James Hall. In 1888, Hall, who was State Geologist of New York, visited the duo and offered to buy Schuchert's collection. Schuchert was loath to be separated from his life's work, so Hall offered Schuchert a position as his assistant in Albany, New York (Kaesler, 1987). After several years in New York, Schuchert removed himself from "Hall's clutches" (Dunbar *in* Kaesler, 1987, p. 409) to take a position at the U.S. National Museum, where he served as Assistant Curator of Stratigraphic Paleontology (Fig. 3C). Schuchert left the Museum in 1904 to become Yale's second professor of invertebrate paleontology after the death of Charles Beecher. Schuchert received the highest honors in his field, including election to the National Academy of Sciences and the Geological Society of America's Penrose Medal. He served as president of both the GSA (1922) and the Paleontological Society (1910), and today a medal of the Paleontological Society bears his name. Schuchert accomplished all this without the benefit of a college or even high school diploma; he had attended school only through the sixth grade (Dunbar, 1942).

Contributions to Trilobite research.—Known primarily for his encyclopedic work on North American brachiopods and his compilation of paleogeographic maps (e.g., Schuchert, 1910), Schuchert's contributions to trilobite research were indirect, and primarily as an advisor to a generation of paleontologists, including Percy Edward Raymond, William Henry Twenhofel, and Carl Owen Dunbar. Raymond, who came to Yale to work with Beecher but had his studies interrupted by his advisor's untimely death, returned to finish his degree with Schuchert and became a prominent trilobite paleontologist as a faculty member at Harvard. Twenhofel did his dissertation work on the fossils and strata of Anticosti Island (and named *Calymene schucherti* in honor of his mentor) and later went on to attain prominence in both paleontology and sedimentology (see discussion, below). Dunbar came to Yale to study with Schuchert on the advice of Twenhofel, who was then at the University of Kansas (Skinner and Narendra, 1985). Dunbar was later hired at Yale, and was positioned to become Schuchert's successor. At Yale, he was the junior author (Schuchert and Dunbar, 1933) of one of the so-called "Yale texts" (Sloss, 1983) that served as the standard in North American geology through its many subsequent editions.

Schuchert (1900) described at least one new trilobite species, *Dalmanites* (*Pterygometopus*) *goodridgii* from Baffin Land, northern Canada. He also had an interest in the habits of early freshwater arthropods (Schuchert, 1916) and non-trilobite arthropods from the Pennsylvanian Mazon Creek fauna (Schuchert, 1897).

August F. Foerste (1862–1936)

Born May 7, 1862, August Frederick Foerste satisfies the temporal criterion for being included as a member of the Cincinnati School (Sandy, 1994). However, his birthplace and workplace in Dayton, Ohio, are not really within the type Cincinnatian outcrop area.Foerste is included here because he was a frequent visitor to and worker within the type Cincinnatian. As a youth, he was an omnivorous collector of natural history specimens of all kinds, especially fossils and plants (Bassler, 1937). He attended Denison University (1883–1887), and co-founded, with Charles L. Herrick, one of his professors, the *Bulletin of the Scientific Laboratories of Denison University*, to which he was an initial contributor with two articles (one on plants and the other on fossils) and a frequent contributor thereafter. After graduating from Denison, Foerste attended Harvard, and completed a dissertation in petrography (Bassler, 1937). While at Harvard, he also served as laboratory assistant in paleontology to N. S. Shaler (discussed above), and worked as a part-time assistant in the U.S.G.S. He returned to Dayton to teach high school, in the words of one eulogist, "because he felt the position interfered less with his scientific research than would a more conspicuous college position" (Bassler, 1937, p. 145). Indeed, the summer school vacations provided Foerste the opportunity for temporary employment with various geological surveys, including the Geological Survey of Canada. From Dayton, Foerste made frequent trips to Cincinnati to visit Ulrich's studio. Foerste lived in Dayton until his retirement from teaching in 1932. That same year he was appointed Associate in Paleontology at the Smithsonian, and he relocated to Washington, D.C. (Fig. 3E). Foerste was one of the founders of the Paleontological Society (1908), and he served as its president in 1928.

Trilobite research.—Among Foerste's paleontological endeavors was the restudy, redescription, illustration, and naming of new species of invertebrate fossils not adequately described or not designated as separate species in their original publications (Bassler, 1937). This includes the most ubiquitous trilobite of the Cincinnatian, then called *Calymene meeki* [= *Flexicalymene meeki*], first described by Meek (1873a) as *C. senaria* but judged by Foerste (1910) as being distinct from the familiar New York species. Foerste had plenty of his own material to describe as well (Table 4).

Foerste's species of *Flexicalymene*, *Amphilichas*, and *Autoloxolichas* have survived taxonomic scrutiny (other than reassignment to newer genera), but the many species of *Flexicalymene* are in dire need of modern taxonomic review. Ross (1967) acknowledged *F. retrorsa*, but with reservation, as it "has little to distinguish it from *F. meeki* except the size, shape, and inclination of the anterior cranidial border" (Ross, 1967, p. 15), which are character states that he was unable to substantiate.

Table 4. A. F. Foerste's trilobite descriptions.

Author(s)/Year	Original Taxonomic designation	Status (ref #)
Foerste, 1885	*Arionellus*	*Phacops* (2)
"	*Dalmanites werthneri*	(2), (5); *Daytonia werthneri* (12)
"	*Illaenus ambiguus*	(2)
Foerste, 1887a	*Acidaspis ortoni*	*Odontopleura ortoni* (2)
"	*Calymene vogdesi*	*Diacalymene vogdesi* (20)
"	*Encrinurus thresheri*	(2); *E. ornatus* (6)
"	*Phacops pulchellus*	(2); *Eophacops?pulchellus* (5)
"	*Proetus determinatus*	(2)
Foreste, 1887b	*Illaenus herricki*	*Thaleops ovata* (2)
"	*Illaenus minnesotensis*	*Nileus vigilans* (2)
Foerste, 1888	*Encrinurus bowningi*	*Batocara bowningi* (11)
"	*Encrinurus mitchelli*	(11); *Pacificurus mitchelli* (18)
"	*Lichas halli*	*Amphilichas halli* (2), (22); *Arctinurus halli* (3); *Platylichas halli* (10); *Autoloxolichas halli* (16)
"	*Phacops serratus*	N.D.
Shaler and Foerste, 1888	*Microdiscus belli-marginatus*	*Serrodiscus belli-marginatus* (15)
"	*Ptychoparia attleborensis*	*Hebediscus attleborensis* (15)
Foerste, 1893	*Phacops trisulcatus*	*P. pulchellus* (2)
"	*Acidaspis brevispinosa*	(2), (21)
"	*Lichas breviceps clintonensis*	(16)
Foerste, 1909a	*Ceraurus miseneri*†	(2)
Foerste, 1909b	*Calymmene* [sic] *callicephala-granulosa*†	*Calymene granulosa* (4); *Flexicalymene granulosa* (9), (23)
Foerste, 1909c	*Dalmanites limulurus-brevicaudatus*	*Dalmanites brevicaudatus* (5)
"	*Illaneus depressus*	(1), (2)
Foerste, 1910	*Calymene platycephala*†	(2); *Platycoryphe platycephalus* (3), (7)
"	*Calymene abbreviata*†	(2); *Gravicalymene abbreviata* (herein)
"	*Calymene meeki*†	*Flexicalymene meeki* (22)
"	*Calymene meeki-retrorsa*†	*Flexicalymene retrorsa* (3), (8)
"	*Dalmanites carleyi-rogersensis*	*Pterygometopus carleyi-rogersensis* (2), (3) *Achatella carleyi var rogersensis* (5)
Foerste, 1914	*Dalmanites achates*	*Pterygometopus rogersensis* (3), *Achatella carleyi var. rogersensis* (5)
"	*Proetus chambliensis*	N.D.
Foerste, 1917b	*Trochurus halli*	(16)
"	*Trochurus welleri*	(16)
Foerste, 1919a	*Acrolichas Gen. nov*	*Amphilichas* (16)
"	*Acrolichas cucullus ottowaensis*†	*Amphilichas cucullus ottowaensis* (16)
"	*Acrolichas (?) shideleri*†	*Amphilichas shideleri* (16)
"	*Calymene cedarvillensis*	N.D.
"	*Calymene retrorsa minuens*†	*Flexicalymene retrorsa* (8)
"	*Encrinurus hillsboroensis*	N.D.
"	*Isotelus brachycephalus*†	*Isotelus maximus* (22)
Foerste, 1919b	*Acrolichas Gen. nov.*	*Amphilichas* (16)
"	*Calymene whittakeri.*	N.D.
"	*Dalmanites brevigladiolus*	(5)
"	*Phacops (Portlockia) mancus*	*Eophacops mancus* (5)
"	*Platycoryphe Gen. nov.*	N.D.
"	*Proetus collinodosus*	N.D.
"	*Pterygometopus confluens*	*Calyptaulax confluens* (5); *Sceptaspis lincolnensis* (13)

continued

Table 4. *continued* A. F. Foerste's trilobite descriptions.

Author(s)/Year	Original Taxonomic designation	Status (ref #)
Foerste, 1920a	*Acrolichas narrawayi*	*Amphilichas narrawayi* (16)
"	*Platylichas miseneri*†	*Autoloxichas (?)miseneri* (16)
Foerste, 1920b	*Bumastus holei*	N.D.
"	*Bumastus rowleyi*	N.D.
"	*Ceraurus plattinensis*	(17)
"	*Remopleurides missouriensis*	N.D.
Foerste, 1924	*Calymene granulosa*†	*Flexicalymene granulosa* (23)
"	*Cryptolithus lorettensis*	(19), *C. tessellatus* (20)
"	*Triarthrus huguesensis*	*T. rougensis* (14)

Notes:

*Key to references: (1) Miller, 1889 (2) Bassler, 1915 (3) Foerste, 1919b (4) Foerste, 1924 (5) Delo, 1940 (6) Best, 1961 (7) Whittington, 1965 (8) Ross, 1967 (9) Hu, 1971 (10) Ross, 1979 (11) Strusz, 1980 (12) Holloway, 1981 (13) Ludvigsen and Chatterton, 1982 (14) Ludvigsen and Tuffnell, 1983 (15) Morris, 1988 (16) Thomas and Holloway, 1988 (17) Hessin, 1989 (18) Edgecombe and Ramsköld, 1992 (19) Whittington, 1992 (20) Shaw and Lespérance, 1994 (21) Edgecomb and Adrain, 1995 (22) Babcock, 1996 (23) Hughes and Cooper, 1999 N.D. = no data.

Ross (1967, p. 16) concluded that "the species may have little stratigraphic use." *Flexicalymene retrorsa minuens* has not been referred to in recent literature, and is generally regarded as a synonym of *F. retrorsa*.

Foerste (1919a) addressed the question of sexual dimorphism in *Isotelus*, and noted that the coeval *I. brachycephalus* and *I. maximus* might be sexual dimorphs. He suggested that the more elongate *I. maximus* was the male form, and the broader *I. brachycephalus* was the female form. Babcock (1996) considered Foerste's *I. brachycephalus* to be a deformed specimen of *I. maximus*, and he recognized only two species of *Isotelus* from the Cincinnatian, *I. maximus* Locke and *I. gigas* Dekay.

As with Meek, Foerste's professional travel took him well outside the Cincinnatian outcrop belt. Notable among Foerste's efforts was his work in the Upper Ordovician of Ontario and Quebec, which he correlated with the type Cincinnatian (Foerste, 1914, 1924).

Foerste was regarded by some of his contemporaries as an inveterate "splitter." This reputation inspired a facetious epitaph (attributed to Sardeson, quoted *in* Weiss, 2001):

Here lies Dr. August Foerste
Who never does his worst. He
Takes the fossil pieces
He makes them into species
And all of them look very thirsty
In rolle of Augustin[i]us
He shows his aweful genius
As out of fractured species
He makes up all the pieces
And calls them each a genus.

William H. Twenhofel (1875–1957)

Credited as one of the founders of modern sedimentology (Dott, 2001), Twenhofel's (Fig. 3D) first love was the fossils of his Covington, Kentucky, boyhood home. Yet another son of German immigrants of modest means, Twenhofel developed a self-reliance that took him to Yale University, where he completed a Ph.D. in 1912 on the fossils and strata of Anticosti Island under Schuchert. Twenhofel taught at the University of Kansas, and became State Geologist in 1915. In 1916, he moved to the University of Wisconsin, where he spent the rest of his productive career. Best known for his contributions to sedimentary geology, Twenhofel was instrumental in founding the *Journal of Sedimentary Petrology* in 1930, and served as its editor in 1933–1946. Twenhofel successfully integrated his interest in the formation of sedimentary rocks with his love of the fossils contained in them. In 1935, he co-authored with R. R. Shrock a widely used textbook on invertebrate paleontology. He was active in the Paleontological Society, and served as its President in 1930. Twenhofel's Canadian field work led to collaborations with fellow members members of the Cincinnati School, particularly Foerste and Bassler.

Trilobite research.—Twenhofel's (1928) work on the stratigraphy and paleontology of Anticosti Island included descriptions of nine new species and three new varieties of trilobites. Another paper (Shrock and Twenhofel, 1939) on Silurian rocks of Newfoundland added three more new trilobite species to his tally (Table 5). Twenhofel's research objectives were more stratigraphic and sedimentologic than taxonomic. He used fossils to interpret paleoenvironments and stratigraphic relationships along the North American Appalachian "geosyncline."

Twenhofel (1945) was an early critic of Ulrich and Resser's (1930) over-splitting (see discussion of Ulrich, above). His criticism was based as much on his own familiarity with the rocks of the upper Mississippi River valley and his understanding of the sedimentology of the Lodi Shale as on his examination of the trilobites. Twenhofel thought it unlikely that 18 species of a single genus would "occur in such a thin lithologic unit," and he noted "no other member of comparable thickness in the geologic column [is] characterized by so many species of one genus" (Twenhofel, 1945, p. 634). He also found deficiencies in Ulrich and Resser's species determinations, and noted that many of their new species were based on few, and always partial, specimens, including many that were impressions and that "extents of variations should have been determined" (Twenhofel, 1945, p. 634).

Table 5. W. H. Twenhofel's trilobite descriptions.

Author/Year	Original taxonomic designation	Status (reference #)*
Twenhofel, 1928	*Cyphaspis anticostiensis*	
"	*Amphilichas arenaceus*	
"	*Amphilichas shallopensis*	
"	*Amphilichas borealis*	(4)
"	*Encrinurus laurentinus*	*Celtencrinurus laurentinus* (1)
"	*Encrinurus anticostiensis*	(2); *Nucleurus anticostiensis* (3)
"	*Chasmops occidentalis*	
Shrock & Twenhofel, 1939	*Dicranopeltis norrisensis*	
"	*Eophacops newfoundlandensis*	
"	*Goldius newfoundlandensis*	

Notes:
*Key to references: (1) Evitt and Tripp, 1977 (2) Strusz, 1980 (3) Ramsköld, 1986 (4) Thomas and Holloway, 1988

Raymond S. Bassler (1878-1961)

Raymond Smith Bassler was born in Philadelphia, but grew up mostly in Cincinnati. According to Caster (1965) Bassler, assumed "Ray," the professional form of his name, as a young man, after having become familiar with the works of the English naturalist John Ray (1627–1705) and Edwin Ray Lankester (1847–1929), one of the most prominent English biologists of Bassler's day. As a fifteen year-old high-school freshman, Bassler knocked on the door of Ulrich's paleontology lab in Covington, Kentucky, and was granted the privilege of working as an unpaid assistant to Ulrich after school hours. He collected and prepared fossils, and made thin-sections of bryozoans. In 1900, Ulrich moved to Washington, D.C., and, in 1901, Bassler followed him (Figure 3E). At the time, Charles Schuchert (see discussion, above) was Assistant Curator of Stratigraphic Paleontology at the Smithsonian. Bassler had met and become acquainted with Schuchert at Ulrich's studio in Covington, and Bassler became Preparator in the Division of Stratigraphic Paleontology at the Smithsonian, with Schuchert as his supervisor (Caster, 1965). By 1929, Bassler had ascended to Head Curator, a post he held until his official retirement in 1948 (Thomas, 1962). At the Smithsonian, Bassler mentored young paleontologists, including Preston Cloud (Dutro, 1999), and rose to prominence in stratigraphic paleontology. Although a bryozoan specialist, Bassler, like his mentor Ulrich, could not resist publishing his opinions on the relationships of some type Cincinnatian trilobites.

Trilobite research.— Bassler considered the recurring issue of sexual dimorphism in *Isotelus* (1919; see discussion of Foerste's research, above) by applying principles of what today would be termed actuopaleontology. He drew comparisons between the fossil organisms and living analogs. On the basis of sexual differences in present-day arthropods, Bassler suggested that the presence/absence of spines was a dimorphic character (males with spines, females not). Sexual dimorphism in *Isotelus* was taken up much later by Hu (1971), and has not been resolved. Bassler (1919) described at least one new trilobite species, *Acidaspis ulrichi*, named for his mentor, from the Ordovician of Maryland.

OTHER EARLY CONTRIBUTORS

By necessity, our catalog of Cincinnatian trilobite paleontologists is dominated by the more prominent members (i.e., those who attained professional status and thus left behind a "paper trail" for their biographers). The amateurs are known primarily through the records of the local scientific societies to which they belonged. Virtually all of the early amateur fossil enthusiasts were associated with the Cincinnati Society of Natural History, which was founded on January 19, 1870 (Anonymous, 1878). Some were also active in the Western Academy of Natural Sciences, which was founded in the 1830s and still existed, albeit barely, in the years just after the American Civil War. [Slightly less than two years after the founding of the Society, the several extant members of the academy voted to turn over the assets of the organization, including its library, collection, and cash, to the new society, with the proviso that the surviving members of the Academy be granted life memberships in the Cincinnati Society of Natural History. This is the origin of the myth that the society dates from earlier than 1870.] In any case, much of the publishing activity of the Cincinnati School was in the *Journal of the Cincinnati Society of Natural History*. It is also obvious that the Society provided a venue for the community that was the Cincinnati School. One is impressed, in reading their various publications, that members went collecting together, described material in one another's collections, and reciprocated in naming taxa after one another. Many of their specimens ended up, either directly or by a circuitous route, in the collections of the Cincinnati Society of Natural History (which, in 1957, became the Cincinnati Museum of Natural History). The bulk of the collections of the professional members (Meek, Foerste, Bassler) resides in the U.S. National Museum.

We briefly mention below three amateur paleontologists whose names are known primarily from the records of the early scientific societies.

John Gould Anthony.—Anthony served as secretary to the Western Academy of Natural Sciences and hosted, with John Locke and others, Charles Lyell when the famous British geologist visited the area in the 1840s (see discussion of Locke). In

1863, Anthony became curator of conchology at the Peabody Museum of Harvard University under Louis Agassiz (Hendrickson, 1947). Anthony described at least two trilobites from the Cincinnatian, *Ceratocephala ceralepta* Anthony 1838, and *Calymene bucklandii* Anthony 1839. Neither taxon, based on incomplete specimens, has withstood subsequent scrutiny. Bassler (1915) referred *C. bucklandi* to *Ceraurus milleranus*. Miller (1889) regarded the pygidium fragment on which Anthony's *C. ceralepta* was based as belonging to *Ceraurus* or *Acidaspis*.

S. T. Carley.—Carley was also active in the Western Academy of Natural Sciences. The honorific *carleyi* serves as the specific name for almost a dozen Cincinnatian taxa, including brachiopods, crinoids, cephalopods, and the trilobite trace fossil *Rusophycus carleyi* James, 1885, that is attributed to *Isotelus* (see Osgood, 1970).

John A. Warder.—A member of the Western Academy of Natural Sciences, Warder also served as President of the Cincinnati Society of Natural History from its founding in 1870 until 1875 (Moore *et al.*, 1883). Warder (1838) described the trilobite *Ceratocephala goniata* based on fragmentary material from Silurian strata near Springfield, Ohio. Miller (1889) regarded the specimen as a fragment of *Dalmanites* or *Acidaspis*.

THE CINCINNATI SCHOOL TODAY

The Dry Dredgers

If the Cincinnati School is, as Caster (1982, p. 27) wrote, predominantly a "long succession of fossil collectors," the tradition continues today under the auspices of the Dry Dredgers, a local club of amateur fossil-collectors (Dalvé, 1951; Kallmeyer and Meyer, 1997; Kallmeyer, 2001). In the early days of the Geology Department at the University of Cincinnati, Walter H. Bucher ran an evening-college *Lecture Discussion Series* in geology, and lead field trips on local geology, paleontology, and other aspects of natural history (Fuchs, 2000). Kenneth E. Caster inherited the Discussion Series when he came to the University of Cincinnati in 1936. A Casterian objective of the field trips was to amass a comprehensive collection of Cincinnatian fossils. In 1942, at the request of local fossil-enthusiasts, Caster sponsored the founding of an amateur society of fossil hunters. Caster suggested the name Dry Dredgers from an article by Charles Schuchert (1895) titled *Dry dredging in the Mississippian sea*. The Dry Dredgers continue the tradition of the Cincinnati School as serious amateurs. The academic and popular culture that permitted Schuchert to rise to Yale professorship with only a sixth-grade education has passed into extinction, along with any hopes of present-day amateur enthusiasts to reach such heights without a formal academic pedigree. However, members of the Dry Dredgers have successfully collaborated with professional paleontologists, published in the peer-reviewed literature, and gained recognition from the paleontological community (for example, Donovan *et al.*, 1995; Morris and Felton, 1993). Moreover, some of the Dry Dredgers have maintained a close association with professional paleontologists. For example, William H. White, Jr., received the Strimple Award from the Paleontological Society in 1985 (Bell, 1986), and Steven H. Felton earned the same honor in 2001 (Meyer, 2002). Felton also was presented the Katherine Palmer Award of the Paleontological Research Institution in 1996. Both awards are designated for non-professionals in recognition of outstanding contributions to paleontology.

Contributions to trilobite research.—Caster (1982) maintained that there had not been a paper written on Cincinnatian fossils at the University of Cincinnati in which Dry Dredger contributions of materials had not had a significant, if not dominant, role. Members of the Dry Dredgers have made gifts and loans of trilobites or trilobite trace fossils for theses by Schweinfurth (M.S., 1958), Osgood (Ph.D., 1965), Hu (Ph.D., 1968), Brandt (M.S., 1980), and Lask (M.S., 1986). Dry Dredgers have jointly authored papers on trilobites with professional paleontologists (e.g., Hughes and Cooper, 1999). The Dry Dredgers provide public forums for the dissemination of trilobite research, through invited professional lecturers at their monthly meetings and at the annual Cincinnati Gem, Mineral, and Fossil Show, and through an internet-based newsletter (http://drydredgers.org/) and web-pages on Cincinnatian trilobites (http://drydredgers.org/trilobit.htm; http://drydredgers.org/fragment.htm). We can reasonably surmise that, had these new media been available at the time, the original members of the Cincinnati School would have produced internet sites with very similar content.

PROFESSIONAL PALEONTOLOGY IN CINCINNATI

Despite the presence of the local fossil lagerstätte and the long history of the Cincinnati School, it was not until 1907 that a Department of Geology was established at the University of Cincinnati (Caster, 1981). It is not that there had been no college-level instruction in geology prior to the early twentieth century. John M. Nickles, a member of the Cincinnati School (although not a trilobite specialist), graduated from the University in 1882, and, in a 1936 letter, said that he studied under A. G. Wetherby, Professor of Geology. According to *Minutes-book no. 2* in the University Archives, Albert Gallatin Wetherby was hired as Assistant Professor of Natural History in April 1877, to begin the next academic year. Early in 1878, he was appointed to Curator of the Museum in the university and, then, to Professor of Natural History, as he is listed in the University Catalogue of 1884–1885. In some of his publications (e.g., Wetherby, 1881), his position is given as Professor of Geology and Zoology at the university. As other members of the Cincinnati School, he was a person with a breadth of interest; he published on fossil arthropods, echinoderms, and cephalopod mollusks.

Department of Geology at the University of Cincinnati.—Professor Wetherby not withstanding, paleontology did not gain prominence at the University of Cincinnati until the appointment of Kenneth Edward Caster in 1936. Caster was not a trilobite specialist; he was known early in his career for his work on Devonian stratigraphy and his support of continental drift (influenced, no doubt, by time spent in Gondwana during fellowships to South America, South Africa, New Zealand, and Australia). He was one of the pioneers of ichnology in North America (Holland and Pojeta, 1995), and his later career was noted for his research on early echinoderms, eurypterids, and aglaspids. The breadth of Caster's experience—he published papers on five phyla, eight geologic systems, and four continents (Holland and Pojeta, 1995)—and his innate curiosity made him adept as an advisor for graduate theses on widely disparate taxa. Caster supervised theses on nautiloid cephalopods, pelecypods, sea stars, edrioasteroids, snails, rugose corals, brachiopods, trilobites, trace fossils, and others. The omnivory of Caster's own research, and that of his students, was reminiscent of the breadth of the research appetites of Cincinnati School members, who aspired to be paleonaturalists familiar with many different taxonomic groups. As some of the original members of the Cincinnati School, Caster's doctoral students left the Cincinnati area to occupy important academic and governmental positions well beyond the type Cincinnatian outcrop area.

Even in the professional boot-camp commanded by Professor Caster, the "publishing-amateur" aspect of the Cincinnati School had not died completely. Elizabeth A. Dalvé, known to her friends as Bettina, was a part-time illustrator and exhibit preparator in the museum in the University of Cincinnati's Old Tech building, the long-time home of the Geology Department. Although especially skilled in the scientific illustration of plants (Braun, 1961), she undertook the preparation of a compilation of the stratigraphic occurrence of taxa reported from the type Cincinnatian rocks. This work (Dalvé, 1948) is strongly reminiscent of some of the compilations of members of the Cincinnati School. As those, it is useful, but it tantalizes the reader with the unanswered questions of just where the actual specimens were collected and where they now reside. Caster used Dalvé's faunal list in revising a mimeographed guidebook to the fossils of the area originally published by Bucher (1939). Caster *et al.*'s (1955) *Elementary Guide to the fossils and strata of the Ordovician in the vicinity of Cincinnati, Ohio* became a classic reference for amateurs and professionals, and it persists, with deliberately few emendations, to this day (see Davis, 1992).

Contributions to trilobite research—Caster supervised three graduate theses on trilobite research: Schweinfurth's (1958) master's thesis (unpublished) on the systematics of *Flexicalymene*, Hu's (1968; published 1971) dissertation on ontogeny and dimorphism in various Early Paleozoic trilobites (including *Flexicalymene*, *Isotelus*, and *Cryptolithus* from the Cincinnatian), and Osgood's (1965, published 1970) dissertation on Cincinnatian trace fossils, including important trilobite trace fossils. In the post-Caster era, despite the lack of a trilobite specialist on the faculty, there have been two trilobite-related master's theses completed at the University of Cincinnati, both supervised by David Meyer, a specialist in modern and ancient echinoderms. Meyer and his students shared an interest in the taphonomy of the Cincinnatian fauna, and this emphasis is evident in the titles of the papers published from their thesis work. These include Brandt's (1985) use of trilobite taphonomic data in reconstructing sedimentary dynamics, and Lask's (1993) study of the hydrodynamic properties of the *Flexicalymene* exoskeleton.

Three University of Cincinnati graduate alumni have gone on to establish professional careers in paleontology that contributed to trilobite research. Osgood's (1970) monograph on Cincinnatian trace fossils secured his credentials as a leader in the nascent discipline of ichnology in North America, and helped to establish ichnology as an important and legitimate line of paleontologic inquiry in this country (see Osgood, 1975 a & b). Osgood's now-classic monograph is a standard reference in trace-fossil compendia (e.g., Crimes and Harper, 1970; Frey, 1975; Häntzschel, 1975; Donovan, 1994; Bromley, 1996). Osgood's (1970) monograph is not simply a catalog of the impressive Cincinnatian ichnofauna, but a truly biological treatise that incorporates observations on the formation of present-day traces, and emphasizing the interpretation of ichnofossils in terms of the behavior(s) they represent. Especially significant trilobite trace fossils included in Osgood's monograph include a *Flexicalymene* trilobite preserved in its *Rusophycus* excavation and several *Rusophycus* traces that preserve details of the ventral anatomy of *Isotelus*.

Hu's dissertation (1968, published 1971) on the ontogeny of Lower Paleozoic trilobites was notable for his comprehensive review of early growth and development in present-day arthropods and his use of these data in interpreting trilobite ontogeny. His dissertation included several type Cincinnatian genera. Hu (1971) somewhat inexplicably assigned specimens of *Isotelus* from the older Edenian beds of the Cincinnatian to *I. stegops* Green, 1832. He might have made this designation on the basis of priority of the species' name and similar stratigraphic occurrence of Green's specimen, but on that basis he might well have chosen to use *I. gigas*. As discussed above, recent workers (e.g., Babcock, 1996) recognize only *I. gigas* and *I maximus* from the type Cincinnatian.

The senior author of this paper shifted her original interest in fossils as sedimentary particles (Brandt, 1985) to using taphonomic principles to interpret trilobite paleobiology (Brandt, 1993, 1996) and evolutionary patterns (Brandt, 2002). She has also been a beneficiary of the Cincinnatian trilobite trace-fossil lagerstätte (Brandt *et al.*, 1995).

EXTRAMURAL RESEARCH ON TYPE CINCINNATIAN TRILOBITES

Other workers on type-Cincinnatian trilobites who were not directly affiliated with the informal Cincinnati School or the University of Cincinnati, but who have made contributions to research on Cincinnatian trilobites, are included here for completeness.

Edgar Roscoe Cumings (1874–1967), although born in northeast Ohio and outside the type Cincinnatian and Professor of Geology at Indiana University for many years, was deeply involved with type-Cincinnatian fossils, especially lophophorates (Shrock, 1970). Cumings compiled a comprehensive stratigraphic and paleontologic summary of the Cincinnatian Series in Indiana (Cumings, 1908) that included descriptions and plates of trilobites. Cumings and Galloway (1913) compiled a comprehensive stratigraphic range-chart for the Cincinnatian fauna, including trilobites, with a vertical resolution of 1.5 m.

Early in his long and illustrious career, Harry B. Whittington spent two years as a post-doctoral fellow at Yale under Carl Dunbar, who had been a student of Charles Schuchert (see Kaufffman, 1984). During this time, Whittington also encountered at least two other members of the Cincinnati School. Whittington (1941) described trilobites originally collected by Ulrich (discussed above), and he acknowledged Bassler for access to collections and assistance while he visited the Smithsonian. Several of Whittington's works included discussions of Cincinnatian types (e.g., Whittington, 1941, an evaluation of Ulrich's *Cryptolithus recurvus*; and Whittington, 1956, a discussion of *Acidaspis cincinnatiensis* Meek, in which *A.*

anchoralis Miller is considered a junior synonym). In addition, Whittington's lavishly illustrated book includes several references to type Cincinnatian specimens (Whittington, 1992, pl. 32 B,C; pl. 89, pl. 90 B).

Nigel Hughes was Curator of Invertebrate Paleontology at the Cincinnati Museum of Natural History (1993–1997). His research and that of his students reflects his time spent among type-Cincinnatian trilobites (e.g., Hughes and Cooper, 1999; Hunda, 2001).

Fossil-arthropod specialist Loren Babcock, of the Ohio State University (just north of the type-Cincinnatian outcrop area), contributed the trilobite chapter to the Ohio Geological Survey's expanded revision of its classic volume *Ohio Fossils* (Babcock, 1996). James St. John, a graduate of Ohio State, and student of Babcock, has written on the history of trilobite research (St. John, 2000; this volume).

Reuben Ross, Jr., of the U. S. Geological Survey, produced two of the most-recent taxonomic treatments of type-Cincinnatian trilobites. Ross (1967) added another species of *Flexicalymene* to the roster of local taxa, *F. griphus*. He was the first to report the genus *Gravicalymene* from the Cincinnati area (Ross, 1967), and he described two new species, *G. hagani* Ross, 1967, and *G. truncatus* Ross, 1979.

Ross' (1979) *Gravicalymene truncatus* (Fig. 2H) is indistinguishable from *Flexicalymene abbreviata* (Fig. 2G). Specimens of each possess a distinctive, bell-shaped, anteriorly truncated glabella. A bell-shaped glabella is a diagnostic character for the genus *Gravicalymene* and distinguishes this genus from *Flexicalymene*. Ross (1979) correctly recognized that his specimen belonged in the genus *Gravicalymene*. *Calymene abbreviata* Foerste, 1910, also is better placed within *Gravicalymene* than *Flexicalymene* on the basis of the same criterion. Both Foerste (1910) and Ross (1967) judged the abruptly truncated anterior glabellar border of their respective specimens to be of species-level significance. Ross was not aware of Foerste's description of *Calymene abbreviata* (Ross, personal communication, 1980), and Foerste's (1910) specific name *abbreviata* has priority. Therefore, *G. truncatus* Ross is appropriately regarded as a junior synonym of *G. abbreviata* (Foerste, 1910).

DISCUSSION

Ray S. Bassler was the last survivor of the original Cincinnati School of Paleontology, so it is fitting that he delivered what could be taken as its valedictory oration. In his 1933 presidential address to the Paleontological Society, Bassler observed that there had been a shift in emphasis in paleontological research away from species descriptions (which had been an essential element of the Cincinnati School). He noted that, although the twentieth century produced college-bred paleontologists, more professional paleontologists, and more paleontological research, the "discovery and study of interesting fossils" as an avocation was in decline, and this resulted in "fewer paleontologies of New York or Minnesota" (Bassler, 1933, p. 269). Perhaps quaintly, from our vantage point in the twenty-first century, Bassler attributed the shift in emphasis in paleontological research to "the mad rush of our machine age." He blamed the automobile, "for in these days of swift transportation few travelers have the time to stop and search the dusty outcrops for fossils, if indeed they can even see them as they speed along."

Ironically, the shift away from describing species and specimens in paleontological research would not have been possible without the efforts of the amateurs and amateurs-turned-professionals of the Cincinnati School and their contemporaries from other fossil-rich locales (e.g., James Hall and his associates in New York State; see Wells, 1987). Their myriad taxonomic descriptions, for better or for worse, comprised the first-order data of paleontology, and were the "elementary particles" of systematics (Cracraft, 2000). Other analyses (e.g., biodiversity, paleobiogeography, etc.) derive from these data.

The quality of the trilobite species descriptions produced by members of the Cincinnati School is variable. If the veracity of taxonomic data were measured by whether the taxon is recognized today, many taxa listed in the tables herein would have to be rejected. It is not surprising that most of the taxa that persist are those authored by School members who attained professional status (for example, Meek and Foerste), but there are exceptions (e.g., *Ceraurus milleranus* Miller and Gurley, 1893). Professional status was no guarantee of success in describing trilobite taxa for posterity, either; even many of Meek's and Foerste's taxon names have fallen into synonymy or disuse.

With the rise of professional paleontology, the work of amateurs, such as those of the Cincinnati School, inexorably led to descriptive paleontology's becoming déclassé in some circles. Inspection of the names in Tables 1–4 leads to the inevitable conclusion that the trilobites of the type Cincinnatian are in need of taxonomic review. Some of these species were included in Bassler's (1915) index, and have not appeared in the literature since. Other species have been judged insufficiently distinct from closely related forms, and have been placed in synonomy. The greater proportion of species listed in Tables 1–4 have been assigned to newer genera, a not-uncommon nomenclatural fate and the logical consequence of taxonomic progress. It remains to be seen whether the type Cincinnatian trilobite species constitute a distinct faunal province, as do type Cincinnatian rugose corals (Elias, 1983) and bryozoans (Anstey, 1986).

The original data compiled by the members of the Cincinnati School (species descriptions, illustrations, locality and stratigraphic data) are still useful, and there is no shortage of new material to be unearthed. Our understanding of the significance of type Cincinnatian trilobites would benefit from researchers taking a new look through the lens of modern phylogenetic sensibilities, using tools not available a century ago. The time is right to convene a "Neo"Cincinnatian School of Paleontology that focuses once again on specimen-based research.

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Both of us were associated with the late Kenneth E. Caster for some years, and are grateful to him for passing on his reminiscences and observations about members of the Cincinnati School of Paleontology and the real contributions they made. We thank R. L. Anstey and E. L. Yochelson for sharing their personal stocks of pertinent antiquarian lore and for their leads and suggestions and L. M. Simonelli, B. Kennedy, and D. Meyer for access to photographs in their archives. D. Meyer and D. Rudkin provided manuscript reviews.

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230 YEARS OF TRILOBITE RESEARCH IN THE CZECH REPUBLIC

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ABSTRACT—The Czech Republic is one of the richest trilobite-producing areas in the world. Exceptionally diverse and abundant assemblages of Cambrian–Carboniferous trilobites are well known from this comparatively small area. Trilobites from this region have played a major role in the study of the group for more than 200 years, and prompted the work of Joachim Barrande who completed some of the most important trilobite research of the nineteenth century. This report summarizes trilobite research in the Czech Republic from its beginning in the eighteenth century. A comprehensive list of publications about Czech trilobites through 2003, with translated titles, is provided because many are obscure and difficult to locate.

INTRODUCTION

Paleontological research, including the study of trilobites, has a tradition of more than 230 years in the small central European region now called the Czech Republic. Remains of diverse fossil plants and animals are common here in Precambrian to Quaternary rocks, and first attracted attention in the eighteenth century. Many of the fossils occur in unmetamorphosed to slightly metamorphosed Paleozoic rocks and show various modes of preservation. However, trilobite exoskeletons in limestone, siliceous nodules, shale, siltstone, and sandstone, or iron ore commonly show good, sometimes even excellent, preservation that may include fine morphological details. Because of such favorable preservation and the common occurrence of complete exoskeletons, trilobites have been collected and studied in Bohemia since the eighteenth century (Fig. 1).

The Barrandian area north of Prague is a classical area of Lower Paleozoic paleontology and stratigraphy. Long-term paleontological research, including the exacting and innovative work of Joachim Barrande in the mid- to late nineteenth century), combined with biostratigraphic, lithostratigraphic, and chronostratigraphic studies resulted in detailed regional syntheses that allowed detailed correlations the Barrandian sequences with other areas. Several horizons in the Barrandian area serve as an international standard, and three Global Stratotype Sections and Points (GSSPs) and several other sections of global importance have been established here.

Because of its long research history and the key role that the Barrandian area has played in Lower Paleozoic stratigraphy and paleontology, collections of fossils from here have been restudied and revised and localities have often been visited by scientists from around the world. Although short reviews of local trilobite research appear in several books (e.g., Snajdr, 1958a, 1990a; Horny and Bastl, 1970; Pek and Vanek, 1989a), no comprehensive list of trilobite papers has been published. Because Czech trilobites have played such an important role in trilobite research and many of the references about them are obscure and difficult to locate, we have compiled a list of all the important papers published about them.

TRILOBITE-BEARING REGIONS AND TRILOBITE ASSEMBLAGES

Trilobites in the Czech Republic are known from several regions and from geological units with different lithologies, metamorphic overprints, and paleogeographic histories. Over the last 230 years, most of the research has been conducted in the classic Barrandian area, which encompaases Cambrian to Devonian sedimentary rocks. Consequently, this area provides quite a comprehensive sequence of trilobite successions. In the Moravo-Silesian Region, trilobite study has a tradition of more than 150 years. Other trilobite-bearing strata in the Czech Republic have a much more restricted geographic extent and stratigraphic range (Figs. 1, 2).

Our contribution focuses on trilobite research in the two best-studied and stratigraphically most complete regions — the Barrandian area and the Moravo-Silesian Region. In other Czech regions, important but poorly known trilobite assemblages reflect inappropriate sedimentary environments or later metamorphic overprint.

In the Czech Republic, the oldest trilobites (*Conocoryphe*, *Ellipsocephalus*, *Ornamentaspis*) occur in the lower Middle Cambrian of the Príbram-Jince Basin (Barrandian area,

FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES, Edited by Donald G. Mikulic, Illinois State Geological Survey, 615 East Peabody Drive, Champaign, Illinois 61820, Ed Landing, New York State Museum, The State Education Department, Albany, New York 12230, and Joanne Kluessendorf, Weis Earth Science Museum, University of Wisconsin-FoxValley, 1478 Midway Road, Menasha, Wisconsin 54952. New York State Museum Bulletin 507.

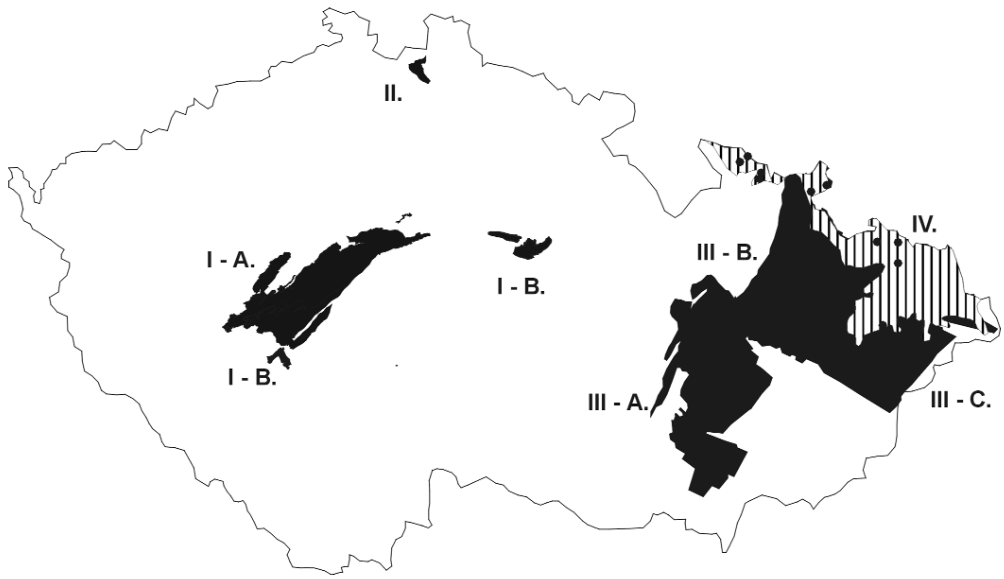

Fig. 1. Geographic distribution of the 'trilobite-bearing rocks' in the Czech Republic.

Bohemicum). The youngest trilobite (*Paladin mladeki*) is known from the upper Namurian A of the Upper Silesian Coal Basin in the Moravo-Silesian Region.

Central Bohemian Region (Bohemicum)

Barrandian Area.—The Barrandian area in the central part of the Bohemian Massif (Figs. 1, 3), represents a terrain, that in the Czech terminology, consists of three tectonostratigraphic megacycles within two main tectonometamorphic units (Fig. 4). The tectonostratigraphic megacycles include: 1) a Neoproterozoic Megacycle without macrofossils; 2) a Cambrian Megacycle; and 3) the Ordovician–Devonian Megacycle of the Prague Basin (Havlícek, 1982).

The Cambrian Megacycle is preserved in two separate areas: the larger Príbram–Jince Basin and the smaller, narrow Skryje–Tyrovice area (Fig. 3). The larger basin is dominated by terrigenous conglomerates and sandstone, with the marine Jince Formation containing more than 30 species of polymeroid and eleven species of miomeroid trilobites. These trilobites are distributed along a bathymetric gradient from shallow-water assemblages on the west-northwest to deeper-water assemblages in the east. The smaller Skryje–Tyrovice area contains a distinct fauna represented by seven miomeroid and 22 polymeroid trilobite species.

Three bathymetrically dependent assemblages have been established and briefly characterized by Fatka (2000) in the Cambrian Megacycle. The shallowest, a *Lingulella*-dominated assemblage, has rare ellipsocephalids (*Ellipsocephalus, Germaropyge*) and conocoryphids (*Ctenocephalus, Conocoryphe*) with rare paradoxidids. A deeper-water assemblage is dominated by *Ellipsocephalus* and *Conocoryphe*, complemented by paradoxidids (*Hydrocephalus, Acadoparadoxides, Eccaparadoxides, Rejkocephalus*), ptychoparioids (*Ptychoparia*), and solenopleurids (*Jincella, Solenopleurina*), which are even deeper water taxa. The more common miomerid trilobites (*Peronopsis, Phalagnostus, Phalacroma*) also occur. An agnostid-dominated assemblage (*Onymagnostus, Tomagnostus, Hypagnostus, Doryagnostus,* and, rarely, *Luhops*) represents the deepest water environment.

Havlícek (1982) designated the area of the Ordovician-Devonian Megacycle as the Prague Basin. Here, mostly siliciclastic Ordovician and Lower Silurian rocks pass upwards into Upper Silurian to Middle Devonian carbonates. The coarse, shallow-water sediments of the initial Ordovician transgression are succeeded by black silty shales with lenticular iron ore bodies as the basin widened and deepened progressively until interrupted by the regression associated with latest Ordovician glaciation in the southern hemisphere. Synsedimentary volcanism markedly influenced deposition during the Ordovician.

An abrupt lithofacies change characterized by dark graptolitic shales occurred at the beginning of the Silurian as Gondwana glaciation waned and sea level rose (Storch, 1986; Kríz 1991, Kríz in Chlupác *et al.*, 1998). These graptolitic shales represent deposition under reducing conditions in offshore pelagic environments. The graptolitic shales were gradually replaced by carbonates (Fig. 4). Shallow-water and locally unstable environments were possibly related to the influence of volcanic activity on water chemistry and seafloor topography. Marine sedimentation continued up to the Givetian Stage of the Devonian (Chlupác and Kukal, 1988).

The fossiliferous succession of the Silurian–Devonian boundary interval in the marine carbonate facies at Klonk at Suchomasty has been selected as the international stratotype of the Silurian–Devonian boundary. An auxiliary stratotype exists at Budnany Rock at Karlstejn (Chlupác *et al.*, 1972, 1998).

Four regional Lower Devonian stages, the Lochkovian, Pragian, Zlíchovian and Dalejan, have been established in the Barrandian area. Two of them (the Lochkovian and Pragian) are accepted as official international stages, and their stratotypes occur in the Barrandian area.

During the Early Ordovician, the shallow-water assemblages are dominated by articulate and inarticulate brachiopods, and trilobites are subordinate. Deeper-water trilobite-bearing

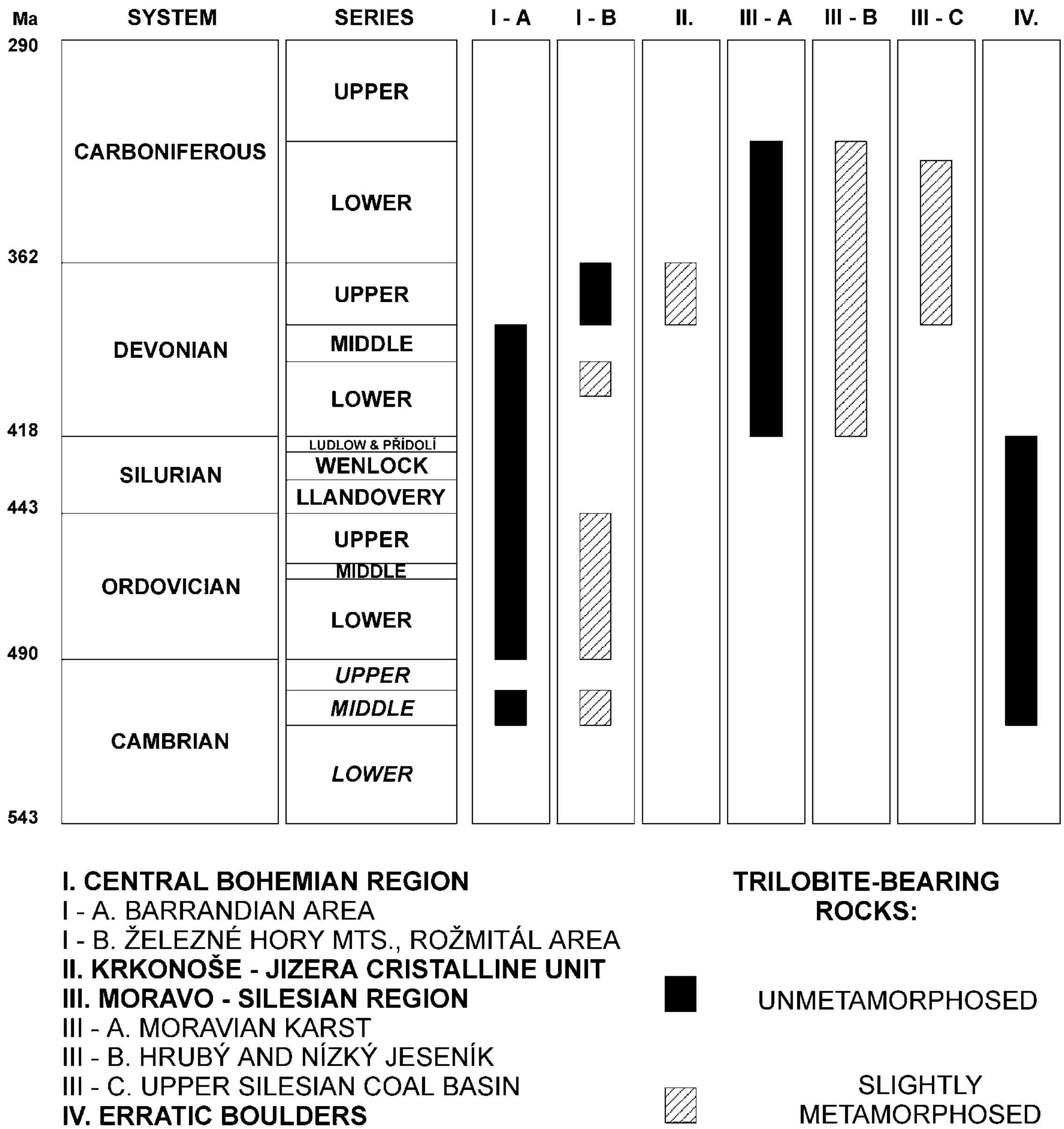

Fig. 2. Stratigraphic range of the 'trilobite-bearing rocks' in separate areas of the Czech Republic.

sediments are nearly absent, with the exception of the poorly fossiliferous Klabava Formation (Fig. 4). Middle Ordovician, shallow-water assemblages are poorly known, but the deeper-water facies contain pliomerid (e.g., *Placoparia*), dalmanitid (e.g., *Ormathops*), and large asaphid (e.g., *Asaphelus*) trilobites, as well as rarer cyclopygids (e.g., *Pricyclopyge*) and agnostids. The deepest part of the basin contains typical elements of the Cyclopygid Biofacies (e.g., *Microparia*). In the Upper Ordovician, quartzitic sandstones are dominated by dalmanitid (e.g., *Dalmanitina*), trinucleoid (e.g., *Deanaspis*) and/or illaenid (e.g., *Cekovia, Stenopareia*) trilobites, although other species of the same families or even genera could also be present in the deeper-water deposits. Cyclopygid trilobites (e.g., *Microparia*, *Symphysops*) with dalmanitids (*Eudolatites*), trinucleoids (*Onnia*), and, in some levels, remopleurids (e.g., *Amphytrion*) and others, are typical of deeper-water shales.

The first discussion of Ordovician assemblages was published by Havlícek and Vanek (1966). Detailed analyses focused on benthic assemblages were compiled by Havlícek (1982), Havlícek and Vanek (1990), and Havlícek *et al.* (1994).

Chlupác (1987) distinguished eighteen Silurian trilobite assemblages in the Prague Basin. The majority of the trilobite assemblages reflect paleoenvironmental changes, and were influenced by the intensity of volcanic activity and coeval fragmentation of the basin into blocks defined by different degrees of subsidence (see Kríz *in* Chlupác *et al.*, 1998). Diverse shallow-

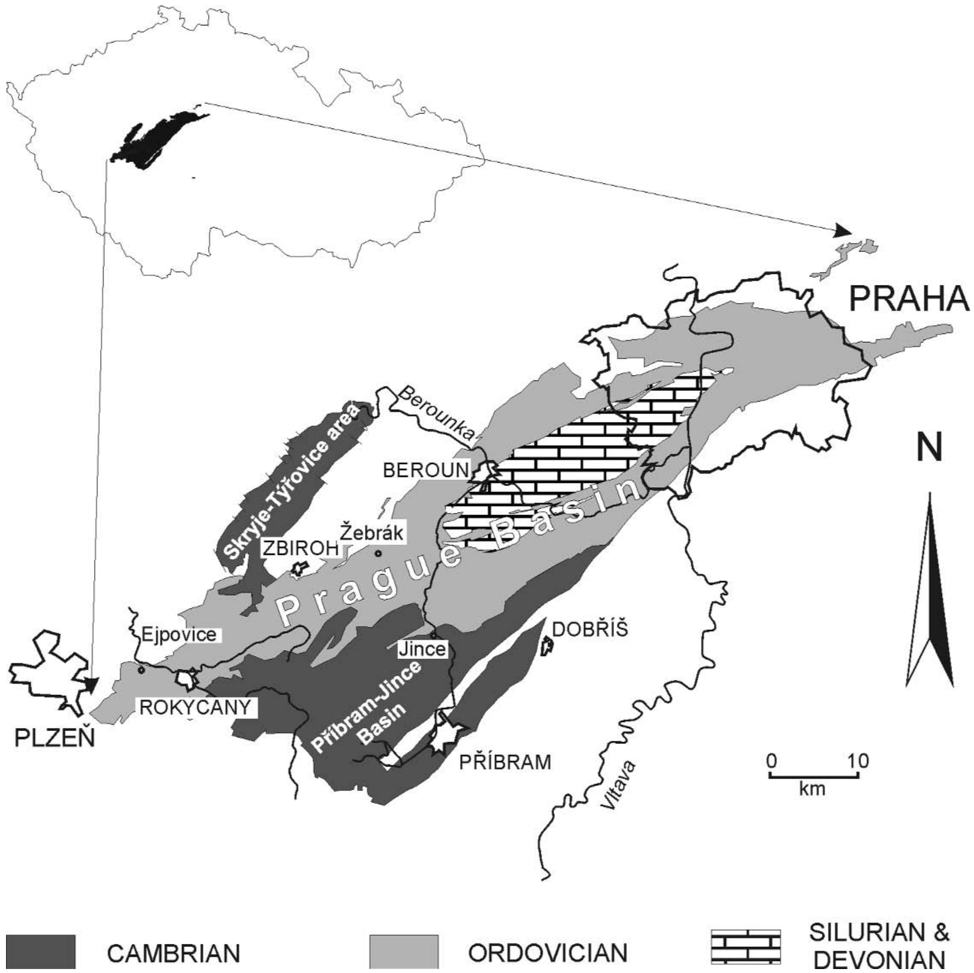

Fig. 3. Sketch map of the Barrandian area.

water assemblages occur in bioclastic carbonates near volcanic elevations; and grade seaward into less diverse, deeper-water assemblages in shale. The distribution of trilobites [benthic assemblages 2–6 in Boucot's (1975) classification] shows analogies with the younger Devonian trilobite assemblages. The most common elements are cheirurid (e.g., *Cheirurus*, *Didrepanon*), proetid (e.g., *Decoroproetus*), otarionid (e.g., *Otarion*, *Aulacopleura*), phacopid (e.g., *Ananaspis*), odontopleurid (e.g., *Miraspis*, *Leonaspis*), lichid (e.g., *Trochurus*), and styginid (e.g., *Kosovopeltis*) trilobites, associated with rare harpetids (e.g., *Bohemoharpes*). Some aspects of the Silurian trilobite and brachiopod assemblages have been discussed by Havlícek and Storch (1990).

Chlupác (1983) identified nineteen trilobite assemblages in the Lower–Middle Devonian of the Prague Basin. The three main assemblages show a close relationship to substrate. The deeper-water assemblage that dominates the micritic carbonate facies includes phacopids (e.g., *Reedops*, *Phacops*), dalmanitids (*Odontochile* in Lower Devonian), odontopleurids, scutelluids, proetids, cherurids, and others. The shallow-water assemblage (e.g., proetids, scutelluids such as *Platyscutellum*, less abundant phacopids such as *Reedops* and cheirurids) occurs in the crinoidal limestone biofacies. The reef assemblages (e.g., scutelluids such as *Radioscutellum*, proetids such as *Gerastos* and locally abundant harpetids such as *Lioharpes*) are locally common in the reef bioclastic limestones. Taxonomic diversity reaches its maximum in the Pragian Stage (Chlupác and Snajdr, 1989; Havlícek and Vanek, 1996). For the Pragian Stage, an alternative synthesis of facies and benthic assemblages, including trilobites, was published by Havlícek and Vanek (1998) and Vanek (1999).

The Barrandian area had a dramatic paleogeographic history, as did the majority of small, predominantly independent terrains. The generally accepted scenario posits a location in very low (peri-equatorial) paleolatitudes during the Early–Middle Cambrian (Fig. 5A), followed by its rapid movement to high, peri-polar paleolatitudes during the Ordovician (Havlícek *et al.*, 1994). Such a European peri-Gondwanan story was constrained by the shift and rotation of the whole Gondwanan supercontinent in the southern hemisphere (Fig. 5B, C). The majority of areas with trilobite-bearing rocks of the Bohemian Massif were characterized by a gradual transfer from high polar paleolatitudes in the Upper Ordovician (Fig. 5C), through the cold and warm temperate belts during the Silurian (Fig. 5D), and to subtropical and tropical environments in the Devonian and Carboniferous, respectively (Fig. 5E, F). This scenario played a

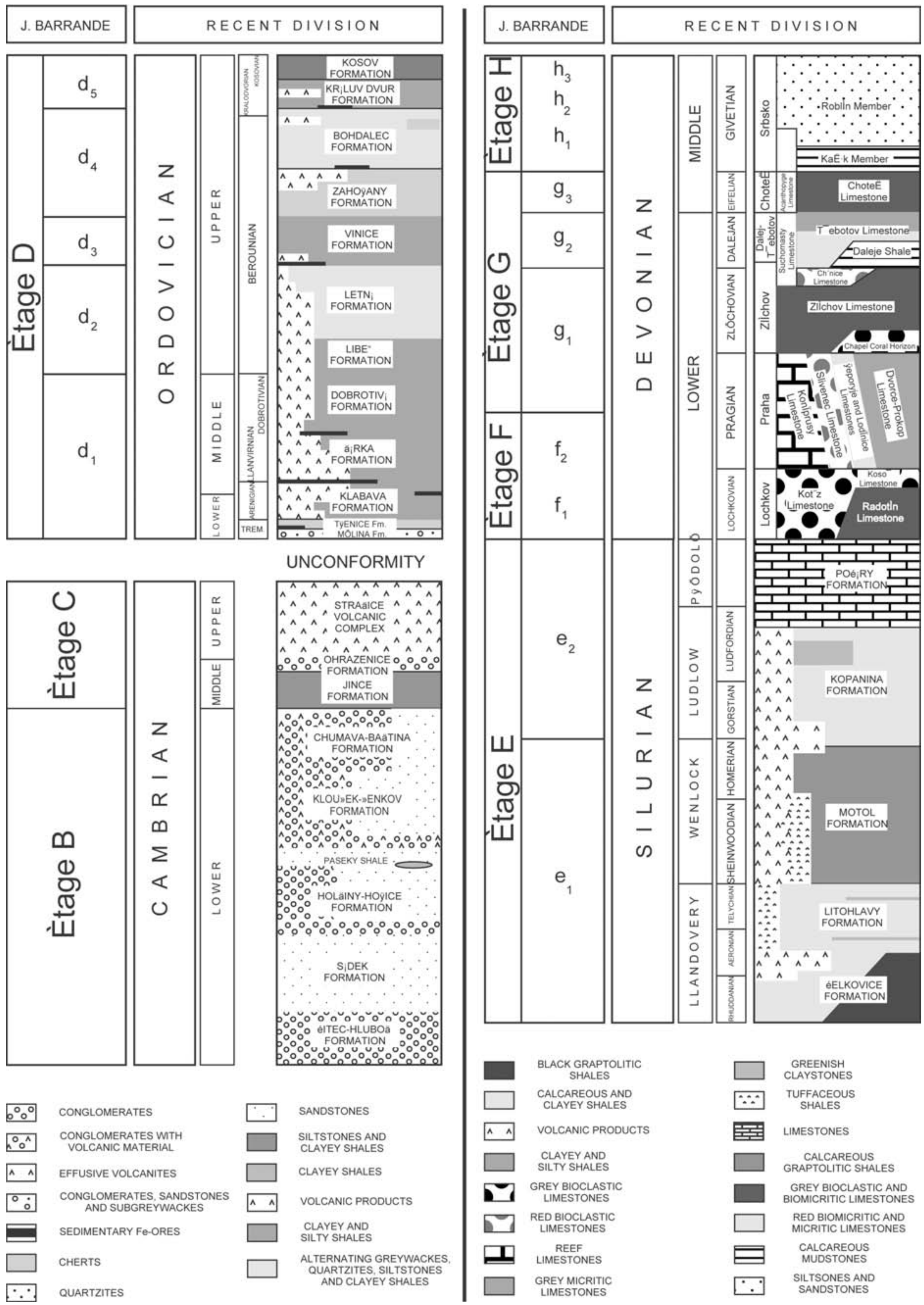

Fig. 4. Stratigraphy of the Barrandian area. A = Cambrian and Ordovician, B = Silurian and Devonian.

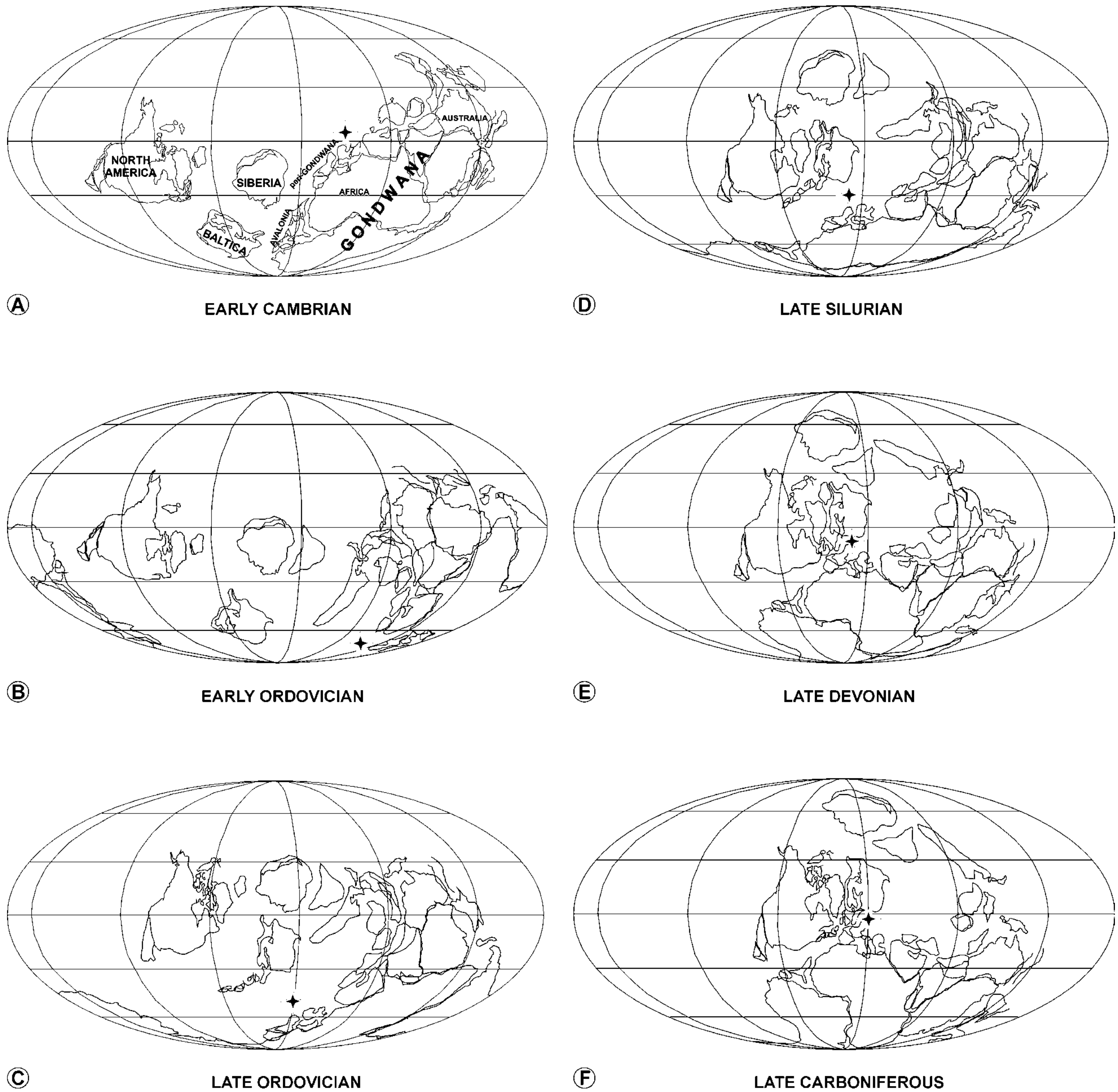

Fig. 5. Paleogeographic reconstructions of the Early Cambrian–Late Carboniferous location of the Barrandian area. A, modified from McKerrow *et al.* (1992); B–E, modified from Scotese and McKerrow (1990).

prominent role in the composition of trilobite assemblages in this area.

Other areas of Central Bohemia.—In the Zelezné hory Mountains, the slightly metamorphosed Middle Cambrian and Ordovician contain trilobites. The poor Middle Cambrian trilobite assemblage shows similarities to the assemblage of the Skryje–Tyrovice area (Havlícek and Snajdr, 1951). The occurrence of *Bavarilla hofensis* in the Lower Ordovician relates this area to the Frankenwald in Germany (Prantl and Ruzicka, 1942; Vanek, 1965a). Rare Upper Ordovician trilobites found in the phyllitic shales (Prachovice and Vápenny Podol) are comparable to equivalent assemblages in the Prague Basin of the Barrandian area.

Trilobite remains in the tectonically disturbed and slightly metamorphosed rocks in the vicinity of Rozmitál pod Tremsínem (the Rozmitál Graben of Havlícek *in* Chlupác *et al.*, 1998) include Upper Ordovician trinucleid and dalmanitid trilobites with rare cyclopygids (Zelízko, 1906, 1917; Pribyl and Vanek, 1972). The material comes from gray-green silty shales of the Voltus Formation, and correlates well with the Berounian (= Caradocian) Stage of the Prague Basin (Barrandian area). In contrast, the common deep-water, small-eyed phacopid trilobite

Plagiolaria aff. *kockeli* from the tentaculite-bearing shales of probable late Zlíchovian age (Early Devonian *fide* Chlupác, 1977c; Havlícek *in* Chlupác *et al*., 1998) shows affinities to those in the Saxo-Thuringian region of Germany.

A sparse assemblage of uppermost Upper Devonian phacopid and proetid trilobites has been collected from limestones in a borehole at Nepasice (at a depth of more than 800 m) near Hradec Králové in the Bohemian Cretaceous Basin (Chlupác and Zikmundová, 1976).

Krkonose–Jizera Crystalline Unit

Very poorly preserved proetid (cyrtosymboloid or archegonid) trilobites occur in phyllitic shales in the Krkonose–Jizera Crystalline Unit. These strata conformably succeed limestones that represent an almost complete sequence of Famennian (Devonian) conodont zones. Superposition suggests they are probably lowest Carboniferous (Chlupác, 1964a, 1993) (Figs. 1, 2).

Moravo-Silesian Region

The Moravo-Silesian Region lies in the Variscan Belt in Central Europe. In the Czech Republic, it includes three main areas with trilobite-bearing rocks: 1) the Moravian Karst; 2) the Hruby and Nízky Jeseník Mountains; and 3) the Upper Silesian Coal Basin (Fig. 1). Devonian and/or Carboniferous trilobites have been found in all of these areas (Fig. 2). Although rare Lower Cambrian and Silurian marine rocks occur in the Moravo-Silesian Region, no trilobite remains are known.

Four principal types of lithofacies developed in the Devonian rocks: 1) Drahany (basinal) development; 2) Ludmírov (transitional) development; 3) Moravian Karst (platform) development, and 4) Tisnov (marginal) development. During the Early Carboniferous, a different pattern of lithofacies development resulted from the diachronous onset of flysch (i.e., Culm) sedimentation in the Moravo-Silesian Region. In general, the same sedimentation continued into the Early Carboniferous. In the Silesian Coal Basin, marine deposition was dominant from the Devonian to Early Carboniferous. This marine cycle was replaced by continental sedimentation that alternates with marine horizons.

Devonian trilobite assemblages.—Devonian trilobite faunas of the Moravo-Silesian Region show distinct relationships to paleoenvironmental changes and such events as the Kellwasser Event. Lower Devonian (Pragian) homalonotids (e.g., abundant *Digonus* in the metamorphic Drabov Quartzites in the Hruby Jeseník Mountains) are gradually replaced by mixed Bohemian-Rhenish assemblages with "acastids" (e.g., *Acastoides*), some homalonotids (*Dipleura*), phacopids (e.g., *Reedops*, *Phacops*), and proetids (e.g., *Cornuproetus*). The uppermost Lower (Dalejan) and Middle Devonian (Eifelian) trilobite faunas are typical of Bohemia (e.g., the phacopids *Struveaspis*, *Chotecops*, *Phacops*; otarionid *Cyphaspides*; proetids *Cyrtosymboloides*, *Cornuproetus*; odontopleurids *Koneprusia*, *Kettneraspis*; and styginid *Thysanopeltis*) (Chlupác, 1969a, 2000). A spectacular deeper-water fauna from the stratotype locality at Chabicov has blind or small-eyed trilobites (*Illaenula*, *Struveaspis*, *Micromma*) (Chlupác, 1965). The fauna from Celechovice (probably lower Givetian) is analogous to communities of the coral-stromatoporoid facies from other regions, including some that are distant (Chlupác, 1992). Rich Upper Devonian (Famennian) trilobite assemblages (phacopids and small proetids) are markedly cosmopolitan, and reflect changes in paleoecological conditions in this time interval (Chlupác, 1966a, 2000).

Carboniferous trilobite assemblages.—Only proetid trilobites have been described from the Carboniferous of the Moravo-Silesian Region. The distribution of Carboniferous trilobites also reflects a pronounced facies dependence. Tournaisian trilobites are known in the Moravian Karst, where two assemblages (shelf slope and limestone communities) have been described (Chlupác, 1966a). Species of both assemblages occur associated at some localities. The shelf slope community is dominated by archegonid phillipsiids. In contrast, *Cummingella*, *Moschoglossis*, and *Piltonia* dominate the Carboniferous limestone assemblage. The Viséan trilobite fauna is represented mostly small-eyed or even blind archegonids that flourished on muddy bottoms of the "Culm" facies under dysoxic conditions.

Viséan limestones have limited outcrop in the Moravo-Silesian Region, and thus the trilobites (e.g., *Griffithides*, *Cummingella*, and *Phillipsia*) were identified only in deep boreholes drilled into the basement of the Outer Carpathians (Král and Pek, 1993) and in exotic boulders in the Carpathian flysch (Hörbinger *et al*., 1985). The youngest trilobite fauna is represented by near-shore ditomopygids (*Paladin*) in Namurian marine horizons of the Upper Silesian Coal Basin (Rehor and Rehorová, 1972).

Erratic boulders

Erratic boulders with Cambrian to Silurian trilobites occur in northeastern parts of the Bohemian Massif. The boulders were transported from Scandinavia (southern Norway, Sweden, and southern Finland) by Quaternary ice (Figs. 1, 2).

The Cambrian to Silurian trilobites in these boulders come from areas located in temperate to tropical paleolatitudes during the Early Paleozoic, and thus represent exotic assemblages. Data on trilobites of different ages that were published in numerous short papers have been summarized by Gába and Pek (1999).

HISTORY OF TRILOBITE RESEARCH IN THE CZECH REPUBLIC

The earliest published information on Barrandian fossils dates from the last quarter of the eighteenth century (Zeno, 1770), and the stratigraphic divisions were proposed at the end of the first half of the nineteenth century (Barrande, 1846a, b). Highly detailed stratigraphic concepts have been worked out for the Cambrian–Devonian (Fig. 4). The original stratigraphic concept of '*Système silurien*' (with eight '*étages*' designated A to H) established by Barrande has been finely subdivided (for a review see Chlupác, 1999).

The *Système silurien du centre de la Bohème* published between 1846 and 1887 by the French engineer and paleontologist Joachim Barrande (1799–1883) represents one of the most important works in our understanding of Lower Paleozoic paleontology and stratigraphy. As this magnificent work was founded on Barrande's life-long research on fossils originating from central Bohemia, Posepny (1895) proposed calling the entire area of the *Système silurien* the Barrandian area.

Trilobite research in the Barrandian area

Barrande played a fundamental role in the Paleozoic paleontological research in the Paleozoic. Thus, we agree with Snajdr (1958a) that four main periods in the study of trilobites in the Barrandian area should be recognized: 1) the pre-Barrande period; 2) Barrande's work; 3) the post-Barrande period; and 4) the post-Second World War period.

Pre-Barrande period.—The oldest note on Bohemian trilobites was produced by the Jesuit priest Franz Zeno (1770), who described and figured 'Cacadu – order Käfer – Muschel' or 'Concha triloba' and 'Echinites.' These illustrations eventually were determined (Horny and Bastl, 1970) to be of species of *Odontochile* and *Phacops*. In general, the earliest papers deal with Bohemian trilobites as "wonders of nature," and were written by hobby-collectors (e.g., Zeno, Sáry, Dusl, Zeidler) who devoted their own time for collecting and/or used their own money to buy such peculiarities.

Two years later, the professor of mineralogy Ignaz von Born (1772) published a catalog of his private collection of minerals, rocks, and fossils. He described several new trilobite taxa, all of which are now considered invalid. According to Horny and Bastl (1970), they represent the Cambrian species *Paradoxides gracilis* and *Conocoryphe sulzeri* and the Devonian genus *Odontochile*.

Prior to the end of the eighteenth century, trilobites were also mentioned by Frantisek Josef, the Count of Kinsky (1775). In his published letter to Ignaz Born, he described and figured some Cambrian forms. The same specimens were later mentioned by Erlacher (1782) and Jirasek (1786). Other trilobites of different stratigraphic range were figured by Lindacker (1791) and Schmidt (1795).

The first specifically Bohemian trilobites were described by Schlotheim (1823) from the Cambrian as *Trilobites hoffii* (now *Ellipsocephalus hoffi*) and *Trilobites Sulzeri* (now *Conocoryphe sulzeri*). Thus, Cambrian and Devonian trilobites were known in Bohemia at this time. A detailed history of research on Cambrian trilobites was compiled by Snajdr (1958a). As noted by Horny and Bastl (1970), the first valid trilobite taxon was published by Brongniart (1822) as *Asaphus Hausmanni* (=*Odontochile hausmanni*).

Fig. 6. Kaspar Maria, Count of Sternberg.

One of the most important scientists of the nineteenth century was Kaspar Maria Count Sternberg (Fig. 6), a paleobotanist and the founder of the Czech Patriotic Museum in 1818. He published important data on trilobite morphology (Sternberg, 1825, 1830, 1833). Cambrian and other trilobites were discussed by Boeck (1827), Emmrich (1839), Zenker (1833) and Beyrich (1845), and some of their species remain valid.

In the second half of the nineteenth century, four additional trilobite workers undertook research. These include Heinrich Ernst Beyrich, Joachim Barrande, Ignatz Hawle, and August Carl Joseph Corda. In the eighteenth and nineteenth centuries, Bohemian trilobites were described and figured mainly by non-Czech scientists, and their papers generally were published outside of the Bohemian part of the Austro-Hungarian Empire.

Barrande's work.—The exception to the domination of research by non-Czech workers was that of the French engineer Joachim Barrande (Fig. 7). Joachim Barrande was an exceptional personality who made a huge impact in understanding Lower Paleozoic stratigraphy and paleontology, including trilobites. All of his studies are characterized by very precise observations, which have stood the test of time both technically and scientifically. Barrande was economically well off, and, therefore, truly independent of the dramatic political events within the Austro-Hungarian Empire following the revolutionary year 1848. In contrast, his only student, Ottomar Novák, demonstrated very promising scientific results; however, his life was tragically brief. Novák may have attained Barrande's expertise had he had better living conditions.

In 1832, Barrande emigrated with the French royal family to the Bohemian part of the Austro-Hungarian Empire. His lifelong employment by Henry Count of Chambord, whom he had earlier tutored, provided him with a secure financial background for his scientific work and with additional funding for collecting and publication (Horny and Turek, 1999). Barrande was soon introduced to Bohemian scholars (Kriz, 1999). Among them, Count Kaspar Sternberk influenced Barrande´s interest in fossils. Barrande was employed by Count Sternberk to examine the railroad extension from Lány to Plzen. The project ran through the Middle Cambrian sequences in the area of Skryje (Kriz, 1999). Traditionally, it is thought that Barrande found his first trilobites while walking along Dívcí hill near Zlichov in Prague (Horny and Turek, 1999, Chlupác, 2002).

Barrande enjoyed his new country and researched the paleontology and geology of the Barrandian area as nobody else had. He investigated not only trilobites of Cambrian to Devonian age, but other fossil groups as well. At a time when the succession of Paleozoic rocks was unknown, Barrande proposed the first stratigraphic subdivision of his '*Système silurien*' into *Étages A–H* (Fig. 4). These étages are now known to represent the Precambrian, Cambrian, Ordovician, Silurian, and Devonian (Horny and Turek, 1999).

Barrande (1846a, b) published his first trilobite studies when he was 47 years old. These reports were preceded by thirteen years of research "in a geologically unknown territory, without good roads and without railways, without elaborate and correct

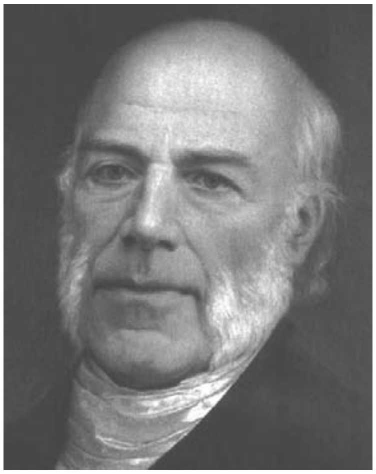

Fig. 7. Joachim Barrande.

Fig. 8. Otomar Pravoslav Novák.

maps and a conception of a detailed stratigraphy, and at the beginning without a good knowledge of the Czech language" (Horny and Turek, 1999, p. 19). Barrande (1846a, b) was motivated to publish because reports on Barrandian trilobites (e.g., Beyrich, 1845) had begun to appear (Horny and Turek, 1999, Chlupac, 2002). Beginning in 1852, Barrande began the publication of his monumental 22-volume work *Système silurien du centre de la Bohème*, with four volumes dedicated to trilobites. Barrande published most of his papers on Barrandian trilobites in Vienna, Paris, Dresden, and Prague (Barrande, 1846a, b, 1852, 1856, 1872; see Horny and Turek, 1999). The large collections and the original types of Barrande's *Système silurien* are stored in the National Museum in Prague, where they form the major part of the Paleozoic collections.

The second half of the nineteenth century, as a whole, was characterized by the initial mapping of selected territories in the Austro-Hungarian Empire. The Barrandian area was one of such regions where collaborators of the "Reichsanstalt" (= geological survey) in Vienna focused their studies, and eventually refined the stratigraphy of Barrande´s "*Silurien Systeme*" in the sense of R. I. Murchison.

Barrande (1852) was the first to describe trilobite larvae and ontogeny. He suggested a method for numbering growth stages during the meraspid period that is still in use (Chatterton and Speyer, 1997). Barrande (1852) also recognized three of the main types of trilobite enrollment (Harrington, 1959), and was the first to describe the presumed infilling of a trilobite alimentary canal (Whittington, 1997).

Barrande's concept of 'colonies' was noteworthy. In 1842, he was informed of Silurian trilobites near Bruska in Prague that occurred in a limestone lens surrounded by an older fauna in Ordovician strata (Horny and Turek, 1999). Barrande thought that the occurrence of a younger fauna surrounded by an older assemblage could be explained by a brief migration of the "younger" fauna from another area. Finding the new conditions unfavorable, the "younger" fauna became extinct. Although he advocated his colony concept until his death, the juxtaposition of these faunas was actually a result of tectonism (Horny and Turek, 1999).

Because they considered Barrande a 'stranger' in their country, two Czech-speaking Bohemian patriots, Ignatz Hawle, a local councilman and avid fossil collector, and August Carl Joseph Corda, a botanist at the National Museum, were displeased with his trilobite work (Horny and Turek, 1999). They responded by publishing a monograph on Bohemian trilobites (Hawle and Corda, 1847). Unfortunately, this paper was compiled in great haste, with idealized drawings and numerous inconsistencies in the text. Barrande (1852, 1872) redescribed and refigured many of their species much more precisely. Thus, Barrande`s names were used by successive workers, although such usage was in apparent conflict with nomenclatorial rules. Because Hawle and Corda`s names were difficult to use, they have been ignored for more than 150 years. According to nomenclatorial rules, it is better to consider them as *nomina oblita*. Unfortunately, the highly talented paleontologist (chiefly a paleobotanist) Corda died tragically in 1849. He did not have an opportunity to defend his and Hawle`s nomenclatoral priority over Barrande's taxa. Hawle, as a non-specialist in paleontology, was unable challenge and critique Barrande`s comments. After the evaluation of Hawle and Corda`s type material by Snajdr (1984a), many of their species have been proven to be invalid.

Post-Barrande period.—One of the most talented Czech paleontologists, Ottomar Pravoslav Novák (Fig. 8), was a student and disciple of Barrande. He was also appointed curator of Barrande`s gigantic collection and authorized to continue Barrande`s work on trilobites. After Barrande`s death, Novák (1880, 1884, 1885, 1886) continued the study of trilobites by publishing several papers on hypostoma and on Silurian and Devonian taxa (Novák, 1883, 1890). These papers included excellent, accurate drawings (Figs. 9–11). Unfortunately, his life and scientific activity were cut short when Novák died after a long illness at age 41 in 1892.

After Novák's death, trilobite study underwent an interruption and crisis which lasted until the end of the nineteenth century (Fig. 12). No person capable of taking the lead came forward to the fill the gap left by Barrande and Novák, although some work on trilobites continued to be produced. Following the deaths of Barrande and Novák, the scientific study of Czech trilobites was interrupted, and several well educated amateurs were responsible for the little that was published on the subject

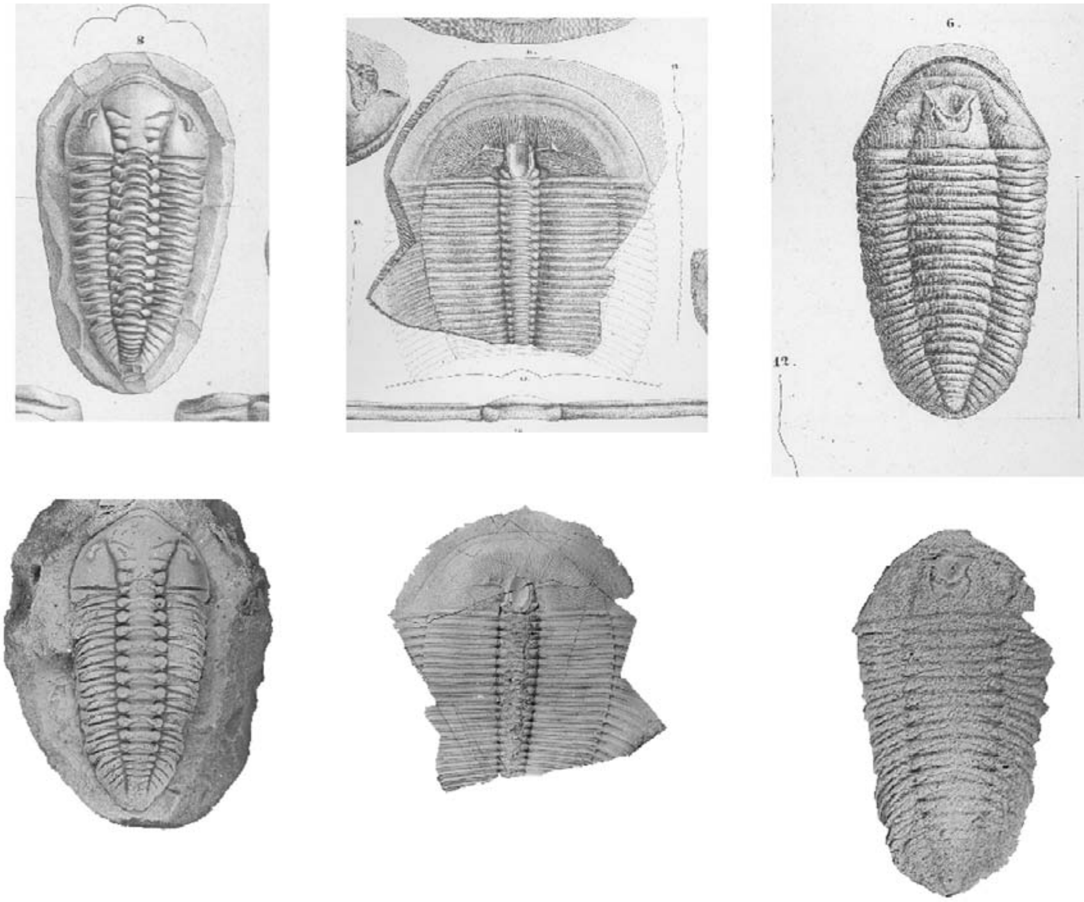

Fig. 9. *Ormathops atavus* NM L 16957. Barrande (1872, pl. 15, figs. 8, 9, 11); *Harpides grimmi* NM L 16606 from Barrande (1872, pl. 1, figs. 11–14); *Platycoryphe bohemica* NM L 16602 from Barrande (1872, pl. 1, fig. 6).

at this time. This situation in paleontological research continued up to the 1920s, when a slow regeneration occurred because of research by amateurs (e.g., Kloucek, Ruzicka) and the next generation of professional scientists (e.g., Boucek, Koliha).

One of Novák`s manuscripts (published in 1918) was arranged and finished for publication by Jaroslav Perner, who was not a trilobite specialist. Several new trilobite species were established in an extensive study by Pompeckj (1895). Other taxa were discussed by Jaekel (1909) and Raymond (1914). Trilobite reports were gradually produced by Holub (1908, 1910, 1911), Kloucek (1916), Zelízko (1921), Ruzicka (1926, 1927, 1935), Smetana (1921), and Suf (1926a), but trilobite research underwent a decline during this period (Fig. 12).

The Second World War resulted in suppression of scientific investigation and a prolongation of the already long period of stagnation. The assembly of fossil collections was the only activity that continued at this time, in part by several young "trilobitophiles" (Snajdr, L. Marek, Chlupác).

Post-Second World War period.—During the Second World War and directly afterwards, several authors occupied an 'open niche of trilobite research' in Czechoslovakia. Prantl and Pribyl, as well as Chlupác, Marek, Snajdr and Vanek, began to publish on trilobites and several other groups of fossils.

Trilobite study became more exacting in this period An emphasis was placed on precise geographic location and stratigraphic ranges as data needed by a new comprehensive geologic mapping of Czechoslovakia as part of a search for raw materials.

In the Barrandian area, the mapping conducted by the State Geological Survey focused on Paleozoic stratigraphy, and the majority of paleontologists, including trilobite specialists, participated in this extensive project. Intensive collecting at classic localities and the documentation of numerous new sections and outcrops provided voluminous new material. As a result, trilobite studies re-examined all of the Middle Cambrian–Middle Devonian.

The time after the Second World War was characterized by extensive geological mapping motivated by the need for raw materials, which rejuvenated trilobite research surprisingly quickly. Large, modern studies and revisions were produced by this rising generation of paleontologists (e.g. Prantl, Pribyl) into the early 1950s, and by their students to the end of the 1950s. All trilobite species assignable to large groups as families and/or superfamilies or major parts of species occurring in one stratigraphic unit were revised with an emphasis on stratigraphic aspects and their applicability (e.g., monographs by Prantl and Pribyl, 1949a; Snajdr, 1958a, 1980a; Chlupác, 1977b; Vanek, 1959; Pek, 1977; Mergl, 1984). Some of the papers published from 1970

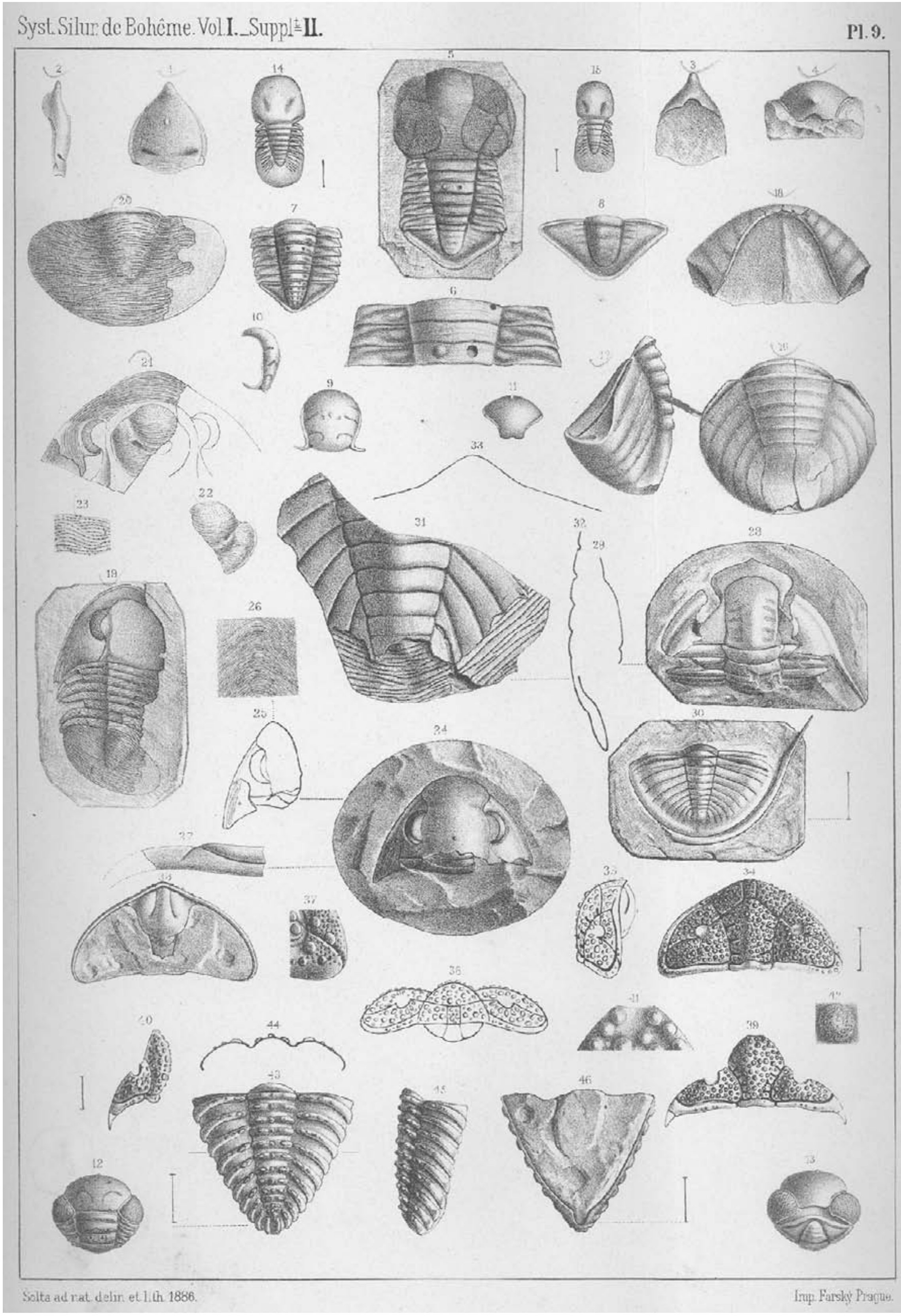

Fig. 10. Ninth plate of Novák's unpublished second supplement to the "*Systeme silurien*."

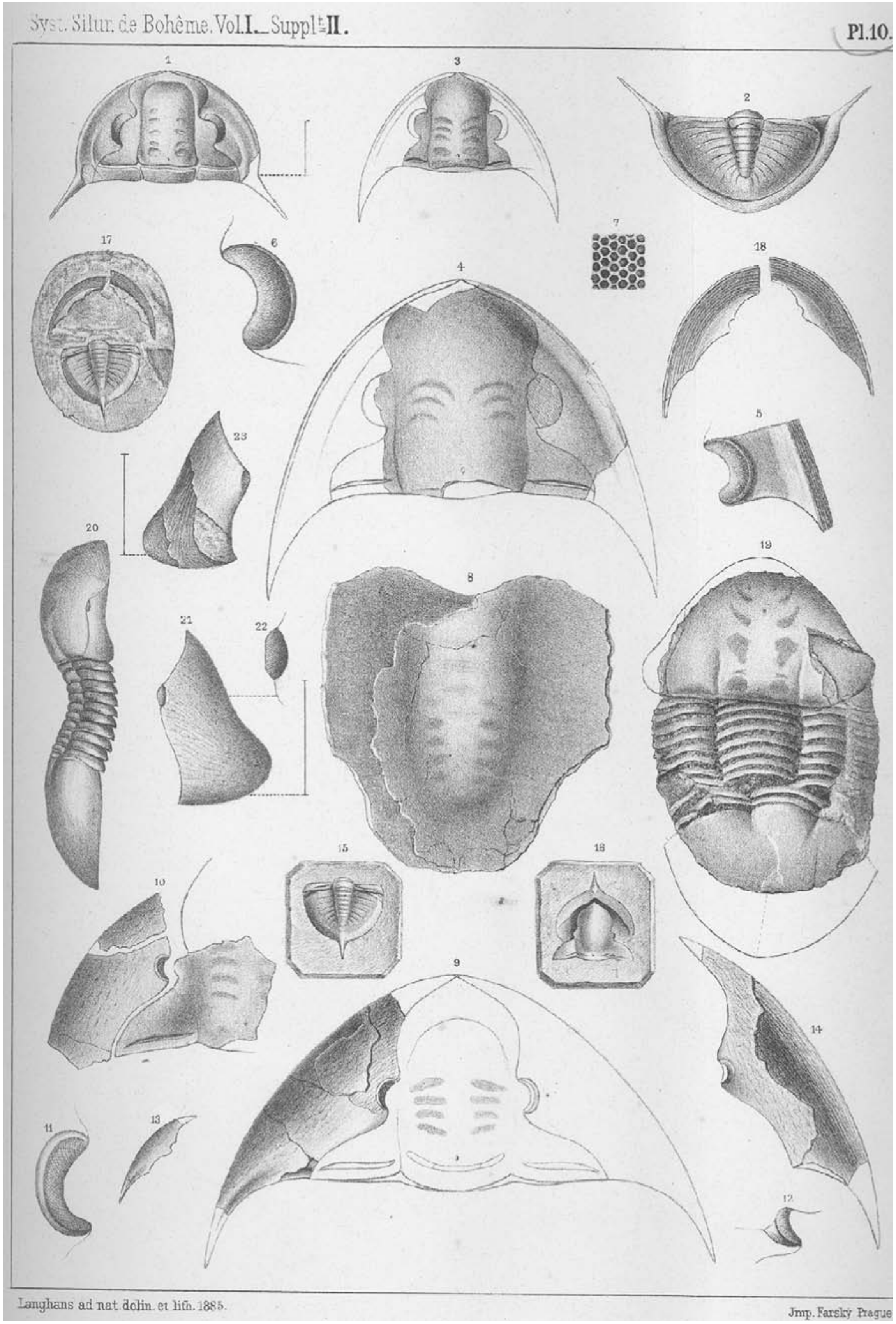

Fig. 11. Tenth plate of Novák's unpublished second supplement to the "*Systeme silurien*."

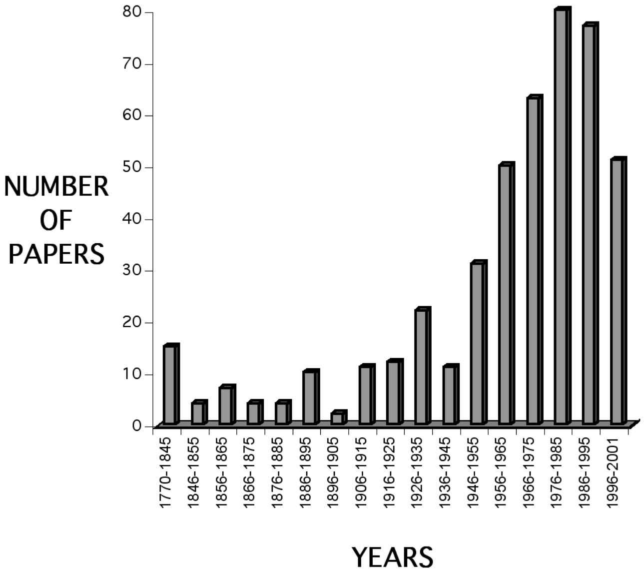

Fig. 12. Rate of publication of papers on trilobites of the Czech Republic between 1770 and 2001.

to the recent include information about molting, ontogeny, and paleoecology (e.g., Pribyl and Vanek, 1969a, 1976; Snajdr, 1960, 1980a; Chlupác, 1977b). Teratologies and pathologies were documented in detail by Snajdr (1978, 1979a, 1981a, 1985a, 1990b) and others.

Comprehensive mapping was connected with extensive field work, which produced immense excavations that permitted fossil collecting in different parts of Czechoslovakia. The years 1950–1980 could be designated as a "golden age of trilobite research" in our country. The generation starting immediately after the war was still active and their students made good use of the opportunity provided by the support to geology given by official state policy.

The decline in geology, including trilobite research, began during the 1980s, when the older generation finished its activities. The attenuation accelerated at the beginning of 1990s after the death of leading personalities, including Snajdr, L. Marek and, most recently, Chlupác. During the second half of the 1990s, however, several permanent positions in state institutions have been occupied by trilobite researchers.

Foreign contributions.—In different periods, trilobites originating from the Barrandian area have been studied by numerous foreign specialists (e.g., Delo, 1935; Kielan 1959; Bruton, 1966; Shaw, 1995, 2000; Hughes and Chapman, 1995; Hughes *et al.*, 1999; Whittington, 1999, and many others). These researchers contributed substantially to modern knowledge, and providing a better understanding of how Bohemian trilobites relate to those in other regions.

Trilobite research in the Moravo-Silesian Region

Compared to the Barrandian area, trilobites are rare in the Moravo-Silesian Region, and are commonly poorly preserved. Generally, younger (Devonian–Carboniferous), less diversified assemblages are present. The earliest reports on this region focused on trilobites from geographically small areas or on isolated, casual finds.

In the Moravo-Silesian Region, trilobite research began in the second half of the nineteenth century when geologists of the "Reichsanstalt" discovered the first fossiliferous localities during mapping of the Austro-Hungarian Empire (Roemer, 1863, 1865, 1870; Stúr, 1866, 1875). Systematic evaluation of trilobites began at the end of the nineteenth century and continued to the Second World War. Trilobites from limestones at the classic Devonian locality of Celechovice (upper Eifelian or lower Givetian) were described by Zimmermann (1892), Smycka (1895a), Remes (1913), and Richter (1914). Rzehak (1910) and Oppenheimer (1916) were the first to report trilobites in the Moravian Karst. Their findings were revised by Richter (1912, 1913). Knowledge about some areas was complemented later by Klebelsberg (1912), Smetana (1916), and Patteisky (1929, 1933), Schwarzbach (1935, 1936), and Pfab (1932).

As in the Barrandian area, the next period of research began shortly after the Second World War. During this time, intensive paleontological research associated with mapping by the State Geological Survey led to the discovery of many new Devonian and Carboniferous localities and stratigraphic levels with trilobites (Fig. 13). These included trilobites from the basal 'Culm' at Hranice (Chlupác, 1956). These new, rich materials allowed a modern revision of the trilobite faunas (see reviews in Chlupác, 1977a, 2000).

The most important studies included: 1) homalonotid trilobites from the Pragian (Lower Devonian) of the Hruby Jeseník Mountains (Chlupác, 1981); 2) the Upper Devonian to Lower Carboniferous trilobites of the Moravian Karst (Chlupác, 1966a) and Devonian trilobites from Celechovice (Chlupác, 1992); 3) Lower and Middle Devonian trilobites from the Nízky Jeseník Mountains (Strnad, 1957, 1960; Chlupác, 1969a); 4) the Devonian of the Drahany Upland (Chlupác, 1960, 1977b); 5) the 'Culm' trilobites from the Nízky Jeseník Mountains (Pribyl, 1951); 6) the rare trilobites from Carboniferous limestones in boreholes in the Carpathians and from exotic boulders from Carpathian flysch (Chlupác and Rehor, 1970; Král and Pek, 1993); Hörbinger *et al.*, 1985); and 7) trilobites from the Upper Silesian Coal Basin (Rehor and Rehorová, 1959, 1972).

FUTURE TRILOBITE RESEARCH IN THE CZECH REPUBLIC

From the preceding historical review, several potential future trends in Bohemian trilobite research may be predicted.

The established understanding of the geographic dispersion of separate taxa provides a good basis for future paleogeographic interpretations, as well as paleoecologic and synecologic studies of trilobite taxa and fossil assemblages. These studies will complement the paleogeographic reconstruction during the Paleozoic of the peri-Gondwana terrane(s) that comprise the Czech Republic.

In the Barrandian area, it seems possible that there are some 'oversplit' trilobite groups for which morphological variability studies should be undertaken. In some instances, the 'endemic Bohemian species' represent subjective synonyms of taxa previously described from other regions.

In the Moravo-Silesian Region, recently collected material from some areas has turned up trilobites from stratigraphic

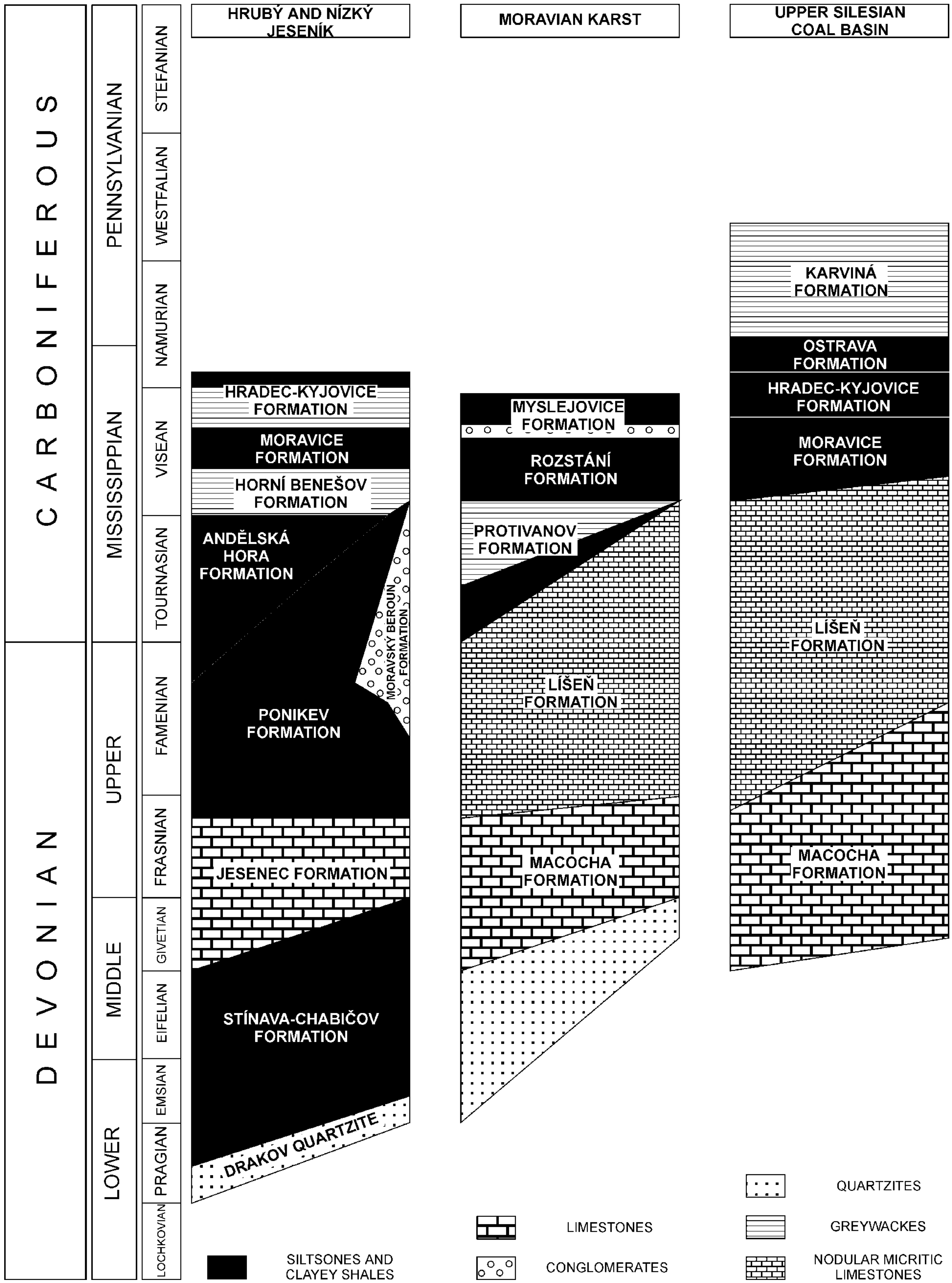

Fig. 13. Stratigraphy of the Moravo-Silesian Region.

levels where they have been previously poorly known or even absent. These new collections need study. Some of the earlier published trilobite assemblages also need to be revised.

TRILOBITE COLLECTIONS

The largest and the most important collections of Czech trilobites are reposited in the following institutions: National Museum, Prague; Czech Geological Survey, Prague; Museum of Dr. B. Horák in Rokycany, District Museum in Beroun; West Bohemian Museum, Plzen; the Moravian Museum in Brno; Ostrava Museum; Silesian Museum in Opava; and the Museum of National History and Art in Olomouc.

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REFERENCES AND ANNOTATIONS

We have attempted to compile a comprehensive list of reports dealing with the systematic treatment of trilobites from the Czech Republic. The majority of references in the list have been published by authors in central Europe. Because of the multinational character of the Austro-Hungarian Empire in the eighteenth and nineteenth centuries, we decided to incorporate all reports involving trilobites from the area of the modern Czech Republic.

Each of the citations in the publication list is accompanied by an English translation of the title. At the end of each citation, we added, if possible, an abbreviation for the geological period in which these trilobites lived. [C] = Cambrian, [O] = Ordovician, [S] = Silurian, [D] =Devonian, and [Ca] = Carboniferous.

Barrande, J., 1846a, Notice préliminaire sur le Système silurien et les Trilobites de Bohème: 97 p. [C, O, S, D]

Barrande, J., 1846b, Noveaux Trilobites. Supplément a la Notice préliminaire sur le Système silurien et les Trilobites de Bohème: 40 p. [O, S, D]

Barrande, J., 1850, *Deiphon forbesi*, *in* Hauer, F., Berichte über die Mittheilungen von Freuden der Naturwissenschaften in Wien. Gesammelt und herausgegeben von W: Haidinger, v. 7, no. 1, p. 4–7. [S]

Barrande, J., 1852, Système silurien du centre de la Bohème: lère partie, Crustacès: Trilobites, vol. 1, 935 p. [C, O, S, D]

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TRILOBITE RESEARCH IN SOUTH KOREA DURING THE 20TH CENTURY

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ABSTRACT—Trilobita are among the most intensively studied fossil groups in Korea over the last century and provide invaluable information on Lower Paleozoic stratigraphy, paleogeography, and tectonics of the Korean peninsula. Six stages of trilobite research in Korea can be defined through the 20th Century: stage I (1924–1934), II (1934–1936), III (1937–1959), IV (1960–1962), V (1963–1991), and VI (1992–present). Important contributions were mainly made during stages II, IV, and VI, whereas trilobite studies in the intervals between these stages are generally less significant. During stages II and IV, the number of species described in the literature exceeds 100, while stage VI is characterized by a marked increase in the number of articles published each year. The future study of Korean trilobites will involve extensive taxonomic revision and a refined biostratigraphic zonation. Trilobite faunal assemblages are important in Paleozoic paleogeographic reconstructions of the Korean peninsula.

INTRODUCTION

Trilobites are among the most abundant and diverse fossil groups in southern Korea. They occur in the Lower Paleozoic Choson Supergroup of the Taebaeksan Basin in the east-central Korean peninsula (Fig. 1). The Choson Supergroup is a siliciclastic-carbonate succession that is late Early Cambrian–early Late Ordovician. Kobayashi *et al*. (1942) recognized five types of sequences in the Choson Supergroup, each with a distinct lithologic succession and geographic distribution. These include the: 1) Tuwibong-type, 2) Yongwol-type, 3) Chongson-type, 4) Pyongchang-type, and 5) Mungyong-type sequences. These sequences have been widely applied in the literature. However, Choi (1998a) noted the inappropriateness of this stratigraphic nomenclature of the Choson Supergroup and proposed the Taebaek, Yongwol, Yongtan, Pyongchang, and Mungyong Groups to replace the Tuwibong-type, Yongwol-type, Chongson-type, Pyongchang-type, and Mungyong-type sequences, respectively. The Taebaek and Yongwol Groups are very fossiliferous, whereas the other groups are poorly fossiliferous. A total of 180 species have been described from the Taebaek Group and 89 from the Yongwol Group (Kobayashi, 1966). Sixteen trilobite species are known from the Mungyong Group, whereas no trilobites have been reported from the Yongtan and Pyongchang Groups.

The geologic structure of the Taebaeksan Basin is characterized by a number of thrust faults and associated folds (Fig. 1) that have led to diverse views on the stratigraphy and age of the Choson Supergroup. Choi (1998a) attempted to resolve the problem by redefining the stratigraphic nomenclature of the Choson Supergroup based on the documentation of trilobite occurrences in the supergroup. The revised Cambrian–Ordovician trilobite biostratigraphy is found to be extremely useful for a better understanding of the Choson Supergroup and the geologic structure of the Taebaeksan Basin.

Most of the current knowledge on Korean trilobites of Korea was developed during the more than thirty years of study by Teichii Kobayashi. In the latest compilation of the Cambrian–Ordovician faunas of South Korea (Kobayashi, 1966), 279 trilobite species assigned to 133 genera were listed from the Choson Supergroup. Since then, relatively little progress on trilobite research was accomplished in Korea. However, recent trilobite studies have required a revaluation of the Korean materials. This should include taxonomic revision, refined biostratigraphic zonation, and paleogeographic and paleoecologic applications. The specific objective of this report is to provide a historical review of trilobite research in South Korea and to propose a guide for future studies.

GEOLOGY AND STRATIGRAPHY

The Taebaeksan Basin occupies the east-central Korean peninsula and comprises mainly the Lower Paleozoic Choson Supergroup (Fig. 1). The Choson Supergroup rests unconformably on Precambrian granitic gneiss and metasedimentary rocks, and is overlain unconformably by post-Ordovician sedimentary rocks. The Lower Paleozoic sedimentary rocks are shallow marine in origin and consist predominantly of carbonates and subordinately of sandstone and shale. In the Early Paleozoic, the Taebaeksan Basin was a shallow marine, mixed siliciclastic-carbonate system with progressively deeper water to the west (Yongwol area), as indicated by the occurrence of coarse siliciclastic sediments in the eastern margin of the Taebaeksan Basin (Chough *et al*., 2000). This siliciclastic-carbonate system persisted throughout the Cambrian, until rapid accumulation of carbonate sediments in the Yongwol area resulted in the formation of a widespread carbonate platform across the Taebaeksan Basin in the Early Ordovician. This carbonate platform seems to have been characterized by shoals, lagoons, and

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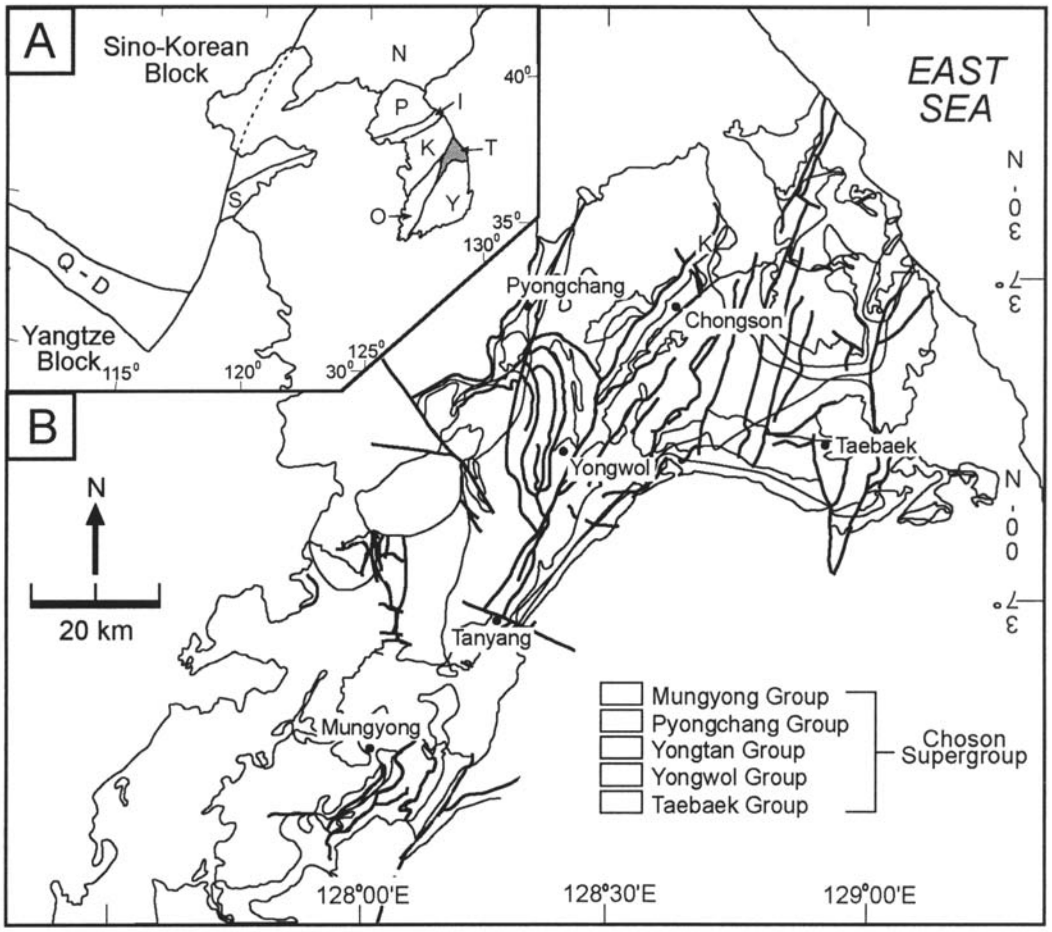

Fig. 1. A, Index map showing tectonic divisions of the Korean peninsula and location of the Taebaeksan Basin (I, Imjingang Belt; K, Kyonggi Massif; N, Nangrim Massif; O, Okchon Belt; P, Pyongnam Basin; Q–D, Qinling–Dabie Belt; S, Sulu Belt; T, Taebaeksan Basin; Y, Yongnam Massif). B, Simplified geologic map of the Taebaeksan Basin (T in Fig. 1A), showing distribution of the Choson Supergroup (modified from Choi et al., 2001).

tidal flats that persisted into the Early and Middle Ordovician (Choi *et al*., 2001). Marine sedimentation virtually ceased over the whole Taebaeksan Basin in the Late Ordovician, and most of the Taebaeksan Basin was emergent during the Middle Paleozoic until marine transgression resumed in the Late Carboniferous.

Taebaek Group

The Taebaek Group occurs in the eastern half of the Taebaeksan Basin (Fig. 1) and comprises the Changsan/Myonsan, Myobong, Taegi, Sesong, Hwajol, Tongjom, Tumugol, Makkol, Chigunsan, and Tuwibong Formations in ascending order (Kobayashi, 1966; Choi, 1998a; Fig. 2). The Changsan Formation is characterized by milky white to light brown, coarse-grained quartzite with occasional cross-beds. Well-rounded gravels with clasts of quartzite, slate, and granitic gneiss locally occur in the lower part. The coeval Myonsan Formation, exposed in the eastern margin of the Taebaeksan Basin, consists of a lower conglomerate, which grades upwards into dark gray to black sandstone and shale. The Myobong Formation is composed mainly of dark gray to greenish gray slate, phyllite, and shale with intercalations of thin sandstone and limestone beds in the middle part. Kobayashi (1966) recognized, in ascending order, the *Redlichia*, *Elrathia*, *Mapania*, and *Bailiella* Zones in the formation.

The Taegi Formation is a monotonous sequence of milky white to light gray, massive- to thin-bedded limestone with oncolitic and oolitic limestone in its lowermost part. Kobayashi (1935, 1966) established three trilobite zones in the formation, the *Megagraulos*, *Solenoparia*, and *Olenoides* Zones, in ascending order, and correlated them with the Changhian Stage (Middle Cambrian) of North China.

The Sesong Formation consists mainly of dark gray slate, fine-grained sandstone, and limestone, and includes two Late Cambrian trilobite zones. These are the *Stephanocare* and *Drepanura* Zones (Kobayashi, 1935, 1966).

The Hwajol Formation is divided into three members (Cheong, 1969). The lower member (up to 100 m-thick) is characterized by alternations of limestone and shale beds that show conspicuous banded structures. The middle member consists mainly of sandstone with occasional limestone intercalations. The upper member comprises limestone, marlstone, shale, and limestone conglomerates. Kobayashi (1935, 1966) recognized the *Prochuangia*, *Chuangia*, *Kaolishania*, *Dictyites*, and *Eoorthis* Zones,

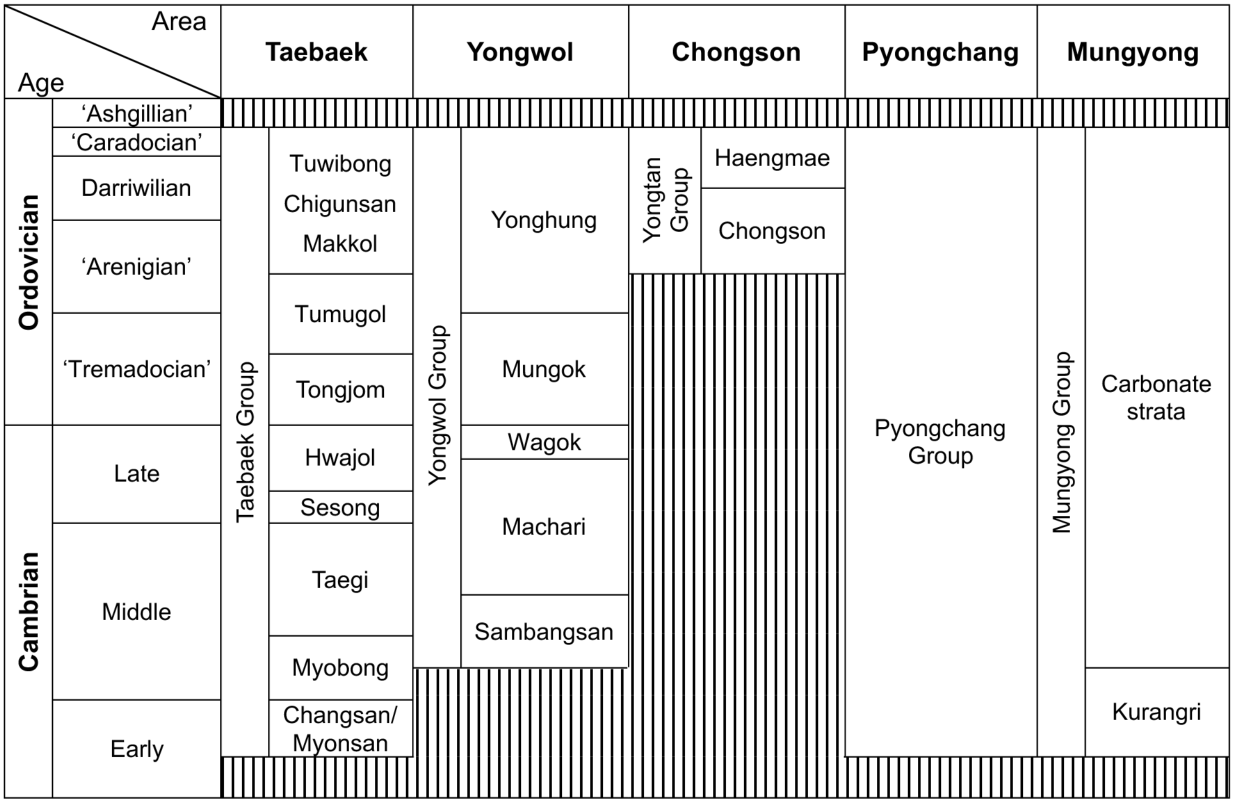

Fig. 2. Lithostratigraphic summary of the Lower Paleozoic Choson Supergroup in the Taebaeksan Basin, Korea (modified from Choi, 1998a).

in ascending order, in the Hwajol Formation. These assemblages show an affinity to the Upper Cambrian faunas of North China.

The Tongjom Formation consists of light to dark gray sandstone, shale, and limestone. *Pseudokainella iwayai* is the only trilobite known from the formation. Kobayashi (1966) placed the Cambrian–Ordovician boundary at the base of the formation. The Tumugol Formation is primarily an alternating sequence of limestone and shale layers with occasional limestone conglomerate beds. The limestone conglomerates were interpreted to be a product of storm activities (Lee and Kim, 1992), whereas Kwon *et al.* (2001) noted that most, if not all, of the limestone conglomerates were formed by diagenetic processes. The formation yields diverse and relatively abundant fossils that include trilobites, brachiopods, bivalves, gastropods, cephalopods, echinoderms, and conodonts (Kobayashi, 1934b; Choi and Lee, 1988; Seo *et al*., 1994). The trilobite faunal assemblages, represented by the *Asaphellus*, *Protopliomerops,* and *Kayseraspis* Zones (Kobayashi, 1934b, Kim *et al*., 1991), are closely comparable to the upper Tremadocian to lower Arenigian faunas of North China (Zhou and Fortey, 1986).

The Makkol Formation is a thick (250 to 400 m-thick) sequence of carbonate rocks that comprise lime mudstone, dolostone, limestone conglomerate, bioclastic grainstone, oolitic grainstone, and cryptalgalaminite. Although fossils are sparse, Kobayashi (1966) proposed the *Clarkella*, *Manchuroceras*, *Polydesmia*, and *Sigmorthoceras* Zones within the Makkol Formation.

The Chigunsan Formation is one of the most fossiliferous units in Korea. The lower part consists of an alternating sequence of dark gray shale and limestone, whereas the upper part comprises mainly dark gray to black shale. Fossils are particularly abundant in the lower part of the black shale unit. They include trilobites, graptolites, brachiopods, bivalves, gastropods, cephalopods, ostracodes, and fossils of uncertain affinity (Kobayashi, 1934a). The Chigunsan trilobite fauna is dominated by *Dolerobasilicus* and *Basiliella* (Lee and Choi, 1992), and shows an affinity to the Middle Ordovician trilobite assemblages of North China (Zhou and Fortey, 1986).

The Tuwibong Formation, the uppermost unit of the Taebaek Group, consists of dark gray massive bioclastic grain- to wackestone and calcareous shale with some limestone conglomerate beds. The formation also yields a diverse fossil assemblage with brachiopods, bivalves, gastropods, cephalopods, ostracodes, and trilobites (Kobayashi, 1934a). Kobayashi (1966) originally assigned the formation to the Caradocian, whereas Lee and Lee (1990) recognized two Llanvirnian (=Darriwilian) conodont zones, the *Plectodina onychodonta* and *Aurilobodus serratus* Zones.

Yongwol Group

The Yongwol Group is divided into the Sambangsan, Machari, Wagok, Mungok, and Yonghung Formations (Kobayashi, 1966; Choi, 1998a; Fig. 2). The lowermost Sambangsan Formation consists exclusively of siliciclastic sediments, whereas the upper four formations are composed largely of carbonates.

The Sambangsan Formation consists of purple to green siltstone and shale in the lower part, and greenish to yellowish gray, fine-grained, micaceous sandstone in the upper part. Middle Cambrian trilobites, such as *Metagraulos* and *Megagraulos*, occur commonly in the greenish gray micaceous sandstone beds (Choi *et al*., 1999).

The overlying Machari Formation has diverse Middle to Late Cambrian trilobites with some brachiopods and gastropods (Kobayashi, 1962). The lower part comprises dark-gray argillaceous limestone, thick-bedded bioclastic (mostly trilobites) grain- to packstone, dark gray dolomitic limestone, brownish black shale, and limestone breccia. The middle part is dominated by laminated dark gray to black shale with occasional intercalations of thin dolomitic limestones. The upper part is primarily an alternating sequence of thin-bedded, light gray dolomitic limestone and black shale beds, but is poorly fossiliferous (Lee, 1995). The *Tonkinella* Zone in the lower part of the formation suggests a middle Middle Cambrian age (Kobayashi, 1966), and is succeeded by an uppermost Middle Cambrian trilobite fauna with *Lejopyge armata* (Hong *et al*., 2000). The abundant trilobites in the middle part allows the recognition of eight Upper Cambrian trilobite zones (*Glyptagnostus stolidotus*, *G. reticulatus*, *Proceratopyge tenue*, *Hancrania brevilimbata*, *Eugonocare longifrons*, *Eochuangia hana*, *Agnostotes orientalis*, and *Pseudoyuepingia asaphoides* Zones in ascending order) (Lee and Choi, 1994, 1995, 1996; Lee, 1995). The succeeding Wagok Formation is a poorly fossiliferous sequence of light gray to gray massive dolostone and is assigned to the uppermost Cambrian (Kobayashi, 1966).

The Mungok Formation in northern Yongwol is divided into four members based on the association of such dominant lithofacies as ribbon rock, grain- to packstone, limestone conglomerate, and marlstone to shale facies (Kim and Choi, 2000b). The basal Karam Member consists mainly of ribbon rock and grain- to packstone with local intercalations of thin limestone conglomerates and chert layers. The superjacent Paeiljae Member is a monotonous sequence of light gray to gray, massive to crudely-bedded dolostone. The Chommal Member is an alternating unit of ribbon rock and limestone conglomerates, and the uppermost Tumok Member comprises ribbon rock, grain- to packstone, limestone conglomerate, and marlstone to shale. Trilobites occur in three stratigraphically separated intervals: the *Yosimuraspis* Zone in the lowermost Karam Member has *Yosimuraspis*, *Jujuyaspis*, and *Elkanaspis* and is lower Tremadocian (Kim and Choi, 2000a). The *Kainella* Zone is based on the occurrence of *Kainella* and *Leiostegium* from the lowermost bed of the Chommal Member and is correlated with the middle Tremadocian of North America and Argentina (Kim and Choi, 1995, 1999). The *Shumardia* Zone has a relatively long stratigraphic range through most of the Tumok Member and is dominated by upper Tremadocian trilobites (Choi *et al*., 1994).

The Yonghung Formation consists of massive to thick-bedded, light to dark gray dolostone in its lower part and bluish gray limestone in its upper part. Its fossils are rather poorly preserved, but include trilobites, brachiopods, cephalopods, conulariids, stromatoporoids, and conodonts (see Choi, 1998a, and references therein).

Yongtan, Pyongchang, and Mungyong Groups

The Yongtan Group is exposed in the Chongson area and has been divided into the Chongson and Haengmae Formations (Cheong *et al*., 1979b; Choi, 1998a; Fig. 2). However, the stratigraphy of the Yongtan Group and its relationship to other groups of the Choson Supergroup is still unclear. The Chongson Formation comprises mainly gray to bluish gray limestone and dolomitic limestone and yields Darriwilian to Caradocian conodonts (Lee, 1985). The Haengmae Formation consists of light brown conglomeratic limestone and milky white to gray limestone and is overlain unconformably by the Silurian Hoedongri Formation.

The Pyongchang Group in Pyongchang and adjacent areas is also poorly understood. Cheong *et al.* (1979a) subdivided it into the Changsan, Myobong, Pungchon, Taehari, Iptanri, and Chongson Formations in ascending order, and suggested it is a lateral equivalent of the Taebaek and Yongtan Groups. No fossils have been reported.

The Mungyong Group has been divided into the Kurangri, Masong, Hanaeri, Sokkyori, Chongri, and Totanri Formations, in ascending order (Aoti, 1942). The Kurangri Formation consists of purple to dark gray shale, whereas the overlying formations are dominantly composed of carbonates. However, later workers failed to confirm the lithostratigraphy proposed by Aoti (1942), and generally subdivided the Mungyong Group into the Kurangri Formation and overlying undifferentiated carbonate strata (Um *et al*., 1977; Lee *et al*., 1993; Choi, 1998a; Fig. 2). Kobayashi (1961) compiled the occurrence of Cambrian–Ordovician trilobites from the group.

HISTORICAL REVIEW

Gottsche (1886) was the first to report trilobites from Korea. The trilobites were found in the Cambrian of the Chosan–Wiwon–Kojang area, North Korea, but neither illustrations nor descriptions were provided. He reported six trilobite genera (*Agnostus*, *Dorypyge*, *Remopleurides*, *Conocephalites*, *Crepicephalus*, and *Anomocare*). The trilobite fauna was later described by Kobayashi and Kim (1931).

Trilobites in South Korea were first reported by Nakamura (1924), who illustrated an incomplete thoracopygidium from the Taebaeksan Basin, and assigned it to *Asaphus*. Yamanari (1926) also reported *Asaphus* and *Ogygia* in the Chigunsan Formation, and noted other trilobites from the Tumugol Formation (Ordovician) and other Cambrian strata. Kobayashi undertook research on the Cambrian–Ordovician of the Taebaeksan Basin by 1926, and subsequently published a series of monographs titled “The Cambro-Ordovician formations and faunas of South Korea” in ten parts from 1934 to 1971. Most of the specimens described by Kobayashi are currently stored in the University Museum at the University of Tokyo (Ichikawa and Hayami, 1978).

In this report, the trilobite studies in South Korea are described chronologically. Six stages of trilobite research are recognized in South Korea: stage I (1924–1934), II (1934–1936), III (1937–1959), IV (1960–1962), V (1963–1991), and VI (1992–present) (Fig. 3). Stages II and IV featured the largest number of species described systematically in the literature (more than 100 species), while stage VI had the highest average number of articles published per year (Table 1).

Stage I (1924–1934)

Six papers published in this interval merely mentioned the

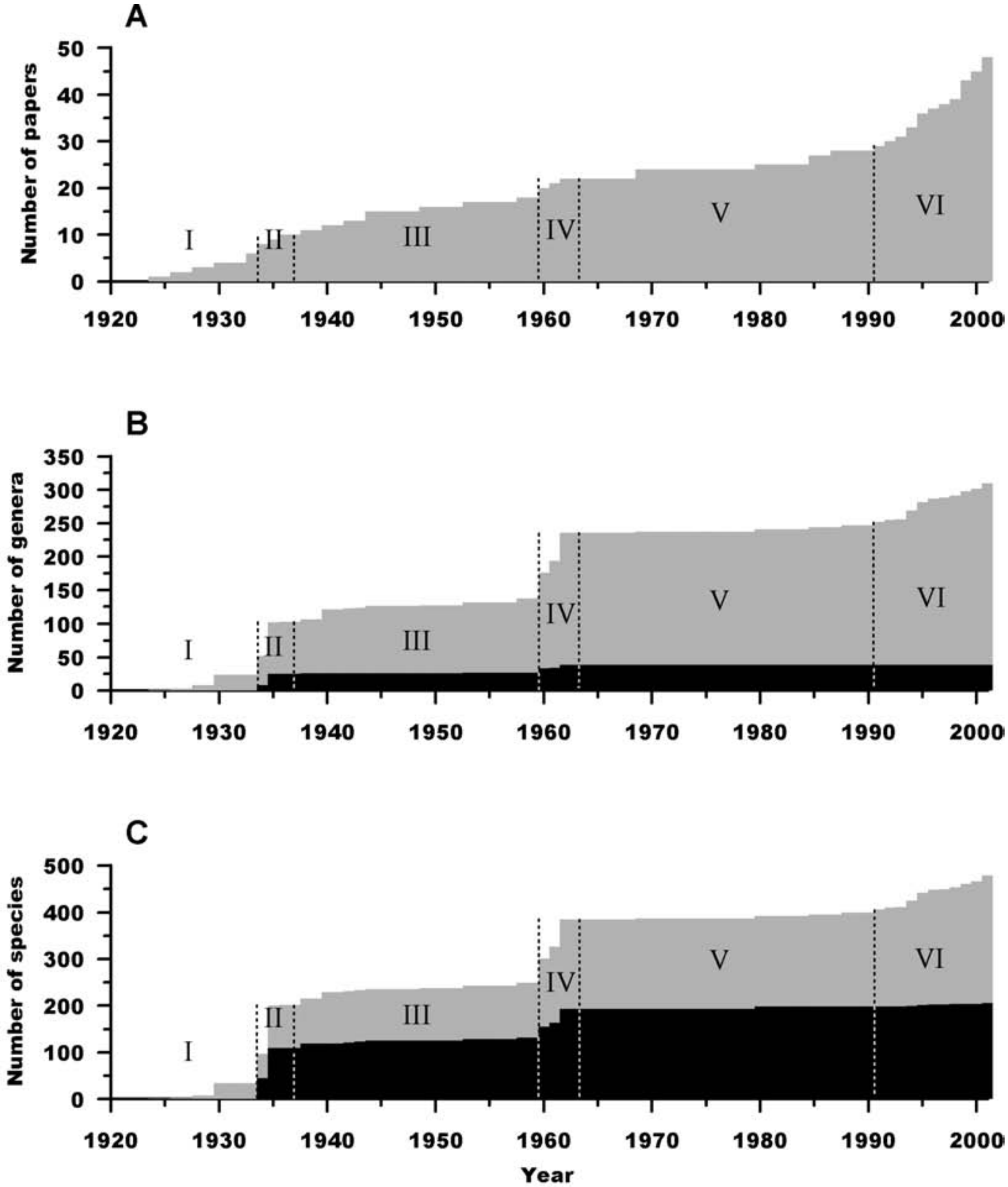

Fig. 3. A, Cumulative number of published articles on Korean trilobites since 1924. B, Cumulative number of total genera and new genera (in black) of trilobites from the Taebaeksan Basin. C, Cumulative total number of species and new species (in black) of trilobites from the Taebaeksan Basin. Six stages of research activities are designated as I, II, III, IV, V, and VI.

trilobites from the Taebaeksan Basin, and did not attempt any systematic treatment. In addition to Nakamura's (1924) and Yamanari's (1926) reports, Kobayashi (1928, 1930, 1933) and Shikama (1934) made some contributions on the Cambrian–Ordovician trilobites of Korea. Kobayashi (1928) briefly commented on the trilobites in the Taebaeksan Basin, and later (Kobayashi, 1930) listed 26 trilobite taxa from the Choson Supergroup and discussed their paleogeographic implications. The first biostratigraphic zonation for the Upper Cambrian of the Choson Supergroup was introduced by Kobayashi (1933, p. 69), and included the *Chuangia*?, *Chuangia*, *Kaolishania*, *Tsinania*, and *Eoorthis* Zones in ascending order (Fig. 4). Shikama (1934) provided line-drawings of several trilobite specimens from the Chigunsan Formation of the Makkol area.

The paleontological significance of these reports appears to be somewhat meager due to the lack of systematic treatments. However, trilobite collections made during this stage undoubtedly led to stage II.

Stage II (1934–1936)

During stage II, Kobayashi (1934a, 1934b, 1935, 1936) published four reports that included three monographs. A total of 168 species assigned to 81 genera were described from the Lower Paleozoic of the Taebaeksan Basin. These included a

Table 1. Number of reports dealing with Korean trilobites, showing total number of genera, new genera, species and new species published during each research stage.

Stage	Paper (paper/yr)	Total genera	New genera	Total species	New species
I (1924-1933)	6 (0.60)	24	0	34	0
II (1934-1936)	4 (1.33)	81	25	168	110
III (1937-1959)	8 (0.35)	34	2	47	22
IV (1960-1962)	4 (1.33)	99	12	136	61
V (1963-1991)	7 (0.24)	16	0	21	5
VI (1992-present)	19 (1.90)	58	0	73	8

number of new taxa (25 genera, 108 species, and two varieties; Table 1).

The first major volume of the monograph series on the Cambrian–Ordovician faunas of South Korea (Kobayashi, 1934a) dealt with invertebrate fossils from the Middle Ordovician Chigunsan and Tuwibong Formations. Trilobites described from the Chigunsan Formation included seven genera, fifteen species, and one variety, with three new genera, eleven new species, and one new variety. The Tuwibong Formation had two genera and two species, one of which was a new species.

The second monograph (Kobayashi, 1934b) described invertebrate faunas from the Lower Ordovician Tumugol and Makkol Formations. Of the 63 species described therein, trilobites comprised 45 species. Trilobites from the Tumugol Formation included twelve genera and 26 species, with two new genera and eighteen new species, and those from the Makkol Formation comprised nine genera and 20 species, of which three genera and fourteen species were newly erected. Based on these faunal assemblages, three biostratigraphic zones were proposed, with the *Asaphellus* and *Protopliomerops* Zones in the Tumugol Formation, and the *Clarkella* Zone in the lower Makkol Formation (Fig. 4). Kobayashi (1936) added the new species *Asaphopsis nakamurai* to the faunal list of the Tumugol Formation.

The third monograph (Kobayashi, 1935) is primarily concerned with the Cambrian faunas of South Korea, but also includes Cambrian trilobites from North Korea, Manchuria, Australia, and North America. The Cambrian faunas of South Korea described therein included 131 species, of which the Trilobita alone constituted 104 species. These trilobites were collected from the Taebaek and Yongwol Groups, with 42 genera and 83 species from the Taebaek Group and twelve genera and 21 species from the Yongwol Group. Of these, seventeen genera and 64 species were newly erected. It is of interest that none of the species occur in both the Taebaek and the Yongwol groups. Based on the faunas of the Taebaek Group, thirteen zones were established (*Salterella*, *Mapania*, *Elrathia*, *Megagraulos*, *Solenoparia*, *Olenoides*, *Stephanocare*, *Drepanura*, *Prochuangia*, *Chuangia*, *Kaolishania*, *Dictya*, and *Eoorthis* Zones, in ascending order) (Fig. 4).

Stage III (1937–1959)

Eight articles dealing with Korean trilobites were published during this stage. Of the 47 species assigned to 34 genera reported during this interval, two genera, 20 species, and two varieties were newly erected (Table 1). Although the number of trilobite species described in this interval was small by comparison with stages II and IV, such Late Cambrian index fossils as *Olenus* and *Glyptagnostus* were reported (Yosimura, 1940; Kobayashi, 1944b, 1949).

Ma (1938) realized that *Basilicus* of the Chigunsan Formation, a genus proposed by Kobayashi (1934a), is morphologically distinct, and erected the genus *Basilicoides* to include *Basilicus yokusensis* Kobayashi, 1934, and *B. deltacaudus* Kobayashi, 1934. However, the name *Basilicoides* was earlier proposed by Harrington (1937), and Harrington and Leanza (1942) subsequently proposed *Dolerobasilicus*, with *Basilicus yokusensis* as a type species, to replace *Basilicoides* Ma, 1938.

The Cambrian–Ordovician sedimentary rocks of the Yongwol area were first surveyed by Yosimura (1940). He also reported fourteen trilobite genera from the area (*Ptychoparia*, *Anomocarella*, *Megagraulos*, *Tonkinella*, *Kootenia*, *Manchuriella*, *Lopnorites*, *Glyptagnostus*, and *Olenus* from the Cambrian, and *Geragnostus*, *Apatokephalus*, *Asaphellus*, and *Shumardia* from the Ordovician Mungok Formation). The material was later systematically described and illustrated by Kobayashi (1944b, 1949, 1953, 1960a, 1962). During the early 1940s, several Cambrian trilobites from the Mungyong area were documented [*Amphoton dercerto spinula* and *A. microlops* by Kobayashi (1942), *Metadiscus bunkeiensis* and *M. bunkeiensis sulcata* by Kobayashi (1943), and *Hedinia regalis* by Kobayashi (1944a)].

In 1953, several Ordovician trilobite species were added to the faunal list of the Taebaek Group [i.e., *Pseudokainella iwayai*

Age		Formation	Kobayashi (1933)	Kobayashi (1934b, 1935)	Kobayashi (1960b)	Kobayashi (1966)	Kim et al. (1991)
Silurian							
Ordovician	'Ashgillian'						
	'Caradocian' Darriwilian 'Arenigian'	Tuwibong					
		Chigunsan					
		Makkol				*Clarkella*	
	Tremadocian	Tumugol		*Clarkella* *Protopliomerops* *Asaphellus*		*Protopliomerops* *Asaphellus*	*Kayseraspis* *Protopliomerops* *Asaphellus*
		Tongjom				*Pseudokainella*	
Cambrian	Late	Hwajol	*Eoorthis* *Tsinania* *Kaolishania* *Chunagia* *Chuangia?*	*Eoorthis* *Dictya* *Kaolishania* *Chuangia* *Prochuangia*		*Eoorthis* *Dictyites* *Kaolishania* *Chuangia* *Prochuangia*	
		Sesong		*Drepanura* *Stephanocare*		*Drepanura* *Stephanocare*	
	Middle	Taegi		*Olenoides* *Solenoparia* *Megagraulos*	*Solenoparia* *Megagraulos* *Bailiella*	*Olenoides* *Solenoparia* *Megagraulos*	
	Middle / Early	Myobong		*Elrathia* *Mapania* *Salterella*	*Elrathia* *Mapania* *Redlichia*	*Bailiella* *Mapania* *Elrathia* *Redlichia*	
	Early	Changsan/ Myonsan					

Fig. 4. History of biostratigraphic nomenclature of the Taebaek Group in the Taebaeksan Basin, Korea.

from the Tongjom Formation and *Kainella euryrachis* from the Tumugol Formation (Kobayashi, 1953)]. In the latter report, four trilobite species from the Yongwol Group were also described [*Hukasawaia cylindrica*, *Apatokephalus hyotan*, and *Pseudokainella* α sp. from the Mungok Formation, and *Pseudokainella*? β sp. from the Wagok Formation]. Trilobites from the Tanyang area were first described by Kobayashi (1958). These included *Chuangia taihakuensis*, *Dictyites longicauda*, *Hamashania* (?) sp., "*Iddingsia*" *orientalis*, *Kingstonia parallela*, *Plethometopus longispinus*, and *Shirakiella laticonvexa*.

Stage IV (1960–1962)

In this stage, four monographs were published (Kobayashi, 1960a, 1960b, 1961, 1962). A total of 136 species assigned to 99 genera were described, and twelve genera and 61 species were newly erected (Table 1).

The sixth monograph (Kobayashi, 1960a) primarily dealt with invertebrate fossils from the Mungok Formation of the Yongwol Group, but also included trilobites from the Wagok, Tongjom, and Tumugol Formations. Trilobites described from the Mungok Formation included fourteen genera, seventeen species, and one subspecies, with two new genera, six new species, and one new subspecies. Of these, five species were previously documented from the Tumugol Formation of the Taebaek Group (Kobayashi, 1934b). Two new species, *Aotiaspis oblonga* and *A. ovalis*, were recognized in the Tumugol Formation, and *Pseudokainella*? sp. was described from the Wagok Formation. Although a fair number of trilobite species were known from the Mungok Formation, the biostratigraphy of the formation was poorly resolved. The *Yosimuraspis* Zone in the lowest part was the only zone recognized in the formation (Fig. 5), whereas the formation above the *Yosimuraspis* Zone was collectively correlated with the *Asaphellus*, *Protopliomerops*, and *Clarkella* Zones of the Taebaek Group (Kobayashi, 1966).

Additional Cambrian trilobites from the Taebaek Group were reviewed in the seventh monograph (Kobayashi, 1960b), which supplemented the third monograph (Kobayashi, 1935). They included 22 genera and 27 species, of which four genera and fourteen species were newly erected. This monograph (Kobayashi, 1960b) provided a modified biostratigraphic zonation for the Cambrian of the Taebaek Group. The *Olenoides* Zone, earlier recognized in the uppermost Taegi Formation (Kobayashi, 1935), was excluded, while the lower part of the formation was referred to the *Bailiella* Zone (Fig. 4). In addition, the *Redlichia* Zone replaced the *Salterella* Zone as the lowest zone of the Taebaek Group.

Age		Formation	Kobayashi (1960a, 1961)	Kobayashi (1962)	Kobayashi (1966)	Lee (1995)	Kim & Choi (2000b)
Silurian							
Ordovician	'Ashgillian'						
Ordovician	'Caradocian' Darriwilian 'Arenigian'	Yonghung			*Basiliella*		
Ordovician	Tremadocian	Mungok	*Yosimuraspis*		*Yosimuraspis*		*Shumardia* *Kainella* *Yosimuraspis*
Cambrian	Late	Wagok			*Aphaeorthis*		
Cambrian	Late / Middle	Machari		*Hancrania* *Olenus-Glyptagnostu* *s* *Komaspis-Iwayaspis* *Eochungia* *Olenoids*	*Hancrania* *Olenus* *Iwayaspis* *Eochunagia* *Tonkinella*	*P. asaphoides* *A. orientalis* *E. hana* *E. longifrons* *H. brevilimbata* *P. tenue* *G. reticulatus* *G. stolidotus*	
Cambrian	Middle	Sambangsan	*Metagraulos* *Yabeia*		*Metagraulos* *Yabeia*	*Tonkinella*	
Cambrian	Middle / Early	Masong	*Kootenia* *Ptychoparia-Dawsonia* *Palaeolenus*		*Kootenia* *Ptychoparia-Dawsonia* *Palaeolenus*		
Cambrian	Early	Kurangri			*Redlichia*		

Fig. 5. History of biostratigraphic nomenclature of the Yongwol Group in the Taebaeksan Basin, Korea.

The eighth monograph (Kobayashi, 1961) described the Cambrian trilobites of the Mungyong Group and the Sambangsan Formation of the Yongwol Group. Seventeen species assigned to eleven genera were reported from the Mungyong Group. Of these, five species were earlier documented by Kobayashi (1942, 1943, 1944a), and one genus and four species were new. Based on these faunas, Lower to Middle Cambrian zones were proposed for the Mungyong Group (*Redlichia*, *Palaeolenus*, *Ptychoparia-Dawsonia*, and *Kootenia* Zones, in ascending order) (Kobayashi, 1961; Fig. 5). Trilobites from the Sambangsan Formation of the Yongwol Group comprise six genera and seven species, with four new species. The *Yabeia* and *Metagraulos* Zones were established within the formation (Fig. 5).

The Machari fauna of the Yongwol Group was comprehensively documented by Kobayashi (1962). The trilobites described therein include 39 genera, 53 species, and two subspecies, of which five genera, 29 species, and one subspecies were new. The trilobite succession of the Machari Formation, however, remained poorly understood, apparently due to the complicated, thrust faulted and folded structure of the Yongwol area. Nevertheless, Kobayashi (1962) recognized a number of biostratigraphic zones in the formation. They include the *Olenoides* (comprising the *Tonkinella* and *Eochuangia* faunas), *Komaspis-Iwayaspis*, and *Olenus-Glyptagnostus* Zones, in ascending order. The *Hancrania* shale was considered coeval with the *Olenus-Glyptagnostus* Zone (Fig. 5).

Stage V (1963–1991)

During the nearly three decades of this stage, trilobites appear to have been almost completely ignored by Korean paleontologists, and only seven short papers on the Cambrian–Ordovician trilobites of Korea were published (Table 1). It should be noted that one of the most important monographs (Kobayashi, 1966) has been excluded from this compilation, because it does not contain systematic descriptions of trilobites. It simply reviewed earlier studies on the Cambrian–Ordovician Choson Supergroup, and described the lithostratigraphy, biostratigraphy, faunal characteristics, and correlation.

Kim (1969) reported *Basilicus* from the Kosong Shale, the age of which was previously uncertain. Consequently, the Kosong Shale was equated with the Chigunsan Formation of the Taebaek Group. Shikama and Ozaki (1969) described *Basilicus yokusensis* from an articulated specimen, and discussed the paleoecologic significance of the Chigunsan fauna. Lee *et al.* (1980) named five new species from the Chigunsan Formation.

In 1985, *Megagraulos semicircularis* Kobayashi, 1961, and

Solenoparia (?) *bisulcata* Kobayashi, 1961, were described from the Sambangsan Formation (Kim *et al*., 1985), and *Redlichia nobilis* Walcott, 1905 was described from the Kurangri Formation (Lee and Lee, 1985). Choi and Lee (1988) reported five trilobite species from the *Asaphellus* Zone of the Tumugol Formation. Subsequently, Kim *et al*. (1991) recognized three zones within the Tumugol Formation (*Asaphellus*, *Protopliomerops*, and *Kayseraspis* Zones, in ascending order) (Fig. 4).

Stage VI (1992–present)

Over the last decade, nineteen articles on Korean trilobites have been published. Many of them focused on the taxonomic revision of Cambrian–Ordovician trilobites from the Yongwol Group. These reports increasingly dealt with the paleobiology of Korean trilobite faunas, and discussed ontogeny, evolution, and paleogeography. The cumulative number of genera and species described in the stage is 58 and 73 (including eight new species), respectively (Table 1).

Lee and Choi (1992) did an extensive taxonomic revision of the Chigunsan trilobite fauna, and synonymized a number of species erected by Kobayashi (1934a). They reduced the number of trilobite species recognized from the Chigunsan Formation to four rather than eighteen (i.e., *Basiliella kawasakii*, *B. typicalis*, *Dolerobasilicus yokusensis*, and *Ptychopyge dongjeomensis*). In particular, the generic concept of *Dolerobasilicus* was emended and clarified. Concurrently, the protaspids and meraspids of *Dolerobasilicus yokusensis* were examined mainly on the basis of internal molds (Choi and Lee, 1993). The results were later utilized to discuss the subfamilial classification of the Asaphidae (D. C. Lee and Choi, 1999).

With relocation of the fossil localities of the Machari Formation in 1990, the material from the formation formed the basis for the first doctoral project dealing exclusively with Korean trilobites (Lee, 1995). Lee (1995) described 72 Late Cambrian trilobite species belonging to 40 genera. Based on the faunas, he proposed eight Upper Cambrian trilobite zones. They are the *Glyptagnotus stolidotus*, *G. reticulatus*, *Proceratopyge tenue*, *Hancrania brevilimbata*, *Eugonocare longifrons*, *Eochuangia hana*, *Agnostotes orientalis*, and *Pseudoyuepingia asaphoides* Zones, in ascending order (Fig. 5). This biostratigraphic zonation differs greatly from that suggested earlier by Kobayashi (1962; see Fig. 6). Some of the results were subsequently published (Lee and Choi, 1994, 1995, 1996, 1997; Choi and Lee, 1995). The Machari Formation also yielded fairly well-preserved juvenile specimens of *Olenus asiaticus* and *Hancrania brevilimbata*. Their ontogenies were analyzed by J. G. Lee and Choi (1999) and Hwang *et al*. (2000), respectively. More recently, Lee *et al*. (2001) discussed the evolutionary significance of an aberrant pygidium of *Eugonocare bispinatum* from the Machari Formation. Hong *et al*. (2003) suggested an evolutionary lineage of *Irvingella* based on the morphological changes of five *Irvingella* species that occur successively in the Machari Formation.

At the same time, the search for trilobites in the Ordovician Mungok Formation led to the location of more than 40 fossil localities in the Yongwol area. Park *et al*. (1994) established a preliminary stratigraphic scheme for the Mungok Formation, while Choi *et al*. (1994) described a late Tremadocian trilobite fauna from the Mungok Formation with seven genera and seven species. These studies triggered the publication of a series of papers on the trilobites and stratigraphy of the Mungok Formation (Kim and Choi, 1995, 1999, 2000a, 2000b), which formed the second doctoral dissertation on Korean trilobites (Kim, 1999). Kim and Choi (2000b) compiled all of the information, and proposed formally four members [from bottom to top, the Karam, Paeiljae, Chommal, and Tumok Members] and three zones [*Yosimuraspis*, *Kainella*, and *Shumardia* Zones, in ascending order] in the Mungok Formation (Fig. 5).

In addition to these trilobite faunas from the Machari and Mungok Formations, a few trilobite faunas have recently been recovered from the Yongwol Group. An Early Ordovician fauna composed of *Asaphellus*, *Kayseraspis*, and *Asaphopsoides* is the first record of invertebrate fossils from the southwestern Taebaeksan Basin (Choi, 1998b). Choi *et al*. (1999) described two Middle Cambrian trilobite species from the Sambangsan Formation, and supplemented the previous works by Kobayashi (1961) and Kim *et al*. (1985). Sohn and Choi (2002) also described the first uppermost Cambrian trilobite fauna in the Yongwol Group. The fauna includes *Micragnostus*, *Pseudorhaptagnostus*, *Fatocephalus*, *Koldinioidia*, *Hysterolenus*, and, questionably, *Amzasskiella*.

All of the faunal data collected during stage VI have been useful in clarifying the lithostratigraphic and biostratigraphic framework of the Yongwol Group. They further provided an important source for recent compilations of the geologic and tectonic evolution of the Korean peninsula (Choi, 1998a; Chough *et al*., 2000; Choi *et al*., 2001).

PROSPECTUS

Systematics and taxonomy

Kobayashi (1966) summarized the stratigraphy and paleontology of the Cambrian–Ordovician Choson Supergroup of South Korea. He reported 279 trilobite species, with 180 from the Taebaek Group, 89 from the Yongwol Group, and sixteen from the Mungyong Group. Of these, 201 species are Cambrian, and 78 are Ordovician (Table 2).

Currently, the revision of the trilobite Treatise is in progress; it will contain new information on trilobite classification accumulated over the past four decades since publication of Part O of the Treatise on Invertebrate Paleontology (Moore, 1959). The first volume of the revised treatise is available and covers the Agnostida and Redlichiida (Whittington *et al*., 1997). Thus, it

Table 2. Number of Cambrian and Ordovician trilobite species documented from five groups of the Choson Supergroup in Korea (from Kobayashi, 1966).

	Age		
Group	Cambrian	Ordovician	Total
Taebaek	115	65	180
Yongwol	71	18	89
Mungyong	16	0	16
Yongtan	0	0	0
Pyongchang	0	0	0
Total	201*	78†	279

* One species occurs in both Yongwol and Mungyong Groups.

† Five species occur in both Taebaek and Yongwol Groups.

seems timely and appropriate to reassess the Korean material in accordance with the revised classification of the Trilobita.

During stage VI, some Cambrian–Ordovician trilobites were examined and emended, although most of these studies were confined to the Yongwol Group. An intensive investigation of the Taebaek Group trilobites is badly needed in order to elucidate the faunal characteristics of the Taebaeksan Basin. At this point, it cannot be overemphasized that we must find good stratigraphic sections with trilobites, and, more importantly, search for all disarticulated parts of trilobites before attempting a taxonomic revision. In doing so, we may be able to reconstruct correct phylogenies, apply the results to a refined biostratigraphic zonation, and discuss the paleogeographic and paleoecologic significance of Korean trilobite faunas.

Biostratigraphy and correlation

The dissimilar faunas of the Taebaek and Yongwol /Mungyong Groups led to two separate biostratigraphic schemes for the Cambrian–Ordovician of the Taebaeksan Basin (Kobayashi, 1966). Over 20 zones or fossiliferous horizons were recognized in the Taebaek Group, whereas thirteen zones were established in the Yongwol/Mungyong Groups (Fig. 6). Until quite recently, these biostratigraphic schemes have been widely employed in Korea without serious criticism (Lee, 1987). During stage VI, Yongwol Group trilobites have been extensively examined (Lee and Choi, 1994, 1995, 1996; Kim and Choi, 1995, 1999, 2000a). Consequently, the revised Upper Cambrian and Lower Ordovician biostratigraphy (Lee, 1995; Kim and Choi, 2000b; Fig. 6) is now better correlated with biostratigraphic schemes established elsewhere (e.g., Geyer and Shergold, 2000).

However, when the Cambrian zonation of the Taebaek Group (Fig. 6) is compared with that of other areas, some discrepancies are easily appreciated. The lowermost zone recognized in South Korea is the *Redlichia* Zone of the Taebaek and Mungyong Groups. The *Redlichia* Zone can be correlated with the *Redlichia* Zone of the Manto Formation in North China (Chang, 1988), which is uppermost Lower Cambrian. The *Palaeolenus* Zone of the Mungyong Group, from which *Redlichia cylindrica* has been recovered, was also considered to belong to the Mantoan Series (Lower Cambrian) of North China. However, it is noteworthy that the *Palaeolenus* Zone underlies the *Redlichia* Zone in North China (Chang, 1988). In Korea, Middle Cambrian trilobites are not abundant, except in the *Solenoparia* Zone of the Taebaek Group and in the *Tonkinella* Zone of the Yongwol Group. Recently, the occurrence of *Mapania* in the Myobong Formation has been discredited by Chang (1988), based on the fact that *Mapania* is characteristic of the *Amphoton* Zone (upper Middle Cambrian) in North China. In addition, the stratigraphic position of the *Yabeia* Zone of the Sambangsan Formation is also incompatible with that of North China. In North China, the *Yabeia* Zone is uppermost Middle Cambrian. As for the Upper Cambrian of the Taebaek Group, Shergold (1980) suggested that the *Chuangia* Zone might underlie the *Prochuangia* Zone, by reference to the faunal succession in Australia. Thus, a number of problems involving Cambrian biostratigraphy must be resolved in the future.

The Cambrian–Ordovician boundary in South Korea had been traditionally placed between the Hwajol and the Tongjom Formations in the Taebaek Group and between the Wagok and the Mungok Formations in the Yongwol Group (Kobayashi, 1966; Lee, 1987). Recently the global stratotype section and point for the base of the Ordovician System has been approved at the lowest occurrence of the conodont *Iapetognathus fluctivagus* at Green Point, western Newfoundland (Cooper *et al*., 2001). Unfortunately, the conodont assemblages across the Cambrian–Ordovician boundary interval in the Taebaeksan Basin appear inadequate to draw any meaningful conclusions, although Lee and Lee (1988) claimed that the Cambrian–Ordovician boundary lies in the uppermost Hwajol Formation. Cooper *et al.* (2001) also noted that the Cambrian–Ordovician boundary closely coincides with the lowest appearance of the trilobite *Jujuyaspis borealis* at the base of the *Symphysurina bulbosa* Subzone in North America. In Korea, *Jujuyaspis sinensis* occurs in the *Yosimuraspis* Zone at the base of the Mungok Formation. This occurrence suggests that the Cambrian-Ordovician boundary in the Yongwol Group lies at the base of the Mungok Formation (Kim and Choi, 2000a). On the other hand, information on the trilobite succession across the Cambrian–Ordovician boundary interval of the Taebaek Group is incomplete at the moment. *Pseudokainella iwayai*, the sole trilobite known from the Tongjom Formation, certainly suggests a Tremadocian age, whereas the *Eoorthis* Zone of the Hwajol Formation is likely largely Cambrian (Kobayashi, 1966). However, the occurrence of "*Pseudokainella*" *maladiformis* (Kobayashi, 1935) in the *Eoorthis* Zone casts doubt on placing the Cambrian–Ordovician boundary at the base of the Tongjom Formation. Much has to be worked out in the determination of the precise location of the Cambrian–Ordovician boundary in the Taebaek Group.

Paleogeography and paleobiogeography

Kobayashi (1967) recognized three Cambrian faunal provinces in eastern Asia. The Hwangho (or North China) fauna contains many indigenous taxa and represents a shallow marine environment. The Chuantien fauna is dominated by redlichiid trilobites of Early to Middle Cambrian age, with later forms in this region poorly represented. The Jiangnan (or South China) fauna is characterized by abundant cosmopolitan and pelagic forms that indicate a deeper-water oceanic setting. The Cambrian trilobite assemblages of the Taebaek Group belong to the Hwangho faunal province, whereas those of the Yongwol group are referable to the Jiangnan faunal province (Kobayashi, 1967). On the other hand, Kobayashi (1969) showed that the Ordovician cephalopod faunas of Korea and North China are distinct from those of South China. Whittington and Hughes (1974) also demonstrated that the Tremadocian trilobites of the Taebaeksan Basin are closely affiliated with those of North China and Australia, but have little in common with those of South China. These faunal contrasts between North and South China have apparently led some authors to conclude that the Sino–Korean (or North China) and Yangtze (or South China) blocks were separated during much of the Paleozoic (Burrett 1973; Burrett and Stait 1986; Metcalfe 1988; Burrett *et al.* 1990; Scotese and McKerrow 1991; Laurie and Burrett 1992). Although these paleogeographic models helped in an understanding of the relationships among the Paleozoic continental blocks that eventually formed the present Asian continent, detailed continental reconstructions involving the Korean peninsula were always unclear due to the lack of reliable paleogeographic information on Korea. The Korean peninsula

Age		Taebaek Formation	Taebaek Zone **(1)**	Yongwol/Mungyong Formation	Yongwol/Mungyong Zone **(2)**	Yongwol/Mungyong Zone **(3)**
Silurian						
Ordovician	'Ashgillian'					
	'Caradocian'	Tuwibong	Actinoceroids	Yonghung	Actinoceroids *Basiliella*	
	Darriwilian	Chigunsan	Orthoceroids			
	'Arenigian'	Makkol	*Sigmorthoceras Polydesmia Manchuroceras Clarkella*			
		Tumugol	*Kayseraspis*			*Kayseraspis*
	Tremadocian		*Protopliomerops Asaphellus*	Mungok		*Shumardia Kainella*
		Tongjom	*Pseudokainella*		*Yosimuraspis*	*Yosimuraspis*
Cambrian	Late	Hwajol	*Eoorthis*	Wagok	*Apheoorthis*	*Fatocephalus*
			Dictyites Kaolishania Chuangia Prochuangia	Machari	*Hancrania Olenus*	*P. asaphoides A. orientalis E. hana E. longifrons H. brevilimbata P. tenue G. reticulatus G. stolidotus*
		Sesong	*Drepanura Staphanocare*		*Iwayaspis*	
	Middle	Taegi	*Olenoides Solenoparia Megagraulos*		*Eochuangia Tonkinella*	*Lejopyge armata Tonkinella*
				Sambangsan	*Metagraulos Yabeia*	*Megagraulos Metagraulos*
		Myobong	*Bailiella Mapania Elrathia*	Masong	*Kootenia Ptychoparia-Dawsonia Palaeolenus*	
	Early		*Redlichia*	Kurangri	*Redlichia*	
		Changsan/ Myonsan				

Fig. 6. Summary of stratigraphic nomenclature of the Taebaek and Yongwol/Mungyong Groups in the Taebaeksan Basin, Korea. Biostratigraphic information in columns **(1)**, **(2)**, and **(3)** from **(1)** Kobayashi (1966), Kim et al. (1991); **(2)** Kobayashi (1960a, 1961, 1962); and **(3)** Lee (1995), Choi (1998b), Choi et al. (1999), Hong et al. (2000), Kim and Choi (2000b), and Sohn and Choi (2002).

was either included in the Sino–Korean block (Burrett and Stait 1986; Laurie and Burrett 1992) or was divided into two parts, with North and South Korea referred to the Sino–Korean and Yangtze blocks, respectively (Burrett 1973; Watson *et al.* 1987).

Over the last decade, paleogeographic studies have made little progress in Korea. On the other hand, recent geotectonic studies have shown that the Korean peninsula records important geological events during the amalgamation of the Sino–Korean and Yangtze blocks (Cluzel *et al.* 1990, 1991). In the Early Paleozoic, part of the Korean peninsula (Kyonggi Massif) belonged to the Yangtze block, while the rest of the peninsula, including the Yongnam Massif, occupied the marginal part of the Sino–Korean block (Fig. 1A). This implies that eastward extension of the boundary or suture zone between the Sino–Korean and Yangtze blocks in China (i.e., the Qinling–Dabie–Sulu Belt) should be located to the north of the Kyonggi Massif. Cluzel (1991) suggested the Imjingang Belt (I in Fig. 1A) as a candidate for the boundary, and this has been supported by subsequent studies (Yin and Nie 1993; Ree *et al.* 1996). Cluzel *et al.* (1991) and Yin and Nie (1993) went further, and drew the boundary between the Sino–Korean and the Yangtze blocks within the Taebaeksan Basin, which divides the Taebaeksan Basin into two tectonically different terranes. Thus, the Taebaek Group was considered to represent a carbonate platform facies of the Sino–Korean block, whereas the Yongwol Group was a marginal facies of the Yangtze block.

However, the Ordovician trilobites of the Taebaeksan Basin (Kobayashi, 1969; Whittington and Hughes, 1974; Choi *et al*., 2001) argue against any major tectonic divisions within the basin. In particular, Choi *et al.* (2001) presented a modified paleogeographic model for the Korean peninsula. By this model, the Korean peninsula in the Early Paleozoic was divided into three major parts.These include the Nangrim, Yongnam, and Kyonggi Massifs. The Nangrim and Yongnam Massifs were considered to be part of the Sino–Korean block, and the Kyonggi Massif was connected to the Yangtze block (Fig. 1A). Cambrian–Ordovician shallow marine sediments accumulated on the margin of the Nangrim and Yongnam Massifs, which were contiguous with the North China craton (Chough *et al*., 2000). Although very little is known about the precise location and orientation of the Yongnam Massif, Choi *et al.* (2001) believed that it was situated adjacent to the Nangrim Massif. The Kyonggi Massif, including the Okchon Belt, was assumed to occupy the northeastern tip of the Yangtze block, following the suggestions of Cluzel *et al*. (1991) and Yin and Nie (1993). These massifs should have amalgamated to form much of the present Korean peninsula during the Late Permian to Early Triassic when the Sino–Korean and Yangtze blocks collided (Ree *et al.,* 1996; Meng and Zhang, 1999).

We are still far from completion of a satisfactory synthesis of the Early Paleozoic continental reconstruction of the Korean peninsula. It is to be expected that a more satisfactory paleogeographic configuration will develop with integration of more refined paleontological data with additional information provided by geotectonics, sedimentology, paleoclimate, and paleomagnetism.

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HISTORY AND DEVELOPMENT OF TRILOBITE RESEARCH IN BRAZIL

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ABSTRACT—Trilobite research in Brazil from 1870 to 2001 can be divided into three main phases of activity. The survey years (1875–1953) were marked by scientific expeditions, particularly to the Amazon Basin, that were mainly headed by American researchers. The Thayer and Morgan expeditions are hallmarks of this period. The large collections obtained during this phase are still an important repository of the trilobites of Brazil, and were the main resources for the first monographs of Brazilian trilobites. This was the period of John Mason Clarke, Karl Friedrich Katzer, and Wilhelm Kegel's contributions. Only a few papers and small notes characterize the 1950–1980 phase. In the mid-1980s, however, Maria da Gloria Pires Carvalho, a micropaleontologist by training, changed her research agenda. She initiated the most important work on Brazilian trilobites, and provided the most consistent taxonomic framework available for this group. At the same time, another woman, Marlene Terezinha Barcellos-Popp, also made an important contribution by her detailed revisions of Clarke's material. An important gap in trilobite research in Brazil occurred after 1991, and only a few reports were published. However, a new group of paleontologists began applying a more modern methodological and conceptual approach in 2000 that included taphonomic, paleoecologic, and sequence stratigraphic techniques to Brazilian trilobites.

THE PIONEER PHASE

Contributions of the North American expeditions

The initial development of Brazilian paleontological knowledge was greatly influenced by North American naturalists and geologists, particularly during the survey years (1865–1871). This was the phase of the Thayer and Morgan expeditions. The latter expedition is particularly noteworthy for trilobite research in Brazil. The first trilobite specimens collected in Brazil were recovered in 1870 and 1871 by the "Morgan Expeditions." In the last decades of the nineteenth century, Charles Frederick Hartt (Fig. 1), a young geology professor from Cornell University, gained the support of Edwin B. Morgan, and organized and lead the first Morgan Expedition to Brazil. In 1870, Orville Adalbert Derby, Herbet H. Smith, and Theo B. Comstock joined Hartt on that expedition. They investigated the geology and paleontology of north and northeast Brazil (Bahia, Pernambuco, and Amazon states) in the Jatobá, Tucano, Sergipe, Amazon, and Recife-João Pessoa Basins. In 1871, Hartt and Derby led the second Morgan Expedition, which mainly focused on the geology and paleontology of the intracratonic Amazon Basin. In both expeditions a number of invertebrate macrofossils were amassed, and reposited in the museum at Cornell University in Ithaca, New York.

With R. Rathbun, Hartt described the first trilobites from Brazil (Hartt and Rathbun, 1875). These included two new species, a calmoniid (*Dalmania paituna*) and a homalonotid (*Homalonotus oiara*), from Devonian sandstones that crop out along the Ererê River (Mendes, 1981; Carvalho, 1985a, Petri, 2001).

Contribution of the Geological Commission of the Empire

By recommendation of Hartt, the Brazilian Emperor D. Pedro II established the Geological Commission of the Empire on May 10, 1875. The directorship of this commission was delegated to Hartt, and during 1875–1877, there were improvements in Brazilian paleontological research. During this time, such researchers as O. Derby, J. C. Branner, R. Rathbun, H. H. Smith, L. Wagoner, and M. Ferrez undertook an energetic collecting of fossils and rocks in different localities in Pernambuco, Sergipe, Bahia, Paraná, Pará, and Amazon states. As a result of their efforts, large paleontological collections were brought together that included Silurian and Devonian trilobites collected by Derby from the Amazon Basin and by Wagoner from the Paraná Basin.

1878 was a difficult year for Brazilian paleontology. On the pretext of cutbacks, the Emperor abolished the Geological Commission on January 1. Then, nearly three months after the closure of the commission, Hartt (1840–1878) died in the capital Rio de Janeiro during a yellow fever outbreak (Mendes and Petri, 1971; Mendes, 1981). During this time, all members of the Geological Commission returned to the United States, except Derby. The material collected by the Commission was sent to a newly built museum, the National Museum of Rio de Janeiro. In 1879, Orville Adalbert Derby (Fig. 2) was appointed director of its Geological and Mineralogical Section. This proved to be an important event. At that time, Ladislau Netto, the director of museum, encouraged Derby to dispatch the material amassed by the Geological Commission to other countries. Derby wanted the Geological Commission collections to be studied as thoroughly as possible. Such researchers as E. D. Cope, C. White, J.

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Fig. 1. Charles Frederick Hartt (1840–1878). The first author to describe Brazilian trilobites. He was the chief of the Geological Commission of Empire and leader of the Morgan Expedition to the Amazon (1870–1871).

Fig. 2. Orville Adalbert Derby (1851–1915). A geologist from the United States who was director of the Geological and Mineralogical Section of the National Museum of Rio de Janiero (1879–1915).

M. Clarke, and R. Rathbun, received the fossil material of the Geological Commission. The results of Derby's efforts were realized several years later with the publication of monographs, such as those of Clarke (1890, 1913) and Katzer (1903), that were the pioneer studies of Brazilian trilobites. In 1907, Rodrigues Alves, President of Brazil, founded the Geological and Mineralogical Survey of Brazil (GMSB). This was significant for Brazilian paleontology because most of the paleontological collections were entrusted to foreign paleontologists to study, and because Derby, its first director, expected high quality paleontological studies at the GMSB. This institution maintained Derby's principles even after his suicide in 1915 (Mendes, 1981).

THE CONTRIBUTIONS OF FOREIGN AND BRAZILIAN PALEONTOLOGISTS

J. M. Clarke´s (1890–1913) view of the Brazilian trilobites

In 1890, John Mason Clarke (Fig. 3) published the first monograph of the Paleozoic marine invertebrates from Brazil. Clarke began his career as a paleontologist in Albany, New York, under James Hall. Clarke succeeded Hall in 1898 as New York State Geologist and Director of the New York State Museum (NYSM). His travel to Brazil allowed him to collect material that still remains in repository in the NYSM from outcrops along the Ererê and Maecuru Rivers in the Amazon Basin. According to Clarke (1890), the rich and diverse fauna of the Maecuru sandstone (now Maecuru Formation) included fifteen species of three trilobite genera (*Homalonotus*, *Phacops*, *Dalmanites*). The Ererê trilobite fauna (Ererê Formation) is, however, of low diversity, and dominated by *Dalmanites* (*Cryphaeus*) *paituna* and *Homalonotus oiara* as Hartt and Rathbun (1875) earlier reported. To Clarke, these latter two species were comparable with those of the Hamilton Group, and were probably a derivative of the New York fauna.

Clarke (1890) suggested an Early Devonian age for both Amazon Basin faunas, and recognized that the Maecuru fauna is probably younger than that from the Ererê sandstone. This was confirmed later by stratigraphic and paleontologic studies in the twentieth century. It is noteworthy that in the appendix of Clarke´s 1890 monograph, there is a clear indication of his scientific relationship with Derby: "Since preparing the foregoing descriptions of Maecuru and Ererê trilobites, I have received from Prof. Derby, accompanied by a request that a description should be prepared, specimens of a trilobite obtained at Jaguarahyva, Paraná, near the southern boundary of S. Paulo" (Clarke 1890, p. 55). The new species *Dalmanites gonzaganus* was erected on the basis of this specimen. The description of the Jaguariaíva material, as well as of the other Devonian localities from the Paraná Basin, the Falklands, and Argentina, appeared much later in his classical monograph, which was Monograph 1 of the Geological and Mineralogical Survey of Brazil and published in 1913.

Clarke (1913a) presented a detailed study of the trilobite faunas from the Paraná Basin in southern Brazil, and described 13 new species assigned to six genera (*Cryphaeus*, *Calmonia*, *Dalmanites*, *Homalonotus*, *Pennaia*, *Proboloides*). Clarke noted the austral nature of this fauna, and concluded that the Amazon and Paraná Basins were not connected during the Paleozoic. A Late Devonian age was attributed to the Paraná Basin fauna. This exhaustive study is probably the most important one published on the Devonian fauna from Brazil.

Curiously, in the same year as Clarke's (1913a, b) two monographs on trilobites from the southern hemisphere, Kozlowski (1913) described three new species (*Acaste lombardi*, *Cryphaeus* sp., *Homalonotus* sp.) from the invertebrate fauna collected at Jaguariaíva, Paraná. Of these, Clarke (1913a) had not recorded *Acaste*. Kozlowski's report appeared in November 1913, while

Fig. 3. John Mason Clarke (1857–1925). A paleontologist and long-term New Yorkl State Geologist and Director of the New York State Museum. He studied Devonian and Carboniferous trilobites from the Amazon and Paraná Basins in Brazil. He wrote important monographs about the Brazilian fossils (Clarke, 1890, 1913).

Fig. 4. Wilhelm Kegel. Geologist with the National Department of Mineral Production. He studied Devonian and Carboniferous trilobites of the Parnaíba Basin.

Clarke's monograph was published at least nine months earlier (Petri, 1948). In 1923, Kozlowski described the Devonian fauna of Bolivia, noted its similarity with the Brazilian fauna, and adopted Clarke's classification and recognized its nomenclatural priority.

Katzer's years at the "Museu Paraense Emílio Goeldi"

At the end of 19th century, two new Brazilian museums were established—the Museu Paulista in São Paulo, São Paulo State, and the Museu Paraense in Belém, Pará State. These institutions participated actively in paleontological research in Brazil, an activity that continued until the beginning of the 20th century. In 1866, Domingos Soares Ferreira Penna founded the Museu Paraense (now Museu Paraense Emílio Goeldi), and thirty years later Lauro Sodré, the governor of Pará State, opened the geology section of this museum. This section was under the supervision of the German geologist Karl Friedrich Katzer, who initiated the study of geology and paleontology of the lower Amazon Basin in 1896.

In 1898, Katzer published a report on the Devonian Maecuru fauna, which was reviewed earlier by Clarke (1890), and tried to establish its global correlation. Katzer (1898) recognized all 13 species previously described by Clarke (1890), and added the new species *Phacops* sp. and *Phacops goeldii*.

Katzer (1903) then published an exhaustive study of the geology of the lower Amazon Basin, including the first geological map of the area. He had traveled along the Amazon River from the Obidos gorge to the river's mouth at the Atlantic Ocean. Based on the geological data he gathered, Katzer proposed a stratigraphical succession from the Archean to Cenozoic. Trilobites were recognized only in the Devonian and Carboniferous. He noted that the Maecuru River section is the best reference for the Devonian in the Amazon. At that time, Katzer knew only of the Lower Devonian Maecuru Formation, and suggesting the following stratigraphic succession:

Carboniferous (top)
Discordance
Level 1. Black Shales
Level 2. Deeply weathered sandstone (fossils in the top)
Level 3. Sandstone
Level 4. Hornstein (chert)
Level 5. Bioclastic sandstone (very rich in spiriferids)
Level 6. Mudstones with intercalated sandstones
Silurian (base)

Invertebrate fossils were noted in levels 2 and 5, which included the trilobites described by Hartt and Rathbun (1875) and Clarke (1890). Katzer (1903) also noted that the sections along the Tapajós River, particularly between the Apuhy falls and the village of Itaituba, constitute one of the most important areas of exposured Carboniferous in the Amazon. In the list of invertebrate fossils found in this section, he mentioned the presence of the trilobites *Phillipsia* cf. *P. major* and *Griffithides tapajotensis*.

W. Kegel's contribution

Wilhelm Kegel (Fig. 4) was employed by the National Department of Mineral Production (NDMP) in 1933 with other Brazilian, American, German, and European geoscientists. In its early years, the NDMP was responsible for the pioneer studies of the mineral resources and soils of Brazil. Kegel devoted most of his time at the NDMP to the geology and paleontology of northeastern Brazil, including the Amazon Basin. In 1951, he published a detailed study of the Carboniferous trilobite fauna from the Piauí Formation in the Parnaíba Basin and the Itaituba Formation in the Amazon Basin. This was based on material collected by the geologists of the NDMP geologists during 1946–1951. Kegel (1951) proposed the new species *Phillipsia*

(*Ameura*) *plummeri* and *P.* (*Ameura*) *duartei*. According to the available data, the *P.* (*A.*) *duartei* has a wide paleobiogeographic distribution, and occurs in the Amazon and Parnaíba Basins. However, *P.* (*A.*) *plummeri* is restricted to the Piauí Formation in the Paraníba Basin. It should be noted that the specimen earlier described by Duarte (1938) as *Anisopyge antiqua* was assigned by Kegel (1951) to *P.* (*A.*) *duartei*. A new brief description, based on the same material studied by Kegel (1951), appeared in a short report by Carvalho and Fonseca (1988). Additionally, Anelli (1999) attributed *P.* (*A.*) *plummeri* to *Palladin plummeri* in his Ph.D. dissertation. As emphasized by Kegel, the material from the Carboniferous of the Amazon Basin (i.e., the Itaituba Formation) is quite fragmentary. D. Brezinski (personal communication, 2001) reports that the cranidium of the Itaituba specimens "shows a general widening between the palpebral lobes. This is characteristic of the genus *Ameura*, not *Palladin*. The middle Pennsylvanian age is also consistent with *Ameura*." Thus, even half a century after the publication of Kegel's pioneer study, his paleontological ideas seem to be correct.

Fig. 5. Maria de Glória Pires Carvalo, Research Associate of the American Museum of Natural History. She initiated modern researchon trilobites from the Parnaíba and Paraná Basins of Brazil.

Another important trilobite paper was published by Kegel (1953) five years after the initial identification of Devonian strata in the Parnaíba Basin by Caster (1948). The data for that paper were gathered during successive collecting trips carried out in northeastern Brazil during 1949–1952. Kegel (1953) provided both a detailed study of the Devonian invertebrate fauna and a critical review of Lower Paleozoic stratigraphy of the Parnaíba Basin. Two trilobite species were record. *Asteropyge* sp. was found in rocks of the three Devonian formations (Pimenteiras, Cabeças, and Longá Formations). However, *Homalonotus* sp. was identified only from the Pimenteiras Formation. Kegel (1953) assigned a Frasnian Age to these formations on the basis of the presence of *Asteropyge* sp.

Fifteen years after the publication of Kegel's paper, Judith de Souza Castro (1968) revised material from the same area previously studied by Kegel. She thought that the material came exclusively from the Pimenteiras Formation. Castro (1968) referred *Homalonotus* sp. to *Burmeisteria notica*, and *Asteropyge* sp. to *Metacryphaeus* cf. *australis*. She was particularly impressed with the similarities between the Parnaíba trilobites and those from the Devonian Paraná Basin in southeastern Brazil that were described by Clarke (1913). However, as noted by Carvalho (1999), the material described by Castro is actually referable to the Cabeças Formation (Lower Devonian). Thus, *Metacryphaeus* cf. *australis* of Castro (1968) is *M. melloi*, a species described by Carvalho *et al.* (1997).

Carvalho's contribution

After 1953, researchers were trained in the universities rather than in museums or scientific institutions or commissions, as earlier. In this context, the name of another woman must be highlighted: Maria da Gloria Pires de Carvalho (Fig. 5).

Carvalho is probably the most important native Brazilian paleontologist to devote a career to Brazilian trilobites. Carvalho began her career in the late 1970s at the Universidade Federal do Rio de Janeiro, where she remained from 1977 to 1985. She taught paleontology, and did most of her research on foraminiferans. At that time, infrastructure and financial difficulties in the university impelled Carvalho to redirect her research. Thus, in 1985 Carvalho published her first paper on Brazilian trilobites, a historical review of trilobite research in Brazil (Carvalho, 1985a). The scope of Carvalho's work mainly covers the taxonomy of trilobites from the Paraná and Parnaíba Basins, and uses a more modern approach (including cladistic analysis). Her work includes other Paleozoic successions in South America and Africa.

Carvalho devoted her career to the study of the Devonian trilobites from the Paraná Basin, especially those from the northwest flank in Mato Grosso do Sul and Goiás States and from the Parnaíba Basin in northeast Brazil. It is noteworthy that the material from Mato Grosso do Sul and Goiás States was not included in the classical monographs by Clarke (1913a, b). Only Ammon (1893),and Oliveira (1937) had previously described trilobites from Mato Grosso, Mato Grosso do Sul, and Goiás states (i.e., *Harpes* sp., *Phacops braziliensis* and *Calmonia* sp.)

Carvalho's career can be divided into two main phases. The first, encompassing the 1980s, was marked by the publication of papers with Brazilian collaborators. The second, starting in 1991, reveals a more international scientific position. In this phase, Carvalho published a series of papers with experts from Venezuela, the United States, and Australia, including J. Moody (University del Zulia, Venezuela), B. Lieberman (University of Kansas), and G. D. Edgecombe (Australian Museum). These were published by the American Museum of Natural History (AMNH), and appeared in the American Museum Novitates (Carvalho and Edgecombe, 1991; Carvalho *et al.*, 1997). This partnership is, in part, a reflection of her admission at the AMNH, as a research associate. In the early 1990s, for personal reasons, Carvalho moved to the United States after her retirement. This gave her the opportunity to study and revise trilobite collections from Brazil, Venezuela, and the Falkland Islands, in part, housed at the AMNH and in the New York State Museum.

Carvalho and her collaborators described Devonian (Emsian–Eifelian) trilobites from Chapada dos Guimarães (Chapada Group), Mato Grosso State, Brazil, based on material in various Brazilian institutions (i.e., Brazilian Oil Company, National Department of Mineral Production, Federal University of Mato Grosso). Carvalho *et al.* (1987) and Carvalho and Edgecombe (1991) identified a trilobite fauna dominated by calmoniids (*Calmonia subseciva*, *C.* cf. *C. signifer*, *C.*? *triacantha*, *Metacryphaeus australis*, *M.* sp., and *Paracalmonia* sp.) and homalonotids (*Burmeisteria* sp.) that showed affinities with assemblages from the Ponta Grossa Formation in Paraná State. In another paper (Carvalho *et al*., 1997), two new species of calmoniid trilobites (*Metacryphaeus kegeli* and *M. meloi*) were described from the Middle Devonian of the Parnaíba Basin in Piauí State, northeast Brazil. The presence of *Metacryphaeus* in the Pimenteiras, Cabeças and Longá Formations confirms faunal affinities with the Malvinokaffric Devonian fauna (Carvalho *et al*., 1997).

In addition to these papers, Carvalho also published a series of abstracts and short notes for Brazilian paleontological meetings. These reports are mostly devoted to Devonian trilobites from the Parnaíba and Parecis Basins (Carvalho and Melo, 1984; Carvalho, 1985b, 1991; Carvalho *et al*., 1997). Recently, Carvalho (1999) revised the material studied by Lieberman *et al.* (1991) and Lieberman (1993), and concluded that the Middle Devonian of the Parnaíba Basin contains only *Metacryphaeus meloi*, *M. kegeli* and *Eldredgeia* cf. *E. venustus* (=*Metacryphaeus* cf. *M. venustus*).

Other researchers

A series of short papers, abstracts, and faunal lists, mostly concerning the trilobite record from the Paraná Basin, has been published since 1954. Lange (1954) published a special edition of the "Paleontologia do Paraná" as part of the commemorations of the Paraná State Centenary. In this volume, Lange (1954) presented a historical review of geological research in Paraná State, and changing the nomenclature of some trilobites proposed by Clarke (1913) based on new taxonomic data. Thirteen years later, Lange and Petri (1967) published another faunal list that including a more rigorous study of the stratigraphic distribution of invertebrates from the Ponta Grossa Formation.

Trilobite research in Brazil almost went into eclipse until the 1980s, when Carvalho (see above) and Marlene Terezinha Barcellos-Popp restarted a study of Paraná Basin trilobites. As is Carvalho, Popp is a university-trained paleontologist. Although employed by the Department of Geology at the Universidade Federal do Paraná, she was trained at the Universidade Federal do Rio Grande do Sul in the early 1980s by an important group of fossil arthropod specialists led by Irajá Damiani Pinto. In her Ph.D. thesis, Popp (1985) revised the trilobites described in 1913 by Clarke (with exception of the Homalonotidae), suggested the presence of new genera and species in the Subfamily Calmoniinae, and proposed a new subfamily of the Brazilian Devonian Acastavinae. In a publication based on her Ph.D., Popp (1989) erected and validated the new Acastinae species *Paranacaste pontagrossensis*. However, Carvalho and Edgecombe (1991) noted that it is a synonym of *Bainella pontagrossensis*, with close relatives in Bolivia and South Africa. In a later paper, Popp *et al.* (1996) presented the first phylogeny for the genus *Paracalmonia* (pro *Proboloides* Clarke, 1913). The authors erected three new species (i.e., *Paracalmonia paranaensis*, *P. salamunni* and *P. mendesi*), and redescribed *P. cuspidata* and rediagnosed *P. pessula*. Unfortunately, Popp retired in 1995.

Other authors (e.g., Copper, 1977; Eldredge and Ormiston, 1979; Eldredge and Branisa, 1980; Cooper, 1982) also mentioned Brazilian trilobites, particularly in reports on Silurian and Devonian paleobiogeography. Because of the scope of these papers and the need for a consistent taxonomic framework of known Brazilian trilobites (Table 1), some modifications to the faunal lists earlier presented by Clarke (1913), among others, are required.

An example of an important advance in the systematics of Brazilian and related Devonian high southern latitude trilobites is seen in Edgecombe's (1994) revision of the calmonid trilobites from the Falkland Islands. Edgecombe's conclusions show the paleogeographic affinities of the Falkland's trilobites with those from South Africa, the Andean shelf, and the Paraná Basin.

RECENT WORK

Another important gap in trilobite research in Brazil took place during the 1990s, when only the reports by Edgecombe (1994) and Carvalho *et al.* (1997) were published. During this decade, Middle Paleozoic paleontological research in Brazil centered on other invertebrate groups (e.g., bivalves and brachiopods). The research occurred mostly in universities, being less represented in museums and research institutions. This was especially the case of the Laboratório de Paleozoologia Evolutiva on the Botucatu campus of São Paulo State University. The laboratory was founded in the early 1990s, and devoted most of its research to the systematics (cladistic-oriented), taphonomy, and paleoecology of Permian invertebrates in the Paraná Basin, where mollusk-dominated fossils occur. In the Paraná Basin, trilobites are virtually absent in this part of the Gondwana sequence. At the end of the 1990s after ten years of intense Permian research, researchers and graduate students of this laboratory started an investigation of Paraná Basin trilobites. They used a more modern methodological and conceptual approach, and had financial support from the São Paulo Research Foundation (FAPESP). This research is focused on the pattern of trilobite distribution and its relationships to the sequence stratigraphical framework. For example, Ghilardi and Simões (2001) integrated the taphonomic data available for trilobites with Bergamaschi's (2001) sequence stratigraphical model for the Ponta Grossa Formation in the Paraná Basin. Although thick and laterally persistant beds with abundant trilobites are unknown, homalonotid and calmoniid are nonrandomly distributed in the sequence. For example, trilobites are virtually absent in obrution deposits near the maximum flooding surfaces (MFS), where epifaunal, sessile, invertebrates (brachiopods, conularids) are commonly preserved in life position (Ghilardi and Simões, 2000, 2001). This seems to be a very promising research agenda, not only because of the data gathered, but also because, it involves the formation of a new generation of broadly trained young paleontologists.

CLOSING THOUGHTS

Several generations of American, European, and Brazilian paleontologists and geologists have made large trilobite collections that are now housed in Brazilian and foreign scientific institutions. Over the last six decades, the study of Brazilian trilobites was clearly neglected in favor of other Paleozoic invertebrates. However, the legacy of the pioneers and their collections still remain. For example, the Kegel collection, now housed at the "Museu de Ciência da Terra", National Department of Mineral

Table 1. Valid trilobite species from Brazil.

Author/year	Parnaíba basin	Amazon basin	Paraná basin
Hartt and Rathbun, 1875		*Homalonotus oiara*	
Clarke, 1890		*Dalmanites australis*	
Clarke, 1890		*Dalmanites galea*	
Clarke, 1890		*Dalmanites gemmelus*	
Clarke, 1890		*Dalmanites infractus*	
Clarke, 1890		*Dalmanites maecurua*	
Clarke, 1890		*Dalmanites tumilobus*	
Clarke, 1890		*Homalonotus derbyi*	
Clarke, 1890		*Phacops menurus*	
Clarke, 1890		*Phacops macropyge*	
Clarke, 1890		*Phacops pullinus*	
Clarke, 1890		*Phacops scirpeus*	
Clarke, 1890			*Dalmanites gonzaganus*
Clarke, 1913			*Calmonia signifer*
Clarke, 1913			*Calmonia subseciva*
Clarke, 1913			*Pennaia pauliana*
Koslowski, 1913			*Acaste lombardi*
Struve, 1958			*Paracalmonia cuspidata* (Clarke)
Struve, 1958			*Tibagya parana* (Clarke)
Harrington *et al.* in Moore, 1959			*Metacryphaeus australis* (Clarke)
Castro, 1968	*Burmeisteria notica* (Clarke)		
Copper, 1977		*Phacopina braziliensis* (Ammon)	*Calmonia ? triacantha* (Ammon)
Cooper, 1979			*Burmeisteria notica* (Clarke)
Cooper, 1979			*Calmonia michrischia* (Clarke)
Eldredge and Orminston, 1979			*Paracalmonia pessulus* (Clarke)
Eldredge and Orminston, 1979	*Metacryphaeus paituna* (Hartt & Rathbun)	*Metacryphaeus paituna* (Hartt & Rathbun)	
Cooper, 1982			*? Gamonedaspis accola* (Clarke)
Cooper, 1982		*Tarijactinoides acanthurus* (Clarke)	
Cooper, 1982		*Metacryphaeus ulrichi* (Katzer)	
Carvalho and Edgecombe, 1991			*Bainella pontagrossensis*
Carvalho and Edgecombe, 1991			*Calmonia ? triacantha* (Ammon)
Lieberman et al., 1991		*Palpebrops goeldi* (Katzer)	
Lieberman, 1993	*Eldredgeia cf. E. venustus*		
Lieberman, 1993	*Metacryphaeus tuberculatus*		
Popp et al., 1996			*Paracalmonia mendesi*
Popp et al., 1996			*Paracalmonia paranaensis*
Popp et al., 1996			*Paracalmonia salamunii*
Carvalho et al., 1997	*Metacryphaeus kegeli* (Kegel)		
Carvalho et al., 1997	*Metacryphaeus meloi* (Clarke)		

Production, at Rio de Janeiro, has yet to be studied and revised. Thus, the coming years are particularly promising.

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AUSTRALIAN TRILOBITE STUDIES

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ABSTRACT—Australian trilobites have been studied since their first report in 1845 by a wide range of people for a variety of different reasons. They are known from all Paleozoic Periods and from all Paleozoic basins or depositional regions. The early phase of discovery in the populated southeast part of Australia made known a few trilobites that were collected with other shelly faunas. Despite the efforts of McCoy; Clarke; de Koninck; Etheridge, Sr.; Etheridge, Jr.; and Tate, very few trilobite taxa were recognized from the entire continent by the end of the nineteenth century. Etheridge and Mitchell's work on the Upper Silurian of the Yass Basin, Mitchell's on the Carboniferous, and Whitehouse's on the Middle and Upper Cambrian of northwest Queensland were pioneering studies that began to detail the size of the Australian faunas and tried to develop a trilobite-based biostratigraphy. After World War II, the Bureau of Mineral Resources began mapping the large sedimentary basins of northern and central Australia, and great numbers of trilobites were discovered and described by Öpik and, later, by Shergold. Trilobite studies were carried on in numerous university geology departments from the 1950s, with the most productive group established by Ken Campbell, who supervised Engel, Chatterton, Jell, and Holloway, among others. Although more than 1000 Australian trilobite taxa are known, knowledge of existing collections shows that many remain to be described.

INTRODUCTION

Explorations of the Australian continent, which began with the voyages of Matthew Flinders during 1801 to 1803 and continued through the efforts of Mitchell, Sturt, Cunningham, Oxley, Leichhardt, and others for most of the remainder of the 19th century, were primarily aimed at establishing the nature and economic potential of the country. Expansion of the agricultural and pastoral industries to feed the expanding population was the primary aim, but the search for coal and any other exploitable minerals also had a high priority. Since they were not a common component of fossil faunas encountered on these expeditions, trilobites remained virtually unreported until the middle of the 19th century.

Even with the appointment of paleontologists by state geological surveys, universities, and museums, beginning with McCoy in 1855, knowledge of Australian trilobites did not significantly increase. Early activity featured reports on spot occurrences of trilobites that were assigned, almost exclusively, to genera known from Europe. These practices did not allow full exploitation of the biostratigraphic potential of trilobite faunas, and it was not until the end of the century and early 20th century that truly pioneering studies were undertaken by Robert Etheridge, Jr.; John Mitchell; and F.W. Whitehouse, who apparently were the first to try to solve stratigraphic problems by the use of Australian trilobites.

However, it remained for the massive national investment in northern Australia and post-secondary education after World War II to trigger the great efforts that lead to our current knowledge of Australian trilobites. The Bureau of Mineral Resources was the very well-funded research support base for the monumental work of A. A. Öpik in northern Australia. The Australian National University hosted K. S. W. Campbell's group, which, although not exclusively devoted to trilobite studies, was the most productive in producing trilobite paleontologists and publications.

EARLY HISTORY

The first report of trilobites in Australia was Strzelecki's (1845, p. 261, 296) record of trilobites in association with *Favosites gothlandica*, another species of *Favosites*, *Amplexus arundinaceus*, *Orthoceras*, and *Encrinites* stems from the Yass Plains and the Boree country. He concluded that the strata were Devonian, and that the Paleozoic of Australia and Tasmania is partly equivalent to the Devonian and Carboniferous of other countries. Clarke (1848) devoted a report to the occurrence of trilobites in New South Wales, and referred to the Yass Plains, to Yarralumla near Queanbeyan, and to numerous localities in the Hunter Valley. He referred to a work by a Mr. MacLeay, in which the trilobites from Burragood in the Hunter Valley were described as belonging to *Trinucleus* and *Asaphus*, with one species named *T. clarkei*, but this report seems never to have been published. However, Clarke's material would be the basis for the first descriptions of Australian trilobites.

The first trilobite described from Australia was *Brachymetopus strzeleckii* McCoy, 1847. This species was in the first collection forwarded in 1844 to Sedgwick at Cambridge University for identification. The collection was made by the

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Fig. 1. Sir Frederick McCoy (1817–1899).

Reverend W.B. Clarke [1798–1878] who had arrived in Sydney in1839. At Sedgwick's request, McCoy examined Clarke's specimens and identified 100 species, of which only two were trilobites. These trilobites included *B. strzeleckii* and *Phillipsia* cf. *P. gemmulifera* Phillips from the Lower Carboniferous of the Hunter Valley. McCoy concluded that all the material he had examined was from Carboniferous or younger strata. Clarke (1878) detailed that he had set out on a new field of research, and sent Sedgwick a second collection of New South Wales fossils in 1855. This collection came from Lower and Middle Paleozoic strata, and underwent a fairly tortuous route to description and publication. As Clarke (1878) related the tale, descriptions of the fossils were unobtainable from Cambridge (presumably as McCoy left for Victoria). Thus, Clarke wrote to Sedgwick and to Sir Roderick Murchison, Director of the Geological Survey of the United Kingdom, with the result that Murchison borrowed the fossils from Sedgwick and submitted them to his staff paleontologists. Lonsdale and Salter did their best, but did not complete this task before their deaths. At one stage, Salter suggested that Clarke ask McCoy to undertake the work, but McCoy declined by citing his public engagements as too time consuming. Clarke next consulted T. Rupert Jones, who suggested that he ask de Koninck of Liége. de Koninck accepted the task, and completed and published the material in 1876–1877. This very important work was published in English in 1898, after a translation from the French by W. S. Dunn and Professor and Mrs. T. W. E. David. It contains descriptions of thirteen Silurian and three Carboniferous trilobite species, and is the most significant 19th century contribution on Australian trilobites. However, its value was enormously depreciated in 1882, when the specimens were lost in the Garden Palace fire in Sydney.

Frederick McCoy [1817–1899] (Fig. 1) was appointed to the foundation Chair in Natural Science at Melbourne University in 1854, and soon after became Palaeontologist to the Victorian Geological Survey and Director of the National Museum. His 1847 paper ensured his place as the first person to name an Australian trilobite, and also began a long running battle with W. B. Clarke over the age of the plants associated with the Australian coals. For this reason, he worked somewhat in isolation in Melbourne. Nevertheless, he made a further significant contribution on Australian trilobites with the first descriptions of Victorian species in Decade 3 of his Prodromus (McCoy, 1876). In this report, he described five species under the names *Phacops* (*Odontochile*) *caudatus* Brongniart, *P*. (*Portlockia*) *fecundus* Barrande, *Forbesia euryceps* McCoy, *Lichas australis* McCoy, and *Homalonotus harrisoni* McCoy. He also and figured a sixth species (McCoy, 1876, pl. 22, fig. 12), which was not referred to in the text, from an Upper Silurian locality between Melbourne and Kilmore in central Victoria. He also identified specimens for the field geologists of the Geological Survey (e.g., see list in Smyth, 1874).

Etheridge's (1878) catalogue of Australian fossils included 33 trilobites (27 Silurian and six Carboniferous species). All of these had been identified by McCoy or de Koninck. Although a few of these existed only as names on lists, most had been illustrated and described by McCoy or de Koninck.

PIONEERING STUDIES

The classical stage of Australian paleontology was regarded by Vallence (1978) as an era when reliance on European scientists declined and paleontologists based in Australia began to provide identifications, correlations, and local infrastructure necessary for the science to progress. Vallence identified this classic Stage with two men, Ralph Tate [1840–1901], who was appointed to the University of Adelaide in 1874, and Robert Etheridge, Jr. [1847–1920]. Both of these men had a role in Australian trilobite studies.

Although his major research dealt with Tertiary mollusks, Tate (Fig. 2) is credited with being the first person to recognize Cambrian strata in Australia. This conclusion was based on his identification of a trilobite collected and reported by Tepper (1879) from a locality south of Parara Station on Yorke Peninsula, South Australia. Tate initially sent trilobites to Henry Woodward (1884) for study, but later published a review paper that erected two new trilobite species (Tate, 1892). However, he made no further contributions on trilobites.

Robert Etheridge, Jr. (Fig. 3) was a geologist in the Geological Survey of Victoria in Selwyn's era and a paleontologist with the Geological Survey of Scotland and the British Museum. He was appointed as a paleontologist to the Geological Survey of New South Wales and the Australian Museum in 1887 (Brown, 1946). He was a prolific worker who was credited with having published a report every six weeks for 48 years on a range of paleontological and anthropological subjects. His paleontological papers generally contained descriptions of new fossil taxa that he recognized as distinct from European relatives. His specialities were focused on New South Wales, in particular, and Australia material, and trilobites were not a major component of his work. Etheridge (1896b) contributed small papers on the

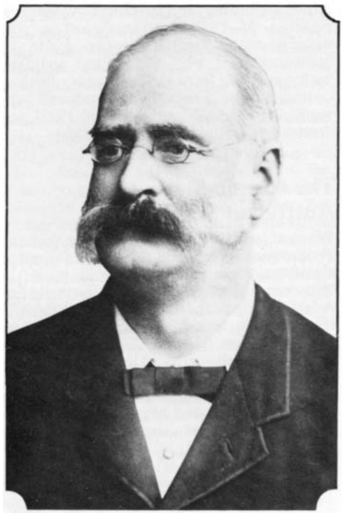

Fig. 2. Ralph Tate (1840–1901).

Fig. 3. Robert Etheridge, Jr. (1847–1920).

Cambrian trilobites of Victoria, in which he proposed *Dinesus*, but incorrectly assigned the pygidium of *Notasaphus*. Other reports dealt with the Cambrian of the Northern Territory (Etheridge, 1896a, 1902) and South Australia (1919), and with the Ordovician trilobites of Tasmania (Etheridge, 1883, 1905). In a comprehensive review, Etheridge (1919) summarized these contributions and all that was then known about Australian Cambrian trilobites. The 21 known species was a paltry record at a time when C. D. Walcott was describing highly diverse faunas from North America and China. Of the 21 Australian species, only two were referred to Australian genera. The other 19, which were referred to northern hemisphere genera, are now known, with one exception, to have been incorrectly assigned.

The Silurian trilobites of the Yass district would be Etheridge's major contribution. These were collected by John Mitchell, a Bowning school teacher, who also collected the Permian Belmont insect material described by Tillyard between 1918 and 1935. Mitchell (1918) also produced the first significant paper on Australian Carboniferous trilobites during his tenure as Head of the Newcastle Technical College. Etheridge and Mitchell (1891–1917) published six significant reports on Yass trilobites. Each of these reports treated a different taxonomic group, and the studies reported 30 new species. Only four European species were confidently recorded in these reports _ this was the first recognition that Australian trilobite faunas were distinct from the Northern Hemisphere even though the same genera were represented.

The first record of a trilobite from Queensland was included in the description of a large Permian shelly fauna by Robert Etheridge, Sr. (1872). This report included the proposal of *Griffithides dubius* for a trilobite collected by Richard Daintree from the Don River, a tributary of the Dawson. In their monumental work on the geology and paleontology of Queensland (Jack and Etheridge, 1892), Etheridge, Jr., described Carboniferous trilobites from eastern Queensland mining areas. He referred his father's species *dubius* and a new species, *woodwardi*, to *Phillipsia*, and described *Griffithides seminiferus* (Phillips) from the Rockhampton district. *Phillipsia dubia* (Etheridge, Sr.) was restricted to the type specimen by Mitchell (1918), but has been lost. Permian trilobites are poorly known in Australia, with only *Ditomopyge* known from Western Australia (Teichert, 1944) and *Doublatia* Wass and Banks, 1971, known from eastern New South Wales and Tasmania.

Little attention was paid to trilobites in Victoria during the latter years of McCoy's era (1880–1899), but the new century saw renewed activity. J. W. Gregory (1903), who replaced McCoy in the university, published only one report. This report proposed *Notasaphus fergusoni* from Heathcote in the same fauna from which Etheridge (1896b) had proposed *Dinesus ida*. These men recognized that the Australian forms were distinct from northern hemisphere faunas.

Frederick Chapman [1864–1944] received an appointment to the National Museum in 1902 with McCoy's departure. Although Chapman's forte was Tertiary foraminiferans, he turned his hand to all manner of fossils. In the 26 years he spent at the National Museum, he wrote at least seven papers on trilobites, and also gave them much attention in books and pamphlets that popularized paleontology. Chapman was reluctant to propose new generic names for Australian forms. In the one case that he did (*Milesia*), it proved to be preoccupied, and was replaced by Whitehouse (1936) with the now well-known name *Xystridura*. However, Chapman (1917a, b) aided the Geological Survey's mapping of the Heathcote region with identifications and taxonomic studies of fossils. In support of E. O. Thiele's work as a geological survey mapper, Chapman (1911a) described an Upper Cambrian trilobite fauna from a fault slice along the Dolodrook River in East Gippsland. Chapman (1911b, 1915) also added to knowledge of the Silurian and Devonian trilobites of Victoria.

In 1925, Chapman was sent a collection of trilobites from the headwaters of the Templeton River 12 miles west of Mount Isa by B. Dunstan of the Queensland Geological Survey. The trilobites had been sent to Dunston for identification by Campbell Miles, discoverer of the Mount Isa ore body, via E. C. Saint-Smith, the company geologist. The timing was unfortunate because F. W. Whitehouse, who would later clarify the nature of this fauna by revising Chapman's determinations, just returned from Cambridge to a position as paleontologist for the

Fig. 4. Frederick William Whitehouse (1900–1973).

Queensland Geological Survey. Although Whitehouse (1927) identified and dated several of the species from the Templeton River as Middle Cambrian, Chapman (1929) again supported the field geologists, and provided a less accurate, undefined (Middle to Late Cambrian) age.

As the Commonwealth government began a search for oil in Australia during the 1920s, Chapman's familiarity with Foraminifera was seen as a major asset. In 1928, he moved to become Commonwealth Palaeontologist. It was not until 1938 that Victorian trilobites again came under scrutiny. Edmund Gill, whose original degree was in divinity, was a youth worker with the Baptist Church, and rose to be director of the church's youth work in Victoria. By the 1940s, Gill's interest in science consumed all his energy. He was an honorary paleontologist at the National Museum from 1944, and in 1948 was appointed Palaeontologist. Gill published profusely on a wide range of subjects (352 papers listed in Carey, 1981), and his contributions on trilobites (e.g., Gill, 1938, 1939, 1940, 1945, 1948a, 1948b, 1949a, 1949b) are only a small fraction of his total output. Nevertheless, he was the only person for nearly four decades to continue the study of the Silurian and Devonian trilobites of Victoria that began with McCoy and has continued to the present.

Frederick William Whitehouse [1900–1973] (Fig. 4) grew up in Ipswich to the west of Brisbane where his parents owned a cake shop. He graduated from the University of Queensland in 1922 with First Class Honours and a University Gold Medal in 1922 and in 1924 with an MSc. He went to Cambridge University on a Foundation Scholarship (250 pounds per annum for 2 years — extended at the request of his supervisors for a third year) where he completed the first PhD awarded by the Earth Sciences Department of that university.The subject was Queensland Cretaceous faunas. On his return to Brisbane, he took up an appointment with the Geological Survey, but almost immediately moved to the University of Queensland to fill in for an injured senior staff member. He remained there for the rest of his career.His Cretaceous work drew him further west in Queensland until he reached the eastern edges of the Georgina Basin. It was in these flat-lying Cambrian sequences that he would become world renowned. Whitehouse's (1936–1945) five-part work on the Cambrian faunas of north-eastern Australia was the first attempt in Australia to use trilobites to establish a modern biostratigraphy. It was a remarkable achievement and should be considered the high point of pioneering trilobite work in this country. The terrain was difficult and mostly desert or semidesert, had few, if any, roads, little good surface water, and only few inhabitants of European descent on huge (3,000–13,000 square miles), isolated cattle stations. The Cambrian strata had undergone extensive weathering since the Cretaceous and, in some areas, since the Cambrian or Ordovician. This weathering produced considerable detrital deposits that obscured the geology in many areas. The weathering also meant few shale horizons remained in outcrop, and then only where they had been heavily silicified. As a university staff member, Whitehouse only had summer vacation to carry out fieldwork in a part of Queensland that lay more than a week's travel from the university. Moreover, summer is the hottest and wettest part of the year, and rocks are almost too hot to handle or floods make travel impossible. Whitehouse's diaries record several occasions when he spent the night sitting up in the car as floodwaters rose to the height of the tires. The university could not provide a vehicle for fieldwork and very little in the way of laboratory equipment. He did all his own photography with very inadequate equipment, and no research grants existed at that time. Whitehouse used his own vehicle, and on several occasions was forced to abandon it in the vast black soil plains between the Georgina Basin and coastal Queensland. He is known on more than one occasion to have walked to the nearest cattle or sheep station and offered to give his vehicle to the farmer if he would pull it from the bog and send all the specimens to the university. The flat-lying Cambrian limestones provided very few sections of any thickness, and Whitehouse was forced to try to fit together the stratigraphy based on widely separated occurrences of trilobites. A stratigraphy based on the sequence of rock units was at that time beyond the reach of a single pioneer, and Westergard's Scandinavian, Middle Cambrian agnostid zonation had not been established. Whitehouse therefore, proposed regional stages based on the occurrence of trilobite genera and correctly placed them in the Middle and Upper Cambrian, though not in the correct order.

Whitehouse recorded 75 species (52 new) assigned to 67 genera. He proposed nineteen genera, most of which remain valid today. He gave us such familiar names as *Aspidagnostus*, *Eugonocare*, *Glyptagnostus*, *Idamea*, *Nepea*, *Papyriaspis*, and *Xystridura*. Despite the extreme field conditions, he laid the foundation for later work on the Cambrian and Early Ordovician trilobites of the Georgina Basin. From the introduction to Part 5 (Whitehouse, 1945) and an examination of his bulk materials reposited in the Queensland Museum, it is clear that Whitehouse intended much more work on Cambrian faunas. However, his work on underground water resources in the Mesozoic Great Artesian Basin, which were of considerable economic significance, took up most of his time until he left the university in the mid-1950s and became a geological consultant on mineral prospects around Queensland.

Fig. 5. Armin Alexander Öpik (1898–1983).

Fig. 6. John Shergold (left) and Peter Jell (Right) with Chinese trilobite worker Zhang Wentang.

POST-WAR DEVELOPMENTS

In 1946, the Commonwealth Government established the Bureau of Mineral Resources (BMR). This organization was comparable to geological surveys in other nations and somewhat similar to those of the various states. In recognizing the need to learn about and develop northern Australia, the Commonwealth Scientific and Industrial Research Organization (CSIRO) and the BMR set about numerous surveys of tropical Australia. BMR geologists were part of a CSIRO survey of the Barkly Tablelands (including most of the Georgina Basin) in 1947–1948.This survey work over the next 30 years was part of a BMR program to map the country at 1:250,000 scale, and provided the basis for the great contribution to Cambrian trilobites made by Armin Aleksander Öpik [1898–1983] (Fig. 5).Two biographical tributes to Öpik (Shergold and Roberts, 1979; Shergold, Casey and Romot, 1984) describe his move from Estonia to Australia at the end of World War II, the great empathy of Öpik for the Australian outback, and the scale of his contribution to Australian geology and paleontology. As noted by Shergold *et al*. (1984), Öpik published 27 contributions to Cambrian stratigraphy and paleontology. Most of these are devoted to trilobites and all, in some way, are related to trilobites. He proposed 294 new trilobite species, or about 50% of the known Australian Cambrian trilobite fauna. Öpik was undoubtedly the most significant personality in the study of Australian trilobites. One of his earlier contributions of particular significance was the coordination of the Australian contribution to the Symposium on the Cambrian System at the 20th Geological Congress in Mexico. This publication was the first comprehensive report on the Australian Cambrian. It detailed virtually all known occurrences of trilobites and put them into their biostratigraphic, sedimentologic, and paleogeographic contexts. Öpik's (1956a–c) reports on Queensland, the Northern Territory, and the paleogeography of the continent are remarkable because he suffered a major loss of his manuscripts and collections in a 1953 fire that destroyed the BMR offices in Canberra. Öpik's (1967) Mindyallan bulletin is a monumental work that introduced 55 new generic names, the greatest number erected in any taxonomic publication on trilobites (i.e., excluding regional atlases). It is the more remarkable when consideration is given to the terrain from which the material was collected (Öpik, 1967, figs. 5–10 and 13). As noted by Shergold (*in* Shergold *et al*., 1984; listed in Shergold, 1973), it made a monumental advance in the study of agnostoid trilobites. The Middle Cambrian agnostoid bulletin (Öpik, 1979) is another remarkable publication for its sheer size. It introduced more than 80 new taxa, and although it has come in for its share of recent criticism, it provides an enormous body of information assembled from collections made by many field geologists as well as Öpik in very confusing terrain.

A mystery remains as to why Öpik never consulted with Whitehouse about his field areas, although both collected in precisely the same remote areas. It is clear that the BMR field parties included geologists (e.g., John Casey) who used Whitehouse's publications and, almost certainly, his field notes as initial starting points to establish the stratigraphic succession. However, Öpik's publications, which cite Whitehouse's work, often comment that inferences were made that were not clarified by personal contacts with Whitehouse. It was a sore point with Whitehouse, even when I knew him in the late 1960s, that his work in the Cambrian of western Queensland had been done under difficult circumstances with many privations. However, the BMR staff had comparative luxury in the field and virtually unlimited logistical support from the Commonwealth government. To make matters worse, Öpik never consulted with him about plans either one of them may have had for future paleontological work on the trilobites nor sought any cooperation between them. Given the greatly increased level of support for fieldwork, Whitehouse's knowledge of the difficult field areas, and his paleontological competence, it is surprising that Öpik never attempted to cooperate with or even contact Whitehouse.

John Shergold (Fig. 6) joined the BMR in the late 1960s. At Öpik's suggestion, he concentrated his efforts on the Upper Cambrian of the Burke River Structural Belt in western Queensland where faulting caused tilting and allowed more extensive sections to be measured and superposition to be better demonstrated. Shergold's (1972, 1975, 1980, 1982) work established a biostratigraphy for the middle and upper Upper

Cambrian between Öpik's Idamean Stage and the Ordovician. He recognized more than 100 new species in this part of the section, and is second only to Öpik in the number of Australian trilobite taxa described. Shergold (1971, 1991) worked on other Cambrian areas in western New South Wales and the Northern Territory, and also promoted work on the Ordovician of the Georgina Basin by enlisting the help of Richard Fortey on the fauna of the Nora Formation (Fortey and Shergold, 1984). He was joined at the BMR by John Laurie in the late 1980s to review the agnostoids for the Treatise revision. Laurie came from the University of Tasmania where he completed a PhD on Ordovician brachiopods under Max Banks. After completing the Treatise work, Laurie (1988, 1989) revised some of Öpik's Middle Cambrian agnostoid work. Laurie and Shergold (1996) also revised the Ordovician fauna of the Canning Basin in Western Australia.

Des Strusz (1964, 1980) of the BMR, although a specialist in corals, made a significant contribution on Australian encrinurid trilobites, as had the geological survey paleontologists McKellar (1969) in Queensland and John Talent (1963, 1965) in Victoria.

Among the many paleontologists trained in or on the staff of Australian universities in the second half of the 20th Century, several have made significant collections and studies of trilobites. Many of these reports have resulted from regional paleontological studies in which trilobites are only one component of the total fauna being investigated. For example, during an investigation of the Upper Ordovician of central New South Wales, Webby (1971, 1973, 1974; Webby *et al.*, 1970) of Sydney University described more than 25 trilobite taxa. Similarly, geological work by his students in far western New South Wales lead to the description of two other trilobite faunas (Webby *et al.*, 1988; Wang *et al.*, 1989). Kruse (1990, 1998) provided biostratigraphic support to field mapping of the Northern Territory Geological Survey, and described 15 trilobite taxa as part of a diverse shelly fauna. Henderson (1976, 1983) of James Cook University in Townsville published on Cambrian and Ordovician trilobites of Queensland as part of broader geological investigations. Similarly, Max Banks of the University of Tasmania has worked with the Tasmanian Department of Mines over many years on the island's Lower Paleozoic faunas (Corbett and Banks, 1974). He has made collections himself, engaged students on particular fossil groups, and invited paleontologists from other parts of the world to study his and the Mines Department collections. From these collections, Jago (1974–1987; Jago and Corbett, 1990; Jago and MacNeil, 1997; Bao and Jago, 2000) has described approximately 100 Cambrian trilobite taxa (Banks, 1982) from many localities across western and northern Tasmania. Heavy soil development and structural complexity are the main reasons for the lack of good measured sections. All of the trilobites are tectonically distorted to some degree, and are difficult to relate to faunas from elsewhere, although their general affinities with faunas of mainland Australia are well documented. Jell and Stait (1985a, b) revised the Tremadoc and Arenig faunas originally described by Etheridge (1883, 1905) and Kobayashi (1936, 1940) from the Florentine River Valley in southwest Tasmania and from near Latrobe in northern Tasmania. Edgecombe *et al.* (1999) described the Upper Ordovician Phacopida, and Burrett *et al.* (1983) discovered deep water Middle Ordovician trilobites in southern Tasmania.

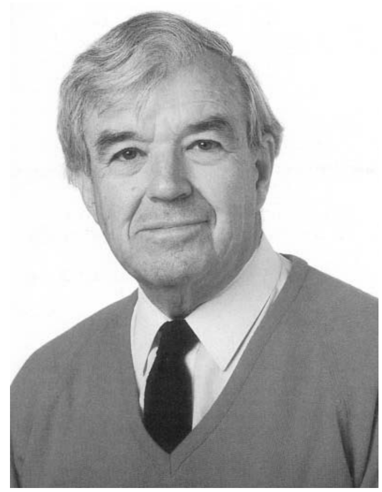

Fig. 7. Ken Campbell.

Ken Campbell's (Fig. 7) research has been considered as consisting of three broad topics (Jell, 1993), one of which was Silurian and Devonian trilobites. His interest in trilobites, though long apparent (Amos *et al.*, 1960; Campbell and Engel, 1963), stemmed mainly from a sabbatical year he spent with Harry Whittington at Harvard in 1965 where he studied North American trilobites that have formed his most prominent contribution to trilobites. Most of his contributions on Australian trilobites are joint studies with his students (Campbell and Durham, 1970; Campbell and Davoren, 1972; Holloway and Campbell, 1974; Chatterton *et al.*, 1979; Chatterton and Campbell, 1980). Campbell is the only Australian paleontologist who developed a school of trilobite workers. His eight students published on Australian trilobites, and four of them (Engel, Chatterton, Jell, and Holloway) remain active trilobite workers after more than 25 years. Brian Engel, with Noreen Morris at Newcastle University, has concentrated on the Carboniferous trilobites of eastern Australia. Their work involves systematic studies (Engel and Morris, 1975, 1983, 1984, 1989, 1991, 1992) and inferred biostratigraphic potential (Engel and Morris, 1990). Although best known for his Canadian work, Brian Chatterton's (1971) PhD on Silurian and Devonian trilobites from the Yass district and subsequent papers completed while on sabbatical leave in Canberra (Chatterton and Campbell, 1980, Chatterton *et al.*, 1979) are important contributions to Australian Silurian and Devonian trilobites and involves about 50 taxa, many of them new. David Holloway finished a degree with Ken Campbell. He then completed a doctorate on North American trilobites at Edinburgh University under Euan Clarkson before returning to the Museum of Victoria where he has worked on Silurian and Devonian trilobites of eastern Australia (Holloway and Neil, 1982; Jell and Holloway, 1983; Holloway and Sandford, 1993; Holloway, 1994, 1996; Holloway and Lane, 1998; Sandford and Holloway, 1998). Peter Jell's (Fig. 6) doctoral work at the Australian National University dealt with Middle Cambrian eodiscoids (Jell, 1975) at Öpik's invitation as this was a group on which he had worked before losing all his manuscripts and collections in the 1953 fire. At the Museum of Victoria, Jell studied Late Cambrian and Early Ordovician trilobites from Tasmania and Victoria (Jell and Stait, 1985a, b; Jell, 1985; Jell *et al.*, 1991) and Early Cambrian trilobites of South Australia (*in* Bengtson *et al.*, 1990). This South Australian work developed the first trilobite biostratigraphy for the Australian Lower Cambrian, and completely revised the previous scheme which had been based on named but unfigured and undescribed trilobites. At the Queensland Museum, he has published on Georgina Basin trilobites (Jell, 1975, 1977, 1978; Jell and Robison, 1978). Among others of Ken Campbell's students, David Legg (1976) was the first to provide an extensive description of the Lower Ordovician trilobites of the Canning Basin in Western Australia. Dick Landrum published on *Warburgella* from the Devonian of the Cobar area of New South Wales (Landrum and Sherwin, 1976).

Owen Singleton's PhD from Cambridge University involved Lower Paleozoic trilobites from Australia and New Zealand. On returning to Australia, he joined the Geology Department of the University of Melbourne, where his father earlier made a significant contribution to the Tertiary of southern Australia. However, Singleton never published the taxonomic work of his thesis. His only legacy is a paper on the Cambrian of Victoria (Singleton and Thomas, 1956). He correlated the stratigraphy of the Cambrian of Heathcote; the Dolodrook Limestone of east Gippsland, Victoria; and the Digger Island Limestone of southern Victoria, and provided faunal lists of the trilobites.

In South Australia, Brian Daily studied the Cambrian of the Flinders Ranges for his PhD under Martin Glaessner. In his long summary paper, Daily (1956) established a regional biostratigraphic succession of 11 "faunas" through the Early Cambrian. This scheme was based mostly on trilobites. Daily identified numerous new taxa and new occurrences of known taxa, but did not provide any illustrations nor indicate any specimens so identified. Although this scheme was quoted extensively by many different authors over more than 30 years, its basis has never been revealed. By recollecting at many of Daily's sites and interpreting his 1956 paper, Jell (*in* Bengtson *et al.*, 1990) sought to relate Daily's scheme to that which he found in well-mapped stratigraphic sections. Nevertheless, Daily maintained a Cambrian research center at Adelaide University with trilobites receiving considerable attention.

Jim Jago, another of Max Banks' students at the University of Tasmania, moved to Adelide University in the early 1970s and completed his PhD on the Cambrian trilobites of Tasmania under Brian Daily. Jago has continued trilobite work in Tasmania at the South Australian Institute of Technology (now the University of South Australia). Ken Pocock, another to complete a PhD under Brian Daily, contributed two important papers on trilobites from the Lower Cambrian of South Australia (Pocock, 1964, 1970)

CONCLUSIONS

Among all the paleontologists who have described Australian trilobites, only Öpik, Shergold, Jago, and Holloway could be said to have been specialists who devoted nearly all their efforts to trilobites. Even Öpik, unquestionably the most prolific worker, had a prominent position among brachiopod workers in his pre-war Estonian career. The inference that Australian trilobites, therefore, have been studied as a sideline to other fossil groups is only reasonable for the many eastern Australian faunas where other taxa dominated the faunas. Öpik and Shergold made the most significant contributions to Australian trilobites, as one would expect with the resources and backing of the BMR and in the virtually untouched platform basins of central Australia.

It is only in the Cambrian that trilobites have been used as the basis for a biostratigraphic zonation. Trilobite-based zonations have been established for the Lower Cambrian by Jell (*in* Bengtson *et al.*, 1990), for the Middle and lower Upper Cambrian by Öpik by application of the Scandinavian agnostid zonation, and for the rest of the Upper Cambrian by Shergold (1975, 1980). In younger periods, graptolites, conodonts, brachiopods, corals, and goniatites have overshadowed trilobites in developing biostratigraphic schemes, but the utility of trilobites has been demonstrated in some local and regional studies, even if not adopted continent-wide.

Approximately 1000 trilobite taxa are known from the Australia at present. How many are yet to be discovered remains to be seen, but it must be a considerable number judging from the existing museum collections and from the continuing rate of publication of new finds. The fields of biostratigraphy, functional morphology and paleoecology require more detailed investigations before they can be considered adequately understood.

It is reasonable to conclude that the pioneering phase of Australian trilobite studies is almost complete. The faunas of the Devonian in the Canning Basin (now being studied by Ken McNamara and Malte Ebach) and all ages in the Bonaparte Gulf Basin are the only totally undescribed faunas. However, there remains an enormous task to bring the state of knowledge to that of the better known northern hemisphere regions. More detailed investigations are required to make the best use of the information offered by the fossilized skeletons of these ancient extinct animals.

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WALCH'S TRILOBITE RESEARCH—
A TRANSLATION OF HIS 1771 TRILOBITE CHAPTER

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ABSTRACT—Johann Ernst Immanuel Walch was a German naturalist who engaged in geological research in the 1760s and 1770s. Walch coined the term "trilobite" in a publication that appears to be the most in-depth, thoroughly-researched, and lavishly-illustrated paleontological work of the 18th century. This was his "The Natural History of Petrifactions." We provide a new English translation of Walch's trilobite chapter as it provides a summary of the understanding of trilobites in the late 1700s. Walch essentially closed the door on the ca. 60 year-old debate on the classification of trilobites as arthropods or mollusks.

INTRODUCTION

The paleontological contributions of the 18th century naturalist J. E. I. Walch (Fig. 1) are not often discussed by historians of geology (see comments by Gayrard-Valy, 1994, and Gould, 2002). Modern paleontologists usually only encounter "Walch" as part of the names of some genera of Late Paleozoic conifers, such as the foliage-genus *Walchia* or the cone-genus *Walchiostrobus*, and as author of the "Class Trilobita" (Walch, 1771). The latter report is frequently cited by trilobite workers, but obtaining this publication has traditionally been difficult (see remarks in Fortey, 2000, p. 49), and it is rarely included in reference lists. Modern trilobite workers are typically familiar with literature that postdates the landmark monographs of Wahlenberg (1818) and Brongniart (1822). However, a number of pre-1800 references (64 or so) describes, discusses, or illustrates trilobites. The most significant of these is Walch's (1771) long and well-researched chapter on trilobites. This chapter was

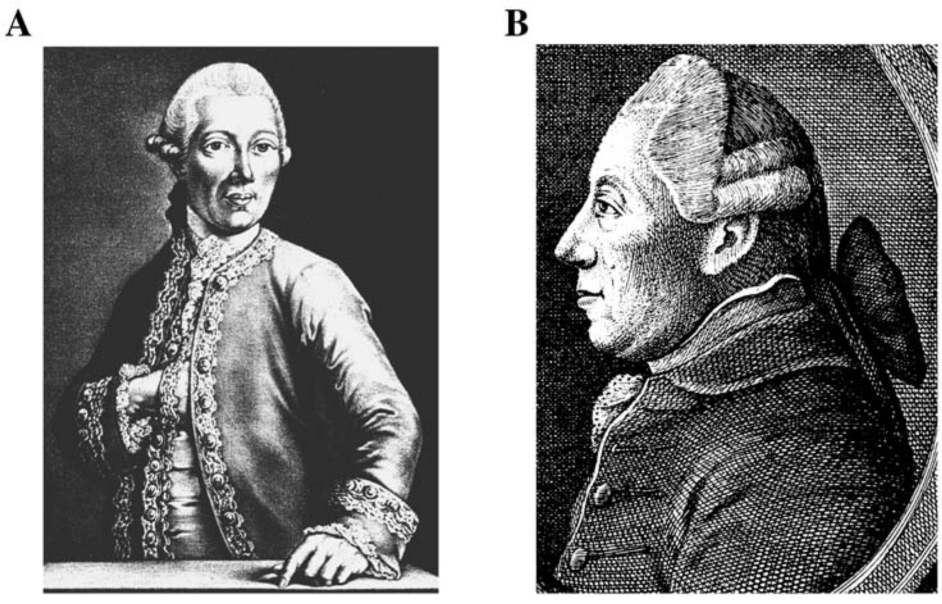

Fig. 1. Portraits of Johann Ernst Immanuel Walch (1725–1778), university professor, theologian, linguist, and naturalist. A, Frontispiece from volume 1 of *Recueil des Monumens des Catastrophes que le Globe de la Terre a Éssuiées* (Walch, 1777). B, Profile by Justus Christian Hennings; appeared as the frontispiece in Schröter (1780).

FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES, Edited by Donald G. Mikulic, Illinois State Geological Survey, 615 East Peabody Drive, Champaign, Illinois 61820, Ed Landing, New York State Museum, The State Education Department, Albany, New York 12230, and Joanne Kluessendorf, Weis Earth Science Museum, University of Wisconsin-FoxValley, 1478 Midway Road, Menasha, Wisconsin 54952. New York State Museum Bulletin 507.

Die
Naturgeschichte
der
Versteinerungen
zur Erläuterung
der
Knorrischen
Sammlung von Merkwürdigkeiten der Natur
herausgegeben
von
Johann Ernst Immanuel Walch
Hochfürstl. Sachsens Weimarischen und Eisenachischen Hofrath, wie auch der Beredsamkeit und Dichtkunst ordentlichen öffentlichen Lehrer auf der Universität zu Jena.
Dritter Theil.
Nürnberg,
gedruckt bey Paul Jonathan Felßecker, 1771.

DE NATUURLYKE HISTORIE
DER
VERSTEENINGEN,
OF
UITVOERIGE
AFBEELDING EN BESCHRYVING
VAN DE
VERSTEENDE ZAAKEN,
DIE TOT HEDEN
OP DEN AARDBODEM ZYN ONTDEKT:
AANGEVANGEN DOOR
GEORG WOLFGANG KNORR:
VERVOLGD EN OMSTANDIG BEREDENEERD
DOOR
JOHANN ERNST IMMANUEL WALCH
HOOGVORST. SAXEN WETMARSCHEN EN EISENACHSCHEN HOFRAAD; HOOGLEERAAR DER WELSPREEKENDHEID EN DIGTKONST OP DE HOOGE SCHOOL TE JENA:
UIT HET HOOG IN 'T NEDERDUITSCH VERTAALD
DOOR
M. HOUTTUYN, MEDICINÆ DOCTOR,
MET VERSCHEIDE AANMERKINGEN.
DERDE DEEL.
TE AMSTERDAM,
BY JAN CHRISTIAAN SEPP, Boekverkooper.
MDCCLXXIII.

RECUEIL
DES
MONUMENS
DES
CATASTROPHES
QUE LE GLOBE DE LA TERRE
A ÉSSUIÉES,
CONTENANT
DES
PÉTRIFICATIONS
DESSINÉES, GRAVÉES ET ENLUMINÉES,
D'APRÈS LES ORIGINAUX,
COMMENCÉ
PAR
FEU Mr. GEORGE WOLFGANG KNORR,
ET CONTINUÉ
PAR
SES HERITIERS
AVEC
L'HISTOIRE NATURELLE
DE CES CORPS
PAR
Mr. JEAN ERNEST EMANUEL WALCH,
CONSEILLER DE COUR DE S. A. SER^{me} MONSGR. LE DUC DE SAXE-WEIMAR, ET EISENAC ET PROFESSEUR D'ELOQUENCE ET DE POESIE A L'UNIVERSITE DE JENE.
TOME TROISIEME.
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Fig. 2. Title pages of the German (1771), Dutch (1773), and French (1775) editions of J. E. I. Walch's "Natural History of Petrifactions," part three.

published in the "Natural History of Petrifactions" series (Fig. 2) that was started by Georg Wolfgang Knorr in 1755 and continued by Walch in the late-1760s to late-1770s. Walch's chapter is an early landmark in the understanding of trilobites that has a significance beyond its nomenclatural importance. Indeed, the work is accompanied by plates of moderately high quality, by comparison with many 1700's and 1800's references, and it shows a near-comprehensive familiarity with earlier literature. Most significantly, its discussion of the debate on trilobite affinities provides insights into how 18th century naturalists dealt with problematic fossil organisms.

BACKGROUND ON WALCH

The summary presented below is mostly derived from Baldinger (1770), Schröter (1773, 1779, 1780), Meusel (1815), Doering (1835), Dobschütz (1896), Zittel (1901), and Geikie (1905).

Johann Ernst Immanuel Walch was born August 30, 1725, in Jena, Germany. He was the eldest of three sons of the famed 18th century theologian Johann Georg Walch. His schooling emphasized theology, philology and linguistics, math, and natural history. His first several publications were completed before he was 20 years old. Jena University hired him as a lecturer in 1745, and as a theology professor in 1750. Walch later switched to the logic and metaphysics professorial position at Jena University in 1755, and then to a position in poetry and elocution in 1759. Most of Walch's interests and publications were on topics in the humanities. These included early Christian church history; New Testament exegesis and commentary; Latin and Greek linguistics, literature, and inscriptions; Roman history and antiquities; Celtic religion; and the history of medicine.

Probably by the mid- to late-1750s, Walch turned his focus to natural history, especially geology and paleontology. He started building what would become a sizable and significant natural history collection. Walch's conversion from the humanities to the natural sciences began during a long study trip in 1747–1748 to cities in central, western, and southern Europe. While in Florence, Italy, Walch viewed the Baillou Cabinet, a large collection of rocks, minerals, and fossils that was on public display until its purchase and transfer to Vienna, Austria, in 1748 by the Holy Roman Emperor, Francis I (Wilson, 1994). Although Walch continued to teach and publish in the humanities, he confessed that the natural sciences overtook his interests in theology and languages. His natural history collection expanded in size and reputation to the point that many European naturalists, even royalty, came to view the Walch Cabinet. The collection included plants and animals. Particularly well represented were fossils, rocks, and minerals of the "Stone Kingdom." Walch's collection was combined in 1779 with that of Karl August, Grand Duke of Saxe-Weimar, to form the foundation of the current museum holdings at Jena University (now the Friedrich Schiller University).

Walch (1762, 1764, 1769) summarized the cataloguing system used for his geologic and paleontologic specimens as *Das Steinreich, Systematisch Entworfen* ("The Stone Kingdom, Systematic Outline"). He envisioned publishing a cataloguing scheme for the plant and animal kingdoms that would rival the Linnaean system, but never completed it. The first volume of *Das Steinreich* (Walch, 1762; 2nd edition, 1769) consists of two major sections: one on rocks and minerals, and one on fossils. The rocks and minerals are arranged systematically on the basis of texture (granular, lamellar, filamentous, fissile, etc.) and other physical properties, such as transparency. The much-longer section on fossils subdivides the animal kingdom into terrestrial, aquatic, and amphibious categories, and the plant kingdom into terrestrial and marine groups. Walch's concept of marine plants principally included corals, milleporid hydrozoans, and rudist bivalves. The fossil descriptions are accompanied by 24 plates that depict a wide variety of mostly Mesozoic and Cenozoic marine invertebrates. The second volume of *Das Steinreich* (Walch, 1764) rarely mentions fossils, but has extensive remarks on the inferred mode of formation for many rocks and minerals. Some early mineralogists preferred a chemically-based classification for rocks and minerals, while others used the textural and descriptive classification of *Das Steinreich* and similar works.

Walch's most significant contribution to paleontology began after the publication of *Das Steinreich*. Georg Wolfgang Knorr, a Nuremberg copper-engraver, art dealer, and fossil collector, had published some works with colored illustrations of such natural history objects as shells, fossils, minerals, and various modern plants, vertebrates, and invertebrates. Knorr prepared copper-engraved plates of fossils for a work titled "Lapides Diluvii Universalis Testes" ("Stones that Testify to the Universal Flood"), which was intended to document the effects of the Noachian flood. Only one portion of the project was published before his death in 1761 (see Knorr, 1755). Over 200 plates that depicted fossils were unpublished. Knorr's heirs contacted Walch about writing text for these plates. Walch agreed, and the result was the beautifully illustrated, four-volume "Die Naturgeschichte der Versteinerungen" ("The Natural History of Petrifactions"). This work was released from 1768 to 1773, and also published in French and Dutch editions (Fig. 2). All of Knorr's plates were printed as hand-colored copper engravings that depicted fossils from private and society collections across Europe. The figured fossils include scleractinian and tabulate corals, bivalves, gastropods, nautiloids, ammonoids, decapods, trilobites, crinoids, echinoids, terrestrial and aquatic vertebrates, leaves, wood, and trace fossils. Few of Knorr's plates illustrate non-biogenic objects, such as manganese dendrites from the Solnhofen Limestone, Liesegang banding, and a large figure of the active Solnhofen quarries.

Walch continued scholarly work in the humanities and natural sciences during the 1770s, and also started a new journal, *Der Naturforscher* ("The Naturalist"). By the end of his career, he had completed over 80 publications (books, chapters, and articles) on various topics in the humanities and about 50 publications in natural history. He became ill in Summer 1778 with the onset of hypochondriac (abdominal) seizures. Walch participated in a last dissertation defense for a Jena University student in late 1778, a month and a half before his death on 1 December 1, 1778, from intestinal infections. He left behind a reputation for being an energetic, practical man and a popular lecturer with a pious Christian character and an enthusiastic concern for his students, colleagues, and university.

SUMMARY OF WALCH'S TRILOBITE CHAPTER

The trilobite chapter in the 1771 volume of the "Natural History of Petrifactions" was accompanied by six plates that showed isolated pygidia and cranidia, as well as complete, partially enrolled, enrolled, and outstretched specimens. Walch's chapter appears to be the most in-depth discussion and description of trilobites published before the 19^{th} century. He began with a documentation of the various names given to trilobites by previous workers, concluded that none was suitable, and proposed the descriptive name "Trilobite." This name was generally accepted after Walch's time, with two notable exceptions. Wahlenberg (1818, p. 18) considered "trilobite" to be "a greatly common name, ... of excessively trivial significance, but unassuming." Dalman (1827, p. 120, 121; 1828, p. 7) noted the "highly unconventional origins and barbaric construction ... of the term."

Walch included some especially noteworthy observations in his lengthy descriptions of trilobite cephalic, thoracic, and pygidial morphology. For example, he rejected the interpretation of a Swedish olenid trilobite that Linnaeus (1759, pl. 1, fig. 1, pl. 2, fig. 1) claimed to have antennae. Walch correctly identified the "antennae" as the anterior cephalic border ("lips" in Walch's terminology). This was well over a century before Charles Beecher's (1896) article on the same topic. Walch also anticipated the discovery of preserved legs within enrolled trilobites. This prediction was about 100 years before Charles D. Walcott discovered appendages in enrolled specimens of *Flexicalymene* and *Ceraurus* from Upper Ordovician limestones of New York State (e.g., Walcott, 1879, 1921; Brett *et al.*, 1999). Walch had numerous trilobite specimens that represented many species. But, he acknowledged his lack of well-preserved specimens, and held back from proposing names and classifications for these species. This restraint contrasts with the enthusiasm for proposing numerous genera and species based on incomplete and poorly preserved material in some of the 20^{th} century trilobite literature.

The remainder of Walch's chapter is devoted to lengthy discussions about the search for the living analogue of trilobites. A concept of extinction was not widespread in the late 1700s, and typically denied based on the argument that God's creation was perfect and extinction could not take place. However, trilobites presented a particularly frustrating problem for some 18^{th} century naturalists. Trilobites seemed to have a paradoxical combination of characters — the segmented body of "crustaceous" animals with the hard mineralized shell of "testaceous" animals. This body plan had not been recorded from any organism in the modern oceans. Walch gave a thoroughly summarized the historical debate of the "testaceous" vs. "crustaceous" affinities for trilobites (i.e., molluscs versus arthropods). He noted the temptation to view trilobites and chitons as similar organisms, but strongly argued against and rejected the chiton hypothesis. Marine isopods were the favorite candidate of many mid- to late-1700's naturalists as the modern analog of trilobites. Walch favored the notion that marine isopods were the closest living analogs of trilobites, but observed that isopods are not hard-shelled as trilobites. He believed that the true living analog of trilobites was yet to be found in the modern seas. This expectation had a reasonable precedent in the discovery of living crinoids in the 1750s (Guettard, 1761), centuries after fossil crinoids were described and illustrated in the literature (e.g., Gesner, 1565; Bauhin, 1598; Imperato, 1599; Lhwyd, 1699).

WALCH'S TRILOBITE CHAPTER

The English translation provided below is from the French edition (Walch, 1775, volume 3, chapter 3) of the "Natural History of Petrifactions." The French edition is titled "Collection of Monuments of Catastrophes that the Globe of the Earth Has Experienced;" Fig. 2). The French version appears to be a faithful translation of the original German edition (Walch, 1771), with occasional, minor differences. Transcription and other inadvertent errors between the German and French editions have been corrected below to correspond with the German edition. Non-proper nouns that Walch capitalized in the French edition are also capitalized herein. City and other place names have usually been modified to correspond with modern spellings. Names of people have usually been modified to correspond with spellings from their original references. Charles Mortimer's (1752, p. 601) quotation in *Philosophical Transactions* was incorrectly rendered by Walch, and Mortimer's original phrasing is used. Words not easily rendered into English and other unusual terms are defined below in the glossary. Walch's footnotes follow the translation.

CHAPTER III - ON THE TRILOBITES IN THE KINGDOM OF PETRIFACTIONS, OR ON THE WRINKLED THREE-LOBED CONCH (*CONCHA TRILOBA RUGOSA*)

If ever during our times, a Petrifaction has excited the attention of Naturalists, it is surely that which has the common name of the wrinkled conch with three lobes, *Concha triloba rugosa*. In the beginning, only the posterior part, or the tail, was discovered, and as it had a Test as in other shells, most have taken it to be a kind of still unknown shell, and have tried to discover its analog. Later, the anterior part of the Test was also found, but isolated, and nobody conjectured that this particular figure was part of the Petrifaction that was previously discovered. Shortly thereafter, some less mutilated pieces were unearthed, both curved and stretched-out, and it was then that was recognized in the Kingdom of Petrifactions a body, that so far had not been observed in all the Kingdom of Nature, a Creature which had a head greatly resembling that of a spider, its back divided into three lobes, and garnished with testaceous rings much like the tail of a crayfish, and with a large tail extremity equally divided into three lobes. At that time, it was observed that this animal must have, under its Test, free movement, and be able to curl, to extend and to contract itself in all directions. Successive Examples were found in the Kingdom of Fossils, which confirmed this observation in an incontestable manner. Until now, we could barely determine positively and with certitude the true analog of this particular Petrifaction, no matter how much effort had been employed; and for the past few years especially, the most learned Naturalists have been piqued, so to speak, at the wish to make such fortunate discoveries, and to approach this analog, by searching and comparing exactly those Examples which have been found. I now will follow this method, and I will detail the Natural History of this Petrifaction, and I will propose my conjectures on its analog, so that the connoisseurs of these subterranean curiosities might investigate them. My friends have furnished me with a quantity of instructive Examples, which I have compared with great care not only with each other, but also with pretended analogous marine specimens. For the past three years, as I have entertained a correspondence on this Petrifaction with some learned Naturalists, and particularly with Provost Gentzmar of Stargard, I have learned several things, which still could be totally unknown, or at least not well known. But I am arriving at the proposal itself.

At the beginning, as only fragments of this Petrifaction were found, and as it was not known under what kind of body to classify it, almost each Naturalist who found it thought it his right to give it a proper name; Bromell[1] named it *Lapis insectiferus, Insectum vaginipenne*, as he thought he found the imprint and Petrifaction of certain Insects having wings covered with hard and horny scales. Mr. Woltersdorff[2] placed it with the Petrifactions of bivalved shells and, as it had three protuberances, he gave it the name of *Conchites trilobus*, a denomination that many others adopted with very little change, and this is where we might recall the names of *Concha trilobos*, *concha triloba rugosa*, *pectunculites trilobus*, as are found in the works of Messrs. Gentzmar,[3] Wilckens,[4] Klein,[5] Bertrand,[6] and several others. It must be said however that, already in a certain sense Mr. Hermann[7] is the inventor of this denomination, as his *Pectunculites trilobus imbricatus* is precisely that shell which we call *Concha triloba*. The celebrated Naturalist Mr. Linné[8] gives to this Petrifaction, because of its peculiar form, the name *Entomolithus paradoxus*; Brander in Davila[9] gives to it the name of *Eruca anthropomorphites*; Brückmann[10] calls it *Petrefactum polypi marini* and *Armata Veneris*; Mr. Baumer,[11] *Trigonella striata*, and Inspector Wilckens,[12] *Entomolithus branchiopodis cancriformis marini*. Several German Naturalists use the names *Cacadumuschel* and *Kaefermuschel*. It is supposed that this first name given to this Petrifaction is because of its resemblance to the erect plumage of the bird which the Ambonese call Cockatoo, and the last name after the name of *Lapis insectifer*, a name given by Bromell. After the report of Mr. Lehmann[13], the narrow kind of tails of this animal also carries the name of Sea-Hare. In England, it is commonly named *Dudley Fossil*, after the locality where it is found, and others call it *Eruca* or *bivalva*, as may be seen in *Philosophical Transactions*, vol. 46, p. 598. Several of these names were given to this Petrifaction before it was well known, and when the extremity of the tail was thought to be one of the two valves of a shell. In examining all these different names, it may be seen that they have been so named either by linking them to the form and to the resemblance of this Petrifaction with other bodies, or else by relating them to a pretended analog which was taken to be the same, although, most often, without base, or even naming them after the locality where these Petrifactions were found. Thus, it is given that designation which is the least studied by naming it a *Trilobite*. The three lobes of the back and of the tail are the characters by which this body is distinguishable from all others, and as these characters are visible, we judge them as appropriate, and accordingly it is not now about giving it a denomination from an analog, particularly as this analog is also subject to many arguments and many doubts.

This particular body, when complete, is composed of three parts, the head, the trunk, and the tail, which, when extended together, form an oblong Oval. The head is covered with a vaulted Test, which is sometimes smooth and sometimes grainy, often the grains being hardly perceptible such as on the armor of a crayfish. Ordinarily, it has certain symmetrical protuberances and depressions dividing it into three parts. The trunk, or the back, as it is usually named, is mostly cylindrical and composed of three lobes. It has a banded armor, that is, the shell which covers it, is composed, the same as a crayfish tail, of rings, each of which is of three arcs, as the back has three lobes. These rings are able to slip by each other, as the animal extends or curls, in a fashion which allows for free movement that doesn't hinder its crustacean armor. The crust, or as it is named, the shell of its tail consists of one piece, as that of the head, and is divided into three elevations. As in the past this tail part was found isolated and as it was believed to be a shell, it was given the name three-lobed conch (*Concha triloba*). The Test (external shell), which is the armor of this animal, is like that of a shell; it separates in laminations and sheets, as I have observed in several Examples, and noted that it was composed of many laminations like the Test of shells. Commonly, this Test is thin, especially in those Examples where several laminations have already become detached; one cannot arrive at a conclusion by the thinness of the test of one Petrifaction as to the thickness of the Test in its analog. There are Examples where the Test has the thickness of a knife blade; the same in the large pieces, there are those the thickness of a quill, and also in larger pieces, the thickness of the Test is a quarter of an inch. Although, it is also observed, at the same time, that the test of the trunk is commonly much thinner than the scale that covers the head and the tail of the animal. The internal surface of the scale, when it detaches from the core, which happens sometimes, is rayed or has very fine lines, often imperceptible, which are slightly undulating and parallel. These lines are even more noticeable on the core which is found immediately below the shell, because of the imprint that they made, and, where these impressions are found, most likely on the tail, it is a sign for sure as to where the test separated. No one has ever been able to discover any vestige of the test on the bottom side; on the cores themselves, the imprint of the internal surface of the superior shell is found all the way to the extremity of the tail, without ever observing anything that holds or unites a shell below with the shell above. Some expert Naturalists thought that they had observed, in the rocks, where one Trilobite was transversely dissected, one shell below[14], which was the same as that above, composed of three arcs, and the two sides holding together. However, this observation proves nothing. As the section had been made across a nearly enrolled Trilobite, its back was dissected twice, and as a consequence, it must be presented on the surface of the stone as two lines with three arcs, facing each other. For the rest, as an animal who is hiding in its shell, and is free to move in all direction, in dying, it is not always in the same attitude. Some are stretched straight[15] and thus have an elongated oval shape. Others are contracted in a manner that the tail is below the head, giving the animal a heart shape[16]. Yet others take a form twisted above and below. Following the difference in attitude, the dorsal rings enter sometimes more, sometimes less underneath others, and thus the rings appear larger or smaller. When the animal is stretched, the rings often enter two thirds into each other, which is distinctly seen in the lateral lobes of some individuals.[17]

Now we must examine more closely the head, the trunk and the tail of this particular animal. Most are found with their head separated from the trunk, and it may be inferred from this that they are only held together by a few muscles, which putrefy rapidly, and which give the head a freer movement. This head, or to state it more clearly, this shell under which the head of the animal is hidden as under a helmet, has forms so varied in the Kingdom of Fossils, that it becomes troublesome to report and determine all these variations. At the same time, we must accept that many pieces, taken to be the head shields of Trilobites when they surely are not, and which are in effect the shells of other marine bodies found among the Trilobites and which were petrified with them.

The shell of the head represents a crescent[18]; it is commonly strongly convex and consists of a single piece. In a few, it is simply a smooth curved surface, without grooving, protuberances, or depressions,[19] and it is probable then that these would be simple cores, their natural test missing; else, they are damaged and their tubercles lost, unless there is effectively a species, which in its natural state has the head covered with a totally smooth head shield. For the most part, they are garnished with protuberances and furrows. In other words, passing from top to bottom up to the extreme edge of the shell, are two fissures or furrows,[20] where the total shell, which covers the head of the animal, is divided into three parts, being that of the middle, and of two lateral parts. We need, to speak more intelligibly, names to identify the different parts of the head. Therefore, we will borrow the names of the parts from the head of an animal, understanding however, that in our animal the parts will not be precisely as those in a quadrupedal animal. Thus, we will name the two lateral parts the *cheeks*, and we will divide the middle part into three parts, which we will name the *forehead*, the *nose*, and the *lips*. There is above on both sides of the forehead two hemispheres or tubercles, which we call the *eyes*. Besides this, we note in some Examples, where commonly are found the eyes, certain cylindrical protuberances, which resemble long ears or horns, and which are covered with small grains and, as regards to the structure, much resemble the eyes of certain Insects. As I do not have all the necessary experience, I dare not determine if these protuberances, in the species of Trilobites which have them, precisely what are in others the hemispheres that we have named the eyes, although it is sure that I have observed two kinds of such Examples. In some which had the protuberances garnished with small grains, it could be seen near these protuberances and toward the forehead, an additional two small, commonly lengthened tubercles, while in others, the forehead was flat, and it seemed that these horns touched above the hemispheres which we call the eyes. Whether they are horns or something else, we will nevertheless call them horns in order to distinguish them from these hemispheric eyes; this is even though we are inclined to accept these for some other thing, and we might discover there a very artificial structure of eyes. All we need is for time to open our eyes in order to judge those of this animal.

We have said that the middle part of the shell, or the forehead, the nose, and the lips, are separated from the cheeks by two furrows. These furrows are sometimes straight and without curves,[21] which gives to the forehead and the nose an equal width, but most of these furrows arc,[22] and the arcs are sometimes narrow, and sometimes wide, sometimes turning inward and sometimes turning outward so that the shape of the forehead and of the nose are presented in a different manner following the difference of these arcs. Some have two similar arcs, while others have three. Most of these Trilobites, which have such furrows curved between the forehead and the cheeks, have united cheeks, where tubercles are not seen, except those formed by these arcs. I have also noticed that Trilobites which have such arcs, have for the most part noses of a mediocre width, but at the same time these are more elevated.

The *forehead* is the superior part of the middle of the shell, which is held close to the shell of the back by a connection. It is sometimes flat, sometimes strongly convex, ordinarily more narrow than the nose,[23] commonly smooth, and marked with a ridge, which consists of a elevated transverse line. Above the forehead is the *headband*, which passes above, on the cheeks and the temples, and which consists of an edge that, bit by bit, takes the shape of the three arcs, and which unites the lobes of the back; that is to say, it unites the first ring of three arcs of the back shell to the head[24]. If we give to this headband the name of *collum trilobum*, and accept it as the neck of the animal, I will be agreeable with this nomenclature. This part is damaged in most of the isolated head shields found, or else, it is pushed in too far forward in the stone to be easily noticed. The *nose* is like the flat nose of a Negro. When, ordinarily, the furrows below, on the lip, form a strong arc directed outwardly, the nose is in this case always larger than the forehead[25]. It is flat even though, the entire shell of the head being convex, it is more elevated than the cheeks. The eyes are hemispheres, and in proportion to the head, smaller or larger, more or less elevated or flattened[26]. Ordinarily these are located at the two sides of the forehead, at the superior part of the cheeks, although in some they are found lower, at the two sides of the nose. At the side of the eyes are found, in some individuals, three or four small tubercles, which differ from eyes only by their size. They are commonly closer to the forehead than the larger hemispheres, which we have named the eyes.[26a] The cheeks are a little convex, in some species more or less large, depending on whether the furrows, which form the shape of the forehead and the nose, make a greater or lesser arc. Consequently, if the nose is quite large, the cheeks are small. They have, in a way, a triangular shape, and they are placed in such a way that, there, where the lateral lobes begin, they terminate in a point which, in some enrolled Examples, come forward a little; we may conjecture that this point or sting may serve as a last defense to this animal, in case its armor or shell, into which it could envelop itself, should fail. Here we give the name of *lips* to the part which Inspector Wilckens[27] names the pivot (*Hängestok*). It forms a round arc, so that, from the extremity of one of its cheeks, which is closer to one of its lateral lobes, it goes to about the same height at its opposite cheek.

What is the most remarkable on the head of this animal is the horns;[28] this is the name that we have given to those cylindrical protuberances, which are raised on both sides of the forehead. We cannot yet determine the use for these for this animal, or for some other parts; in any case, I am convinced that these parts, as found on this Trilobite, if found on an Insect, I would take them, without hesitation, to be eyes. Meanwhile, we leave them the name of "horns," to distinguish these from the hemispheres, which we have named the "eyes." We do not find these horns in all the animals found, nor in any which British authors have written about in the *Philosophical Transactions*; this difference, as well as several others which we have already noticed on the head shield of this animal, informs us that the Trilobite is a widespread type of animal consisting of a very large number of species and subordinate species. When the horns are found on a Trilobite, they are located on the superior part of the cheek, on both sides. Some terminate in points; others have, above, instead of the point, a small surface in the shape of a crescent, in the middle of which is a small conical protuberance. These horns are garnished with very fine grains, with such regularity, that it would be hard to imagine something finer and neater. These grains are closely packed, are all perfectly of the same size, and go in straight lines around the horns. They present themselves in three different manners: firstly, they are whole, undamaged, and they are found on the horns like grains of millet, in a manner so that one half are ensconced in the stone, and the others stand out, brilliantly, just like Onyx; or secondly, they are found blunted, and it is then that one does not observe the grains, but simply the circular shapes which enclose each the other half of the small grains; or thirdly, these grains have fallen off, and it is then that may be well seen circular shapes, which instead of being filled, are each a hemispherical cavity. In this last case, which is not observable without the aid of a microscope, one may see very clearly, but small, a kind of beehive cells, also symmetrically arranged as such cells are.

We must not fail to mention here a certain crustacean Insect whose eyes exactly resemble those parts, which we have here named above the Horns of the Trilobites. Here I allow my readers to reflect, if these parts can be utilized to find the analog, and I am content to add here, that this testaceous Insect has its back composed of similar rings as that of Trilobites, except that it is not divided into three lobes. This crustacean Insect is given the name of Iceland Sea Aselle, Cloporte or Scolopendra (*Oscabiörn*) and, after the reports of Thorlenius and of Borrichius, there is, in the *Neue Gesellschaftliche Erzählungen*,[29] the following description for the eyes: The eyes of this marine louse merit being admired; they are infinite in numbers, are solidly encased in a horny membrane, of oblong shape and greenish color, ... being yet in the head shield they present themselves as a network composed of a thousand scales, somewhat greenish; with the aid of a magnifying glass it is seen that they consist of two oblong and convex horns, where are observed in each at least two hundred little eyes with their eye sockets; but it is with difficulty that they may be exactly counted ... with their cells, they seem like a honeycomb. Until the anonymous author of *Neue Gesellschaftliche Erzählungen*, Borrichius gives to this crustacean Insect, whose back resembles the tail of a crayfish, the name of *Argus Islandicus* because of the great number of its eyes, and because it is native to the sea of Iceland.

I was not able to discover other parts to the head of this animal. In the Swedish *Kongliga Vetenskaps Academiens Handlingar*, there is represented a similar Trilobite with antennae. Even though I have examined a great number of Trilobites, and that my colleagues, principally Provost Gentzmar, Dr. Hempel and Pastor Woltersdorff were kind enough to provide me, for this purpose, the best and the most instructive pieces, I have not been able to find, other than these horns, which I described above, the least vestige of any antennae, things that I believe impossible by itself in a Petrifaction. For this reason, I reject as questionable the authenticity of this figure until I may be convinced otherwise. Anyhow, if we would suppose that this animal has, under its shell, antennae like a snail, they could not have petrified any better than another fleshy part subject to putrefaction. Perhaps part of the inferior and slightly raised edge of its lips were mistaken for antennae.

The *back* has the character by which this animal is distinguished from all other crustacean animals. It is divided into three lobes, and is covered similarly by a scale, whose three lobes are composed, like the tail of a crayfish, of rings which pass one into the other when the animal extends itself or bends upward, and which move one under the other, and enlarge when the animal enrolls unto itself in such a manner that the head and the tail approach each other.[30] Ordinarily, these three lobes are of the same width, although there are Examples where the middle lobe is more narrow, and other Examples where it is wider, larger and considerably higher than the two side lobes. The rings are ordinarily of a thinner shell than that which covers the tail and the head of the animal, probably because it is there that the animal can least bear any lesion. The delicacy of this part may well be the reason that these Trilobites are mostly broken and destroyed before they pass into the Kingdom of Fossils. It is rare that is found such a ring, where its three arcs have remained entire. These rings are united at a small furrow which they have near the two extremities, where they cover the lateral lobes.[31] Each ring consists of three inflections or three arcs, so that they always cover part of the entire back, which is composed of three lobes; thus the number of rings is the same for each lobe. These three curves appear in some Examples to not consist of a one piece shell, since the two furrows of the back, which is divided into three lobes, sometimes appears separated and interrupted.[32] Perhaps this is due to a hardened mud, which clings to it; if we could remove it from the scale which is hidden below, we could see that each ring of the back consists of three arcs, which together form an entire ring. The most remarkable thing about these rings is the way that they mesh into each other and yet how they are separate from each other. Each ring is composed, so to say, of two raised, rounded striations, in such a manner that one striation is more elevated than another. This last striation, less elevated, is hidden below the ring which immediately follows it, when the animal is extended, but when the animal is curled, this less elevated striation only shows between the rings of the center lobe, although when the animal turns, the rings separate one from the other such as with the tail of a curled-up crayfish. Inspector Wilckens has noted this same particular circumstance in Trilobites, in his fine Treatise: *Nachricht von Seltenen Versteinerungen*, page 7. I will report his description: "there is," he says, "between each articulation, in the middle a spherical prominence, which meshes perfectly into the cavity of a ring, and meets it, without adhering to it. Instead, it is rather attached to the greatest elevation of the ring which is below it as if it were part of it, and all being jointed together, it fills the cavity of the articulation, which was previously curved, and it advances even a little, as it seems, below this articulation. However, each of these prominences is separated by a little furrow from the ring on which it is."

The number of rings is not the same for all individuals. Eight, ten, twelve, and more rings have been counted; some Naturalists have counted twenty four. It is possible however that they have taken the furrows of the tail for rings, and counted these. Probably these rings hold to each other by certain nerves, in such a manner that the animal living underneath is able to turn as it will, and thus, following their movement, the rings can easily mesh one into the other, or separate each from the other. After the death of the animal, these nerves putrefy, as it seems, must happen soon, so it must be that these rings detach one from the other, and separate from the head shield and the tail. There must be, as we may conjecture from some Examples, under these rings, as well as below the shell of the tail, a membranous skin, which retains it after death. This could explain a certain phenomenon. The rings being crustacean, and by that being disposed to curve or to furrow, are symmetrically placed, whether the animal is extended or enrolled on itself, and represent scales that are united, and the furrows are never irregular or contorted. However, Examples have been found, which on the three lobes up to the extremity of the tail, do not present as many of the rings united, and even that they pull away from each other, so that the folds are not too regular. It appears that these Examples have been stricken bare from their natural shell, or else they remained in their matrices when it was separated, in such a way that only the core was found, thus presenting the ridges of its contracted skin. In this case, this skin still exists, or else, only its imprint is seen on the core. These wrinkles then go to the extremity of the tail, which for this reason is much more curved in those Examples which are contracted, than in those which still have their natural shell. It seems to me that it is this type under which we must place Linck's well known Example.

The tail, or rather the extremity of the tail, is not less different than the head shield, or the shell which covers the head. If, however, each type of head shield suggests its own type of tail, which particular one belongs to which type of head shield or another, is something that one could not yet determine, it being that we only find the shells of the head and of the tail mostly separated and isolated from each other. The shell of the tail consists only of one piece, like the head shield, and has two longitudinal furrows, thus dividing it into three lobes, so that, near the extremity of the shell, the middle lobe terminates in a blunted point.[33] The shell, in itself, has the shape of a semi-oval or a semi-circle,[34] or else it is sometimes conical.[35] There is not in all others the same proportion between their width and their length. There are some that are longer and more narrow than others.[36] All three lobes are convex,[37] and end below in the middle of the edge as a more or less blunted point. The middle lobe is ordinarily narrower and shorter,[38] but also more convex than the two lateral lobes. However, there are some that have the middle lobe quite wide, and where the inferior extremity doesn't have a blunted point, but are perfectly round in shape.[39] When the two lateral lobes still have their natural shell, they meet below under the middle lobe,[40] or else, the extremity of the tail is either pushed too far into the shell, or the shell was destroyed. Around the lateral lobes may be seen in several a smooth edge[41] which is continuous with the rest of the shell, and it is this circumstance that makes us believe that this edge is not the skin of the animal,[42] although otherwise this skin could not be contiguous with the shell itself. We observe on top, there where the tail is attached to the back, a narrow edge which is somewhat raised. This edge, which when separated, presents a slanted surface, thus justifies the conjecture that the tail is attached to the back only by a strong ligament which is in the middle.

The three lobes of the tail differ in several manners in regard to the surface of the shell. I only know one single species, which has the shell totally smooth and without folds,[43] all others have folds, but at the same time, they also differ much between each other, so we must refrain, where the shell is missing, from taking for the shell itself, the contracted and folded skin which is below. In some of these it is merely the middle lobe which is transversely folded, and it is there that the lateral lobes are smooth, and thus neither too convex nor too curved,[44] and the transverse folds of the middle lobe are more or less flat or pushed in. We must place here a very small species of tail shells, which is found in a black Stinkstone in the environs of Berlin, and which, unless I am in error, is also found in the countryside of Mecklenburg. Its three lobes are smooth, but the middle one has certain prominences, which on both sides project obliquely toward the top, unite in the center of the middle lobe, and appear to form, so to say, an obtuse angle. The shells of the tail, which are found in the alum shales of Andrarum, and which are known of in the *Mineralogia et Lithographica Svecana* of Bromell, are this same species, but finer and sharper, and with this difference, that toward the inferior extremity they show a compressed arc, and there it is observed both at the extremity of the edge, and also where the middle lobe ends, an elevated transverse striation. I thought at the beginning to see in this shape a particular type of head shield of the Trilobite, but I was disenchanted when examining with more attention this shale of Andrarum. It is, as all the circumstances prove, the tail of a particular species of Trilobite. In others all three lobes are folded,[45] and these folds, as they go toward the extremity, become narrower and finer, but they differ from each other in that, in some, they are quite large and few in number,[46] and in others narrow and numerous,[47] or there are also cases where, the sides, which are elevated between the folds, are sometimes finer or thicker. In some the sides always unite, two by two, to the extremities, where they bifurcate.[48] In some species the number of folds on the lateral lobes is equal to that of the folds of the middle lobe,[49] while in others, the middle lobes have more folds than the two lateral lobes.[50] The folds themselves are either smooth or garnished with grains; in this case the grains are found either simply on the middle lobe,[51] or in one row, or in two rows, or these grains are found also on the lateral lobes. The number of these small protuberances or grains, especially on the middle lobe, is sometimes larger, sometimes smaller, but all these grains become successively smaller and more closely spaced toward the extremity. The disposition of the furrows, on the side where they begin, is also not the same in all the individuals. On the middle lobe, these furrows are always transverse. On the lateral lobes, it is not always the same, but they descend in an oblique direction, and form an angle where they join the furrows of the middle lobe.

Here is another circumstance of the tail of the Trilobites which should not be neglected. The difference in size of the shells of the head and of the back is not as perceptible as in the shells of the tail. The reason must be due to the large quantity of the latter. Had we found as many shells of the head and of the back, as of the tail, we would find among these the same differences in size. There are shells of the tail that are barely the size of a pin head, but there are also some the size of a hand and larger, and even pieces half a foot long.[52] It can be judged that this important difference is not simply due to growth, but also due to generic size, and it must be that in the sea there are creatures of this kind, where their length must be greater than one-half ell, it being that the shell of the tail is one-third or one-quarter of the total length of the animal. Independently of this, we cannot yet determine exactly, by the shape of the tail, the actual genus with respect to its natural size. It was discovered, even among the little ones, with the help of a magnifying glass, these same species differences, as we have indicated above, and I have noticed this same difference in the Trilobites which are the size of a hand.

In the countries which are preferably the home of the Trilobites, are found, mixed with the Trilobites, certain Petrifactions where we are not positive if they should be classified as the genus of Trilobites; else, these are other bodies, which by hazard have mixed with the Trilobites, and whose analogues are also unknown. These bodies are not all of the same type. We could easily divide these into four Classes. For those that belong in the first Class, it is most probable that they are the tails of certain particular species of Trilobites; there we can, for example, place the Petrifactions of Westgötland, which Mr. Bromell has communicated in his *Mineralogia et Lithographica Svecana*.[53] Apparently, we should also mention here all the squarish Trilobites that this Naturalist[54] and Mr. Linné[55] have observed in the alum shales of Andrarum. These are commonly found mixed with the tail of Trilobites, and they could be isolated pieces of the back shells with three arcs, and even of that species, where the middle lobe is more convex than the lateral lobes.[55*] For the bodies of the second Class, it is still very doubtful that they belong to a genus of Trilobite. It is there that we are to classify this Petrifaction of which Inspector Wilckens[56] gave us a detailed description, and which we generally take to be the fry of Trilobites. We can only attest on those stones where Trilobite bodies are found in such great quantities that it is as if they had been sown; here there are only isolated pieces which have great resemblance to Trilobite tails. However, for the most part, they do not resemble them at all, and, up to now, I have not found any at all where I could discover the least vestige of any furrows or striations as are seen on tails, even with examination using the best Microscopes. However, it is for sure that these small bodies consist of a shell where its inferior surface has a concave shape and where in the upper convexities we note something which resembles lobes. If these small shells are also found with larger pieces, and this I can not tell, but I am certain, that on all the pieces which up to now fell into my hands, that I have never found any vestige of a true Trilobite tail. We will place in the third Class all those bodies which truly resemble Trilobites, but where it is noted that they belong to bivalves, where one valve has in the middle a round fold which is much raised, and where the other has this same fold, but where instead of being convex, is pushed in. Of these there are many species in the Kingdom of Petrifactions. Some are classified with ammonites, other as pectunculites, and particularly those that are striated, and also those among the false arches; here principally are those where the extremities of the hinge are far from each other. It is among these true bivalved conchs with three lobes that we also need to report that species, for which Inspector Wilckens[57] has provided a drawing. In the fourth Class, we place certain bodies which are found among and with the Trilobites, but which evidently must be taken as unknown, and which we do not have the time or the space to handle here as a treatise. Perhaps, these are the shells of certain crayfish of the North Sea that are still unknown, and of other crustacean Insects.[58]

Up to now, I have thus described with all possible exactitude all the parts of this creature which has been given the name of Trilobite. Before I talk about its analog, the question comes: should it not be possible to make a certain classification of the different species and subordinate species which we have noted? I think that up to now, it is too soon to think about it. Up to now, we have found too few perfect and instructive Examples, notwithstanding the quantity of isolated pieces and tail shells produced in the Kingdom of Fossils. We are thus not yet capable to advise exactly as to the shape of each species of Trilobite, and neither to determine which species of head shield belongs to what tail. For sure, at least when we have found more, the division will be founded principally on the form of the head; by this same reasoning, I suggest to make a small attempt and propose as a prelude a sketch of the Classification of Trilobites. The principal division should be founded on the difference in the furrows of the head shield. Some species have no furrows at all, and actually the shell is convex without any depression;[59] others have furrows which are not curved, and where the two furrows which divide the head in three equal size lobes, descend in a straight line from the forehead to the lip;[60] and others yet have curved furrows. It is this kind of Trilobite which is the most common, and thus the direction of the curve determines the different subordinate species. So as the arcs of these furrows are larger or smaller, or more or less numerous, these animals have the forehead and the nose sometimes narrow, sometimes wide, and the cheeks sometimes large, sometimes small. In this manner, some have, for example, the forehead narrow, the nose large and the cheeks narrow,[61] others have the forehead narrow, and most often enlarge as a vase toward the extremities by curved grooves, and have a narrow nose and large cheeks,[62] others which have the forehead wide, the nose wider and the cheeks almost imperceptible,[63] and to finish this list, there are others which have the forehead wide, the nose narrow (which does not widen until near the lip, at the bottom) and the cheeks round and quite large.[64] I am doubtful here, if I should place for now into a particular class the Trilobites which have horns, as mentioned above, for who knows if most of the heads of Trilobites which have been found don't have similar horns on their tubercles, and these have been lost. Perhaps this will be clarified in the future.

What, then, is the present analog of this particular creature, which the Kingdom of Fossils allowed us to find? Has it already been found, or where should we search for it? Is there already a kind of animal, under which we could classify the analog in case it is found? Should we look among the Insects, or among shells, or somewhere else? These are the most difficult questions where we need a positive response, questions which our best Naturalists have tried to resolve. As to this analog, I will firstly report the different opinions, examine them, and then add my own opinion.

The opinions of the Naturalists with regard to the analog of the Trilobites may easily be sorted into three classes. This is because some believed it is to be found among the Insects, others among the shells, and yet others among other kinds of marine bodies. The Partisans of the first opinion are Lyttleton,[65] Mortimer,[66] Bromell,[67] Sir Linné,[68] Wilckens,[69] Davila,[70] Guettard,[71] Emanuel Mendez da Costa[72] and several others, and these differ still between each other on several points. Several, and in particular, Mr. Bromell, have taken the Trilobites to be Petrifactions of Coleopteran Insects, Scarabs, and other Insects of this kind, and have thought they had seen in these stones the vestiges of these small animals (*Scarabæorum vel aliorum vaginipennium animalculorum vestigia*.). Others, on the contrary, have classified these with the wingless Apteran Insects, but they have not agreed as to whether they should search for the analogue in the crayfish or among the Monocules. Mr. Guettard and Mr. Davila place them among the Astacoliths, and believe that these are crustacean animals, which have an articulated back, since all crayfish have an articulated tail. They classify the Trilobites among the sea lice (*Pediculus marinus*), and if these Naturalists such as Mr. Emanuel Mendez da Costa, of whom I will talk later, understand this animal under the name of *Pediculus marinus*, the Insect of the Sea, which is named *Oscabiörn* in Iceland, and whose back resembles a crayfish tail, they have, following my opinion, come nearest to the true analog of the Trilobite, as I will prove later. In examining the Insect which carries the name *Oscabiörn*, I myself fell into the conjecture that the analog of the Trilobites must belong to this genus, before I became aware of the thoughts of three knowledgeable Naturalists. Messrs. Linné, Mortimer, and Wilckens supposed that their analog belonged to the genus of animals that are called Monocules (*Monoculus*). The first is in some doubt yet, as to whether it should not be classified as a middle genus among the crayfish, the monocules and the Aselles (*Oniscus*), being that the distinction between them is that they have an oval shape with twenty intersections; as to the feet, he adds, which in this genus separate easily with the animal destroyed, they have not yet been seen distinctly. In *Museum Tessinianum*, p. 98, he declares this Petrifaction to be a *Monoculus*, and he also gives it feet, although here some error must have slipped in. For if the Example which is represented on Plate 3 effectively has feet, its back cannot be divided into three lobes, and thus it is not a Trilobite. However, if he has taken the two lateral lobes, which are ensconced too far into the matrix, for the feet, and that these supposed feet are really lobes, there is no longer any reason to give feet to this Example. He has confirmed this same opinion in a letter addressed to Provost Gentzmar dated 9 November 1767, "*It cannot be a Testacean or a Chiton. I am convinced that it may be a species of Monocule, although the animal has not yet been discovered*." Mr. Mortimer supposes that the analog to the Trilobite is in affinity with the *Scolopendra aquatica scutata*, the same one that Mr. Klein has described with that name in the *Philosophical Transactions*, vol. 40, number 447, p. 150, but this is precisely the Monocule of which Mr. Schaeffer[73] gave a detailed description. Inspector Wilckens thought he had found the analog among the Monocules, and even among these same Monocules a form of crayfish, although he could not precisely say that the Monocule, which Monsignor Schaeffer gives a description, is in fact the analog of our Trilobites, but he supposes that it belongs, as another unknown species of the genus *Monoculus*, and that it is probably a species that is more likely found in swampy lakes, and maybe even the sea, rather than in fresh waters. Mr. da Costa[74] gives as its analog the Sea Louse name (*Pediculus marinus*), which belongs, as I see it, as well as to the Chitons, as to a marine Insect of the North, which has feet, and of which I will talk in more detail later. However, he believes that the true analog has not yet been discovered, and rather he gives to our Trilobite the name of *Pediculus marinus maior trilobus*. Mr. Lehmann has inserted in volume 10 of *Novi Commentarii Academiae Scientiarvm Imperialis Petropolitanae*, p. 410 and following, a treatise on *Entrochis* and *Asteriis columnaribus*, where he yet has some doubt as to why he has to have the name of Three-Lobed Conch. Later, and after this Volume was already printed, he added in the Summary an Annotation, where he declares that the *Oniscus*, which he believes properly, and as assured by Professor Beckmann of Göttingen, the *Oniscus entomon* of Mr. Linné is, according to his opinion, the analog of the Trilobite.

Following the second principal opinion about the analog of Trilobites, it is not an Insect, but a testaceous animal, which should be searched for among the shells. Scheuchzer,[75] Pastor Torrubia,[76] Provost Gentzmar,[77] Professor Franz Zeno[78] and several ingenious and expert Naturalists have taken this opinion. Or, as the shells are divided between conchs and snails, each has found their partisans. There was no other Naturalist, except the English scholar Leigh[79] who classified them with the snails. He believed that this Petrifaction was a piece of a Nautilus, an opinion which likely would not be adopted by anyone. All the other Naturalists thus decided on the genera of conchs as the place to find something resembling a Trilobite. Since Shells are univalved, or bivalved or multivalved, none of these classes failed to pick up some Partisan. Scheuchzer classified our Trilobite among the univalved Shells, by supposing it could well be a species of Patellite, an opinion that later the expert Professor Zeno[80] of Prague adopted. Most of the Naturalists went for bivalved Shells. Several of them took the tail of the Trilobite, before understanding it, not for a part of the entire animal, but for the entire animal, that is for an entire shell, and even for the entire valve of a bivalved conch; this is because such a tail, especially when it is described, as it often happens, as a semi-circle, and its circumferences has some resemblance to a conch. Hermann[81] was already of this opinion, and by this reasoning gave this tail the name of *Pectunculites trilobatus*. Mr. Woltsersdorff[82] also places it among the bivalved conchs, which is also done by an Anonymous author in the *Berlinisches Magazin*[83]. Some Naturalists who are of this opinion, and who know the entire shell of the Trilobite, maintain that the place of the Trilobite in the Kingdom of Shells cannot be disputed, as this animal may, as all other conchs, hide its entire fleshy body in its shell, as it may open it and close it, and that, which in other conchs is its hinge, is here its articulated back. In modern times, some Naturalists have begun the search for its analog among the multivalved conchs.

There is among these a certain genus which, as the Chiton, has a shell composed of rings, and which, like the Patellites, does not have any valve below, which attaches itself to rocks, and which, when pulled from the rocks, contracts itself like the Trilobites. It has different names; Sir Linné names it *Chiton*, others *Oscabrion*, Sea Louse, Whale Louse, *Pediculus marinus*, etc. Thus this multivalved animal must, following the opinion of some, be the genus to which the analog of our Trilobite could well belong to as a species. Two expert Naturalists are of this disposition, one being Father Torrubia,[84] and the other is my friend, Mr. Gentzmar of Stargard, with whom I have maintained correspondence, most instructive for me, for three years, on the subject of Trilobites. Father Torrubia said, that from the beginning, he took the Trilobites for a species of sea crayfish, but that later, after having seen the Ambonese Rarity Cabinet of Rumphius, and seeing what was a *Limax marina*, he had changed his mind; now he is convinced that this same *Limax* is the analog of our Trilobite.

And finally, we must make mention of the third principal opinion on the subject of the Trilobite analog, and it is the one that will classify it neither with the Insects nor with the shells. This is the way that Brückmann[85] says that the Trilobite is the Petrifaction of a Sea Polyp, without further explanation, and that others maintain, following the report of Inspector Wilckens,[86] classifying it within the genus *Tethys*. Whatever animal species is properly understood by that, this I cannot tell. I do not expect that they will search for the analog among the Molluscs where, as is known well enough, the Tethys belongs.

Several of these opinions do not have the least probability, and a verbose refutation would be easy but superfluous. Other opinions are more plausible, and merit examination with more attention. All these opinions agree on the principal point, that is the analog must belong to the Animal Kingdom, and even to the marine animals. The Partisans of this opinion agree furthermore that the true analog has not yet been located, it being that up to now, of all the marine bodies, none have yet been found which have the back divided into three lobes, and additionally it being articulated. Consequently, when they talk about the analog to the Trilobite, and when they propose their conjectures about it, they only propose to indicate the category, to which the analog, yet to be discovered, must belong, a species to date unknown in its natural state; or else, they determine a species, to which this unknown body could be considered as a subordinate species. It is there that they all agree, but then divide into two principal camps, so that one side places the supposed analog, yet to be discovered, among the shells, and the other side among the Insects. To be sure, this will easily be decided when the analog is found, and meanwhile, numerous things can be said as a preamble of this topic, it being that it can be judged by the character of Classes and of genera, which were adopted and established in the Animal Kingdom.

When it is a question in general, if it is more proper to place the analog among the shells or among the Insects, I must admit ingenuously that here and there, some of these opinions have good arguments, however several difficulties will assail them. The Test, and principally that of the tail, perfectly resembles, in all its substance, and its laminated tissues, that of seashells, and as we already know there are shells whose back resembles a crayfish tail, as for example the Chitons; beyond that, there are shells, which have only a shell on one side, and whose other side clings firmly to rocks, as for example the Patelles; and also, following Rumphius' report, those snails, when they are ripped from their place, contract upon themselves the same as our Trilobites, and give their oblong bodies a round shape; it almost seems that the *Limax* of Rumphius, which we will learn at closer hand later, is the analog of our Petrifaction. Independently from those who take the analog to be an Insect, they are not yet willing to concede, and they still have good reasons for it. In their opinion, the total form of a Trilobite is repugnant to the constant and essential characters of a shell, and even the specific difference that there is between a shell (*animal testaceum*) and a crustacean Insect (*Insectum crustaceum*) removes doubts to the opinion about the Trilobites' analog so that it cannot be a shell, but must be a crustacean Insect. The Test of a testaceous animal never has, as we know, articulations in a manner where can be distinguished in the shell, the head, the back and the tail, and that even in these principal parts, may be distinguished yet other parts, as for example, the tubercles and the Horns of the head of a Chiton. Rather, the shell of a testaceous animal is continuous, without it having separate members and parts of the body, whether the shell is jar shaped or in the shape of a pipe or some other shape. In contrast, we observe in the Insects, for example in the crayfish, the Aselles, the Monocules, etc., that their distinctive Character consists in these visible characters, which constitute the difference in the head, the back and the tail, and as they purport, not without good reason, manifest against all the Zoological Principles, leading to the conclusion that an animal such as the Trilobite is a testaceous animal. Truly, there is not much to be said about that. But no matter, the opposite party fights in the same way the idea that Insects are the pretended analogs of the Trilobite, and would we not think that they would find repugnant even the idea of representing an Insect without feet? The Trilobite has no feet, since they have never been discovered in the petrified Examples that have been found, and as a consequence it could not be a crustaceous animal, and, as there is not a third type, we must place it among the testaceans. This objection has much likelihood, although I think that there are many things to be retold here with further thought. We should suppose meanwhile, that we have not yet discovered feet in Trilobites, and we could infer by that positively, especially when we have paid attention to several particulars, which are found in this Petrifaction, and that is those feet are also missing in the analog? When only the tail of the Trilobite was known, and that it was thought to be a shell, and that this pretended shell was given a back which resembled the tail of a crayfish, when actually this had yet to be observed? Nevertheless, later this back was found, and at present, we see this rare Petrifaction from a viewpoint much different from before. How long have we not known the Trochites, the Entrochites and the Asteries before knowing the crown which they wear? If then someone had conjectured the existence of such a head or crown, they would surely have encountered many contradictions, and this would principally be based on that which has not yet been discovered about the Entrochites which up to then had been found.

There can be reasons, why the Trilobites are mostly stripped of their feet after death. The reason, why for most Trilobites the rings of the back separate from each other, and that within some hundreds of tails one can find only a single one where the rings of the back still hold firm, is the same which causes the loss of feet in Trilobites. No one will discover that the living animal, which is the analog to the Trilobite, will not have nerves by which, not only will the testaceous articulations hold to each other, but that they will also extend and contract them, and thus have free movement of their body. The ligaments, which attach the rings of the back to each other, must, as no one will also discover, be much stronger and compact than those, by which they allow movement to the soft feet.

As, for the most part, the rings of the back are separated from each other by the reason that the ligament was destroyed by the putrefaction which occurred before the dead Trilobite passed into the Kingdom of Fossils, how much more can it not be that by this same reason it was stripped of its feet? It is the same with Encrinites; why do we find such immense quantities of Trochites, why much fewer Entrochites and why yet more rarely Encrinites? Because the nervous system of this Zoophyte was destroyed before it found, in the Kingdom of Fossils, a tranquil place, and because by this destruction it must be that all these pieces separate. Thus we will not find any Echinite that will still have its spines, since the skin and the nerves, which give free movement to the spines on the test, have been destroyed by putrefaction. They must fall before the Sea Urchin passes into the Kingdom of Fossils. By consequence if the analogs of the Echinites were still unknown, no one could easily convince himself that the animal in its natural state had spines, which it used as feet.

We must still add a circumstance which merits attention. The Trilobites found in the Kingdom of Petrifactions are either stretched-out or contracted. It is probable that this animal, in dying, contracts, and if in this state it passes rapidly into the Kingdom of Fossils, it maintains its rounded form. But when its nervous system putrefies, it cannot maintain its contracted form, the dead body, being half putrefied, decomposes, and it is probable then that the feet, due to the thinness of the nerves, are first to separate, the shell of the back stays still attached a little at the head and at the tail, and by a fortunate chance, a few Trilobites find themselves in a tranquil place before being totally destroyed, but for most, the shells of the head and of the tail, being in the shape of a vase, are soon transported by water and sunk whereas the more fragile rings of the back are not. For this reason, it is not possible to find feet on stretched-out Trilobites. Beyond this, the number of stretched-out Trilobites is much too small to allow anything to be inferred in general; principally, because of the rarity of perfect Examples, no one will easily be convinced to take apart a well preserved piece to search under its shell for feet, which could well yet be hidden in its core. As for closed Trilobites, it is quite possible that, should we wish to try and cut them through the middle, that we might still find the vestiges of feet. But as the beautiful and perfect Examples are still a rarity in the Cabinets of those most knowledgeable, no one is willing to sacrifice these so as to resolve this Problem, although it would certainly be worth the effort. And after all, even if such an attempt was not successful, we still could not infer by this that Trilobites, in their natural state, had no feet. We should remember here for example the Echinites; were not many different bones contained in their shells, when they were still alive? One would think that we would find these bones in the Echinites turned to pieces, seeing that they are all around enclosed in a shell; and yet, we almost did not find at all the bones of Echinites enveloped in the cores.

All that I have just stated about the feet of the analog of the Trilobite, is well confirmed by an observation of Dr. Charles Mortimer, inserted in the *Philosophical Transactions*, vol. 46, p. 600. As I have just received this volume, in scanning it I find that among the Examples of Trilobites, which had been sent to the Royal Society of Sciences, I noticed one stretched-out Trilobite, which is referenced there as fig. 10, and below which is something that advances to one side, and which perfectly resembles feet, which up to now has not been willingly attributed to this animal. Mortimer himself is of this opinion. In explaining f. f. on fig. 10, he says there "appear some traces of feet, which seem to lie under the belly: but, as the belly, or under side, was not distinct, not being cleared from its stony and earthy matter, I could not discern any other legs." I have read Mortimer's observation with great satisfaction. As my conjecture was effectively based on such, and I do not regret at present the difficulties which I went through to make probable the existence of feet in Trilobites, before I had heard from England that they had found vestiges on one Example. And even presently I find that in France, the same discovery was made on one Example which is located in the Cabinet of Mr. Davila, as may be seen in Mr. Guettard's Treatise in the *Histoire de l'Académie Royale des Sciences* for the year 1757, p. 82. The opinion of finding the Trilobite's analog among the shells thus falls by itself.

Up to now, we have only considered in general the question of whether the Trilobites should be classified with the shells or with the crustacean Insects. We are now arriving at the opinions of the Naturalists, in particular to the subject of the analog of the Trilobites. I am here only reporting on those which merit our examination and our attention.

The opinion that the Trilobite is half of a bivalved conch, falls by itself, as this idea only took place with regard to the tail, and as long as we had not yet the entire body of the Trilobite, and that we were persuaded that this tail was its entire body. If some Naturalist maintains that, notwithstanding this, we can take the entire body as a bivalved conch, and that instead of a hinge, has an articulated and flexible back, this is repugnant in general for the bivalved conch organisms, and in this case, I would much prefer to classify its analog among the Patellites or among the multivalved conchs.

The opinion that the Trilobite belongs to the Chitons, seems to have more probability, and I confess that in the beginning, I had myself adopted this idea, upon which Provost Gentzmar suggested first in Germany. Later, I obtained some species of these Chitons, in their natural state, which furnished me with the occasion to examine them more exactly, and to compare them with our Trilobites. Different names were given to the Chitons; they are called Lice of the Sea, *Pediculus marinus*, Whale Lice, Elephant Lice and Oscabrion, but manifestly it is by this last denomination that has been mistaken the Icelandic Oscabiörn, which is a crustacean Insect having fourteen feet, and which we will understand better later on. For Chitons belong to the shells, and not to the articulates; in contrast, the Oscabiörns belong to the Insects and much resemble the Cloportes (*Oniscus*) and for this reason most Naturalists classify them thus. The shells of the Chitons perfectly resemble an egg cut longitudinally in two pieces, it is hollow below, and hemispherical above, and because of this, it is comparable to a large nacelle. The entire shell is composed, as the Trilobite, of rings, that following the movement that the animal makes to stretch or contract, enter or slip one under the other. We count at least six and at the most eight of these rings. As this is a mollusc which lives in this shell, there is no visible articulation, as in the crustacean Insects, and for this reason, it is not possible to distinguish the shell of the head or of the tail, but its entire hemispherical testaceous armor is composed of rings, with this difference, that it has an oval contour, and the rings are shorter and more blunt toward the extremities than in the middle. There are on the same rings elevated sheets, wide at the base, and pointed higher toward the back, which Rumphius[87] calls spines. Below, at the edge of its shell there is all around a large, tough roll, to which the rings are attached. This roll is garnished with very fine scales, making it appear as grainy leather. The Chitons grab hold of rocks at the bottom of the sea, like the Patelles, so that they are only removed with great difficulty, and then they contort and enroll upon themselves. There are several species of these Chitons,[88] but they all are similar with regards to this generic character to which I am referring. They are represented in the Works of Mr. d'Argenville,[89] Seba,[90] Rumphius[91] and Knorr,[92] without even mentioning others. In the meanwhile we have not said with reference to this multivalved marine body more than was necessary for this. There is still the question which is, could this Chiton be the analog to our Trilobites? Here are the arguments which have made me doubt it. The Chiton has neither a helmet, nor a shell for a tail, and cannot have it as long as it is classified with the shells; in opposition, in the Trilobite may be seen distinctly testaceous articulations, a helmet and a test on the back and on the tail. The rings or the scales of the Chiton are garnished with a kind of elevated sheets and pointed or flattened spines, characters which are entirely missing in the Trilobites. All around the shell of the Chiton is a rolled edge, elevated and scaly, but this scaly roll is not found in the Trilobites. Mr. Davila has in his Cabinet a considerable quantity of Chitons and even several species of Trilobites. He makes an effort with Mr. Guettard, who knows Chitons only too well, to show their analog, and yet among all these Chitons, he has not found a single species that has any resemblance to the Trilobite. For this reason he classifies the Chitons among the multivalved conchs, and on the other hand he classes the Trilobites among the crustacean Insects and even with the Astacoliths.

To give my ingenuous opinion, I find much less resemblance between a Monocule and a Trilobite than between a Trilobite and a Chiton. It is thus a must that in all the Examples the convex and horny skin of the back has been lost, and yet in all the members and the parts of its body it is the most disposed to become petrified. The articulated or ringed body hidden below this shell is of a substance much too soft to resist putrefaction, to not contract, and, which is the most remarkable, to change it to a layered and hard scale. As to the shell of the tail, which already in its natural state must be either crustaceous or testaceous, there is not the least vestige. If it was supposed that the body of a Monocule was petrified and stripped of its shell, it would be that only the soft flexible skin was petrified, or else that the soft fleshy substance followed the same change. In the first case, we would not understand how this soft skin could, without putrefying, and without contracting, separate from the flesh, and without suffering any compression, be enveloped in stone with such regularity. In the last case, there must at least be found under the shell of the back of the Trilobite a spathic substance born of the petrified soft parts of the animal; anyhow, as well as I know, this was never found, and this makes us conjecture that it is nothing but a simple shell that was either crustaceous or testaceous, which passed into the Kingdom of Fossils, and which is now presented as the body which we call a Trilobite.

To state my opinion on the subject of the analog of this Petrifaction, up to now I believe that it has not yet been discovered, since among all the animals, testaceous as well as crustaceous, we have not found a single one, which has all and at the same time, an armor of the back divided in three lobes, a shell of the head or a helmet and a shell of the tail. I could not be less convinced that we must search for the analog in the sea, as it is generally found in marbles and calcareous stones, which get their origins from the sea, and that are found in the company of marine bodies and not with terrestrial bodies. I also believe that if we discover the true analog, it could well constitute a separate genus, as it cannot be conveniently placed under known genera, unless that we wanted to establish characteristics too expansive and not determined enough, and in determining the genus, neglect those characteristics which are essential to these bodies. I am also of the sentiment that up to now it is too early to determine the genus of the Trilobites, even to establish with certitude a species of a genus already known, be it either shells or be it Insects. As much as the affair does not have to be decided but only by appraising those, for the most part, imperfect Petrifactions which we have, we can always make negative conclusions rather than positive ones, being that it would be easier to say what the animal is not rather than what it is. Besides, in the Kingdom of Petrifactions, hidden from our eyes are several parts of these bodies which are for the most part destroyed, and which are after all necessary to determine the genus, and in opposition are presented several parts, which we must consider from a different perspective, that we are quite pleased to be able to compare with the body itself an analog which is unknown up to now, and which will then be known. The Belemnite and the Trilobite will justify some day well enough the conjecture that I have proposed here. But when some day the analog of the Trilobite will be discovered, the Zoologist will have no problem in assigning its place among the animals, and to classify it either in a genus already established or, as I suppose it, to establish it as a separate genus. At present, the best position is that of searching among the marine testaceous bodies which have already been found, without paying attention to their Classes, families and genera, or to the Classification methods, which anyway are quite variable, for this body within the confines of which our Trilobite would most likely be placed, if it could be found. All depends to the more or less great resemblance that there is between our Trilobite and marine bodies which have already been discovered. Either I find the greatest resemblance, or in the marine body I find essential qualities with regard to the external and visible organic structure, or the entire shape of the Test, or the ringed back, (because it is there that are the essential and visible characters, that Nature presents us so as to discern bodies from each other); or I find, I say, these marks and these characteristic traits, which agree the most, and in the most natural way and without the help of our imagination, with the Trilobite; in the meanwhile, it is within the confines of the Animal Kingdom that I must place the Trilobite, until we are proposed a more founded and a more probable opinion, and then I will be the first to recognize and retract my error. In the seas of the North, and thus by consequence in the countries, where principally, solid earth is the home of the Trilobites, there is a certain marine testaceous Insect, which the habitants of Iceland call Oscabiörn. It is also named Aselle of the Sea, since it is found in the sea, and much resembles the Aselle or Cloporte. I have myself, in my cabinet, such an Insect, and I have compared it exactly with the descriptions and the drawings that have been given me as well as with my Trilobites. Each lobe of the Trilobite has much resemblance with the testaceous back of this Insect, and it is only missing the two grooves to have it become three lobed like that of the Trilobites. Hannes Thorlev, born in Iceland, gave us a description of this Insect which may be found in Bartholin's *Acta Physico-Medica*.[93] After this author, another anonymous author has inserted a very exact description of this Insect in the *Neue Gesellschaftliche Erzählungen*.[94] The body of this Insect is oval. The head, the back and the tail are covered by a smooth shell, which is similar in several ways to that of a crayfish, but which appears to be of a more compact substance than that of a river crayfish, so that I am almost tempted to believe that this shell, especially when it is strong and thick, must have divided into sheets. The shell of the head or the helmet, as in the Trilobites, only consists of a single piece. In some, as may be seen in *Museum Wormianum*,[95] this shell is large and perfectly proportioned to the size of the head of the Trilobite and to the rest of its body. In others, as in my Example, this shell is considerably smaller, although it has, as do the Trilobites, two fine curved furrows, which start above near the first articulation of the back, and which disappear slowly, below, near the lip. This back is similarly composed, as I just stated, in all the Trilobites, of rings, which enter or slip one under the other, and it is only missing the double furrows to give it the shape of a three-lobed back. The number of these rings of the back is unequal; in my Example, I count twelve, and in Worm's Example, the shell of the tail is very small, unless it had been mutilated, because in my Example, I have noted that the smallest violence is enough to separate the articulations of the back. On the other hand, in the Example which I have in my Cabinet, and that which Monsignor Gesner has communicated in *Insectis Marinis*, p. 268, the shell of the tail is much larger than in that of Worm's, which ends as a blunted end, and its shape totally resembles the shell of the tail of a Trilobite, except that it is not divided into three lobes, and that the transverse folds are missing, as it is completely smooth. As to the rest, the shell is pretty well at the proportion of the body; and as my Example is about an inch long, it must be that in the larger Examples that have a length of four or five inches, the shell must be of a considerable thickness. We see at the inferior part fourteen very soft feet, with their extremity furnished with a recurved hook such as the claw of a bird. With these nails, these Insects attach themselves to fish, such that they cannot remove themselves readily. They hold firmly in place where they attached themselves, and kill the fish by sucking its blood. In some of these small animals, the shell of the head is furnished with two prominences; it is with reason that I say in some, because in my Example there are none. These protuberances are the eyes of this Insect. Following Thorlev and Borrichius' description[96] they resemble exactly the granulated horns of some Trilobites. Below the shell of the back we have not yet discovered, besides the feet, any viscera, however a viscous and gelatinous substance, which hardens in time, was found. This substance is scissile, half transparent, and generally reddish yellow. The inhabitants of Iceland call it Stone of St. Peter (*Peters-Stein*). As we have not found in this animal other soft and fluid parts, and that it is for the most part hollow, it is perhaps here the reason that it can hide its feet under the shell of the back and to contract them in such a manner that they are totally hidden as in a bowl, and that from the outside, we cannot perceive any trace of feet. Thus this animal, laying on its stomach, cannot even be suspected of having a hint of feet; they even almost touch the internal surface of the shell. The individual that Worm describes with a side view of the back and the stomach shows no feet. It must already have been stripped of them because, according to Sir Linné, the feet of this testaceous Insect fall readily. Perhaps these animals hook on so tenaciously to fish with the help of their highly curved claws, that in death they remain attached. Whether the fish escapes or not, it is easy to conceive, that in putrefaction, the feet thus hooked remain attached to the fish, and that the shells that cover the head, the back and the tail, fall either together, or, which happens more often, fall in pieces.

Any impartial Naturalist agrees, that of all the marine bodies known, there is not one known which resembles more to our Trilobite than this marine Insect; at least, we can remove more easily the difficulties that are encountered with the other opinions. It suffices for me to offer a testaceous Insect, whose species include the analog of the Trilobite. I leave it to the Zoologist to find the Family and the Genus under which it may be classified. Perhaps among the Aselles (*Onisci*), shall we say. As for myself I find great difficulty with this opinion. I cannot myself classify our cloportes and other apteran molluscan Insects with the same genus as the animals which have a testaceous armor, a head shield and a shell on the tail. I admit that a cloporte has fourteen feet and as many folds on the back: must we understand, by this, that all which has fourteen feet and has folds on the back, must be an aselle? The difference that there is between a soft skin and a testaceous armor, is too essential to be neglected in the classification of the apteran Insects. It suffices then to separate all the cloportes which are covered with an armor such as the crayfish from those that have a soft skin, and to make these a particular genus, which I would place between the crayfish and the soft-skinned cloportes. This middle genus could be given the name Armadille, which anyway is given to a certain species of cloportes, and the description would be the following: *Body ovate-oblong, crustaceous, VII-XII articulated dorsal segments, shell of head & tail integrated, XIV feet*. Maybe we could classify under this new genus, which we would establish between the crayfish and the cloportes, several marine animals, which have been classified, in my opinion wrongly, among the crayfish or among the cloportes. For when we establish for the characteristic of the crayfish an articulated tail, we cannot well classify under a particular genus the marine animals that have the back articulated and armored, and to place them before the cloportes, which do not have a crustaceous armor. We would classify then, in this middle genus, most of the Insects which Mr. Linné has placed under the name of *Macroura manibus adactylis*, *Systema Naturæ, 12th Ed., Tom. I, Pars II*, p. 1054. And certainly, if we consider the *Scyllarus* in Rumphius, *D'Amboinsche Rariteitkamer*, pl. 3, fig. F, the *Pulex marinus* in Frisch, *Beschreibung von Allerley Insecten in Teutschland*, part 7, pl. 18, whose back is practically divided into three lobes, and if we pay attention to other similar aquatic Insects, we will note a very natural analogy between them and our Trilobites. I would also classify, without difficulty, in this same class the testaceous insect, whose petrifaction was communicated in the *Histoire de l'Académie Royale des Sciences* of Paris for the year 1757, p. 82, pl. 7, fig. 2. For upon close examination, we easily find a very great resemblance between the *Scyllarus* or the *Squilla arenaria marina* in Rumphius, pl. 3, fig. F, and a stretched out Trilobite, so that all these species of bodies could well constitute a middle genus under the name Armadille.

I must still deal with the condition in which this body is found in the Kingdom of Fossils, the matrix in which it is mounted, and the localities where it is found. The Trilobites which are found, are for the most part imperfect and in pieces. The shell of the tail and of the head is ordinarily isolated and separated from the lobes of the back, while their rings are found much more rarely in the stone, isolated or only partially coherent. We can allege here a most probable reason. As the shell of this animal is composed of mobile parts, tied to each other by some soft ligaments, it must be that after the death of the animal, when the soft parts and fluids putrefy, the shell falls in pieces, just as in the same situation the spines of the sea urchins fall off ordinarily. But the principal reason why so few isolated rings of the back have been found, must well be that they are for the most part too thin and too fragile that they may, as the shell of the head and of the tail, pass into the Kingdom of Fossils without being destroyed. Perhaps we have not until now examined them with enough attention for these were not known, and that probably these were taken to be fragments of papyraceous shells, as these are actually found.[97] I possess myself a slab found in the country of Mecklenburg, covered with similar isolated rings, which are spread on the stone, with several tail shells. Often the test is no longer there, or else, when the piece is fractured, there remains in this half the imprint of the animal. However, when there are some remains, they are typically white in color, or a yellow gray, sometimes dark yellow brown, which also often depends on the color and the quality of the stone in which the Petrifaction is found. The test is either petrified or calcinated,[98] or metallized; in this last case, it is ordinarily pyritized.[99] Trilobites are commonly found in the company of other marine bodies. They are found in particular with Belemnites around Prague, with Pectinites and with Pectunculites near Frankfurt-on-Oder, with Orthoceratites in the region of Mecklenburg,[100] and with Corallioliths, as may be distinctly seen on one of my examples, which offers on one side a Trilobite of average size, and on other side a *Tubularia fungiformis*.

The matrix is, particularly in the North of Germany, of a gray or reddish marble, and often it is but a piece of limestone. In other regions they are found in a smelly black stone, such as at Neuruppin, and in Sweden, as attested by Mr. Bromell, and especially in the areas around Prague. The region of Stargard also provides an arenaceous black shale, which encloses Trilobites. I have received some from Gnoyen in the area of Mecklenburg that are enveloped in a very fine greyish sandstone that is poorly compacted. In the region of Mecklenburg, they are also found in half-decomposed flint.

As for localities, they are found much more frequently in the septentrional regions than in other places. In the North of Germany, Uckermarkt and Mecklenburg offer them in abundance, and, notwithstanding that, even in those regions, nothing is rarer than a perfect Example. Very expressive specimens have been found besides in the environs of Berlin and of Frankfurt-on-Oder; the Cabinet of Mr. Woltersdorff contains some beautiful ones. The same thing can be said of several provinces of Sweden. Particularly in the regions of East-Götland and West-Götland, in Öland and in Scania, the shells of the tail of Trilobites are found in such great quantities that, referring to the report of Mr. Linné[101], they appear to form rocks. We find in particular beautiful Trilobites in England, where they are named *Dudley-Fossils*, after a place in the County of Worcester with the name of Dudley, where they are extricated from limestone quarries, sometimes loose, and sometimes fixed in their matrices, and often in large and beautiful slabs. Near Colebrookdale in Shropshire are even found very nice Trilobites, as are seen in vol. 25 of *The Gentleman's Magazine*, p. 24. Already, Lhwyd knew them under the name of *trinucleus*, and found some in Merionethshire (*Comitatus Mariduniæ*), as he tells in his first letter inserted in his *Lithophylacii Britannici Ichnographia*, p. 96.

They are also found, but much more rarely, in other regions in, as well as out of, Germany. Brückmann[102] obtained some from Stemme, in the Bishopric of Paderborn. In the *Berlinisches Magazin*[103] there was mention of those that are found near Aachen, and near Burgwenden in Thuringia. Similarly, they are found near Prague, and, apparently, they are found there as far as the chain of calcareous mountains that stretch from there toward the South-East, and where is drawn this pungent black stone. Following the remark of the late Mr. Klein[104], Mount Cyngal near Danzig also supplies these Petrifactions; however, it seems that there they are not found too frequently. They are also found in Switzerland,[105] although the simple tails that are found there are quite rare. They are also found in France, although, it appears, very rarely, in the slates of Angers.[106] In Spain, Father Torrubia, as may be read in his Natural History of Spain, has also found some at the edge of Pardos, two leagues from Molina of Aragon, in the environs of Anchuela.

To date, we can only say very little about the history of this petrifaction. During the past century, it was totally unknown; at least, I do not know any author who mentioned it. At the end of the past century and during the beginning of the present one, the English made known the first ones, without knowing what they were. Lhwyd[108] names it *trinucleus*, and admits that he does not know where to classify this petrifaction. Soon after him Leigh[109] attempts to do so, but not too successfully, considering that he decided it to be a fragment of a Nautilite. It is only ten years later that Hermann[110] located the first Trilobite in Germany, in Silesia; but he did not know, any more than the others, what to do with it; nevertheless, he conjectured that the shell of the head, which he found, could be an Echinite, and the shell of the tail, a Pectunculite. Sixteen years later, Scheuchzer[111] also found some in Switzerland. He did not guess either that it was a Trilobite, and took it to be a type of Patellite, or even an Ostracite. These knowledgeable Naturalists ignored the discoveries of each other.

Since this time, we neither heard nor saw anything until the year 1730, in which Bromell, in his *Lithographiæ Svecanæ*, made known the shells of the tail of our Trilobites under the name of petrified vaginipennous Insects. The German translation of this Work also made them known to German Naturalists, and while they did not take them to be petrified scarabs, as did Bromell, neither did they know what they were, until Mr. Woltersdorff, in 1748, assigned them, in his System of Mineralogy, to a place among the bivalved shells. Since this epoch, the German Naturalists placed them among the petrified shells, in their lithologic Systems and Works, and there things generally remained until the year 1750.

Since that year the Trilobite has been the subject of research for several Naturalists, who have published several scholarly Works, as follows:

1. Mr. Gentzmar, Provost of Stargard in Mecklenburg. This learned Naturalist was the first to describe the Trilobite in a particular memoir under the title: "Description of a petrified shell with three lobes (*conchæ rugosæ trilobæ*)." It is found in vol. 2 of *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, 1751, in octavo, p. 285. The continuation of this scholarly memoir is found in vol. 3, p. 183. There, he compares and writes very exactly about the Trilobites which have been found in the country of Mecklenburg, particularly of those that he has himself in his elegant cabinet. At first, he took the Trilobite to be a species of shell; however, in the continuation here mentioned, he proposed, reasonably, that its analog is an unknown marine animal, whose test is composed only of crescent-shaped rings. He is disposed, at the same time, to look at the Chiton, described here above, to be the analog of

this unknown marine animal. We owe, to this same scholar, that information on the Trilobites, which is found in article 11 of the *Neues Hamburgisches Magazin*, p. 440. Also in 1771, he inserted a small memoir on the three-lobed conch as article 2 of vol. 3 of *Berlinische Sammlungen*, where he proposes the possibility that a Chiton is the analog of the Trilobite.

2. Emanuel Mendez da Costa. We obtain from him: “A description of a curious fossile animal,” which is written in *The Gentleman's Magazine*, vol. 25, p. 24. This curious animal, which he describes, is precisely our Trilobite; he gives it the name *pediculus marinus maior trilobus*.
3. Guettard. We obtain from him the “Mémoire sur les ardoisiéres d'Angers”, which are written in the *Histoire de l'Académie Royale des Sciences* for the year 1757, p. 82 and following. Here he also deals with certain *Chevrettes*, which he finds on these slates, and he includes, under this name, our Trilobites and some other species of astacoliths that he found on these slates.
4. “Peculiar Petrifactions of an insect, *Entomolithus paradoxus*,” described by Mr. Linné from the Cabinet of Count Tessin. This is the title of a little, but scholarly memoir inserted in the German edition of the Swedish *Kongliga Vetenskaps Academiens Handlingar*, vol. 20, p. 20. He supposes, as we have said above, that the Trilobites hold an intermediate place among crayfish, monocules and aselles.
5. Charles Lyttelton. He has published: “A letter concerning a non descript petrified Insect.” This letter is found in the *Philosophical Transactions*, vol. 46, number 496, p. 598. Here may be seen very exact illustrations of extended and curled Trilobites, which were found in the Dudley quarries in Worcestershire. Dr. Charles Mortimer has added here several items that serve as an explanation to Lyttelton's description.
6. Johann Gottlob Lehmann. In vol. 10 of *Novi Commentarii Academiae Scientiarvm Imperialis Petropolitanae*, there is on p. 401 and following, a Treatise from this learned Naturalist: “De entrochis et asteriis covmnaribvs trochleatis,” to which he has added a “Problema de petrefacto incognito noviter invento” name, under which he includes precisely our Trilobite. When he wrote about this problem, he did not declare why he specified this petrifaction. However, he added to the summary of this volume a supplement, where he recognizes an oniscus indigenous to these waters (*Entomon* of Sir Linné) to be the analog of the Trilobite. Professor Beckmann of Göttingen, who then was in Petersburg, and Mr. Staehlin, Secretary of the Academy of Sciences of Petersburg, sent a live oniscus of this species to Mr. Lehmann, and those two scholars thus assured the latter that the analog should be searched for among the onisci. Mr. Bergmann in his *Physikalischen Beschreibung der Erdfugel*, p. 161, reports that Mr. Staehlin, while at his country home, found in nets, among small fish, a certain aquatic Insect (probably in fresh water) barely as thick as a fishing line, with skin as white as snow, but on which he could find neither feet nor any opening. It had no scales, but had unfolded wrinkles (*rugæ explicatæ*), where, upon touching, they contracted, so that the animal, which had a large and flat shape, when it contracted, took on a round shape. Mr. Staehlin showed this Insect to Mr. Lehmann, who recognized it to be an oniscus, and initially took it to be the analog of our Trilobite.
7. “Nachricht von einigen seltenen Anomiten, oder Bohrmuschelsteinen.” This is the title of a scholarly memoir found in the *Berlinisches Magazin*, vol. 4, p. 36. The author also talks about our Trilobite on p. 54, and places it among the bivalved shells with unequal valves.
8. *Nachricht von Seltenen Versteinerungen, Vornemlich des Thier-Reiches, welche bisher noch nicht genau genug beschrieben und erkläret worden, in drey Sendschreiben an seine Gönner und Freunde abgefasset von Christian Friedrich Wilckens, Inspectore der Cothusischen Diöces und Pastore Primario*. Berlin & Strasbourg, 1769, in octavo with 8 Plates. The author of this scholarly work gave a well detailed description of Trilobites. He proposed, as was mentioned above, that the analog of this petrifaction should be searched for in the genus of aquatic cloportes (*Branchiopus*).

TRANSLATION OF WALCH'S TRILOBITE PLATE CAPTIONS

Following the order of the Plates which compose this Supplement, I arrive at the Trilobites, and at the same time at some echinites which for the most part are quite rare. I will add some explanations with reference to both.

Supplemental Plate 9 (see Fig. 3)

Number 1. The shell of the tail of a trilobite of considerable size; from Öland. It is of the group whose edges form a semi-circle. The three lobes have raised striations, but that of the middle has more of them than the two side lobes. The analog, when complete, must have been of considerable size, and at least of eight to ten inches. This piece is still covered with its natural test, and it may be seen distinctly, that in these animals the shell of the tail consists of a single entire piece, and that it is not furrowed like the back.

Number 2. A semi-rounded shell of a tail of medium size, from Mecklenburg, covered with its yellow-grayish thin natural test, detached at one of its extremities. The middle lobe is narrow, and shows the same number of raised striations as the two side lobes. There, where the back was, the shell slants into the stone, and it may be inferred from this that the shell of the tail must have been united to the shell of the back only by some large muscles.

Number 3. A little shell of the tail, from Gnoyen, in Mecklenburg. It is still covered with its test, brown in color, set in a grayish calcareous stone. The middle lobe is very narrow, and advances nearly to the edge. The two lobes are very smooth, and have no striations.

Number 4. A shell of the tail of mediocre size, from Mecklenburg, set in a gray calcareous stone. The petrifaction is of the same color, the test is whole, of the thickness of a knife blade. The middle lobe has the same number of striations as the lateral lobes. These striations disappear little by little toward the edge, as if the painter had missed, and the middle lobe does not advance all the way to the edge.

Number 5. A very large shell of the tail, set in a reddish marble, from Stargard. The test, still there, is thicker than the blade of a knife. The width of this piece allows for the conjecture that in its natural state, it would have been longer.

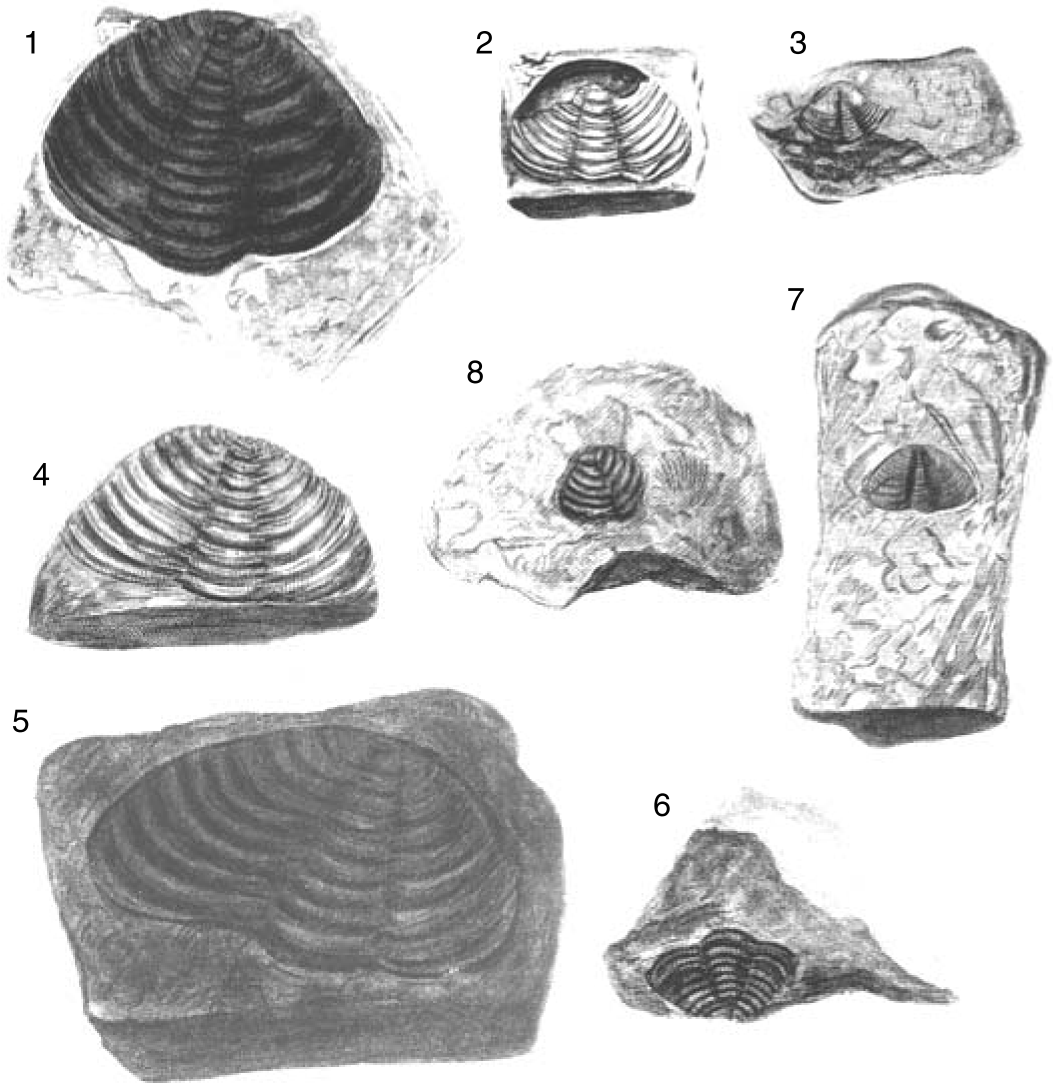

Fig. 3. Trilobite pygidia from Supplemental Plate 9 of Walch (1771). Numbers correspond to the original figure designations. Number 1 is from the Gdansk Physical Society collection. Numbers 2–8 are from Walch's collection.

Number 6. This piece is from Gnoyen, and is cloaked in its natural test. It is set in a yellowish brown calcareous stone.

Number 7. A piece that has been found around Stargard. The test is very thin, and it remains attached to the imprint of its body in the other half of the stone, as often happens when rocks are broken open. Therefore, seen here is the internal surface of the test, and noticeable also are elevated striations, in a manner so that, what is ensconced on the external side is in relief here, and that which is relief is ensconced here, somewhat the same as the embossed relief work of a jeweler. In these stones, the trilobites are sometimes found in the company of orthoceratites.

Number 8. A whitish yellow calcareous stone, from Frankfurt-on-Oder. One of its lobes is sunken in the stone, and thus there are only two that are visible. The elevated striations are, in proportion to the size of the piece, quite wide. The test, which is still there, is spathic. In the same stone there are pectunculites and turbinites which have very fine striations. Other strange bodies are mixed in without any regularity.

Supplemental Plate 9a (Fig. 4)

Numbers 1, 2. This trilobite is found in the famous Cabinet of Mr. Linck of Leipzig. It is enclosed in the manner that this testaceous insect, in death, bends and contracts. Number 1 represents the shell of the tail along with the lower portion of the back, and number 2 the helmet or the shell of the head with the upper portion of the back. This piece was found near Leipzig by a servant, and as, since that time, no one else has discovered, in all the environs, the least vestige of this petrifaction, it is not probable that this area contains such a piece, and most likely it was found by accident, and perhaps someone had lost it there. This petrifaction could have been transported into the Cabinet of Mr. Linck, and as at that time it was still completely unknown, Mr. Linck corresponded with other learned Naturalists on this subject, principally with Messrs. Klein, Breyn and Brückmann, and with the intention of molding the piece in wax, so as to communicate copies for them and to learn of their impressions. The correspondence continued on with the first

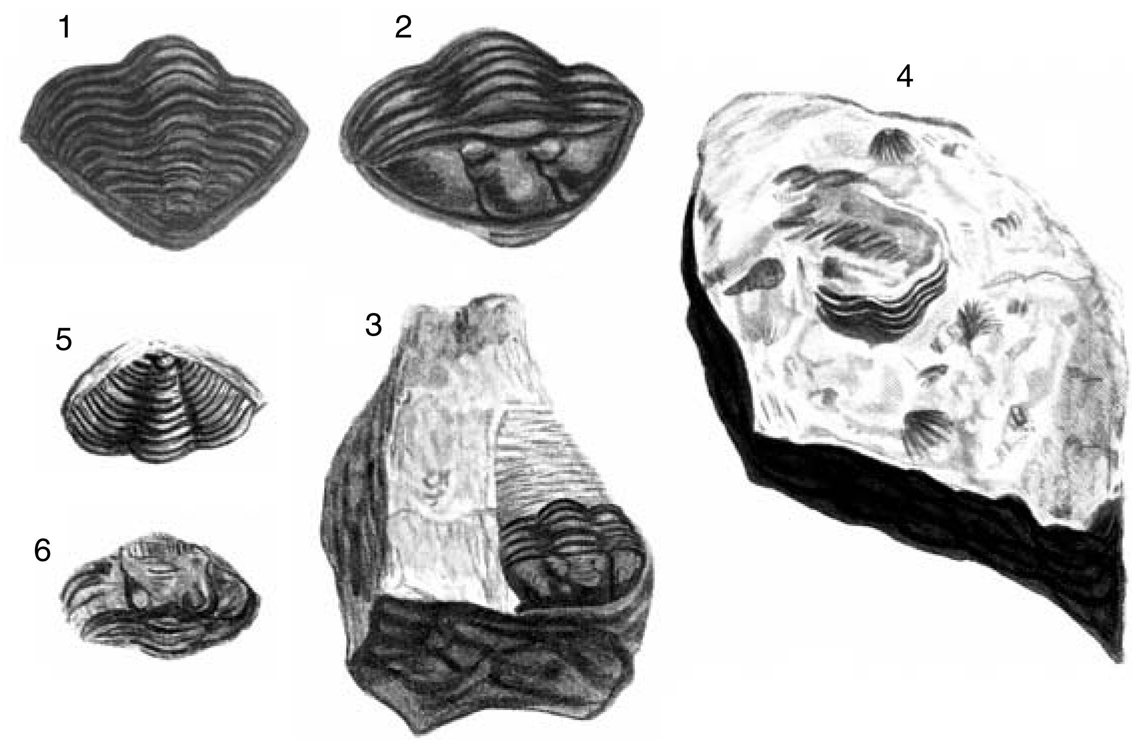

Fig. 4. Trilobites from Supplemental Plate 9a of Walch (1771). Numbers correspond to the original figure designations. Numbers 1, 2 are from the Linck collection. Numbers 3–6 are from the G. A. H. Heydenreich collection.

two, may still be found in Danzig at the famous Academy of Curiosities; but the petrifaction itself is still in Leipzig in the Cabinet of Mr. Linck. There is a slight misunderstanding because Mr. Wilckens, in his *Treatise on Petrifactions*, page 3, says in a note, that only Mr. Linck had the good fortune of possessing copies of this petrifaction in a copperplate engraving and in wax. Actually the continued correspondence on the subject of this body caused it to be known soon and to be copied many times. Mr. Brückmann was the first to do so in his *Centvria Epistolarvm Itinerariarvm*, Epistola itineraria 23, pl. 2, number 6. Later this same piece was described, probably after another example, in the *Berlinisches Magazin*, vol. 4, and a not very exact copy was made on a plate that was added. This body appeared a third time in the *Specimen Oryctographiae Gedanensis* of the late Mr. Klein, pl. 15, numbers 3 and 4, similarly copied on a form of wax, and this representation is most nearly the same as the one I offer here. It is only because of the conviction that this piece was the complete animal, that it earned the honor of being engraved on a copper plate. It may be observed here, it is true, that the principal parts of the body, therefore the head, the back and the curved tail, are in a certain sense complete and undamaged. But the best part and the principal part is missing, that is the natural test, which, following all conjecture, remained in the matrix when the body was removed from the stone, which often happens to this petrifaction. I had my doubts already, while examining a wax copy with attention, before I had obtained any trustworthy information. This is difficult to see, as the raised rings of the back are not segmented, and that they form a continuum with the shell of the tail, which is never observed in the examples which still have their natural test. I described my suspicion already when I composed my Chapter on the trilobites, and I find it now well founded following the advice which Baron von Zorn had the kindness of communicating to me on this subject. This learned Naturalist assures me that the late Mr. Linck, in his letters, which are still preserved in Danzig, expressly states that this petrifaction is only a simple core. The hood or the shell of the head is what holds the most interest in this piece, since it is rarely found complete. We see that the interior of the shell expresses perfectly, by its recesses, the protuberances of the external surface, and that this trilobite belongs to that type which has curved furrows, the forehead and the nose fairly wide and with triangular cheeks. The small protuberance on the right side of the lower part of the nose is probably only a defect made during fusion, as in this area, no other trilobite has any tubercle, and especially as there is none to be seen on the other side. Nothing is observed of the headband on this core. I add a few more words of remarks. It is observed on the cores of trilobites, that they never present the protuberances and the arcs as regularly as those that are still covered with their test. Why is that? It is because it is not so much the test that leaves its imprint, but rather the wrinkled skin which is under the test; and this is also the reason why in these cores the back always makes a continuum with the tail, which after all is only held by certain muscles.

Numbers 3, 4, 5 & 6. All these pieces are found in the Cabinet of Mr. Heydenreich; they are all from England and probably from Dudley, the Storehouse of trilobites. Number 3 presents the trilobite extended, although the posterior part is missing, and only a vestige of its place remains. Here is seen distinctly the headband of the forehead, and the trilobite belongs to the type

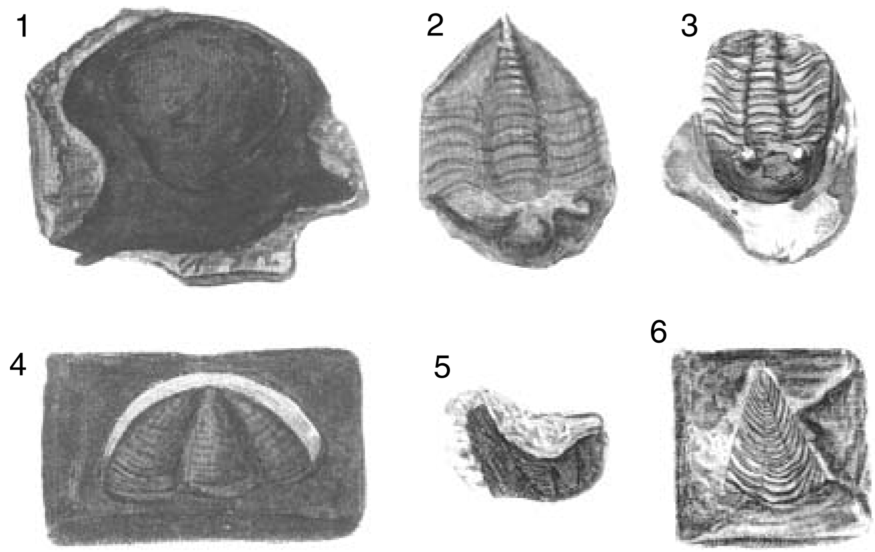

Fig. 5. Trilobites from Supplemental Plate 9b of Walch (1771). Numbers correspond to the original figure designations. Specimens are from the J.B. Gentzmar collection.

whose head shield has straight furrows and whose forehead, nose and cheeks are of regular proportion. The piece number 4 is shown only because of its situation. With individuals that lay horizontally in their matrix, never is found the least vestige of a lower test, which would be expected if there was one it its analog. This circumstance then confirms the conjecture that I proposed above, that the animal is not like bivalved conchs, with two valves, but that they have, under the shell of the back, testaceous feet hidden like a crayfish. Numbers 5 and 6 represent both sides of a very well preserved curved trilobite. Above is distinctly seen the slanted edge where the nearest rings of the back are joined. The other half of this trilobite, number 6, is presented here at a bias. There, where the tubercles are located, is the forehead of the trilobite. It has a flattened head shield without apparent furrows. How many different species of this testaceous insect, which is still so poorly known, must there be in the sea?

Supplemental Plate 9b (Fig. 5)

All the petrifactions presented on this Plate are from the beautiful Cabinet of the late Provost Gentzmar in Stargard. He thinks that number 1 is the shell of a trilobite of a peculiar configuration. He means probably the front of the shell or the head shield. However, this conjecture is subject to doubt. I have already stated above that usually, where trilobites are found, are fragments of unknown shells, and that because of this they are thought to be fragments of trilobites. But they could be just as well be fragments of other testaceous insects, which possibly are still unknown. Anyhow, this piece has little resemblance to the head shield of currently known trilobites. Mr. Gentzmar did not indicate where it was found, but, as well as we can conjecture from the type of reddish marble, it is a Petrifaction from Mecklenburg. More recognizable and more beautiful is the yellowish-brown extended trilobite of number 2, cloaked in its natural test. The lateral lobes of the tail are smooth, and this one, instead of having a rounded contour below, terminates in a blunted point. The back consists of eight rings composed of three arcs, but the head shield is a little damaged. Still, with difficulty, it may be seen that it has a curved furrow, a narrow forehead, and large cheeks. The entire body is, proportional to its length, larger than usual, which could be due to some violent compression it may have suffered in the Kingdom of Fossils. This piece is from Woggersin, near Neubrandenburg. Number 3 is an extended trilobite from Suckow in the Uckermarkt, which has eight well preserved rings on its back. The back is slightly retracted inward, which proves that the animal, independent of its testaceous armor, has free movement in all directions. The head shield consists of a smooth test without furrows, but it has two well raised tubercles, which we have above named the eyes. Number 4 is a shell of the tail, which has a smooth border around the circumference, which is not observed in all. In the example of Linck it is also very apparent. If number 5 must also be counted among the fragments of trilobites, that is a decision which I leave to others. Number 6 is the shell of a conical tail, from Stargard. Normally conical shells look much more beautiful than the rounded ones. They have for the most part more fine elevated striations, and the two lateral lobes have only sixteen. The piece was found near Stargard.

Supplemental Plate 9c (Fig. 6)

Number 1 is very beautiful and large, extended trilobite; it is the most beautiful of those that are presented in this work. Neustrelitz is its native country. It was found in a gray calcareous stone. It has eight rings on the back, of which the little one is quite large. The shell of the tail is missing part of both sides, which makes visible, on the imprint, very fine parallel striations; this is as if the fine lamellae are laying one upon the other, and one advances slightly under the other. All three lobes have the same number of elevated striations. The head shield is no less

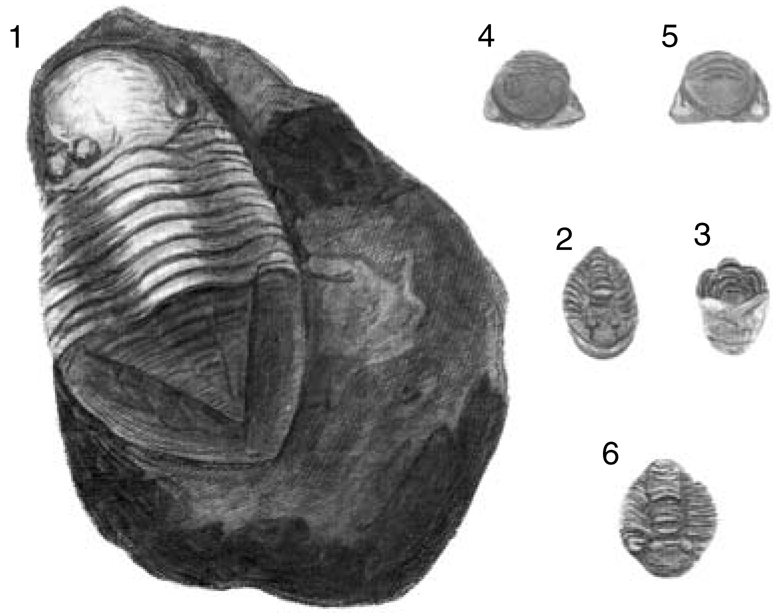

Fig. 6. Trilobites from Supplemental Plate 9c of Walch (1771). Numbers correspond to the original figure designations. Specimens are from the Hempel collection.

remarkable. It has the forehead and the nose so large that it results in the cheeks being only slightly apparent. Tubercles are distinctly visible. It seems that on one side there are two of them together, and in this case this phenomenon is quite rare. The small trilobites, numbers 4–6, are from Neubrandenburg, very well preserved, and distinctly presenting all their parts. Number 3 shows the posterior face of number 2 or the shell of the curved tail, and numbers 4 and 5 show a piece presented from both sides. Number 2 has very large tubercles, and number 4, although of the same size, has them quite small. On number 5 the three lobes of the shell of the tail are not very distinct, unless this is a particular species of trilobites where the shell of the tail does not curve; this reminds me of a piece that I have in my Cabinet.

Supplemental Plate 9e (Fig. 7)

Number 1. The middle part of a trilobite of considerable size, from Havelberg. It is, as may be seen, only a core. What is the most peculiar is that little is visible of the three lobes of the back. Effectively, if were found together in the Kingdom of Fossils bodies whose back resembles the tail of a crayfish, and which is not divided into three lobes, our trilobites would not constitute a particular species of these bodies, and in this case, could not we dispense with taking this individual for the body of the *oniscus crustaceus* described above, or to be the *Oscabiörn* of the Icelanders? This body, shown here, belongs to the so-called tails of petrified crayfish, which are mentioned by Gesner and other Naturalists of that time.

Number 2. Here is the description given by the late Mr. Gentzmar for this trilobite: *the shell is certainly a single trilobed smooth valve, of which the median lobe is short & ends in a depressed furrow leading down to the margin*. In other words, he takes the entire piece to be the shell of the tail, with the middle lobe terminating halfway and this changes, so to say, into a furrow which goes to the extreme edge. As for myself, the inferior part appears to me to be a piece of the shell of the back, upon which lays the shell of the tail. This is because we observe very fine rings which are pushed under each other, a characteristic which only fits the shell of the back, and not that of the tail. Very little of the lobes are seen here. This piece is from Stargard in Mecklenburg.

Number 3. The head shield of a trilobite from Stargard. It is of the type whose curved furrows form a narrow forehead and nose. At both sides are protuberances where the eyes are.

Number 4. Another head shield, where the furrows form a very narrow forehead, and the nose and the lips are all the larger. The hardened earth deposited between the forehead and the cheeks makes it so that the head shield is not seen distinctly in its entirety. This piece is from Ripkerfield, near Stargard.

Numbers 5 and 6. The fields of Stargard have a type of argillaceous stone, which once was hard and compact, but exposure to air has caused it to lose its ancient hardness. It is normally thought of as decomposed cornstone. However, it is completely opaque, even to the edge of a fracture seen in the light. Trilobites are found in this rock, in addition to several other petrifactions, and I communicate here a beautiful and complete example. There are two peculiarities. One is the way it is bent, which proves clearly that the animal had, under its armor, totally free movement, and the other is the two large horns, which it has at the side of the forehead.

Number 7. A trilobite, of which only the shell of the back is preserved. This example distinctly shows the way that the rings disappear one under the other. This piece is from Neuruppin, and is enclosed in calcareous stone. The cores of the head shield and the shell, especially those of the latter, are damaged, and do not now distinctly show their true shape.

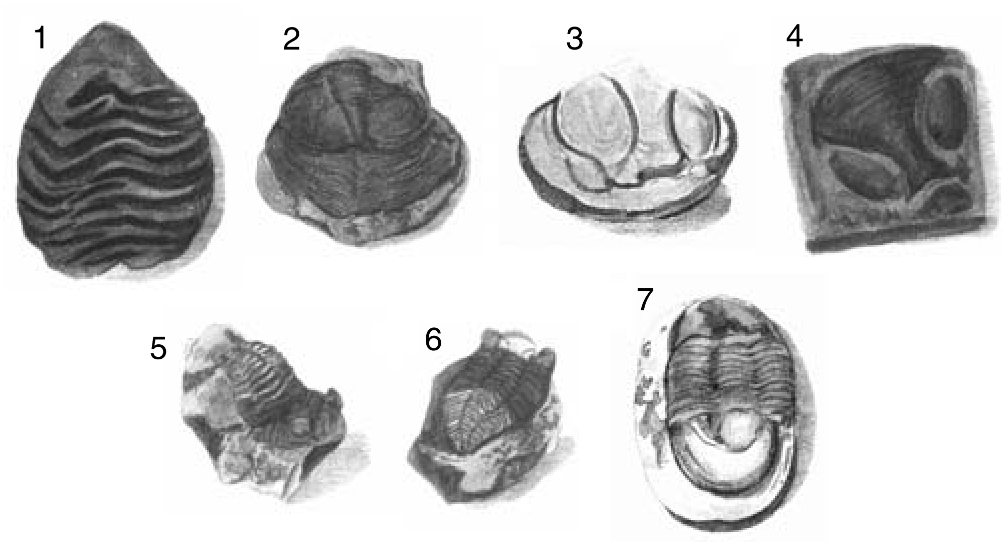

Fig. 7. Trilobites from Supplemental Plate 9e of Walch (1771). Numbers correspond to the original figure designations. Specimens are from the J. B. Gentzmar collection.

Supplemental Plate 9f (Fig. 8)

Numbers 1, 2, 3, 4, 5. Up to this point, we have given preference, above all other trilobites, to those from Dudley, in England, because of their beautiful preservation and of their expressive character. This Plate shows a few beautiful pieces, from the magnificent Cabinet of Mr. André, a learned and celebrated apothecary from Hannover. I find it unnecessary to stop here, being that the parts of this insect, described above in Chapter 3, that is the forehead, the eyes, the horns, the nose, the lips, the forehead band, etc., are seen so distinctly that it would be superfluous to restate here what I said above. I only need to add here that, at the right, number 1, and at the left, numbers 3 and 5, the double prominences are very well distinguished, which I named the eyes, and the others the horns, and that the rings of the back, numbers 1, 2 and 3, do not appear to be similar, but the cause is that hardened earth is deposited between the furrows of the back. If this earth could be detached from the shell of the back, not only would the rings appear differently, but also it would be seen that each shell of the back which by itself consists of three arcs, constitutes one total ensemble. Mr. André had intended to publish a Memoir on this petrifaction, which to date was the favorite subject of the many Curious, and to add copies of the most beautiful pieces from his Cabinet. He supposes that its analog is to be found among the monocules, and even among the sea monocules, and not among the freshwater monocules. He tells me in a letter that a friend from London assured him that the analog of these trilobites was in a Cabinet in London, but upon inquiring more exactly, was given a response that the Cabinet had been sold and dispersed, thus there was no hope of finding the true analog there.

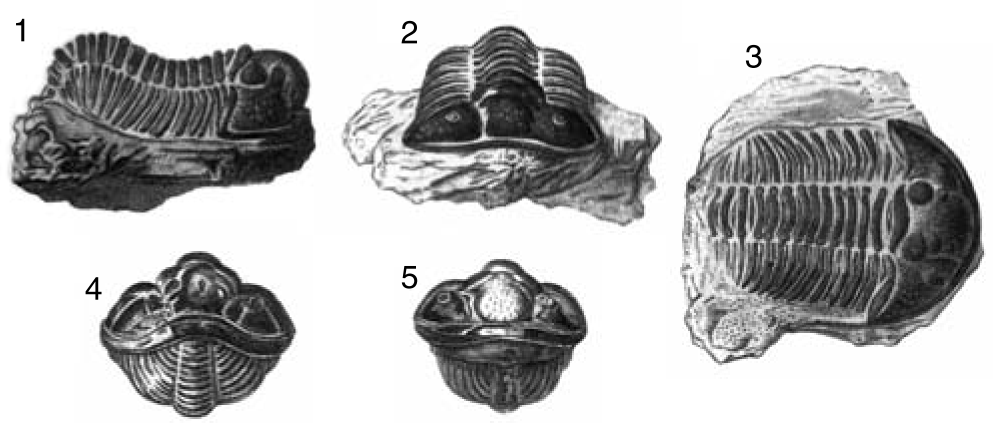

Fig. 8. Silurian (Wenlockian) calymenid trilobites from Dudley, England, from Supplemental Plate 9f of Walch (1771). Numbers correspond to the original figure designations. Specimens are from the André collection.

WALCH'S FOOTNOTES

Bibliographic information in Walch's footnotes is sometimes translated, paraphrased, incomplete, ambiguous, or erroneous when compared with the originals. These problematical citations have been corrected below, and additional information is provided in brackets to assist in locating the original references. For additional information about of the references given below, see St. John (1998, 1999, 2000). The "supplemental plates" noted below are the plates that accompany Walch's 1771 trilobite chapter (reprinted in the 1773 Dutch and 1775 French editions) (see Figs. 3–8).

1. *Lithographiæ Svecanæ*, p. 76, 79. [= *Mineralogia et Lithographica Svecana*, 1740]
2. *Mineral-System*, p. 42. [= *Systema Minerale*, 1748]
3. In the Description of a shell whose back has three lobes. See *Researches of a Society in the Upper-Lausitz*, vol. 2 & 3, 1751, 1752, in octavo. [= Beschreibung einer versteinten Muschel, mit dreyfachen Rücken (conchae rugosae trilobae). *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, v. 2, p. 285–298, 1 pl., v. 3, p. 183–201, 1 pl.]
4. *News of Rare Petrifactions, Primarily from the Animal Kingdom*, at Berlin, 1769, in octavo, p. 28. [= *Nachricht von Seltenen Versteinerungen, Vornemlich des Thier-Reiches*]
5. *Specimen Oryctographiae Gedanensis*, pl. 15.
6. *Dictionnaire Universel des Fossiles Propres, et des Fossiles Accidentels*, part 2, p. 213.
7. *Maslographia*, pl. 9, fig. 50, p. 214, no. 50.
8. *Systema Naturæ* [12th edition], volume 3, p. 160 and Transactions of the Swedish Academy of Sciences, vol. 20, p. 20. [= *Kongliga Vetenskaps Academiens Handlingar*, 1759]
9. *Catalogue Systématique et Raisonné des Curiosités de la Nature et de l'Art*, volume 3, p. 204; compare with volume 46 of *Philosophical Transactions*, p. 600.
10. Epistola itineraria 64, pl. 3, fig. 5 [= 1737] in *Centvria Epistolarvm Itinerariarvm*. [= 1742 compilation of all published epistolae]
11. Natural History of the Mineral Kingdom, p. 328. [= *Naturgeschichte des Mineralreichs*, 1763]
12. In his Work mentioned above, p. 43. [see footnote 4]
13. Treatise on Layered-Mountains, p. 72. [= *Versuch einer Geschichte von Flötz-Gebürgen*, 1756]
14. See the treatise of Provost Gentzmar, which is inserted in the *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, p. 184. Compare with Plate number 7.
15. See Supplemental Plate 9b, number 3 and Suppl. Pl. 9b, number 1 in this Work.
16. Supplemental Plate 9a, numbers 1 and 2.
17. Supplemental Plate 9e, numbers 5 and 6.
18. Supplemental Plate 9a, number 2, 9f, number 3; Mr. Gentzmar in *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, pl., number 3; Wilckens, pl. 1, fig. A.
19. *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, pl., number 1. Supplemental Plates 8d, number 17, 9b, number 3 of this Work.
20. See Supplemental Plate 9, number 3 and Wilckens pl. 1, fig. A and Mr. Gentzmar, in the Work mentioned above, vol. 3, pl., number 11. In some Examples, the furrows only go to the center, and anyway as they have little resemblance to Trilobite head shields, it remains to decide if these are not the shells of other marine bodies. A similar shell, which I mention principally here, was communicated by Provost Gentzmar in the *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, on the Plate that is mentioned, number 6.
21. See Supplemental Plates 9a, number 3, 9c, number 2, 9f, number 3 and *Philosophical Transactions* number 496, pl. 1, p. 604, fig. 9.
22. Mr. Wilckens, pl. 1, figs. A, B, C. Mr. Gentzmar, *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 2, pl., numbers 13, 17, vol. 3, number 4. *Philosophical Transactions* in the passage mentioned above, figs. 3 & 7.
23. Mr. Gentzmar, in the same place, vol. 3, number 11.
24. See *Philosophical Transactions* in the place mentioned here above, fig. 6.
25. In Supplemental Plates 9a, number 2, 9e, number 4. Mr. Gentzmar in the same place, vol. 3, number 11.
26. In Supplemental Plates 8d, number 17, 9a, number 3, 9b, number 3, 9f, number 3.

26a. See *Philosophical Transactions*, at the place mentioned here above, figs. 8, 9, 11 & 12.

27. In the Treatise mentioned above, p. 11. [see footnote 4]
28. See Supplemental Plate 9e, number 6.
29. Part 4, p. 39. [= 1762]
30. Provost Gentzmar in the *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, p. 194.
31. This furrow is expressed as an obliquely drawn line, in the Memoirs of the Royal Academy of Sciences of Sweden, part 20, pl. 1, fig. 1. [= *Kongliga Vetenskaps Academiens Handlingar*, v. 20, 1759]
32. See the Supplemental Plates in this Work, pl. 9f, number 3.
33. Supplemental Plate 9b, numbers 2 & 6.
34. Supplemental Plates 9 & 9e, number 2.
35. Supplemental Plate 9b, number 4. Mr. Wilckens, pl. 2, fig. 2.
36. See Mr. Gentzmar, *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 2, pl., numbers 5 & 6.
37. Mr. Wilckens, pl. 2, fig. 3. Supplemental Plate 9.
38. Supplemental Plate 9, numbers 1, 7. Mr. Wilckens, pl. 2, fig. 5, pl. 3, figs. 7 & 10.
39. Bromell, *Lithographiæ Svecanæ*, p. 77. [= *Mineralogia et Lithographica Svecana*, 1740]
40. Mr. Gentzmar in the same Work, number 4. [see footnote 3] Mr. Wilckens, pl. 3, figs. 6, 7. Supplemental Plate 9, number 1.
41. Mr. Wilckens, pl. 4, fig. 17, pl. 5, fig. 19.
42. This is the opinion of Inspector Wilckens in his Treatise: *News of Rare Petrifactions*, p. 33, 34. [= *Nachricht von Seltenen Versteinerungen*, 1769]
43. I myself am in possession of this species, embedded within a black Stinkstone from Mecklenburg, on which cannot be found the least vestige of any furrow. Besides this, Mr. Woltersdorff communicated to me an Example of a large fragment of tail, where the middle lobe, which still has its natural shell, does not present the least vestige of any transverse furrows.
44. Mr. Gentzmar in the place mentioned above, vol. 2, pl., number 2. [see footnote 36] Supplemental Plates 9b, number 2, 9e, number 2.
45. Supplemental Plate 9b, number 6.
46. Supplemental Plate 9, number 8
47. Supplemental Plates 9, numbers 2, 6, 9b, number 6.
48. Provost Gentzmar, *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, pl., number 7.
49. See the treatise of Professor Franz Zeno on the Petrifactions that are found in the environs of Prague, in vol. 1 of Prague's Physical Entertainments, pl. 1, fig. 1. [= *Neue Physicalische Belustigungen*, 1770]
50. See Supplemental Plate 9, number 1. Inspector Wilckens in the treatise mentioned above, pl. 2, fig. a. [see footnote 4] Mr. Gentzmar, *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 2, number 7.

51. Mr. Gentzmar, vol. 2, pl., number 6. Mr. Wilckens, pl. 4, fig. 17.
52. See the New Hamburg Magazine, article 11, p. 440. [= *Neues Hamburgisches Magazin*, v. 2, part 11 ("*Silftes Stück*"), 1767]
53. p. 80.
54. p. 77.
55. In the Memoirs of the Royal Academy of Sciences of Sweden, vol. 20, pl. 1. [= *Kongliga Vetenskaps Academiens Handlingar*, 1759]

55*. I have been confirmed in this supposition on the Alum Shale of Andrarum, which Pastor Woltersdorff was kind enough to send to me later, and upon which we can observe, quite distinctly, that the square shapes were isolated pieces of the three-arcs armor of the Trilobite.

56. *News of Rare Petrifactions*, p. 75. [= *Nachricht von Seltenen Versteinerungen*, 1769]
57. Plate 6, figs. 26, 27.
58. Here we must perhaps report on the shell, which is found in the Treatise of Mr. Wilckens, pl. 6, numbers 33 and 34, and that which I have mentioned above, after the Memoir of Mr. Gentzmar in the *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, on the Plate, number 6.
59. See Supplemental Plate 8d, number 17, 9b, number 3 & *Philosophical Transactions*, vol. 46, number 496, pl. 1, p. 604, fig. 10.
60. Supplemental Plate 9a, number 3, 9c, number 2, 9f, number 3, and *Philosophical Transactions* in the same place [see footnote 59], fig. 9.
61. Supplemental Plate 9e, number 4. Mr. Wilckens, pl. 6, fig. 24.
62. See *Philosophical Transactions*, at the place mentioned above, fig. 3, fig. 7 & fig. 12. [see footnote 59] Mr. Gentzmar, *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, pl., number 11. Sometimes the shell of the forehead, cut out in the shape of an arc, is found alone. See in the same Work, vol. 2, pl., numbers 11 & 13. Mr. Wilckens, pl. 5, figs. 21, 22, compare with pl. 1, figs. A, B, E, F.
63. Supplemental Plate 9b, number 1. Mr. Wilckens, pl. 9, fig. 15. In some of this species the forehead and the nose have a rounded convexity, the same as found in the Treatise of Professor Franz Zeno on the Petrifactions of marine bodies in the environs of Prague, pl. 1, fig. 2. [see footnote 49]
64. Supplemental Plate 9c, number 3.
65. "A letter, concerning a non-descript petrified insect," with remarks by Mr. Mortimer in *Philosophical Transactions*, vol. 46, number 496, p. 598.
66. In the same place.
67. *Lithographiæ Svecanæ*, p. 76 and following. [= *Mineralogia et Lithographica Svecana*, 1740]
68. A peculiar Petrifaction of an Insect, in the Memoirs of the Royal Academy of Sciences of Sweden, vol. 20, p. 20 and following. [= Petrificatet *Entomolithus paradoxus*. *Kongliga Vetenskaps Academiens Handlingar*, 1759]
69. *News of Rare Petrifactions, Primarily from the Animal Kingdom*, p. 37 and following. [= *Nachricht von Seltenen Versteinerungen, Vornemlich des Thier-Reiches*, 1769]
70. *Catalogue Systématique et Raisonné des Curiosités de la Nature et de l'Art*, vol. 3, p. 204.
71. In the Memoirs of the Royal Academy of Sciences of Paris for the year 1757, p. 82. [= *Histoire de l'Académie Royale des Sciences of Paris*, vol. 1757 (published 1762)]
72. *The Gentleman's Magazine*, vol. 25, p. 24, 25.
73. This Treatise on the Monocule in the form of a crayfish was published at Regensburg in 1756, in quarto. [= *Der Krebsartige Kieferfub mit der Kurzen und Langen Schwanzklappe*]
74. Description of a curious fossil animal, in *The Gentleman's Magazine*, vol. 25, p. 24.
75. *Museum Diluvianum*, number 759. *Meteorologica et Oryctographia Helvetica*, p. 316, fig. 131.
76. In the Natural History of Spain, pl. 3, fig. 4 [= *Aparato para la Historia Natural Espanola*, 1754], following the German Translation of Mr. Murr. [= *Vorbereitung zur Naturgeschichte von Spanien*, 1773]
77. *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 2, p. 288 on.
78. Treatise on the Sea-Petrifactions and Fossils of Prague, 1769, octavo. [= *Abhandlung von Versteinerungen, Welche bey Prag Gefundenen Werden*, the separate edition of the 1770 journal article; see footnote 49]
79. *The Natural History of Lancashire*, pl. 7, fig 1.
80. In the Treatise on the Petrifactions & the fossils in the environs of Prague, p. 5. [see footnotes 49 and 78] In the *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, p. 184. Provost Gentzmar has from the beginning also proposed this conjecture.
81. *Maslographia*, p. 214, compare with pl. 9, fig. 50.
82. *Mineral-System*, p. 42. [= *Systema Minerale*, 1748]
83. Vol. 4, p. 54. The beautiful Treatise, which is found here, is titled "Beschreibung einiger Anomiten," among which our Trilobites are also placed. The author, whom I do not have the honor of knowing, supposes there, p. 53, that I take the cores of the White Strawberry of Rumphius to be Trilobites, in my Kingdom of Fossils, vol. 1, p. 112 [= *Das Steinreich Systematisch Entworfen*]. Never has this entered my mind. Perhaps I did not explain myself clearly enough, as what I said there about the *Nucleus quandrandis fragi albi*, does not relate to Trilobites, but to Trigonelles, upon which also are the words which immediately follow.
84. In his Natural History of Spain, pl. 3, fig. 4. [= *Aparato para la Historia Natural Espanola*]
85. Epistola itineraria 23 [= 1730] *in Centvria Epistolarvm Itinerariarvm*. [= 1742 compilation of all published epistolae]
86. *News of Rare Petrifactions*, p. 36. [= *Nachricht von Seltenen Versteinerungen*]
87. Cabinet of Ambonese Rarities, p. 38. [= *D'Amboinsche Rariteitkamer*, 1705]
88. See the *Systema Naturæ* of Mr. Linné, p. 1106, 12th edition; Davila, *Catalogue Systématique et Raisonné*, vol. 1, p. 392; and the remarks of Professor Müller on the Description of Shells of the late Mr. Knorr, part 4, p. 29. [= *Vernügen der Augen und des Gemüths, in Vorstellung einer Allgemeinen Sammlung von Schnecken und Muscheln, Welche im Meer Gefunden Werden*, 1769]
89. Conchyliologie, pl. 25, figs. L, M. [= *L'Histoire Naturelle Éclaircie dans Deux de ses Parties Principales la Lithologie et la Conchyliologie*, 1742]
90. *Locupletissimi Rerum Naturalium Thesauri*, vol. 2, pl. 61, number 3 on. [= 1735]
91. Cabinet of Ambonese Rarities, pl. 10, fig. 4. [= *D'Amboinsche Rariteitkamer*, 1705]
92. *Vernügen der Augen und des Gemüths, in Vorstellung einer Allgemeinen Sammlung von Schnecken und Muscheln, Welche im Meer Gefunden Werden*, part 4, pl. 17, figs. 3, 4. [= 1769]
93. Vol. 5, number 90, p. 219. [= 1740]
94. Vol. 4, p. 37. [= 1762]
95. p. 241.
96. New Society Reports, p. 36. [= *Neue Gesellschaftliche Erzählungen für die Liebhaber der Naturlehre*, vol. 4 (1762)]
97. See Mr. Gentzmar, *Arbeiten einer vereinigten Gesellschaft in der Oberlausitz*, vol. 3, p. 192. Mr. Wilckens, *News of Rare Petrifactions*, pl. 6, figs. 8, 9. [= *Nachricht von Seltenen Versteinerungen*] We should mention here the beautiful Plate of Trilobites in *Philosophical Transactions*, vol. 46, p. 598, on which may be seen, here and there, isolated fragments of the shell of the back of the Trilobite which protrude from the stone.

98. Gentzmar, same citation, vol. 3, p. 191. [see footnote 97]

99. Davila, *Catalogue Systématique et Raisonné des Curiosités de la Nature et de l'Art*, vol. 3, p. 205, number 261, p. 206, number 266. Bromell, *Mineralogia et Lithographica Svecana*, p. 77.

100. *Neues Hamburgisches Magazin, Silftes Stück*, p. 440. [= vol. 2, part 11, 1767]

101. See his voyages to Öland and Götland, p. 162, German edition [= *Reisen durch Oeland und Gothland*, 1764], & Transactions of the Royal Swedish Academy, vol. 20, p. 20. [= *Kongliga Vetenskaps Academiens Handlingar*, 1759]

102. Epistola itineraria 23 [= 1730] in *Centvria Epistolarvm Itinerariarvm*. [= 1742 compilation of all published epistolae]

103. Vol. 4, p. 56.

104. *Specimen Oryctographiae Gedanensis*, pl. 15.

105. *Berlinisches Magazin*, vol. 4, p. 56. Scheuchzer, *Museum Diluvianum*, number 759. Compare with his *Meteorologica et Oryctographia Helvetica*, p. 316, fig. 131

106. Davila, *Catalogue Systématique et Raisonné des Curiosités de la Nature et de l'Art*, vol. 3, p. 206.

107. In the German translation, which Mr. Murr has published [= *Vorbereitung zur Naturgeschichte von Spanien*], these Trilobites are found on pl. 3, number 4.

108. *Lithophylacii Britannici Ichnographia*, epistola 1, p. 96, compared with the plate that appears on p. 120.

109. *Natural History of Lancashire*, pl. 7, fig. J.

110. *Maslographia*, pl. 9, fig. 50, pl. 11, fig. 44, pl. 12, fig. 31.

111. *Museum Diluvianum*, number 759, compared with his *Meteorologica et Oryctographia Helvetica*, fig. 132.

GLOSSARY OF SOME OF WALCH'S TERMS

articulates - early term for arthropods and many worms.

aselles - terrestrial and aquatic isopod crustaceans; terrestrial forms are often given the common names "pill bugs" or "sow bugs." Walch often used this term (e.g., sea-aselles) when referring to local names for marine isopods (see also Beekman, 1999, p. 412).

astacoliths - fossil crayfish, lobsters, and crabs, or fossils that resembling these groups.

asteries - individual, star-shaped, crinoid stem columnals (rounded columnals are "trochites").

back - thorax.

bones - calcified elements that make up the jaw apparatus ("Aristotle's lantern") in sea urchins.

cacadumuschel - "cockatoo-mussel" or "cockatoo-shell", an early term for trilobite.

cheeks - genal areas.

chevrettes - "shrimp".

cloportes - terrestrial isopods ("wood-lice"), often given the common names "pill bugs" or "sow bugs." Walch often used this term when referring to local names for marine isopods or branchiopods.

core - rock matrix underneath the exoskeleton of a fossil; an internal mold.

cornstone - early term used in Britain for "earthy concretionary limestone, mottled red and green," "a rock of a pseudo-brecciated appearance," or "red limestone" in part of the Old Red Sandstone succession (Conybeare and Phillips, 1822; Roberts, 1839; the *Oxford English Dictionary*; and the discussion on cornstone in Bertrand, 1763, p. 181–183).

corallioliths - coral or coral-like fossils.

echinites - fossil sea urchins (regular echinoids).

ell - an obsolete unit of measure used in western Europe; its length was not universally agreed upon, and varied from region to region. "Elle" is used in the 1771 German edition (p. 129), while "aune" is used in the 1775 French edition (p. 113). Colburn (1831) equated the aune and the ell, and gave their lengths as 42 English inches. Beekman (1999) reports the ell as about 27–28 inches; the *Oxford English Dictionary* and Colburn (1831) define the English ell as 45 inches, the Scotch ell as 37.2 inches, and the Flemish ell as 27 inches.

encrinites - complete or nearly complete fossil crinoids (crowns attached to stems).

entrochites - segments of rounded to subrounded fossil crinoid stems that consist of many articulated columnals.

forehead - appears to correspond with the posterior lobe (L1) of the glabella.

fossil - the classic definition of a fossil, referring to any object dug from the ground, including rocks, minerals, fossils, archaeological artifacts, etc.

headband - appears to correspond with the occipital ring and posterior cephalic border.

horns - prominent palpebral lobes, or combination of prominent eyes and palpebral lobes.

insects - early term for arthropods; "arthropod" was introduced by Siebold (1845).

Kaefermuschel - "beetle-mussel" or "beetle-shell", an early term for trilobite, inspired by Bromell's (1729) description of Swedish olenid and agnostoid trilobites as vaginipennous insects (= beetles).

lips - anterior border of cephalon.

monocules - early term that principally encompassed various arthropods (for example, limulids (king-crabs) and several small branchiopod crustaceans), from the eponymous genus *Monoculus* (e.g., Bradley, 1721, p. 157; Linnaeus, 1735, 1758, p. 634, 635).

nose - appears to correspond with all parts of the glabella anterior to the L1 lobe.

oniscus - early general term for marine isopods, from the eponymous genus *Oniscus* (e.g., Linnaeus, 1758, p. 636, 637).

orthoceratites - straight-shelled, fossil nautiloids.

ostracites - fossil oyster shells.

patelles - limpets (patellid gastropods).

patellites - fossil limpet or limpet-like shells.

pectinites - fossil pectinacean or pectinacean-like bivalves, and some strongly-ribbed brachiopods.

pectunculites - includes fossil brachiopods and some strongly-ribbed fossil bivalves.

petrifaction – identical the modern concept of a fossil (also spelled "petrification").

scolopendra - early general term for centipedes (chilopod myriapods), from the nominal genus *Scolopendra* (e.g., Linnaeus, 1758, p. 637–639). Walch mentioned "Iceland scolopendra" as a local name for a variety of marine isopod, and also used Klein's (1741) name, "*Scolopendra aquatica scutata*," for tadpole shrimp (notostracan branchiopod crustaceans).

sea-hare - a group of sea slugs (anaspidean opisthobranch gastropods) with a pair of prominent, slender extensions on the head and a lightly mineralized, internal, asymmetrical, cap-shaped shell.

sea louse/sea lice - early common name applied to chitons (polyplacophoran molluscs) and various marine isopod crustaceans.

Scyllarus of Rumphius - the Holocene stomatopod crustacean *Odontodactylus scyllarus* (Linnaeus, 1758), illustrated in Rumphius (1705, pl. 3, fig. F, G) (see Beekman, 1999, p. 22, 23, 396).

stinkstone - strong-smelling, petroliferous or bituminous carbonate; "Stinckstein" is used in the 1771 German edition (p. 128), while "Pierre-porc" (pig-stone) is used in the 1775 French edition (p. 112), in reference to the use of this rock as an early remedy for a pig disease (see Regnéll, 1949, p. 19).

test - traditionally refers to the hard shell of molluscs ("testaceans" or "testaceous animals"), but was extended to include the mineralized exoskeleton of trilobites.

trigonelles - distinctly trigonal bivalve shells.

trochites - individual fossil crinoid stem columnals (rounded to subrounded; individual star-shaped columnals are "asteries").

turbinites - high-spired fossil snail shells that resemble turbinid archaeogastropods.

vaginipennous insects - beetles (coleopteran insects).

white strawberry - the Holocene cardiacean bivalve *Fragum fragum* (Linnaeus, 1758), illustrated in Rumphius (1705, pl. 44, fig. G) (see Beekman, 1999, p. 197–199, 459).

wrinkles - refers to furrows on exoskeletal surfaces or internal molds.

zoophyte - "plant-like animal", from Order Zoophyta of Linnaeus (1758). Walch used this term when referring to crinoids.

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LEGACY OF THE LOCUST—DUDLEY AND ITS FAMOUS TRILOBITE *CALYMENE BLUMENBACHII*

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ABSTRACT—The trilobite *Calymene blumenbachii* from the Silurian at Dudley, England, had a fundamental role in the early study of this prominent group of extinct arthropods. Discovered during the mid-1700s, this was the first trilobite known from numerous complete and well-preserved fossils anywhere in the world. Commonly known as the Dudley Fossil or Dudley Locust, exceptional specimens of this trilobite became widely distributed in collections throughout Europe. As a result, they were central to the most influential trilobite papers of the time including those of Walch (1771) and Brongniart (1822). Many basic characteristics of the group, including their ability to enroll, were first established through the study of these fossils. In turn, this information provided the key evidence used to establish the arthropod affinities of this group. During the late eighteenth century, all trilobites were commonly referred to as Dudley Fossils, and demonstrate the initial importance and prominence of this species. It became the standard of comparison in trilobite research, as well as the textbook example for these fossils. No other trilobite contributed as much to the early understanding of these ancient animals.

The scientific prominence of *Calymene blumenbachii* derived from geologic and economic factors. The limestones at Dudley contained an exceptionally rich biota of well-preserved Silurian fossils, of which this trilobite was the most notable. These specimens, however, only became available to the scientific community through industrial-scale quarrying and mining at Dudley, and the collecting efforts of miners, fossil dealers and amateur naturalists. As the importance and value of these fossils became known, local individuals assembled large collections of exceptional specimens, which were then studied by some of the most prominent scientists of the day. As a result of this research and commercial trade, Dudley achieved worldwide recognition as the best source for exceptional trilobite fossils and for Silurian fossils in general. The Dudley Locust, as it was called by the local miners became a cultural icon in the community, a role that has continued for 250 years.

INTRODUCTION

A vast number of extinct plants and animals have been discovered in the fossil record. Although they all contribute to our understanding of evolution and the history of life, a few taxa have had a disproportionately greater role than others. Because of their uniqueness, excellent preservation, or scientific importance, the discovery of notable fossils provided an opportunity to make important advances in paleontologic knowledge.

The trilobite *Calymene blumenbachii*, popularly known as the Dudley Fossil or Dudley Locust, is one of these notable fossils. Found in the Silurian rocks of Dudley, England, its rise to prominence was not a random event, but resulted from a combination of factors including the need for certain natural resources at the beginning of the Industrial Revolution, the development of scientific knowledge to meet these needs, and the concomitant changes in society. The key role of the Dudley area in these events was described by Chandler and Hannah (1949), "Man has built up an industrial civilization largely on the coal, limestone, fireclay and iron found in Dudley and the Black Country. The geological structure of this area made the Industrial Revolution possible and perhaps also made the British Empire possible." They also observed, "Dudley's history is rooted in the limestone on which it stands." It was the mining of this limestone, linked with the social and economic changes of the Industrial Revolution that resulted in the discovery, fame and importance of this trilobite.

Fossils of *Calymene blumenbachii* were first found at a critical time in the study of trilobites and the establishment of paleontology as a science. Prior to the eighteenth century, little was known about fossils, as superstition, folklore, and speculation were most commonly used to explain many aspects of the natural world. This situation would start to change significantly during the 1700s when the beginnings of the Industrial Revolution necessitated a more comprehensive and accurate understanding of the Earth. Geologic and paleontologic information became critical in locating many of the natural resources required by the expanding industrialized population. As the new economic and societal conditions provided practical reasons to study fossils, they also created new social groups with the interest, leisure time, and money to undertake natural history studies, either for professional reasons or as personal intellectual pursuits. The

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Industrial Revolution also created new opportunities to collect fossils as the rapidly expanding number of quarries, mines, and construction projects provided many new sites where fossils could be collected. At the same time, it added a multitude of potential collectors in the guise of workers employed in these activities. It was under these conditions that the scientific study of trilobites began.

Trilobite fossils had been known for thousands of years (see Peng, St. John, Kihm and St. John, this volume); however, until the end of the seventeenth century, these early discoveries did not result in any important contributions to paleontological knowledge. Edward Lhwyd (1699a, b) was the first person to illustrate and discuss trilobite fossils, although he didn't recognize their arthropod affinities, and even labeled one a fish (Burmeister, 1843, 1846; Vogdes, 1890; Owens, 1998). He referred to a specimen of *Ogygia* as an "ichthyomorphous stone," which "swims spread out on its side," similar to a "sole fish" (Vogdes, 1890). Moreover, he did not believe fossils were truly the remains of animals and plants (Gunther, 1945; St. John, 2006). During the early 1700s, a number of other individuals published illustrations and descriptions of trilobite fossils, while speculating on their origins (see Burmeister, 1843, 1846; St. John, 2006, for reviews). Adhering to earlier ideas such as Lhwyd's, some of these authors continued to support an inorganic origin for fossils during this period. However, many others began to recognize that trilobites and other fossils were the remains of ancient plants or animals.

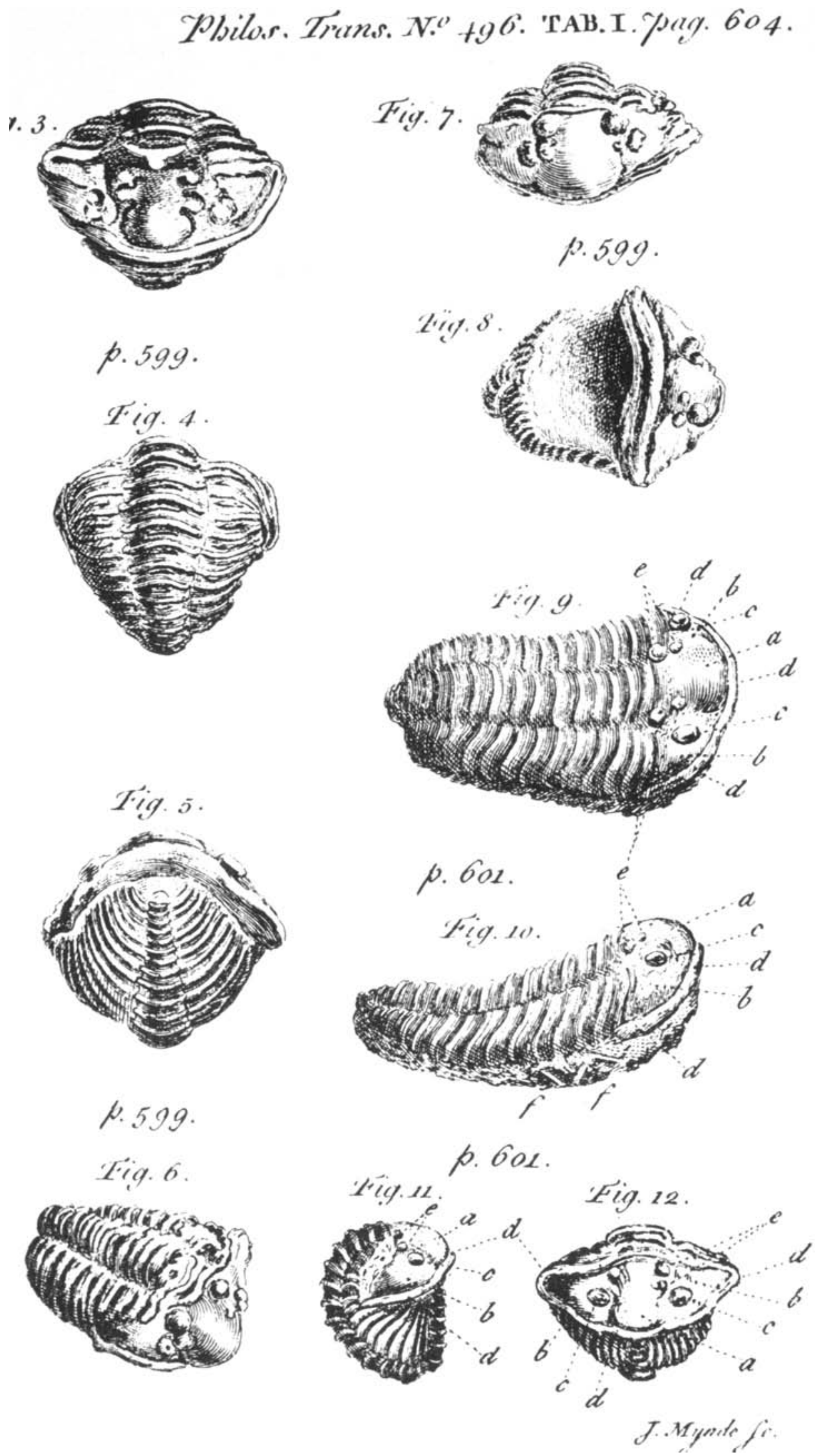
Interestingly, there was little consensus as to the type of animal that trilobite fossils represented, as they were more problematic to interpret than those of many other animals. Representing an extinct life form, trilobites were not as readily compared to living organisms, as were other taxonomic groups with such familiar extant relatives as snails or clams. Perhaps even more important in prolonging the quandary about their affinities was the special nature of the trilobite fossil record itself. Trilobite fossils are preserved primarily as isolated skeletal elements because they, like other arthropods, molted their exoskeleton periodically in order to grow. In turn, these molts, along with the carcasses of dead individuals, disarticulated easily and were scattered across the sea floor before fossilization. As fossils, many of these individual parts no longer conveyed the appearance of the entire animal or their arthropod affinities, but, instead, could be confused with other living creatures. For example, some trilobite pygidia were identified historically as "mollusks" (probably meaning brachiopods in many cases) because they bear some resemblance to the shells of these bivalved animals. Even finding articulated trilobite fossils did not establish their arthropod relationships conclusively. Prior to the late 1800s, none had been found with preserved appendages, which are of prime importance in recognizing and classifying most arthropods, and their general absence in trilobite fossils was one of the main reasons for the initial confusion about the affinities of this group (see Yochelson, this volume).

Following its eighteenth-century discovery and first scientific descriptions, the unique Dudley Fossil rapidly became a primary focus for research on this strange group of extinct marine animals. *Calymene blumenbachii* was the first trilobite known from numerous complete and well-preserved fossil specimens. Other trilobite taxa were known, but even complete specimens of these rare fossils usually were poorly preserved and lacked detail. In contrast, the relatively common and robust specimens of the Dudley Fossil provided the first good information on many of the basic characteristics of the group, while their unrivalled quality and ready availability attracted the attention of scientists and collectors alike. Moreover, they not only represented an unusual type of fossil, but they also were among the oldest known at the time. The scientific prominence of *Calymene blumenbachii* lasted for nearly one hundred years, from the 1750s through the 1840s. This period embraced not only the development of modern paleontology and trilobite studies, but also the establishment of a stratigraphic framework for Early Paleozoic rocks. The role of Dudley and its fossil in these developments was critical to early geologic studies, and involved the efforts of some of the most prominent scientists of the day.

THE DUDLEY FOSSIL: A NAME FOR ALL TRILOBITES

The discovery and description of trilobite fossils from Dudley, England, in the eighteenth century mark the true beginnings of trilobite research. These events would play a central role in determining the arthropod affinities of this extinct group, establishing the general features of their exoskeleton, and helping to define the nature of early marine life. Prior to the mid-1700s, trilobite fossils were usually mentioned only in broad geological works that covered fossils in general. The short initial papers on the Dudley Fossil were the first devoted entirely to this specific group. The earliest of these publications appeared in 1752 in the *Philosophical Transactions of the Royal Society of London* (republished in abridged versions, Lyttleton, 1756, 1809). In 1750, Charles Lyttelton submitted a letter to the Society concerning a "petrified In[s]ect" he had found in 1749 in the "Lime[s]tone Pits at Dudley" (Figs. 1, 2). [Note, the expression "[s]" here and below replaces the letter "f," which was used for the letter "s" at the time.] He hoped that in submitting his letter other members of the society could help to determine "what Cla[ss] of the Animal Kingdom" his specimens represented. Lyttelton stated that these fossils had not been mentioned by any of "our own Writers," but that he had seen similar but imperfectly described fossils by some "foreign Lithographi[s] ts."

Fig. 1. (right) Earliest known illustrations of the Dudley Fossil (Table I, Lyttelton, 1752; Mortimer, 1752). Specimens show "extended" and "rolled" forms. Mortimer described these as follows: "At Fig. 9 is one of these In[s]ects completely extended at its whole Length; wherein it appears, that the Head is cover'd with a Shell or Crust con[s]i[s]ting of three Parts; the middle part is broad and round, a. which I [s]hall therefore call the No[s]e: The two [s]ide Pieces are of a triangular Form b.b. in each of which is [s]ituate a large protuberant Eye, c.c. The anterior Part of the Whole is encompa[ss]ed by a round Border, d.d.d. which looks like an upper Lip; tho' I do not take it to be [s]o; but that the Mouth is [s]ituate lower down, as in the Crab-kind, and does not appear in any of the Specimens I have yet [s]een. On each Side the Crown of the Head, towards the back Part of it, are two [s]mall Knobs, e.e. At f.f. in Fig. 10 appear [s]ome Traces of Feet, which [s]eem to lie under the Belly: But, as the Belly, of under Side, was not di[s]tinct, not being cleared from its [s]tony and earthy Matter, I could not di[s]cern any other Legs."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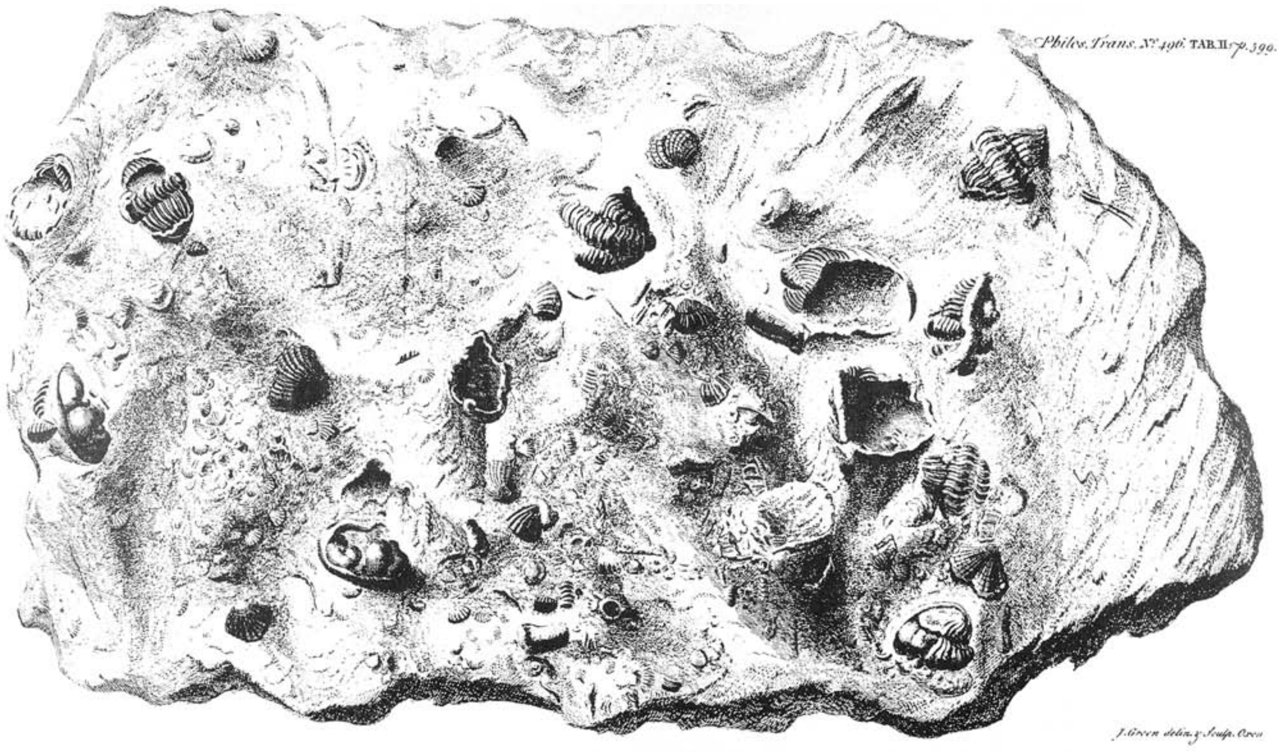


Fig. 2. Table II from Lyttelton (1752) and Mortimer (1752), which they described as "Repre[s]ents a large Ma[s]s of Lime-[s]tone dug up at Dudley, in which are embodied many of thefe Fo[ss]ils, together with [s]everal other petrified Shells."

In a footnote to this paper, the editor of the *Transactions*, Cromwell Mortimer, speculated that one of the unnamed individuals Lyttelton referred to might be a Dr. Bruckmann who had identified similar fossils collected by Mr. Linck as "a [s]ort of *Polypus marinus*" in 1742. It is also possible that Lyttelton was referring to papers by Bromell who used the name "stone insects" for arthropod fossils in general (see St. John, this volume). In an addendum to his paper, Lyttelton discussed the importance of an "extended" specimen of the "Dudley Fo[ss]il" that had been sent to him recently by Dr. Shaw of Oxford. This new specimen contrasted with those he had previously collected, which were all enrolled. He noted that there had been disagreement about their identification among the "Fo[ss]ili[s]ts," with some thinking these fossils were of a bivalve (a name then used for both clams and brachiopods), while others thought they were an "Eruca" (a name then used for arthropods with a caterpillar-like morphology). In view of this controversy, Lyttelton previously "thought it be[s]t to leave the Reader to judge for him[s]elf from the Engravings" as to which group these fossils belonged. After having seen this outstretched specimen, however, he recognized that because the animal could both enroll and outstretch it should be called an "Eruca," which would place it with the arthropods.

The same volume of the *Transactions* contained a follow-up paper by Mortimer (1752, republished in abridged versions in 1756, 1809), in which he further discussed the characteristics and affinities of Lyttelton's fossils. Using additional Dudley specimens that had been submitted to the Royal Society by Rev. Dr. Pocock (Fig. 1), Mortimer was the first person to describe the morphology of these "In[s]ects," and elaborated on features of the head and correctly identified the eyes. Unfortunately, he mistakenly identified "feet" on one of the specimens, which would cause confusion for later authors. After checking the available literature, he suggested that these fossils were similar to the living notostracan branchiopods described by Jacob Klein in 1741 (see Burmeister, 1843, 1846; St. John, this volume), and proposed that the Dudley specimens could be referred to Klein's *Scolopendrae aquaticae facutatae affine animal petrifactum* until more information was obtained. It is important to note that both Lyttelton and Mortimer recognized the arthropod affinities of the Dudley Fossil, based largely on the animal's ability to "roll up."

Following the publication of Lyttelton's and Mortimer's papers, the Dudley Fossil assumed a prominent role in trilobite research, and stimulated interest and commentary by a number of individuals. For example, Emanuel Mendez da Costa (1754a, b, republished in abridged form, 1809) published a note in direct response to the Lyttelton and Mortimer papers; he referred to their trilobite as "the famous fo[ss]il," and indicated its growing reputation. He specifically credited the extended specimens illustrated in those papers (in comparison with those that are enrolled) as proving the Dudley Fossil belonged to "the cru[s]taceous tribe of animals." He further described an "extended" trilobite fossil from Coalbrookdale, Shropshire, which he thought confirmed their views, and proposed that both his and the Dudley specimens should be called *Pediculus marinus major trilobos* because of their resemblance to *Pediculi* *marini* (living sea louse; see Burmeister, 1843, 1846; St. John, this volume) which also could enroll. This last name in various forms continued to be associated with the Dudley Fossil well into the nineteenth century.

Mendez da Costa also pointed out that Edward Lhwyd had previously figured similar fossils. Interestingly, a few years later, illustrations thought to be of the Dudley Fossil (Vogdes, 1893; Shirley, *in* Gunther, 1945) were included in the 1760 edition of Lhwyd's (1699) book titled *Lithophylacii Brittanici Ichnographia*. Some authors (e.g., Brongniart, 1822; Burmeister, 1843, 1846) mistakenly thought that these 1760 illustrations of the Dudley Fossil were included in the 1699 edition of Lhwyd's work and, as a result, erroneously extended the first scientific mention of this specific trilobite back more than fifty years.

Although the Dudley Fossil was mentioned or figured in many late eighteenth century publications on fossils and natural history, its most important contribution to trilobite research of the time is found in the classic work by the German naturalist Johann Walch (Kihm and St. John, this volume). In 1771, Walch published the first truly comprehensive investigation of this group, and combined a thorough examination of the appropriate literature with the study of a large variety of fossils available primarily from central European collections. The most noteworthy result of his research was his proposal to use the name "trilobite" for this group of fossils. He chose this name because he believed it was more appropriate to name them after their unique three-lobed character instead of their supposed analogous living relatives or the localities at which they are found, as had been common previously. Walch also made other fundamental contributions to trilobite research by convincingly establishing their arthropod affinities and accurately defining many of their basic characteristics.

Although his study included other European trilobites, the Dudley Fossil had a central role in Walch's paper, and his definition of the group was probably based more on its features than any other single trilobite taxon. Evidence of the importance Walch placed on this trilobite can be derived in part from several noteworthy comments he made in his paper. For example, he observed, "We find in particular beautiful trilobites in England, where they are named Dudley-Fossils, after a place in the County of Worcester with the name of Dudley, where they are extricated from limestone quarries, sometimes loose, and sometimes fixed in their matrices, and often in large and beautiful slabs." (translation from Kihm and St. John, this report). He also referred to Dudley as "the storehouse of trilobites," and, most importantly, he later stated, "we have given preference, above all other trilobites, to those from Dudley, in England, because of their beautiful preservation and of their expressive character." When discussing the features of specimens illustrated on his plates, he pointedly bypassed descriptions of his figures of the Dudley Fossil by stating, "I find it unnecessary to stop here, being that the parts of this insect, … are seen so distinctly that it would be superfluous to restate here what I said above." (translation from Kihm and St. John, this volume).

Walch's prominent use of specimens and the published information on the Dudley Fossil to define various basic trilobite features further attest to the importance of this species in his work. No other trilobite is specifically mentioned by Walch as often as the Dudley Fossil, nor was any represented by more illustrations. His figures of Mr. Andre's Dudley specimens (Supplemental Plate 9f) are the best of his paper, and are among the most detailed and accurate trilobite fossil illustrations of the time period (Fig. 3). Ironically, Walch made one important mistake based on the Dudley Fossil when he used Mortimer's (1752) erroneous report of "feet" to confirm his principal idea that trilobites were not bivalved animals, but were arthropods with "testaceous feet hidden like crayfish" under the shell of their back. Clearly, the Dudley Fossil was a critical component of Walch's study, which, in turn, further enhanced its prominence in later research by others.

The new name "trilobite" for this group of fossils was slow to be adopted and, even when used, was sometimes mistakenly credited to other authors. But other trilobite workers, such as the Danish biologist Morten Thrane Brünnich, readily adopted the name. In addition to being one of the first papers to use Walch's name, Brünnich's (1781) work also has the distinction of being one of the oldest to have defined a still-valid trilobite species, *Trilobus caudatus* (now *Dalmanites caudatus*). Whereas Walch refrained from naming any species in his paper, Brünnich described several under his single genus *Trilobus*. His work included a description, but no illustrations, of the Dudley Fossil, which he named *Trilobus tuberculatus*, the first trilobite named in his paper. Although this work included the earliest species name proposed for the Dudley Fossil, it was little used and, for a variety of reasons, has been suppressed officially (Whittington, 1983; Siveter, 1985; Whittington and Siveter, 1986). The distinction of being the first trilobite species designated in his work is symbolic of its importance in early trilobite studies. The Dudley Fossil would hold the position as the first-discussed species in the succeeding studies of many other authors well into the nineteenth century. Although not stated, it is probable that the reason the Dudley Fossil was placed first in these papers was because of its fame and importance as the best-known and best-preserved trilobite fossil of the time.

In addition to more formal research papers through the late eighteenth and early nineteenth centuries, the Dudley Fossil was mentioned or illustrated in numerous general natural history books and other types of publications. In many of these works, it is the only trilobite figured or discussed, and served as the representative for the entire group. A typical example is found in the works of the famous German naturalist Johann Friedrich Blumenbach. In the 1780 edition of his *Handbuch der Naturgeschichte*, Blumenbach included a brief section on petrifactions of insects (arthropods) listing the "Dudley fo[ss]il[s]" as one of the trilobites. In the 1797 edition of this work, he further discussed the classification of these fossils, and stated that, while trilobites are found at a number of places, they are nowhere more beautiful than at Dudley, where they are preserved with their crab-like shells. Blumenbach (1800) also discussed trilobites under the name *Entomolithus paradoxus* [a name proposed by Linneaus (1753) for trilobites in general; see St. John, this volume] in Part 5 of his *Abbildungen Naturhistorischer Gegenstande*. The Dudley Fossil was the primary example of trilobites used in this discussion, and he illustrated two specimens of this species from his collection (Fig. 4), and noted that the best-preserved trilobites were from Dudley. These figures also were reproduced in a 1803 French translation of his *Handbuch* in an interesting combination of both of Blumenbach's earlier works.

Although Blumenbach's work is not, in itself, unusually

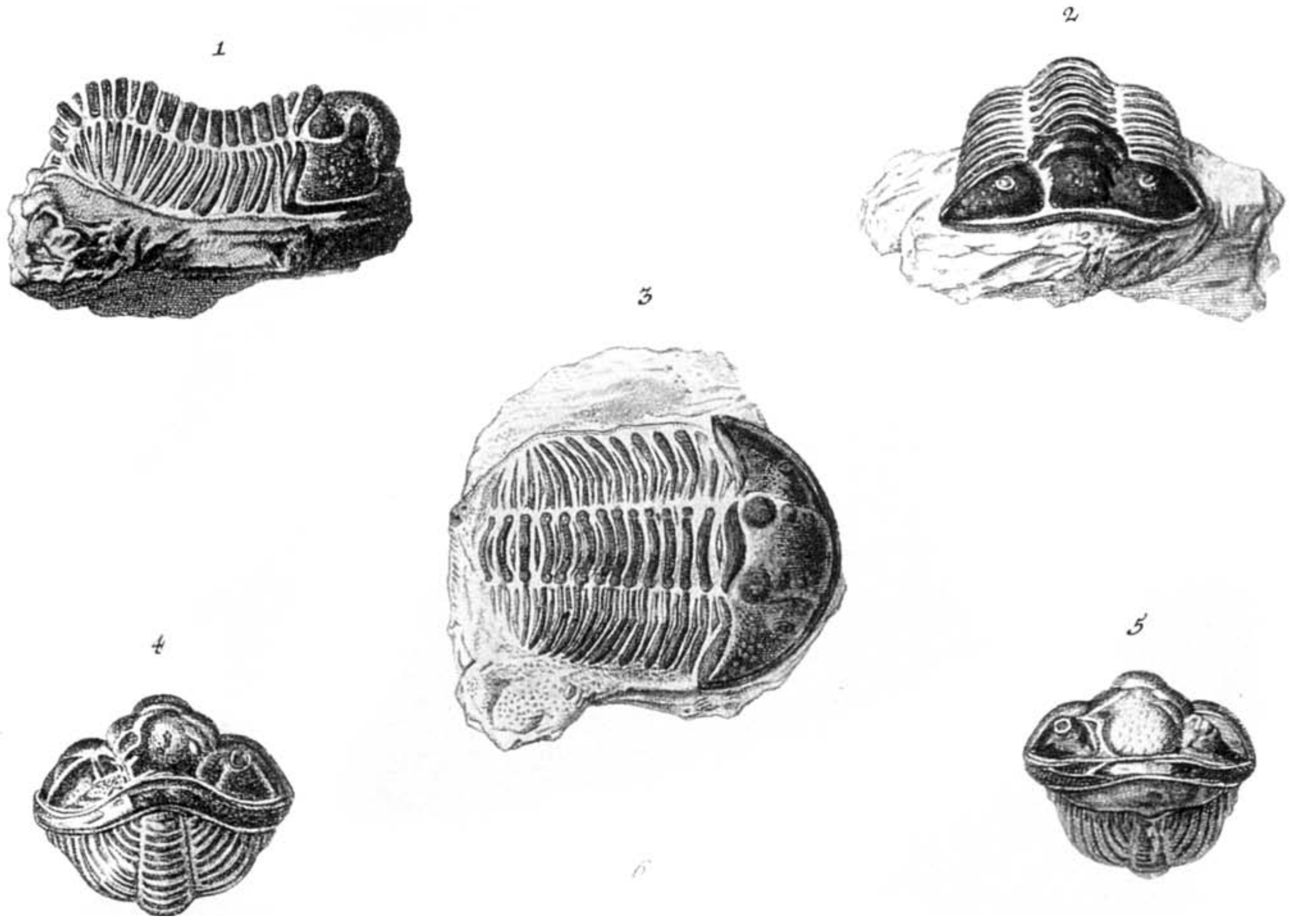


Fig. 3. Supplemental Plate IXf, figs. 1–5, of Walch (1771), with trilobites (*Calymene blumenbachii*) from Dudley in the André collection, Hannover.

important in early trilobite studies, it is noteworthy that his 1800 publication probably inspired the French scientist Alexandre Brongniart to formally name the Dudley Fossil *Calymene blumenbachii* in his honor (see Brongniart, 1822; Desmarest, 1816, 1817). This is the scientific name used today for this trilobite (see Whittington, 1983; Siveter 1985, 1996; and Whittington and Siveter, 1986, for discussions on the history of naming this species). Brongniart's paper, like that of Walch's, is considered to be one of the most important early trilobite studies. Whereas the main accomplishment of Walch's work was to establish the arthropod affinities of trilobites, Brongniart's paper marked the beginning of modern trilobite classification. He was the first author to define still-valid genera to which he assigned a number of new or previously defined species. Burmeister (1846) considered this work to be the "most perfect" and influential on trilobite workers of the time, whereas Vogdes (1893) stated that Brongniart is considered to be "the first systematic writer upon the Trilobites."

Brongniart (1822) became interested in trilobites while gathering information for a lecture on "Transition Terrain" fossils in 1812, and the Dudley Fossil apparently was critical in initiating his research on the systematics of the group, and lead to his classic 1822 paper. Recognizing that the use of Linnaeus's name *Entomolithus paradoxus* for all trilobites had created confusion, Brongniart specifically mentioned that the name had even been given to the Dudley Fossil, and indicated his perception of the uniqueness of this taxon. Ironically, it appears that Blumenbach's questionable use of the name *Entomolithus paradoxus* for the Dudley Fossil in 1800 might have initiated Brongniart's interest in the group, and resulted in his naming the fossil *Calymene blumenbachii*.

The naming and systematic description of the Dudley Fossil had a prominent role in Brongniart's paper. As Brünnich (1781), Brongniart placed the descriptions and figures of his genus *Calymene* along with its type species *blumenbachii* at the beginning of his systematic section (Fig. 5); this made *Calymene* the first and oldest genus of modern trilobite systematics. He commented that the first genus, which he named *Calymene*, included the trilobite that has been described under the name "Dudley Fossil." Although wrongly stating that it had been found over a century before (probably because of the inclusion of figures of this trilobite in the 1760 edition of Lhwyd's 1699 book), he correctly indicated the importance of these unique, common, and well-preserved fossils in determining the distinct nature of these animals.

Dudley's role in Brongniart's research was not limited to the trilobite *Calymene blumenbachii*. He also named a second species found at Dudley, *Calymene variolaris* (known today as *Encrinurus variolaris)*, and described and illustrated Dudley specimens of *Asaphus caudatus (Dalmanites caudatus*) and an unnamed trilobite (now known as *Hemiarges bucklandi*).

Calymene blumenbachii also played an important part in the classic 1843 trilobite study by the German zoologist Herman Burmeister [see Burmeister (1846) for an English translation by T. Bell and E. Forbes]. Expanding on the work of Brongniart and others, Burmeister published a comprehensive examination of trilobites that was highlighted by a more detailed comparison between trilobites and living arthropods, as well as a proposed high-level classification of the group. He believed that previous work on these fossils had shortcomings because of the limited zoological background of most of the authors, and that his expertise in this field might allow him to resolve some of the questions raised by others. One of his new families, the Calymenidae, which represented, in part, "trilobites having the power of rolling themselves into a ball…" was, undoubtedly, inspired and based to a large degree on *Calymene blumenbachii* specimens. [This family is now credited to Milne Edwards (1840), who proposed a similar family name for a group with many of the same trilobite taxa; see Whittington (1983.)] Even though the number of trilobite taxa and specimens available to Burmeister had grown considerably since Brongniart's work, *Calymene blumenbachii* apparently was still one of the most important because of the excellent preservation and wide availability of its fossils. Burmeister specifically noted the rarity of trilobite specimens with their "real shell" preserved and that fossils of the "Dudley Trilobites" were among the few taxa in which he could "observe the external layer with its granulations in a well-preserved state." He believed this was an important feature of the group.

The historical importance of this species is acknowledged in Burmeister's (1843, 1846) discussions of previous studies of trilobites in which he mentioned the Dudley Fossil "as the Trilobites were usually called in England, from the principal locality where they were found." He also acknowledged the key role that the Dudley Fossil played in establishing the arthropod affinities of trilobites, and stated, "Their anomalous form induced a number of collectors to search for them in England, where the most beautiful and perfect specimens have always been found, and their admirable condition in that country readily caused the impression that they must be Articulata to gain ground."

In summary, the publications of Lyttelton, Mortimer, Walch, Brünnich, Brongniart, and Burmeister are among the most influential pre-1850 works on trilobites. Collectively, they demonstrate a significant progression in understanding the group based on a combination of insights, new discoveries, and cumulative knowledge. In each paper, the Dudley Fossil, *Calymene blumenbachii*, played a critical role. It was clearly the single most important trilobite taxon used in research on the group during this initial period of investigation (1750–1850) and was discussed in numerous publications. The American paleontologist James Hall (1852) stated, "Perhaps no other single species has been so generally cited in works upon this subject as the *Calymene blumenbachii*."

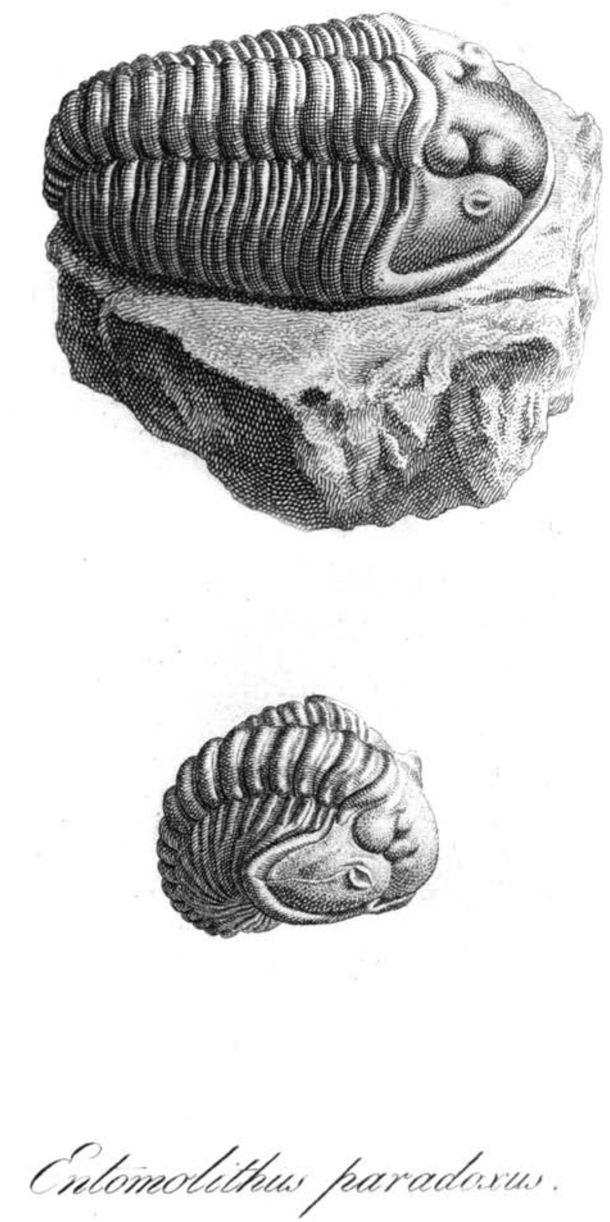


Fig. 4. Illustrations of the "Dudley-fossil" (*Entomolithus paradoxus*) reproduced from Alexandre Brongniart's personal copy of the 1803 French edition of Blumenbach's work (University of Illinois at Urbana-Champaign Library).

Following the mid-1800s, *Calymene blumenbachii* began to lose its central role in trilobite research, although it remained important as one of the first and best-known members of the group. The main reason for this decline probably was the growing discovery and description of new trilobites, some of which were based on equally well-preserved specimens (including other taxa found at Dudley). In addition, the focus of trilobite research was also changing from the original discussions on the relationships and basic characteristics of the group to more focused descriptive works on other taxa and on geographic localities and stratigraphic intervals where *Calymene blumenbachii* did not occur. As a result, scientific interest in this species shifted to more specialized research, such as its role in the composition and biostratigraphy of specific Silurian trilobite faunas. For example, the Dudley Fossil had been recognized as a characteristic fossil of

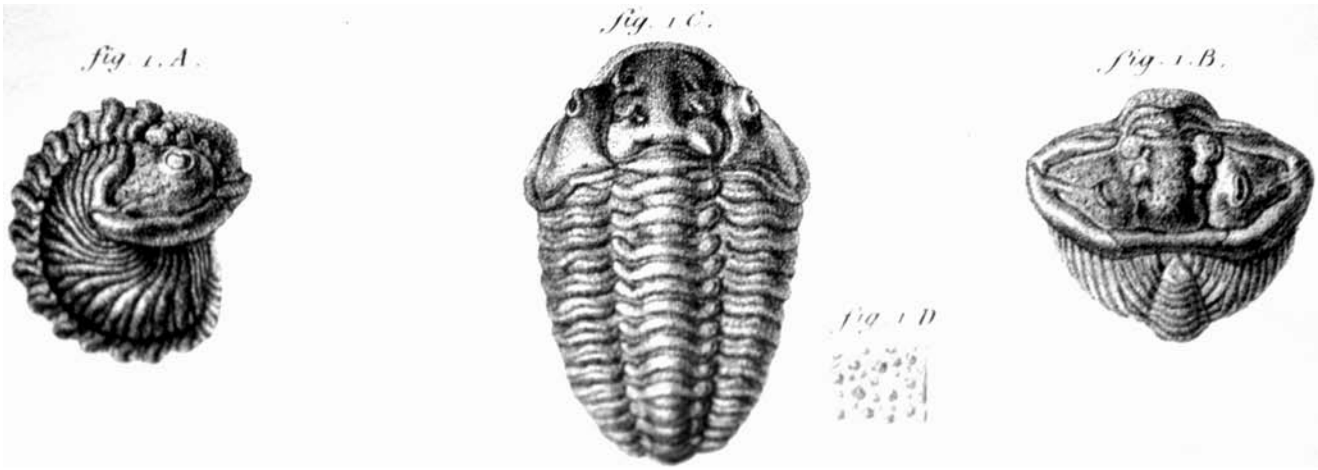


Fig. 5. Brongniart's (1822) Plate I, fig. 1A, B, C and D, illustrating specimens of *Calymene blumenbachii* from Dudley.

the Transition Series, then thought to represent the oldest fossiliferous rocks on Earth. With revisions of this portion of the stratigraphic column, it remained an index fossil of the more refined Silurian System (Upper Silurian), which was named by Murchison in the 1830s. The apparent abundance and widespread distribution of this species made it one of the best trilobites for this type of research. Its special importance was indicated by Salter (1859), who called it "an universal Silurian fossil."

Although losing some of its prominence in trilobite research of the mid-1800s, the Dudley Fossil had become even better known to a broader audience through its appearance in a wider variety of publications. Encyclopedias, popular works on natural history or science, and more specialized books on geology and paleontology were published with increasing frequency throughout the early nineteenth century. Many of these publications (e.g., Buckland, 1836; Mantell, 1844), especially those written for other naturalists, included discussions and illustrations of trilobites, which usually portrayed *Calymene blumenbachii* from Dudley as a primary representative. For example, Mantell (1844) included several trilobites in his discussion of the group, but highlighted *Calymene blumenbachii* with his introductory comments, "Among the numerous petrifactions which are found in the limestones in the neighborhood of Dudley, in Staffordshire, there are certain fossil bodies which, from their extraordinary form and appearance, have for more than a hundred and fifty years been objects of great interest to the naturalist, and of wonder to the general observer, and have long been provincially termed Dudley insects, or locust." This use was not confined to Great Britain, but was common throughout Europe (e.g., Vogt, 1854, 1878; Lardner, 1860; Figuier, 1864; Credner, 1883; Blanchard, 1890; Haas, 1902) and North America (e.g., Dana, 1864, 1875, 1880; LeConte, 1899). During the nineteenth century, the Dudley Fossil truly served as the "textbook" example for all trilobites. Most publications that discussed these arthropods figured outstretched and enrolled specimens of *Calymene blumenbachii*, as they were then the best-known examples that illustrated this important feature of the group. Most of these illustrations were reproduced from a limited number of older works, of which Brongniart (1822) and Burmeister (1843) were most frequently used (Fig. 6). Few publications, including books written by British authors, included figures of the Dudley Fossil from the older British works, with the exception of the poor illustrations of Parkinson (1811, 1833). Even more surprising, Walch's and Blumenbach's illustrations do not seem to have been used by anyone despite their high quality.

The number of publications that discussed and illustrated *Calymene blumenbachii* did not begin to change appreciably until the 1870s, when the first trilobite fossils were discovered with preserved appendages. At that time, illustrations of these new specimens, represented by taxa such as *Triarthrus eatoni*, began to replace *Calymene blumenbachii* as the "standard" trilobite in popular literature and textbooks. Because of its compelling popular name and historical importance, however, the Dudley Fossil remained one of the most widely cited trilobites.

THE NAMING OF A FOSSIL: A TRILOBITE BY ANY OTHER NAME

The scientific importance of *Calymene blumenbachii* is, to a large part, the result of its featured role in early trilobite research. Its long lasting notoriety, however, is due primarily to the popular and scientific names with which it has long been associated. With the exception of a few vertebrates, such as dinosaurs, rarely have other ancient organisms been identified with such a variety of widely recognized popular names as has this trilobite, and few for as long. Dating back to the 1750s, some of these names reflect the manner in which paleontology developed as a science as well as the role of *Calymene blumenbachii* in early trilobite research. Others seem to have originated with the public because of the trilobite's importance to the miners, collectors, and other inhabitants of the Dudley area. While some of them overlap in time, these names can be divided into several basic categories that relate to their origin and application. These categories include "scientific" names used in the initial studies of these fossils, formal scientific designations derived from "modern" systematic

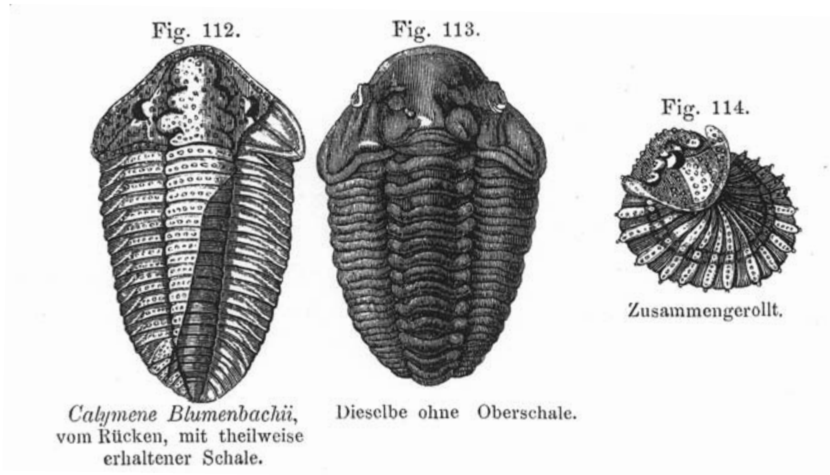


Fig. 6. Illustrations of *Calymene blumenbachii* published by Burmeister (1843, figs. 112 and 114) and Brongniart (1822, fig. 113), reproduced in Vogt (1854).

studies, and "popular" nicknames by which this trilobite has long been known. An examination of these categories demonstrates the difficulties of studying extinct organisms without close living relatives, as well as the significance of *Calymene blumenbachii* fossils to scientists and the public.

In the mid-eighteenth century, when fossils of this trilobite were first described, paleontology and biology did not really exist as scientific disciplines. Even many modern organisms were unfamiliar to the naturalists of the time, and there was no accurate classification system that could be used to establish the relationships between most living plants and animals. It is no surprise, then, that the fossils of strange forms such as trilobites were problematic to the few individuals who contemplated them, with even their organic origins having been questioned. The best approach was to find similar-appearing extant organisms that could provide clues to the nature of these fossils and identify them by the then-"scientific" terms applied to them.

As a result, during the late eighteenth century, the trilobite now known as *Calymene blumenbachii* was labeled with a variety of names. These included *Scolopendre aquatic scutate affine animal petrifaction, Pediculus marinus major trilobos, Monoculus, Onifcus, Anthropomorphite,* and *Entomolithus paradoxus monocul* (all with variations) based on a perceived resemblance to specific living or fossil arthropods. The origins of most of these names predate the beginnings of Linnaean binomial nomenclature, and, for a number of reasons, are not valid in modern systematics. They are, however, of historical interest for their role in the early study of trilobites. Initially used in scientific papers that focused only on trilobites, these names later appeared in early papers on the geology of the Dudley area (e.g., Keir, 1798; Thomson, 1816; Smith, 1836a, b; 1838). They also appeared in contemporary regional natural history volumes, tourist guides, local histories, and business directories (Nash, 1781; Payton (1794; Shaw, 1801; Booker, 1825; Bentley, 1841; Harris, 1845). The use of these old terms ended quickly in scientific circles after the publication of Brongniart's (1822) paper, which provided an accepted scientific name. In the popular press, however, these old terms, sometimes in combination with valid or invalid scientific terms along with popular local designations, remained in use until well after 1850.

Following the adoption of Linnaean binomial classification in the late eighteenth and early nineteenth centuries, *Calymene blumenbachii*, along with a few now-invalid names such as *Trilobus tuberculatus, Calymene ceratophthalama, and Calymene lata,* represented the "modern" scientific rubric for this trilobite (see Siveter, 1985). The derivation of *Calymene blumenbachii* has been discussed above. It should be noted, however, that, although that name is used for all specimens of the Dudley Fossil discussed in this paper, taxonomic studies such as those by Siveter (1985, 1996) have demonstrated that several other related trilobites (*Calymene aspera, C. fuliginata, Diacalymene allportina*) now also are known from the Silurian of Dudley. Many of the original specimens depicted in historical descriptions and illustrations of trilobite fossils from Dudley have been lost through time, therefore, it is difficult to confirm with absolute certainty that *Calymene blumenbachii* was the species those fossils represented. As these other species are generally rare compared with *Calymene blumenbachii* in museum collections, it is likely that most of this lost historical material was of the latter species.

Following the description of this species by Brongniart (1822), trilobites identified as *Calymene blumenbachii* were described or reported from many localities worldwide. Brongniart believed that fossils from distant localities in North America and Europe were of the same species. Other authors such as Burmeister (1846) stated that *C. blumenbachii* "has a very wide range, and is found in Europe, in South Africa, and North America." It now is known that many similar calymenid trilobites of different genera and species are common in Ordovician and Silurian rocks worldwide, whereas *C. blumenbachii* is restricted to the Silurian of the British Isles.

The popular names for *Calymene blumenbachii,* for which it has long been famous, are historically the most interesting. Since the eighteenth century, this trilobite has been known as the Dudley Fossil, Dudley Locust, Dudley Insect, Dudley Trilobite, or Dudley Bug. Having a widely recognized nickname for over 250 years is a feat that can be claimed by few other fossils. [The amazing record of over two thousand years goes to rocks with

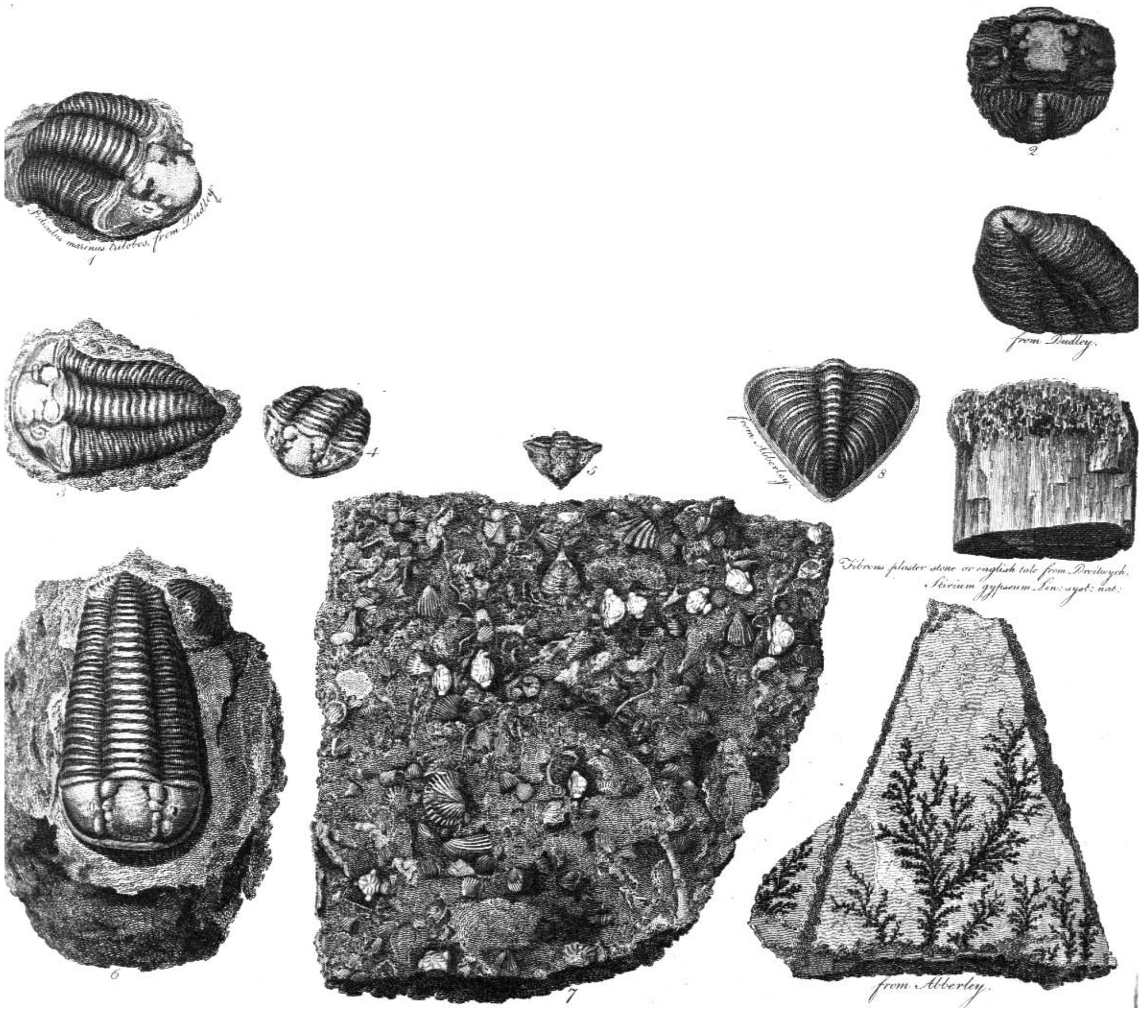


Fig. 7. Illustrations from Nash's (1781) natural history plate, with several specimens of *pediculus marinus trilobos* from Dudley (figs. 1–6) and a slab from Dudley (fig. 7), showing a variety of fossils including numerous trilobite "heads" (cephala), which may be *Acaste*.

the Chinese trilobite fossils called "batstones"; see articles by St. John and Peng, this volume.] The origin of these nicknames is unrecorded, but it is possible to establish a general history of their use by examining the extensive literature on this trilobite. These publications show clearly that the popular names fall into two categories based primarily on who used them: those used by early scientists or naturalists, usually from outside the region (i.e., Dudley Fossil, and to a lesser extent Dudley Trilobite and Dudley Insect) and those used locally by the miners (i.e., Dudley Locust and, more recently, Dudley Bug).

The first of these, Dudley Fossil, may be traced to the scientific papers of Lyttelton (1752) and Mortimer (1752). Dudley Fossil, as used by these authors, probably was not intended as a formal term, but merely reflected the locality at which these fossils were found. If it had been a locally derived name or another was then in use by Dudley residents, it wasn't noted in their reports. As the fame of these exceptional fossils spread, they generally became well known as Dudley Fossils by scientists and popular authors alike, to the exclusion of all other fossils found at Dudley. Because it was the best-preserved and most common trilobite of the time, many authors also used Dudley Fossil as a name for trilobites throughout Europe or for all trilobites from Dudley, even after Brongniart (1822) proposed the scientific name *Calymene blumenbachii*.

This usage was not limited to England, as illustrated by its prominent use in Walch (1771) and its listing as a separate subject by Defrance (1819) in the *Dictionnaire des Sciences Naturelles*. Used in a historical context or as a reference to popular usage, "Dudley Fossil" appears in many scientific and educational works into the mid-1800s (e.g., Jukes, 1829a; Sowerby, *in* Jukes, 1829a; Parkinson, 1833; Bakewell, 1833; Comstock, 1836; Murchison, 1839). Rarer variations of the name, such as "Dudley insect," (Mantell, 1844) or "Dudley trilobite" (Lyell, 1852; Owen, 1860), were also used but, eventually, all of them disappeared from scientific publications in favor of *Calymene blumenbachii*.

The most famous popular term for *Calymene blumenbachii* is "Dudley Locust." Still appearing in current publications, the continuing use of this compelling name is the primary reason for this trilobite's long-lived public renown. In contrast to the

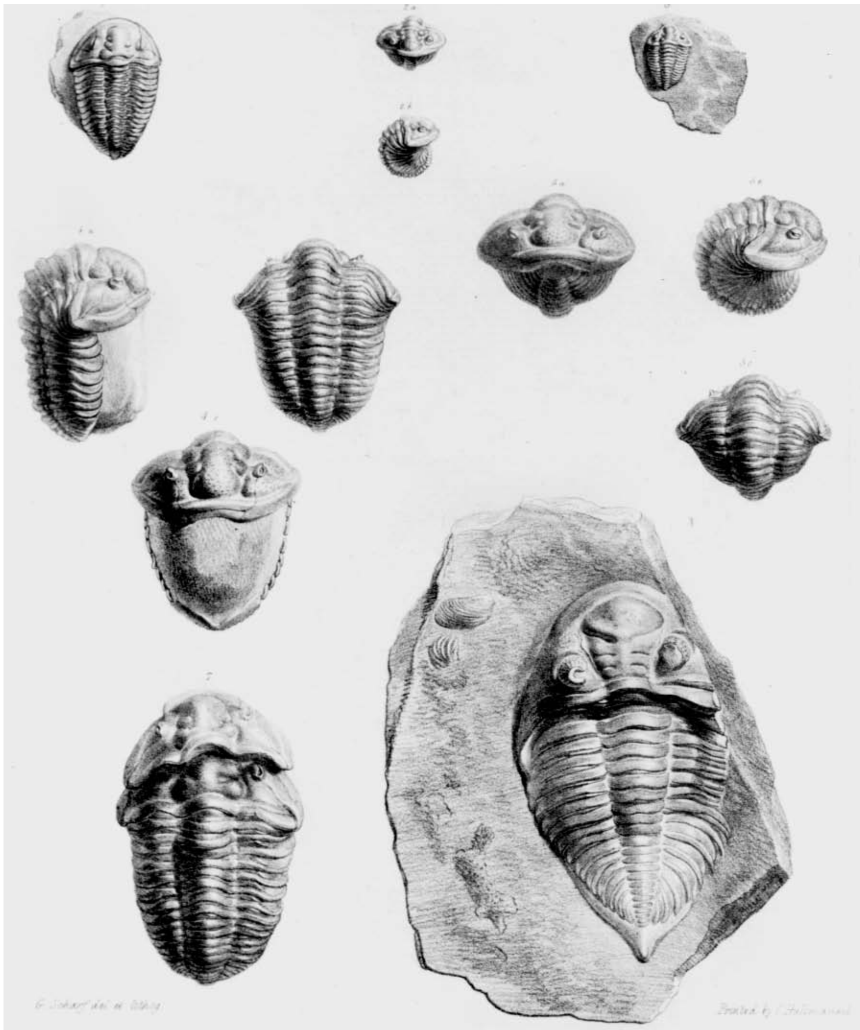


Fig. 8. Plate I from Payton (1827) showing Dudley specimens of *Calymene blumenbachii* (figs. 1–5, 7) and "*Asaphe caudatus*" (fig. 6) from his collection.

origin of "Dudley Fossil," "Dudley Locust" was not derived from the scientific work of the time, nor was it used as a name for trilobites by these investigators. Instead, it seems to have begun as a local term used by the miners and general population of Dudley. Because of this origin, the exact date when its use began and the reasons why it was chosen do not seem to be recorded.

"Dudley Locust" first appeared in print in 1781. In Brünnich's classic paper, he observed that Dudley limestone miners called these fossils [locusts] or [grasshoppers] because they thought the trilobites resembled these insects. Treadway Nash (1781) also used "Dudley Locust" in a tome titled *Collections for the History of Worcestershire*. Although generally ignored in trilobite research, this volume included several interesting observations on trilobite fossils from Dudley, and is comparable in content to some well-known contemporary works on the group. Nash began his trilobite discussion with "In lime-[s]tone quarries near this town is frequently found a kind of fo[ss]il called by the workmen the Dudley fo[ss]il or Dudley locu[s]t." He included in his discussion a brief review of the different ideas and names used in previous trilobite studies, listing some of the "[s]ynomyns of the Dudley fo[ss]il" [he apparently was unaware of Walsh's (1771) paper]. He also provided exceptionally high-quality illustrations of a number of fossils found in Worcestershire, most of which appear to be specimens of *Calymene blumenbachii* (Fig. 7). Nash recognized that there were several different trilobite species found at Dudley, and did not exclude trilobite parts from his contribution to trilobite terminology.

The next popular reference to this trilobite was supplied by Joseph Payton (1794), a businessman, author, and one-time mayor of Dudley, as well as a prominent collector of and dealer in local fossils. In 1794, Payton published a guide to Dudley Castle, in which he described a variety of interesting features of the area, including the fossils. Specifically, he observed, "In the Lime-[s]tone Quarries near this place, is found that rare fo[ss]il called by the workman, the Dudley Locu[s]t." In part, his comments may have been paraphrased from Nash, but he does include information on the other types of fossils found at Dudley absent from Nash's work. A few years later, Keir (1798)

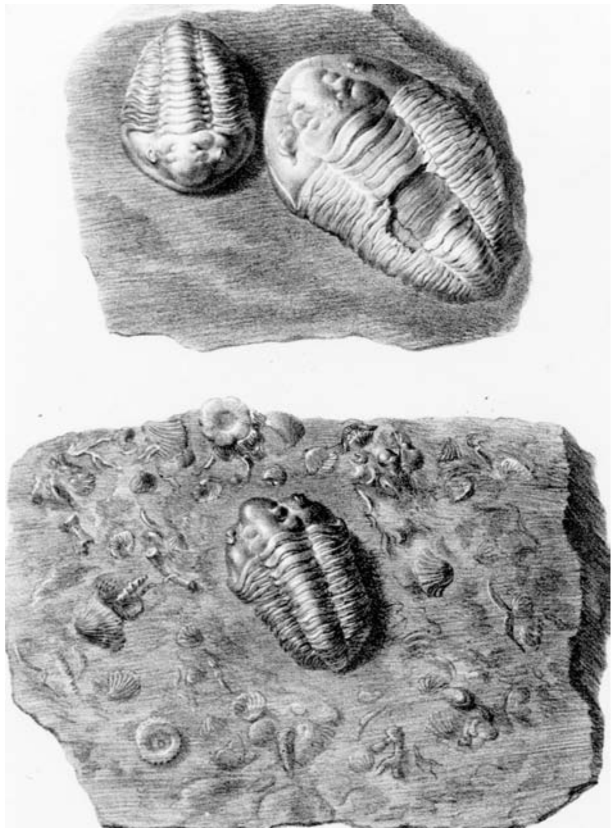


Fig. 9. Plate II from Payton (1827), showing fossiliferous slabs with specimens of *Calymene blumenbachii* from Dudley.

stated, "Among the[s]e [s]hells there is nothing [s]ingular, but one very rare fo[ss]il repre[s]entation of an animal, called by the workmen a locu[s]t, by others, the Dudley fo[ss]il, and by tho[s]e naturali[s]ts who de[s]ignate by peculiar names tho[s]e petrified [s]hells, although the [s]ame [s]pecies are not known to exi[s]t now, at lea[s]t in our climate, *Pediculus marinus trilobos* and *Anthropomorphites*." Nash (1781) stated, "[s]ome authors call it *anthropomorphites,* becau[s]e the head bears [s]ome [s]mall re[s]emblance to a man's face." Warner (1802) stated, "the rarest productions of this sort is the *pediculus marinus*, or sea-louse, the *entimolithus paradoxus monoculi deperditi* of Linnaeus, but called, in the homely naturalist's vocabulary of the place where it is found, the Dudley locust." In 1827, Payton published a short article on Dudley trilobites (Figs. 8, 9), and stated that these fossils are called "Locusts" by the miners, "a local name, of which it would be difficult to trace the origin, as no living animal at all resembling it has been yet discovered in any part of the world." Dugdale (1854?) reported that the workmen called the fossil the "Dudley locust," and added, "What is called the locust stone is the most rare and curious."

Collectively, these comments present some intriguing possibilities about the origination and use of the name "Dudley Locust." Using the earliest information from Brünnich (1781) and Nash (1781), it appears that the "workmen" were calling these fossils "locust" or "Dudley Locust" at that time (Nash also claimed they used Dudley Fossil; he is the only author to do so). Later reports, including those by such members of the local community as Payton (1794), suggest the miners used only "Dudley Locust." Other authors, such as Keir (1798), Payton (1827), Pye (1825), and Dugdale (1854?), indicate that just "locust" or even "locust stone" might have been the moniker preferred by miners.

Payton's (1827) comments should be considered the most accurate in this regard as he had long been the premier Dudley collector, and, presumably, was most familiar with the local name for this fossil. In addition, James Keir (from nearby West Bromwhich Tipton), clearly stated that the workmen called it "a locu[s]t" while the naturalist used "Dudley fossil." In any event, the likelihood that miners or other Dudley area residents coined the name "Dudley Locust" has interesting implications. Did the miners see an arthropod in their fossils before any scientists ever laid eyes on them? Was the name in use before 1781, or even before the time of Lyttelton's visit in 1749? Was it inspired by Lyttelton's use of "petrified insect" or by later scientific discussions of the arthropod affinities of trilobites? Hopefully, information might still be uncovered to answer these questions, but it is clear that the name "Locust" or "Dudley Locust" was not coined by scientists but by members of the Dudley community.

The popular appeal of the name Dudley Locust has ensured its continuous use for well over 200 years, not only by locals, but also by the world of science and the general public. As one of the few fossils with an intriguing popular name, it still is used regularly in a wide variety of publications. Many academic works that mention *Calymene blumenbachii* also note the common name "Dudley Locust," as do publications for the general public. Although "Dudley Locust" may be more widely recognized now than ever before, in recent decades, a new name, Dudley Bug, has become increasingly popular.

ENROLLMENT, EYES AND DIVERSITY: THE SCIENTIFIC CONTRIBUTIONS OF DUDLEY TRILOBITES

Dudley trilobites were involved in a number of important contributions to the early study of this group. *Calymene blumenbachii* played a central role in establishing the basic morphological characteristics of trilobites, their ability to enroll, and their relationships to other arthropods. Over time other Dudley taxa became important in documenting additional features of the group. Noteworthy trilobite features, such as their highly developed compound eyes, were first defined by the use of Dudley species. The increasing number of new species reported from the area also provided insights into trilobite diversity. This was an important discovery in itself, as most other localities known at the time yielded only a few trilobite taxa.

Enrollment was the first and most important trilobite characteristic derived from the study of the Dudley specimens. As discussed above, the recognition that trilobites such as *Calymene blumenbachii* could enroll was a key factor in establishing the relationship between trilobites and arthropods. Because of their greater resistance to destruction, enrolled specimens of the Dudley Fossil probably were easier to collect than outstretched specimens. Therefore, it is no surprise that some of the first illustrated specimens were enrolled. Lyttelton (in the addendum to his 1752 paper) reported that he had obtained an "extended" specimen of the Dudley Fossil in addition to the enrolled specimens he collected initially. Possessing enrolled and outstretched specimens, he decided that this fossil undoubtedly represented an arthropod because of the similar construction and function of its thorax to that of modern arthropods. Arthropod enrollment is a well known feature of the group, even to many people situated far from the sea, because of the ubiquitous terrestrial isopods referred to as woodlice, pill bugs, or sow bugs. This similarity was noted by Warner (1802), "In form it resembles that common wood-louse, except that it is trilobated, and exceeds in considerable size, some specimens being nearly five inches long, and few so small as the recent insect is." Many other authors, such as Miller (1847) and LeConte (1899) commented on this conspicuous trait, and the Dudley Fossil became the main example of enrollment in trilobite research and popular discussions during the 1800s. One of the most frequently used trilobite illustrations since the nineteenth century is the combination of outstretched and enrolled specimens of *C. blumenbachii* (see Dixon, 1993; Molyneux, 1999).

Spectacular compound eyes were also discovered through the study of trilobites from Dudley. In this case, *Calymene blumenbachii* had no role. Instead, *Asaphus caudatus* (*Dalmanites caudatus*) was the important species. Although its conspicuous eyes were noted by earlier authors, William Buckland (1836) provided the first insightful and extensive commentary on their character and significance. A man of many remarkable discoveries in geology, he was very impressed with these fossils, and remarked that finding trilobite eyes "in so perfect a state of preservation, after having been buried for incalculable ages … is one of the most marvellous [sic] facts yet disclosed by geological researches." In determining the structure of trilobite eyes to be the most important point of resemblance to living crustaceans, he presented detailed comparisons of these features to show that these groups were related. Equally interesting was his observation that the similarity of the eyes of these groups indicated that modern crustaceans and ancient trilobites lived under similar conditions of light, atmosphere, and water clarity. Buckland's figure of the eye and head of a specimen of *Dalmanites caudatus* from Dudley joined those of the Dudley Fossil as repeated illustrations in numerous nineteenth-century publications. More recently, Clarkson (1966a, b; 1969) and Thomas and Lane (1984) used Dudley specimens to investigate how the character of trilobite eyes was related to their behavior.

Although the Dudley Fossil was the first and most famous trilobite taxon found at Dudley, additional taxa were discovered at the locality by the early 1800s, and further enhanced the site's importance and reputation. Parkinson (1811, 1833) figured a specimen of the Dudley Fossil along with two other trilobites (a dalmanitid and an encrinurine), which probably were found at Dudley. In addition to naming *Calymene blumenbachii*, Brongniart (1822) described three other Dudley taxa, one of which he designated as the new species *Calymene variolaris* (*Encrinurus variolaris*). Some later authors seemed to be unaware of the additional species reported in these earlier works. At least some of this confusion resulted from the rarity of articulated specimens of taxa other than *C. blumenbachii* at Dudley, and that isolated trilobite parts generally were ignored. Payton (1827) commented on this rarity, and illustrated only a single complete specimen of another trilobite, *Asaphe caudatus* (now *Dalmanites caudatus*). He remarked that, whereas parts of the former trilobite were common, complete specimens were extremely rare. He seemed unaware of some of the new taxa described in Brongniart (1822). In his paper on the famous specimen of *Bumastus barriensis* from nearby Hay Head, Jukes (1829a) stated that two trilobites were known from Dudley, "the one which is commonly called the Dudley fossil…and another…which, I believe, has not yet been particularly noticed, arising, probably, either from their scarcity, or from the imperfect condition in which they are usually found, the head and tail being generally apart." Sowerby (*in* Jukes, 1829a) identified these two trilobites as *Calymene blumenbachii* and *Asaphus caudatus,* but also believed, incorrectly, that "these are all that were known at or near Dudley."

Afterward, the number of trilobites known from this locality grew significantly, probably as the result of increased mining, collecting, and study. For example, Murchison (1839) listed thirteen different trilobite taxa from Dudley, a number that he had almost doubled to 22 in his 1859 book *Siluria* (Fig. 10). During the remainder of the nineteenth century the diversity of Dudley trilobites increased notably through a series of papers by Salter (1849, 1853, 1864a, b, 1865, 1867, 1883), Fletcher (1850a, b) and Lake (1896). Continuing work on the trilobites of Dudley further enhanced the area's reputation as one of the world's premier nineteenth-century trilobite localities. Many of the taxa described in these publications were based on articulated specimens not found elsewhere, and provided some of the best available examples of many prominent trilobite groups.

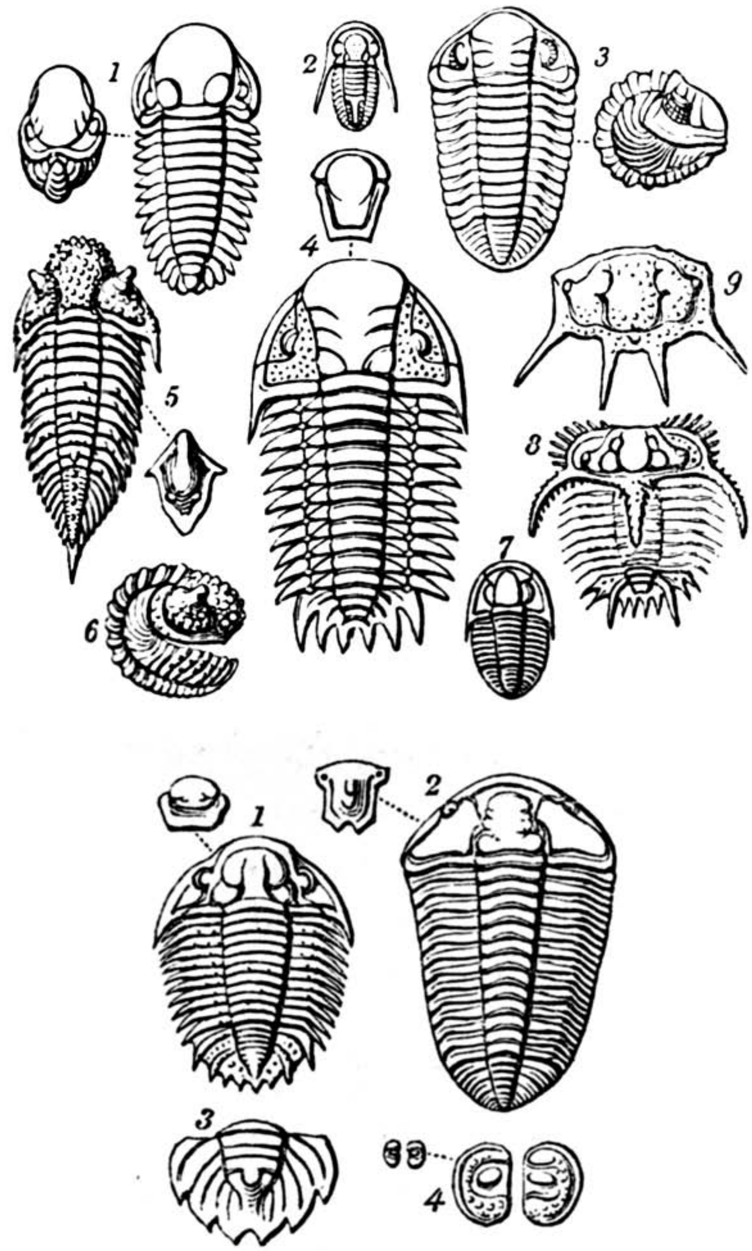


Fig. 10. Illustrations from Murchison (1859, 1872) of Wenlock trilobites, most of which are found at Dudley.

Consequently, numerous generalized publications on geology and paleontology continued to illustrate Dudley specimens as representatives of all trilobites. For example, Lyell (1866) figured a specimen of *Sphaerexochus* from Dudley on the title page of the sixth edition of his classic work *Elements of Geology*, to represent the life of the Primary [i.e., Paleozoic] Era.

After Salter's work on British trilobites was curtailed by his untimely death in the 1860s (Secord, 1985), research on trilobites from Dudley diminished, although they retained their prominence in more general and popular works. In recent decades, however, there has been an increased research interest in these fossils. Most importantly, Thomas (1978, 1981) began a study of all British Wenlock trilobites, including those from Dudley. Thomas (1979) reported at least 37 trilobite genera from the Silurian Much Wenlock Limestone Formation at Dudley, with some represented by more than one species. Some of these taxa have never been described, whereas others have not been restudied since their initial descriptions in the nineteenth century. Surprisingly, the entire Dudley trilobite biota has not yet been described fully despite its fame and over 250 years of research.

WORTH MORE THAN ITS WEIGHT IN SILVER: THE RISE OF THE TRILOBITE

A unique combination of geological and socio-economic conditions fostered the prominence of the Dudley Fossil in early trilobite research. Geologically, the Silurian rocks at Dudley contain an exceptionally diverse biota with an unusual abundance of well-preserved fossils. However, these fossils only became available for scientific research because extensive mining had developed to supply limestone for the local iron furnaces at the beginning of the Industrial Revolution. This mining provided an opportunity for discovery and collection of fossils by the miners who, along with private and commercial collectors, supplied sought-after specimens for the expanding community of professional scientists, amateur naturalists, educational institutions, and museums. During the eighteenth and early nineteenth centuries, few, if any, other sites witnessed an industry-dependent fossil collecting on as large a scale as that at Dudley. Because of this unique combination of factors, Dudley was the trilobite center of the world for almost 100 years.

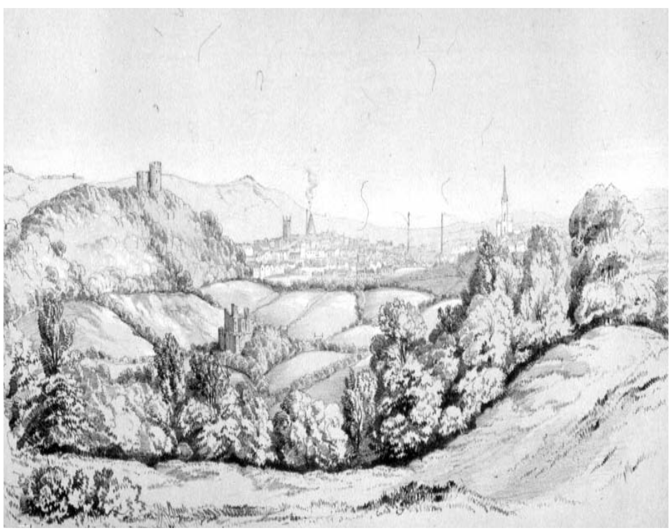


Fig. 11. Sketch of the town of Dudley and Dudley Castle Hill as seen from Wren's Nest, from Murchison (1839), as drawn by his wife.

The Geology

The characteristics of the Silurian rocks of Dudley are well known, and are described in a long series of papers (Keir, 1798; Thomson, 1816; F. Jukes, 1829a; Smith 1836a, b, 1838; Murchison, 1838, 1839; J. B. Jukes, 1859, 1866; Myers, 1866; Lapworth, 1898; Moore, 1898; Butler, 1939; Strachan, 1967; Hamblin *et al.*, 1978; Oliver, 1981; Cutler *et al.*, 1990; Thomas and Radcliffe, 1988; Siveter, 2000; Ray, 2001). Dudley is located in the South Staffordshire Coalfield, which lies north and northwest of Birmingham, England.

Throughout much of this area, Silurian rocks are buried by a thick sequence of Late Carboniferous coal-bearing strata. At the north edge of Dudley, however, the Silurian has been folded upward and projects through the Carboniferous in three prominent anticlinal inliers (Dudley Castle Hill, Wren's Nest Hill, and Hurst Hill) (Fig. 11). These hills consist primarily of limestone and shale strata of the Much Wenlock Limestone (Wenlock), which is underlain by shales of the Coalbrookdale Formation (Wenlock) and overlain by shales of the Elton Formation (Ludlow) (Fig. 12). The Much Wenlock Limestone here consists of a lower 16.2 m-thick Lower Quarried Limestone Member and the 8.6 m-thick Upper Quarried Limestone Member, which are separated by the 31 m-thick Nodular Member (Ray, 2001).

These rocks, especially the limestones, have long had an economic importance. Chandler and Hannah (1949) observed that the limestone was used originally for building the local castle and priory in the twelfth century, later to make lime for general building purposes, and, finally, "the easily worked limestone was exhausted through its use as flux in the blast furnaces engaged in the iron industry." Outcrops of these strata probably were extensive on all three hills originally, but are now very limited in extent, having been considerably altered and reduced by hundreds of years of mining and quarrying.

Although the limestones of the hills north of Dudley were quarried for the lime at least as early as the late seventeenth century (Plot, 1686), little information was published on their geology until the nineteenth century. Undoubtedly, miners and mining engineers understood the basic geology of the area because limestone, ironstone, and coal mining had become major local industries. During this time, an enhanced geologic knowledge of the region would have been needed in mining. Other than references to the Dudley Fossil, however, few geological observations were published about these rocks over this long period.

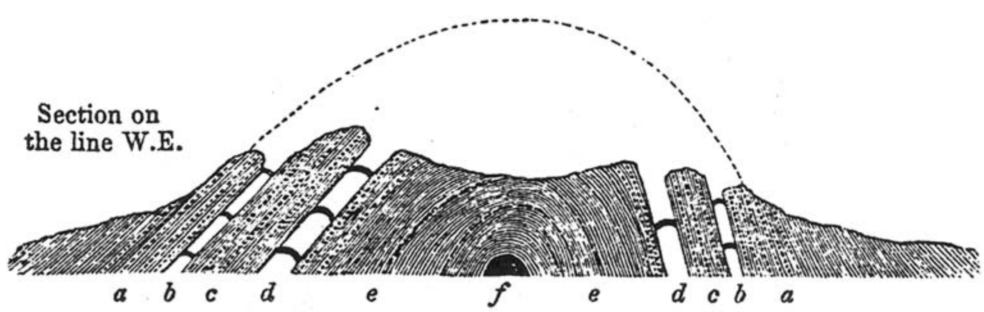


Fig. 12. Cross-section through Wren's Nest, showing the stratigraphy of Silurian rocks applied by Murchison (1839) figure: a) Elton Formation, b) Upper Quarried Limestone Member of the Much Wenlock Limestone Formation, c) Nodular Member of the Much Wenlock Limestone Formation, d) Lower Quarried Limestone Member of the Much Wenlock Limestone Formation, e and f) Coalbrookdale Formation.

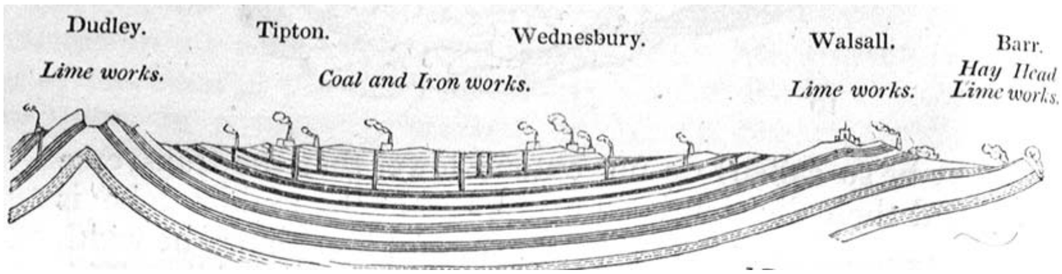


Fig. 13. Eleven-mile-long cross-section showing the presumed relationship of the Silurian limestone beds at Walsall and Barr with those at Dudley (from Jukes, 1829a).

Keir (1798) and Thomson (1816) provided the first detailed descriptions on the Silurian limestones in the Dudley area. These works have general observations about the composition, distribution, and structure of the limestone strata, and Thomson recognized that the limestone was "formed in the sea" because of its fossil content. Other geological accounts of these rocks appeared through the early 1800s, many of which were written by such local authors as Booker (1825) and Bentley (1841), in tourist guides, business directories, and other publications outside of the scientific literature. Because of their growing economic importance and scientific prominence, the Dudley limestones became the focus of increased study by a wider range of naturalists and geologists, including some of the most prominent of their day. These studies documented the local geology and paleontology, afforded early comparisons with rocks from distant localities, and helped establish a framework for understanding Lower Paleozoic rocks. The limestone beds of Dudley were recognized as part of the "Transitional Series," which in the early 1800s, was a group of poorly understood sedimentary rocks under the younger Old Red Sandstone and over a group of older, unfossiliferous, "primary" metamorphic and volcanic rocks (Thackray, 1978; Bassett, 1991). As one of the most prolific sources of what were then thought to be the oldest fossiliferous strata, the Dudley limestones provided an opportunity to study the paleontology of this ancient time.

By the 1830s, a detailed understanding of at least part of the Transitional Series of the Dudley area had been realized, as indicated in papers such as those by Jukes (1829a, b), Smith (1836a, b; 1838), and Murchison (1838). The first of these (Jukes, 1829a), although primarily a description of a new trilobite, provided a simple but accurate cross-section of the "Lime formations" from Dudley to Hay Head, a distance of about eleven miles (Fig. 13). Although he worked with discontinuous exposures in a geologically complex area, Jukes based his cross-section on observations of the distribution and dip of several limestone units, which he distinguished by their fossil content. Jukes's work is remarkably accurate, especially when viewed in comparison to the more recent cross-section by Cole (1987) based on a wealth of information including mine records and modern subsurface data. Except for identifying numerous faults in the area, Cole's cross-section is little different from Jukes's 150 years earlier. Jukes's work also inspired commentary by Sowerby (*in* F. Jukes, 1829a) who emphasized the importance of the observation that specific trilobite species "are peculiar to different beds," and could be used to identify beds or strata of the Transitional rocks "at immense distances." Murchison (1834, 1835, 1838, 1839) employed this kind of biostratigraphic approach, including the use of trilobites, to establish and subdivide his Silurian System from rocks of the old Transitional Series.

Murchison used this understanding of Dudley geology to establish his Silurian System, and made the first detailed comparisons of the rocks in this area with similar strata elsewhere. Prior to the 1830s, the fame of its fossils and industry ensured that the Dudley Limestone was a widely recognized part of the Transitional Series. However, when Murchison investigated this part of what would become his Silurian System, he used outcrops of the same strata in the vicinity of Wenlock Edge in nearby Shropshire to formally name this unit the Wenlock Limestone (now Much Wenlock Limestone Formation). Even though they were much better known, Murchison believed the limestone beds at Dudley did not show a complete enough stratigraphic section. Murchinson (1839) observed, "For these reasons therefore it is obvious, that however long known to collectors for the beauty of its organic remains, the name of Dudley limestone could not be used in stratigraphical classification, and hence I was compelled to adopt the term of Wenlock." In particular, he had found that the exposures at Wenlock Edge better demonstrated relationships with adjacent units. This new name was later the basis of the Wenlock Series, which is now recognized internationally as the term for this middle part of the Silurian—an honor lost by Dudley with the demise of the term "Dudley Limestone." However, Murchison's decision was probably correct. It should be remembered that the fame of the Dudley Locust was a primary reason that the Dudley Limestone almost became the foundation of this Silurian series.

The Fossils

The Much Wenlock Limestone beds in the Dudley area have long been known as one of the best sources of well-preserved, abundant, and diverse Silurian fossils in the world. Since the 1750s, more than 600 fossil taxa have been identified from these rocks (Cutler *et al.*, 1990), and are represented by thousands of specimens in museums worldwide. The study of these fossils has resulted in many important contributions to geology and paleontology, but has also produced a few misconceptions. Among the most notable misconceptions about trilobites are that the fossils at Dudley belong to a single biota and that articulated trilobite specimens are, or were, common in these rocks.

The idea of a single biota came about during the early development of the disciplines of geology and paleontology. When fossils from Dudley were first studied, scientists had little understanding of the ecological complexity of the modern world, much less of its ancient past. Moreover, many of their specimens were obtained from dealers, collectors, and miners who did not record the details about the environmental and stratigraphic occurrence of their discoveries. More recent research by Butler (1939), Thomas and Radcliffe (1988), and Ray (2001) has shown that the preservational nature and distribution of the fossils at Dudley vary considerably through the 70 meters of Silurian rocks locally exposed there. This variation results from temporal differences in living and burial conditions, as these rocks were deposited as sediments in a variety of marine environments and over a significant period of time (Ray, 2001). Consequently, the distribution and preservation of different taxa vary, with some being found throughout the section and others occurring only in specific intervals or environments. Similarly, some taxa may be well preserved or abundant at one horizon, and rare or fragmentary in another. This is especially noteworthy with the trilobite and crinoid fossils, as their skeletal elements are common in many beds, but only a few horizons contain significant numbers of the articulated specimens for which the locality is famous. These studies also have shown that the Dudley biota does not represent a single group of organisms living together in the same place and time, but, rather, a variety of different communities that lived at different times and under different conditions. Although not representing a single biota, Dudley remains one of the most diverse, best-known, and historically important Silurian trilobite localities in the world.

Dudley has been famous as a source of complete trilobite fossils for more than 250 years. An examination of museum collections or the scientific literature would suggest that articulated trilobite fossils, especially *Calymene blumenbachii*, were common here. In reality, this was only true relative to other localities then known in this early period of trilobite studies. At Dudley, articulated specimens were readily available in the late eighteenth and nineteenth centuries because of the large-scale industrial excavations and the financially-motivated collecting activities of the miners. Not only did the quarries and mines here produce more articulated trilobite fossils than at other contemporary sites, but these specimens were also among the best preserved. At most other localities, articulated trilobite fossils were rare, commonly compressed or distorted, and had a poorly preserved test or no test at all. In contrast, the Dudley trilobite tests typically were uncompressed, three-dimensional, and well-calcified. The availability of such Dudley specimens led to their prominence in early trilobite research.

The most numerous trilobite fossils at Dudley, however, are individual, disarticulated skeletal elements, which are plentiful in many beds. Even today, long after mining has ceased, it is not difficult to find cranidia, pygidia and other parts of the more common trilobite taxa, especially *Calymene blumenbachii*. Although noted in some of the earliest papers, these parts had little or no role in early trilobite research. The brief report by Nash (1781) was one of the few exceptions. In addition to figuring several complete specimens, he also illustrated a fossiliferous Dudley slab with common cephala of what might be *Acaste* and other trilobite parts, including a dalmanitid pygidium. Even though he did not appear to have a complete specimen of the latter taxa, Nash recognized the relationship of these parts to complete trilobites, as indicated in his comment, "where likewi[s]e is found the head without the body, as in the ma[s]s here engraved, which was found at Dudley, wherein are feveral *[s]emipediculi*, or bodies without heads, and many heads without bodies." In this regard, his creative use of the term "*femipediculi*" [semipediculi] for the headless bodies or for tails is noteworthy as it appears to have been derived from the better-known name *pediculis,* which was then used for complete specimens of *C. blumenbachii*.

In contrast with Nash's observations, some individuals did not seem to make the connection between exoskeleton parts and entire trilobite specimens. For example, Parkinson (1811, 1833) figured a *Calymene* cranidium from Dudley, which he identified as "fossil remains of some crustaceous animal, which are frequently found with the trilobite in the Dudley lime-stone" on the same plate on which he figured two articulated specimens of the same taxon labeled as "Dudley fossils." It was only after the 1830s that the use of trilobite skeletal elements became more common in research, at least for the rarer Dudley taxa for which articulated specimens had not been found.

Mining for Trilobites

Dudley became an important source of Silurian trilobites and other fossils for two basic reasons. The most obvious factor, as already discussed, was the exceptional abundance, diversity, and preservation of the fossils. The mere existence of these fossils, however, did not insure that they would be collected or available for scientific research. More important to Dudley's paleontological prominence was the early development of its local limestone industry, which provided the means for fossils to be collected and distributed on a large scale. This industry created extensive collectable excavations, and employed large numbers of miners who probably were the original source of many specimens. Dudley is one of the best examples of how early paleontological research was dependent upon industrial and engineering excavations for many of its discoveries.

The mines.—Mining played a prominent role in Dudley's history and economic development. Located in the South Staffordshire Coalfield, the community is part of the Black Country, a region named for its industrial appearance and economic prominence in Britain's nineteenth-century iron industry. Mining prospered here because of the local abundance of coal, iron ore, and limestone—the basic materials for iron smelting—and a well-developed canal system that made transportation of resources and products economical (Davies and Hyde, 1970).

Carboniferous rocks are found throughout much of the Black Country and, as a result, coal and iron ore were widespread. In contrast, Silurian limestones, used primarily to make flux for iron smelting were localized in a few outcrops near Dudley and Walsall. Although poorly documented, the quarrying of these exposures began long before the advent of the iron industry. Silurian limestones were already a source of building stone during the initial construction of Dudley Castle and Priory in the twelfth century (Chandler and Hannah, 1949; Powell, 1999). Robert Plot (1686) described late seventeenth century quarrying and burning of limestone in this area to produce lime, which was used in agriculture and as mortar in construction. One hundred years later, however, the demand for lime increased dramatically as it was needed as a flux in the growing iron industry. As quarrying exhausted surface outcrops during the eighteenth century, extensive underground mining of these rocks began, and created the impressive caverns for which Castle Hill and Wren's Nest became famous. Limestone mining and lime burning continued as major industries during much of the nineteenth century (Warwick, 1967; Powell, 1999), with as much as 300,000 tons of stone produced in 1873 (Davies and Hyde, 1970). By 1900, however, limestone mining had diminished greatly, and finally ended in 1924. Although mining at increasingly greater depths became more difficult, it was the demise of the local iron industry, the main market for limestone, that was probably the most critical factor in the cessation of mining (Davies and Hyde, 1970).

To a large degree, the commercial excavations of these limestones controlled the availability of Silurian fossils at Dudley. Undoubtedly, natural outcrops of these rocks were much smaller than the later manmade exposures, and would have consisted predominantly of highly weathered, thick-bedded limestones, which would have made collecting highly desirable fossils, such as complete trilobites, difficult. During active mining, however, the exposures and piles of rock rubble from the industrial-scale excavations increased the availability of fossils and made them much easier to collect. (Today, the weathered exposures in old quarries and mines produce very few specimens of complete trilobites and other rare fossils.) Without intensive mining activity, it would have been impossible to collect the magnitude and quality of Dudley fossils now found in museums worldwide, and the area never would have played a major role in the scientific research of trilobites and other aspects of Silurian geology and paleontology.

The collections.—It is not surprising that the number of reports on Dudley area fossils increased with the growth of the local limestone industry. Robert Plot (1686) of the Ashmolean Museum at Oxford University was the first to comment on these fossils. As part of a study on the natural history of Staffordshire, he described and illustrated a few fossils from the limestone pits at Dudley, including a specimen given to him by the owner of the pits, Edward, Lord Ward. Most of Plot's material seems to be of the easily found brachiopods, corals and crinoids that abound in these rocks.

John Woodward (1729) listed, but did not figure, a number of fossils from Dudley that he had in his collection. Neither Plot nor Woodward described any Dudley specimens that can now be recognized as trilobites, which is surprising in view of the conspicuous nature of these fossils and the abundance of their skeletal elements. Little or nothing more was published on fossils from Dudley until Lyttelton's (1752) report. Lyttelton reported that he found his first specimen from the "Lime[s]tone Pits at Dudley" in 1749. Between the time his letter was read to the Philosophical Society in 1750 and his paper was published in 1752, several individuals had sent additional specimens to him and Mortimer for examination. This indicates that other British collectors had acquired specimens from the locality before 1752. These fossils soon found their way into other parts of Europe, as indicated by Walch's (1771) classic paper with its specimens of the Dudley Fossil from German collections.

By the early 1800s, specimens of the Dudley Fossil seemed to be commonplace, but limited information is available as to who collected this material and how it was disseminated. It is likely, however, that the scientists who studied this material were typically not the ones who found it. Many, such as Murchison and Salter, clearly indicated that much of the impressive material they were using was borrowed from private collectors. For example, Salter (1859) noted, "Indeed, the quarries of Dudley are the most famous in the world for Upper Silurian organisms. Shells, corals, encrinites of very numerous genera and species, and trilobites are all in a state of perfection such as no other locality in Britain exhibits. The well known collections of Messrs. Gray and Fletcher at Dudley, and the cabinets of nearly every public museum in Britain or elsewhere, are evidences of the great labour expended in collecting and developing these beautiful remains."

One of the few documented visits by scientifically minded individuals to collect fossils at Dudley was Hugh Miller's in 1845. Although experienced in finding fossils, his efforts on that trip were not as rewarding as he had hoped. Whereas common fossil brachiopods and corals were easy to find, he wrote disappointedly, "I will be unable, I find, to add materially to my collection here" (Miller's 1845 letter *in* Bayne, 1871). Miller bought a few complete trilobites from a fossil dealer after an unsuccessful weeklong collecting effort.

Although the more common fossils were never difficult to find in Dudley's mines and quarries, collecting rare specimens was a challenge for the casual visitor. The wealth of exceptional trilobites, crinoids, and other unusual fossils from Dudley in the world's museums is, therefore, misleading. Although for a critical period in early trilobite research, specimens of the Dudley Fossil were the most common complete trilobites available to scientists, these fossils probably were never easy to find at Dudley, and their great numbers in collections are most likely the product of an intensive effort by financially-motivated individuals to find them. As described by Lapworth (1898), "Bed for bed it is probable that these Midland Silurian rocks are no more prolific in fossils than their Shropshire representatives; but the Dudley limestones have been worked for centuries as a flux for the ironstones of the surrounding South Staffordshire Coalfield, and consequently abundant—and, indeed, unrivalled—opportunities have been afforded for the discovery and collection of the fossils … For many years—especially about the middle of the present century, when the limestone workings were open to the surface—these fossils were assiduously collected personally, or were purchased from the workmen, by local geologists and others."

Although fossils from remote locations or those that are expensive and hard to recover, such as large dinosaurs, always have tended to be collected by scientists, the majority of fossils in most older museum collections were discovered and collected by quarry workers, miners, private collectors or commercial dealers. These individuals provided the vast amount of manpower needed to explore the world and collect samples of its geology and paleontology, something that never could have been accomplished by the small number of contemporary naturalists or scientists (Mikulic, 1983). Rather than the result of planned "digs" or chance discoveries during exploration, many of the fossils used in science have been the byproduct of excavations for quarries, mines or the innumerable construction projects needed by an industrialized society. Most of these collections cannot be duplicated due to the decline in extractive industries at many classic localities, to increased mechanization of these industries, and to the diminished interest shown by the people to invest time and money in assembling comparable collections (Mikulic, 1983). Even today, this process continues, however, with some of the most scientifically valuable specimens found at such famous localities as the Liaoning fossil beds of China (Norell, 2005) and Mazon Creek in Illinois collected by labor-intensive work by non-scientists. Without the efforts of these collectors, regardless of their motivation, we would know dramatically less about paleontology, as well as botany, archeology, and a broad range of other natural history topics.

Dudley is an important example of this collecting phenomenon. With a history extending back to the seventeenth century, it is one of the earliest sites in the paleontological literature. Its long-term scientific prominence resulted from large-scale industrial excavations and the efforts of local collectors, both of which can be tied to the rise and fall of the local iron industry. The fossil-bearing limestone, needed for flux, was undoubtedly mined at an increasing rate as iron production grew. Records on yearly production of iron and limestone in this area are incomplete, but some indication of the trends in these industries can be derived through changes in the numbers of local iron furnaces. This trend shows a dramatic increase in the number of iron furnaces from the origin of the local iron industry in the 1790s, a peak in the mid-1850s, and a dramatic decline to 1900 (Gale, 1966; Davies and Hyde, 1970). Limestone production seems to have followed the same trend. The numbers of fossils found, doubtless, was related to the amount of limestone produced. The number of fossils described from Dudley and the number of collections assembled seem to follow the same trend, with a gradual increase towards the middle of the nineteenth century and a gradual decline to 1900. After 1900, limestone mining at Dudley was limited. Although little documentation exists about the identity of the leading Dudley collectors or the conditions under which they toiled, there is enough information to establish the general roles that miners, dealers, and collectors played in acquiring these fossils and supplying them to the scientific community.

The miners.— Quarry workers and miners were the mainstay of the fossil-collecting process, and constituted a chief source of specimens at many localities worldwide in the nineteenth century (e.g., Mikulic, 1983; Mikulic and Kluessendorf, 1998), and this was also probably true at Dudley. By the mid-eighteenth century when the earliest scientific studies of the Dudley Fossil were published, Silurian limestone had been quarried at Dudley for several hundred years. Surely, Dudley quarriers and miners had long been familiar with specimens of these conspicuous fossils.

Undoubtedly, these workmen found a major portion of the rarer and larger Dudley specimens because mining was labor-intensive. During their 12-hour shift, a crew of nine or ten men would produce nine tons of stone daily, much of which they handled manually (Hemingway, 2000). With the financial incentive of supplementing their meager incomes by selling fossils, they probably became diligent collectors. Between 1837 and 1850, when complete Dudley trilobites were selling for at least ten shillings, most miners were earning only three to six shillings a day (Warwick, 1967). Because of their work, miners also would have had the advantage of knowing the best strata and localities with the rare specimens. Brünnich (1781) observed that because specimens of the Dudley locust were much desired by the English collectors, the workers also learned to appreciate the ones that were found almost complete.

Unfortunately, direct evidence about the miners' fossil collecting is scarce. A possible clue to their collecting is the name Dudley Locust. Most authors make a point of attributing this name to the miners, and indicate that they were familiar with these specific trilobite fossils. John Gray, one of the most prominent early nineteenth-century private collectors in Dudley, reportedly directed workmen in his quarry to save fossils for him, and this constituted the main source of specimens for his collection (British Museum, 1904). In addition, Gray informed Woodward (1868) that miners had been collecting trilobites from Dudley for fifty years. Woodward (1868) also mentioned a specimen at the center of a controversy that was reportedly derived from a workman. In another note, Miller (1847) implied organized collecting, and recorded that a barber in Dudley "holds a sort of fossil agency between the quarrier and the public."

The large Dudley collection (now part of the Lapworth Museum of Geology at the University of Birmingham) assembled by the wealthy Birmingham ironmaster Charles Holcroft is accompanied by a registry (Strachan, 1979). This registry lists the individuals from whom he purchased specimens, although it does not record the livelihood or other details about his sources. Between 1876 and 1897, Holcroft acquired 140 specimens of *Calymene* from the Dudley area. Of these, 104 specimens were purchased from William Woodall and 28 specimens from James Woodall. These two men also provided the vast majority of his other Dudley trilobites. Contemporary census records show that there were several individuals with these same names in the Dudley area, some of whom were limestone miners. It cannot be determined conclusively if these were the same Woodalls from whom Holcroft purchased his specimens, much less whether his sources were miners, mine foremen, fossil dealers, or worked in some other trade, or even whether they actually lived in Dudley.

Commercial collectors and dealers.—Local commercial collectors, dealers, and private collectors are the best-documented source of fossils from Dudley in the nineteenth century. Most of the important specimens now in museums or used by scientists in research can be traced back to these individuals. Certainly, they collected some of their own material, but, most likely, they relied heavily on miners for specimens. Socially, these individuals were members of the new middle class, who had at least some leisure time and financial resources to devote to their paleontological interests. In contrast, miners have not been recorded as having personal collections and probably could collect only to earn much needed extra cash.

Although commercial collectors probably purchased most of their specimens from miners, some are known to have collected specimens on their own. For example, Blocksidge (1905) provided the following description of this pursuit, "Years ago it was a favourite resort of men who made a precarious living by finding fossils, and selling them to well-known collectors. These men were in the habit of going into the Cavern in the morning and lighting a fire, the light from which, with the aid of few candles, enabled them to proceed with their self-imposed task." This may have been an atypical example of collecting. However, according to Blocksidge's map, the cavern appears to be now known as Stores Cavern on Castle Hill, which is famous as the only location in the entire Dudley area where rare and spectacular specimens of the trilobite *Trimerus* have been found

(Hollier, 1868; Reid, 1994; Ray, 2001). As these were among the most sought-after fossils from Dudley and commanded a high price, it is likely that special efforts were made to collect them, perhaps as described by Blocksidge.

Joseph Payton may have been the one of the earliest Dudley fossil dealers. In his 1794 guide to Dudley Castle, he included a footnote to his description of the variety of fossils found there, "The Public may be [s]upplied with any of the[s]e articles, upon application to J. Payton, Dudley." Payton apparently maintained a fossil collection, published an article on trilobites (1827), served as mayor of Dudley in 1839, and was instrumental in establishing the spectacular exhibit of Dudley fossils set up for the visit by the 1839 British Association for the Advancement of Science trip to the area.

Bentley (1841) listed three fossil dealers in Dudley: Payton, who was also listed as an "auctioneer, & c.," William Roberts, also listed as a "hair-dresser," and John Tomkins, who is listed only as a fossil dealer. Having three individuals selling fossils in such a small town as Dudley indicates a great demand for these specimens. However, it is important to point out that two of the three had other sources of employment. Hugh Miller (1847) mentioned purchasing trilobites from a Dudley barber who "…had been in the way of selling Dudley fossils, he told me, for a good many years; and his father had been in the way of selling them for a good many more." Perhaps this barber was the "hair-dresser" listed by Bentley (1841). One other notable individual was Elliot J. Hollier, a Dudley chemist. Like Payton, he was a mayor of Dudley (1858) and a collector of and dealer in local fossils. In 1881, he advertised his fossil trade in a large advertisement (Fig. 14) in *The Curiosities of Dudley and the Black Country* (Clark, 1881). The only other fossil dealer in a Dudley area business directory was P. Tomkins, whose listing appeared in the 1839 directory of W. Robson and Company.

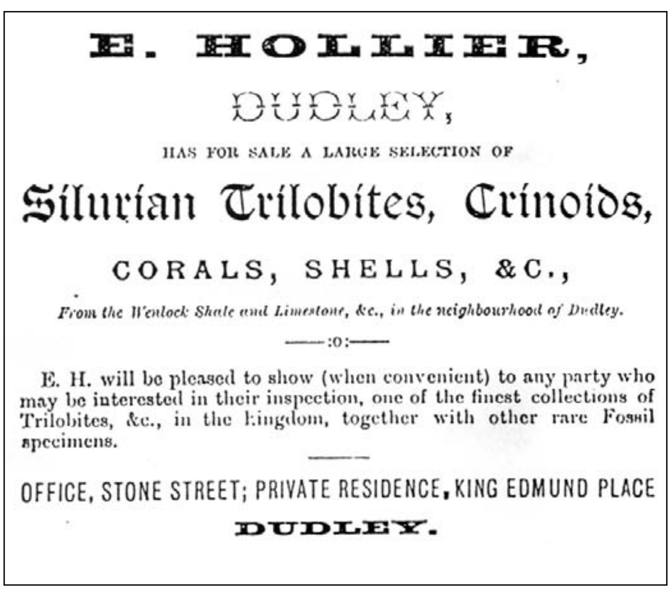


Fig. 14. Advertisement offering Dudley fossils for sale by Elliot Hollier (from Clark, 1881).

Private collectors.—Private collectors from Dudley and vicinity assembled the best collections of fossils. However, the earliest descriptions of Dudley trilobites were based on specimens from such individuals as Lyttelton, who lived in the region, as well as those from outside the area, such as Dr. Shaw of Oxford (Lyttelton, 1752; Mortimer, 1752). Some specimens, such as those used by Walch (1771), were borrowed from the fossil collections of private individuals, who did not specialize in Dudley fossils or even live in the region. This demonstrates that the Dudley Fossil had already found its way into distant collections as far away as Germany by the 1770s.

A shift in the source of specimens is recorded with the publication of *The Silurian System* (Murchison, 1839), which marked the first time that fossils from private Dudley area collectors were used extensively in research. Murchison used these fossils to help establish a biostratigraphic framework in order to subdivide rock units and to provide a comprehensive paleontological treatment of the taxa found in each unit. This material played a critical role in establishing the paleontological characteristics of his Upper Silurian Wenlock Limestone. In addition, this was the first attempt to describe all of the Dudley trilobites systematically. Murchison demonstrated conclusively that the old Transition beds could be subdivided based on their fossil content, and trilobites were essential to this work. Dudley trilobites were some of the best specimens available for illustration and description, and Murchison made good use of specimens from local private collectors. Ironically, Murchison was reputed to understate the amount and importance of much of the information he received from key contributors to his work (Torrens, 1990), although he did make a few references to Dudley collectors who supplied many of the spectacular trilobites from Dudley. He acknowledged the use of specimens from collectors, including Blackwell, Gray, Cartwright, Mrs. Downing, Stokes, and Morris. Murchison also commented, "The reputation of Mr. Peyton [sic], of Dudley, as a purveyor of these beautiful fossils, is widely spread." The origins of a few Dudley specimens he figured are not indicated, and this suggests that Murchison may have collected them. Clearly, most of the best trilobites he figured were borrowed from collectors.

After this time, scientific studies on Dudley trilobites came to rely on specimens from local private collectors for the best and rarest material, most of which was eventually acquired by museums. Salter (1849, 1853, 1864a, b, 1865, 1867, 1883) demonstrated this repeatedly in a series of papers in which he credited such Dudley collectors as Gray, Fletcher, Ketley, Hollier, and Mushen for loaning many of the best Dudley trilobites. Salter even solicited, in print, individuals to send him their best specimens.

The increasing number of trilobite taxa appearing in the literature over time correlates well with the rapid expansion of fossil collecting. Payton (1827), a veteran collector and dealer, reported only two taxa (although he missed a couple, such as *Encrinurus*, which already had been described). Murchison (1839) listed six. Salter's attempt to describe all British trilobites was cut short by his premature death. However, in conjunction with the papers by Fletcher (1850a, b), it is clear that many of the rarer Dudley taxa were discovered by the 1860s. By 1900, collecting dropped off significantly, and most of the Dudley collections found their way into museums. Most of these had been sold to museums by the collectors or by their heirs; however, some passed through larger commercial collectors (see sections on Gray, Johnson, and Madley, in British Museum, 1904; and Rayska, 1994). A few collections, such as Holcroft's, were donated to local museums (Strachan, 1979). Sadly, some, such as Payton's, seem to have vanished, although some of his specimens may have been incorporated into the original Dudley Museum, which was established around the time of his death in the 1840s. Whatever the means, Dudley specimens were widely distributed and are now found in museums around the world.

Undoubtedly, the reduction in quarry and mine sites and the closing of the Dudley mines around 1900 had a negative impact on collecting. A similar situation occurred at the same time in other areas (Mikulic, 1983; Mikulic and Kluessendorf, 1998). Social changes at this time also produced fewer private collectors, while increasing mechanization in quarries and mines meant that workmen had fewer opportunities to collect specimens.

Trilobite prices.—The demand for trilobites and other Dudley fossils was probably high during the late eighteenth and early nineteenth centuries, although little documentation exists. The fact that Payton was selling them to tourists in 1794 shows that there has long been a market for these objects. Warner (1802) remarked, "Being discovered only at Dudley and another place in the kingdom, the fossil is the more valuable; a circumstance not unknown to the venders [sic] of these productions of the mines at Dudley, who charge most unconscionably for all their specimens." Booker (1825) noted that the availability and prices of trilobites changed as the limestone operations shifted underground, "Formerly, when the limestone was raised by what is termed 'open work,' this singular fossil was so frequently discovered that the finest specimens of it were purchased for a trifle; whereas now when the stone is got from much deeper measures, and immediately carried to neighboring kilns for calcination, the fossil is so seldom found, that a good specimen is worth more than its weight in silver."

The price for quality trilobites and other fossils probably remained high throughout the nineteenth century. Pye (1825) observed that "In these rocks there are numerous marine productions, and among others, one which the miners denominate a locust, for which they have been known to refuse its weight in gold; it being understood that there is only one other place in the kingdom where they are to be found." Drake (1839) mentioned that the limestone at Dudley "…is remarkably rich in fossil treasures; trilobites, or as they are vulgarly called, 'Dudley locusts,' have been found here in great variety, but from the eagerness of collectors, and the inadequate supply of these ancient creatures yielded by the rocks, they have become scarce and costly…" Bentley (1841) stated, "The price of this fossil is according to size, and can seldom be bought for its own weight in silver; in fact, very few can be purchased that are worth having at less than one sovereign each." Miller (1845, in Bayne, 1871) observed, "It is rare to find a well-preserved trilobite,—so rare that the fossil dealers charge for them from ten shillings to five pounds, and I can not afford to collect specimens at such a price." He did buy some a few days later, however (Miller, 1847). Beyond the purchase price of some specimens, collectors apparently paid to have them prepared, sometimes at high cost. The diaries of Henry Johnson, Sr., of Dudley note that he paid as much as 5£ for this service (C. Knipe, 2005, personal communication).

The fossil registry for the Charles Holcroft collection recorded the prices he paid for each specimen between 1876 and 1893 (I. Strachan, 1976, personal communication), with prices for the 666 trilobites listed ranging from as little as 3 pence to as much as 600 pence each. The most expensive were specimens of *Trimerus* from Dudley Castle Hill, followed by a few specimens of *Calymene blumenbachii* and rare trilobite taxa. Even though they were high priced, it is surprising that the spectacular large slabs of crinoids from Dudley were not as expensive as the several isolated trilobite specimens he purchased. The evidence also suggests that the price was less at Dudley than at more distant places. For example, a specimen for which Holcroft paid seven shillings in Dudley in the 1880s was worth 5£ in London, according to the prominent Dudley collector Henry Johnson (Rolfe, *et al.*, 1988). Apparently, the Dudley Locust was also prized for its aesthetic value. Oakley (1985) noted that during Georgian and Victorian times these fossils were mounted in gold and worn as brooches and tie-pins.

Dudley may have been one of the first locations to manufacture and sell fake fossils. When demand exceeded supply, the commercial fossil trade apparently resorted to this method to furnish specimens. The prominent Dudley collector John Gray (*in* Woodward, 1868) reported, "…the miners have not only collected and developed Trilobites, but even *made them* when they did not turn up in sufficient abundance…New and undescribed species are still to be purchased, composed of parts of *Calymene* and *Phacops* united together, either by accident or by the aid of a knife and a little gum." Ironically, the trilobite discussed in Woodward's (1868) paper turned out to be a specimen that a workman had enhanced. As a result, Woodward mistakenly named it a new species (Fig. 15). Debate at a meeting of the Dudley and Midland Geological Society confirmed that the "fossil in question has been mutilated" (Dudley and Midland Geological Society, 1869). Bassett (1971, 1982) and Dance (1976) have discussed faked Dudley trilobites. Museums with a large number of Dudley fossils commonly contain at least a few

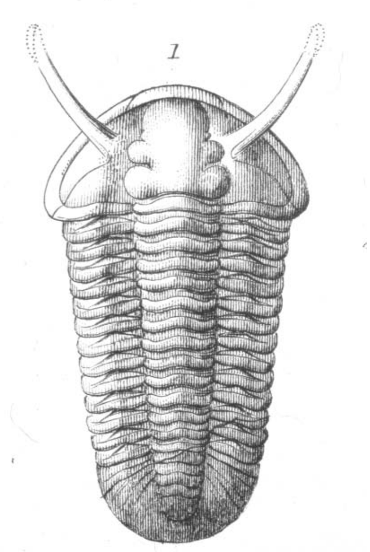
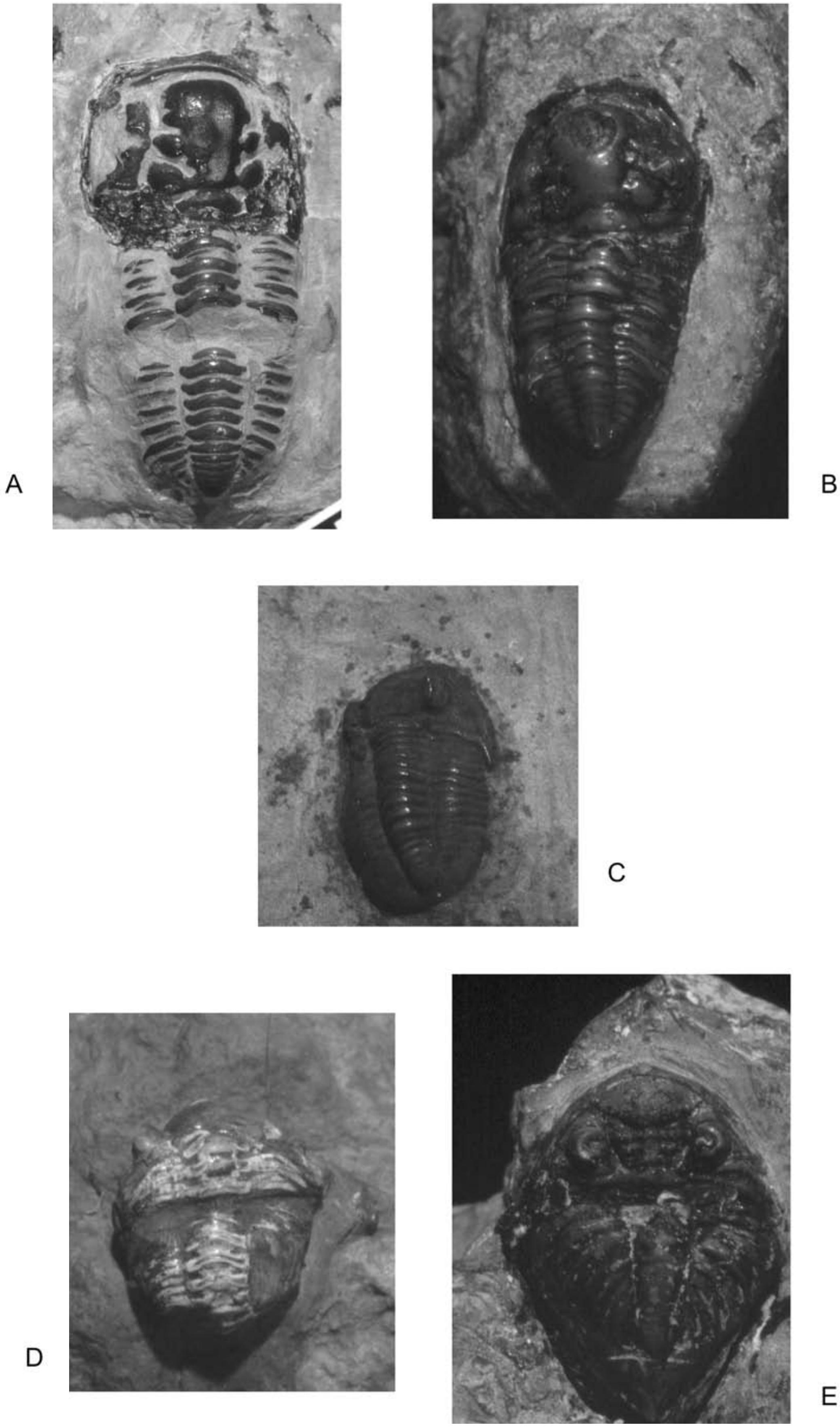


Fig. 15. Woodward's (1868) restoration of an artificially enhanced *Calymene blumenbachii* specimen, which he designated as a new species (*C. ceratophthalma*).


A
B
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D
E

examples of these manufactured trilobites, and reveal the variety of methods by which this fakery was accomplished (Fig. 16). The most obvious specimens, as Gray pointed out, are taxonomic mixtures of heads and tails glued together, and suggest a lack of taxonomic sophistication by the manufacturer or buyer. Fake fossils from Dudley may still be making their way into the literature. For example, Ager (1963) illustrated what he considered to be a naturally fortuitous association of a Dudley calymenid cephalon and a dalmanitid pygidium. However, the cephalon in his figure looks suspiciously like a glued-on specimen.

DUDLEY AND ITS LOCUST

The impact of mining, geology, and paleontology on Dudley has been considerable. Historically, each subject has made specific contributions to the importance and success of the community by providing economic or social opportunities as well as outside recognition. These factors were interrelated, and helped provide Dudley with an identity and fame that few other similarly sized communities could claim. For over 300 years, this fame drew numerous scientists, businessmen, and tourists to view its attractions. While some were interested only in specific subjects, others found the combination of mines, hills, fossils, canals, factories, parks, and museums both unique and impressive. No other locality could tout such a bounty of related attractions, and many people seized the opportunity to capitalize on this geological heritage.

Initially, Dudley Castle was the focus for visitors to the region. However, during the eighteenth century, industrial development added a variety of new attractions, especially for geologists and individuals interested in the technology of the local industry. If accessible, the spectacular mines in the steeply-dipping Silurian strata (Fig. 17) and their connecting tunnels to the local canal system were among the most impressive sites of the Black Country. They were described as the largest manmade underground caverns in the British Isles. Many individuals and tours visited these mines and canals. For example, in 1799, the Russian ambassador was given a canal tour that included the caverns of Dudley Castle Hill during a review of Black Country industry (Uglow, 2002). In 1844, a trip by the Duc de Bordeaux was described in the popular *London Illustrated News* (Anon., 1844).

Some of the most notable tours, however, were geologic in nature, such as those organized for the 1839 and 1849 meetings of the British Association for the Advancement of Science (BAAS) in nearby Birmingham (Anonymous, 1839, 1849). On both occasions, Lord Ward, the owner of the property, illuminated some of his Castle Hill caverns with thousands of candles for the large crowds. An estimated 15,000 people, including the French Ambassador, toured the mines during the 1849 trip (Anonymous, 1849). Among the most famous events during this trip was the subterranean lecture that Murchison gave about local Silurian geology, which was followed by his enthronement as "King of Siluria" by the Bishop of Oxford (Geikie, 1875).

Interest in the mines and geology was responsible for the formation of new institutions and organizations in Dudley. A temporary fossil exhibit mounted by Joseph Payton for the 1839 BAAS meeting inspired the town to assemble a local fossil collection, which, eventually, was housed in a municipal museum, the forerunner to the current Dudley Museum and Art Gallery. This meeting also inspired the founding of the Dudley Geological Society in 1841 (Cutler, 1981). This organization started with 150 subscribing members, including Lord Ward, who became its president, along with 30 local industrialists, geologists, and members of Parliament who became vice presidents. This Society was short-lived, but the more successful Dudley and Midland Geological Society was formed in 1862 (Cutler, 1981). This group lasted into the early 1900s, and sparked local geological research, field meetings to area geological sites, and, most importantly, re-established the Dudley museum.

Although not as economically important as mining, the Dudley Locust played a role in attracting attention to the community. For some, this trilobite was as much a symbol of Dudley as its mines, canals, and castle, and few other communities could boast of such a well-known fossil. Emmerich (1846, translation by Taylor) reflects this relationship, "The Dudley fossil bears the name of the principal place for Wenlock fossils, and has carried the name of the picturesquely-situated Dudley through the world." As early as the nineteenth century, museums worldwide had specimens of this trilobite, and a plethora of scientific publications featured it. The general public was also directed to this fossil in a wide variety of publications. During the mid-1800s, national and regional guides, such as those published for the railroad system, frequently mentioned the Dudley fossil. From 1818 to at least 1940, many directories for Worcestershire, Staffordshire, and even Birmingham in Warwickshire mentioned the Dudley Locust, even when they discussed the town only briefly. On a more specialized level, the Dudley Locust was discussed and figured in guides to the region (Payton, 1794; Booker, 1825; Bentley, 1841; Harris, 1845; and Baker, 1848), which also detailed Dudley Castle and its history, as well as local limestone mining and geology (see Powell, 1999, for other examples). Demonstrating its prominence in local culture, the Dudley Locust even graced the cover of an early book of photographs about Dudley in 1868 (Laxton, 1868).

As a result of its fame and importance, *Calymene blumenbachii* became an official symbol of the community. The Dudley Borough Seal (Fig. 18), which was adopted in 1866, featured the Dudley Locust in a prominent central position (Grazebrook, 1873; Perkins, 1905). A similar image is also featured on the Dudley Mayoral Chains. In 1957, an official coat-of-arms was

Fig. 16. (left) Trilobites from Dudley showing a variety of fakery styles in the collections of the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (U.S.A.): A, MCZ153342, *Calymene* cranidium glued on rock with partial thorax and partial thorax and pygidium, length 50 mm. B, MCZ153346, large partial cranidium of *Calymene* glued on rock with *Acaste* thorax and pygidium, which is also glued on rock, length 21 mm. C, MCZ153343, artificial cast of proetid glued on rock, specimen length 17 mm. D, MCZ153345, *Acaste* cephalon and partial thorax with pygidium and partial thorax, glued on rock, length 13 mm. E, MCZ153344, *Dalmanites* cephalon with *Dalmanites* pygidium glued on rock; no thorax present, specimen length 33 mm.

Fig. 17. View of a limestone mine near the entrance to the Seven Sisters Caverns in the Lower Quarried Limestone, west side of Wren's Nest (from J. Jukes, 1859).

granted to Dudley that incorporated much of the original Seal, including the Dudley Locust (Basset, 1971, 1982). In various older buildings in Dudley, such as the Town Hall, Police Department, Library, and Dudley Museum, representations of the Dudley Locust are rendered in carved stone or stained glass as part of the old Borough Seal, and, more rarely, are seen as a freestanding figure.

In recent decades, Dudley has revived its interest in promoting its industrial and scientific heritage, and the Dudley Locust continues to play a part in this legacy. Visits to the mines by the public continued until the late 1800s, when safety concerns curtailed access to most of them. Dudley Castle remained a popular attraction, particularly after the opening of the Dudley Castle Zoo in 1937. New interest in the geology and paleontology of the region began in 1956, when Wren's Nest became the first geology-based National Nature Reserve in the United Kingdom. Now visited by nearly 10,000 people a year (Connah, 1999), Wren's Nest National Nature Reserve highlights the geological, paleontological, and industrial heritage of this heavily mined area. Tourist development further expanded with the reopening of the Dudley Canal Tunnel in 1973, through the efforts of the Dudley Canal Trust, which later began canal tours to one of the limestone mines. In 1975, the Black Country Geological Society was established (Shilston, 1988). This Society has similar functions to the preceding organizations, but, in addition, helps conserve local geological features.

The Black Country Living Museum, which was opened as a cultural and industrial heritage site in 1978, now boasts a yearly attendance of 250,000. Several of the exhibits at the museum recognize the importance of geology and mining to local history. The exhibits include limekilns, a reconstructed coal mine, and a reconstruction of a fossil shop. The Dudley Locust is part of the Museum's logo. More recently, the importance of Castle Hill, Wren's Nest, and Hurst Hill to geological and industrial heritage was the impetus for a 1994 proposal to include them as part of a UNESCO World Heritage Site. Scientific groups continue to visit the area, including the 1989 field trip by The Murchison Symposium, an international meeting on the Silurian System, and the international conference on Trilobites and Their Relatives held in 2001. Thus, although the nature of scientific and industrial activities has changed dramatically over the years, they have remained an important part of Dudley's cultural heritage and, as such, provide new opportunities for the future.

CONCLUSIONS

The development of geology and paleontology as scientific disciplines were important events in the late eighteenth and early nineteenth centuries. Then, as now, progress in various aspects of these endeavors was tied to the discovery of fossils and their availability for research. Specimens of *Calymene blumenbachii* were especially important in the early development of these fields, as they were the best trilobite fossils known at the time and had a wide distribution in collections throughout Europe. The study of these specimens helped to characterize both a critical portion of geologic time (then thought to represent the oldest fossiliferous rocks) and to define trilobites as an important group of extinct animals. Because of its unique role, this trilobite became one of the best known of its group and remains so today.

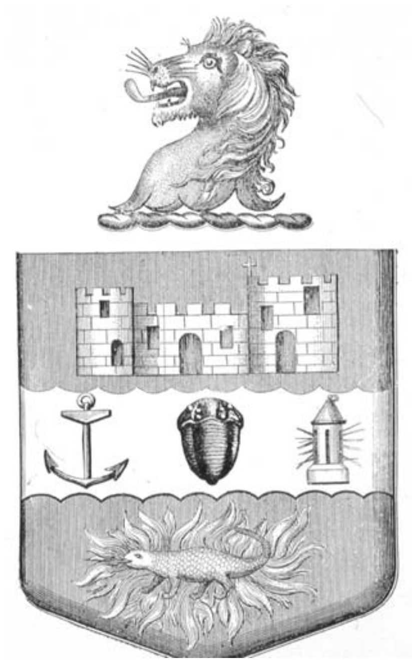

Fig. 18. Dudley Borough Seal with image of the Dudley Locust (from Perkins, 1905).

As with many other fossil taxa, the discovery and initial study of *Calymene blumenbachii* was made possible by a combination of geologic, economic, and social conditions. Exceptional fossils were present in the rocks, but the opportunity to collect these specimens would not have existed if an extensive mining industry had not developed at Dudley. Similarly, these fossils would not have been collected if miners and others did not have an economic interest. Scientists had to depend on the efforts of these individuals to secure the best research material, a situation that has changed little to the present day. The history of Dudley fossil collecting is an outstanding example of the interdependence of these factors and is one of the oldest known. Through this research, Dudley became famous to collectors and scientists as one of the best sources of trilobites and other Silurian fossils, and this had a significant social impact on the community. Tourists came to the area to see the castle, mines, and fossils, and guidebooks highlighted the Dudley Locust as one of the more interesting local features. A museum was established specifically to exhibit the fossils. Because of its fame, the Dudley Locust became a cultural icon for which the community was known internationally. Over the last 250 years, few descriptions of Dudley have failed to mention its famous fossil, while few discussions of the fossil have failed to mention the town. The Dudley Locust has been the centerpiece to the rich and related geological and industrial heritage of the region, and Dudley has promoted it to good advantage. In fact, Dudley may be the first locality to exploit geotourism, a supposedly modern concept that seeks to highlight an area's geological heritage for economic benefit. That Dudley has enjoyed the attention of both the general public and the scientific community for more than two centuries is the legacy of the "locust."

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HISTORICAL REVIEW OF TRILOBITE RESEARCH IN CHINA

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ABSTRACT—Trilobites were known as "stone silkworms" in China for more than one thousand years. The term "stone silkworm" in some ancient Chinese pharmacopoeias may refer to the pygidial axis of a trilobite. The "stone bats" that appear in ancient Chinese literature are pygidia of *Drepanura*. The earliest mention of "stone silkworm" may be traced back as early as in Tang Dynasty (659 A.D.). The oldest verified mention is in the pharmacopoeia "Kaibao Benchao," which was printed at the beginning of Song Dynasty (973 A.D.). The beginning of modern research on Chinese trilobites is marked by the appearance of Dames' (1883) paper on Cambrian trilobites from Liaoning in northeast China. Many impressive works were completed by foreign paleontologists in the early stage of Chinese trilobite research (1883–1924). During this interval, the most important work was done by C. D. Walcott (1913), who described 180 species of Cambrian trilobites from north and northeast China. The monograph published by Sun Yunzhu (1924) on the Cambrian trilobites of north China was the first scientific report on trilobites by a Chinese paleontologist. Since then, native paleontologists have played leading roles in research on Chinese trilobites. During the late 1920s–1940s, more research on systematic paleontology of trilobites was done in north, northeast, central, and southwest China, and investigations on trilobite-bearing strata extended to the remote areas in northwest and southwest China. Sun (1937) established the first trilobite-based biostratigraphy of the Middle–Upper Cambrian in north China. From 1949 on, many Chinese paleontologists have been involved in research on trilobites and trilobite-bearing strata. Almost all areas with Paleozoic strata in the country were investigated for trilobites. Many scientific papers, atlases, and monographs on trilobites and related disciplines were published, and great progress was made in almost all fields of trilobitology in China during this interval.

INTRODUCTION

China is one of the richest countries in trilobites. These fossils have now been found throughout the Paleozoic of all the provinces and autonomous regions on the mainland. The earliest written record of trilobites in the world may be from China. The trilobite was called a "stone silkworm" or "stone bat" in ancient China for the resemblance of the pygidial axes of trilobites to silkworms, and the resemblance of *Drepanura* pygidia to flying bats. The term "stone silkworm" in an ancient pharmacopoeia, the Kaibao Benchao, which was printed in the beginning of the Song Dynasty (973 A.D.) is probably the earliest record of trilobites in the world. In ancient China, "stone silkworms" were used in Chinese mineral medicine, and "batstones" were used in material for handcrafted articles. Today, *Drepanura*-bearing rocks are still widely called "bat-stones," and are quarried for commercial purposes by local people. Because "stone bats" are so well known in China, a drawing of a *Drepanura* pygidium has been used as a logo on the cover of each issue of *Palaeontologica Sinica* since the Palaeontological Society of China started publication of the journal in 1921.

F. F. von Richthofen is the first geologist, who investigated trilobite-bearing strata in China. Some trilobites collected by him in Liaoning, northeast China in 1868–1872 were studied by Dames (1883). As the first scientific publication on Chinese trilobites, Dames' paper marked the beginning of modern scientific research on trilobites in China. In the following forty years (1883–1924), a number of foreign geologists investigated the trilobite-bearing strata of China. B. Wills, E. Blackwelder, and R. H. Sargent investigated the Cambrian of Liaoning and Shandong in 1903–1904. Their investigation, with additional material collected by P. J. Iddings from Liaoning, resulted in C. D. Walcott's (1913) monumental work on Chinese trilobites. In that book, Walcott described 180 Cambrian species of trilobites from the North China Platform.

Sun Yunzhu's (1924) monograph "Contribution to the Cambrian faunas of China" is the first publication on trilobites by a Chinese paleontologist. Sun described the Fengshan trilobite fauna for the first time, and divided the Cambrian of north China into three series and five lithological units. Sun (1935) once more described the Cambrian trilobite faunas of north China, and established five trilobite zones in the Upper Cambrian Changshan and Fengshan Formations, which was the first biostratigraphic subdivision of the Upper Cambrian of China. Other important works appeared in 1924–1949 on the systematic paleontology and stratigraphy of Chinese trilobites, including the monographs of Endo and Resser (1937) and Troedsson (1937). Endo and Resser described a number of new Cambrian taxa and refined Cambrian biostratigraphy, and Troedsson described a diverse Cambrian trilobite fauna from

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Qurq-tagh, northwest China.

From 1949 to the present, great progress has been made in trilobitology in China, with hundreds of scientific papers, atlases, monographs, and books being published. Lu (1962) refined the litho- and biostratigraphic scale of China with eight formations and 21 trilobite-based zones. Lu *et al*. (1965) published a two-volume book, "Trilobites of China," in which almost all Chinese trilobites known to date were included. In the late 1970s–early 1980s, many regional or provincial paleontological atlases were compiled that included trilobites. Other important works during this interval include the studies on the Ordovician trilobite faunas of central and southwest China (Lu, 1975), the Cambrian trilobites of southwest China (Lu *et al*., 1974b; Zhang *et al*., 1980), the Cambrian trilobites of northwest China (Xiang and Zhang, 1985), the Cambrian and Tremadocian trilobites of the Jiangnan Slope Belt (Yang, 1978; Peng, 1990, 1992; Yang *et al*., 1991), the Devonian and Carboniferous trilobites of south China (Yuan, 1984; Yuan and Xiang, 1998), the trilobites of the Chengjiang and Kaili biotas (Shu *et al*., 1995; Yuan *et al*., 2002), and the agnostoids of south China (Peng and Robison, 2000). Recently, trilobite-based biostratigraphy and chronostratigraphy were further refined for north China (Xiang *et al*., 1979; Zhang and Zhu, 2000), and were developed for south China (Peng, 1987, 1992, 2000a, b; Peng and Robison, 2000; Peng *et al*., 2000a, b, 2001; Peng and Babcock, 2001).

YEARS BEFORE 1883

Chinese trilobites were first described by the German paleontologist W. Dames (1883), but they were documented in Chinese literatures at least nine centuries earlier. Needham (1959, p. 614–623) noted many records of fossil animals, including trilobites, from ancient Chinese literature in his great work "Science and Civilisation in China" and regarded the "stone silkworm" and the "bat-stone," both of which were mentioned frequently in ancient Chinese literature, as trilobite-containing rocks. The "stone silkworm" refers probably to the appearance of the axis of the trilobite pygidium with the pleural field obscured by matrix, and "stone bat" to the pygidium of a damesellidean trilobite.

"Stone silkworm" was recorded in the "Kaibao Benchao" (Kaibao reign-period Pharmacopoeia), the earliest printed pharmacopoeia in China, and in some of the subsequently printed pharmacopoeias. Kaibao Benchao was spelled as "Khai-Pao Pen Tshao" by Needham (1959). "Benchao" is a sort of ancient book on drugs used in traditional Chinese medicine, just like a modern pharmacopoeia. They contain entries on medicinal herbs, animals, and minerals etc. with descriptions of their characters, medicinal efficacy and application. They were usually issued by official authority, written by famous doctors from the imperial medical academy, Taoists, and pharmacologists, and have been used by practitioners of Chinese medicine for prescribing.

The first edition of the "Kaibao Benchao" pharmacopoeia appeared in the sixth year of the Kaobao reign of the Song Dynasty (973 A.D.), and the second and revised edition in the seventh year (974 A.D.). It was edited by Liu Han (Fig. 1), Ma Zhi, and seven other medical academy officials in accordance with the first emperor's decree of the Dynasty. [Ma Zhi, spelled as Ma Chih by Needman (1959), was a Taoist and famous doctor employed by the first emperor of Song Dynasty.]

Fig. 1. Liu Han, from Linjing, Canzhou (now Ninjing, Shandong), high official of the Medical Academy of the Song Dynasty. He is the first author of the "Kaibao Benchao" pharmacopoeia, in which the earliest written record of trilobites probably occurred.

The "stone silkworm" in the Kaibao Pharmacopoeia was described to be "like silkworm in appearance, but actually of stone" (see Lin, 1998, p. 78). This probably was the first reliable documentation of trilobites. Coiled fossils like ammonites or gastropods could not have been compared with silkworms, because a silkworm is usually straight. Coiled fossils, particularly gastropods, were called "stone snakes" in ancient China (Needham, 1959, p. 618). Some nautiloids are straight-shelled, but they could not be referred to as "stone silkworms" as this kind of fossil had never been recognized as an animal remain before modern paleontology was introduced to China. They were called "stone pagodas" or "stone bamboo shoots" in ancient and contemporary times.

However, the term "stone silkworm" may have appeared even earlier. According to a recent study by Lin (1998), this entry had appeared originally in a hand-written pharmacopoeia, the "Xinxiu Benchao" (Newly Revised Pharmacopoeia). This pharmacopoeia was compiled as early as 659 A.D. (the third year of the Xianqing reign, Tang Dynasty) by Su Jin and 18 other famous doctors, and was the original version of the "Kaobao Benchao." If so, it may be the earliest documented mention of trilobites in the world. However, this record remains unverified because some of volumes of the "Xinxiu Benchao" were lost over a period of almost 15 centuries. According to the historic records, the "Xinxiu Benchao" pharmacopoeia should consist of 20 volumes, but only eleven volumes survive today. Unfortunately, no entry of "silkworm" has been found in these existing volumes.

Rock containing trilobites has been called 'bat-stone' in North China, especially in Shandong and southern Liaoning Provinces, where the lower Upper Cambrian rocks of the Kushan Formation are richly fossiliferous. The bat-stone is usually a yellow-colored, thin-bedded, platy, and muddy limestone with numerous disarticulated cephala, pygidia, and isolated

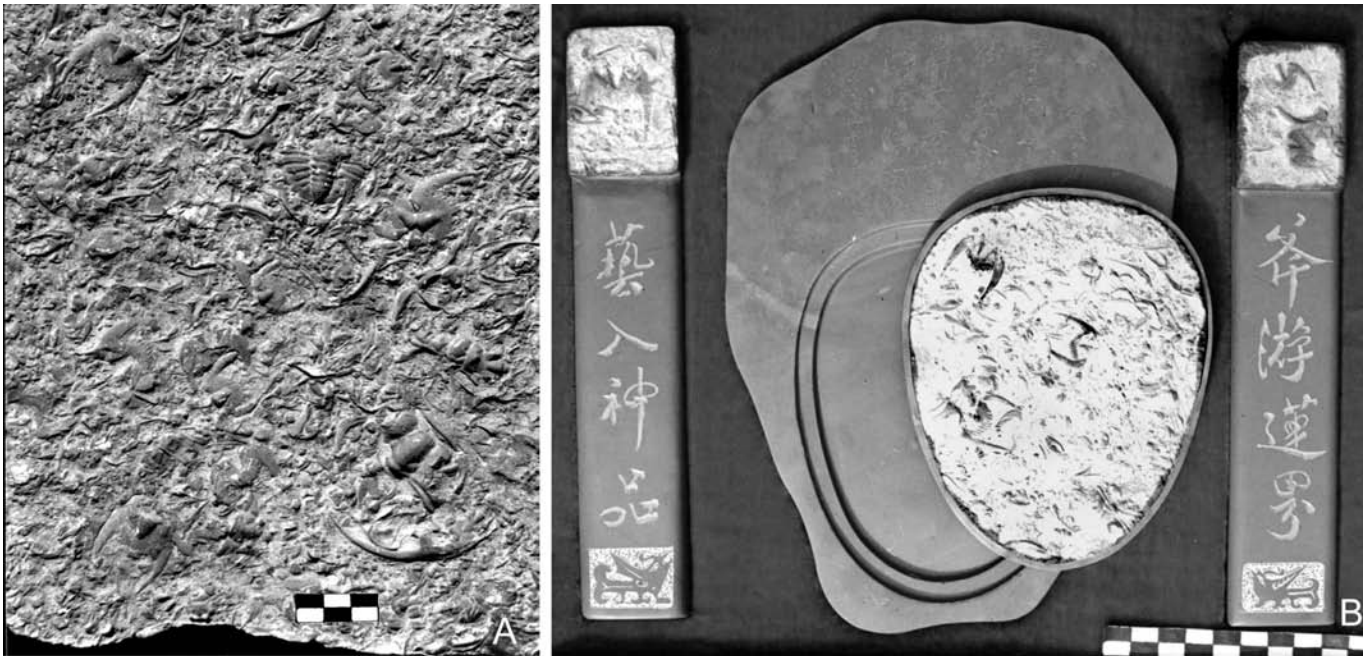


Fig. 2. A, Part of a "bat-stone" from the famous locality at Dawenkao, Shandong Province. Cranidium on lower right and the middle-upper pygidium are *Blackwelderia sinensis* (Bergeron); other pygidia of *Drepanura premesnili* Bergeron. Cranidium of *Drepanura premesnili* just below larger pygidium in left upper photo. B, Inkstone and two stone paperweight bars, all made recently from "bat stones" (scale bars in A = 3 cm and B = 8 cm).

thoracic segments preserved on the surface (Fig. 2A). It gained the name because of the resemblance of *Drepanura premesnili* pygidia, with their large anterolateral spines that are usually predominant and distinctive on rock surfaces, to flying bats.

Needham (1959, p. 619) mentioned an ancient Chinese dictionary "Er Ya" (Erh Ya), and referred the earliest documented mention of trilobite-containing "bat-stone" to Guo Pu's commentaries in that dictionary, but this seems to be not true. "Er Ya" is the first dictionary in China's history, and has been considered to be one of the great ancient classical works of China. The dictionary was compiled in the Han Dynasty (~100 B.C.) by unknown authors, and annotated by Guo Pu of the Jin Dynasty (~ 300 A. D.) and again by Xing Bing of the Song Dynasty (~ 1000 A.D.). [Guo Pu, spelled as Kuo Pho by Needham (1959), was a scholar of the Jin Dynasty, and was famous in annotating the Er Ya dictionary.] A mention of the "bat-stones" by Guo Pu could extend the earliest record of trilobites back to the beginning of the 4th century. However, my inspection shows that the dictionary gave only an explanation of the word "bat," and Guo Pu's commentaries were related to the secondary name of the bat, and the places where that name was used. Therefore, there seems to be no record to support Needham's conclusion. This mistake may have been caused by a misunderstanding of a later work that appeared in 1691 A. D. by Wang Shizhen. [Wang Shizhen, spelled as Wang Shih-Chenby by Needham (1959), was a scholar of Song Dynasty, and the author of the famous book "Chi Bei Ou Tan."]

Unlike western countries, where the bat is commonly considered to be a terrible blood-sucking animal, the bat in China is considered to be a symbol of happiness because the word "bat" is homophonic with the word "happiness" in Chinese. As recorded by Wang Shizhen (1691), a famous scholar of the Qing Dynasty, in his book "Chi Bei Ou Tan" [Chance Conversations north of Chizhou; spelled as Chhih Pei Ou Than by Needham (1959)]), the bat-stone was used by local people in Shandong for making inkstones in Chinese calligraphy and traditional painting (Fig. 2B). Bat-stone has long been also utilized as the material for making handcrafted articles, such as desk knick-knacks or house ornaments.

An article titled "Zhimo Inkstone" in the book "Chi Bei Ou Tan" detailed a story about bat-stone. Zhimo (Chi Mo) was another name for "bat" in Qi State (Shandong Province) in ancient times. The story related that a gentlemen, Zhang Huadong, walked along a stream and, by chance, found a slab of stone in water during his overnight stay at Dawenkou in Tai'an County, Shandong, on his tour to the Taishan Mountain in April 1637. This stone contained "numerous flying and resting bats together with a silkworm", and was taken back by Mr. Zhang. The stone was finally made into an inkstone, which was named Duofu (lots of happiness) Inkstone and was admired by many of his friends. Dawenkou is one of many famous fossil localities with *Drepanura premesnili* Bergeron, *Blackwelderia sinensis* (Bergeron), *Stephanocare richthofeni* Monke, and some other damesellidean genera of the Kushan Formation. It is also well known for supplying slabs of bat-stone commercially. Judging from Wang's description and the collecting locality as well, there is no doubt that the 'bats' and the 'silkworm' on the slab found by Zhang are trilobites.

Zhang Hongzhao (Fig. 3, 7), the first president of the Geological Society of China, and probably the first Chinese geologist who made a collection of trilobites for scientific purposes, visited Dawenkou with about two dozen students from the

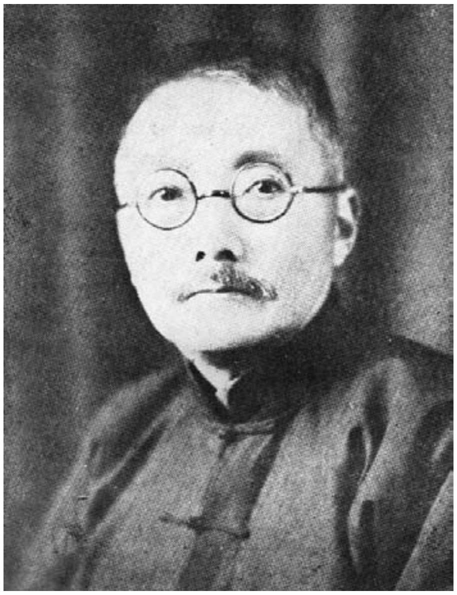
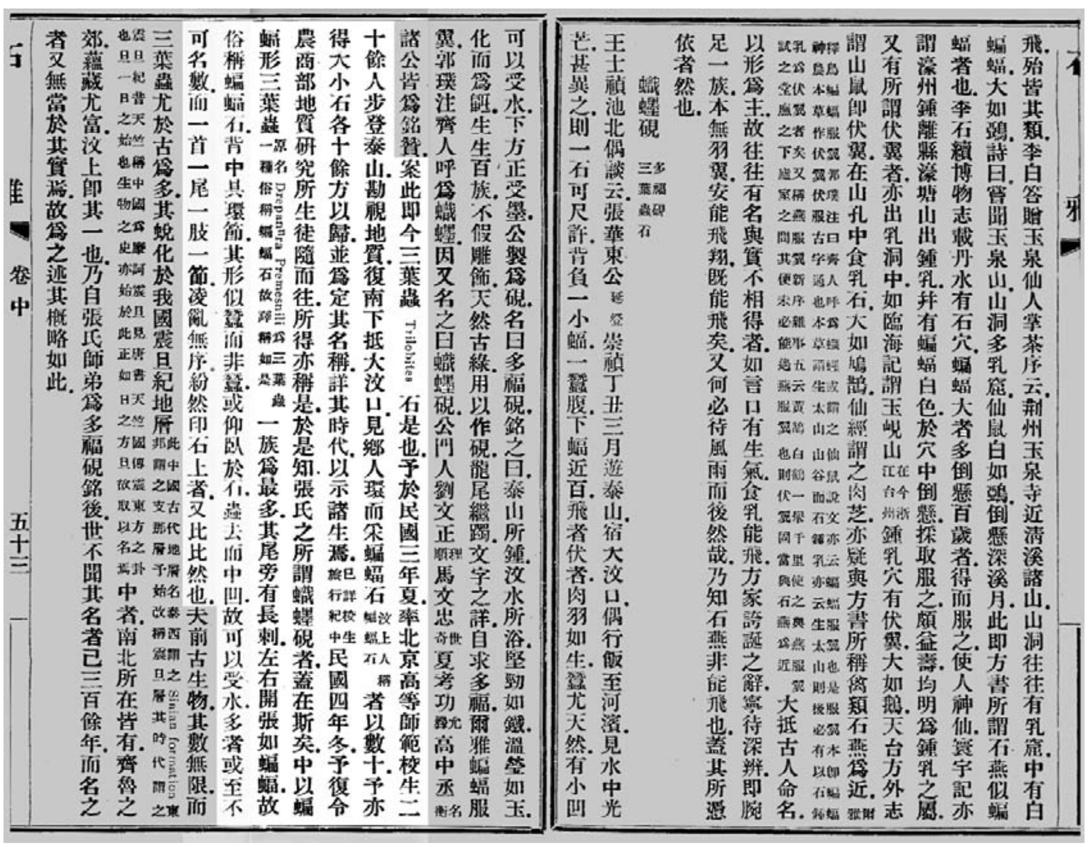


Fig. 3. Zhang Hongzhao (1877–1951), first President of the Geological Society of China who greatly influenced trilobite research in China; the first Chinese geologist to collect and illustrate trilobites.

Peking Normal School in Summer 1914. They collected trilobites at the locality of bat-stones, where there were several dozen local people quarrying bat-stones. Zhang (1921, p. 52, 53) cited the story of "Zhimo Inkstone" in his book "Shi Ya" (Lapidaries of China), and realized, for the first time, that the stone bats and silkworms in China are the trilobites of western scientists. He correctly pointed out that the "bats" are pygidia of *Drepanura premesnili*, and the "silkworms" are axes of trilobites (Fig. 4). In Shi Ya, Zhang also figured a slab of "bat stone" from Dawenkou on a whole-page plate, which was the earliest photo of trilobites illustrated by a Chinese geologist.

1883–1924

During the late nineteenth and early twentieth century, many scientists and explorers from western Europe, America, Hungary, and Russia made expeditions to China to investigate geology, geography, and topography, and collected rock and fossil specimens. Among the expeditions, those made by F. F. von Richthofen and by B. Willis and E. Blackwelder were particularly important and influential for scientific research on the stratigraphy and paleontology of China. In particular, these two expeditions are closely related to research on Chinese trilobites.



飛。殆皆其類。李白答贈玉泉仙人掌茶序云。荊州玉泉寺近清溪諸山。山洞往往有乳窟。中有白蝙蝠。大如鴉。詩曰。嘗聞玉泉山。山洞多乳窟。仙鼠白如鴉。倒懸深溪月。此即方書所謂石燕似蝙蝠者也。李石續博物志載丹水有石穴。蝙蝠大者多倒懸。百歲者。得而服之。使人神仙。寰宇記亦謂滁州鍾離縣濠塘山出鍾乳。并有蝙蝠白色。於穴中倒懸。採取服之。頗益壽。均明爲鍾乳之屬。又有所謂伏翼者。亦出乳洞中。如臨海記謂玉岘山（在今浙江台州）鍾乳穴有伏翼。大如鵝。天台方外志謂山鼠卽伏翼。在山孔中食乳石。大如鳩鵲。仙經謂之肉芝。亦疑輿方書所稱禽類石燕爲近。（爾雅釋鳥蝙蝠服翼。郭璞注曰。齊人呼爲蟙蠌。或謂之仙鼠。說文亦云蝙蝠服翼也。是服翼卽蝙蝠。神農本草作伏翼。伏服古字通也。本草謂生太山山谷。而石鍾乳亦云生太山。則接必有以石鍾乳谷伏翼者矣。又稱燕服翼。新序雜事五云。賈誼白鶴一擧千里。使之與燕服翼試之堂廡之下。處室之間。其便未必能遠燕服翼也。則伏翼固當與石燕爲近。）大抵古人命名。以形爲主。故往往有名與實不相得者。如言口有生氣。食乳能飛。方家誇誕之辭。寧待深辨。即腕足一族。本無羽翼。安能飛翔。既能飛矣。又何必待風雨而後然哉。乃知石燕非能飛也。蓋其所憑依者然也。

蟙蠌硯（多福硯 三葉蟲石）

王士禎池北偶談云。張華東公（延登）崇禎丁丑三月遊泰山。宿大汶口。偶行飯至河濱。見水中光芒。甚異之。則一石可尺許。背負一小蝠。一蠶腹。下蝠近百。飛者伏者。肉羽如生。蠶尤天然。有小凹可以受水。下方正受墨。公製爲硯。名曰多福硯。銘之曰。泰山所鍾。汶水所浴。堅勁如鐵。溫瑩如玉。化而爲鼫。生生百族。不假雕飾。天然古綠。用以作硯。龍尾纖蜀。文字之詳。自求多福。爾雅蝙蝠服翼。郭璞注齊人呼爲蟙蠌。因又名之曰蟙蠌硯。公門人劉文正（理順）馬文忠（世奇）夏考功（允彝）高中丞（名衡）諸公皆爲銘贊。案此即今三葉蟲（Trilobites）石是也。予於民國三年夏。率北京高等師範校生二十餘人步登泰山。勘視地質。復南下抵大汶口。見鄉人環而采蝙蝠石（汶上人稱蝙蝠石）者以數十。予亦得大小石各十餘方以歸。並爲定其名稱。詳其時代。以示諸生焉。（已詳校生旅行紀中）民國四年冬。予復令農商部地質研究所生徒隨而往。所得亦稱是。於是知張氏之所謂蟙蠌硯者。蓋在斯矣。中以蝙蝠形三葉蟲（原名Drepanura Premesnili爲三葉蟲一種。俗稱蝙蝠石。故譯稱如是）一族爲最多。其尾旁有長刺。左右開張如蝙蝠。故俗稱蝙蝠石。背中具環節。其形似蠶而非蠶。或仰臥於石。蟲去而中凹。故可以受水。多者或至不可名數。而一首一尾一肢一節。淩亂無序。紛然印石上者。又比比然也。夫前古生物。其數無限。而三葉蟲尤於古爲多。其蛻化於我國震旦紀地層（此中國古代地層名。泰西謂之Sinian formation。東邦譯之支那層。予始改稱震旦層。其時代謂之震旦紀。書天竺稱中國爲摩訶震旦。見唐書天竺國傳。震東方之卦也。旦一日之始也。生物之史亦始於此。正如日之方旦。故取以名焉）中者。南北所在皆有。齊魯之郊。蘊藏尤富。汶上卽其一也。乃自張氏師弟爲多福硯銘後。世不聞其名者已三百餘年。而名之者又無當於其實焉。故爲之述其概略如此。

石雅 卷中 五十三

Fig. 4. Two pages of Zhang Hongzhao's "Shi Ya" (Lapidaries of China, p. 52, 53) that cite the story of "Zhimo Inkstone", which was recorded and commented on by Wang Shizhen (1691) in "Chi Bei Ou Tan." The unshaded area recorded his visit to the "bat-stone" quarry at Dawenkou, Shandong, in Summer 1914. He pointed out that the "stone bats" and "silkworms" of ancient Chinese literature, were trilobites; the "stone bats" are *Drepanura premesnili* Bergeron, and the "silkworms" are axes of trilobites.

Richthofen was a German geologist and geographer. He traveled in China for a long period. He came to Shanghai in 1868 (Qing Dynasty), and did not return to Germany until 1872. During the four years of his stay in China, he made seven investigations of stratigraphy and geography over a vast area. He described many sections, and made collections of fossils of different groups and different ages. His investigations resulted in the publication of the book "China" in five volumes, a monumental work for Chinese geology and stratigraphy (Richthofen, 1877–1912). Willis (1907) commented, "Baron Ferdinand von Richthofen, by his extensive exploration and penetrating research, laid the foundation for all future geologic work in China. In his journeys from the extreme south to the far north, from the eastern plains to the western ranges of the Empire, he observed all phases of geographic and geologic phenomena presented in that vast area, and grasped the problems broadly and strongly."

The trilobites gathered by Richthofen were mainly from three localities at Saimaji (Sai-ma-ki), Daling (Ta-ling), and Wulupo (Wu-lo-pu), eastern Liaoning, northeast China. Other small collections were from localities in Sichuan and Jiangxi Provinces. The material from Liaoning was later studied by Dames (1883) (Fig. 5), and that from Sichuan and Jiangxi by Kayser (1883a, b) and Frech (1911). All these results were published in volumes 4 and 5 of the book "China." As the first scientific research on trilobites in China's history, Dames (1883) described fourteen Cambrian species assigned to five genera, two questionably assigned cranidia, and two undetermined pygidia. Specimens described by Kayser include the Carboniferous species *Pseudophillipusia obtusicauda*, which was later revised by Frech (1911) and Lu *et al*., (1965), and four unnamed species assigned to four genera. The species described by Kayser were the first record of trilobites from south China.

Richthofen's material as reported by Dames (1883) was revised by Kobayashi (1937) and Schrank (1974, 1975, 1976, 1977). Except for *Dorypyge richthofeni* Dames, all species assigned originally by Dames were later transferred to other genera (Walcott, 1913; Kobayashi, 1937). The material is reposited in the Museum of Natural History (Museum für Naturkunde) in Berlin. I had an opportunity to examine and photograph those specimens in 1998, and G. Geyer and I are planning to revise them.

Richthofen's expedition and Dames' paper impressed C. D. Walcott. Walcott realized the need to study the stratigraphy and to collect fossils extensively in China in order to compare the Cambrian sections and faunas between North America and east Asia. With the support of the Carnegie Institution, he sent B. Willis and E. Blackwelder to China in order to study the Cambrian and collect trilobites. In July 1903, Wills and Blackwelder sailed for Europe, and after a conference went by the Trans-Siberian Railroad to Beijing in late September 1903. From October 1903 to June 1904, Willis, Blackwelder and R. H. Sargent from the U. S. Geological Survey, who joined them in December, made investigations of the Cambrian geology in Shandong, Liaoning, Shanxi, Shaanxi, Sichuan, and Hubei Provinces, where they measured a number of sections. The trilobites collected from sections in east Liaoning and Shandong, were studied preliminarily by Walcott (1905, 1906, 1911). With the addition of a large collection made by J. P. Iddings of the University of Chicago, which was made at Walcott's request from eastern Liaoning, Walcott (1913) finally completed his monumental work on Chinese Cambrian trilobites of the North China Platform. In this work, "The Cambrian faunas of China," he dealt with eleven fossil groups, including Foraminifera, Porifera, Anthozoa, annelids, brachiopods, gastropods, "pteropods" (i.e., hyoliths), cephalopods, ostracods,

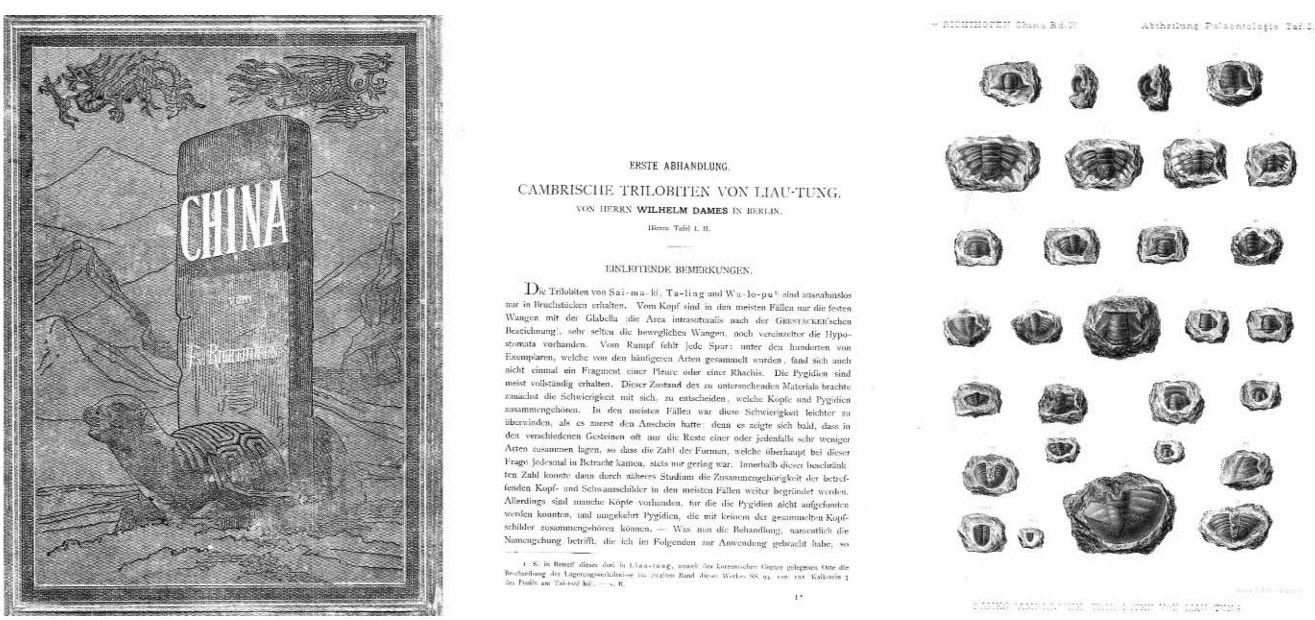


Fig. 5. Cover page of Richthofen's "China" (left), the first page of W. Dames' paper "Cambrian trilobites from Liaotung" (middle), which was the earliest scientific paper on Chinese trilobites, and the first plate in the paper, in which the upper two rows are *Dorypyge richtofeni* Dames.

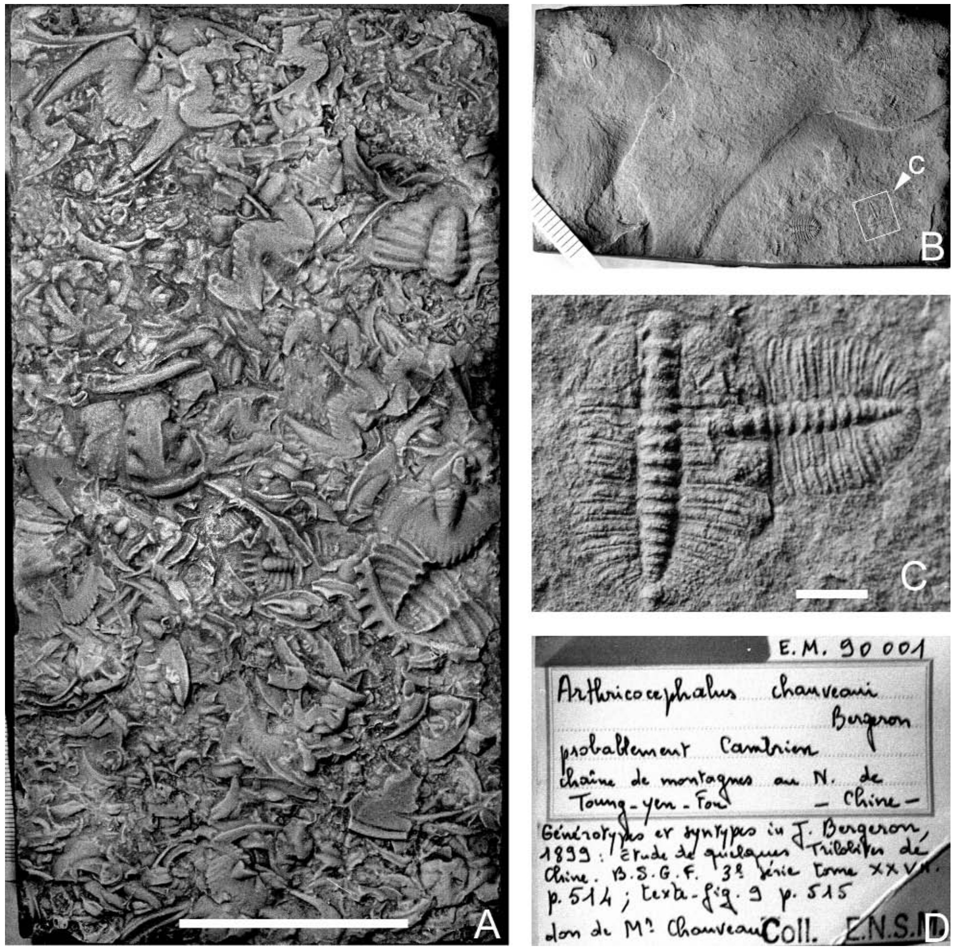


Fig. 6. Material from Bergeron's paper of 1899. A, Gypsum replica of limestone slab with syntypes of *Blackwelderia sinnesis* (Bergeron) and *Drepanura premesnili* Bergeron, bar = 5 cm. The original specimen was purchased in Beijing and is believed to be a "bat-stone" from Dawenkou, Shandong. Dawenkou's bat-stones were marketed by local people much earlier than the appearance of Bergeron's paper. B, Slab with syntypes of *Arthricocephalus chauveaui* Bergeron, about natural size, specimen collected near Tongren, eastern Guizhou. C, Enlargement of two exoskeletons from 6B, bar = 1 mm. D, museum label of the Tongren specimen.

merostomes, and trilobites. Walcott described 36 genera and 180 species of trilobites, with a few Lower Cambrian trilobites recorded for the first time from north China. Walcott's work was the most comprehensive study on Chinese trilobites at that time, and had great influence on future trilobite studies in China. Walcott's specimens are in the Smithsonian Institution. More recently, trilobites in Walcott's collection have been restudied by Zhang and Jell (1987).

Other papers on Chinese trilobites were published by the French geologist Bergeron (1899), the Hungarian geologist Lóczy (1899), the German geologists Monke (1903) and Lorenz (1906), and the British geologist Woodward (1905). Bergeron's paper was important even though he worked only on two small collections now housed in the Museum of University Claude Bernard, Lyon, France. One collection is a slab of limestone with *Blackwelderia*, *Drepanura*, and *Pseudagnostus* (Bergeron, 1899, fig. 1; Fig. 6A). By describing that specimen, Bergeron named, for the first time, the "bats" as *Drepanura premesnili*. The specific name was for M. A. R. Prémesnil, a collector of antiques who bought the specimen in Beijing in 1858. This slab contains also the types of *Blackwelderia sinnesis* (Bergeron) and *Pseudagnostus douvillei* (Bergeron). This slab was said to be from north of Pékin (Beijing) (Bergeron, 1899), but it is now believed to have been collected from the Kushan Formation at a locality in Shandong Province (see Walcott, 1913), which is south of Beijing. The slab had probably been returned to Prémesnil after Bergeron studied it (A. Prieur, Museum of the Universite Claude Bernard, Lyon, personal communication, 2002); as this collection now contains only a gypsum replica (plastotype). The second collection is a small slab of dark greenish grey marl, collected from the Balang Formation near Tongren (Toung-yen-Fou), eastern Guizhou, by M. Chauveau, who gave it to Bergeron for study. This specimen contains several exoskeletons, isolated cephala, thoracopyga (trunks), and a single pygidium (Fig. 6B, C). These fossils represented a new form that Bergeron named *Arthricocephalus chauveaui.* These were the first recorded trilobites from Guizhou Province.

In the same year, Lóczy (1899) illustrated four fragments of

Fig. 7. Zhang Hongzhao, Ding Wenjiang, A. W. Grabau, Sun Yunzhu, and other founders of the Geological Society of China. Photograph taken in front of Grabau's house at Douyacai Hutong (Bean Sprouts Lane), Peking (Beijing), in 1933. Seated in the first row, left to right: Zhang Hongzhao (H. C. Zhang), President of the Geological Society of China; Ding Wenjiang (V. K. Ting), Secretary of Academia Sinica; A. W. Grabau, professor in the National University of Peking and head of the Paleontological Section of the Geological Survey of China; Weng Wenhao (W. H. Wong), Director of the Geological Survey of China; and P. T. de Chardin, French vertebrate paleontologist and geologist, Researcher of the Geological Survey of China. Sun Yunzhu, Secretary of the Geological Society of China, is the fifth from the left in middle row.

trilobites from the Silurian at Pupiao, near Baoshan, Yunnan, southwest China, and three pygidia and one fragmental cranidium from the Qilian Mountain area, Gansu Province, northwest China. The specimens in the latter collection were assigned to the new Carboniferous species *Phillipsia kansuensis*. Although Lóczy found only fragments of trilobites at Pupiao, Yunnan, the locality has since become a classic site for trilobite hunting (Mansuy, 1916; Reed, 1917; Sun, 1939; Luo, 1974; Sun and Xiang, 1979). Lóczy was the first paleontologist to describe trilobites from northwest China.

The material of Monke, Woodward, and Lorenz is all from the classic study area in Shandong, and, except for one Ordovician species described by Lorenz, all are from the Middle and Upper Cambrian. Monke's material was probably lost during the Second World War. I have searched for it several times in Germany since 1998, but failed to find it. Lorenz's material, however, is now in the University of Freiburg.

In the early 1900s, French geologists investigated the geology of Yunnan Province and collected rich trilobite faunas. The Cambrian trilobite material published by Mansuy (1912, 1916) was collected by H. Lantenois in 1903 and J. Deprat in 1909, respectively. Mansuy (1912) described Lower Cambrian species of *Redlichia* and *Palaeolenus*. This material is reposited in the museum of the Universite Claude Bernard. Mansuy (1916) described Middle and Upper Cambrian trilobites in a nearby area between Yunnan and Vietnam, which was apparently similar to that in Liaoning and Shandong, north China. During 1908–1910, J. C. Brown from the Indian Geological Society also investigated the geology in Yunnan. The trilobites collected by Brown from the Ordovician at Pupiao, southwest Yunnan, were later studied by Reed (1917). The research of both Mansuy and Reed was of great significance in the study of the paleogeography of Chinese trilobites. It showed that the Cambrian and Ordovician trilobites of Yunnan belonged to platform habitats, and are closely related to the faunas of the Yangtze and the North China Platforms.

1924–1949

The first fossil group that Chinese paleontologists began studying was trilobites (Lu *et al.*, 1981). Sun Yunzhu (1924) published a monograph on the Cambrian trilobites of north and northeast China. This was the first substantial publication on trilobites by a Chinese scientist, and was a milestone for Chinese trilobite research. The years 1924–1949 constitute a period in which Chinese geologists began to be involved in trilobite research, and they have played important roles ever since.

The founding of the Republic of China in 1911 made it possible to establish a national geological institution, the Geological Section, under the Ministry of Industry. In that year, two young geological students, Zhang Hongzhao (H. C. Chang) (Figs. 3, 7) and Ding Wenjiang (V. K. Ting) (Fig. 7), graduated and returned to China from Japan and England, respectively. They had a great influence on Chinese geology and trilobite research thereafter. Zhang was appointed head of the section soon after his return. The following year, when the Geological Section was renamed the Geological Institute under the Department of Mine Affairs, Ministry of Industry and Commerce, Ding was appointed director of that section. One year later, the Ministry was moved from

Fig. 8. Sun Yunzhu (1896–1979) in his youth. Photograph given to A. A. Öpik, the famous Australian trilobite worker (then at the Estonian State University at Tartu, Estonia), by Sun at the 14th International Geological Congress, Madrid, Spain, 1926.

Nanjing to Beijing, and it established a section of the Geological Institute as one of its branches. In October 1913, the Geological Institute began to recruit students and offered geological courses in the Department of Geology of the National University of Peking, which was founded in 1909, but closed one year later. The Institute then became the basis for the second Chinese geological education institution. The teaching staff included Zhang and a German teacher, F. Solgor. In 1915, Ding joined the teaching staff.

After a training period of three years, 21 students graduated in 1916, and became the professional geologists trained by the Chinese government. By employing some of the graduates in that year, the government set up a new national geological institution, the Geological Survey of China, to replace the Geological Institute. Ding was appointed director of the survey. Afterward, local institutions of geological education and geological surveys were established everywhere in China. The establishment of those additional institutions strongly promoted geological and paleontological research in China. In 1917, The National University of Peking decided to resume its geological department. Sun Yunzhu (Y. C. Sun) (Fig. 8) was one of the students recruited after the department was restored. Twenty students graduated in 1920, known as the "second year's" graduates. As a distinguished student, Sun was employed by the department on his graduation.

In 1920, another important event for Chinese paleontological research was the arrival in China of A. W. Grabau (Fig. 9), a professor at Columbia University. Invited by Ding, then the director of the Geological Survey of China, Grabau accepted two posts: the Paleontological Professor at the Department of Geology, National University of Peking, and the Chief Paleontologist of the Geological Survey. In the university, he took complete responsibility for training Chinese paleontologists and geologists. He gave lectures on paleontology and stratigraphy and on zoology for the students and research workers. Sun Yunzhu was appointed his teaching assistant. Under his guidance, Sun later became the first Chinese trilobitologist, and went on to great achievements in Chinese trilobite research. In the survey, Grabau was in charge of the Paleontological Laboratory and began to issue *Palaeontologia Sinica*, the famous English monograph series published by the Paleontological Society of China (then the Geological Survey of China), in which nine monographs, to date, on trilobites have been published.

During 1920–1937, dozens of young Chinese paleontologists were trained under Grabau, and studied almost all the major fossil groups. Besides Sun Yunzhu, his students Sheng Xinfu (H. F. Sheng), Wang Yu, Yin Zanxun, and Lu Yanhao (Fig. 10), also devoted themselves to Chinese trilobite research. Until his death in Beijing on March 20, 1946, Grabau had stayed in China for 26 years, and devoted more than one-third of his life to China's paleontological education and research. No other foreign geologist has made so great a contribution to the development of modern Chinese stratigraphy and paleontology, including trilobitology. He contributed to Chinese trilobite research by describing two species of Ordovician *Asaphelus* from north China in 1922, and Silurian trilobites from the eastern Yangtze Gorge area in 1925. In the latter paper, Grabau (1925) described seven species assigned to six genera, including three new species, among which was the famous Silurian trilobite *Coronocephalus rex* Grabau.

Under Grabau, Sun Yunzhu (1924) published his first monograph "Contributions to the Cambrian faunas of North China." It described 38 trilobite species belonging to 25 genera from Hebei, Shandong, and southern Liaoning, north China (Fig. 11). It was the first paleontological monograph, published by a

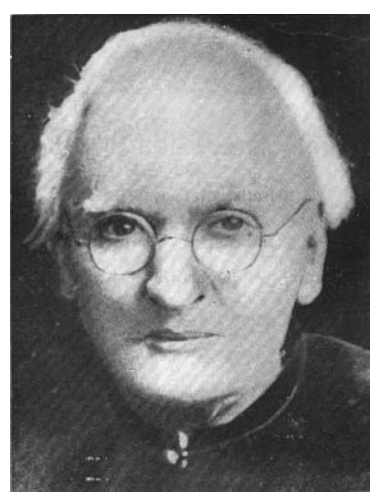


Fig. 9. Amadeus William Grabau, born in Cedarburg, Wisconsin, in 1870; died in Beijing in1946. As a paleontological Professor at Peking University (1920–1946), he had significant influence on the development of trilobite work in China.

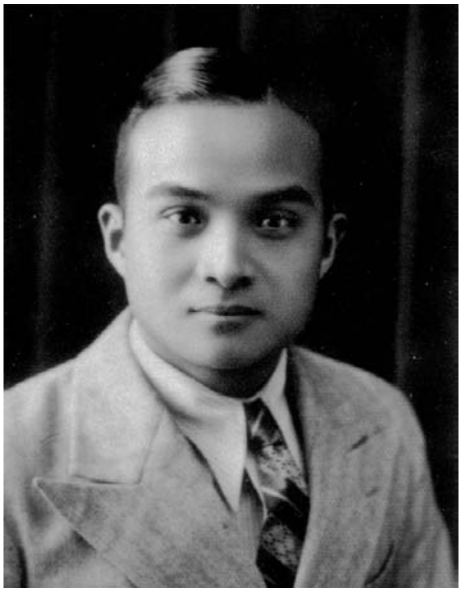


Fig. 10. Lu Yanhao (1903–2000) in 1937 at his graduation from the Geology Department of the National University of Peking.

Chinese paleontologist. The most important contribution of this monograph was the discovery of the late Late Cambrian Fengshan limestone and the post-*Chuangia* fauna in north China. In this study, Sun divided the Cambrian of north China into a Lower, Middle and Upper series and five lithostratigraphic units.

Sun (1931), then a professor in the Department of Geology of Peking University, published a second monograph, "Ordovician trilobites of central and southern China", and then (Sun, 1935) his third, "The Upper Cambrian trilobite faunas of north China." In the latter work, he described nine new genera and 32 new species and divided the Upper Cambrian of north China into the Changshan and the Fengshan "series" (i.e., formations) and five trilobite zones.

One year before Sun's third monograph on trilobites, Sheng Xinfu (1934) published a monograph "Lower Ordovician trilobite fauna of Zhejiang" with the descriptions of four genera and nine species. This is a relatively small assemblage, but he documented important Ordovician trilobite faunas from southeast China, which were poorly known.

Sun (1937a) subdivided the Kushan Shale of Shandong into four trilobite zones. He established for the first time a Cambrian biostratigraphic sequence for north China:

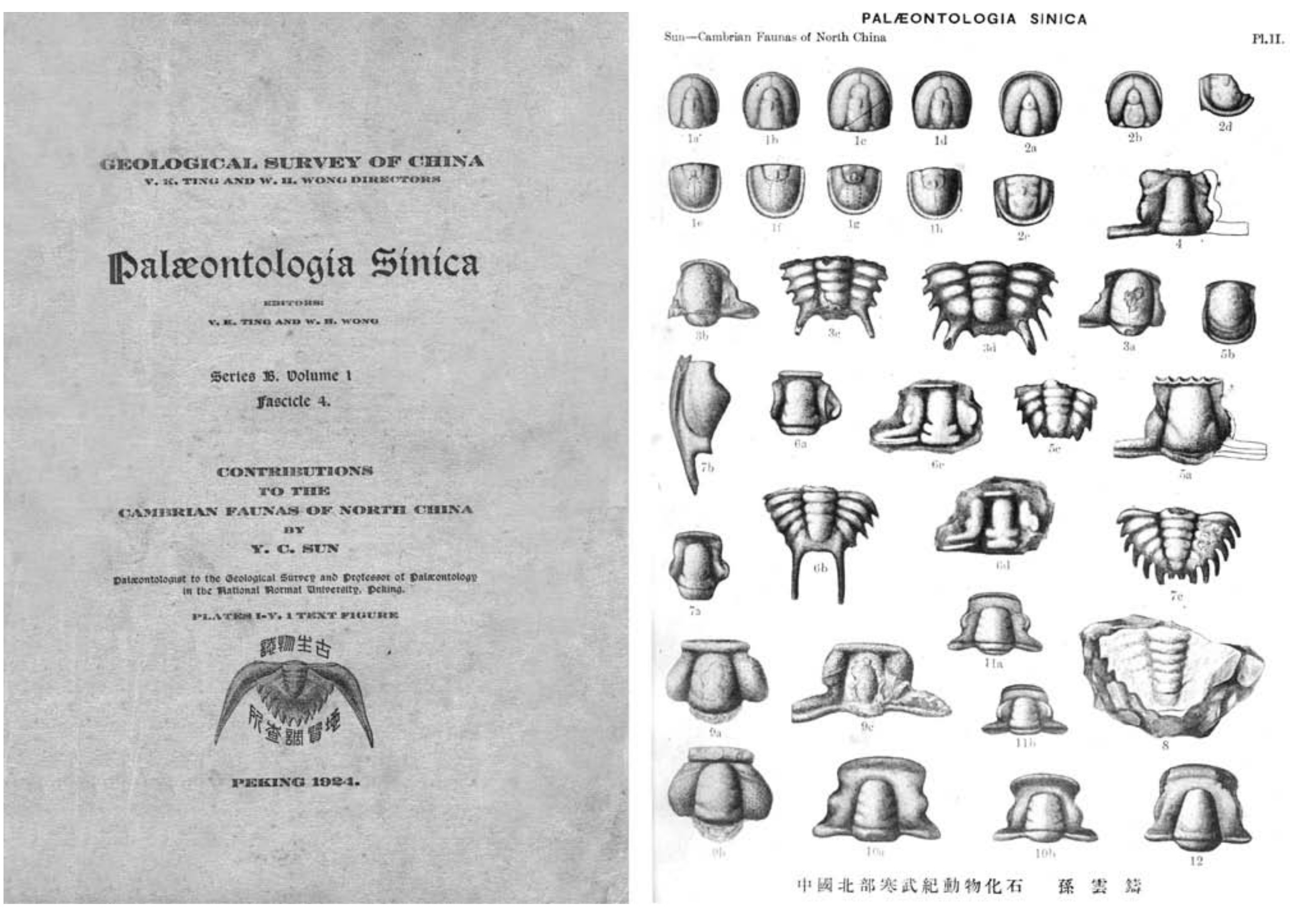


Fig. 11. Cover and the first plate of trilobites of Sun Yunzhu's (1924) monograph, the earliest study on trilobite taxonomy published by a Chinese paleontologist and a milestone in the history of trilobite research in China.

Upper Cambrian	
Fengshan Formation	9, *Quadraticephalus walcotti-Saukia acamus* Z.
	8, *Ptychaspis subglobosa* Zone
Changshan Fm.	7, *Kaolishania pustulosa* Zone
	6, *Changshania conica* Zone
	5, *Chuangia batia* Zone
Upper Kushan Shale (Kushan Fm.)	4, *Drepanura premesnili* Zone
	3, *Blackwelderia sinensis* Zone
Middle Cambrian	
Lower Kushan Shale (Wenshui Fm.)	2, *Damesella blackwelderi* Z.
	1, *Amphoton typica* Zone
Lower Cambrian	
Manto Formation	

In addition to this study, Sun (1937b) published a paper on two new Devonian trilobite species from Hunan, south China. Three more papers by Chinese paleontologists were published in 1937. Wang Yu (1937) described a new Permian trilobite from Gansu, northwest China; Yin Zanxun (Yin T. H., 1937) described Ordovician and Silurian trilobites from western Yunnan; and Ma Xirong (1937) discussed the geological distribution of *Redlichia*.

Also in 1937, two important monographs on Chinese trilobites were published by foreign paleontologists. "The Sinian and Cambrian formations and fossils in southern Manchoukuo" was a collaboration by the Japanese geologist R. Endo and the American trilobite worker C. E. Resser. It described Cambrian trilobites from Liaoning, northeast China. "On the Cambro-Ordovician faunas of western Quruq-tagh, eastern Tienshan" by the Swedish paleontologist G. T. Troedsson (1937) dealt with Cambrian and Tremadocian trilobites from the Quruq-tagh Mountains, Xinjiang, northwest China.

The work of Endo and Resser (1937) was completed in the United States. Beginning in 1924, Endo did fieldwork during his school vacations each year on the Cambrian and Ordovician stratigraphy and trilobites in southern Liaoning, northeast China. The collecting lasted for over 10 years, and was done at a number of localities. During his earlier collecting, Endo communicated with C. D. Walcott who still actively worked on Cambrian trilobites. In response to Walcott's suggestion, Endo sent his material to the Smithsonian Institution in order to collaborate with Walcott. Before they could carry out the project, Walcott passed away in 1927. Afterward, Endo gathered more trilobite material, and collaborated with C. E. Resser, then the curator of invertebrate paleontology in the United States Museum. Walcott had transferred Endo's earlier collections to Resser as he felt that he did not have sufficient time to complete the study.

Endo and Resser (1937) described nearly 300 Middle and Upper Cambrian trilobite species, which were assigned to 62 genera. Most of them were described as new taxa. Their new litho- and biostratigraphic subdivision for north China, with three series, nine formations, and fourteen trilobite zones, was not widely accepted.

Troedsson's (1937) material was collected from Quruq-tagh,

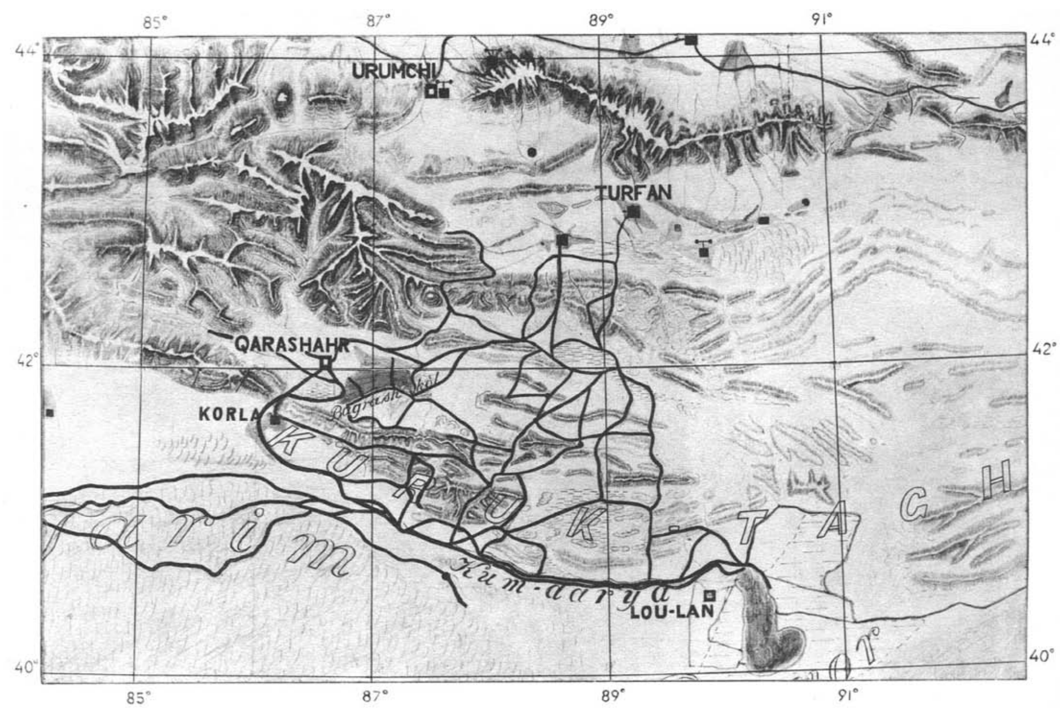


Fig. 12. Map from E. Norin (1937), showing the routes taken by E. Norin and N. Ambolt of the Sino-Swedish Expedition in Quruq-tagh and Chöl-tagh, Xinjiang. The expedition resulted in the report on Quruq-tagh trilobites by Troedsson (1937).

Xinjiang, by E. Norin, the head geologist of the Sino-Swedish Expedition to the North-Western Provinces of China, which was carried out in 1927–1934 (Norin, 1937) (Fig. 12). The expedition was under the leadership of Sven Hedin, who organized the team with support from Weng Wenhao, the Director of the Geological Survey of China, and Ding Wenjiang, the Secretary of Academia Sinica. Troedsson's work was the most extensive study of Cambrian–Tremadocian trilobites of northwest China up to that time, and showed that the fauna was very different from that of north and northeast China. It proved to be similar to the Cambrian–Tremadocian fauna from Zhejiang, east China, which was named by Lu Yanhao (Lu *et al*., 1974a) as the distinct trilobite fauna of "Southeast China-type."

Just as trilobite research was becoming productive in China, the Japanese government launched a war against China in July 1937. Soon after the military incursion, Japanese troops rapidly occupied northeast China, and pressed on towards north China. The universities and geological institutions in Beiping (previously Peking, now Beijing) and Tianjing were forced to move to Hunan, and then, after the occupation of North and Central China, to Kunming, Yunnan Province, and Chongqing, Sichuan Province. The war had a seriously negative impact on China's trilobite research and limited field studies on trilobites to southwest China.

After the surrender of the Japanese army in 1945, the situation still did not improve because a three-year civil war followed. Though 1937–1949 was an extremely difficult period, Chinese paleontologists were able to obtain important scientific results in trilobite research. Lu Yanhao (1939, 1940, 1941, 1942, 1945) investigated the trilobite-bearing formations in the Kunming area, eastern Yunnan, and published a series of papers on trilobites, mainly of Early Cambrian age. Among these papers, Lu did the first ontogenetic and phylogenetic research on Chinese ptychopariid and redlichiid species (Lu, 1939, 1940). Sun Yunzhu (1939) did a study of the Upper Cambrian of western Yunnan, and published on trilobites collected from those formations. Meanwhile, Wang Yu (1938a, b) published on Ordovician and Silurian trilobites from western Hubei, and Yin Zanxun (1938) described a Devonian trilobite from eastern Yunnan. Chen Guanyan (1948) described two odontopleurid species from the Silurian of western Yunnan; and Xu Yujian (S. C. Hsü) and Ma Zhentu (C. T. Ma, 1948) detailed the Ordovician trilobites from the Yangtze Gorge area. All this work laid a foundation for developing the Paleozoic biostratigraphy of southwest China, particularly that of the Lower Cambrian.

In the late1920s–1940s Kobayashi investigated the Cambrian and Ordovician of northeast China and Korea during the Japanese occupation. He obtained a great deal of Chinese trilobite material, on which he published a series of reports (Kobayashi, 1931, 1933, 1937, 1938, 1941a, b, c, d, 1942a, b, 1944a, b, c). These papers described and reinvestigated many Chinese Cambrian taxa, particularly the damesellid genera.

The studies carried out by 1949 enriched the content of Chinese trilobite faunas. These publications involved trilobite systematic paleontology, ontogeny, phylogeny, biostratigraphy, and paleogeography, and covered a wide geographic area that included fourteen provinces. As a result of the efforts by Sun and his colleagues, trilobite study became one of the most important research areas in Chinese invertebrate paleontology in the 1930s and 1940s.

1949–PRESENT

For over half a century since 1949, unprecedented progress has been made in Chinese trilobite research. The founding of the People's Republic of China in 1949 ended the long-term unrest caused by war. In the beginning of the republic, the necessary geological surveying and exploration for mineral resources for China's reconstruction provided a good opportunity for research on stratigraphy and paleontology. In the 1950s and 1960s, the number of workers engaged in trilobite research increased continuously, and the investigation of trilobite-bearing strata was extended into such new areas as the Zhuozishan Ranges in Inner Mongolia, the Qilian Mountains in Qinhai, the Qinling Ranges, the Wuling and Xuefeng Mountains in western Hunan and eastern Guizhou, the Hinggan Ranges in Heilongjiang, and areas in Anhui, Jiangsu, Guangdong, Guangxi, and Fujian Provinces.

Since 1949, hundreds of scientific papers, monographs, atlases, and books on Chinese trilobites were published by Chinese paleontologists. These publications involved almost all the fields of trilobitology and covered all the Paleozoic periods. Some papers dealt with material from abroad.

In 1951, the Chinese Academy of Sciences founded China's first paleontological research institution, the Nanjing Institute of Palaeontology (predecessor of the Nanjing Institute of Geology and Palaeontology). Lu Yanhao, one of the world's leading trilobitologists by then, was appointed deputy director, and maintained this position for over 30 years. Under his leadership, the institute became a focus of Chinese trilobite research, and its members increased to as many as ten in the 1980s.

In the 1950s, the Ministry of Geology also set up its own research institutions in Beijing, which included the Geological Institute of the Chinese Academy of Geology (with a paleontological section), local research institutions in all major administration regions, and regional surveying teams in almost all provinces. Those institutions and teams employed many geologists to work on trilobites and trilobite-bearing strata, and formed a large research group which subsequently became the Trilobite Section of the Palaeontological Society of China.

During the 1950s and early 1960s, the first generation of Chinese trilobite workers, Sun Yunzhu, Lu Yanhao (Fig. 13), and Sheng Xinfu, were still active in research on Chinese trilobites. A number of young paleontologists including Zhang Wentang, Guo Hongjun, Zhu Zhaoling, Qian Yiyuan, Xiang Liwen, Yi Yongen, Lin Tianrui, Li Shanji, Guo Zhenming, and Chen Renye began their trilobite research. The most significant single work in this period was the two-volume "Trilobites of China" (Lu *et al*., 1965). Altogether 1,233 species in 376 genera previously recorded in China were redescribed and revised. It was the most comprehensive work on Chinese trilobites up to that time (Fig. 14). "The Index Fossils of China" and the handbooks of regional fossils were edited as atlas-style series of publications with figures and descriptions of many index trilobites (Lu, 1957, Lu, Zhu and Qian, 1962; Lu, Zhu, and Zhang, 1963; Xiang and Yi, 1963; Lu and Qian, 1964). They were considered to be very useful for field investigation. Significant papers published in this period include the studies on the Cambrian trilobites from Yunnan and Guizhou (Lu, 1951, 1956, 1961), the Lower Paleozoic trilobites from the Qilian Mountans (Zhu, 1960a, b; Zhang and Fan, 1960), the Lower Cambrian and Ordovician

Fig. 13. Lu Yanhao, Deputy Director of the Nanjing Institute of Geology and Palaeontology of the Chinese Academy of Sciences, working on trilobites in his office in the hot summer of 1954.

Fig. 14. The two volume atlas "Trilobites of China," compiled by Lu Yanghao and four other Chinese trilobite workers (1965), and one of the most important works on Chinese trilobites published since 1949.

trilobites from the Yangtze Gorge area, Hubei, (Zhang, 1953; Yi, 1957), the Ordovician trilobites from southwest China (Sheng, 1958), the Middle Cambrian trilobites of Hebei (Zhang, 1959), the Cambrian trilobites from the Kushan Formation of north China (Zhu, 1959), and the Middle Cambrian trilobites from western Henan (Xiang, 1962).

According to the agreement between China and the USSR, the government of the Soviet Union sent L. E. Yegorova, a female trilobite specialist from the Institute of Geology, Geophysics, and Mineral Resources in Novosibirsk, to work in China in May 1956. She collaborated for three years with Xiang Liwen until she returned in May 1959. Accompanied by Xiang and other Chinese paleontologists, she investigated Cambrian trilobites in the Qingling and the Wuling Mountains, and published two papers, including a monograph (Yegorova and Xiang,1958; Yegorova *et al.,* 1963). Yegorova *et al.*'s (1963) monograph on the Cambrian in western Hunan and eastern Guizhou described 43 species in 33 genera, including two new genera, eleven new species, and 12 species left in open-nomenclature. It was the most extensive study of trilobites from an area where trilobites were poorly known. Later research has shown that the Cambrian and Lower Ordovician in the border area between western Hunan and eastern Guizhou were deposited in a slope environment, and have transitional trilobites. This area is significant for trilobite taxonomy and stratigraphic research (Yang, 1978; Peng, 1984, 1987, 1990, 1992; Peng and Robison, 2000).

During 1949–1965, research on trilobite biostratigraphy progressed considerably. In a reinvestigation of the Cambrian of Liaoning and Shandong, Lu and Dong (1952) refined the Cambrian stratigraphy of North China by subdividing the Cambrian into three series, seven formations, and seventeen trilobite zones. Lu (1962) subsequently proposed a stratigraphic framework for the Cambrian of China by combining the Cambrian litho- and bio-stratigraphy of north China and eastern Yunnan:

Upper Cambrian	
Fengshan Formation	21, *Calvinella-Tellerina* Zone
	20, *Quadraticephalus-Dictyella* Zone
	19, *Ptychaspis-Tsinania* Zone
Changshan Formation	18, *Kaolishania* Zone
	17, *Changshania* Zone
	16, *Chuangia batia* Zone
Kushan Formation	15, *Drepanura* Zone
	14, *Blackwelderia* Zone
Middle Cambrian	
Changhia Formation	13, *Taitzuia* Zone
	12, *Amphoton* Zone
	11, *Crepicephalina* Zone
	10, *Liaoyangaspis* Zone
Hsuchuang Formation	9, *Bailiella* Zone
	8, *Metagraulos abrota* Zone
	7, *Sunaspis* Zone
	6, *Kochaspis hsuechuangensis* Zone
Lower Cambrian	
Lungwangmiao Fm.	5, *Shangtungaspis* Zone
	4, *Micmacca-Redlichia chinensis* Zone
Tsanglangpu Fm.	3, *Paragraulos-Yuehsienszeella* Zone
	2, *Palaeolenus* Zone
Chiungchussu Fm.	1, *Yunnanocephalus-Redlichia walcotti* Zone

Lu *et al*. (1974a) and Qian (1977) subsequently proposed the Maochuang and the Meishucun Formations, as the upper and the lower units of the Lower Cambrian, respectively. On the basis of Lu's work, Xiang (1979) developed a stage nomenclature for China's chronostratigraphy. He refered to the formations as stages, and shifted the Maochuang Formation upward as the basal stage of the Middle Cambrian. This framework has long been used as the standard subdivision of the Chinese Cambrian, although it is conceptually based on lithostratigraphy.

The "Cultural Revolution" of 1966–1976 was a disaster for Chinese scientific research. After July 1966, China's paleontological research was forced to cease, and all publications on paleontology were discontinued. Some scientists were forced to settle in the countryside to do manual labor, and others had to "carry out revolution" by participating in political activities rather than doing research. Almost no scientific papers on trilobites were published until 1974, when the situation changed slightly, and some scientific results could again be published. Lu *et al.* (1974a) published the first paper on trilobites since the beginning of the "Revolution." In this paper, they proposed a bio-environmental control hypothesis based chiefly on the provincialism of Cambrian trilobites. The report divided the world's trilobites into three distinctive faunas: the Oriental, the Western, and the Mixed faunas. The Chinese trilobites represent the Oriental Fauna, and comprise three subfaunas: the North China, the Southeast China, and the transitional types. Each type of fauna was formed under the control of environmental factors. This hypothesis was significant in research on Cambrian paleogeography and plate tectonics. It led to the recognition of the four major, Cambrian blocks that constitute modern China (the North China, Yangtze, Tarim, and Tibet blocks). It also established the Cambrian paleogeography of the Yangtze and the Tarim blocks, which are characterized by a progressive environmental change from a shallow-water platform to an ocean-facing slope and finally to a deep-water basin.

In this same year, the atlas "Handbook for Stratigraphy and Paleontology of Southwest China" was published by the Nanjing Institute of Geology and Palaeontology. It included descriptions of Sinian–Jurassic invertebrates and plants. The portions of the atlas involving Cambrian–Devonian and Permian trilobites came from work by nine experts of the institute (Lu *et al*, 1974b; Lu and Zhang, 1974; Zhang, 1974a, b; Lu, 1974). In the next year, Lu (1975) published, in Chinese and English, his monumental "Ordovician trilobite faunas of central and southwestern China," which described 187 species belonging to 75 genera (Fig. 15). Its trilobites were collected by Lu and many other paleontologists from 33 Ordovician sections and localities in four provinces in central and southwest China in the 1930s–1950s. This book also presented details on the Ordovician biostratigraphy of south China. As an internationally recognized trilobite worker, Lu's fame was enhanced by the publication of this book.

Though a few papers were published, trilobite research did not return to normal until the end of the catastrophic "Cultural Revolution" in 1976. In that year, *Acta Palaeontologica Sinica*, which has been the important journal for publishing trilobite papers, was resumed.

During the late 1960's-1970's, some young graduates, Lin Huanling, Liu Yiren,Yang Jialu, Zhou Zhiyi, Zhou Zhiqiang, Zhang Jinlin, Yuan Jinliang, Wu Hongju, Zhao Yuanlong, Yin Gongzheng and Peng Shanchi, were employed by universities, regional institutions of geology, and the Nanjing Institute of Geology and Palaeontology. They became paleontologists who specialized in trilobites. Some of them still actively working on trilobites.

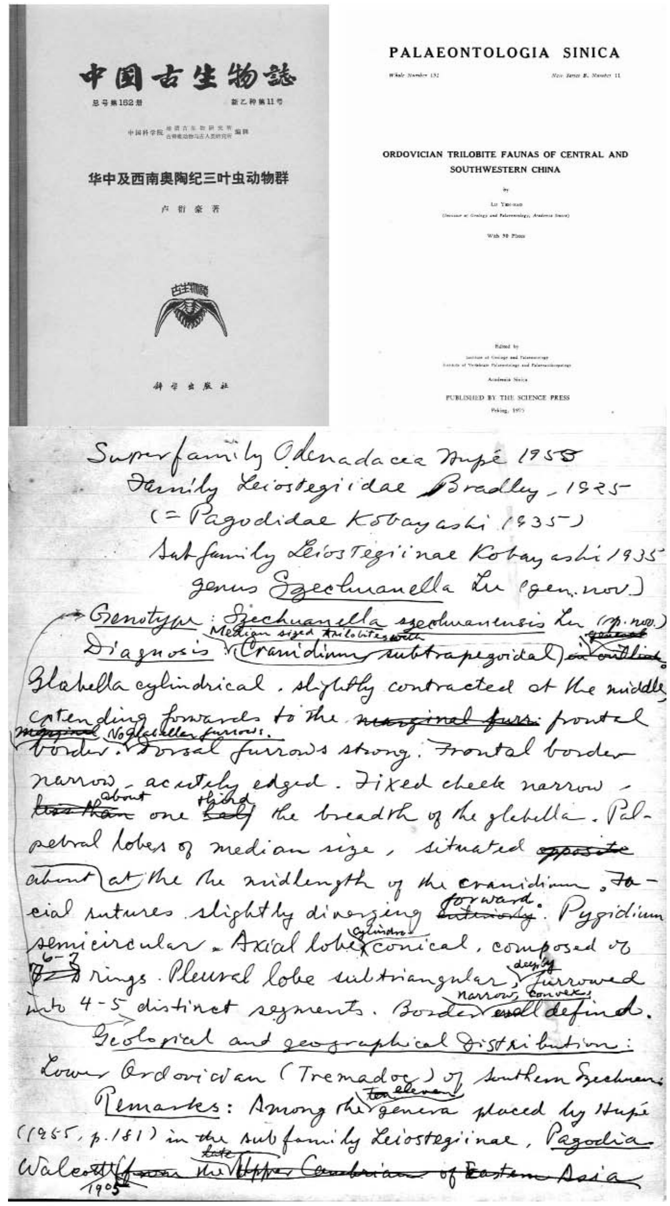


Fig. 15. Cover and title page (above) of Lu Yanhao's monograph on Ordovician trilobites of central and southwest China, and a sheet of his handwritten draft for this work (below).

From 1976 on, a series of regional paleontological atlases have been compiled by the Ministry of Geology and Mineral Resources. More than 30 atlases have been published, of which nineteen contain a portion on trilobites (Luo, 1974; Nan, 1976, 1985; Zhou *et al.*, 1977; Zhou, 1977; Yin and Li, 1978; Yin, 1978; Li, 1978; Zhu *et al.*, 1979; Zhang, 1981, 1983; Zhou *et al.*, 1982; Lin *et al.*, 1982; Liu, 1982; Zhou, 1983; Qiu *et al.*, 1983; Sun, 1984; Zhang and Wang, 1985; Zhu, 1992). Known trilobites and new taxa were figured in the atlases. They provided good trilobite

Fig. 16. Participants at the second conference of the Trilobite Section of the Palaeontological Society of China, in Cili, northwest Hunan, in 1985. From left to right in the first row: Yan Enzeng, Zhu Zhaoling, Xiang Liwen, Lu Yanhao, Zhang Wentang, Chen Runye, Yi Dingrong, Li Shanji, Yi Yong'en. Standing in middle row: Peng Shanchi, Zhang Tairong, Zhang Wei, Luo Huilin, Zhang Zhenghua, Zhou Zhiqiang, Yuan Kexing, Qiu Hong'an, Liang Zongwei, Yang Jialu, Lin Tianrui, Zhou Tianmei; standing in the third row: Ju Tianyin, Zhang Jinlin, Guo Ying, Lin Huanling, Li Changwen, Zhang Sengui, Tan Yugang, Liu Yiren, Zhu Naiwen, Zhang Quanzong, Zhu Hongyuan, Chen Yong'an, Ji Zailiang.

information for each region, and were useful for field geologists and trilobite researchers. However, many of the atlases were compiled in a short period, and this resulted in taxonomic problems. Moreover, the type specimens of new taxa that appeared in some atlases have not been well cared for, and are sometimes very difficult to access. This has caused trouble in current research.

In the late 1970s, scientists from the Chinese Academy of Sciences conducted expeditions to the Himalayan area in Tibet. An important discovery of the expeditions was the first record of trilobites from Tibet. Two species from the Lower Ordovician Jiacun Formation near Nyalam, southern Tibet, were described by Qian (1976). Additional Tibetan trilobites were recorded from the Lower Paleozoic (Qian, 1981). Important work during this period included the study of Middle–Upper Cambrian trilobites from western Hunan and eastern Guizhou (Yang, 1978). This was a more detailed study than Yegorova *et al.*'s (1963) for the area. More papers on trilobites were published in the journal *Acta Palaeontologica Sinica* and other journals.

In recent years, investigations of Cambrian and Ordovician trilobites of key regions have resulted in the publication of a series of monographs on systematic paleontology. These monographs include studies of the trilobites from the Cambrian of southwest China (Zhang *et al.*, 1980); the Cambrian of western Tianshan, Xinjiang, northwest China (Xiang and Zhang, 1985); the Cambrian of Zhejiang, northeast China (Lu and Lin, 1989); the Cambrian and Tremadocian of the Jiangnan Slope Belt in northwestern Hunan, South China (Peng, 1990, 1992); the Cambrian of the east Qingling-Dabashan Mountains, Central China (Yang *et al.* 1991); the Changshanian from north and northeast China (Qian, 1994); the Cambrian of eastern Liaoning, northeast China (Guo *et al.*, 1996), and the Ordovician of the Hinggan Ranges, northeast China (Zhao *et al.*, 1997). These monographs significantly improved knowledge of Chinese trilobites, and described numerous new genera and species. The comprehensive study of the agnostoids of western Hunan (Peng and Robison, 2000) allowed development of an agnostoid-based Middle–Upper Cambrian biostratigraphy that allows intercontinental correlation of this interval in South China.

Chronostratigraphic research on the Cambrian–Ordovician and Ordovician–Silurian boundaries has advanced the study of trilobite biostratigraphy and systematic paleontology of the boundary strata (Lu and Lin, 1984; Peng, 1984; Zhou and Zhang, 1984; Zhu and Wu, 1984; Qian, 1985a, 1986). In recent years, Chinese trilobite researchers did comprehensive research on the systematic paleontology and the biostratigraphy of Silurian–Carboniferous trilobites, which were earlier poorly known (Wu, 1977, 1979, 1987a, b; Lu and Wu, 1982; Yuan, 1984, 1988; Yuan and Li, 1995; Yuan and Xiang, 1998). Zhang and Zhu (2000) further refined the Cambrian chronostratigraphy of north China. A chronostratigraphy with four series and nine stages with 29 zones has been developed for south China (Peng, 2000a, b; Peng *et al.*, 2000a, b; Peng and Babcock, 2001). Most of these zones are trilobite-based, and some are globally correlatable. A

Fig. 17. Participants at the third conference of the Trilobite Section of the Palaeontological Society of China in Xinxian, Shanxi, in 1988. The photograph was taken in front of a temple at Wutai in the Wutai Mountains. From left to right, in the first row, Zhang Sengui, Ju Tianying, Zhu Zhaoling, Yi Dingrong, Lu Yanhao, Zhang Quanzong, Zhang Jinlin, Yi Yong'en, Zhou Tianmei, Zhu Hongyuan, Luo Huilin; Han Nairen, Liu Huaishu, Yin Gongzheng, Qian Yi, Yang Qinghe, Zhao Yuanlong, Liu Yiren, Yuan Jinliang, Jiang Lifu, Wang Huaiqing, Zhou Zhiyi, Peng Shanchi (Photo by Lin Huanling).

study of the *Glyptagnostus*-bearing interval resulted in the establishment of the first global stage of the Cambrian, the Paibian, and the first intra-Cambrian "golden spike" (Global Standard Stratotype-section and Point) (Peng *et al.*, 2001).

Many other reports on trilobites have been published in recent years. Although these papers dealt mainly with trilobite systematic paleontology and biostratigraphy, more attention has been directed towards aspects of this fossil group. These include studies on ecology (Han, 1985; Zhou, 1996), ontogeny and phylogeny (Lu and Zhou, 1979; Lu, 1980; Lu and Wu, 1982; Lu *et al.*, 1984; Qian, 1984; Yi, 1988; Peng, 1994, Yang, 1992; Yuan *et al.*, 2001), molting (Han and Wang, 2000a, b), enrollment (Han, 1985, 2001b; Liu, 1987), morphology and function of eyes (Han and Zhang, 1985; Han, 1989a, b, 2001a), panderian structures (Han, 1978, 1984, 2001b), sexual dimorphs (Peng, 1990), malformation (Han and Zhang, 1991), heterochrony (Zhou *et al.*, 1994), and taxonomic cluster analysis (Lin and Chen, 1982; Lin and Zhu, 1985, 1990; Lin, 1988, 1990). The research has also included trilobite biofacies and biogeography (Zhou *et al.*, l979, 1989, 1992, 1999, 2000, 2001; Zhou and Dean, 1989). Significant research on taxonomy in the 1980s and 1990s included studies on the Cambrian–Tremadocian trilobites of Guizhou (Lu and Qian, 1983; Lu and Zhou, 1990); the subfamily Coronocephallinae (Zhang, 1983); the *Onychopyge* faunas of Gansu and Inner Mongolia (Lu *et al.*, 1984); the Cambrian trilobites of southern Anhui (Qian, 1985b), the Jiangnan Slope Belt in northwest Hunan (Peng, 1987, Peng *et al.*, 1995), and western Henan (Zhang *et al.*, 1995); and the Ordovician trilobites of northern Guizhou (Zhou *et al.*, 1984), north and northeast China (Zhou and Fortey, 1986), Gansu (Zhou and Dean, 1986), western Yunnan (Zhou *et al.*, 1998a), and Tarim (Zhou *et al.*, 1995, 1998b); and Ordovician agnostoids and trinucleids (Zhou, 1987; Zhou and Hughes, 1989).

More recently, the Lower Cambrian Chengjiang Biota with exceptionally preserved fossils of many groups was found at several localities in Chengjiang area, Jinning County, near Kunming, Yunnan Province. It is considered to be one of the most amazing scientific discoveries in the last century. The Chengjiang Biota includes trilobites. Four trilobite species, *Eoredlichia intermedia, Kuanyangia pustulosa*, *Wutingaspis tingi,* and *Yunnanocephalus yunnanensis* in the biota have been described and figured (Shu *et al.*, 1995; Chen *et al.*, 1996; Luo *et al.*, 1999; and Hou, 1999). They are preserved with antennae and other appendages, articulating devices, the alimentary canal, and other structures.

Well-preserved trilobites are also known from the Cambrian Kaili Biota from the Kaili Formation near Taijiang, Guizhou Province. The trilobite fauna consists of mainly primitive ptychoparoids, dorypygelloids, redlichids, bathynotids, and oryctocephaloids (Zhao *et al.*, 1994, 1999); Yuan *et al.*, 1999, 2001, 2002; Guo *et al.*, 1999).

In 1982, the Palaeontological Society of China established several of its fossil-group sections, and about 40 members joined the Trilobite Section. In that year, the section held its first meeting at Qingyang, southern Anhui, and Professor Lu was elected the head of the section.The section held its second and third meetings in 1985 at Cili, northwest Hunan (Fig. 16), and in 1988 at Xinxian, Shanxi (Fig. 17). Unfortunately, after the third meeting, it almost completely ceased its activities. Recently, retirement and the loss of positions in all the geological institutions and universities have reduced the number of trilobite workers. At present, only about 10 trilobite workers are still engaged in research in China.

SUMMARY

From 1883 on, research on Chinese trilobites has made great progress. More than 1000 Chinese genera have been established and nearly 2000 trilobite species have been described, which is about one-sixth the total described species in the world. However, most of the systematic work was conducted in the Yangtze region and north and northeast China on Cambrian and Ordovician trilobites. However, trilobites are also well represented in the vast remote areas of northwest China and Tibet, and Silurian–Permian trilobite-bearing strata are well developed in many regions of the country. Much work on trilobites remains to be done, and Chinese trilobitologists shoulder heavy responsibilities.

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BIOGRAPHICAL NOTES ON SUN YUNZHU (1895–1979) AND LU YANHAO (1913–2000)

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ABSTRACT—Sun Yunzhu and Lu Yanhao were founders of modern Chinese trilobite research. As the first Chinese trilobite worker, Sun published three monographs and a number of papers on Chinese trilobites, and laid a foundation for the development of the Cambrian biostratigraphy of the North China Platform. Lu was one of the most highly productive Chinese trilobite workers. He devoted himself to trilobite research throughout his lifetime, and accomplished particular achievements in systematic paleontology, biostratigraphy, and provincialism of Cambrian and Ordovician trilobites. By their publications, organization of geological and paleontological institutions, and their training of students, Sun and Lu gained great respect and won international recognition. A selected bibliography, mainly inclusive of their work on trilobites and trilobite-related stratigraphy, is part of this report.

INTRODUCTION

Since Richthofen's investigations around 1870 in China, dozens of foreign and native geologists and paleontologists have engaged in research on Chinese trilobites (see Peng, this volume), and have published hundreds of papers. These contributions appeared as short papers, monographs, books, and paleontological atlases, which have greatly expanded our knowledge of trilobites and trilobite-related biostratigraphy and paleogeography of China. Among these researchers, Sun Yunzhu and Lu Yanhao are two of the outstanding native Chinese trilobite workers.

Sun Yunzhu was the first Chinese trilobite paleontologist and stratigrapher. He received his Ph. D. at Halle University in Germany in 1926 and a professorship at the National University of Peking in 1929. He published three monographs and many papers on trilobites and trilobite-bearing strata. The first monograph, published in 1924, dealt mainly with Cambrian trilobites and stratigraphy of north China, and recorded, for the first time, the post-Chuangia trilobite faunas and formations of that region. The next two monographs, published in 1931 and 1935, dealt with the Ordovician trilobites of central and southern China and the Upper Cambrian trilobites of north China, respectively. Sun proposed the first trilobite-based biostratigraphy of the Middle–Upper Cambrian for north China in 1937, and this formed the basis of the modern biostratigraphic framework of the North China Platform.

In the 1920s–early 1950s, Sun devoted himself to teaching geology, paleontology, and stratigraphy. Under his influence, a number of his students chose trilobites as their primary research field. In addition, more than forty of his students became academicians of the Chinese Academy of Sciences in earth science. Sun was one of the primary founders of the Geological Society of China, and was twice elected president of the society.

As a great trilobite paleontologist and stratigrapher, Lu Yanhao focused on the group through his professional life. He received a B.Sc. at the National University of Peking in 1937, and started a career in trilobite research in 1938. For more than 60 years, Lu investigated trilobites and trilobite-bearing strata over a vast area in southwest, central, east, north, and northeast China. In about 160 papers on trilobites and trilobite-related subjects, Lu raised the academic status of Chinese trilobite research remarkably, and had a significant influence on future trilobite work in China. His most important works include the two-volume "Trilobites of China," which was compiled chiefly by him in 1965, and is still an important reference. The monograph "Cambrian of China" (1962) laid a foundation for China's stratigraphical subdivision and provincialism of the Cambrian. Two monographs, "Ordovician trilobite faunas of central and southwestern China" (Lu, 1975) and "The Cambrian trilobites of western Zhejiang" (Lu and Lin, 1989), are magnificent pieces of scientific scholarship. Lu was a senior academician in the Chinese Academy of Sciences and deputy director of the Nanjing Institute of Geology and Palaeontology (1950–1984). He was elected president of the Palaeontology Society of China (1984–1989) and the vice-president of the Geological Society of China (1979–1996).

SUN YUNZHU (Y. C. SUN) (1895–1979)

Biographical notes

Sun Yunzhu (Fig. 1) was the most renowned Chinese geologist and educator in geology, and the first Chinese paleontologist to specialize on trilobites. Over 50 years of paleontological study, he published numerous papers, including three monographs dealing with trilobites, and greatly influenced research on paleontology and stratigraphy of China.

FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES, Edited by Donald G. Mikulic, Illinois State Geological Survey, 615 East Peabody Drive, Champaign, Illinois 61820, Ed Landing, New York State Museum, The State Education Department, Albany, New York 12230, and Joanne Kluessendorf, Weis Earth Science Museum, University of Wisconsin-FoxValley, 1478 Midway Road, Menasha, Wisconsin 54952. New York State Museum Bulletin 507.

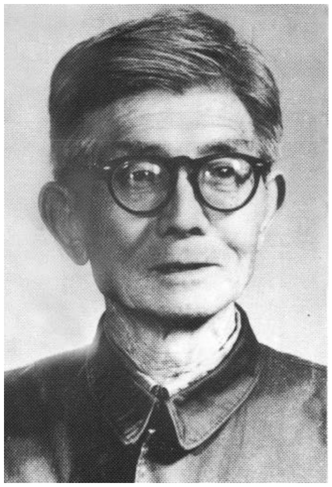

Fig. 1. Professor Sun Yunzhu (Y. C. Sun) (1895–1979) about 1960.

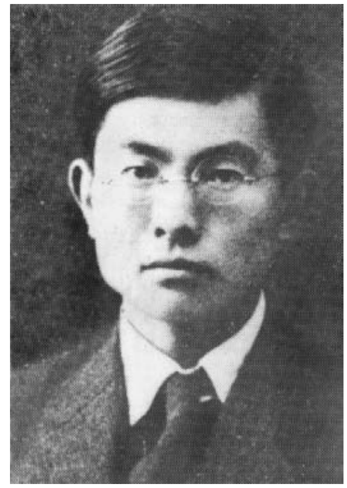

Fig. 2. Sun Yunzhu in 1929, when he was promoted to professor of the National University of Peking.

Sun was born in 1895, the eldest child in a governmental officer's family during the late Qing Dynasty in Gaoyou County, Jiangsu Province. Gaoyou is a famous and historic town, where the first post office in China was set up during the Qin Dynasty (221–206 B. C.), soon after the first emperor unified China from separate warring states. It also may be the oldest post office in the world. Before Sun went to school, he was well educated at home, as his parents thought highly of education (Sun *et al.*, 1995). At age eleven, he went to Nanjing, the capital of the province, for elementary and high school education. In 1914, he entered one of the colleges of Baiyang University in Tianjing, which was upgraded in 1916 to the Mining Department of the university (Wang, 1995). In 1918, he transferred to the Department of Geology of National Peking University to study geology after the university had reopened the department in 1917. The Department of Geology was founded in 1909, but had been closed for seven years. As one of the second year's graduates of the department, Sun finished his university education in June 1920. After his graduation, he was immediately employed by the Department of Geology and joined the teaching staff as the first teaching assistant of A. W. Grabau, who was invited to come to China in 1920. Sun also held a concurrent post in the Geological Survey of China until 1933.

In 1922, Sun was active in founding the Geological Society of China, and became one of its first 26 members. He was twice elected president of the Society (1943, 1952), and was frequently secretary (1924, 1925, 1929, 1931–1934, 1949–1951).

In 1926, Sun was representative of the Chinese government and the Geological Survey of China at the14th International Geological Congress in Madrid, Spain, and submitted the paper "Cambrian, Ordovician, and Silurian of China." This was the first scientific presentation by a Chinese geologist at an international congress in geology, and the paper was well received. At the recommendation of Grabau, Sun was sent to Halle University in 1926, where he studied under J. Walther. During his stay in Germany, he traveled to London to visit W. W. Watts and C. J. Stubblefield at Imperial College in London. Sun received his doctorate at Halle University in 1927; his Ph. D. dissertation dealt with Triassic ammonites. After his return to China in 1927, Sun was employed by Peking University.

When the Paleontological Society of China was founded in 1929, Sun was elected its first president. Sun continued teaching courses, including paleontology, historical geology, stratigraphy, biology, and geology of the world. In 1929, he was appointed professor of paleontology at the Department of Geology of Peking University (Fig. 2).

During the war years of 1937–1945, Peking University was temporarily moved to Kunming, Yunnan Province, and Sun was the head of the Department of Geology as well as the director of the Department of Geology, Geography, and Meteorology of the Southwest Associated University, which was merged with Peking, Tsinghua, and Nankai universities. After the reopening of Peking University in 1946, he continued as director of the Department of Geology until 1952, when he was appointed Superintendent of the Education Bureau under the Ministry of Geology, the State Counsel of China. Sun attended the 18th International Geological Congress in London in August 1948 (Fig. 3), and the meeting of the International Paleontological Association (IPA) during the congress. He was elected Vice-President of the IPA, with his tenure running from 1948 to 1952. In 1950, he joined the Ocean and Lake Society of China, and was elected its first president (Yu, 1995). In 1955, he became an academician of the Chinese Academy of Sciences.

In 1956, Sun was appointed deputy president to the Chinese Academy of Geological Sciences (formerly deputy director of the Institute of Geology, Ministry of Geology). He held this position for 23 years until his death on January 6, 1979, at the age of eighty-four. During this time, Sun established the paleontological section for the Academy of Geological Sciences by inviting some well-known paleontologists from other institutions in China and employing young graduates as well. Through his efforts, the paleontological section of the academy become the second largest paleontological research institution in China after the Nanjing Institute of Geology and Palaeontology (Xiang and Hou, 1995).

Sun was always kind, generous, and helpful, and was con-

Fig. 3. Sun Yunzhu (center) and other Chinese participants at the 18th International Geological Congress, London, 1948.

Fig. 4. Sun Yunzhu (center, front row) and students from the Beijing College of Geology investigating geology in the Yangtze Gorge area in 1956.

sulted and respected greatly by all his colleagues and students. As his first assistant, Sun established a particularly close friendship with Grabau. When Sun (1924) published his monograph on Cambrian trilobites of north China, Grabau hosted a party at his home to celebrate the first paleontological monograph by a native Chinese. On the tenth anniversary of his arrival in China, Grabau (1930) published a report on the progress of Chinese paleontological research during the previous ten years. In it, he placed a high value on Sun's scientific achievements. Following Grabau's death in 1946, Sun (1947) edited a special issue of the Bulletin of the Geological Society of China to commemorate Grabau.

As an outstanding paleontologist and stratigrapher, Sun Yunzhu was a pioneer in the research of paleontology and stratigraphy of China. He made significant achievements in his primary research on trilobites and Paleozoic stratigraphy. Sun (1937) completed the first litho- and biostratigraphic framework of the Cambrian with three series, five formations and nine trilobite zones for the North China Platform, which was later developed into a standard scale for the Cambrian of China. Sun published nearly 100 papers. In addition to his trilobites, his interests and contributions extended into Ordovician and Silurian graptolites; Lower Paleozoic echinoderms; Devonian corals; Devonian, Permian and Triassic ammonoids; stratigraphic principles; and geotectonics. Beside those on trilobites, his monographs include two on graptolites and one on corals. Sun's (1961) "Problem of classification of the Cambrian System in China" subdivided the North China Platform Cambrian into 10 stages and 20 zones.

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LU YANHAO (1913–2000)

Biographical notes

Lu Yanhao (Fig. 5) was an outstanding trilobite paleontologist and stratigrapher, who pursued trilobite research as his lifelong work and achieved an excellent national and international reputation.

Lu Yanhao was born in Kanshi, Yongding, Fujian Province, on April 16, 1913. His grandfather and father were teachers. He began his education at age four at a private school owned by his grandfather, and then at an elementary school at Kanshi in Yongding. He entered Yingding Junior High School at fourteen, and Ligong High School in Fuzhou, the capital of Fujian Province, in 1930 (Pan, 2000). After graduation from high school in 1933, he was accepted at three universities. He chose the Department of Geology at the National Peking University (Fig. 6), where A. W. Grabau, Li Siguang (J. S. Lee), Ding Wenjiang (V. K. Ting) and Sun Yunzhu were teaching geology and paleontology. Lu Yanhao graduated from the department in 1937 with a B.Sc. He joined the teaching staff as a teaching assistant in the Department of Geology on his graduation, and was sent to a coal field in Cixian, Hebei, to investigate the geology. Soon after Lu and his colleagues began their field work, the Japanese launched a war against China.

With the occupation of the Japanese Army of northeastern and northern China, Lu and his colleagues abandoned their investigation and returned home to Fujiang. During this time, Peking University temporally moved to Kunming, and merged with Tsinghua University of Peking and Nankai University from Tianjing to form the Southwest Associated University in April 1938. After Lu heard the news, he traveled from Fujiang on the east coast to Kunming, Yunnan, in southwest China, to join the teaching staff. On his arrival, he was employed as an assistant to Sun Yunzhu, director of the Department of Geology, Geography, and Meteorology, and he began to teach geology and paleontology. Under the influence of Sun who worked on trilobites, Lu chose trilobite research for his lifelong work.

Fig. 5. Lu Yanhao (1903–2000), about 1981.

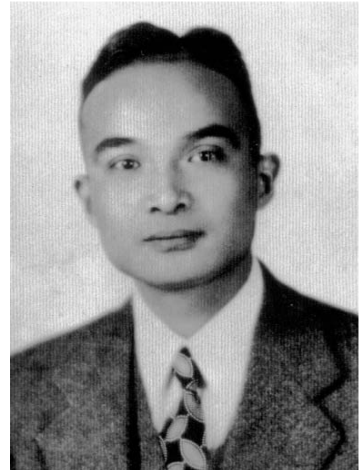

Fig. 6. Lu Yanhao in his youth, about 1935.

During the Second World War, from 1937 to 1945, Lu undertook fieldwork around Kunming, and conducted studies on Cambrian stratigraphy and trilobites in southwest China. Lu (1939) published his first paper "Ontogeny of *Ptychoparia szechuanensis*," which initiated research on trilobite ontogeny in China, and published (Lu, 1941) the "Lower Cambrian stratigraphy and trilobite fauna of Kunming, Yunnan." By studying the details of the Cambrian of Yunnan, Lu made a radical change in the stratigraphy set up by the French geologist J. Deprat. Lu's Lower Cambrian trilobite succession formed the basis for the standard of Chinese Lower Cambrian biostratigraphy.

In 1941, Lu Yanhao was employed by the Geological Survey of China. The survey had been moved to Chongqing in Sichuan Province, the temporary capital of China during the war years. In the following years, Lu undertook geologic investigations in the Qinling and the Dabashan Mountains, a then desolate and uninhabited mountainous region with dangerous wild animals, and made a large collection of trilobites. In 1945–1946, the Chinese government sent him as a visiting scholar, to the United States, where he spent his time at the Smithsonian Institution and the Unite States Geological Survey and visited a number of geological institutions and universities. These include the laboratory of the Shell Oil Company, the University of Chicago, the New York State Geological Survey, the State University of New York in Albany, Yale University, and the Buffalo Museum of Natural History. He also went on a field trip to examine the Paleozoic of the Appalachians of Tennessee. On his way home to China, he visited E. Blackwelder at Stanford University.

Soon after his return, he was employed as a researcher by the Geological Survey of China, which had moved back to Nanjing, then the capital of China, and he began to edit the journal "Dizhi Lunping" (Geological Review). During the late 1940s, he continued his trilobite research, but extended his interest to fossil charophytes, and published several papers on them. This research made him the first charophyte worker in China, and filled in the research gap on this fossil group. For his work on trilobites and charophytes, he won the V. K. Ting Prize from Academia Sinica in 1947, then the highest scientific award in China.

In the second half of 1947, Lu contacted Chinese paleontologists in an effort to reestablish the Palaeontological Society of China. Because of his efforts, the society held its first meeting since the end of the war in December 1947. At this meeting, Lu was elected Council Member of the Society, and at a meeting in 1948, a member of the Standing Committee of the Society.

In 1951, Lu was appointed deputy director of the Nanjing Institute of Geology and Palaeontology, the Chinese Academy of Sciences, a post that he held for 34 years. During his tenure, he was in charge of the scientific research at the institute, and expanded its staff from eleven to about 300 paleontologists. He was an energetic leader—his enthusiasm affected all who worked with him. He was always cheerful and welcomed by his colleagues and students. Although his administrative duties were burdensome, he achieved great success in his own research. For a long time, he was concurrently engaged as a professor by Peking University and Nanjing University, and gave lectures on paleontology, especially on trilobites. He was active in organizing the Geological Society of China, the Palaeontological Society of China, and the All-China Stratigraphical Commission. He was elected the deputy president of the Geological Society of China (1969–1996), the president of the Palaeontological Society of China (1984–1989), and the deputy president of All-China Stratigraphical Commission (1959–1999).

Beginning in 1952, Lu studied the Ordovician trilobites of central and southwest China, and completed the work over twelve years. In 1965, Lu and four of his colleagues compiled the important atlas "Trilobites of China", which comprised two volumes with 776 pages and 135 full-page plates.

While reading the proofs for his monumental work, "Ordovician trilobite faunas of central and southwestern China," the "Cultural Revolution" began, and political unrest made it impossible to publish the book. From 1966 to early 1974, Lu Yanhao was forced to stop doing research. Scientific research began to return to normal in 1974, and Lu had the opportunity to finish his proof on Ordovician trilobites. Lu *et al.* (1974) were also able to publish "Bio-environmental control hypothesis and its application to the Cambrian biostratigraphy and palaeozoogeography" (Li, 2000). In this latter paper, Lu divided the Chinese trilobites into three major types, and explained that the distribution of each type was controlled by or closely related to

Fig. 7. Lu Yanhao collecting trilobites at Lunshan, Nanjing Hills, Jiangsu Province, in 1981 (Photo by Shanchi Peng).

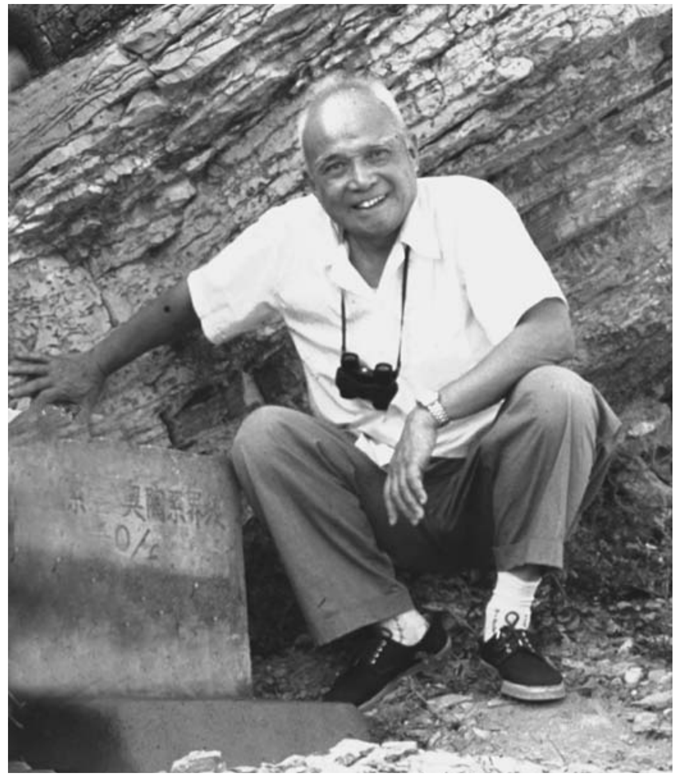

Fig. 8. Professor Lu Yanhao seated on the Cambrian–Ordovician boundary at Wushan, Lulong, Hebei, north China, in October, 1983, during the post-symposium field trip of the International Symposium on the Cambrian–Ordovician and Ordovician–Silurian Boundaries. (Photo by Shanchi Peng).

the environment in which they lived. In 1975, his work "Ordovician trilobite faunas of central and southwestern China" was finally published. It comprised large (787 x 1092 mm) pages, was written in Chinese and English, and contained 50 full-page plates. This book described 187 species of trilobites collected from 33 localities. It remains the most thorough report on Ordovician trilobites in China.

In 1980, Lu was elected an academician of the Chinese Academy of Sciences when the membership of that organization returned to normal following a 23 year suspension. He was also named a member of the International Subcommission on Ordovician Stratigraphy and of the Cambrian–Ordovician Boundary Working Group in the 1980s (Fig. 7).

In 1983, Lu organized the International Symposium on the Cambrian–Ordovician and Ordovician–Silurian boundaries in Nanjing, and its field trips to Hebei, Zhejiang, and Hubei Provinces (Fig. 8). The symposium was the first international conference on geology in China after the "Cultural Revolution." Lu was also the chairman of the Organizing Committee of the Second International Congress on Paleoecology in Nanjing (1991).

In 1997, Lu became seriously ill, and finally lost most of his mental faculties. After lengthy treatment in a hospital in Nanjing, he died on February 20, 2000, at the age of 87.

Lu's scientific career was remarkable in many ways. For his excellent work and great contribution to science, he received eleven awards, including four State Natural Science Prizes, and seven prizes in natural sciences from the Chinese Academy of Sciences and local governments.

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THE EARLIEST TRILOBITE RESEARCH (ANTIQUITY TO THE 1820S)

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ABSTRACT—Trilobite research before the 19th century centered principally on attempts to link trilobites to a living group of organisms. Early naturalists suggested trilobites had affinities with marine fish, bivalved mollusks, chitons, certain sea slugs, and various arthropods, such as decapods, isopods, limulids, and some branchiopods. Disarticulated trilobite pygidia were often misidentified as shells of coarsely-ribbed bivalves from the 1710s to the 1770s. A variety of designations for this group of fossils was used from the earliest 1700s into the 1820s, but Johann Ernst Immanuel Walch's term "trilobite", proposed in 1771, emerged as the most preferred name.

INTRODUCTION

Trilobites are among the most conspicuous and well-known Paleozoic fossils. They are well documented in a corpus of literature that includes thousands of reports. Humans have been aware of trilobite fossils for at least 15,000 years, and first documented them about 1700 years ago. A logical break-point between "classical" and "modern" trilobite studies probably took place around 1820. The early 1820s mark the beginning of a dramatic increase in trilobite publication frequency, as well as the appearance of key taxonomic monographs. Close to 90 references are known that illustrated, mentioned, or focused on trilobites before 1822. Not unexpectedly, the overwhelming majority of these works are European, while a few are Chinese, and only one is American (M'Murtrie, 1819). Most of the classic trilobite literature treated these fossils as novelties, as many fossils were during the 1600s and 1700s. Some late-1700's or earliest-1800's works were taxonomic in nature, and only a few 18th century naturalists wrote extensively on the inferred biology and lifestyle of trilobites. Early discussions on trilobite biology were hampered in part by a prolonged debate about what modern group of organisms trilobites represented. They were variously regarded as mollusks or arthropods. The duration of this debate reflected the belief that extinction had not taken place through time and the perception that trilobites had an unusual combination of morphologic features (see Kihm and St. John, this volume). The debate about their taxonomic relationships was expected to be solved by the eventual discovery of living trilobites. Although this expectation went unfulfilled, disagreements diminished after the 1770s as their interpretations as mollusks became rarer.

ANCIENT KNOWLEDGE ABOUT TRILOBITES

Trilobites are known from some archeological sites. The best documented occurrences are in France, Utah, British Columbia, and Northern Australia. Specimens of a dalmanitid trilobite, probably *Ormathops*, and the ptychoparioid trilobite *Elrathia kingii*, have been reported with drill holes. These specimens were apparently used as charms or amulets or pendants.

The probable *Ormathops* specimen (Fig. 1) was found in the 1880s from a ca. 15,000 year-old, late Paleolithic site in Yonne, central France (Oakley, 1965, 1985; Chlupác, 2000; Henry, 2001). This discovery was the inspiration for naming the site the "Trilobite Grotto." The trilobite is worn, which prevents identification of the species and its provenance. Several earlier reports indicated it was *Zeliszkella hawlei* (formerly *Dalmanites hawlei*) derived from central Germany (Salmon, 1889; Oakley, 1965, 1985; Rudkin and Barnett, 1979). Re-examination indicates that it is a Middle Ordovician zeliszkelline dalmanitid likely from the lower Loire River Valley area of northwest France or the Morvan Mountains of central France (Chlupác, 2000; Henry, 2001).

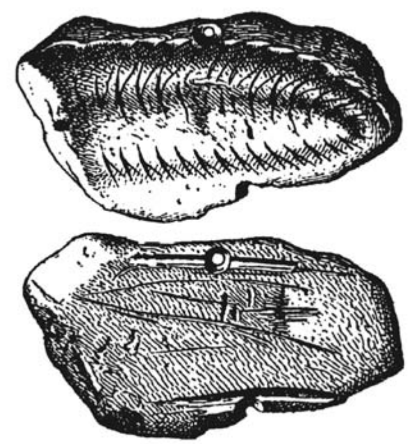

Fig. 1. Drilled for use as a pendant, this worn Ordovician zeliszkelline dalmanitid trilobite from "Trilobite Grotto," Yonne, France, was found associated with ca. 15,000 year-old artifacts (from Salmon, 1889, fig. 280).

FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES, Edited by Donald G. Mikulic, Illinois State Geological Survey, 615 East Peabody Drive, Champaign, Illinois 61820, Ed Landing, New York State Museum, The State Education Department, Albany, New York 12230, and Joanne Kluessendorf, Weis Earth Science Museum, University of Wisconsin-FoxValley, 1478 Midway Road, Menasha, Wisconsin 54952. New York State Museum Bulletin 507.

A similar pendant, consisting of a drilled *Elrathia kingii*, was discovered in the early 1900s in the Sevier Valley of west-central Utah at a Pahvant Ute Indian burial of undetermined age (see Beckwith and Pickyavit, 1939; Beckwith, 1947, 1975; Taylor and Robison, 1976; Kennedy, 1976; Oakley, 1985). *Elrathia kingii* is a late Middle Cambrian trilobite common in the nearby House Range. Historically, Pahvant Ute tribespeople used *Elrathia* specimens for protection, and named them "lizard foot bead things" and "like a little water bug in a stone house" (Taylor and Robison, 1976). This suggests that they recognized trilobites' affinities with arthropods. Whether prehistoric tribes also related trilobites to animals is unknown.

Other reports of trilobites in archeological sites or as artifacts include an external mold of a complete late Middle Cambrian ptychoparioid, *Lyriaspis alroiensis*. This specimen occurs on the surface of a worked chert implement found in the Barkly Tablelands, Northern Territory, Australia (Etheridge, 1919; Whitehouse, 1939; Oakley, 1965, 1985). The age of the implement is undetermined, and it was transported only about 5 kilometers from the inferred outcrop of its origin (see Whitehouse, 1939). In Canada, a specimen of the early Late Cambrian aphelaspid trilobite *Labiostria westropi* was recovered with points, scrapers, and knives at an archeological site along the Fraser River in southwest British Columbia. This species is currently known only from a site along Tanglefoot Creek in southeastern British Columbia, about 450–500 kilometers east of Fraser River. The specimen appears to have been transported by early native(s) sometime in the last 2000 to 5000 years (Ludvigsen and Pugh, 1995; Chatterton and Ludvigsen, 1998; Ludvigsen, 1999, 2003; Nisbet, 2003).

Several works of ancient literature mention fossils (e.g., Marsh, 1879; Adams, 1938; Needham, 1959; Edwards, 1967; Thompson, 1988; Mayor, 2000). However, the oldest recorded works devoted entirely to fossils appear to be by the Greek philosopher Theophrastus (ca. 372 to ca. 287 B.C.), the famous pupil of Aristotle. Theophrastus apparently wrote two books on fossils titled *Peri ton Aithoumenon* ("On Petrifactions"), but both are lost, likely by mishandling and careless storage of Aristotle's and Theophrastus' combined libraries (Hicks, 1925; Jaeger, 1963; Eichholz, 1965; Fortenbaugh *et al.*, 1992). Whether either book mentioned trilobites is, of course, unknown. Surviving works by Theophrastus contain a few passages that mention vertebrate fossils.

From very early times, the Chinese were well aware of fossils, including trilobites, although the first taxonomic descriptions of Chinese trilobites did not appear until the late 19th century (Dames, 1883). Trilobite-bearing limestones from the uppermost Middle Cambrian Kushan Formation of northeast China have been known for over 1700 years. These limestones have abundant, well-preserved sclerites of *Drepanura*, *Liostracina*, *Stephanocare*, *Teinistion*, and other trilobites (Monke, 1903; Woodward, 1905; Sun, 1924; Zhang and Jell, 1987; Sun, 1989). The long, curving spines at the anterolateral corners of *Drepanura* pygidia inspired a comparison with flying bats (Fig. 2A), and led to the term "batstones" for *Drepanura*-bearing limestone slabs (Chang, 1921, 1927; Kobayashi, 1942; Needham, 1959; Oakley, 1985; Xia and Wang, 1996). Batstones have long been sold and used as decorative pieces and inkstones in China. Kushan Formation batstones are mentioned in the oldest written reference to trilobites, a 4th century A.D. commentary in a Chinese dictionary (Guo, ~300 A.D.; Needham, 1959; Xia and Wang, 1996). Some trilobite material from these limestones has been referred to as "stone silkworms" (Liu and Ma, ~970 A.D.; Chang, 1921, 1927). This term apparently referred to the annulated appearance of the axial lobes of trilobites when the pleural lobes are obscured in matrix.

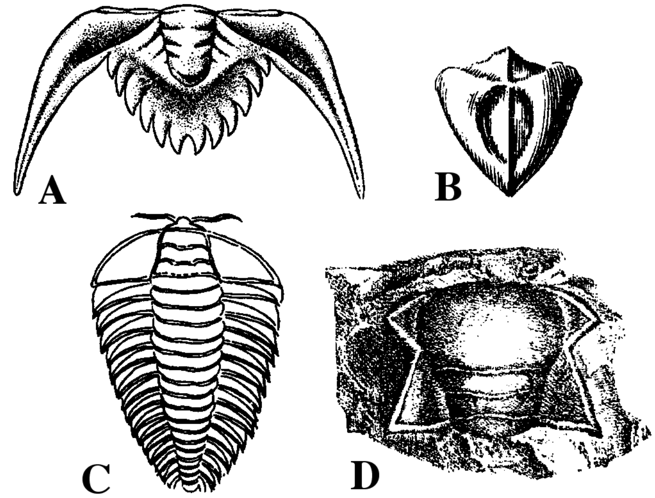

Fig. 2. A, Pygidium of *Drepanura* from the Kushan Formation, uppermost Middle Cambrian, Shandong Province, North China. *Drepanura*-bearing limestones were traditionally called "batstones" (from the Geological Survey of China logo on the cover of Sun, 1935). B, Anterior view of a bivalve internal mold, considered by some early naturalists to be a trilobite tail (from Lange, 1708, pl. 39, fig. 7). C, Late Cambrian olenid trilobite from Sweden, originally called *Entomolithus paradoxus*; the anterior cranidial border was originally identified as preserved antennae (from Linnaeus, 1759, pl. 1, fig. 1). D, Paradoxidid cranidium from the Middle Cambrian Jince Formation, Czech Republic, originally called *Entomolithus incognitus* (inverted and slightly modified from Born, 1775, pl. 3, fig. 6; external shadow lines omitted).

The earliest European literary reference to trilobites is possibly in Albertus Magnus' work *Mineralia* (~1260s). Albertus Magnus' book includes descriptions and occurrences of various rocks and minerals. His discussions of "borax" and "nusae" refer to "toadstones." Toadstones were often described as jewels found in the heads of toads or as pictures of toads in stones. They probably included fossil shark teeth, ray teeth, neopterygian fish teeth, and concretions (e.g., Plot, 1676, p. 128, pl. 7, fig. 8; Pennant, 1769, p. 9; Page, 1865, p. 121; Bandy and Bandy, 1955, p. 143; Wyckoff, 1967; Oakley, 1975; Kennedy, 1976). Wyckoff (1967) speculated that Albertus Magnus' reference to stones with pictures of toads could be a description of trilobite-bearing concretions, based on the presence of bumpy heads and bulging eyes in some trilobites, especially phacopides.

THE SEVENTEENTH CENTURY

Few books before the seventeenth century contain illustrations of fossils (Su Sung, 1070; Munsterus, 1550; Encelius, 1551; Gesner, 1565; Bauhin, 1598; Imperato, 1599), but they became increasingly common after the mid-1650s (see compilation by

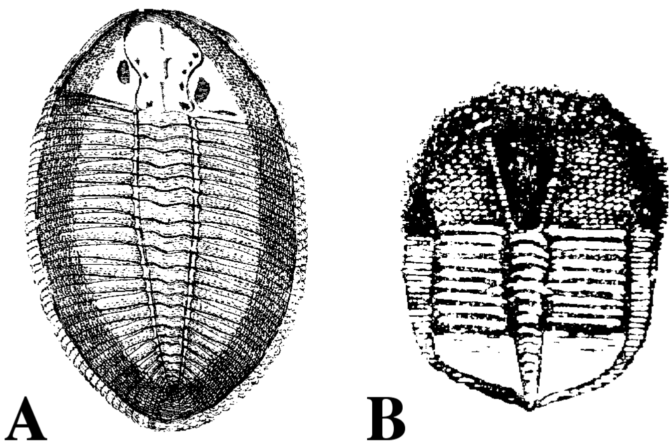

Fig. 3. Earliest illustrations of trilobites. A, Ordovician asaphid *Ogygiocarella debuchii* from southern Wales, originally identified as the skeleton of a flatfish (slightly modified from Lhwyd, 1698, fig. 15; matrix surrounding original figure has been omitted). B, An Ordovician trinucleid from southern Wales, originally termed *Trinucleum fimbriatum* (from Lhwyd, 1699, pl. 23).

Edwards, 1931, 1967). Of the several "protogeological" works published in the 1600s, only three are known that mention, describe, or illustrate trilobites. In North China, the Kushan Formation "batstones" from the Taishan area of Shandong Province were mentioned by Wang Shizhen (1689). Edward Lhwyd (1698, 1699) first illustrated trilobites in a short journal article and a book titled *Lithophylacii Britannici Ichnographia*, (Fig. 3).These illustrations featured late Middle Ordovician material from southern Wales: a complete *Ogygiocarella*, a trinucleid cephalon and complete exoskeleton, and a cybeline cranidium (for locality information see Owens, 1999). Lhwyd did not recognize the arthropod nature of his trilobite material, and interpreted *Ogygiocarella* as a flatfish (Lhwyd, 1698, 1699, p. 96). He stated that none of these fossils represented once-living animals ("not that I conclude that either these, or any other Marine-terrestrial Bodies, were ever really, either Parts or *Exuviæ* of Animals", Lhwyd, 1698, p. 279, 280). This view reflected a then-popular, but not universal, notion that fossils formed within rocks by various processes (Gunther, 1945; Eyles, 1947; Roberts, 1989; Hellyer, 1996). A few original fossils from Lhwyd's collections have been identified and preserved in museums (Gunther, 1945). Two *Ogygiocarella* specimens (a near-complete exoskeleton and a pygidium) housed in the Oxford University Museum of Natural History have been identified as possible Lhwyd specimens (Eliza Howlett, personal communication, 2006). The existing near-complete exoskeleton cannot be confidently identified as one of Lhwyd's figured specimens (Lhwyd, 1698, fig. 15; 1699, pl. 22, fig. 2; 1760, p. 101, pl. 22, fig. 2).

TRILOBITES AS FOSSIL MOLLUSCS

During the 18th century, several publications illustrated and described trilobites. Isolated trilobite sclerites were frequently found, but they were not regularly recognized as parts of a larger organism until about the 1750s and 1760s. Sometimes trilobite remains were not even recognized as biogenic (Tilas, 1740, p. 208, pl. 2, fig. 22; see Regnéll, 1949, p. 53; Hedberg, 1988, p. 87, 88, 94). Two main opinions emerged among naturalists about the affinities of trilobites: 1) trilobites represented a group of mollusks, and 2) trilobites represented a group of arthropods. Most of the pro-mollusk opinions were based on incomplete material, typically isolated trilobite pygidia. Occasional pro-mollusk arguments appeared even after the complete trilobite body plan was widely understood.

Although the oldest known published figures of trilobites included complete specimens (Lhwyd, 1698, 1699), isolated pygidia were usually misidentified as coarse-ribbed bivalves in the early- and mid-1700's literature. The bivalve interpretation appears to have begun with Leonhard Hermann's (1711, p. 214, pl. 9, fig. 50) figure and intepretation of an encrinurid pygidium in gray limestone as a trilobed bivalve shell: "Pectunculites marmoreus trilobus imbricatus in medio dorsi punctatus, & striis exiguis per transversum notatus." Hermann depicted this encrinurid tail in and inverted position and alongside a brachiopod, which was also identified as a variety of coarse-ribbed bivalve (Fig. 4A). Hermann also identified trilobite cranidia as "Echinites" (Fig. 4B, 4C), but apparently had no reason to conclude they were parts of a larger organism. Trilobite tails, and sometimes complete enrolled trilobites, were referred to as trilobed shells by later authors (Woltersdorff, 1748, 1755; Baumer, 1763; Klein, 1770; Zeno, 1770; Lindacker, 1791), typically without much discussion, and under such Latin or German designations as *Conchites trilobus*, *Trigonella striata*, *conchae rugosae trilobae*, cockatoo-shell, or beetle-shell (Fig. 5A).

More complete trilobite material that included outstretched specimens prompted Johann Gentzmar (1751, 1752, 1771) and Father Joseph Torrubia (1754) to conclude that trilobites had affinities with chitons (i.e., polyplacophoran mollusks) (Fig. 5B,

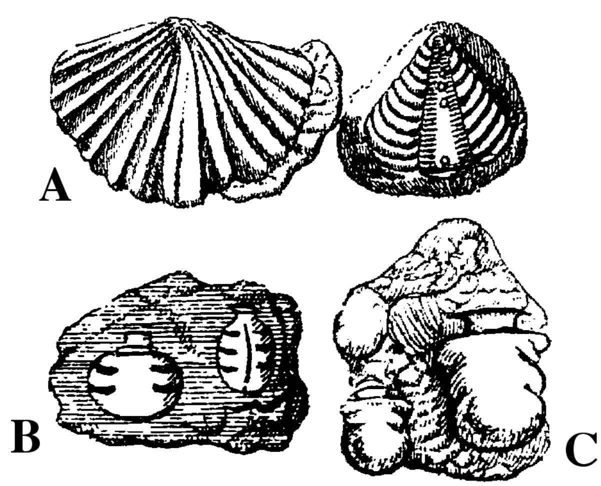

Fig. 4. Trilobites figured by Leonhard Hermann. A, Brachiopod and inverted encrinurid trilobite pygidium, both originally identified as varieties of the bivalve *Pectunculites* (from Hermann, 1711, pl. 9, fig. 49, 50). B, Inverted trilobite glabella, originally called a variety of *Echinites* (from Hermann, 1711, pl. 11, fig. 44). C, Inverted calymenid glabella, originally identified as a variety of *Echinites* (from Hermann, 1711, pl. 12, fig. 31).

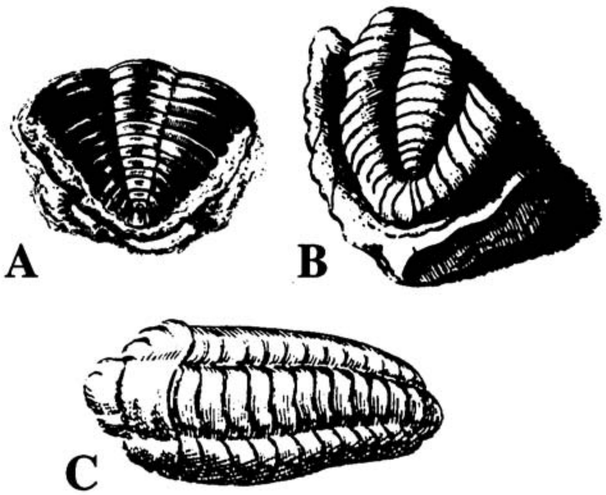

Fig. 5. Trilobite material identified as fossil molluscs. A, Early Silurian *Odontochile* pygidium from Prague, Czech Republic, originally identified as a "Cacadumuschel" or "Käfermuschel" ("cockatoo-shell" or "beetle-shell") (from Zeno, 1770, pl. 1, fig. 1). B, Partial thorax and pygidium of an undetermined trilobite (from Gentzmar, 1751, fig. 4). C, Outstretched trilobite identified initially as a stone crab or crayfish, and afterward as a chiton (from Torrubia, 1754, pl. 3, fig. 4).

5C). After comparing Spanish trilobites with fossil decapods from China's Hainan Island, Torrubia (1754, p. 83, pl. 3, fig. 4) initially interpreted trilobites as crabs or crayfish in his *Aparato para la Historia Natural Española*. However, the plate captions of this book note that the trilobites are actually comparable with the *Limax Marina* figured by Rumphius (1705, pl. 10, fig. 4), a modern *Acanthopleura* polyplacophoran (see Beekman, 1999).

The chiton interpretation was revived later by the early 19th century naturalist Pierre Latreille (1817) in the last serious attempt to demonstrate trilobites had affinities with mollusks. Latreille (1817) noted that trilobites could be classified in a position between myriapod and crustacean arthropods. However, he was deeply troubled by the lack of appendages in any trilobite fossil. Thus, he later concluded that trilobites are better considered as allied to chitons or as the ancestral stock that gave rise to mollusks and arthropods (Latreille, 1821, 1831).That other contemporary naturalists still held onto the chiton view in the early 1800s was acknowledged by Göran Wahlenberg (1818, p. 18), apparently based on the imperfectly articulated and imbricated segments in some trilobite specimens.

An intriguing variant of the trilobites-as-mollusks interpretation was proposed by Johann Gottlob Lehmann (1756) who identified isolated trilobite pygidia as shells of sea hares (Fig. 6). Sea hares, or anaspidean opisthobranch gastropods, sea slugs that have a pair of rabbit-ear shaped extensions on the head and a reduced, slightly asymmetrical, cap-shaped, internal shell. These shells vaguely resemble some trilobite pygidia, although they lack the strong furrowing commonly seen on most trilobite tails. After acquiring complete, outstretched trilobite material, Lehmann (1766) realized that his supposed fossil sea hare shells were actually the posterior portions of an arthropod.

The occasional referral of genuine mollusk material to trilobites probably aided in prolonging the arthropods vs. molluscs debate. Some 18th and 19 century workers identified a bivalve internal mold figured by Carl Lange (1708) as a trilobite pygidium (Fig. 2B; see Baumer, 1763; Burmeister, 1843, 1846). Others considered that the descriptions and illustrations of some coarsely-ribbed mollusk shells published by Johann Jacob Scheuchzer (1702, p. 46, fig. 66; 1716, p. 82, no. 759; 1718, p. 316, no. 759, fig. 132) referred to trilobites. Johann Gentzmar (1751, p. 292) pointed out the potential for confusion of some non-trilobite fossils that were described as a "trilobed shell" or "trilobed conch." For example, some brachiopods were figured and described as "Conchæ Anomiæ striatæ triloba Columnæ" by Georg Helwing (1717, p. 74, pl. 9, figs. 9–11).

Other early "mollusk" interpretations of trilobite material were regarded by later authors with a hint of incredulousness and ridicule (see Walch, 1771; Parkinson, 1811). For example, a pygidium-like object from Lancashire, England was depicted by Charles Leigh (1700, p. 192, pl. 7, fig. 1), and identified as a piece of a *Nautilus*. Francis Brückmann (1730) had complete, enrolled calymenid specimens from northeast-central Germany (Fig. 7), but regarded them as remains of marine polyps or of some unknown marine conch-bearing animal. Walch (1771) was perplexed by this identification, due in part by use of the term "polyp" for a wide variety of organisms in the 16th to 18th centuries. Although "polyp" is now usually associated with cnidarian terminology, the designation was often applied to cephalopods (nautiloids, octopods, teuthids, and sepiids) before the 1750s. Brückmann (1737) later figured additional trilobite material, including an isolated encrinurid tail that he described as a marine bivalve shell, and trilobite glabella described as petrified insects or scarabs.

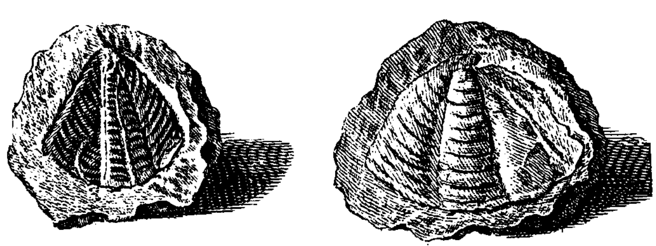

Fig. 6. Inverted trilobite pygidia originally identified as the shells of sea hares, or anaspidean opisthobranch gastropods (from Lehmann, 1756, pl. 1, fig. A, B).

Fig. 7. Cephalic and pygidial views of an enrolled calymenid trilobite, originally described as a "sea polyp" (from Brückmann, 1730, pl. 2, fig. 6).

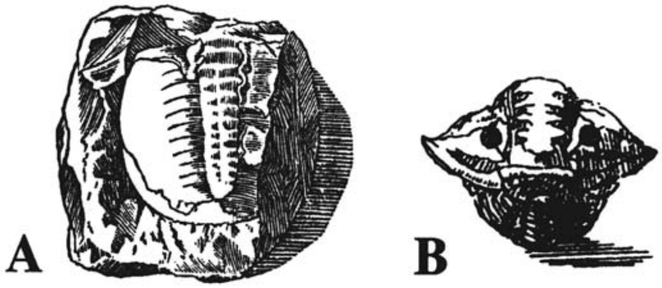

Fig. 8. Trilobites figured by early Swedish naturalists. A, Pygidium of Ordovician *Megistaspis* from eastern Sweden, originally called a petrified marine crab (from Roberg, 1715, fig. H). B, Enrolled Silurian calymenid, likely from Götland, Sweden (from Swedenborg, 1717, unnumbered figure).

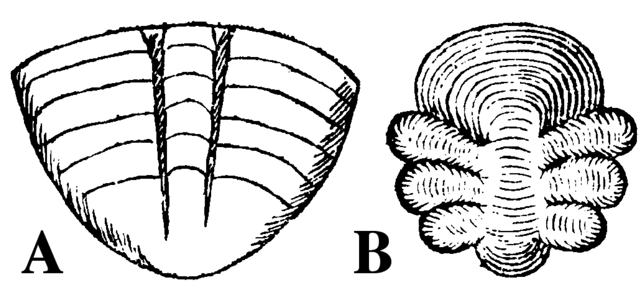

Fig. 10. Trilobite material figured by Carl Linnaeus. A, Pygidium of Ordovician *Megistaspis* from Öland, Sweden, originally compared with an "Echini valve" (from Linnaeus, 1745, p. 147). B, Middle Cambrian paradoxidid glabella from Västergötland, Sweden (from Linnaeus, 1747, p. 88).

TRILOBITES AS FOSSIL ARTHROPODS

Early Swedish naturalists were familiar with trilobites (Fig. 8A, 8B, 9; Roberg, 1715; Swedenborg, 1717; Bromell, 1729, 1739, 1740), and apparently published the first conclusions about trilobites' affinities with arthropods. In Lars Roberg's travel journal and in his treatise on crustaceans, an Ordovician *Megistaspis* pygidium from eastern Sweden is identified as a petrified marine crab (Fig. 8A; Roberg, 1715; Vogdes, 1893; Wiman, 1905; Regnéll, 1949; Reyment, 1973). Beginning the 1720s, Magnus von Bromell described his collection in fifteen articles. In addition to figuring and discussing various fossil plants, corals, mollusks, bryozoans, and graptolites, Bromell also illustrated Swedish trilobites (Fig. 9). Bromell had olenid, asaphid, nileid, and agnostoid material, and illustrated the olenids, *Olenus* and *Peltura*, and a block of *Agnostus pisiformis* packstone (Bromell, 1729, 1739, 1740; Regnéll, 1949; Reyment, 1973, 1974). Most of Bromell's trilobites are still preserved at the University of Uppsala (Reyment, 1973, 1974). Bromell's trilobite descriptions referred to them as "stone insects from Scania and Götland." "Insects" was a pre-19th century umbrella term for arthropods. He more identified his *Peltura* specimens as the remains of scarabs or beetles or small butterflies and his *Agnostus* specimens as small vaginipennous (i.e., beetle-like) and crustaceous, worm-like insects.

The great 18th century Swedish naturalist Carolus Linnaeus (or Carl Linné and Carl von Linné; born Carl Oldenberg) is best known for his zoological, botanical, and nomenclatorial contributions to science. The bulk of the Linnaeus' studies focused on living plants and animals, but he also engaged in geological field work and the study and description of rocks, minerals, and fossils (Nathorst, 1907, 1909; Regnéll, 1949). The earliest of Linnaeus' publications that illustrate trilobites do not include much speculation about their affinity. Linnaeus (1845) figured a large *Megistaspis* pygidium from Öland, Sweden, and noted its similarity to an "Echini" valve (Fig. 10A). A few years later, Linnaeus (1747, p. 24) described agnostoids in petroliferous concretionary limestone ("stinkstone") from the Gösätter Farm in Västergötland, Sweden, and identified them as impressions of coleopteran insects (beetles). This 1747 report also contains illustrations of polymeroid trilobites, including a large paradoxidid glabella (Fig. 10B). Linnaeus (1751, p. 121, 122) also identified some olenid trilobites from Andrarum, southern Sweden, as coleopteran insects, while Andrarum agnostoids were likened to compressed peas.

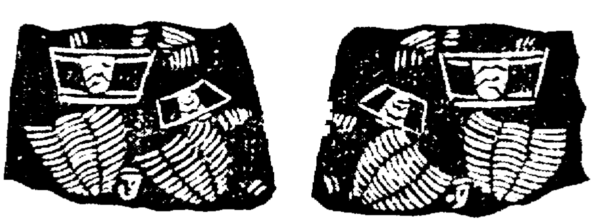

Fig. 9. Late Cambrian *Olenus truncatus* from the Alum Shale Formation at Andrarum, Scania, Sweden, originally identified as stone scarabs (from Bromell, 1729, p. 496, fig. b).

In the late 1740s to early 1750s, the beginnings of the Industrial Revolution resulted in increased quarrying at many localities in Great Britain. Some excitement developed with the discovery of well-preserved, complete Silurian calymenid trilobites, particularly *Calymene blumenbachii*, from quarries in the Much Wenlock Limestone at Dudley, England (Fig. 11). Calymenids from the Dudley area were given such names as "Dudley fossils," "Dudley locusts," and "Dudley bugs." Charles Lyttelton (1752) collected some of these Dudley fossils in 1749 and 1750, and illustrated them (Fig. 11A). He refrained from discussing trilobite affinities, apart from referring to them as "non-descript petrified Insect[s]." But Lyttelton did point out that earlier "fossilists" saw this type of fossil as representing a bivalve or an "eruca", an early term for a caterpillar or larval insect (e.g., Bauhin, 1598, book 4, p. 214; Brander *in* Davila and Romé de l'Isle, 1767, p. 204, 205). Cromwell Mortimer (1752) immediately followed up Lyttelton's short note with a morphological description of the Dudley calymenids (Fig. 11B), and proposed that trilobites were covered during life with beetle-like elytra. Mortimer was particularly impressed with similarities between the Dudley trilobites and the trilobed bodies of notostracan branchiopods, as illustrated by Jacob Klein (1741, pl. 1, figs. A-C; copied from Frisch, 1732, pl. 1, figs. a-c). Notostracans, or tadpole shrimp, have a moderately convex axial lobe under their carapace that is reminiscent of the trilobite thorax. Klein

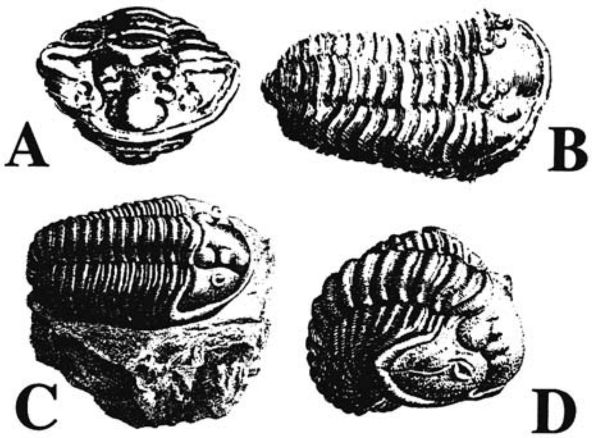

Fig. 11. *Calymene blumenbachii* from the Much Wenlock Limestone (Silurian), Dudley, England. A, Enrolled specimen (from Lyttelton, 1752, pl. 1, fig. 3). B, Outstretched specimen (from Mortimer, 1752, pl. 1, fig. 9). C, Outstretched specimen (from Blumenbach, 1800, pl. 50). D, Partially enrolled specimen (from Blumenbach, 1800, pl. 50).

called his notostracans *Scolopendram Aquaticam Scutatam*, and Mortimer suggested that the Dudley trilobites were "petrified animals having affinities with *Scolopendræ aquaticæ scutatæ*."

After more Dudley material became available, Emanuel Mendez da Costa (1754, 1755) confidently identified trilobites as belonging to a "crustaceous animal, of that kind called *Pediculi marini*." *Pediculus* is now known to be a genus of terrestrial phthirapteran insects, or lice. During the 1700s, names close to *Pediculus marinus*, or "sea-louse," were applied to various marine organisms, including isopod crustaceans and polyplacophoran mollusks. However, it appears that Mendez da Costa was referring to isopods (Burmeister, 1843, 1846). The Dudley calymenids were considered so significant that figures of them were added to the updated edition of Edward Lhwyd's (1760, p, 101) *Lithophylacii Britannici Ichnographia* a half-century after Lhwyd died. High quality illustrations of Dudley calymenids also appeared in Walch (1771) and Blumenbach (1800) (Fig. 11C, 11D).

While the term "Dudley fossil" was applied to trilobites in England, Linnaeus (1753) introduced "*Entomolithus paradoxus*", or "paradoxical stone insect," for Swedish trilobites. This 1753 work is titled *Museum Tessinianum*, and was a descriptive catalog of a collection of fossils and minerals owned by Count Carl Gustav Tessin. Linnaeus' system of binomial nomenclature was applied to all of the geologic objects described from the Tessin collection. Thus, *Entomolithus paradoxus* appears to be earliest Linnaean-style scientific name applied to a trilobite. *Entomolithus* was actually proposed much earlier for fossil crabs in Linnaeus' (1735) first edition of *Systema Naturæ*. The binomial name *Entomolithus paradoxus* was originally intended for all trilobites, and Linnaeus figured a calymenid pygidium and a large, complete Middle Cambrian paradoxidid as examples (Fig. 12). The name "*Entomolithus paradoxus*" later became more closely associated only with the paradoxidid. The original paradoxidid specimen, found at Dimbo in Västergötland, Sweden, still exists, and is preserved in the Mineralogical Museum of the University of Copenhagen, Denmark (Nathorst, 1907, pl. 2; Levi-Setti, 1993, pl. A10; Nielsen and Jakobsen, 1993, 1995, fig. 2). This paradoxidid trilobite has been sometimes been referred to as *Paradoxides paradoxus* (Linnaeus, 1753), although the name is invalid for modern nomenclatorial purposes since it predates 1758. In one of the best examples of taxonomic irony, this oldest named trilobite may actually represent a new species of *Paradoxides* (see Westergård, 1953; Bergström and Levi-Setti, 1978). However, a formal, modern name for "*Paradoxides paradoxus*" is probably not warranted on several grounds. Indeed, its glabella form is obscured by crushing and a strong impression of the underlying labrum, and, secondly, a thorough systematic reevaluation of the 143 or so named species and subspecies names of *Paradoxides* sensu lato should be done before new names are proposed for less-than-ideal material.

Olenid, encrinurid, and phacopide trilobite material was described and figured under the umbrella name of *Entomolithus paradoxus* by Linnaeus (1759). Among the figures is a remarkable illustration of an olenid trilobite with what appears to be a pair of antennae (Fig. 2C). Linnaeus identified these structures as antennae, but subsequent trilobite workers were divided over whether his identification was correct (see Törnquist, 1896a, b; Beecher, 1896; Nathorst, 1907, 1909; Regnéll, 1949; Bergström and Yochelson, 1991). Linnaeus suggested that the inferred antennae proved trilobites' affinities with arthropods. He also surmised that trilobites represented a separate arthropod group close to crabs, isopods, and "monocules", an early term for horseshoe crabs, and small branchiopod crustaceans. Although Linnaeus was correct in concluding that trilobites were antenna-bearing arthropods, Walch (1771), Brünnich (1781), and Beecher (1896) demonstrated that the supposed antennal structures were the anterior cranidial border. This was not the only early misidentification of appendages in trilobites. Linnaeus (1753) described the thoracic pleural lobes of "*Paradoxides paradoxus*" as legs (Fig. 12), which helped fuel confusion over the identification of trilobites as arthropods or chiton-like mollusks (see Walch, 1771).

The earliest potentially available scientific names for trilobites appeared in the "Stone Kingdom" volume of the 12th edition of Linnaeus' (1768) *Systema Naturæ*. Linnaeus (1768) briefly described an asaphid, an olenid, and an agnostoid as three subspecies of *Entomolithus paradoxus*: *E. p. expansa*, *E. p. cantharidum*, and *E. p. pisiformis*. None of these named taxa is available for use in modern nomenclatural schemes. The International Commission on Zoological Nomenclature (1954, Opinion 296) ruled Linnaeus' (1768) designations as invalid due to irregularities among the fossil brachiopod names in the work. The third of Linnaeus' subspecies names carried over into modern trilobite taxonomy as the name of the "type agnostoid trilobite" *Agnostus pisiformis* (St. John, 1997).

An extensive discussion of everything then known about trilobites was provided by Johann Ernst Immanuel Walch (1771) (Kihm and St. John, this volume). Walch was a philologist and a theologian by training, but undertook studies of many fossils during the 1760s. He is principally credited for formally proposing the term "trilobite." Walch (1771) also summarized all the arguments of the mollusk-versus-arthropod debate about trilobite affinity. He agreed with Linnaeus and other earlier naturalists that trilobites were undoubtedly arthropods, despite

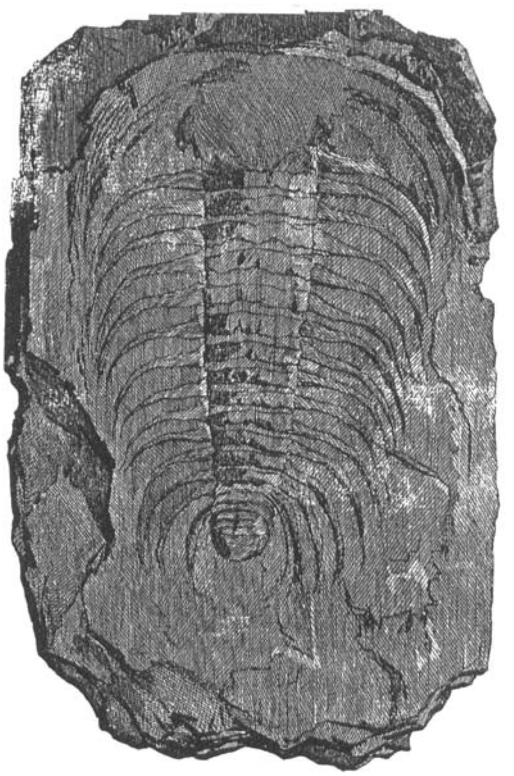

Fig. 12. Complete specimen of a Middle Cambrian paradoxidid from Västergötland, Sweden, originally named *Entomolithus paradoxus* (from Linnaeus, 1753, pl. 3, fig. 1); the pleural lobes were initially identified by Linnaeus as appendages.

their superficial similarity with chitons, and that isopods probably represent the closest living forms (see also Beckmann, 1773; Martin, 1809). Few serious considerations of the trilobites-as-mollusks view appeared after Walch's contribution.

Many other names were in use during the mid- to late-1700s, and there was some initial reluctance to use Walch's term "trilobite" for these fossils (but see Brünnich, 1781; Gehler, 1793). *Entomolithus paradoxus*, or just *Entomolithus* and its variant *Entomostracites*, continued to be used to refer to most trilobites (Fig. 2D; Born, 1775; Schmidt, 1795; Blumenbach, 1800; Martin, 1809; Wahlenberg, 1818). By the 1810s, "trilobite" was more widely used (Schlotheim, 1810; Parkinson, 1811; Desmarest, 1816, 1817; Latreille, 1817). A noticeable increase in publications on trilobites occurred after about 1820 (see list in Burmeister, 1846, p. viii). This coincided with the end of turmoil in mainland Europe from the French and Napoleonic Wars. Examination of this new literature suggests that "trilobite" was universally accepted by the late 1820s, with the exception of Johann Wilhelm Dalman (1827, 1828). He suggested that "palæades" should replace "trilobites," because a trilobed body does not occur in all specimens of this fossil group. Indeed, Dalman noted the weakly impressed axial furrows in the Ordovician trilobite *Nileus*.

The monographs of Göran Wahlenberg (1818) and Alexandre Brongniart (1822) essentially marked the beginnings of a trilobite literature with modern taxonomic importance. Only a few minor works of modern taxonomic significance appeared before this (e.g., Brünnich, 1781; Martin, 1809; Desmarest, 1817). An increasingly significant portion of the trilobite literature after Wahlenberg's and Brongniart's publications was taxonomic. The notion that trilobites were a group of crustaceans was predominant from the 1820s onward, a view that persisted well into the 20th century.

CONCLUSIONS

Several aspects of the history of trilobite research before the 19th century parallelled the history of discovery of some problematic fossil organisms in the 20th century. A key point of discussion for early naturalists was whether trilobites had affinities with mollusks or arthropods. Many modern studies have focused on the problems of determining phylogenetic positions for peculiar fossil metazoans, particularly from Konservat-Lagerstätten. Advances in understanding the biology and phylogenetic relationships of such problematic Cambrian organisms as *Microdictyon*, anomalocaridids, and halkieriids depended on the discovery of complete and articulated specimens (Whittington and Briggs, 1985; Chen *et al.*, 1989; Conway Morris and Peel, 1990, 1995). Separate parts of anomalocaridids were traditionally identified as entire organisms, and attributed to shrimp, sea-cucumbers, sponges, and jellyfish (e.g., Whiteaves, 1892; Walcott, 1911; Conway Morris, 1978; Collins, 1996). Individual pieces of complex, multicomponent fossil organisms are not always initially recognizable as such. This was a problem in the study of trilobites in the early 1700s, and continues to be a problem for scientific study some small shelly fossils and the often extraordinary, nonmineralized fossil organisms from Konservat-Lagerstätten. The temptation is there for modern paleontologists to chuckle slightly at such early naturalists as Hermann, Lehmann, Torrubia, and Latreille for interpreting trilobites as clams, sea slugs, or chitons, just as one might upon recalling the once seriously held and widespread view that the Earth was flat, or that earthquakes were caused by ignition of underground deposits of naturally-occurring explosives. Science discards those ideas shown to be wrong. However, some historians of science remind us that it is not entirely appropriate to pass harsh judgment upon past naturalists and scientists whose opinions are now known to be incorrect. The early views of naturalists about the affinities of trilobites should remind modern workers about the risks of making incorrect and premature phylogenetic conclusions based upon insufficient characters.

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NIGHTMARE ON RESSER STREET—DEALING WITH RESSER'S TRILOBITE TAXONOMY

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ABSTRACT— Charles Elmer Resser (1889–1943) was an influential Cambrian paleontologist who worked at the Smithsonian Institute, first as an assistant to Charles Doolittle Walcott in 1914 and then in various curatorial positions from 1915 until his death. During his career, Resser discussed over 1400 Cambrian trilobite taxa, including over 900 new species and 100 new genera. He disliked using a suprageneric classification in his papers, and believed that more species needed description before a meaningful classification could be undertaken. Resser used any variation in diagnosing his new species, including that resulting from ontogeny, normal biological variation, preservation, and tectonic deformation. Compounding the problems generated by using any source of variation, Resser often provided poor descriptions and used poor or no photographs. He commonly used only one or two specimens or poorly preserved material. These practices were not typical of trilobite workers of this time. Most of Resser's species, and specifically his type species, need to be reevaluated to determine if they should continue to be recognized or be placed in *nomina dubia*.

Resser was one of the most productive Cambrian workers of his time. Due to his taxonomic practices and influence on other workers, we presently have difficulties understanding the phylogeny and diversification history of Cambrian trilobites. Given the importance of trilobites in the Cambrian fauna, this further inhibits our understanding of the Cambrian explosion and the early modes of evolution.

INTRODUCTION

Charles Elmer Resser (Fig. 1) was an intriguing person. If you read Howell's (1944a) memorial to Resser, you would think that he was second in Cambrian studies to only Charles Doolittle Walcott and that he was as highly respected. However, this is not the case.

Curators are confounded by Resser's procedure of gluing new labels over old (Walcott) labels, and his practice of removing type specimens from their proper location to a new location in the type collection or into the biological or stratigraphic collections. Trilobite workers curse his oversplitting of taxa, poor or lack of illustrations, poor descriptions, and the use of poorly preserved or single specimens. Rumors suggest that Resser never went into the field, and believed that any specimens found 40 km (25 miles) apart had to be a different species, and that he named the same specimen twice. Who was this man?

RESSER'S BACKGROUND

Charles Elmer Resser was born to George M. and Sallie Resser on April 28, 1889, in East Berlin, Pennsylvania (for details of his early life, see Howell, 1944a). As a child, he was interested in the fossils that occurred in the area where he lived, and later he decided to study natural science. He attended Blue Ridge College in Maryland, where he met Anna Mae Evans. After he graduated at age 19, Resser married Anna Mae on July 18, 1908. He then attended Penn State Teachers College, where he became a student of H. Justin Roddy. He graduated with a Bachelor of Pedagogy in 1912. Roddy introduced Resser to Walcott and Gilbert Van Ingen of Princeton University. At Roddy's urging, Resser attended Franklin and Marshall College, and a year later he received his B.A. degree. He then entered the graduate program at Princeton University, where he met fellow graduate student and lifetime friend Benjamin F. Howell. Resser left Princeton after one year.

In 1914, an event occurred that changed the nature of Cambrian taxonomy for years to come; Charles Doolittle Walcott offered a position to Charles Resser. Resser, now 25, accepted and, became an assistant to Walcott (Fig. 1). On April 1 Walcott noted in his diary that Resser was being hired (E. L. Yochelson, personal communication, 2001).Yochelson (personal communication, 2000) has also suggested that it was Raymond S. Bassler, Curator of Stratigraphic Paleontology at the Smithsonian and a bryozoan and ostracod expert (Fig. 2), who suggested the hiring of Resser. This opinion was based on Bassler hiring a most unsatisfactory field assistant for Walcott in 1912. In the course of the correspondence connected with the firing of this earlier field assistant, Walcott told his correspondent in Washington, D.C., to tell Bassler he would have to try again (Yochelson, personal communication, 2001).

Bassler and Resser were at least close colleagues if not friends. Bassler arranged for Resser to finish his masters at

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Fig. 1. Charles Elmer Resser at the Smithsonian Institute, ca. 1925 (Bassler Collection, Smithsonian Institute).

George Washington University (GW) in Washington D.C., which he did in 1915. Bassler also supervised Resser's Ph.D. dissertation, which was completed only two years later in 1917, also at GW. Bassler also accompanied Resser and his son during the Rocky Mountain field season during Summer 1927 (Resser, 1928a). Resser's and Bassler's photographic collections include photographs of each other and of them together.

Resser worked for 29 years (1914–1943) at the Smithsonian. Only one year after joining the staff, Resser became an Assistant Curator of the Division of Paleobiology. In 1923, he became the Assistant Curator of the Division of Stratigraphic Paleontology; in 1924, an Associate Curator; and in 1929, a Curator of Paleontology and Paleobotany, the position he held until his death.

In addition to his work at the museum, Resser was also an educator, initially teaching as an Instructor, then as an Assistant Professor at GW from 1915 to 1931. He also taught at the University of Maryland for several years after 1931.

Resser was a religious man. He was president of the Washington, D.C., Sunday School Association, secretary/treasurer of the Church of Brethren, and later (1938) the Chairman of

Fig. 2. Left to right, Charles Resser, Edward O. Ulrich (U.S. Geological Survey Paleozoic Paleontologist), Ray S. Bassler (Smithsonian Curator of Stratigraphic Paleontology, bryozoan and ostracod expert), and Charles D. Walcott (Secretary of the Smithsonian Institute), ca. 1920. (Bassler Collection, Smithsonian Institute).

Fig. 3. Resser in the field. Left to right, C. E. Resser, R. D. Mesler (U. S. Geological Survey, Ulrich's assistant), Irwin Pohl (Paleontological staff, Smithsonian Institute), Charles E. Butts (U.S. Geological Survey), R. S. Bassler, Sarah Evens, Willis Popinot, Gilbert O. Raasch (Assistant Curator, Geology Department, Milwaukee Public Museum), Harry Warner, Alexander Wetmore (Assistant Secretary, Smithsonian Institute), unidentified boy, Captain of lunch, ca. 1926 (Bassler Collection).

the Board of Trustees. Resser was a family man. His wife, Anna, bore him a son, Harold, and a daughter, Helen. Resser loved roses, and one of his last publications was "Very ancient roses" for the *American Rose Annual* (1942, vol. 27, p. 11–15). He was apparently a friendly and generous man, willing to help any scientist wanting to know about the Cambrian or use the museum collections. "He had many warm friends and not a single enemy" (Howell, 1944a, p. 220). Resser died September 18, 1943, at the age of 54, after a short illness.

RESSER'S CONTRIBUTIONS TO SCIENCE

Resser's first documented scientific work is his 1915 master's thesis from George Washington University. This 27-page thesis, *The Stratigraphy and Fauna of the Waldron Shale*, reports on faunas in the Smithsonian collection from a 1–1.5 m-thick Silurian shale unit in Indiana and Tennessee. The thesis has eight pages of discussion, three pages of annotated bibliography, and fifteen pages of taxonomic lists with each species rated as very rare to very common. No thesis committee was mentioned, and no fieldwork was involved.

Resser's next contribution was his 1917 Ph.D. dissertation from GW, the 60+ pages *The Stratigraphic and Geographic Distribution of North American Cambrian Fossils*. For the heart of his dissertation, Resser assembled 3000 cards with the bibliographic summary of Cambrian genera. He did this in his spare time over three years. The first part of his thesis presented information from 500 of the 3000 cards. Other parts included a list of Cambrian genera, formations, and taxa by age/state, and the systematics of the taxa. Perhaps he was the early Jack Sepkoski in his tabulation of the known diversity and distribution of Cambrian taxa.

An interesting aspect of his dissertation was his explanation for the Cambrian Explosion—that the abundant appearance of life in the Cambrian was due to their development in the open ocean prior to the Cambrian. He believed that this earlier record would be preserved in the present deep ocean. He also suggested that the Cambrian was only 1 to 4 million years in length based on the thickness of its stratigraphic units.

There was no fieldwork involved with his dissertation. It was to be published by either the United States Geological Survey or the Geological Society of America, but it never was, nor was it published by the Smithsonian. It is possible that this information was the basis of his Contribution to Cambrian Paleontology series (Resser, 1935, 1936, 1937a, 1938b, 1942b).

Resser published 11 abstracts and 40 papers from 1920 to 1945. A complete bibliography, excluding Resser, 1945, was published by Howell (1944a). It is interesting to note that his first paper was co-authored with Walcott in 1924 (the only paper that Walcott co-authored) on the trilobites from the "Ozarkian" sandstones of Novaya Zemlya, Russia. Resser's next scientific publication was not until 1928, after Walcott's death in February 1927. It has been suggested that there was some professional distance between Walcott and Resser. The absence of Walcott's name in Resser's dissertation and the lack of Resser's publications between 1924 and Walcott's death may support this conjecture. But, if this distance existed, Walcott did not carry it home, for Walcott's widow provided "generous assistance" to purchase a new "motor truck" for "strenuous field-work" for Resser's 1927 summer fieldwork (Resser, 1928a, p. 17).

Resser also worked with other renowned paleontologists and geologists, including C. E. Butts (Fig. 3), C. Diess, R. Endo, T. Kobayashi, B. F. Howell, E. H. McKee, and E. O. Ulrich. Resser published on Cambrian strata, faunas, its time scale, and trilobite life habits. He provided information for the *Index Fossils of North America* (Shimer and Shrock, 1944) and the "Cambrian Correlation Chart for North America" (Howell, 1944b). He named numerous trilobites, brachiopods, hyolithids, "mollusks," and other taxa from the Appalachians, Rocky Mountains, Great Basin, Grand Canyon, Mississippi River valley, China, and other locations. Resser worked with Lower, Middle, and Upper Cambrian faunas.

Resser has been accused of never going into the field, but there are several comments about his field work in the Annual Reports for the Smithsonian Institute (e.g., Wetmore, 1932, 1943). In addition, there are field notebooks in the Smithsonian Archives for Pennsylvania for 1913, 1918, and 1920; Montana for 1914; Virginia, Tennessee, and Alabama for 1923 and 1934; the western states for 1923–1924; and the Rocky Mountains for 1923–24 and 1927–30. Some of the photos in the archives are indeed field shots, but the later photographs after 1930 look like tourist photos taken not far off the road. According to Howell's (1944a) memorial, Resser accompanied Walcott on field trips to the Rocky Mountains (Fig. 4) and Great Basin. The only report of him being in the field with Walcott is during his first year at the Smithsonian (1914) where Walcott (1916) reported Resser and Mrs. Walcott helping collect trilobites in the Rocky Mountains. Resser (1928a) reported going to the Rocky Mountains of Wyoming, Utah, Idaho, Montana, and Alberta with his son and Bassler during Summer 1927. In 1930, he spent four months in the field, and started at the Grand Canyon and then traveled to Delta, Utah (Wetmore, 1932).

Resser also journeyed into the field late in his career (Fig. 5). In May 1941, at age 52, he traveled to Virginia and Tennessee to collect faunas from the Maryville Formation (Resser, 1942a). In 1942, he spent part of the summer in Montana and the Canadian Rockies (Wetmore, 1943). He was accompanied by George B. Maxey, and they visited the Wasatch Mountains in Utah, and then spent a few weeks in the Canadian Rockies. They collected fossils high on Eiffel Peak and traveled the three-mile-long path from Field, British Columbia, which climbs 900 m, to make base camp. From there, Resser followed the trail on the north side of Kicking Horse River to Burgess Pass (Wetmore, 1943). It is unknown whether Resser did this traveling by horse or by foot, but he was still in relatively good health in his early fifties.

It is obvious, based on Resser's comments in various papers, that he obtained most of his trilobites from museum collections and other collectors, although he did visit some of the sites and collected some material (see Resser, 1928a). In 1935, Resser received a Penrose grant from the Geological Society of America for fieldwork in the Appalachians (Resser, 1938c), but many of the specimens came from other collections. Material for the *Olenellus* Zone paper (Resser and Howell, 1938) was derived from museum collections made by Walcott, H. J. Roddy, and others. Given that some of the material came from Resser's old professor, Resser was probably familiar with the localities. The Spence Shale fauna (Resser, 1939a) was probably based on

Fig. 4. Resser at age 34 in the field at Yellowstone, Wyoming, August 21, 1924 (Resser Collection, Smithsonian Archives).

Walcott's collections, although Resser did collect one locality (locality 20x). The "Ptarmiganian" fauna was from Walcott's 1898 and 1906 collections and a private donation from Mr. Roundy (Resser, 1939b), although Resser also reports the same locality (20x) as in his earlier paper. [It is interesting to note that locality 20x in the Ptarmiganian paper consisted of disarticulated specimens in limestone, whereas the same locality in the Spence Shale paper consisted of articulated specimens in shale or sandstone.] The Pend Oreille report (Resser, 1938a) was based on Mr. Sampson's field collections of 1921 to 1924. The Upper Cambrian trilobite fauna (Resser, 1942c) was derived from Walcott's collections. The material for the Grand Canyon fauna (Resser, 1945) was collected by a variety of geologists, but Resser collected at least two localities. In 1930, Resser traveled with Alexander A. Stoyanow (University of Arizona) to Peach Springs and localities near the mouth of Nankoweap Valley. Nankoweap Valley is one of the most difficult and steepest official trails in the Grand Canyon (E. Rose, personal communication, 2001). This horse trail was built under J. W. Powell's supervision in November 1882 so Walcott and his crew could collect fossils in the canyon during Winter 1882 (Yochelson, 1998). The

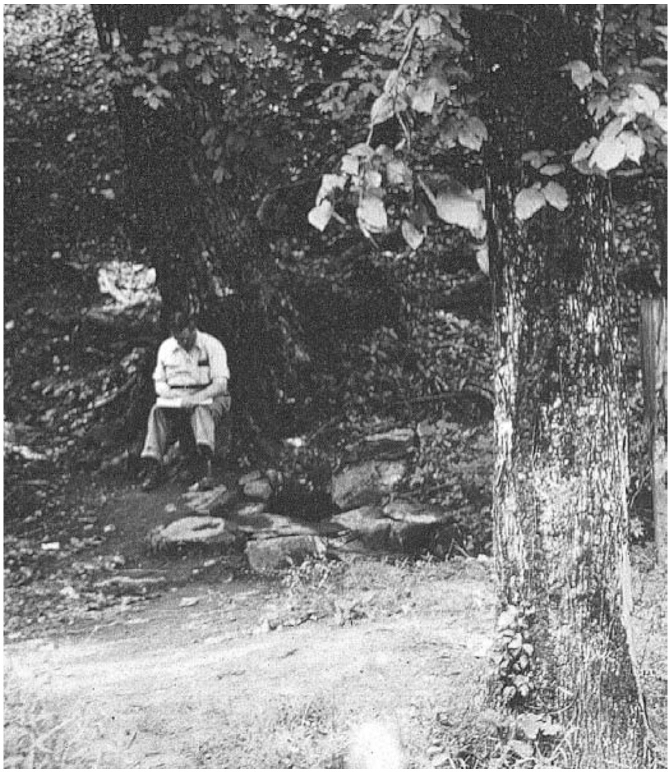

Fig. 5. Resser at age 50 in the field at Herskill, Tennessee, June 28, probably 1940 (Resser Collection).

Table 1. Number of species discussed, reassigned, or named and number of genera named by Resser. "Species discussed" includes all new, reassigned, and/or other species that had some type of information presented about it, including species left in open nomenclature.

Publication Date	Species Discussed	Species Reassigned	New Species	New Genera
1928b	7	2	3	0
1935	120	75	30	14
1936	71	48	18	8
1937a	85	63	21	17
1937b	10	0	10	0
1937c	24	4	13	2
Resser and Endo, 1937	193	12	167	17
1938a	19	0	18	1
1938b	52	28	20	1
1938c	285	22	225	25
Resser and Howell, 1938	36	6	23	2
1939a	53	0	36	3
1939b	75	0	73	3
1942b	143	90	40	2
1942c	205	2	194	5
1945	47	0	32	1
Totals	1425	352	923	101

trail starts at the canyon rim and extends to the Colorado River some 1000 m below. Resser visited the Peach Springs locality again in 1940 at age 51. The Peach Springs locality has relatively easy access.

In summary, Resser did go into the field, although he was not a Walcott-style paleontologist who spent a considerable amount of time collecting and measuring stratigraphic sections. Resser measured no sections, but apparently visited fossil localities and relied on measured sections of such geologists as Walcott, Diess, and Butts, a common practice among paleontologists.

RESSER'S TAXONOMIC PHILOSOPHY

Examples of Resser's taxonomic philosophy can be derived from his publications. He believed that any variation was justification to define a new species. In a personal communication to G. O. Raasch (Fig. 3), Resser "categorically stated that 'trilobites do not vary. If two specimens are different, they represent different species'" (Raasch, 1951, p. 140). Given the number of species named by Resser (Table 1), he apparently took this to heart. His synonymies rarely consisted of two earlier named species that he considered the same. In fact, many of Resser's new species are the result of splitting taxa previously named by Walcott.

Resser's goal was to document as many species as possible to promote a better understanding of taxonomic diversity and to facilitate suprageneric classification and biostratigraphy. He was apparently set on this course by Walcott. Resser (1942c, p. 1; Figs. 6, 7) stated, "In the two years remaining before his death, in 1927, Dr. Walcott set aside some of the specimens here presented, and less than 2 weeks before his passing he urged me to carry on and describe species as rapidly as possible so that they would become available for use." It took 15 years for Resser to follow through on this request. Resser's biostratigraphic and taxonomic intentions are illustrated by the following quote, "Since 1925 there has been increased activity in the study of Cambrian geology. Numerous papers describing many new genera have appeared, but in most cases, they also include only one or two species in addition to the genotype. This situation leaves many of the genera inadequately portrayed and fails to make available the species needed for stratigraphic purposes. Hundreds of undescribed species contained in the National Museum collections need to be described, both to improve the concept of genera and to supply species for stratigraphic work" (Resser, 1942c, p. 1, 2).

Resser obviously believed that numerous species were needed to properly describe each genus. Although he emphasized species for biostratigraphic use, he, in fact, used genera as the essential biostratigraphic tool, and supplemented them with the number of species within a genus (see Resser, 1933, 1938a, 1939b, 1945).

Resser disliked applying suprageneric classifications in his papers. He considered the agnostids as a separate, but related, group to the trilobites (e.g., Resser, 1938c) and the Olenellida as a valid trilobite order (Resser, 1938c, 1942b). Resser (1935, 1938c, 1942c) refrained from placing other trilobites into previously named suprageneric groups. He stated, "Trilobites cannot yet be satisfactorily classified, and to attempt to do so merely adds to

Fig. 6. Left to right, C. E. Resser, R. D. Mesler, Ehrenberg, R. S. Bassler, and E. O. Ulrich. November, 1921 (Bassler Collection).

Fig. 7. Left to right, R. S. Bassler, Riuji Endo (Japanese paleontologist, Educational Institute, Mukden, Manchoukuo), and C. E. Resser in Washington, D.C., ca. 1929 (Bassler Collection).

the confusion now existing" (Resser, 1942c, p. 2). He felt that many more trilobite species needed to be described before a suprageneric classification was warranted. This is illustrated by his (1942b, p. 2) comment, "Today there are still too many undescribed species on hand to warrant the erection of a classification intended to embrace the whole of the class." This attitude mirrors that expressed earlier by his colleague E. O. Ulrich (1929). Resser (1942b) also provided several comments about the suprageneric classifications that did exist. This approach of not using suprageneric taxa was not followed by his contemporaries, who were actively naming suprageneric taxa [e.g., Whitehouse, 1936, 1939; Kobayashi, 1936; Lochman, 1936; including Resser's good friend Howell (1935a, b)]. In fact, at the same time, Resser was inconsistent in his use of suprageneric classifications, as he (Resser, 1937b) placed new taxa into the family Conocoryphidae. In his Spence Shale publication (Resser, 1939a), he provided suprageneric classifications (families), and later (Resser, 1942c, p. 79) named the new family Burnetidae.

Rumor has it that Resser believed that no trilobite species ranged over a distance greater than 40 km. Thus, any specimen found 40 km from another congeneric specimen had to be a new species. A survey of Resser's (1938c) publication on Appalachian faunas, suggests that this is an overstatement, but not by much. Of the 261 ptychopariid and corynexochid species discussed, only 25 species (9.6%) were reported from two or more localities. Only twelve species (4.6%) were reported from localities greater than 40 km apart. For five of these twelve species, his published information says that the species is known from "…other localities in…" Alabama or Tennessee. I am assume that these localities are separated by at least 40 km, but this may be incorrect.

Resser may have believed that widely separated specimens *could not* be conspecific. In his publication *Fourth Contribution to Nomenclature of Cambrian Fossils*, Resser (1938b, p. 43) proposed the new species *Tonkinella kobayashi* for specimens from Korea, because the name *T. breviceps* Kobayashi, 1934, was used by Kobayashi (1935) "…previously used for a species in Kashmir [India]" (Resser, 1938b, p. 43). No other justification was given. Sundberg (1994) and Jell and Hughes (1997) synonymized several *Tonkinella* species, including *T. kobayashi* with *T. breviceps*, which is now recognized from Newfoundland, the Appalachians, the western United States, Korea, Kashmir, and Russia.

Resser's belief that taxa have limited geographic ranges resulted in his once using the same species name twice. *Elvinia utahensis* was originally named by Resser (1938b) based on a specimen from the Dugway Range, western Utah. Resser (1942c) later reused the name for a different specimen from Blacksmith Fork in the Bear River Range, eastern Utah. [Both species are considered synonyms of *E. roemeri* by Palmer (1960).] If Resser had believed that species could have broad geographic ranges, then he would have checked his own publications for taxonomic comparison, and would have discovered that the name had been already used.

RESSER'S CAMBRIAN WORK

Resser was one of the most productive Cambrian workers of his time, and generated a large volume of work. However, he is known for his oversplitting of taxa, providing poor or no illustrations and poor descriptions, and using tectonically distorted, poorly preserved, single, or juvenile specimens. These problems hinder the use of Resser's work.

Oversplitting taxa

Resser was an extreme taxonomic splitter. Chang and Jell (1987, p. 186) used the phrase "over zealous" to describe some of Resser's splitting. He would construct new taxa based on small differences among specimens from the same stratigraphic horizon. This was common among paleontologists of the time. For example, Ulrich and Bassler (1931) named thirteen species of the bradoriid *Walcottella* from the Grand Canyon. They reported all thirteen species from a single locality, which was the type locality for eleven of these species. In contrast, the over-splitting of trilobite taxa by Resser and Endo (1937) was recognized at the time by Kobayashi (1941a, c).

Resser may have learned the art of splitting from Ulrich (Figs. 2, 6). Ulrich was a U.S. Geological Survey employee who moved to Washington, D.C., in 1901 (Bassler, 1953), where he became an associate paleontologist at the Smithsonian. Thus, Resser and Ulrich would have first met when Resser arrived in 1914. Resser and Ulrich worked together naming new trilobites from the Midwest, first in 1924 (Ulrich and Resser *in* Walcott, 1924), and then in two monographs (Ulrich and Resser, 1930, 1933) in which they named 123 species. In addition, during Summer 1924, Resser and Ulrich spent two months touring the important Lower Paleozoic outcrops in Europe (Wetmore, 1926). Raasch (1951) made many of the same comments about the quality of Ulrich and Ressers' work, as noted above. Raasch reduced the number of taxa recognized in the two monographs to about one-third. For example, Ulrich and Resser (1930) recognized 26 species of *Dikelocephalus*, which Raasch reduced to eight species. Labandeira and Hughes (1994; Hughes, 1994) later re-analyzed this group with the use of museum collections, additional field collections, and morphometrics. Consequently, Hughes (1994) synonymized all 25 species named by Ulrich and Resser with *D. minnesotensis*.

How much did Resser split? There is no one synopsis of Resser's species and their present standing. However, Chang and Jells' (1987) review of the Chinese Cambrian trilobites in the Smithsonian gives us a modern analysis of Resser and Endos' (1937) taxonomic work. Riuji Endo (Fig. 7) was a Japanese paleontologist at the Educational Institute at Mukden, "Manchoukuo" (the name for Japanese-occupied Manchuria), who worked on the Cambrian stratigraphy and faunas of China. Resser and Endo (1937) reported 193 trilobite species from the Cambrian of China, of which 167 (87%) were new (Table 1). Chang and Jell (1987) reviewed 186 (96%) of these species, and concluded that 78 species (40 percent) were *not* correctly assigned and that 108 (56%) were "valid." Nineteen of these "valid" species were named prior to Resser and Endo (1937). Therefore, of the new species named by Resser and Endo, only 89 (53%) were considered valid by Chang and Jell. This suggests that the number of trilobite species named by Resser and Endo was inflated by 100%. Furthermore, of these 89 "valid" species, 41 were named from damaged, weathered, and/or one or two specimens (Chang and Jell, 1987).

Elvinia, *Irvingella*, and *Pterocephalia* are other examples of taxa oversplit by Resser. Resser (1937a, 1938b, 1942c) assigned eleven species to *Elvinia*. Palmer (1965) reassigned all of them to *E. roemeri*, including the original type lot used by Shumard (1861) that Resser split apart. Resser (1942c) recognized 23 species of *Irvingella*, but Palmer (1965) assigned eighteen of these to *I. major*, two to *I. flohri*, and three to *I. angustilimbatus* (also see Frederickson, 1949, and Gaines, 1951). Resser (1938b) assigned seven species to *Pterocephalia*, all of which were referred to *P. sanctsabae* by Palmer (1965).

Resser probably had a very strong influence over Poulsen (1927), Endo (Part III *in* Resser and Endo, 1937), and Diess (1939). These authors also generated a high number of synonymous species in their publications.

Poor illustrations

Charles Resser was known for his outstanding photography, and some of his photographs were excellent (e.g., Resser, 1939a, b, 1942c). I even found a three-page manuscript by Resser (not dated) in the Smithsonian Archives on how to photograph trilobites. However, in his 1938 publication on the Cambrian faunas of the Appalachians, many of the trilobite photos are so small that the printing screen is coarser than some of the diagnostic features. I specifically remember trying to identify the key morphological features of *Tonkinella appalachia* Resser (1938c, p. 8, fig. 36) with a handlens and saw the print screen clearer than the morphological features. It was not that larger printing of the photographs was impossible, at least technologically. For example, Resser (1938c) illustrated the holotype of *Rimouskia typica* twice, once at x2 (pl. 3, fig. 21) and another at x4 (pl. 3, fig. 22). The larger photo is much clearer.

Resser's (1938a) paper on the fossils from Pend Oreille Lake, Idaho, provides another example of poor illustrations. The single 4 by 7-inch plate contains 58 figures of 25 species of hyolithids, brachiopods, and trilobites, 24 of which were new. The illustrations are at either x2 or x4 magnification, and most are nearly useless. A similar example can be seen in Resser's (1937c) paper on the fossils from Labrador and Vermont.

Why the limited photograph size? A brief survey of the contemporary literature on trilobites (Mansuy, 1916; Poulsen, 1927; Saito, 1934; Whitehouse, 1936, 1939, 1945; Kobayashi 1937, 1941a, b, c, 1942) illustrate a range in photographic magnifications from x1 to x6. Most photographs are x1 to x3. Thus, Resser may have been following the standard magnification of the time. However, only Poulsen (1927, e.g., pl. 17, figs 2, 3, 7, 12, 25, 28, 29) produced postage stamp size photos similar to those of Resser's photographs.

No illustrations

Perhaps Resser's most "important" publications were his five *Contributions to nomenclature of Cambrian fossils* (1935, 1936, 1937a, 1938b, 1942b), which consisted entirely of the re-analysis of earlier published material. In these publications, Resser named 129 trilobite species and 42 genera, and reassigned 304 species (Table 1) without a single illustration or photograph. Although the reassignment and splitting of some species were necessary, Resser only referred to previous lithographs of Walcott's and other turn-of-the-century paleontologists. In the first paper of the series, Resser (1935, p. 2) stated, "For the sake of lowering publication cost illustrations are omitted from this article, even though they would be desirable, particularly since most papers describing Cambrian fossils are now out of print." Josiah Bridge of the U. S. Geological Survey had Resser's papers bound and on the spine was "Contribution to the confusion of nomenclature" (Yochelson, personal communication, 2001).

Resser was unique in not providing an illustration of a new species. A brief survey of the contemporary trilobite literature produced only one publication (Raymond, 1920) where no illustrations were provided, even though new species were described.

Poor descriptions

One of my favorite descriptions discovered while preparing this paper was that for *Kootenia troyensis*. For this new species, Resser (1937a, p. 17) stated, "The illustrations, *poor as they are*, show the specific difference of this species in *size*, contour, and width. *It may* have scattered granules on the test." [my italics]. The illustrations referred to are of *Solenopleura*? *nana* Walcott (1891, [sic. 1890] pl. 98, figs. 1a, 2; Fig. 8). To base a new species on the poor illustrations of Walcott without refiguring or redescribing the specimen is useless. In addition, the specimen referred to by Resser is a very small cranidium, 3 mm long, and is probably an early holaspid, which does not exhibit the characteristics used to distinguish *Kootenia* species. Resser split this species off from *Kootenia nana* (Ford), but used only Walcott's specimens for comparison (Ford's specimens could not be located; Resser, 1937a, p. 16). *Kootenia nana* and *K. troyensis* are from the same locality. Resser (1937a, p. 17) states about *K nana* that, "Unfortunately, the lectotype [which Resser assigned] is an imperfect specimen, for which reason reference of the specimen subsequently described from Washington County to the species must remain somewhat doubtful. The pygidia illustrated in 1891 show two species, but whether the difference is merely one of drawing cannot now be determined, since one specimen cannot be found." Although the type of *K. nana* is too poorly preserved to allow comparison, Resser still proceeded to separate *K. troyensis* based on a juvenile specimen.

Such brief descriptions were not typical of contemporary and earlier trilobite workers. Walcott (1886, 1890, 1916, 1917), Wanner (1901), Barton (1913), Raymond and Barton (1913), Raymond (1916, 1920), Mansuy (1916), Lochman (1936), Whitehouse (1936, 1939, 1945), Poulsen (1927), Saito (1934), and Kobayashi (1937, 1941a, b, c, 1942) generally provided moderate to long descriptions for new species. Brief descriptions for new taxa were not common, and were generally limited to taxa that have strong similarities to other more fully described taxa (e.g., Walcott, 1916; Raymond, 1916, 1920; Walcott and Resser, 1924). Resser did provide better discussions and descriptions for some of his species. For example, Resser (1935, p. 8) provided a full description for *Alokistocare piochensis*. In addition, Resser (1937c) provided extended diagnoses for the new species and more full descriptions in his paper on Upper Cambrian faunas (Resser, 1942c).

As mentioned above, Resser reassigned 304 previously named species to different genera (Table 1). This was indeed needed for many species, but the justification for such transfers was not always provided. For example, Resser (1938b, p. 34) transferred *Conocephalites verrucosus* to *Lonchocephalus*, and provided only an age, location, and type number. There was no comment or justification about the transfer. The lack of information is the same for fourteen of the other 27 species transferred in the same publication.

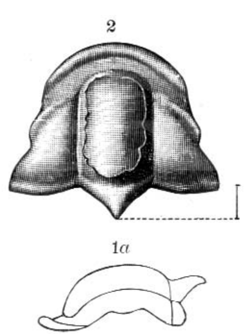

Fig. 8. Walcott's lithograph of *Solenopleura*? *nana* Walcott (1890, pl. 98, figs. 1a, 2), a form that Resser (1937a) assigned to *Kootenia troyensis*.

Poorly preserved or single specimens

One of the most frustrating aspects of Resser's taxonomy was his use of fragmentary, poorly preserved, or too few specimens to name species. This frustration is compounded when he used these new species to define genera. Resser acknowledged that some of his specimens were either poorly preserved or limited in number. For example, Resser and Endo (1937, p. 178) in naming *Aojia punctata* stated, "Two peculiar cranidia, one lacking about half of the brim, hardly suffice for a specific description, but a name is assigned for the purpose of easy reference." In naming *Asaphiscus transversus*, they (p. 183) cited only a single cranidium that was poorly preserved. In naming a new species and genus, *Hsiaella striata*, they (p. 228) stated, "Unfortunately, the single enrolled specimen is rather poor for establishing a new genus, but since it finds no other place it has been given a new name." *Manchuriella prisca* was based on a "…single cranidium compressed in micaceous red shale" (Resser and Endo, 1937, p. 248). The difficulty of using specimens defined on incomplete specimens was recognized at the time. Kobayashi (1941a, c, 1942) commented on the difficulty of using Resser and Endo's (1937) poorly preserved specimens. Chang and Jell (1987) described the type material of 43 species of Resser and Endo, and used phrases such as "small cranidium;" "two specimens;" "internal molds;" "no features are distinctive;" "very poorly preserved;" "badly damaged;" "better left in open nomenclature;" and "the name should be allowed to lapse." Chang and Jell (1987) retained many of the species, but indicated that the species were uninterpretable, and the names should be restricted to the type specimens.

Resser and Howell (1938) also used tectonically distorted specimens to name species. While describing the trilobites from the Lower Cambrian Kinzer Formation, Resser and Howell (1938) recognized seven species of *Olenellus*. Many of the features they used to define species are characters that are easily produced by compaction and tectonic distortion. Campbell and Kauffman (1969) analyzed the deformation of these specimens and reduced the number of species to two.

Two problems arise when poorly preserved or single specimens are used as type material for type species. First, there is no way of assessing the variation of a species based upon one or a few specimens. In turn, if this species is the type species, then it cannot provide a key to the potential morphological range within the genus. Second, when poorly preserved specimens are used for type species, the morphological details are not fully known and this could lead to the assignment of unrelated and morphologically distinct species to the genus. This has an impact on broader evolutionary, biostratigraphic, and taxonomic studies.

An example of the difficulty generated by Resser's practice is *Antagmus*. Resser (1936) reassigned *Ptychoparia teucer* Walcott, 1886, to his new genus *Antagmus* because the name was preoccupied. Resser cited only Walcott's (1886, pl. 26, fig. 3; Fig. 9a)

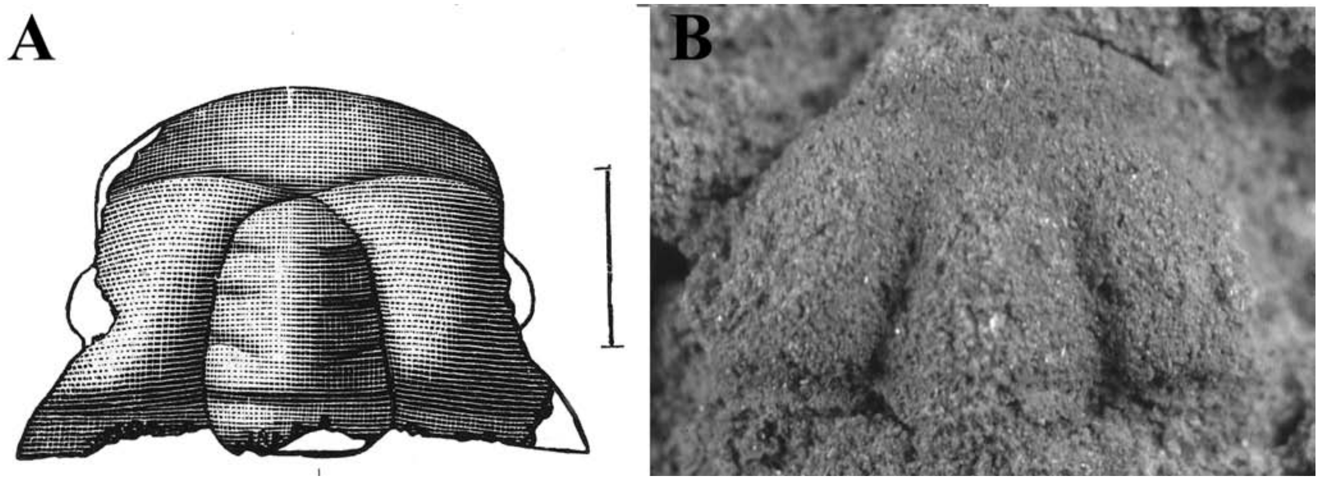

Fig. 9. A, Walcott's original figure of *Ptychoparia teucer* (Walcott, 1886, pl. 26, fig. 3) that Resser (1936) used to establish *Antagmus*. B, The type specimen of *Antagmus typicalis* Resser, 1937c, the type species for the genus. The specimen is a nearly complete, internal mold of a cranidium preserved in a medium grained, friable, limonite-cemented sandstone, x7.0, specimen uncoated.

lithograph. Resser (1937) then reassigned the specimens to the new species *A. typicalis,* and provided a small photograph (x1) of the type specimen (1937c, pl. 8, fig. 64). A larger photograph of the type specimen later appeared in Shimer and Shrock (1944, pl. 253, fig. 6). In the Smithsonian's type collections, *A. typicalis* is represented by a single, incomplete internal mold of a cranidium preserved in a medium-grained, limonite-cemented, friable sandstone (Fig. 9b). Other than the general shape of the cranidium and glabella, this specimen contains little information about the external morphology and, thus, little about the diagnostic morphology of a species that is important in determining phylogenetic relationships. Inspection of the Smithsonian's systematic collections produced some additional cranidia, all more poorly preserved. Librigenae, thoracic segments, or pygidia of the taxon, which can be important in determining phylogenetic relationships (e.g., Palmer, 1965; Sundberg, 1994, 1999), are lacking in the collections. Consequently, *Antagmus typicalis* does not contain characters that can be used to identify the species, or characterize a genus. To add to the problem, *Antagmus* is also the nominal taxon for the subfamily Antagminae Hupé, 1953, which contains 13 genera (Harrington *et al*., 1959), six of which were named by Resser. This example of *Antagmus* is especially poignant because it has been a widely recognized Lower Cambrian trilobite (e.g., Resser, 1945; Lochman, 1947, 1952; Rasetti, 1955; Shaw, 1955; Fritz, 1968, 1972; Chang *et al*., 1980). Because the type species is poorly preserved and the associated sclerites are not known, Sundberg and McCollum (2000) considered *Antagmus* a *nomen dubium*.

Resser is not entirely to blame for these taxonomic problems. Lochman (1947) and Rasetti (1951, 1955, 1957) perpetuated the problems by trying to make sense of Resser's work. Lochman set forth identification guidelines, assigned new species to *Antagmus*, and removed others. Rasetti redescribed and assigned new taxa to *Antagmus* . Rasetti's better material, excellent photographs, detailed drawings, and good descriptions (some included in the *Treatise of Invertebrate Paleontology*) have been used subsequently to identify these taxa (e.g., Fritz, 1972). However, Rasetti's material is not of the type species, and thus is of secondary importance to the generic concept.

Resser and Endo (1937) also defined genera based on type species named from poor material or limited specimens. For example, *Eilura* was based on a single pygidium; *Temnoura* was based on two pygidia, each belonging to a different species; and *Hsiaella* was based on a single enrolled specimen, and it is "…unfortunate that this indeterminate fossil carries a generic name as it is impossible to determine any generic features" (Chang and Jell, 1987, p. 245).

Juvenile specimens

Resser based some species on small specimens, and sometimes used their small size to help define them. *Kootenia troyensis* (Fig. 8), discussed above, is a prime example. Resser paid little attention to morphological changes with growth. This is not to say that he did not recognize protaspids or early meraspids; I have found no example where he had named such specimens. However, *Kootenia troyensis* is either a late meraspid or an early holaspid [given that meraspids and holaspids are defined on the total number of thoracic segments, it is difficult to tell which growth stage is present in disarticulated material]. The cranidium is only 3 mm long, and more mature cranidia are typically 10–20 mm long (e.g., *Kootenia* species discussed by Sundberg, 1994). Kobayashi (1941a, c) commented on Resser and Endo's use of juvenile specimens for new species of *Drepanura* and *Damesella*. Chang and Jell (1987) provided other examples where Resser and Endo (1937) based taxa upon immature specimens.

Plagiura and *Plagiurella* are other examples of where Resser defined taxa, and ignored ontogenetic changes. Resser (1935) proposed *Plagiura* for *Ptychoparia*? *cercops*, which was named by Walcott (1917) for a lower Middle Cambrian trilobite of the Mount Whyte Formation of Canada. Later, Resser (1937a) erected *Plagiurella* for the smaller species, *Ptychoparia cleadas,* also named by Walcott (1917) from the same formation. Lochman (1947, p. 66) recognized that the characters used to define *Plagiurella* were not significant enough to define a new genus.

She synonymized *Plagiurella* with *Plagiura*, and noted, "The type cranidium of this species and several associated cranidia are all smaller than the smallest cranidium of *P. cercops* (Walcott)…" She continued to differentiate the two species based on glabellar convexity, glabellar furrow depth, frontal border convexity, and shorter posterior area of the fixigena. These features change during ontogeny, and Rasetti (1951) with a larger sample concluded that they were one species, *P. cercops*.

IMPACT OF RESSER'S WORK

Resser's taxonomic practices have an impact on our understanding of the early evolution of animal life. To understand this early evolution and later evolutionary events, it is important to understand the phylogenetic relationships of Cambrian organisms. It was during the Cambrian that metazoans became abundant in number and diverse in form. Documenting this diversification and the phylogenetic relationships of the early metazoans is important in detailing the modes of evolution and extinction present during their beginnings and the potential contrasts to these modes recognized in post-Cambrian metazoans (e.g., Jacobs 1987, 1990; Sundberg 1989, 1990, 1995, 2000). However, phylogenetic relationships and even the generic abundance of trilobites, a major clade of Cambrian and post-Cambrian organisms, are poorly known. This is particularly true for the ptychopariid trilobites, which first arose in the Early Cambrian (Briggs and Fortey, 1992) as part of the Cambrian Explosion. They survived other groups of trilobites and became the most common and diverse group in the Middle and Late Cambrian world. These Cambrian ptychopariids were also the ancestors of later trilobites (Briggs and Fortey, 1992).

Thus, understanding the phylogenetics and diversity history of Cambrian ptychopariids is crucial to understanding the evolution of a major Paleozoic group. However, doing analyses based on the present database will generate erroneous results. Why? Because of Resser's poorly defined taxa, other species have been incorrectly assigned.

To promote more accurate studies in the phylogeny and diversity of trilobites, particularly the ptychopariids, all of Resser's species need to be restudied to discern if they are valid, recognizable taxa or if they should be considered *nomina dubia*. If they are not recognizable taxa, then their names should be restricted to the type specimens and removed from consideration in diversity and taxonomic studies. This is particularly true for the type species. Based on the *Treatise of Invertebrate Paleontology* (Harrington *et al*., 1959), Resser named or was a coauthor of 76 ptychopariid genera, of which only four were considered unrecognizable. Reanalyzing Resser's species and type species in studies such as Campbell and Kauffman (1969), Labandeira and Hughes (1994), and Hughes (1994) will be of great assistance in determining the phylogeny of trilobites.

CONCLUSIONS

From all accounts that I have heard and read, Resser was a kind, giving, and helpful man. "Nightmare on Resser Street" refers to my experience dealing with his trilobite work, an experience that other paleontologists have also related to me. Resser's lack of concern whether type specimens were exfoliated, broken, weathered, tectonically distorted, or crushed when he named new taxa has created many named forms that cannot be accurately characterized and differentiated from other related trilobites. He apparently felt that any variation from the type specimens was cause enough to name a new species. This included biological outliers and different growth stages.

Most paleontologists working with his taxa are aware of these problems, but a strong warning needs to be issued to all who try to use Resser's work. It would be wise to not rely on the information provided by Resser unless you have checked it personally or it has been independently checked by a well-documented, modern publication. Even the well-respected Franco Rasetti tried to make Resser's taxonomic schemes work, but this led him and other paleontologists astray.

By using such poor type specimens to name taxa, Resser hindered the progress of determining the phylogeny and taxonomic diversity of Cambrian trilobites, which has frustrated many a trilobite worker. One should not use a Resser taxon without looking at the type material, seriously considering if the criteria that Resser used for defining that taxon are still valid, and recollecting the type localities for larger specimen sets to provide a clearer understanding of the species. Resser was a productive man (Table 1), and now we must systematically reanalyze his taxa to discern what should be considered valid and useful and what should be placed into a black hole (*nomina dubia*) and never seen from again until better material is found. Of course, I am only talking about Resser's trilobites, he also named brachiopods, mollusks, and other taxa.

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REFLECTIONS ON THE CLASSIFICATION OF THE TRILOBITA

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ABSTRACT—The continued use of a division of trilobites into Agnostina and polymerids (i.e., trilobites having at least several thoracic segments) reveals the lack of agreement on higher categories in classification. Only in post-Cambrian trilobites do family or superfamily groups find wide acceptance. Adult morphology and early growth stages in Cambrian species are inadequately known; thus taxonomic groups are not clearly diagnosed and lines of descent unknown. This is particularly so in the transition to the distinctive family groups of the early post-Cambrian. Characters of value in classification recognized in recent years include the distinction between trilobites with a natant hypostome and those with the hypostome conterminant. Protaspides of post-Cambrian trilobites are known to differ between families; the same may prove to be more widely true in the Cambrian. Characters of the cheek and pleural regions differ markedly, and need greater recognition, and the importance of paedomorphic processes in evolution needs further investigation. Knowledge of trilobite limbs points to the unity of the class; only the relationships of Agnostina are questionable. The evolution of trilobites took place in differing biofacies, accompanied by ever-changing paleogeography, sea levels and ocean current patterns; consequently, it offers a wide field of study in improving trilobite systematics.

INTRODUCTION

Trilobites were first illustrated in a work published at the end of the seventeenth century, and "trilobite" was coined in the following century (see Kihm and St. John, this volume). The rapid growth of paleontological work in the nineteenth century showed that hard parts of trilobites frequently were dominant among the fossils of the oldest system, the Cambrian. In the successively younger systems of the Paleozoic Era, trilobite remains become progressively fewer, while those of other animal groups become more abundant and varied. Before the end of the era, the trilobites had vanished.

Groups of trilobites with similar appearance, the families, were recognized and became widely accepted in the twentieth century, particularly those from the post-Cambrian systems. These latter trilobites are morphologically more varied, and workers on them have elaborated and enlarged the family groups, clarified their distinctive characters, and explored their evolutionary relationships. The relative abundance of complete exoskeletons and enrolled specimens and the exploitation of silicified material have enabled detailed studies of morphology and ontogeny.

In the Cambrian System, trilobites are the principal fossils used for dating and correlating strata, and emphasis has necessarily been put on this aspect of their study. The value of the Agnostina and of the Olenidae in biostratigraphy, for example, has been established. In addition, the paleogeographic distinction between the olenellid faunas of northern Europe and Laurentia and the redlichiid faunas of Asia and Australia has become obvious.

However, many Cambrian trilobites, particularly those currently embraced within the Orders Ptychopariida and Corynexochida, show only a limited range of morphology, and have proved difficult to divide into widely acceptable groups, or families. Hence evolutionary relationships within them are poorly understood, and the lines that may lead from them as originators of post-Cambrian families have not so far been traced. This is the major deficiency in understanding evolution in trilobites, and until it is at least partially remedied, a widely acceptable classification of Trilobita will remain elusive.

Since the mid-twentieth century, a time when authors were preparing their contributions to the first edition of the Treatise of Invertebrate Paleontology, there has been a spectacular rise in knowledge of modern and ancient oceanic sedimentology and biology, in the development of ideas on biofacies, in understanding paleogeography, and in methods of determining geological time. The evolution of trilobites has to be placed within this new and rapidly changing context, and, for example, the role of deeper water faunas as progenitors of new forms must be considered more fully.

The segmentation of trilobite exoskeletons was long recognized as showing their relationships to arthropods, and the discovery of their jointed limbs late in the nineteenth century confirmed it (see Yochelson, this volume). Subsequent studies point to the unity of the class; but debate continues as to how this class is related to other arthropods. The paragraphs that follow expand on some of the statements made above.

CLASSIFICATION OF TRILOBITES

In his opening remarks on this subject, Fortey (1997, p. 289) stated that a satisfactory natural arrangement is still not possible, any more than it was in 1959 (Harrington, 1959b, p. 145).

FABULOUS FOSSILS—300 YEARS OF WORLDWIDE RESEARCH ON TRILOBITES, Edited by Donald G. Mikulic, Illinois State Geological Survey, 615 East Peabody Drive, Champaign, Illinois 61820, Ed Landing, New York State Museum, The State Education Department, Albany, New York 12230, and Joanne Kluessendorf, Weis Earth Science Museum, University of Wisconsin-FoxValley, 1478 Midway Road, Menasha, Wisconsin 54952. New York State Museum Bulletin 507.

This is because we do not know the lines of evolutionary diversification which led from the origin of trilobites to the widely-accepted families of the Ordovician and younger systems, as the diagrams of Henningsmoen (1951, fig. 2) and Fortey (2001, fig. 1) show. Since the realization that a higher classification could not be based solely on the pattern of facial sutures, attempts have been made to use other characters — those of paedomorphic processes, of differences in morphology of growth stages, of the shape and position of the hypostome, and of the manner of enrollment.

Following their early use, thoracic characters have been long neglected, and much new information on trilobite limbs has been discovered. Two processes were essential in the life of trilobites, that of periodic molting to allow growth, and that of enrollment for protection. The exoskeletal characters linked with these processes may have value for classification, as well as those for monitoring the environment and for seeking food and conveying it to the mouth. The history of the ways in which trilobites have been classified into higher groups was reviewed by Stubblefield (1936) and by Harrington (1959b, p.145–170), with a recent consideration of the subject being by Fortey (1997), who has also reflected on trilobite systematics and progress towards a phylogenetic classification (Fortey, 2001).

PHYLOGENY IN THE CAMBRIAN

The diagram in Fortey (2001, fig. 1) makes clear how little is known of the phylogeny of Early Cambrian trilobites and their descendants in younger Cambrian rocks. Jell (2003) made a major new contribution in outlining lineages in Early Cambrian trilobites, and how particular lineages may have led to the origin of the possibly polyphyletic Ptychopariodea, the Agnostida, Redlichiidae, and Corynexochida. He also noted how lineages may have arisen and spread by migration to give descendants in Gondwana that differ from those in Laurentia.

Rasetti (1954, p. 599) earlier remarked that "understanding the phylogenetic relationships among Upper Cambrian trilobites and the derivation of the Ordovician families from them, is one of the main problems for the trilobite taxonomist." This statement remains true today, for all Cambrian trilobites and their successors. The difficulty in proposing a plausible phylogeny is illustrated in the same work by Rasetti (1954), who concluded that catillicephalids were almost certainly of ptychopariid descent. Only two years earlier, Shaw (1952) regarded the catillicephalids as corynexochoids, and the possible ancestors of the Ordovician Sphaerexochinae (and hence possibly the Phacopida). Further, we now are to understand (e.g., Gradstein and Ogg, 1996; Landing *et al*., 1997; Bowring and Erwin, 1998) that Middle and Upper Cambrian time was less in duration, a mere 20 million years or so, than the succeeding Tremadoc and Arenig Series of the Ordovician, when many long-recognized family groups (Fortey, 1997, p. 290, fig. 216) appeared, and began to diversify. When, where, how, and along what evolutionary pathways, did these new and distinctively different groups emerge in so seemingly brief a time? Was some particular evolutionary process operative?

Stubblefield (1936) first proposed that paedomorphism played a role in the evolution of trilobites, and his suggestions were further explored by Størmer (1942) and Hupé (1954–1955). McNamara (1986) investigated paedomorphic processes in depth, described their importance in the evolution of Cambrian trilobites, and argued that poor control of growth and molt systems may have led to their rapid diversification. These suggestions need further investigation. The problem of the Ptychopariina has been discussed by Fortey (1990, p. 562; 1997, p. 295). Equally problematic relationships exist within the Corynexochida, and in tracing their possible post-Cambrian descendants. These groups need to be the focus of future studies, and the search for ontogenetic series and for entire exoskeletons will be crucial in leading to the solutions of some of the problems (cf., Fortey, 2001, p. 1148).

Description and interpretations of stratigraphic sequences of trilobites in Middle and Upper Cambrian strata of Laurentia (e.g., Palmer, 1965) and Baltica (Henningsmoen, 1957; in process of re-examination by Clarkson and Taylor, 1995) were discussed by Fortey (2001, p. 1144). These throw only a limited light on the origin of post-Cambrian families. The apparently short duration of many genera poses a problem (see Davidek *et al*., 1998), and perhaps reflects rapid evolution, but the manner of this is not yet understood. It is evident that a great challenge before us is to understand the evolution of trilobites (and indeed of other kinds of invertebrate animals) in the relatively short time between the late Early Cambrian and the end of the period (see Landing *et al*., 1998). This challenge is as great as is that of understanding the earlier Cambrian explosion.

THE CORYNEXOCHIDA

A cardinal character of trilobites placed in this order is that in the protaspis the hypostome is conterminant and remains so during development and in the holaspid. This contrasts with the Ptychopariida, in which the hypostome is also conterminant in the protaspis, but becomes natant early in development and remains natant in the holaspid. A long-held view (Harrington, 1959b, p. 161; Hahn, 1989) is that the Corynexochida are only Cambrian, and had no post-Cambrian descendants. A different view was taken by Poulsen (1927, p. 320), Richter (1932), and Henningsmoen (1951) who regarded the Illaenidae and Styginidae as derived from Corynexochida, and gave the order a far longer range in time. Fortey (1990, 1997, p. 298; 2001, p. 1147) agreed with this interpretation, which has support from studies of ontogeny (Chatterton and Speyer, 1997; Lee and Chatterton, 2003). Fortey (1990) was primarily concerned with the Ptychopariida, and considered Corynexochida in less detail. Families in this latter order are inadequately discriminated in the Early Cambrian (Jell, 2003). While some genera appear to be widespread, others are restricted to Laurentia or Gondwana.

In describing the rare Middle Cambrian *Hanburia* (Whittington, 1998), I discussed some of the problems in evolutionary relationships within Corynexochida, and referred briefly to the role of deeper-water forms in evolution. Furthermore, studies of the Illaenidae and Styginidae have led me (Whittington, 2000) to question the inclusion of these two families in one superfamily. I drew attention to illaenid-like trilobites in rocks dated as Late Cambrian in Russia and China

(Whittington, 1997a, p. 886). However, the possible Cambrian origins of the Styginidae remain obscure.

THORACIC CHARACTERS

J. Barrande (1852, 1872) made a massive and unrivalled contribution to the knowledge of trilobite exoskeletons of Middle Cambrian to Middle Devonian age (see Bruthansová *et al.*, this volume). His meticulously-drawn illustrations show the form and convexity of the exoskeleton; the longitudinal and transverse sections show the extent of the doublure, and his plates depict the thoracic segments, in situ hypostomes, and the cephalic sutures. Well-preserved specimens, either casts and molds or in limestone (as was much of that studied by Barrande), and, in particular, isolated exoskeletal sclerites of silicified specimens freed from the matrix by acid have revealed in detail how sclerites articulate with one with another, and the extent and form of the doublure. A more extensive discussion of the thorax was thus possible in the revised Treatise (Whittington, 1997b). Another example is in the photographs in Chatterton and Campbell (1993, figs. 4, 8) that show articulation devices and the distinctiveness of the doublures of the outer portions of the pleurae of different groups. The pocket-like doublure of asaphids (Siegfried, 1936), with its panderian opening, which projects and acts as a stop in enrollment, is a characteristic of this large group (e.g., Balashova, 1976, pls. 6–8).

I have also shown the distinctive morphology of the thorax in a homalonotid (Whittington, 1993), in illaenids (Whittington, 1997a), and the inward extent of the doublure in Scutelluinae (Whittington, 1999) and lichids (Whittington, 2002). Such characters of the axial and of the cheek and pleural regions of the exoskeleton need to be investigated because they lead to a better understanding of the morphology and anatomy of each family group, and reveal characters of value in suggesting superfamily relationships. For example, these characters show the marked contrast between the ventral morphology of a lichid and that of an odontopleurid (Whittington, 2002, p. 314). Whether or not trilobites of these two families should be united in a single order continues to be a matter of debate, as my discussion and those of Fortey (1997, p. 299; 2001, p. 1145, 1147) show.

ENROLLMENT

Characters of the thorax, such as the presence or absence of the fulcrum, the hinge line, articulation devices, and the facets, are intimately linked with enrollment. The classification of Bergström (1973) is unique in including consideration of these matters. Trilobites that tucked the pygidium against the cephalic doublure in enrollment were considered by Bergström to be derived and to be placed in a separate order, for which he redefined the Ptychopariida. In such trilobites, as well as those which in enrollment brought the ventral surfaces of the cephalon and pygidium into contact, the shape of the cephalon, its doublure, and the pygidium must conform throughout meraspid and holaspid life, to ensure a close fit. This is the coaptation of Clarkson and Henry (see references in Clarkson and Whittington, 1997).

Some of the necessary progressive changes in the shape of the cephalon and pygidium during growth are shown in the analysis of Hughes and Chapman (1995). An important point in assessing the significance of particular characters in trilobites is the linkage that must obtain, for example, between the characters directly concerned in enrollment and coaptation. These include the shape of cephalon and pygidium (and of changes in these shapes during growth), articulation, facets, vincular notches and grooves. All of these characters are significant, not in isolation, but in combination.

In their discussion of enrollment in classification, Fortey and Owens (1979) argued that characters associated with enrollment were in peripheral parts of the exoskeleton and hence of less significance than axial characters. However, enrollment is activated by musculature (e.g. Whittington, 1993, p. 79, 80), and the muscles are housed in and attached to the axial exoskeleton, so that enrollment is linked to the axial region. This provides a further example of the complex linkage between exoskeletal characters. Fortey and Owens showed that different types of enrollment occurred within a single family, between species of a single genus, and even within specimens of a single species. They concluded that the family was the highest level at which enrollment may be useful in taxonomy. Bruton and Hass (1997) have shown in detail how coaptative structures of the pleural tips differ between species placed in different genera of phacopids.

HYPOSTOME

Features of the axial region are agreed to be important in higher classification, and one of these is the hypostome, with its different forms so strikingly characteristic of post-Cambrian families. Whether the hypostome is attached to the exoskeleton (conterminant) or not so attached (natant) has been brought into higher-level classification by Fortey and Chatterton (1988) and Fortey (1990). I have argued (Whittington, 2000, p. 879) that a third condition of the hypostome (impendent), described by them is probably of no significance in higher-level classification, because it appears to be a homeomorphic trend in particular species.

The conterminant condition, in which the hypostome is firmly braced against the cephalon, allowed the evolution of hypostomes which function to protect the vital cephalic region, and aid in the comminution of food and the guiding it into the mouth (Bruton and Haas, 1997; Whittington, 2002, p. 314). This contrasts with the conservative, simpler form of the natant hypostome (Fortey, 1990, fig. 11).

ONTOGENY

Barrande's great work, referred to above, included descriptions of a series of growth stages of species of five genera of Cambrian and Ordovician trilobites. Beecher (1893) first described silicified specimens of the earliest larval stage, the protaspsis. It was Beecher's studies of growth stages that led to his classification (Beecher, 1897) that divided trilobites into three orders, each based on a type of facial suture. Difficulties with such a classification, which relied on a single character, soon arose. The attempt by Størmer (1942) to provide a classification that used emended definitions of Beecher's orders was not adopted by Harrington (1959b, p. 160). The function of cephalic sutures is to facilitate molting, and their pattern must serve this function. The pattern may have been modified rapidly in evolution, and to attach high taxonomic significance to, for example, the width and shape of the rostral plate or the presence of a median suture in any particular group of trilobites may be incorrect. My study of Late Cambrian trilobites (Whittington, 2003) led me to doubt that the median suture is a character unique to the Asaphina, as thought by Fortey and Chatterton (1988).

A masterly review of what is known of the development of trilobites was given by Chatterton and Speyer (1997). Their many new figures covers all aspects of the history of this study and of the deductions that have been made from it. One such conclusion is that related, monophyletic groups of trilobites appear to have similar larvae, and this conclusion has significance for classification, at family and seemingly higher levels. Hence, as Fortey (2001, p. 1148) emphasized, the discovery of early growth stages of Middle and Late Cambrian trilobites, in particular, may be crucial in helping to solve the Ptychopariina problem and other uncertainties in evolutionary relationships. How significant evolutionary changes in the earliest developmental stages may be, and whether or not these stages will help to determine affinities at the superfamily or higher levels of classification are uncertainties yet to be clarified.

TRILOBITES AS ARTHROPODS

The discovery of trilobite limbs at the end of the nineteenth century confirmed the view that they were arthropods. How they may be related to other fossil and living arthropods has been discussed by Fortey (2001, p. 1141–1143). The abundant living marine animals that have a head, segmented body, and tail are the Crustacea (e.g., crabs, shrimps and lobsters), and trilobites were first thought to be their ancestors. That trilobite limbs consisted of a single pair of antennae and a series of similar, biramous limbs from head to tail cast doubt on this view. Størmer (1933, 1944) championed the suggestion that trilobites were more closely related to arachnids, a large group in which he included spiders and the Cambrian to Recent merostomes, which embrace fossil eurypterids and the living horseshoe crab *Limulus*. The renewed study of the Burgess Shale soft-bodied arthropods of the Middle Cambrian, and discoveries of similar faunas in the Lower Cambrian of Greenland and Yunnan, China, has revealed the world-wide variety of these marine animals, so that arthropod relationships, and the ancestry of the phylum are much-debated subjects. Størmer's view of the trilobite-merostome relationship is currently widely accepted (e.g., Fortey et al, 1997, fig. 1).

APPENDAGES

The earlier history of the study of specimens of trilobites with preserved limbs is provided by Harrington (1959a, p. 76–85). The first volume of the revised Treatise (Whittington, 1997c, p. 87–111) reviews more recent work, and the anatomy and movements of the limbs are considered. Since then, a major contribution to such studies was made by Bruton and Haas (1997, 1999). In *Phacops,* not only is the exoskeleton in its dorsal and ventral aspects known in great detail, but some specimens show the pyritized limbs in similar detail, and make this genus the best known holaspid trilobite with limbs. Specimens of *Eoredlichia* and *Yunnanocephalus* with appendages have also been described from the upper Lower Cambrian Chengjiang fauna of China (Shu *et al*., 1995).

It can now be seen how similar trilobite limbs were from the late Lower Cambrian to Early Devonian (ca. 120 million years). Trilobites have an antenna and three pairs of limbs on the cephalon, and a series of similar limbs on the thorax and pygidium that decrease in size posteriorly.

The limbs of meraspid *Agnostus pisiformis* (all that are known among the Agnostina) are different, and providing one of the reasons for considering that this group may not be referable to the trilobites (Fortey, 2001, p. 1143). In a discussion that has new figures of *A. pisiformis*, Mass *et al.* (2003, p. 181–184) treat the group as crustaceans.

In the trilobite *Olenoides* there are posterior cerci, but it does not have the many pairs of tiny posterior limbs that *Triarthrus* and *Phacops* display. The limited knowledge we have of appendages, however, points towards the unity of the class and its conservative anatomy.

THE WAY AHEAD

These reflections, like those of Fortey (2001), show that factual data need to be gathered on the entire exoskeleton and its development in as many species as possible to clarify and expand the basis on which all inferences on phyletic relationship rest. The history of trilobite studies shows that current ideas are heavily biased towards what is known of European, North American, and Australian faunas, and by the views that authors from these countries have expressed. The discussion has been dominated by authors familiar with faunas from Laurentia and parts of the fringes of Gondwana. Knowledge of South American and Asiatic trilobite faunas has grown rapidly during the last fifty or more years, but much further study is needed for a better-balanced view of trilobite evolution in time and space.

Figure 1 of Fortey (2001) reminds us that Agnostina, Olenellina and Redlichiina are contemporaneous in Lower Cambrian rocks, and we are only beginning to understand the relationships between them. Furthermore, Lower Cambrian rocks have yielded a ptychoparioid with spiral enrollment (Palmer, 1958), species with an effaced cranidium (Palmer and Gatehouse, 1972, p. 26; Palmer and Rowell, 1995, p. 12), and unusual forms such as *Alacephalus* (Lane and Rushton, 1992) and *Perissopyge* (Blaker *et al*., 1997).

The data show that trilobites had evidently diversified considerably by the late Early Cambrian, but may be unknown earlier because the exoskeleton was uncalcified, and hence not preserved in any rocks so far known. That their appearance as fossils was because of calcification of the exoskeleton is not a new idea. Rasetti (1948, p. 5) invoked calcification as a was to explain abrupt appearances of taxa not only in the Lower Cambrian, but subsequently, such as those of the Middle Cambrian *Hanburia* and *Burlingia* or younger examples. Landing and Westrop (2004) proposed that trilobites were the first mineralized group that were able to compete with a diverse infauna and diversified in off-shore paleoenvironments at the end of the Cambrian evolutionary radiation. This evolution was taking place in a world of changing geography, fluctuating sea level, and probable alterations in oceanic circulation. The pioneering attempt by Fortey and Owens (1997, p. 271–287) to place biofacies and events in evolution within this context needs to be developed more fully. The way ahead offers ample scope for investigations in all aspects of trilobite studies, in the search to clarify understanding of evolution and improve systematics.

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CHARLES DOOLITTLE WALCOTT AND TRILOBITE APPENDAGES (1873–1881)

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ABSTRACT—C. D. Walcott began to suspect in 1873 that some flexed to partially enrolled specimens of *Ceraurus* had preserved legs. He began their study in February 1876 by preparing cut sections of trilobites in limestone from the W. P. Rust farm at Trenton Falls, New York. In November 1876, Walcott, now employed by James Hall, moved to Albany. In a preliminary notice of trilobite appendages, published December 1876, Walcott insured he alone, and not Hall, was credited with the discovery of trilobite legs. The New York State Museum had a new steam-powered saw, and with its use, Walcott made thin-sections. Grinding and polishing was done by hand, mainly in his boarding house, after the regular work day. An 1877 preprint provided details on legs and gills. In Fall 1877, Walcott first observed and dissected living marine Crustacea, and though his preprint was formally published in 1879, the text remained unchanged. Walcott continued to prepare and study sections, and, in 1881, published a definitive paper on the paleobiology of trilobites.

INTRODUCTION

Charles Doolittle Walcott (1850–1927) accomplished much in a variety of fields. His biography only summarizes his early investigations of fossils (Yochelson, 1998; 2001a). His discovery and study of trilobite limbs was a fundamental contribution to paleobiology; a preliminary note was published when he was 26. How the young man, lacking formal training in geology or biology, accomplished this study deserves a detailed account. His daily diary provides some scanty data. The diary entries given herein are direct quotes, including abbreviations, and commonly do not underline taxonomic names. A few entries are reproduced in full, but, in the main, comments which are not germane to this report are omitted.

The trilobites were embedded in limestone, and to aid in their interpretation, one must consider the preparation techniques that were available to Walcott. In his time, the cutting, grinding, and polishing rocks required far more time and effort than making sections today. From the diary, Walcott's mental state and the general environment in which he lived may also be surmised as he made the transition from a professional fossil collector to someone who studied fossils scientifically. Science is concerned with "what," "where," and "who." History cares about "who," but is more interested in the "how" and particularly "why."

NINETEENTH CENTURY BACKGROUND

It was generally accepted before the middle of the 19th century that trilobites belonged within the Arthropoda. The hope still existed that a living trilobite might be discovered. In a widely circulated work, Burmeister (1846) discussed what was known or assumed about these striking extinct forms. Nevertheless, comments by J. W. Salter (1864, p. 8, 9) a quarter of a century later, which reinforced similar earlier remarks, cannot be ignored:

"Every author who has written on Trilobites has more or less perceived their analogy with Limulus or King-crab, to which tribe there is, indeed, a good deal of external resemblance. But this resemblance totally fails when we examine the under side of the animal; for all the researches hitherto made (and they are many) fail to detect the slightest trace of limbs in the Trilobite. It is impossible, seeing the state of preservation in which they occur, to suppose that in every case — in fine shale, in limestone, in arenaceous mud — all traces of these organs should have been lost, had they ever existed.

"We are compelled to conclude that Trilobites had not even membranaceous feet, and that the ventral side was destitute of appendages. It is of course difficult to prove this."

Only a few years later, Geological Survey of Canada paleontologist Billings (1870), described legs on *Asaphus platycephalus*. At a meeting of the Geological Society of London, Henry Woodward corroborated his discovery. J. D. Dana, A. E. Verrill, and S. I. Smith also examined the specimen. However, they rendered a collective verdict that was not to be taken lightly "that the organs are not legs, but the semi-calcified arches in the membrane of the ventral surface to which the foliaceous appendages, or legs, were attached" (Dana, 1871, p. 321). Dana, a leader in American geology, was also an expert on living Crustacea.

Thus, the scientific stage was set for Walcott to show that these extinct forms had legs. Furthermore, he documented that at least some of those appendages were jointed, which proved conclusively that trilobites were arthropods. Walcott later reexamined Billings' specimen, which had engendered the unfavorable comment from Dana and his colleagues. "A glance showed

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that Mr. Billings's interpretation was the correct one, and that as far as the thoracic legs are considered, the Canadian trilobite has a pair for each segment" (Walcott, 1884, p. 281).

TRENTON FALLS, NEW YORK

On the southwest flank of the Adirondack dome, West Canada Creek has cut a gorge through limestones and shales of the Upper Ordovician Trenton Limestone; this is the type Trentonian. The Grand Honeymoon Tour for newlyweds was to Saratoga Springs, then Trenton Falls, and finally Niagara Falls in the 19th century. The romantic aspects of the falls inspired poetry, oil paintings, and water colors, but fossil collecting by tourists was also highlighted.

Trenton Falls is significant in the history of American paleontology. "In 1824, the physician James De Kay used the first zoologically named fossil species [*Calymene blumenbachii*] as an index to the age of a New York rock" (Aldrich, 2000, p. 30). Local farmers collected trilobites, and during the long winters prepared them; specimens of *Isotelus* were particularly striking. "Otis Borden's novelty shop... sold trilobites and other geological curiosities to gullible tourists. He also palmed off a few imitations .... pouring plaster of Paris into frames in the shape of trilobites" (Thomas, 1951, p. 116). In addition, pieces were glued together to make saleable items, and young Walcott bought one of these fakes (Yochelson, 1998, p. 5).

When Walcott was eight, his widowed mother moved her family from New York Mills to Utica, a larger town to the east so that he could attend a good school. According to an obituary, Walcott had difficulty with his teachers and several times left primary school. He next entered the Utica Free Academy. The school burned shortly before Walcott attended, and classes were necessarily makeshift. According to the same account, he left without graduating at age eighteen. During the Civil War, if not earlier, the family summered at Trenton Falls, which is higher and cooler than Utica, rather than swelter in the Mohawk Valley. How many summers they spent there is not known, but by age sixteen Walcott (1916, p. 254) had a good knowledge of local fossils and was able to recognize an exotic fauna in a glacially transported block. At some point, Walcott met William Palmer Rust, a farmer/paleontologist with an impressive collection of trilobites.

WALCOTT AT TRENTON FALLS (1870–1875)

During 1869–1870, Walcott worked in a Utica hardware store, and corresponded with the Rust family, particularly Lura, one of Rust's sisters who was seven years his senior. By April 1870, he abandoned clerking and moved to the Rust farm. To partially pay room and board, Walcott assisted with the innumerable farm chores, but spent much of his time collecting and studying. He exchanged fossils with other collectors, including Elkanah Billings in Ottawa. Walcott then became partners with Rust in the commercial sale of fossils. In January 1872, he married Lura, whom he loved deeply. His mother had doubts about the marriage and his rich uncle William refused help when asked to buy Walcott's fossil collection. These two events may have steeled Walcott's determination to succeed (Fig. 1).

Fig. 1. Charles Doolittle Walcott as a young widower at age 27 (Smithsonian Institution Archives).

His mother gave occasional financial support when Walcott first moved, but that may have ended with his marriage. To provide income to set up housekeeping, Walcott tried buying wool, raising chickens, and other ventures, though none proved a success. Ever since he first mentioned Lura in his diary, she was intermittently ill, and after they wed, illness waned and waxed for several years. Prospects for buying his own home faded, and crowded conditions in the Rust house made the isolation of the long, hard winters worse. Never-ending farm chores governed by the cycle of the seasons were always present, and Walcott was intellectually worn down. He began his diary while clerking, but before the end of 1873, he abandoned even this minimal daily activity and did not start again until 1875.

LOUIS AGASSIZ (1873)

James Hall, State Paleontologist, repeatedly promised to purchase the Rust-Walcott fossil collection, though he never obtained funds from New York State (Yochelson, 1998). Finally, in October 1873, the partners made a sale to Louis Agassiz, founder of the Museum of Comparative Zoology (MCZ) (Winsor, 1991). Thus, New York State, by claiming its typical concern with the budget, lost an opportunity to preserve part of its own heritage within the state. Walcott spent a week unpacking and arranging the collection in the MCZ, during which he stayed in the Agassiz home (Yochelson, 1998). This was his total college experience, and Walcott considered Agassiz his mentor who had urged the study of trilobite appendages. Because there are no diary entries during this interval no details are known.

Following Walcott's trip, Agassiz (1873) published a short note. "I have received the fine collection of Trenton fossils of Mr. E. [sic] Walcott of Trenton Falls. It is particularly rich in trilobites. Mr. W. called my attention to one which he was confident would settle the only question of the presence or absence of legs in trilobites. And truly there can be no doubt left upon this point." This was the last writing of Louis Agassiz, who died December 14, 1873. Any hope that Walcott might have become an assistant at the MCZ also died.

Walcott (1881, p. 191) later wrote, "In the month of October 1873 the attention of Professor Louis Agassiz was called to certain markings on the inner surface of the pleurae of a specimen of Asaphus platycephalus, 'Panderian Organs.' He considered them as proving the existence of true crustacean legs (Amer. Nat. VII, 741, 1873)." Billings (1870, p. 481–483) had earlier discussed Panderian Organs, and almost certainly Agassiz was aware of that paper.

THE FOSSIL QUARRY

Adjacent to the Rust farm is the little valley of "Gray's Brook," unnamed on any known map, which drains into West Canada Creek. The thin-bedded strata quarried from the valley walls yielded excellent fossils. In particular, the *Ceraurus* bed at creek level provided numerous complete, small trilobites on its upper and lower surfaces. Within the bed, some trilobites are flexed or partially enrolled, but are almost impossible to extract or prepare as they break across the matrix rather than free from it.

More than a century later, the small quarry was reexcavated by T. E. Whiteley of Rochester, New York (Brett *et al.*, 1999). The most fossiliferous units were collectively termed the Prospect Beds, and the Rust Member of the Coburg Formation, in which they occur, was upgraded to formation-level status. It is interesting to compare Brett *et al.*'s (1999) measured section to a detailed section prepared by Walcott in 1874. Subsequently, the trilobite-bearing beds were named the Walcott-Rust Quarry beds, and are about 12 meters above the base of the Rust Formation (Whiteley *et al.*, 2002 p. 75).

Some of the trilobites from this quarry were redescribed and illustrated (Brett *et al.*, 1999). Quotes from Walcott's diary and publications record the taxonomic names he used. Current generic and specific assignments may be determined from the 1999 publication, or from Whiteley *et al.* (2002, p. 75), which lists 21 trilobite species from the quarry.

The Grays' Brook locality is the Walcott-Rust quarry (Brett *et al.*, 1999). Higher in the section, Rust had a quarry for limestone that he burned for agricultural lime. Walcott (1918, p. 133, footnote) mentioned " .... the trilobite quarry near Trenton Falls, New York, that I discovered about 1870." The modern name for the quarry is appropriate as Walcott used the fossils scientifically. Still, Rust taught Walcott the local stratigraphy and instructed him in the art of collecting. Above all, Rust was a remarkable preparator, and showed Walcott the patience needed for this work. Specimens in the National Museum of Natural History document his skill.

As he collected to replace the fossils he sold in 1873, Walcott noted calcite spots near trilobites in the *Ceraurus* layer; these fossils had been smothered by an influx of lime mud. He realized the spots might be connected to complete trilobites and perhaps were the legs. "This unique mode of preservation is believed to result from anoxic bacterial-induced calcite precipitation within the appendage, followed by calcite in-filling as the appendage material decayed" (Whiteley *et al.* 2002, p. 41). Walcott (1881) mentioned that the quarry was the only locality where appendages were preserved. Although the Prospect Beds crop out elsewhere in the Trenton Falls area, T. Whiteley, (oral communication, 1995), confirmed the uniqueness of the quarry locality.

The search for appendages may have been inspired by Agassiz's comments, but their discovery was due entirely to Walcott's observations. When he first discovered preserved appendages in the *Ceraurus* layer is unknown, although a date can be approximated. If these structures were known in 1873, they would have been mentioned by Agassiz in his note or by Walcott in the introduction to his 1881 paper.

Following his week at the MCZ, Walcott began writing scientifically, and his first two published notes may have been written during Winter 1873–1874. Meeting Agassiz could have been the inspiration to describe two new trilobite species (Walcott, 1875a, b). Walcott was possibly encouraged by Lura or wanted to show her that he could actually have his work published. These notes were in a short-lived journal. Walcott had exchanged fossils with its editor, S. A. Miller of the *Cincinnati Quarterly Journal of Science*. These notes were followed by more substantial reports on *Ceraurus pleurexanthemus* Green in a more widely distributed journal (Walcott, 1875c, d). He noted, "The writer has had the opportunity, by his residence at the type-locality of the Trenton Limestone, to make some investigations upon the structure and habits of the trilobites of that interesting horizon" (Walcott, 1875c, p. 155). In neither article did Walcott mention appendages.

Internal evidence suggests that one *Ceraurus* manuscript was completed in late 1874 or early 1875. By Fall 1875, Lura's health declined dramatically and Walcott spent considerable time at her bedside. Thus, one may surmise Walcott noticed the calcite flecks in the *Ceraurus* layer during the spring or summer of 1875.

After a long painful interval, Lura died January 23, 1876. Walcott was devastated by her death; no other term describes his written words of anguish. It could only have been worse if she had died on their fourth anniversary, two weeks earlier. A few days after Lura's funeral, he left Trenton Falls to visit his mother and sister in Utica, New York.

PREPARING FOR INVESTIGATION OF TRILOBITE APPENDAGES

The first Sunday in February, Walcott commented in his diary that Lura had been gone for two weeks, a sentiment to be expected from a recently bereaved husband. However, the next entry is a surprise, "Busy during the morning at my lathe at Mr. Hackets" (February 6). "Working on lathe in the morning" (February 8). "Working on lathe all day, hope to finish it tomorrow. It is the first attempt I have made to work up limestone scientifically and I hope to reap good results" (February 9). "Worked on my lathe at Mr. Hacket's in the morning" (February 10). Perhaps to soothe his loss, Walcott was suddenly possessed by the need to pursue research, and the next day he wrote James Hall about the possibility of employment in Albany.

A reasonable surmise is that discussion with the presently unknown Mr. Hacket may have occurred during late Summer or early Fall, 1875. This would have been before Lura became so ill and before the first snows made travel to Utica difficult. After discovery of the appendages in limestone, Walcott must have speculated as to how to investigate this difficult material. Agassiz may have suggested cutting sections through fossils, although this seems unlikely. When Walcott exchanged fossils with Billings, he received from him some books and papers. Billings (1870, p. 481) mentions cutting the trilobite specimens which showed legs and ".... others of which I had made sections ...." Perhaps this was the inspiration for a lathe.

At Newport, southeast of Trenton Falls, quarrying of Black River Group limestone produced dimension stone. Walcott may have seen the saws in operation, although there is no mention in his diary. Jewelry manufacture was a more germane source of data on cutting and polishing small rocks. Handbooks for mechanics were available and some of the information on early methods and machines given below is from Byrne (1870) and Knight (1875).

MACHINERY FOR CUTTING LIMESTONE

Today, making thin-sections is so routine and easy that almost no one recalls how it was done in the past. Considering the machinery Walcott may have used to "work up limestone scientifically" helps to understand the difficulties he faced. As no details are known, several possibilities must be considered. Limestone and harder rocks have been sawed by the back-and-forth movement of a wire coated with an abrasive paste. The first use in American paleontology of what may have been wire to slice several sections involved a Devonian plant described by J. W. Dawson in 1859 (oral communication, F. Hueber, 1999). If Walcott used this approach, a "lathe" would not be mentioned in his diary.

Prior to electric motors, small machinery was powered by human labor. Hand cranks were used, but unless an assistant provided the muscle power, all other work had to be done with one hand. The most common alternative was a foot treadle, and one of the earliest uses of foot power was the potter's wheel. Back-and-forth treadle motion may be converted to rotation in one direction by a Pitman, a rod attached eccentrically to a wheel. About a decade after Walcott began his work, a Seneca Falls, New York, company advertised a lathe with right and left treadles to ease the strain on the knees. When electric motors became common, the foot treadle lingered on in older models of the Singer sewing machine. Foot-powered machinery for polishing jewelry is still used in some third-world countries.

A country modification of the treadle is a "spring pole lathe." A limber tree branch is pulled down by a rope attached to a treadle, and when it springs up, the operator again presses down on the treadle. It is slightly easier than unaided foot power, and is used in good weather near a young tree, though a limber pole can be rigged indoors. Because Walcott's work began in late winter, a limber pole is unlikely. Walcott's machine probably used a treadle for its power.

In regard to cutting limestone, the term "lathe" is not clear. One occasionally hears the redundant "turning lathe," as the rotation is in a vertical plane. Lathes equipped with a saw blade developed, where the piece to be cut is rotated and the blade is still, or the piece can be moved slowly by hand to speed the process (Fig. 2). Using a Pitman, a blade could be moved up and down. In light of Walcott's meager finances, such complicated machines seem unlikely.

A different term is a "mill," probably named with reference to mill stones, where rotation is in a horizontal plane. "Mill" and

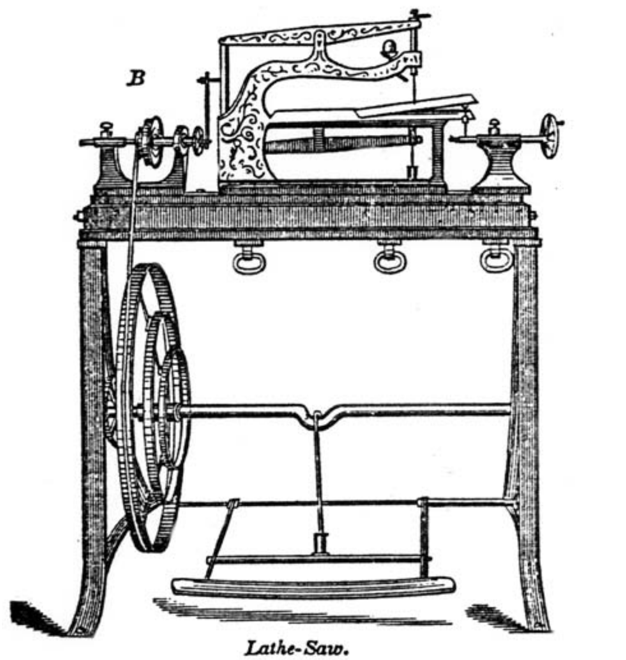

Fig. 2. Diagram of a treadle-powered lathe saw (from Knight, 1875, p. 1275. fig. 2439).

"lathe" may have been more or less interchangeable words, or Walcott may have confused them. Indeed, "table lathe" appears in some literature. The term "lap" or "polishing lap" for a horizontally rotating wheel is more familiar (Fig. 3).

Byrne (1870, p. 208, 209) described, "When the stone to be sliced is too large and heavy to be conveniently held in the hand, it is mounted on a crane, ... The crane consists of an upright rod ... and upon this rod slides vertically a horizontal arm ... provided with a binding screw .... The stone ... is carefully clamped, so that the line of the intended division is exactly horizontal .... The weight then suffices to keep the stone continually pressing

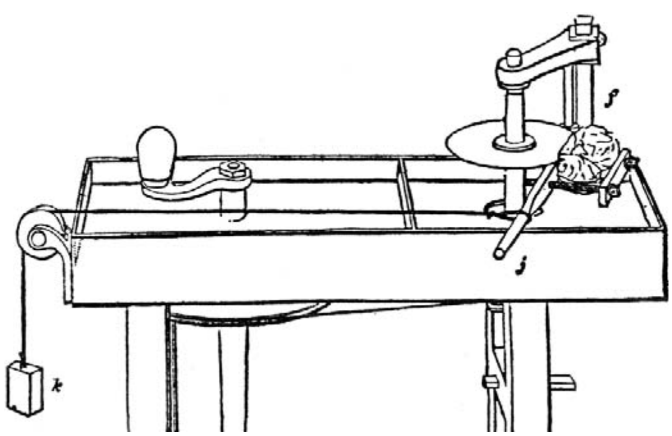

Fig. 3. Diagram of a lapidary mill designed to cut slices of a rock; the motive power, not shown, was a treadle (from Byrne, 1870, p. 207, fig. 118).

against the edge of the slicer, and the operator has merely to keep the lathe in motion, and supply the oil. For cutting parallel slices, it is only requisite between every cut, to shift the horizontal arm upwards upon the vertical rod." Some of these devices described by Bryne (1870) would have made Rube Goldberg proud, but the techniques were proven. Accordingly, a plausible interpretation of Walcott's "lathe" is a machine like that shown in Fig. 3. The steam-powered saw in Albany discussed below supports the idea that a horizontally rotating blade was used.

By the 1860s, expensive diamond-studded saw blades existed, although an iron blade charged with abrasives would have been sufficient to cut limestone. If the blade was horizontal, Walcott could keep replenishing the abrasive and ladling lubricating water with little trouble. Common quartz sand could be used for cutting, although emery, a commercial corundum, was available in the 1870s. The still harder carborundum, an artificial silicon carbide, was not produced until about a decade after Walcott first did his sectioning. Whatever the mechanism, to cut even a small piece of limestone involved a great deal of time and much pumping of the treadle.

Walcott's diary notes, "After dinner went down to Mr. Hackets & made standard for magnifying glass" (February 16). Brett *et al.* (1999) noted that a *Ceraurus* cross-section is only about 2 cm in width, and cutting was best done under magnification. "Wrote description of B. Longispinus in the morning" (February 17).

Concurrently with his investigation of trilobite legs, Walcott (1877a) described new fossils from the Trenton Group limestones (Walcott, 1877a). Entries on that project provide a comparison of how much time Walcott spent in study and preparation of a typical manuscript on descriptions of new species relative to his work on the appendages.

CUTTING LIMESTONE AT THE RUST FARM (1876)

"About the house in the morning, sketching B.l. and waiting for W. P. R.[ust] who did not arrive" (February 18). The next day Rust came to Utica, loaded Walcott's trunk and lathe into his sleigh, and returned to Trenton Falls. Walcott followed in a few days and was still actively preparing a manuscript. ".... copied description of Bathyurus longispinus" (February 24). "Wrote a little & copied finishing description of B. l." (February 25). "Working at Trenton fossils mostly with caustic potassa [potassium hydroxide]. Had fair success" (February 28). "Drawing on B. l in the morning. .... After dinner worked at lathe getting it ready for cutting up C.[eraurus] p. [leurexanthemus]'s" (February 29).

Because of snow and cold weather, Walcott could not have collected *Ceraurus*-bearing limestone later than early Fall 1875. The diary supports the inference that he decided to make sections no later than Summer 1875 and had stockpiled rock. The harsh winter precluded setting up the lathe outside, and the house was so crowded that Walcott probably set his lathe up in a barn. If Walcott worked indoors, the only light sources were kerosene lamps or candles. Because of the fire hazard, it is almost inconceivable that anyone would use candles in a barn. One can almost picture him pumping the treadle, peering through the magnifying glass by the light of a lantern, and dashing outside to check his observation in the winter sunlight.

"Prof. Hall wrote that he will be here this month or in April. I hope to obtain work under him for the ensuing summer. Cut up several C.p.'s had fair success. I think I shall determine their interior structure if it can be determined" (March 1). "Finished sketch of B. l. in the morning" (March 4). Unfortunately, when his description of Trenton fossils was published (Walcott, 1877a), no illustrations were included.

"Busy the entire morning cutting & grinding C.[eraurus] p.[leurexanthemus]'s. Found three sections which will be of use to me in working up C. p." (March 6). "Cut up C. p. and worked out Trenton fossils in the morning. After polished & mounted several C. p.'s C. s's & 1 As[aphus] g[igas]. Had good success in finding interior structure. Wrote description of Bathyurus tuberculatus & studied on several trilobites. Read in the evening" (March 7).

A cut surface is never entirely flat and may show saw marks. To smooth the surface, it is rubbed on a glass plate covered with a paste of abrasive and water. The rock is moved in a figure eight pattern, as back-and-forth motion bows the limestone surface, and the glass itself is ground into a hollow. When the rock is reasonably smooth, coarse abrasive is washed away and fine abrasive used for polishing. If coarse abrasive grains are present, the smooth surface is ruined. Even after the technique is mastered, continually moving a small rock with the fingers is tedious. Hand grinding and polishing a cut limestone surface may take half an hour.

Walcott may have seen cut sections mounted on glass at the New York State Museum (NYSM) or the MCZ. A medical doctor or local naturalist could also have had specimens on glass slides. Mounting keeps the polished surface pristine, and a glass slide is easier to handle than a rock chip. Currently, many glues and plastics are in use, but for nearly a century, the typical attachment was by "Canadian balsam." This resin is heated, which drives off volatile components to the point where the material is sticky. To test the consistency, a needle is used to pull out a string, like pulling taffy, from a spot of Canadian balsam on the glass slide. The rock slice will not stick if the balsam is too soft or too hard. As an extra problem, should the contact between the balsam and rock be done improperly, air bubbles will mar the section. A glass plate for grinding on could be obtained in Trenton Falls or Utica, and there were many trees around to provide a resin, although "Canadian balsam" was generally available as a balm for cuts.

"Busy at sorting and working out Trenton fossils most of the day" (March 8). "Drawing a sketch of Bathyurus tuberculatus in the morning. After dinner cut up C. p. found nothing new" (March 9). "Arranging fossils in collection, studying n. sp. of Conularia, etc during the morning. Ground sections of trilobites in the afternoon. Found the Calymene seriana has the same character of appendages that c. p. has. Wrote description of c. p. after supper" (March 10). "Wrote de[sci]pt[ion] of Conularia quadrata n. sp & drew sketch to accompany it. Also cut 10 C. p. a.m."

Farm workers rose early for work, and "a.m" after chores may mean three to four hours. This translates to about 15–20 minutes per limestone cut. Walcott did no cutting on Sunday, though he "Mailed extras on c.p. to friends etc." (March 11). This was probably a reference to copies of his publications in the *Annals* (Walcott, 1875c, d).

"Not feeling very well. Worked at fossils very easily during the greater part of the day. Commenced to block out notes for an article on c. p. in relation to the evidence I have obtained by cutting sections. I now need to be at Cambridge in order to study the recent crustacea. As it is, I shall try to do the best I can with the means at hand" (March 13). "Reading on the structure and affinity of the trilobite, as given by various authors. Polished a number of section of c.p. nothing especially new revealed. I am not feeling very well. Worked beyond my strength last week" (March 14). Walcott's copy of Burmeister (1846) bears a few annotations, and one dated "March 1876" proves he had access to this report while at the Rust farm (Yochelson, 2001b). What other literature was at hand is unknown. "I find that I have 3000 specimens in my collection & 1500 duplicates collected the past three summers" (March 15).

"Reading in the morning on the Phyllopoda, handling of specimens after dinner and then drew a section of c.p. Wrote Dr. A. S. Packard respecting trilobite legs" (March 16). Packard was the outstanding American student of living Crustacea. "In the morning cut up trilobites. Found a beautiful section of the appendages in a Calymene senaria. It is fascinating work. The hope of finding something new or more definite keeps spurring one on" (March 17). "Very cold. Worked with lathe in the morning" (March 18). "Polished sections of C. p." (March 20).

"In the afternoon drew a section of C. p. Studied section of "[c.p. in quotes in dairy] " in the evening" (March 21). "Working on section of C. p. 2/3 of the day. Prospecting for the appendages about the head" (March 23). "Cut up & ground sections of c. p. in the morning. After dinner arranged blocks of small fossils in the hall" (March 24).

A late snowstorm forced unexpected shoveling and road plowing, which may have disturbed Walcott's concentration. "Drew on section of C. p. a.m. Not able to work long at close work on account of a weakness in my eyes" (March 29). "26 years old this day. I feel more like 36" (March 31). Walcott's research effort was slowing, perhaps because of malaise, and for months nothing more is recorded concerning use of the lathe.

Walcott was in Utica for a few days. "Spent a portion of the day a[t] Mr. Blaikie's examining specimens with his microscope" (April 13). He was next in Albany trying to arbitrate a bitter argument between Hall and his assistant Whitfield, who was leaving, and this meant that Hall would not have an assistant. There is no indication that Walcott discussed his discoveries with either man, but his next activity suggests he mentioned it to Hall. "Wrote a little on a preliminary note, noticing the discovery of appendages in trilobites" (May 6). "Returned [from Trenton Fall to Utica] & wrote a little on C. p."(May 10). "Coppied [sic] a little of my article on C. p. & C. s" (May 25). "Finished copying article on C. p. & C. s. & wrote Prof. Hall respecting the publication of my descriptions of fossils, etc." (May 26). The descriptions may refer to specimens from the Trenton Limestone (Walcott, 1877a), but the "etc." could equally well refer to his note on appendages.

The need to pursue research left as abruptly as it began. Walcott commented that for 26 days in June he made no attempt to break rocks at the brook. He visited friends in the Finger Lakes and then moved back to the farm. His mother and sister lived in rooms in Utica, and there was little space for another person, no matter how much they doted on him.

During July, Whitfield visited him at the farm, and on August 1, Hall offered Walcott a position as of November 1. This would be his first job in his chosen field. The offer improved Walcott's spirits, and he went off to vacation in Maine. En route, he stopped at the MCZ and spoke with the zoologist-nobleman Count Pourtales. He "... wrote Mother, Cynthia, Dr. A. S. Packard..." (August 10). After an extended stay at the seashore where he met several young ladies, Walcott retraced his route homeward. "... went into Boston 8. a. m. Called to see Mr. Bicknell & learned from him respecting sawing limestone etc. Went out to Cambridge at 10 a.m." (September 2), and had another conversation with the Count.

Walcott never forgot Lura, but he was back collecting and considering fossils. "Received letter from Count Portales [sic] & specimens of Branchipus. Also diamond dust from New York. Tried using it on wheel - failed - shall try using it again" (October 7). The enigmatic "wheel" could refer to a turning lathe, a horizontal cutting blade, or a polishing lap. Most likely, the diamond dust was used as an abrasive for cutting limestone, rather than polishing. Grinding and polishing rates are related both to the hardness and size of the abrasive, but diamond dust grinds limestone down so rapidly that there could be little control of the process. "Experimented in cutting stone. Half a failure this time" (October 9).

Over the next few days, Walcott collected at the quarry, especially from the *Ceraurus* layer. "It seemed like old times to be on the spot where I spent so many pleasant hours of work, and to me, play" (October 12). His mother dragged him off to the Philadelphia Centennial Exposition, but upon return, he plunged into research. "Busy nearly the whole day working at specimens of Asaphus" (November 6). "Also prepared C. p.'s for grinding & cutting" (November 8). "Cutting sections of C. p. in the morning" (November 9). Two days later, Walcott left the Rust farm and Utica behind him to be Hall's special assistant in Albany (Yochelson, 1987).

In the first part of a note, Walcott (1876) mentioned sections of 41 trilobites. In the second part he mentioned "numerous microscopic, transparent and opaque sections." This tends to support the idea that Walcott's earliest investigations were based on opaque [i.e. polished] sections. He had to learn new techniques and labored under primitive conditions at Trenton Falls where thin sections may have been beyond his capabilities. The estimated times for preparation accord with this supposition.

ALBANY (NOVEMBER 1876)

Once in Albany, Walcott needed several days to find a place to live. His first day in the Hall household made him realize that staying with the professor was not a good idea. However, he immediately plunged into Hall's assigned tasks. "Busy during the day at the State Museum assisting Dr. Hall at cutting sections of cephalopods. Wrote notes & sent notice of trilobite remains to Profs Dana, Packard, Newberry & Worthen" (November 16).

Walcott contacted four of the most senior geologists in America to advise them of his research. This "notice" may have been what he wrote at the end of May. In pondering why he did not distribute it earlier, one guess is that once Walcott was in Hall's employ, it seemed vital to establish his claim to the discovery of appendages. Perhaps the kindest remark one can make about Hall is that he was never shy in assuming that anything done by anyone in Albany was his to publish. If he was in a particularly good mood, Hall might extend a junior authorship to the discoverer. Walcott was the only one of Hall's assistants who was never involved in a joint publication with him. The appropriate cliche is that the "irresistible force had finally met the immovable object."

To clarify a point of possible confusion in the above quotation, the "Dr. Hall" was the son of James Hall, and was nominally in charge of the new saw (Fig. 4), as described by J. W. Hall (1884). The elder Hall (1878, p. 8, 9) noted, "In the progress of the Museum work, it has been frequently necessary to cut and polish specimens of fossils, ... Until the past year [1875] this work was done at marble cutting establishments which afforded proper facilities. This mode, however, became too expensive and uncertain as to time, and the requirements of the subjects also demanded that more delicate and perfect adaptations should be at command. It became, therefore, necessary that we should have the means at hand within the Museum building.

"In the first place, an ordinary turning lathe, operated by a treadle, was adapted to the requirements of such work, but this was found unsatisfactory, and the labor of cutting large specimens too severe. At the present time, a small steam boiler and the necessary machinery have been adapted to the lathe.... The study of the microscopic structure of rocks and fossils, has, within a few years, become an essential part of the science, and facilities of this kind are required." The small upright steam boiler was about the size of a cylindrical stove.

Determining how to study embedded trilobite legs may have been nearly as much of an accomplishment as originally discovering them. In geology, thin-sections of rock were first extensively used by petrologists, but cutting fossils to examine inner structure was a relatively new idea, despite the early work in paleobotany (discussed below). It is difficult to date when the standard use of thin-sections in studying fossils came to America, and even harder to determine when the technique came to Hall's attention.

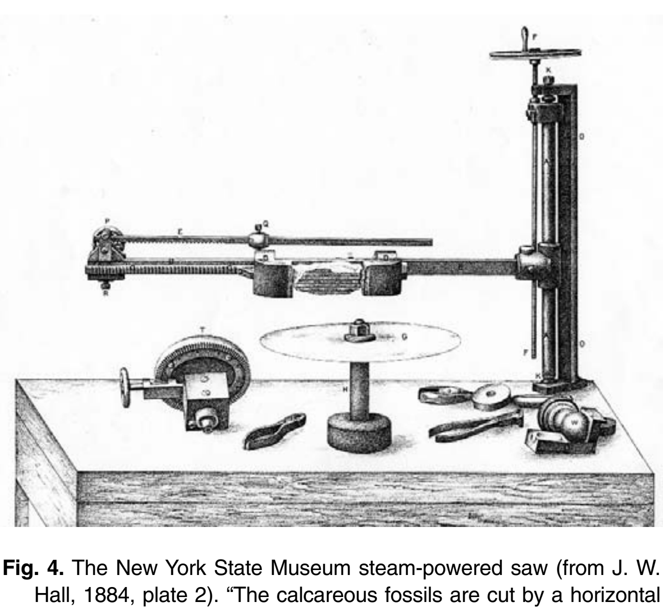

Fig. 4. The New York State Museum steam-powered saw (from J. W. Hall, 1884, plate 2). "The calcareous fossils are cut by a horizontal disk of tin, which moves at a rate of five hundred revolutions per minute; and is fed with emery and water." The funnel or hose used for feeding in the water and abrasive mixture is not shown. Plate 1 shows the devices to hold a specimen, and the key to the lettering on both plates is in the text.

The coral work of Hall (1876) includes a few polished sections, but no thin-sections. To what degree they were polished cannot be determined from Hall's (1876) figures. For a brief time in 1877, Walcott studied bryozoans, and his diary does not mention sections. Perhaps thin sections, other than Walcott's, were not then used in Albany. A decade later, a widely used British text included drawings of thin-sections of fossils (Nicholson and Lydecker, 1889). W. A. Oliver, Jr. (oral communication, 2002) restudied Simpson's (1900) coral thin-sections, and suggests that they were prepared years before Hall died. The 33rd New York State Museum Annual Report lists 69 translucent sections of brachiopods, and the 34th has a ten page list of fossils and rocks which had been sectioned, although this need not mean thin-sectioned. Both reports post-date Walcott's efforts and interesting enough, no trilobites are listed as having been sectioned. So far, the oldest thin-section published by Hall is dated as 1888 (Lindemann and Melycher, 1997).

The development of techniques, especially those of the 19th century, is not easy to trace. It is commonly accepted that opaque and thin-section investigations were early associated with sedimentary rocks and, especially, igneous rocks. Zirkel (1876) is reputed to have been the first to publish results of the microscopic petrography of American igneous rocks. An earlier British study by Henry Sorby was discussed by Dawson (1992).

Thin sections of paleobotanical specimens were prepared by techniques similar to those used in the petrographic study of rocks. Amos Eaton made several sections in 1837 by following directions received from the botanist John Torrey (Aldrich, 2000). Torrey copied this information from a British publication (Witham, 1833). Credit for the first thin-sections of petrified wood goes back even earlier to William Nicol, of Nicol prism fame (Zittel 1901; Andrews, 1980, p. 76, 77). Witham (1831) credited Nicol in the first edition of his work, but later (Witham, 1833) ignored Nicol (Morrison-Low and Nuttall, 2003). Later, Nicol gave full credit for the development of thin sections to "Mr. Sanderson," an Edinburgh lapidary. It is unlikely that Hall or Walcott knew of this literature, despite its early date, although both probably had some knowledge of thin-sections of biologic material.

PREPARATION OF THIN SECTIONS

After his brief tutelage by Dr. Hall, Walcott was cutting rocks and fossils without supervision the following day. Later, Walcott (1881, p. 191) stated "The succeeding year [1876] thin sections of Trilobites were cut from both Lower and Upper Silurian rocks." So far as is known, Walcott never published any observations on Silurian trilobites, and "Lower Silurian" at that time referred to the Ordovician System. "At 5.p.m returned to the [sic] my room. Washed emery for the purpose of making sections and then wrote an hour copying descriptions of two n. sp. of Asaphus for publication" (November 24). The abrasive, emery, is a dark variety of natural aluminum oxide, or corundum, and has a hardness of approximately 9 on the Moh's scale (limestone has a hardness of 3).

Bryne (1870, p. 352) has noted, "... particles of emery and other powders may be separated, according to their magnitudes, in a more accurate manner than can be accomplished by sieves. A portion of emery powder of uncertain size is thoroughly well mixed in a large quantity of water, as in a common wash hand-basin, and at the end of ten seconds the liquid is poured off from the sediment which has fallen down in that period; the sediment is laid aside in a separate vessel. The bulk is again stirred and poured off at ten seconds and this second sediment added to the first, and which process is repeated until no farther [sic] sediment is deposited in the period of ten seconds; the process requires watchfulness and a steady hand. A fresh deposit is similarly collected from the residue after a period of rest, say twenty seconds … ."

The sizing of emery is a strong indication that Walcott planned considerable grinding and polishing. The inference is that he now intended to make thin-sections. Distinctions between "grinding" and "polishing" refer to stages in essentially the same process. In grinding, a coarse abrasive wears away the rock relatively rapidly. When the surface is nearly smooth, a finer abrasive is used to remove the smaller irregularities. The art of polishing was known for centuries and the Taj Mahal is reputed to be the world's most highly polished building; this work may have been done with common sand. Even a few grains of coarse abrasive inadvertently mixed with the fine will destroy the polished surface.

The November diary has no further reference to trilobite preparation. On the last day of the month, Walcott recorded eating Thanksgiving dinner alone in the Museum basement, and it is a safe assumption he was there to use the saw. "The calcareous fossils are cut by a horizontal disc of tin, which moves at a rate of 500 revolutions per minute; and is fed with emery and water" (J. W. Hall, 1884, p. 122). The illustration of the saw does not indicate how the abrasive and lubricant were distributed to the saw blade (Fig. 4).

Walcott may have been able to make two parallel cuts in moments, and then trim excess limestone from the sides of the slice to form a smaller surface to grind and polish. One may infer that he made limestone pieces about two x three cm and about one cm thick. By aligning a rock with the blade, turning on the steam, adding abrasive, and sawing several cuts, a reasonable assumption is that a quarter hour or so was required to make each trimmed slice. It was a quantum leap forward in the time required. If a cut was not in the right place, the piece could be discarded for another. As a bonus, the steam-powered saw was easier on the legs.

To make a thin-section, after one surface has been polished and attached to a glass slide, grinding then begins to thin the other side of the limestone piece to transparency. If the adhesive comes loose, all is lost. More detail may be seen, but it is even more tedious to grind down the thickness of the slice than simply to grind and polish one surface. Because abrasive size is so critical, both coarse and fine laps are used, with abrasives for each kept separate, in modern work. If the NYSM had steam-powered laps at that time, one would expect them to be mentioned in connection with the saw. Walcott ground his sections during evenings in his room. If he had access to any grinding/polishing machinery, it must have been minimal. As a final step, the thinned rock may be covered with adhesive, and a cover slip of thin glass attached to protect the upper surface from harm. If not done properly, air bubbles may spoil the product. Cover slips had become common by the 1870s (James Connor, written communication, 2002), but it is impossible to determine if Walcott used them during this period; the thin-sections could have been completed later.

A number of these assumptions are based on Walcott's few words and the recollections of old-time preparators, but they form a coherent pattern. Combining the various points, each of Walcott's thin-sections probably represented two to three hours' effort. These figures should be kept in mind when considering just how busy December was for Walcott's research on trilobite appendages.

FIRST PUBLICATION OF RESULTS (DECEMBER 1876)

Walcott wrote Count Pourtales in mid-November and again in the second week of December. It is likely that Walcott was discussing his findings and was asking for advice. Unfortunately, no letters to or from Pourtales have been found. "After tea cut a thin section of C. senaria two, showing the ventral membrane beneath the axial lobe & the appendages. They end on the outside of it. It furnishes strong proof & was what I had long hoped to discover" (December 5). "Spent the evening working on sections of C. p. Mr. L. Brown watched the process. He is assistant at Prof. Hall's & seems to be a good young man & earnest in his desire to learn" (December 9). This entry shows that while cutting was performed at the Museum, grinding and polishing was done in the rooming house.

"In the evening cut & polished sections of Calymene Senaria showing appendages etc" (December 11). "Working on sections until bedtime" (December 13). "Worked on sections in the evening" (December 15). "Read, wrote & worked on sections" (December 18). "Working on sections in the evening" (December 19). "On the hill during the day. Wrote on structure of trilobites for 28th Rpt & did not return to room until 8.45 p.m." (December 20). "The hill" refers to Hall's laboratory, as the Museum was on State Street and faced toward the Hudson River.

On December 23, Walcott left for Utica. His manuscript may have gone through several hands, but it was at the printers in time for the four-page, unillustrated paper to be published in December, in advance of the 28th New York State Museum Annual Report. In January 1877, his new species from the Trenton Limestone appeared as another preprint. No copy of either preprint is in the bound set of publications that Mary Vaux Walcott prepared after her husband's death, and no copies of the 1876 preprint have been identified with certainly. Both papers appeared as part of an Executive Document in 1877. The 28th New York State Museum Annual Report was not published until 1879, but because this is the source most readily available, pagination is cited from it.

Fortey (2000, p. 61) noted about the report—"It carried the ponderous title 'Preliminary notice of the discovery of the remains of the natatory and branchial appendages of trilobites.' While true to the letter of the discovery, it could scarcely be a best-seller with that title." The title's first two words indicate the caution that Walcott practiced though his career. An interesting aspect of this report is that two and one-half pages of text end with an address "TRENTON FALLS, *May* 26, 1876. This made abundantly clear that the ideas were Walcott's and Walcott's alone. From what is known about Hall, it seems almost incredible that the address line was printed. Slightly more than another page of text follows. It is titled "Note of Additional Evidence Obtained since the above was Written," and concludes with the address "N.Y. State Museum of Nat. Hist., *December*, 1876."

Walcott (1876, p. 89) noted, "In only two layers of a fine, bluish-gray sediment, were trilobites found which had structural remains preserved beneath the dorsal shell." T. Whiteley (oral communication, 2000) observed that no other layer in the quarry has quite a comparable fauna or fossil preservation. Thus, the second layer is unknown today, but it could have been the source of the *Calymene* specimens that Walcott sectioned.

"The remains, with the exception of the hypostoma, appear to be of a semi-calcified nature, as if a thin membrane had enclosed them until the organic substance had been replaced. Frequently all traces of structure are destroyed by the presence of crystallized calcite" (Walcott, 1876, p. 89). He listed four species which showed "organic structure" below the carapace.

Most of the data came from twenty-one sections of *Ceraurus pleurexanthemus*; both transverse and longitudinal sections are mentioned. Walcott noted short and unjointed, cylindrical supports for swimming lobes, or rudimentary walking legs. "The three pair of appendages beneath the head, present an obscurely jointed structure" (Walcott, 1876, p. 89). Jointed appendages are a key feature that place trilobites within the Arthropoda.

Fifteen of these sections showed branchial appendages "... beneath the pleural lobes near the union with the free pleurae" (Walcott, 1876, p. 90). Walcott reported obliquely inclined bars, which varied slightly in position, and suggested they were attached to fleshy material no longer preserved. The branchial appendages were longer than the axial appendages. He also indicated the presence of a membrane below the axial lobe, but found no evidence of a ventral membrane.

Walcott indicated that twelve specimens of *Calymene senaria* showed axial appendages, and one specimen had twenty-one on one side. He mentioned that the branchial appendages were generally similar to those of *Ceraurus,* and in one specimen, were in life position. Walcott remarked that *Acidaspsis trentonensis* had a ventral surface like that of *Ceraurus pleurexanthemus*. It is unlikely that Walcott's reference to a second layer was where he obtained *Asaphus* and *Acidaspis* for sectioning, as no appendages are mentioned for either of these forms.The penultimate paragraph is concerned with *Asaphus gigas platycephalus*. He confirmed Billings' discovery that the ventral surface was strengthened by arches which formed the attachment for the double row of appendages. He then remarked that this was further evidence to reinforce the interpretation that trilobites swam on their backs. This hypothesis is discussed below in Appendix 1.

"The central or axial series were either attachments of swimming lobes, or rudimentary, ambulatory legs. The lateral series were branchial in their structure, the bars serving as points of attachment for the lamellae. It is probable that they were also used in swimming. Many sections show appendages beneath the head, but nothing satisfactory can be established from them. As the writer has a large amount of material from the same locality, which is unworked, he hopes to present in a future article a series of descriptions and illustrations, giving the structure of the ventral surface and appendages of the trilobite" (Walcott, 1876, p. 91).

His further discussion involved the branchia. "The perfect state of preservation of the delicate branchial appendages and the ventral membrane precludes the idea of the destruction of any thing of a stronger texture than fleshy swimming lobes attached to the axial appendages. The axial appendages could not have reached to the surface upon which the edges of the pleurae rested, which negates the view that their being in any way ambulatory, in case the non-presence of articulations, in the appendages, should be called into the question" (Walcott, 1876, p. 92).

The preprint received a review of nearly a full page (Packard, 1877a) and an equally complimentary one half as long (Dana, 1877a). Walcott was in new territory, and was a long way from a clear understanding of trilobite appendages, but he had found them. It was a first step toward establishing Walcott's reputation as a serious scientist. Equally impressive to those who knew Hall and his ways, the two-part nature of the note was unchanged when it appeared in the long-delayed 28th New York State Museum Annual Report.

ALBANY (JANUARY–JUNE 1877)

Hall kept his special assistant fully occupied without any official time for private research. Walcott was involved in the final stages of preparing Volume V, Part II of the Palaeontology of New York. He divided his time between the Museum and Hall's private laboratory, as the Professor's priorities shifted almost daily. The preparation and study of trilobite appendages continued after regular work hours in Walcott's rented room.

"Busy with sections during the evening" (January 10). "After tea busied myself sending away a notice of my trilobite work etc." (January 12). "Also sent off copies of my notice of trilobite remains" (January 14). This was Sunday and while Walcott took his religion quite seriously, mailing reprints, a pleasurable activity for a budding scientist, could not be considered breaking the Sabbath.

"After tea working on sections" (January 15). "... in museum until 5.30 p.m... . Worked on sections until 8.30 p.m." (January 18). "Worked on sections in the evening had unusual success. Found a lot of eggs (?) In a c.p. & also the attachment of the axial appendage" (January 19). "In the evening worked at sections & cleaned up for Sunday" (January 20). " Polished sections during the evening. Am getting along nicely with sections. Hope to have all the material I have worked up by March 1st" (January 22). "After tea worked on section until 8. p.m." (January 23).

On January 24, Walcott noted working on sections at the Museum. This may have involved cutting specimens, as he added, "In the evening busied myself on my own sections. I hope to get through this work soon, so that I can read & write evenings" "Returned to room at 5. p.m. Mounted several sections and blocked out a letter to Henry Woodward, Esq. Eng. .... This has been a very severe week, as I am nearly exhausted & feel dispirited over my health" (January 27). "Working on Prof. Hall's collection at his private museum. I am hardly in fit condition to work as both my nerves and physical condition is [sic] anything but good. Shall keep at it however, as I may improve in a week or two. After examined & worked at sections. Found jointed appendages, probably antennae by the side of the hypostoma. Retired at nine o'clock" (January 30).

Despite concerns about his health, Walcott ended the month on a positive note. "After tea worked on sections until 8.p.m.

My work on sections has advanced rapidly & successfully" (January 31).

February diary entries have fewer references to this work. "After supper worked on sections until 8.15.p.m" (February 1). "Feeling better this evening & working on sections" (February 2). "... returned to room & spent half an hour sorting out sections" (February 5). "Wrote letter to Woodward and sent it to Josie to copy. Post card to A. S. Packard" (February 6). His sister Josie had handwriting that was far better than his, and a neatly copied letter was required for Henry Woodward, who was perhaps even more important to Walcott than Packard.

Walcott sectioned all the rock he had taken to Albany, and took a quick trip to the Rust farmhouse. "Busy most of the day searching for trilobites that I can cut up for evidence in relation to the anatomy of the trilobite. Succeeded in getting 30" (February 22). When Walcott returned to Albany, he cut these additional rocks, as four items of preparation are mentioned in March. "Working on sections after supper" (March 1). "Quite tired at night but worked on sections until bed time 9.p.m" (March 5). "Worked on my sections from 5. p.m. until 6.30" (March 8). "Worked on sections in the evening" (March 9). There are no other similar entries, but he could hardly have finished 30 sections in that short time, and it may be that some material he had selected turned out to be useless when cut.

In addition to other duties, Hall had Walcott spend much of his time at the state Capitol to watch legislative actions of concern and lobby on Hall's behalf. This was nearly Walcott's final straw in his relationship with Hall, but shortly thereafter life became a little better. In mid-March, Walcott moved to more congenial lodgings at 184 South Swan Street where he shared a sitting room with Mr. Brown. The house was midway between Hall's laboratory and the Museum, and this reduced the time spent walking. A large portion of old Albany was razed in the 1960s to build the modern Empire State Plaza government complex. However, Walcott's old rooming house remained for years, and, fittingly enough, was close to the present location of the New York State Museum.

Three further diary entries for the month suggest Walcott's varying states of mind. "When tired and lonely how naturally the mind returns to thoughts of home & loneliness" (March 19). "Letter from Mr. Henry Hicks of London. He confirms my view of the trilobite swimming on its back as far as circumstantial evidence can" (March 20). On Walcott's 27th birthday, he noted, "Am recovering from the shock of Lura's illness & death as rapidly as I can expect" (March 31). At least this was better than the despair of the previous year.

The legislature remained in session afternoons and many evenings, and Walcott found his lobbying duties for Hall increasingly onerous and eroding his private time. "After tea examined sections of trilobites" (April 13). "After tea busied myself with d[e]s[cri]pt[ion]s of fossils & comparisons of same" (April 16). "After tea working on descriptions of fossils until my head ached & then used battery & retired" (April 17). Walcott was indeed hooked himself up to an electric storage battery to receive a jolt; he had been doing this for some years in Utica. There are no further diary entries that spring on trilobite sections.

Once the legislative session ended, Hall had Walcott moving from one chore to the next. Late in May, he visited the Rust farm again. "Read papers ate supper & then wrote an hour on note respecting trilobite eggs" (May 24). In the January 19 entry he reported finding "eggs [?]." On the fourth of June, Walcott recorded writing for an hour, though the subject was not specified. In mid-June, he collected at Saratoga Springs, and late in June went off to collect Devonian fossils in the Helderberg Mountains.

RESEARCH, VACATION, AND FIELD WORK (JULY–DECEMBER 1877)

After Walcott returned from the Helderbergs, he recorded a key sentence in his diary. "Worked at reviewing what I have written for the 29th Regents R[e]p[or]t. Also commenced a note on some of my trilobite sections" (July 10). The first comment refers to a manuscript on Chazy and Trenton fossils (Walcott, 1877d) which also appeared as a preprint. Printing of the Annual Report had fallen far behind, and this paper reappeared in the 31th report, issued in 1879.

"Wrote a little in the morning .... Worked on my paper after dinner...." (July 11). "Busy two thirds of the day studying on my trilobite sections. Find that they show much more than I anticipated they would. The more I study them & compare them with the recent Crustacea the more readily I can see the true relations of the various fragmentary parts" (July 12). "In my room writing until 3. p.m. Found that the branchial & axial appendages of trilobites belong to the same central system of appendages" (July 13).

The following day, Walcott "... packed up my things at my room and worked a little on sections of C.s. & C.p." (July 14). He took a quick trip three day trip to Trenton Falls. Back in Albany, he "Examined sections until dark" (July 17). "Spent most of the day writing & studying on section of trilobites. I find that my knowledge is not equal to the work. I wish to publish a note of progress & delay further action until I obtain better material & can study it more throughly" (July 18). "Returned [to my room] & wrote to Jessie [at Rust farm] & worked on my paper for an hour" (July 18). A later letter mentions that he submitted his manuscript at this time.

Walcott left for a vacation in Maine, and then went to Saint John, New Brunswick. To a paleontologist, a vacation can involve visiting new outcrops. At Saint John, he met George Frederic Matthew (see Landing and Miller, 1988), and collected Primordial fossils. Barrande's Primordial Silurian was being equated with Sedgwick's Cambrian, but "Primordial" was still in common use (Yochelson, 1993). In Saint John, he met Alpheus Hyatt, his first extended contact with someone familiar with both living and fossil marine invertebrates. "He advises me to publish immediately as he thinks it worthwhile" (August 4). Walcott met Hyatt the previous day, and that may have prompted him to write to J. A. Lintner, an entomologist and museum senior curator responsible for its publications. "You were very kind to push forward my article at the cost of delay of your own. I was not aware but that the entire amount to be printed could be set up & proofs struck within a week or two. I like to push things through & get them off my hands as soon as possible, and in this case there was a little more of an incentive so I used more persuasion than may have been needed" (Yochelson, 1998, p. 62).

After collecting in Saint John, Walcott returned to Eastport, Maine. "Found Prof Hyatt in his room. Also Messrs. Van Vleck & Gardiner. Spent the afternoon studying on the structure of the macroran [?] Decapods and talking over the structure of trilobite with Mr Van Vleck (August 15). "Worked at Prof. Hyatts laboratory. Determined from my present knowledge that the trilobites' branchia arm[?] or appendage is homologous with the expodite [sic] of the lobster etc at its third stage of development (m.i[?]) before the branchiae are withdrawn into the branchial cavity" (August 16). "Returned at 4.p.m. and worked until 9.30 p.m. on my attempt to homologize the trilobite with recent crustaceans. Prof. Hyatt & Mr. Van Vleck are assisting me in every way they can" (August 17).

"Spent the day at the laboratory working on crustacea etc." (August 18). He ended up talking with Hyatt until 10 PM. The following day was Sunday, but Walcott bent his rules on his last day in Maine, and went sailing with Prof. Hyatt and the students. Walcott returned via Boston, where he tried unsuccessfully to contact A. S. Packard.

By the last week of August, he was back at the Rust farm breaking rocks at Gray's Brook and commenting that it was like old times. The idyll persisted, with Walcott collecting material from his "C.p. layer." Saturday, September 15, he was back in Albany, and the following day Walcott called on Mr. Ast, one of Hall's lithographers. "Before tea went down to see about my trilobite article. It is ready for its final printing. It is not as full & complete as it should be, but still must answer as I have no more time for it now" (September 20) (Fig. 5).

Shortly after the paper was published, Hall sent Walcott to collect in the Silurian of Indiana, though a few younger outcrops were investigated. More germane to this study, Walcott spent a few days in Cincinnati with a number of local collectors. At Trenton Falls, he had exchanged fossils with several of them, but this was his first and only meeting with these early members of the "Cincinnati school." He absorbed several tales of intense dislike of James Hall, but the locals had the opportunity to judge he was of different sort. This visit paid dividends in a later study of trilobite appendages as he eventually obtained a unique specimen (Walcott, 1884; Yochelson, 2003).

A few more diary comments for the year are of interest. "Letter from Dr. Packard" (October 24). "Wrote Dr. Packard after breakfast. Told him about my view[s?] of my working on the trilobite" (October 25). When Walcott summed up events on December 31, after his first full year in Albany, he remarked in his diary that 1877 was a good year.

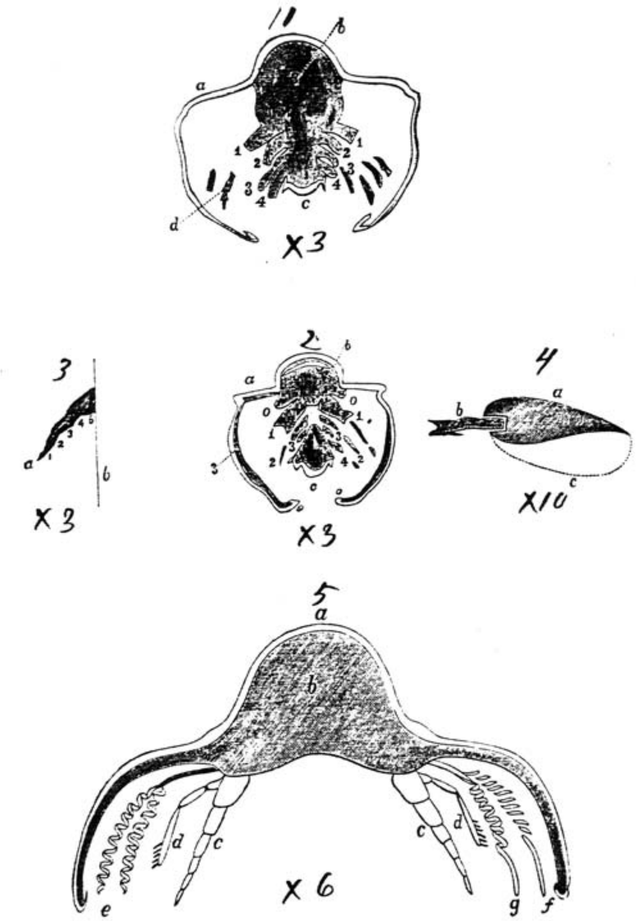

Fig. 5. Copy of the illustration from the preprint (Walcott,1877a). Figure 1 is a transverse section of the head of *Calymene senaria*. Key: a = dorsal shell; b = visceral cavity; c = hypostoma; d = terminal joints of manductory legs. 1 = coxa of posterior manductory leg; 2 ,3, 4 = manducatory appendages or legs. Figure 2 is a transverse section as in figure 1; e = membraneous crust that connects visceral cavity and doublure; o = base of fourth pair of manducatory legs. Figure 3 is a "Section of the leg or axial appendages of *Ceraurus pleurexanthemus*." The joints of the leg are numbered 1–5; a = terminal claw, and b = edge of section. Figure 4 is the "Supposed swimming foot or terminal joint of posterior manducatory leg" with a = terminal joint; b = three small joints and spines; c = restored outline. Figure 5 is a "Transverse section of the thorax of *Calymene* partially restored." Key: a = dorsal shell; b = visceral cavity; c = legs, restored; d = epipodite; e = spiral gills as seen in detached condition in other sections; f = actual section of spiral gill; g = same restored; o = continuation of visceral cavity to edge of dorsal shell [this is not evident unless it at the lower right near "f." Walcott noted that with the exception of part of figure 5 which was restored, "the figures are each a copy of a section." In the 1879 version, figures 6 and 7 were added

"NOTES ON SOME SECTIONS OF TRILOBITES, FROM THE TRENTON LIMESTONE"

This work appeared first as a preprint, and the top of an unnumbered page states "Printed in advance of Report of New York State Museum of Natural History, September 20, 1877" (Walcott, 1877b). The title is written below this statement, with "from" and the remainder of the words in smaller capitals. "Plate I" is on the unnumbered caption page after page 7, but not on the plate; the five figures are unnumbered, and the magnifications were added by hand. The page after the plate is blank. Page 11 has the heading "NOTE UPON THE EGGS OF THE TRILOBITE" (Walcott, 1877b), a report that continues onto page 13. Both articles bear the name of C. D. Walcott. This preprint is followed by Walcott's (1877a) paper on "Descriptions" beginning with page 15. The copy has a title page, hand-written by Walcott that lists the two works.

Another version of this report exists with the title page printed, but the text of the two parts unchanged in typography and pagination. The text for the plate is identical, but the plate has two extra figures, with no explanation. "Plate I" is written in at the top, and another ink was used to write in the magnifications and numbers for all seven figures.

When the 31st New York State Annual Report came out, the pagination was changed. A note inserted between text on the "sections" and the "eggs" clarified figures 6 and 7 (Walcott, 1879a). S. A. Miller had sent Walcott a slab from Cincinnati that had on its surface "a slender size jointed leg of some crustacean" and other fragments. Walcott noted a "strong resemblance" to the legs discussed by Billings (1870). Miller later lent another slab showing several legs. Curiously, what might be the figured leg is in the trilobite collections of the National Museum of Natural History in Washington rather than the MCZ (F. Collier, oral communication, 2001).

To add one more layer of confusion, there is also an 1879 reprint paginated 1–12 that contains all three notes. This reprint and the annual report carry a footnote mentioning the 1877 preprint, and also note the figures (6 and 7) which were not in the original. It is best to cite the pagination from the more widely distributed 1879 printing, even if this makes an editor apoplectic (see Appendix 2).

Walcott packed a great deal of information into a few pages. "Within a month after the above was written [i.e., the notice of December 1876], a section was obtained that showed that the axial appendage articulated to the ventral surface, but, also, that it was a jointed appendage. Six months later the branchial appendages were found" (1877b, p. 61). Walcott went on to describe the appendages in *Calymene* and *Ceraurus*.

Five points are "... intended to show the progress made up to the present date, and not as a final publication" (Walcott, 1877b, p. 63). A summary of four of them includes: 1) ventral membrane supported appendages; 2) the appendages are on either side of the trilobite; 3) the jointed appendage, attached to the leg basal joint, may be equivalent to the epipodite of living crustaceans; and 4) posterior of the hypostoma, the mouth consists of four pairs of jaws. Based on the apparent equivalence of the epipodites, Walcott placed the trilobites as a third order within the Class Crustacea and in the Subclass Gnathopoda, along with Xiphosura and Eurypterida.

The remaining point was "The respiratory apparatus consists of a gill bearing appendage attached to the thoracic leg and a bifed spiral gill attached to the side of the thoracic cavity. The setiferous appendages attached to, or above, the manducatory legs are modified thoracic branchiae" (Walcott, 1877b, p. 64). The basic error of a spiral gill was never corrected. Walcott's note has a better interpretation. In thin-sections, one does see short parallel segments which could easily be interpreted as the whorls of a spiral. It is perhaps understandable that, with the walking legs so similar to living forms, one might hope this was a different feature of trilobites, and was more exotic.

The second and final paragraph of the little note on legs is a single sentence. "A discussion of the views of various authors upon the structure and relations of the Trilobite is reserved for a future article, in which, also, the structure of the mouth and branchiae of the Trilobite will be given more fully than in the preceding article" (Walcott, 1879a, p. 64).

A. S. Packard (1877b, p. 694) reviewed Walcott's paper, and ended on an attempt at humor. "The discovery of the nature of the limbs of trilobites 'adds a fresh laurel,' to use a fossilized expression, to American palaeontology." Walcott's opinion of the review was "It says very little about it" (November 15). He should have been happy with Packard's comments, for the following month another review of twenty lines doubted the organic nature of the eggs, and for good measure included "More sections are needed before the facts observed can be satisfactorily interpreted" (Dana, 1877b).

Packard (1882, p. 408) later used one of Walcott's figures in a major study of crustaceans. "In the trilobites, however, as may be seen by Mr. Walcott's able reconstruction, we have attached to the thoracic ambulatory feet a respiratory epipodial portion. In some respects, then, in the trilobites we have a style of structure intermediate between the Merostomata and Decapoda." A section of this major paper was reprinted and widely distributed (Packard, 1882b). Dr. Packard did well by Mr. Walcott.

SUBSEQUENT EVENTS (1879–1881)

During his stay in Albany, Walcott continued making thin-sections as time permitted (Yochelson, 1998). In his 1878 diary, Walcott had a little note that 122 sections were made before 1878, and 95 in 1878. The total of 217 were labeled "trilobites," and below that figure is "Opaque 25". This year was not so satisfactory as 1877, and in December 1878 Hall terminated Walcott's contract. They had had several arguments, and Hall believed that Walcott was disloyal.

Walcott remained in Albany for another six months, and continued his trilobite studies (Walcott, 1879b). In mid-April 1879, Walcott lectured on trilobites at the Albany Institute. The [Albany] *Argus* newspaper recorded that James Hall noted that this talk was the "first definite statement of the facts in the history of this animal, and has only been obtained by several years study of over 2,000 sections made by Mr. Walcott." The figure of 2,000 sections has been confirmed elsewhere (Mickleborough, 1883; Yochelson, 2003), and must include the rocks which were cut, though not necessarily polished. Except as quoted above, use of the saw is not mentioned in Walcott's diary. Assuming five cuts of limestone per hour, 2,000 sections constitutes a great deal of overtime effort, quite apart from the slices made into thin sections.

Early in 1879, Walcott wrote to Clarence King, Director of the new U. S. Geological Survey (USGS), as did Hall, despite their previous falling out, but neither received a reply. Late in June, with no prospects whatsoever, Walcott began packing to move back to the Rust farm. Quite unexpectedly, a letter arrived from Washington, with the result that on July 21, 1879, Walcott became USGS employee number 20. He was a geological assistant, at $50 per month and at only two thirds of the salary that Hall had paid him. Unexpectedly, Walcott was sent to southwest Utah, and assigned to measure and collect from all the strata. After measuring 13,000 feet of rocks he returned to Washington, and during the winter and spring of 1880 prepared his reports.

Walcott performed an outstanding job in the southwest, and July 1, 1880, he was promoted to assistant geologist, a permanent position that paid $1000 a year. Because Walcott had been so prompt and efficient in his assigned project that spring, King allowed him official time to complete study of his trilobite material (Walcott, 1881). This work fulfilled his promise of 1879 for a more complete paper.

REPOSITORY OF WALCOTT'S TRILOBITE SECTIONS

L. Hernick, NYSM (written communication, 2001), searched the New York State Museum fossil collections for any of Walcott's sections. She noted, " We do not have any specimens [*Calymene senaria* and *Ceraurus pleurexanthemus*] specifically of Walcott's. We do, however, have several from the William Rust collection. On several specimens from Rust there are cuts perpendicular to the bedding plane, and parallel cuts. There are no polished slabs and no glass slides. There are no specific dates of collection or preparation available on the cut specimens — the NYSM purchased the collection in 1890. There is no way, then, of knowing when the cuts were made." Walcott had maintained full control of all material during his years in Albany. Perhaps Walcott reasoned that none of the complete trilobites, thin-sections, nor the intellectual ideas they provided were the property of the Museum, and especially not the property of James Hall.

An alternative interpretation of Walcott's failure to reposit his trilobite sections in the NYSM is that it was more than ethically questionable. Walcott was indeed a salaried employee of the State Museum, and should not, at least by modern standards, have put together a collection that competed with the museum. Similarly, the museum had published a number of Walcott's first reports on trilobite appendages, and he had removed a part of his employer's (i.e., the state's) heritage that the museum could have cared for. By such personal decisions, the NYSM lost a number of important collections over the years. For example, at a time of state budget crisis, James Hall sold most of the existing type specimens during the 1890s to such institutions as the American Museum of Natural History and Field Museum. Similarly, with his departure as Assistant State Paleontologist, the late Rousseau Flower took most of the Lower Ordovician cephalopod type specimens that he had collected in eastern New York, and reposited them at the New Mexico Bureau of Mines.

Because the MCZ published his 1881 work, it is somewhat understandable that the figured material would be deposited there. T. Whiteley (written communication, 2002) has begun a project to digitize Walcott's slides, and has made observations on the sections. He notes, "There are 285 slides in the MCZ and 38 in the USNM [catalogue designation for National Museum of Natural History] (6 in the type files). I can identify 21 slides which Walcott used in his 1881 paper; 15 of these have cover slips. 10 slides in the MCZ have black masking paint around the specimen and 7 of these have no cover slip. 25 slides in the MCZ have maroon masking around the specimen and 14 of these have no cover slips. The black and maroon masking was something later applied to improve the photograph. Since these were backlit it would reduce the glare into the lens" (Fig. 6).

The sections were numbered, probably during P. E. Raymond's tenure at the MCZ, but from these numbers one cannot determine the sequence in which they were made. It is like-

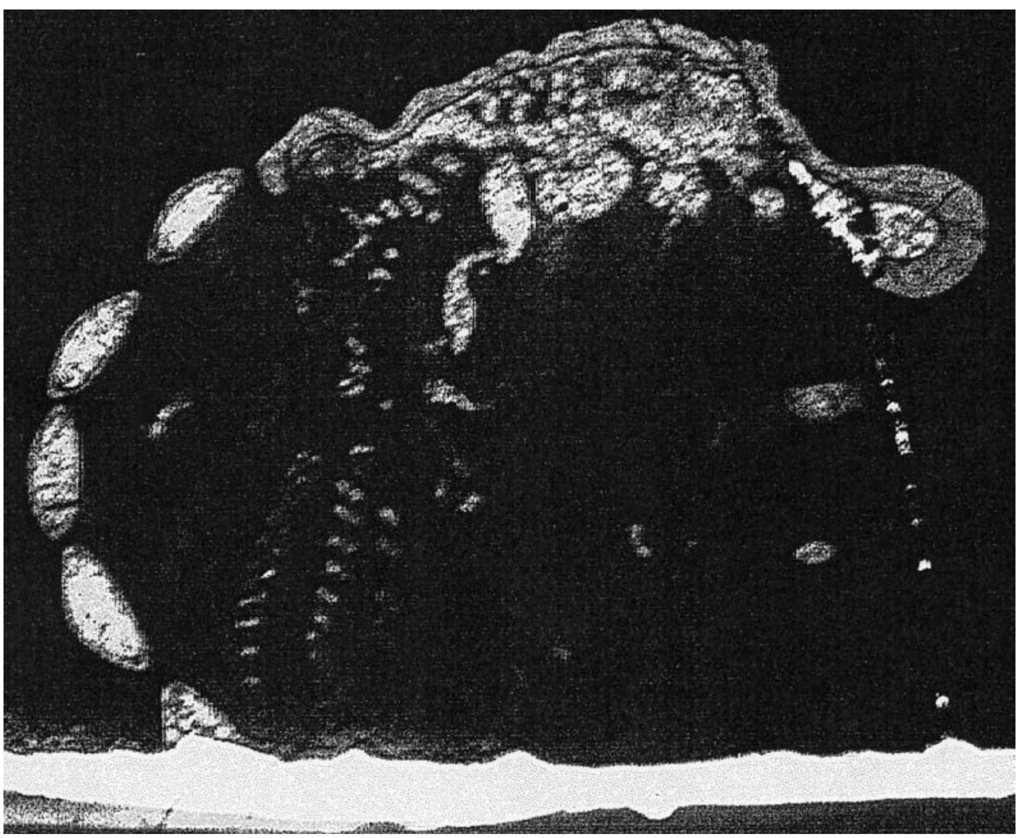

Fig. 6. Photograph of Walcott slide 8867, MCZ, showing the apparent "bifed spiral" gills or appendages, ca. x 10. Photograph by T. E. Whiteley.

ly that those with cover slips were made later than the others, and eventually the early Trenton Falls material might be sorted out. "The glass used in the slides varies a great deal in thickness and except for the USNM slides most appear to be cut from larger pieces of glass, possibly single strength window glass. The glass used [for mounting] varies from 1.1 to 2.4 mm in thickness and the specimens from 0.1 to 0.2 mm in thickness. This figure is highly variable because the specimen thickness on those with cover slips is at best a guess" (T. Whiteley, written communication, 2002). T. Whiteley (oral communication 2002) judges that because of their thickness, the thin-sections are better described as translucent rather than transparent. More than 30 sections were illustrated by Walcott, but matching sections to figures is a challenge.

One cut blank of limestone attached to a glass slide fits the speculated dimensions discussed in connection with the steam-powered saw in Albany. Indeed, all of my notions on preparation technique were written prior to examining the slide collection. Insofar as one can reconstruct technique from the finished product, they confirm the comments given herein.

DISCUSSION

The English translation of Burmeister (1846), based on his German publication in 1843, had a profound impact, as it was essentially a compendium of all that was then known of trilobites. In a sense, it may have been comparable to a section of the modern Treatise on Invertebrate Paleontology. During the latter part of the 19th century, paleontologists tended toward increasing specialization as both the number and kinds of known fossils proliferated. Walcott's work could never have had the impact of a more general work three decades earlier. In terms of its "impact," today's publication of yet another volume of the Treatise does not rank as high.

Burmeister's publication was monographic, whereas Walcott's was far smaller, and had only 33 pages and six plates (although Whiteley notes at least 21 slides were illustrated by drawings, but there may have been as many as 34). Most of Walcott's text was devoted to a specialized feature of morphology hardly mentioned by earlier investigators. Thus, any comparison to an older publication is difficult. Perhaps a fair evaluation is that during the next four decades, Walcott (1881) would have been required reading for anyone interested in trilobites. The bulletin was a milestone in trilobite studies, and, in a more general sense, a major contribution to paleobiology, long before that term was coined.

At that time, there were only two journals in America likely to publish Walcott's (1881) effort, and it was mentioned in both. Dana (1881) gave it 21 lines, rather than the 20 for his 1876 paper. The first half of his comments were supportive, but he remarked about the "ambiguous organ" which Walcott thought to be gills. Then, "A restoration' of *Calymene senaria* is given ... The series of legs looks very doubtful, for ... it seems incomprehensive that ... dissections should be needed for their discovery" (Dana, 1881, p. 79). The argument was that a large trilobite ought to have large legs unless they were "thin membraneous articulated appendages such as have hitherto been attributed to Trilobites." Dana did not record who had expressed that particular view, but indicated that Walcott had misinterpreted what he had seen.

In contrast, Packard (1882c) summarized in nearly a full page all of Walcott's main points and presented a fair review and a minor tribute. "We congratulate the author on the success of his long-continued efforts and well-directed labors; he has fully demonstrated that Trilobites have slender jointed limbs on the general plan of those of Limulus, and not phyllopodous ones; while he has also shown that the branchiae were also attached to certain of these limbs, though we may not be satisfied with his interpretation of the nature of these gills, and wait for further light on this extremely difficult point. His restoration of a Trilobite will be useful, although it does not seem entirely natural, but yet may express the results of Mr. Walcott's work thus far. He has settled, however, in an admirable way the general nature of the appendages of the Trilobite, and is entitled to the thanks of palaeontologists" (Packard, 1882c, p. 41).

The first sentence of Walcott's paper set the tone. "This publication terminates, for the present, an investigation that has occupied much time and attention during the last seven years" (Walcott, 1881, p. 191). On the next page, he mentions "... there are but 270 sections, affording more or less satisfactory evidence of their presence [appendages]." As regards preparation, the caption for figures 1 and 2 on plate 1, suggests they were cut from the same specimen. If these were serial sections, it was a major step forward in technique.

Walcott still interpreted the gills as spiral features, and included drawings of *Cyamus scammoni* Dall, an arthropod that lives on the skin of whales, to support his reconstruction. He never changed his view on the gills, and was wrong in his interpretation. Inasmuch as the description of trilobite legs started from essentially zero, subsequent studies indicate he had the essential features mostly correct. When better preserved trilobites from the Upper Ordovician near Rome, New York, and the Middle Cambrian Burgess Shale became available, Walcott reviewed his 1881 work, but that story is too long to be considered here.

Walcott (1875c) supported Burmeister's interpretation the trilobites swam with carapace down. However, " .... with the discovery of ambulatory thoracic legs the view of their living in that position was necessarily abandoned" (Walcott, 1881). Despite what Walcott now wrote, the swimming of trilobites though the water with their legs upward persisted from some years, especially in a few artistic renditions. Although it is unlikely that trilobites swam with the legs upward, similar to the habit of *Limulus*, this statement of Walcott cannot be proven.

An old aphorism regards genius as 1% inspiration and 99% perspiration. Walcott (1881) reported he had 2,200 trilobites "... in a condition to warrant sections being made. ... It is very difficult, after obtaining the material, to cut a section so as to show what might be preserved within the dorsal shell" (Walcott, 1881). To downplay Walcott's time and effort is easy, for given the right material and modern machinery, almost anyone could duplicate his preparations in a few weeks. This view recalls a demonstration by Columbus of how to stand an egg on end; one need only support it in a pile of salt, and then obviously anyone can do it.

Having the right material is a consideration, as Walcott emphasized that only the quarry yielded appropriate specimens for sectioning. "This fact once established led to the working of the prolific stratum. The soil and rock to a depth of nine feet was removed over a large area, to obtain the fossils scattered through the thin layer of limestone. From this area there were taken over 3,500 Trilobites ..." (Walcott, 1881, p. 191, 192). During mid-

October 1875, he had 1160 specimens on hand. To have tripled that number required a great deal of pick and shovel work. There may be some truth, after all, in that well-worn saying about the amount of sweat needed. It may be wise to end on a more recent comment on trilobite legs. "Those limbs with two branches that C. D. Walcott laboured so hard to reveal turn out to be very common among all manner of Cambrian soft-bodied arthropods, too" (Fortey, 2000, p. 137).

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Archivists at Brown and Harvard universities searched unsuccessfully for the correspondence of A. S. Packard and L. F. Pourtales. The Smithsonian Institution Archives staff was helpful with Walcott's diaries and papers from Record Unit 7004. The location of other archival material cited herein may be determined from notes in Yochelson (1998). In 2001, Collier allowed me to see the Walcott sections; he also read and improved an earlier draft. This same chore was performed by T. Whiteley, who added significant comments to the text, shared his unpublished information on the Walcott sections, and supplied the original of one illustration. F. Shaw and an anonymous reviewer critiqued the manuscript. Paragraph two in the section "Repository of Walcott's trilobite sections" was added in editing by E. Landing.

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APPENDIX 1—THE LIFE POSITION OF TRILOBITES

Walcott's (1875a, b) third and fourth papers are on *Ceraurus pleurexanthemus* Green. Nowhere in the two pages of description or the illustration in the latter (Walcott, 1875d) is there mention of appendages or life position. The larger work (Walcott (1875c, p. 158) also does not mention legs, but does paraphrase Burmeister (1846) on the life habit of trilobites, "2. That they swam in an inverted position, the belly upward, the back downward and that they made use of their power of rolling themselves into a ball, as a defense against attack from above." The thrust of the paper was to support this interpretation, based on Walcott's collecting. It closes with "Note. To October 16, 1875, 1160 specimens of *Ceraurus pleurexanthemus* have been noted on the under surface of the thin layer ("Ceraurus layer"). Of these 1110 lay on their backs; while but fifty presented the dorsal surface up. Forty-five of these fifty were very small, the remaining five of medium size" (Walcott, 1875c, p. 159).

Walcott's support of Burmeister's view was based on careful observation. In the Walcott papers (Smithsonian Institution Archives, box 32, folder 6) is a small booklet written in pencil, "Record of Trilobites to September 4" 1875. Calcareous Band Gray Brook." Part of the booklet lists dates and number of specimens, and records whether they were in dorsal or ventral position. Lists for "under surface of thin layer" begin July 30, 1874, and continue for six days, to which are added some earlier observations for 222 specimens. The list begins again on April 24, 1875, and notes two more days in April, seven in May, four in June, three in July, five in August, and two in September. He also made notes of trilobite positions in the "Upper surface of c.p. layer."

No attempt has been made to correlate the days listed with diary entries, but it is clear from those dates that farm chores often prevented Walcott from going to the quarry. The long cold season in the Trenton Falls area did not permit much collecting before April or after early October. Walcott also made some records for the "Starfish layer," where a greater variety of trilobites were found. In the quotation below is the recognition of three co-occurring species of *Asaphus*. Apparently at the start of his career, Walcott had a poor idea of population variation.

Between several pages of lists is a section dated "July 11, 1874, 4.P.M.," some parts of which appear in his 1875 and 1881 papers. These comments might mark this point where Walcott made the transition from being a professional collector of fossils to a paleontologist. The transcript is as accurate as can be made, and distinguishing punctuation from blemishes in the poor paper is uncertain. One should recall that "Silurian" of 1874 was divided into Upper and Lower, the latter becoming the Ordovician (Yochelson, 1997). It is also likely that the "corals" referred to below are actually bryozoans.

"On the brook resting after half a day of hard work, which has resulted in a few poor specimens. The spot where I am now working was formerly the bed of a quiet sea. The fine even deposit of blue limestone & the perfect preservation of the delicate corals proves this. The lower layer is a fine sediment containing an occasional Ceraurus, which however cannot be saved, as in cleaning the stone from [the words 'the trilobite' are crossed out] the fragile crust of the Trilobite breaks and clings to the matrix. It is upon the exterior surface of this layer that illustrates the profuseness of life in the Silurian sea of this spot. The upper surface holds Poteocrinus and an occasional Ceraurus dorsal side up. The under surface has 7 species Trilobites, 3 of Crinoidea, 6 of corals, 2 Conularia, 5 of brachiopods. The Ceraurus were gregarious, and when found in great numbers generally occupied the surface to the exclusion of other species. The crinoids, corals, Asidaspis, Calymene associated, and few scattered Ceraurus were met with among the crinoids etc. Over a surface about 10 feet sq[uare], the curcul [?circle] on bases of Chaetetes lycopora nearly covered the rock. Crinoids lay over them, and several Asidaspis were attached to the hollow surface of the coral. Some of the corals were complete, as found in other localities. All have the appearance of having been stopped in their growth by a deposit of fine clay which covering and protecting the fossils at the same time formed a base upon which they adhered. Of 300 ceraurus found attached to under surface of this layer about 1/10 had the ventral surface up. All the rest were back down which probably was the position in which they swam, as specimens ranging from 1/8 to 2^{in} in length were found in this position. The most perfect & delicate specimens always occur in that position. The Acidaspis the same [?]. The Calymene are few in number and are in all positions.

"The succeeding layer is from 6 to 8^{in} in thickness and composed of two distinct parts the lower is usually a fine grayish sediment containing Asaphus gigas megistos & Iowensis in a perfect state of preservation 2/3 of the specimens are ventral surface up. The other 1/3 in all positions. The A. gigas & megistos are equally represented. Of the Iowensis 5 sp[ecimen]s have been found associated with upwards of 250 megistos & gigas. The lower surface has Heteocrinus simplex, H. tenuise, Spherocoryphye (only locality Orthis lynx, Stroph[omena] alternata, Berychia [?] Lichas Acidaspis [space left] & cystid). Dalmanites, Anomalocystites & numerous bryozoans. The upper surface is a coarse irregular, ["surface" is crossed out] joined closely to the upper portion of the layer which contains fragments of Asaphus and an occasional Lingula & Trematis, Rhynchonella recurvirostra & a small Tellinomya abound in local spots in the layer. Over this layer there is a layer of slaty lim[e]s[tone] 2^{in} thick, composed of dark sediment & broken crinoid stems. above this is a layer of buff colored clay 1^{in} thick containing immense numbers of L.[eptaena] serecia, Rhy. Recurvirostra, Orthis testudinaria, C. lycoperdon [?] & many other species of corals, crinoid columns etc. All are young specimens. Attached to the lower surface of the succeeding layer we find the above species in great profusion. The next layer a fine blue limestone 3 to 4^{in} thick. Asaphus gigas, megistos, Lingula, Trematis, L. serecia & alternatus."

APPENDIX 2—BIBLIOGRAPHIC NOTES ON SEVERAL PREPRINTS

In Hall's domain, manuscripts often had a complex history, of which Walcott (1877) is an example. It is amazing that printers could make changes and reset type without errors. Determining publication dates of some early Walcott papers varies from difficult to impossible. For example, Marcou (1885) indicated the New York Lyceum work appeared in 1875, but he listed only one paper, perhaps because the reprints contained both. Anonymous (1928) lists both with an 1875 date. U.S. Geological Survey Bulletin 746 (Nichols, 1923) lists it as 1876. Darton (1928) also listed both as 1876. A printer's note at the bottom of the first page indicates November 1875. The entire volume was issued in parts, with parts 7 and 8 coming out in February 1876; individual papers may have been issued as preprints. No new taxa are involved, and the precise date of publication is not critical; the weight of evidence suggests 1875.

Three of these sources agree that Walcott's "Preliminary Notice" came out in 1876. However, Darton listed the date as 1877. Seemingly the 28^{th}–31^{st} reports appeared in 1879.

The "Description of New Species of Fossils from the Trenton Limestone" involves the issue of priority. Nichols (1923) gives 1876, and Marcou (1885) gives December 1876, as well as for the preliminary note. However, both cite page numbers from a later publication. Anonymous (1928) gives January 1877, and Darton (1928) gives 1877. In view of the late December printing date of the "Preliminary Notice," 1877 seems more logical.

Darton, Marcou and Nicols date "Notes on Some Sections" and "Note on the eggs" as 1879, when the New York State Museum Annual Report was published. Anonymous (1928) lists September 20, 1877; and the preprints support this without question. Neither Marcou nor Nicols mention the partial page on "legs," whereas Darton dates it as 1879. Anonymous (1928) gives this as "Sept. 20, 1877 or later." In view of the plate without the two figures, the date of "later" seems to fit the evidence.

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