

# RELATIONSHIPS OF CAMBRIAN ARACHNATA AND THE SYSTEMATIC POSITION OF TRILOBITA

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**ABSTRACT**—Cladistic relationships of Trilobita, Naraoiidae (five ingroup taxa), Helmetiida (five ingroup taxa), Xandarellida, and the Cambrian arachnates *Retifacies*, *Sinoburius*, *Emeraldella*, and *Sidneyia* are investigated based on 29 characters. Documentation of appendage morphology and other ventral structures in *Saperion* from the Chengjiang fauna permits an appraisal of helmetiid relationships. A monophyletic Trilobita [=“Olenellida” (Emuellida + Eutrilobita)] is defined by numerous synapomorphies, including exoskeletal calcification and dorsal eyes with calcified lenses and circumocular sutures. Helmetiida is a robust clade, resolved as (Helmetiida (Tegopeltidae (Saperiidae + Skioldiidae))). Naraoiid monophyly is well-supported, but neither a naraoiid-trilobite nor a naraoiid-*Retifacies* clade are parsimonious, the latter grouping (“Nectopleura”) being explicitly paraphyletic. A sister group relationship between Xandarellida and *Sinoburius* is endorsed, although character support is novel compared to previous groupings of these taxa. The fourth postantennal limb pair in trilobites, naraoiids, and apparently helmetiids is based beneath the cephalothoracic articulation. Reweighted characters favor Trilobita and Helmetiida as closest relatives, with Petalopleura and then Naraoiidae as sister groups.

## INTRODUCTION

THE SYSTEMATIC position of trilobites within the Arthropoda has long been a source of controversy. A range of mostly Cambrian taxa that have been dubbed trilobitomorphs (Størmer, 1944) or trilobitoids (Størmer, 1959) serve as the best supported candidates for closest relatives of the Trilobita. The objective of this paper is to examine cladistic relationships in trilobite-allied Cambrian Arachnata based upon parsimony analysis of 29 characters.

Among Cambrian arachnate groups that have been of uncertain phylogenetic position (because of inadequate morphological knowledge) are the Helmetiidae Simonetta and Delle Cave, 1975, and Tegopeltidae Simonetta and Delle Cave, 1975. Until recently helmetiids and tegopeltids were known solely from rare examples of the nominate genera, *Helmetia* Walcott, 1918, and *Tegopelte* Simonetta and Delle Cave, 1975, in the Middle Cambrian Burgess Shale. Documentation of the Early Cambrian Chengjiang fauna of Yunnan, China, revealed helmetiids and tegopeltids to be widespread Cambrian groups including additional taxa. Hou (1987) identified two new helmetiids in the Chengjiang fauna, *Kuamaia lata* and *Rhombicalvaria acantha*, and Hou, Ramsköld and Bergström (1991) diagnosed a tegopeltid, *Saperion glumaceum*, more recently assigned to a monotypic Family Saperiidae Hou and Bergström, 1997. Hou and Bergström (1997) have since added the new taxa *Skoeldia aldna* (Family Skoeldiidae Hou and Bergström, 1997) and *Kuamaia muricata*, and united the helmetiids, *Skioldia*, *Tegopelte*, and *Saperion* as the Order Helmetiida. One of the objectives of this work is to present morphological findings on the best known helmetiid, *Kuamaia lata*, and tegopeltid/saperiid, *Saperion glumaceum*, as they bear on character analysis of the Cambrian Arachnata. We draw on recently illustrated specimens of these species (Chen et al., 1996) housed in the Early Life Research Centre of the Nanjing Institute of Geology and Palaeontology. Localities for Chengjiang specimens cited in this work are described by Chen, Zhou, and Ramsköld (1995).

Our study complements the recent consideration of early arachnate relationships by Hou and Bergström (1997). Differences in our results are in part empirical and in part analytical. On the first score, we present differing interpretations of morphology, include new characters, and reject some characters used by those authors. Methodologically, we depart from Hou and Bergström in not accepting plesiomorphy as phylogenetically informative, in attempting to track all implied character transformations, in

rejecting paraphyletic groups, and in avoiding erection of monotypic taxa out of adherence to Linnean categories. The basis for our study is cladistic parsimony.

## TERMINAL TAXA

The history of research has seen Trilobita closely allied to a wide range of arthropod taxa. Most of these hypotheses have been convincingly refuted and are not subjected to further testing herein. All recent studies that have employed phylogenetic systematics recognize trilobites as more closely related to Chelicerata than to Crustacea (Bergström, 1992; Wills et al., 1994, 1998), with trilobites and related stem-group chelicerates being classified in Arachnata (Lauterbach, 1980, 1983; see Chen et al., 1997, for phylogenetic definition). An especially close (i.e., ancestor or sister group) relationship between trilobites and chelicerates (Lauterbach, 1980, 1983, 1989) has not been supported in recent work (e.g., Wills et al., 1998). Instead, trilobites are part of an imprecisely resolved grade of Early Paleozoic taxa. This analysis considers taxa that have been allied to trilobites in recent analyses and those that may occupy a nearly basal position on the lineage leading to chelicerates.

A controversy concerning the systematic position of agnostids is not examined here because neither of the two main competing hypotheses postulates that agnostids are especially relevant to the questions being addressed. The traditional view that agnostids are ingroup trilobites derived from eodiscids (Fortey and Theron, 1994, text-fig. 8) negates a branchpoint below the Trilobita—coding agnostids as a terminal taxon would then be as irrelevant as coding any other deeply-nested ingroup trilobite clade (e.g., Odontopleurida or Asaphida). The alternative, agnostids being more closely allied to Crustacea (Shergold, 1991; Bergström, 1992) than to trilobites, can only be tested by including a comprehensive range of schizoramian arthropods as terminals (e.g., stem-lineage crustaceans of Walossek and Müller, 1990). Under this hypothesis, agnostids are only distantly relevant to trilobite-allied arachnates, and indeed are less relevant than extant chelicerates. Views such as agnostids and naraoiids sharing a close relationship (Babcock, 1994) would render agnostids an appropriate terminal taxon in this analysis, but no compelling support has been offered for this hypothesis, only a crude correspondence in the relative size of the tagmata.

*Trilobita*.—The traditional concept of Trilobita (e.g., Moore, 1959) restricts this taxon to “Olenellida” (a paraphyletic group;

Geyer, 1996) and Trilobita sensu Lauterbach (1980), i.e., Emuellida + Eutrlobita. Apart from upholding convention, this scope for Trilobita has merit because such a clade can be diagnosed by a substantial body of character evidence (Fortey and Whittington, 1989; Ramsköld and Edgecombe, 1991; Hou and Bergström, 1997). For the purpose of coding characters in Trilobita we have selected two Cambrian taxa known from soft-part preservation, *Eoredlichia* (see Shu et al., 1995; Ramsköld and Edgecombe, 1996) and *Olenoides* (see Whittington, 1975, 1980). These representatives of the Redlichiiida and Corynexochida serve as adequate estimates for the basal node of Eutrlobita. We have not included the purported trilobite *Kleptothule* Budd, 1995, because of a preponderance of missing data and imprecise homologies.

*Naraoiidae/Nectaspidida*.—Several genera have been assigned to a naraoiid or nectaspidid taxon in recent years, and such a group has been defended as a clade (Fortey and Theron, 1994; Chen et al., 1997). To test this hypothesis of naraoiid monophyly in the broader context of arachnate phylogeny, we consider naraoiid genera as separate terminal taxa. These are *Naraoia* Walcott, 1912, *Liwia* Dzik and Lendzion, 1988, *Tariccoia* Hammann et al., 1990, *Soomaspis* Fortey and Theron, 1994, and *Misszhouia* Chen et al., 1997. We do not further consider alleged naraoiids (*Maritimella* and *Orientella* Repina and Okuneva, 1969) that have not unreasonably been interpreted as mudflakes. The view that naraoiids should be regarded as trilobites (Whittington, 1977; Fortey and Theron, 1994) is opposed by Hou and Bergström (1997), who resolved naraoiids as especially closely related to the Chengjiang taxon *Retifacies* Hou et al., 1989 (see below) and trilobites as more closely related to several other groups, including chelicerates.

*Helmetiidae*.—Helmetiids have been allied with trilobites, naraoiids, and tegopeltids (Delle Cave and Simonetta, 1991). Hou and Bergström (1997) grouped helmetiids, skioldiids (Family Skioldiidae Hou and Bergström, 1997), tegopeltids, and saperiids in an Order Helmetiida Novozhilov, 1969 (equivalent to the redundant Subclass Conciliterga Hou and Bergström, 1997). The status and position of the helmetiids is evaluated by coding *Helmetia expansa* Walcott, 1918, and *Kuamaia lata* Hou, 1987.

*Skioldiidae*.—Hou and Bergström erected this monotypic family for *Skioldia aldna*, a rare taxon in the Chengjiang fauna. Codings are based on their published material (two specimens), and our study of an unpublished specimen (ELRC 19502).

*Tegopeltidae/Saperiidae*.—Given the sister group relationship between *Tegopelte* and *Saperion* advocated by Hou and Bergström (1997), their separation as monotypic families (Tegopeltidae and Saperiidae) is questionable. Both genera are coded in this analysis.

*Xandarellida*.—Chen et al. (1996) grouped three Chengjiang arachnates in Xandarellida: *Xandarella* Hou et al., 1991, *Sinoburius* Hou et al., 1991, and *Cindarella* Chen et al., 1996. *Almenia spinosa* Hou and Bergström, 1997, is a junior subjective synonym of *Cindarella eucalla* Chen et al., 1996, and is not further considered. The Family Almeniidae Hou and Bergström, 1997, is accordingly dismissed. Our earlier study of xandarellids (Ramsköld et al., 1997) uncovered many similarities to trilobites and other Cambrian arachnates, so the relationships of xandarellids are tested here.

*Sinoburiida*.—*Sinoburius lunaris* Hou et al., 1991, is a rare taxon in the Chengjiang fauna; Hou and Bergström (1997) reported no new specimens additional to the holotype and a paratype. Only two further specimens have been examined by us (Chen et al., 1996, fig. 215; Chen and Zhou, 1997, figs. 88, 89; Fig. 1 herein), and a specimen is figured by Luo et al. (1997). Originally compared with *Xandarella*, merostome chelicerates, and aglaspidids, Chen et al. (1996) formalized a relationship

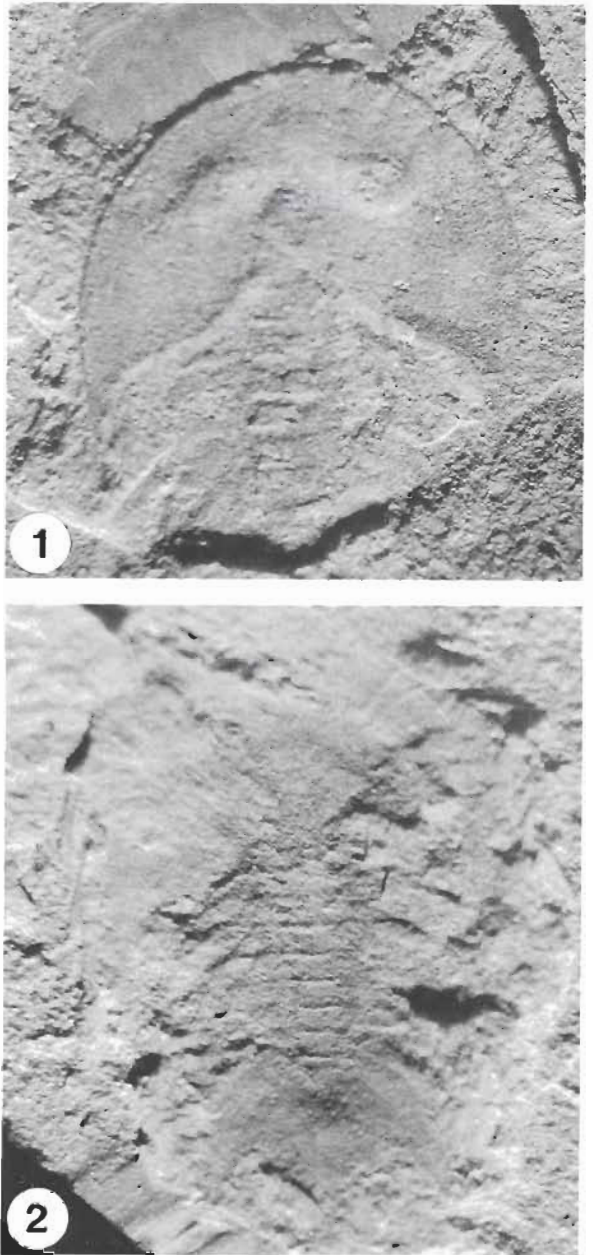


FIGURE 1.—*Sinoburius lunaris* Hou, Ramsköld and Bergström, 1991. 1. Ventral view of head and thorax ELRC 19550, from MN5,  $\times 11.9$ ; 2. dorsal view of partial head shield and complete trunk ELRC 19551, from MN5,  $\times 10.6$ .

with xandarellids. Hou and Bergström (1997) recognized a monotypic higher taxon for *Sinoburius*, the Order Sinoburiida, which they grouped with Xandarellida in the new Subclass Petalopleura.

*Retifacies*.—*Retifacies* Hou et al., 1989, has been of uncertain systematic position. Delle Cave and Simonetta (1991, table 1) indicated a branchpoint for it near that of the naraoiid *Liwia* and the Helmetiidae. Hou and Bergström (1997) assigned *Retifacies* (Order Retifaciida Hou and Bergström, 1997) to a Subclass Nectopleura, along with the naraoiids. Our codings for *Retifacies* incorporate data from specimens in the Early Life Research Centre, Nanjing Institute of Geology and Palaeontology (ELRC 19630–19633).

*Emeraldella* and *Sidneyia*.—The Burgess Shale taxa *Emeraldella* Walcott, 1912, and *Sidneyia* Walcott, 1911, have been recognized as arachnates in many studies. They are included in this analysis to sample taxa that may be more crownward on the chelicerate stem lineage, and thus serve as a proxy for Chelicerata. This phylogenetic placement was suggested for *Sidneyia* by Bruton (1981), and also by Hou and Bergström (1997), who assigned both *Sidneyia* and *Emeraldella* to a taxon Xenopoda that is most closely allied to Aglaspidida and Chelicerata. Some analyses by Wills et al. (1998, fig. 2.6) likewise resolve *Emeraldella* and *Sidneyia* basally within an arachnate clade that is sister to aglaspidids and chelicerates.

#### CHARACTERS

Under discussion of several characters we present new data for *Saperion glumaceum*. Previous illustration of a key specimen (Chen et al., 1996, fig. 217) does not convey details of appendage morphology, and a reconstruction of the limb by Chen et al. (1996, fig. 218B) differs in many respects from our interpretation, which is substantiated by enlarged photographs and camera lucida drawings.

1) Calcified cuticle: 0—absent; 1—present.

Calcification of the exoskeleton serves as a classic apomorphy for Trilobita (Fortey and Whittington, 1989; Ramsköld and Edgecombe, 1991; Shu et al., 1991, fig. 20A).

2) Number of cephalic somites/appendages: 0—antenna only; 1—antenna and three limb pairs; 2—antenna and three limb pairs, fourth limb pair at head/trunk articulation; 3—antenna and four limb pairs; 4—antenna and five limb pairs; 5—antenna and six limb pairs.

The number of cephalic somites, as determined from the number of cephalic appendage pairs, is a classical character in the definition of extant major clades of arthropods. This is so because the number is stable in living arthropod groups; Crustacea fundamentally have five, Chelicerata six, Hexapoda four. In contrast, Cambrian arthropods display a bewildering variation in the number of appendage pairs in the head. For this reason, Hou and Bergström (1997) and Bergström and Hou (1998) have criticized the use of head segment numbers in phylogenetic analyses of early arthropods. However, if this character is cladistically unreliable, as they claim, this must be demonstrated empirically by incongruence with other characters rather than asserted a priori and dismissed from further consideration. An unordered multistate coding makes minimal assumptions.

Prior to the discovery of the Chengjiang fauna and the renewed interest in the Burgess Shale fauna, a cornerstone in the discussions on the stability of the number of cephalic appendage pairs in early arthropods was the condition in trilobites. The axiomatic view that the trilobite cephalon possessed antennae plus four pairs of biramous legs (A+4), was challenged when Stürmer and Bergström (1973) presented evidence for A+3 in *Phacops*. Subsequent studies have claimed three (Cisne, 1975; Whittington, 1975) or four (Bergström and Brassel, 1984; Hou and Bergström, 1997) pairs of postantennal cephalic limbs in trilobites.

For many of the taxa under consideration here, the number of cephalic appendage pairs can be determined with some confidence. The major difficulty is that cephalic appendages are not morphologically differentiated from trunk appendages, so the position is the sole criterion for judging whether an appendage belongs to the cephalon or to the trunk. This is the reason why different workers have reported different counts for the same taxa. We here detail the evidence for several taxa coded where this differs from recently published accounts.

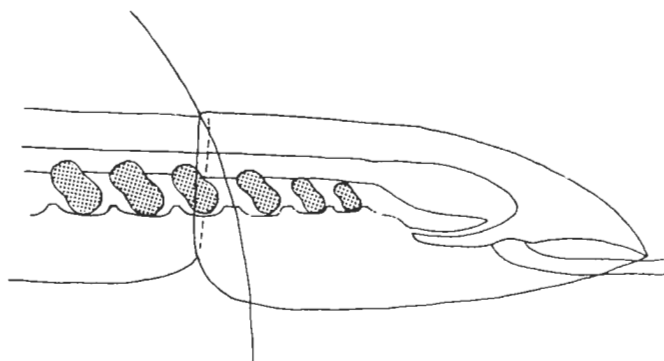


FIGURE 2—*Misszhouia longicaudata* (Zhang and Hou, 1985). Simplified reconstruction in cross-section to show relationship between limb attachments and tergites and illustrate the concept of the three and one-half state for the number of postoral limb pairs in the cephalon (character 2, state 2). The limb attachments to the trunk stem are stippled. Note that the shape of the attachments is drawn schematically to indicate their position relative to other structures, not to indicate the detailed shape of the junction between the limb and the trunk stem, which is structurally complex and has different parts at varying angles to the vertical plane illustrated. The gently curved line passes dorsally through the joint between the head and trunk shields, and ventrally between the third and fourth sternites, indicating the obliqueness of the plane of flexure.

*Misszhouia*.—In the Chengjiang fauna, more appendage-bearing specimens are known for the naraoiid *Misszhouia longicaudata* than for any other arthropod. It may therefore be somewhat surprising that the number of postoral biramous appendages has not been settled. In the original description, the number was given as three (Zhang and Hou, 1985), but later the figure was changed to four (Hou, 1993), and reinstated as three (Hou and Bergström, 1997). The uncertainty stems from the ambiguous position of the fourth postoral appendage pair. The present authors described this pair as positioned at the head/trunk articulation, with only the three first appendage pairs being structurally and functionally part of the head (Chen et al., 1997, p. 7). The condition in *Misszhouia* (Fig. 2) is neither three nor four, but an intermediate state here termed three and one-half. This state is also encountered in other taxa under consideration here, and is used in the phylogenetic analysis.

In *Misszhouia longicaudata*, the tendinous bar between neighboring hourglass-shaped sternites is marked by a well defined ridge (e.g., Ramsköld et al., 1996, fig. 2B; Chen et al., 1997, figs. 2b, 8a, 13a; Hou and Bergström, 1997, fig. 41E, not overturned as stated but figured upside down). The third and fourth postoral sternites are separated by twice the normal distance, and between them the transverse ridge is set between smaller, anterior and posterior ridges or folds. In one of the most detailed specimens (Ramsköld et al., 1996, fig. 2B; Chen et al., 1997, fig. 9a), the three anterior sternites are set at a small angle (to the individual's left side) to the succeeding sternites. This strengthens our interpretation that the presence of the additional folds between sternites 3 and 4 allowed increased flexibility between these segments, indicating that this is the point of flexure between head and trunk. However, this point is not exactly at the position of the head/trunk juncture, but half a sternite in front of it, i.e., the fourth sternite is centered right under the articulation between the head and the trunk shields. This articulation involves only a small overlap of the shields (in dorsoventral view, as preserved in numerous specimens). An appendage pair is based in the lateral embayments in the sides of each of these sternites, and based on this criterion, there are three postoral

appendage pairs in the cephalon. The fourth appendage pair would have underlain the cephalic shield in all attitudes except when strongly posteriorly deflected. Functionally, however, it would have been part of the trunk but not of the head, being based posterior to the point of flexure. The position of the ventral point of flexure half a sternite-length anterior to the dorsal one means that the boundary between head and trunk, when traced through a cross-section of the animal, would not be vertical but would form an anteroventrally inclined plane or curve (Fig. 2).

We will not here enter into a detailed discussion on whether the tergite boundaries in these arthropods coincide with somite boundaries (see, e.g., Minelli and Bortoletto, 1988). Arbitrarily assuming that they do, the somites in forms like *Misszhouia* must be obliquely inclined, with the ventral part more anterior than the dorsal. The condition where the fourth appendage pair is based at the articulation between the head and first trunk tergite is also encountered in *Helmetia*, *Naraoia*, and in *Trilobita*.

*Helmetia*.—The holotype is the only published specimen with parts of limbs preserved. The interpretation presented here combines features showing relief (Simonetta and Delle Cave, 1975, pl. 16, fig. 1) with those best observed in reflected light (Briggs et al., 1994, fig. 141). The extent of the head can be estimated with some accuracy from interpolating the missing central part of the apparently fused junction between the head shield and the first trunk tergite. Three sets of segmentally arranged structures are preserved. One is the series of exopods, mainly of the right side. This series is incomplete, but the anterior two exopods of the right side are entirely within the extent of the head. Other structures (see below) indicate that these exopods are the second and third, whereas only the attachment of the anteriormost exopod is evident. The second series is formed by deep, irregularly shaped pits to the right of the sagittal line. The seven or eight pits are set at intervals equal to segment lengths, demonstrating their segmental nature. The pits range through the head and the trunk, the posteriormost being at the second last thoracic segment. The third serial structure is a row of paired, reflective spots. Anteriorly the transverse midline of this row begins slightly to the right of the centre of the eye-pair, and it then describes a curve convex to the right, until the row fades at the penultimate thoracic segment. The strong deviation from the sagittal line indicates that the structures in question are positioned far ventrally, on the trunk stem (see discussion on character 6). The reflective spots on the right are set more anteriorly than those on the left. The right hand spots are transversely elongate, set perpendicular to the curve they describe. The left hand spots are strongly obliquely oriented, and their shape is different, being rounded crescentic. This difference in shape and orientation indicates that the spots are not gut caeca, structures that also may form pairs of reflective spots. They are also considerably smaller and differently shaped than known gut caeca in *Kuamaia*. The spots are thus likely part of the proximal limb construction, perhaps muscular attachments. Each of spots 2, 3, and 4 (counted from anterior) on the right side are positioned directly at the proximal end of the exopod shaft. We conclude that whatever their exact nature, they indicate the number and position of limb bases. The spots on the right side all have a pit (from the pit series described above) anteriorly, a quarter to one-third of the distance to the next anterior spot. If the spots are correctly interpreted as associated with the most proximal part of the exopod, the pits are in the expected position for the basis and its attachment.

In the head of *Helmetia*, a weak anterior spot pair is followed by two stronger pairs. The inferred line between the head and trunk passes between the third and fourth pairs. The pits in front of the fourth spot pair lie on the inferred line of junction. If the above interpretation is correct, then the fourth postoral limb pair

is based directly under the head/trunk junction in *Helmetia*, and we have accordingly coded it as showing the three and one-half state.

*Trilobita*.—The limb attachments in trilobites have previously been thought to be positioned centrally (in the exsagittal plane) under each thoracic tergite. Tendinous bars have accordingly been placed underneath each joint between thoracic segments (e.g., Campbell, 1975; Cisne, 1975; Whittington, 1993b).

Among trilobites preserving soft tissues, a single specimen of *Placoparia* is unique in showing the tendinous bars, sternites, and appendage attachments preserved, even in full relief. We reinterpret this specimen (Whittington, 1993a, figs. 1–4, 6) as having the tendinous bars positioned half way between the anterior and posterior margins of each thoracic segment rather than underneath each articulation. Between each neighboring pair of tendinous bars is an hourglass-shaped area that we interpret as a sternite (by comparison to the sternites in *Misszhouia* and other taxa). As recognized by Whittington (1993a), the most proximal part of the limbs is preserved as a circular pit extending ventrally from the concave lateral side of the sternite. Tracing the slightly obliquely preserved junctions between thoracic segments 2, 3 and 4 across the central area reveals that each limb is based centrally under each tergite junction and not centrally under each thoracic segment.

The specimen is complete and the count, from posterior, of thoracic segments is unambiguous. In Whittington's (1993a) figure 4, the limb bases on the left side are labelled "p," and the second of these from posterior is situated under the cephalo-thoracic articulation (rather than under the first thoracic segment as is implied by the labelling of the figure). An oblique view of the specimen (Whittington, 1993a, fig. 6) reveals a set of three tendinous bars and limb bases anterior to this one. The anteriormost of these limb bases is set anterior to the first tendinous bar, in front of which is the posterior edge of the hypostome. There is no space for any more tendinous bars, and an even more anterior appendage would have to be based half-way to the anterior wing of the hypostome, a position already occupied by the antennal attachment. We conclude from this configuration of soft anatomy relative to the dorsal exoskeleton that the number of postoral biramous limb pairs in *Placoparia* is three and one-half.

Another trilobite that shows the three and one-half distribution is *Rhenops* (Bergström and Brassel, 1984). A single specimen preserves the complete set of limbs. The exoskeleton is exposed from the ventral side, and all appendages are based on the tergite junctions, best seen in the five anterior thoracic limbs on the individual's left side (Bergström and Brassel, 1984, fig. 1).

Well-preserved specimens of *Triarthrus eatoni* also show that the fourth postoral limb pair was based at the cephalo-thoracic junction. Specimen USNM 400940 is exposed from the ventral side but has been prepared to expose the occipital ring and the posterior border furrow (Whittington and Almond, 1987, figs. 24–26). The basis ("coxa") of the fourth limb pair overlies the cephalothoracic articulation on both sides.

Other trilobite species preserving soft parts are too incomplete or distorted to permit a definite statement on the position of the limb attachments. The two taxa used in our analysis, *Eoredlichia* and *Olenoides* do not, in spite of their otherwise exquisite preservation, show unequivocally the number or position of postoral appendages in the cephalon. However, the longitudinal position of the tendinous bars, sternites and limb attachments affects the basic construction of the muscular system, and we regard it as unlikely that *Placoparia*, *Rhenops* and *Triarthrus* show anything but the normal trilobite condition. For *Eoredlichia* and *Olenoides*, as representatives of *Trilobita*, we have accordingly coded the three and one-half state.

3) Antennal orientation: 0—directed anterolaterally; 1—strongly deflected laterally; 2—placed well inside shield margin, curving posteriorly from a transverse proximal extent.

Chen et al. (1997) used lateral deflection of the proximal part of the antennae as a shared derived character within Naraoidae, present in *Livia* and *Naraioia*. Among other taxa considered in this analysis, *Sidneyia* also has a similar strong lateral deflection of the antenna. Antennal orientation is considered to be less prone to taphonomic distortion than leg stance, particularly in cases in which the limbs were pendent in life. Vertical compaction will be expected to affect the preserved postures of limbs, with rotation and reorientation occurring during burial. The proximal part of antennae, having a more horizontal posture in life, will be flattened but not substantially reoriented by compaction.

The antenna of *Saperion* has not been previously described. One pair of antenniform cephalic appendages is present (Figs. 3.1, 4; Chen and Zhou, 1997, fig. 72). The antenna attaches near the anterolateral corner of the hypostome, but the hypostomal margin is too fragmented to determine whether or not an anterior wing is present. Antennomeres cannot be discerned on the proximal quarter of the antenna, but ten are distinct along the distal three-quarters. As such a relatively small number of antennomeres characterizes *Saperion* (in contrast to trilobites or naraoids). Proximal antennomeres are considerably longer than distal ones; the former are cylindrical, longer than their diameter, whereas the distal five antennomeres are of about equal length and diameter. The distal segment is blunt and conical. Comparison with *Tegopelte gigas* (Whittington, 1985, fig. 3) shows the position of antennal attachment to be variable within the tegopeltid-saperiid group. The antenna can be traced farther back in *Tegopelte* than is the case for *Saperion*. This also indicates that the hypostome is more posteriorly displaced in *Tegopelte*, a finding consistent with Whittington's (1985) identification of an ill-defined hypostome in the appropriate position. The antennal orientation of *Saperion* is shared by *Skioldia* (Hou and Bergström, 1997, figs. 63, 65A), in both cases being oriented laterally proximally, then curving backwards and lying entirely under the tergal shield. This unique morphology (coded as state 2) appears to provide a compelling synapomorphy.

4) Position of lateral faceted eyes: 0—ventral; 1—dorsal; 2—absent.

Alternative codings were attempted for eye position, including scoring dorsal and ventral eyes as separate characters (note that "lateral faceted" refers to both positions, being the standard term to distinguish the "compound" eye from median eyes). This has the advantage of allowing some taxa to be scored for the definite absence of dorsal eyes although the presence of ventral eyes is uncertain (e.g., *Soomaspis* and *Tariccoia*). Such a coding was rejected because it denies the likelihood that dorsal and ventral eyes are homologous (merely being different positions of the lateral faceted eye) and also because spurious optimizations resulted. For example, naraoids and trilobites group based on the lack of ventral eyes, but this "absence" is very different—trilobites lack ventral eyes because they have incorporated them into the dorsal surface of the head shield whereas naraoids have evidently lost the lateral faceted eye, which is primitively ventral in the group under analysis. We have used a partial uncertainty coding in PAUP for instances in which a taxon is known to have either state 0 or 2 (eyes ventral or absent) but definitely not state 1 (eyes dorsal). An alternative coding would be to employ two characters, one for presence and absence of eyes, and another for dorsal versus ventral position of eyes. The latter would, however, require "inapplicable" codings for blind forms.

Hou and Bergström (1997) cited a primitive ventral positioning of the compound eyes as a diagnostic character of their Nectopleura. We do not accept their reasoning that symplesiomorphies are indicative of closest relationships. Furthermore, no evidence for compound eyes—in any position—is known for naraoids (see discussion of character 11 for evidence that ventral eyes in naraoids are median eyes rather than compound/lateral faceted eyes) and thus it is unclear how any state of this character except absence can serve to unite naraoids with any group. Hou and Bergström (1997) regard dorsal eyes as a synapomorphy for all arachnates except their Nectopleura. The fact that the eyes of *Cindarella* are ventral, as are those of *Xandarella*, helmetiids, and *Saperion*, in our opinion (see discussion of character 6 below), renders this dubious.

5) Visual surface with calcified lenses, bounded by circumocular suture: 0—absent; 1—present.

Fortey and Whittington (1989) cited the calcified visual surface of trilobites as a synapomorphy. Rasmköld and Edgecombe (1991) cautioned that calcification of the visual surface may be obligately coupled with exoskeletal calcification. Fortey and Theron (1994) upheld the independence of these characters, based partly on the independent (phosphatic) mineralisation of eye lenses in aglaspids. We tentatively accept a calcified visual surface and circumocular sutures as independent evidence for the monophyly of Trilobita.

6) Bulge in exoskeleton accommodating drop-shaped ventral eyes: 0—absent; 1—present.

A pair of reflective spots situated behind and slightly distal to the anterior sclerite in *Helmetia* has been interpreted as eyes (Briggs in Conway Morris et al., 1982). As documented below, eye-like organs are identified in the same position in *Kuamaia* and in *Saperion*, corroborating Briggs' interpretation, and we demonstrate that they are ventral structures.

*Helmetia*.—The type specimen of *Helmetia expansa* has been figured in various illuminations, enabling some interpretation of the morphology (Walcott, 1931, pl. 23; Simonetta and Delle Cave, 1975, pl. 16, fig. 1; Conway Morris et al., 1982, pl. E; Briggs et al., 1994, fig. 141). The specimen is exposed in nearly dorsal view, which is conclusively shown by the dorsal shield overlying the anterior sclerite (Simonetta and Delle Cave, 1975, pl. 16, fig. 1). A slight rotation has resulted in the left side being slightly tilted down. Due to the original convexity of the dorsal side, the right side is preserved to occupy a larger area than the left side. Another effect of the tilt is to cause progressively more ventral structures to show a progressively increasing displacement to the right of the dorsal sagittal line.

The anterior sclerite is attached posteriorly to the dorsal exoskeleton, and shows almost no displacement. Clearly this sclerite was positioned only slightly ventral to the dorsal shield, whereas in *Kuamaia* it was at a more ventral level. On the dorsal shield just posterolateral to the anterior sclerite are the two rounded, reflective areas interpreted by Briggs as eyes. The eye-pair is markedly displaced to the right relative to the anterior sclerite. Due to the tilt of the specimen, such preservation would be impossible for dorsal, sessile eyes, but is consistent with a ventral position. Our interpretation is that after entombment, the eyes were preserved in close contact with the ventral cuticle, and after complete compaction of the organic material, they are now virtually level with the adjacent structures. The holotype is the only published specimen showing the eyes, and it is so strongly compacted that it is not possible to determine if the dorsal exoskeleton was raised above the eyes.

On the right side, in the angle between the anterior sclerite and the dorsal shield, a portion of a structure is protruding in front of the anterior head margin. The anterior edge of the structure is anteriorly curved. Structures that could occur in this area



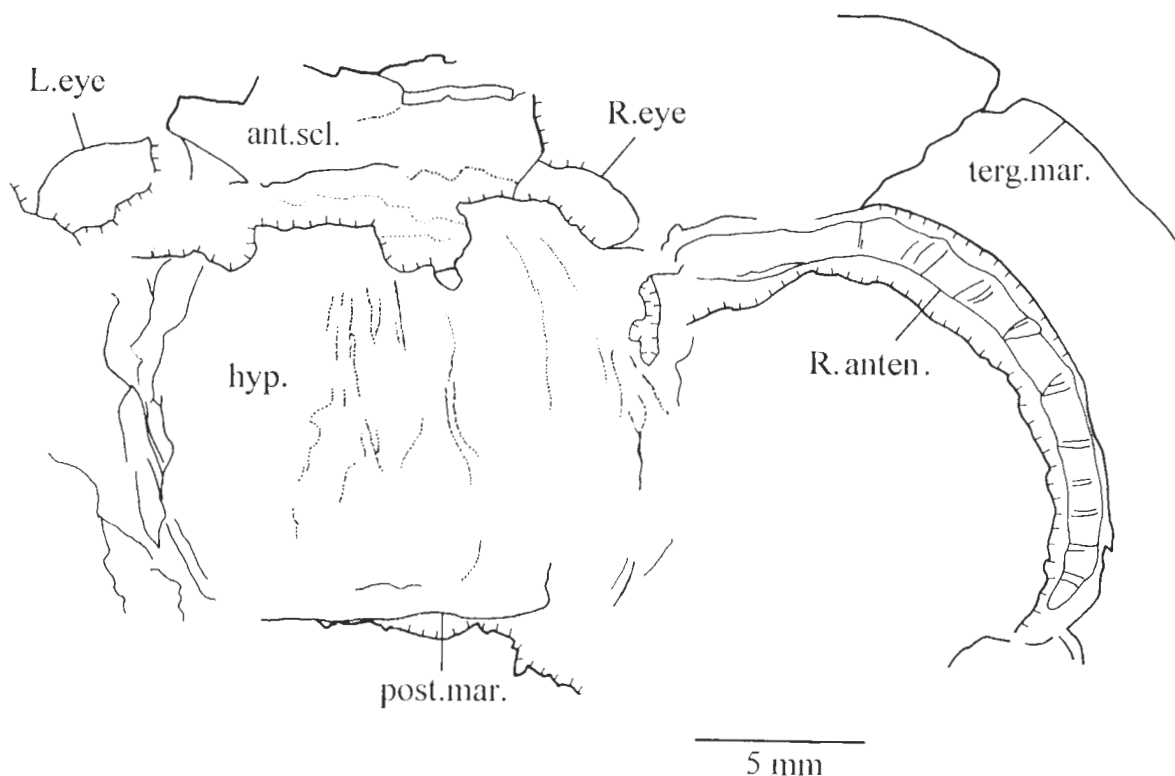


FIGURE 4—*Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991. Camera lucida drawing of ELRC 19500a (Fig. 3.1). Abbreviations used in this and other figures: anten., antenna; ant.scl., anterior sclerite; hyp., hypostome; L, left; post.mar., posterior margin of hypostome; R, right; terg.mar., margin of tergum.

are either a proximal part of the antennule or of the eye stalk. Considering that in *Kuamaia* the antennule attaches to the ventral body surface some distance posterolateral to the anterior sclerite (Hou and Bergström, 1997, fig. 61A), whereas the eye stalk is based on or near the posterolateral corner of the same sclerite, the eye stalk is presently the most likely interpretation. Excavation of the specimen would be necessary to confirm this suggestion.

*Kuamaia*.—A pair of weakly swollen ovate or tear-shaped organs occur in *Kuamaia lata* in a position corresponding to the eyes of *Helmetia* (Figs. 3.2, 5, 6). These are regarded as originating ventrally and appearing in low relief on the dorsal surface of the exoskeleton (the same circumstance as in *Saperion*; see below). The narrowest part of the eye lobe is at its anteromedian edge, which extends very close to, but apparently not against, the anterior sclerite. It is not known if the eye lobe actually originates on the anterior sclerite (as is the case for the eye stalks and an anterior cephalic sclerite in *Fuxianhuia*; Chen et al., 1995).

The positioning of the eyes underneath the dorsal exoskeleton is particularly well seen in ELRC 19584a (Figs. 3.2, 5.1, 5.3). The right eye is completely preserved, with the eye stalk curving anteromedially to a transverse direction. The eye, distinguished by its dark color and teardrop-shape, fits into a dorsally convex exoskeletal bulge. The adaxial edge of the bulge is broken or

forms a sharp fold, caused by compactional compression, and forms a laterally-directed scarp. The left eye in ELRC 19584a is preserved as a weakly concave, rounded area, apparently indicating that the split of the rock has gone down to the ventral surface of the eye. The presence in all well-preserved specimens of similar tear-shaped, raised exoskeletal bulges above the eyes shows that they are primary structures.

*Saperion*.—Two symmetrically placed, swollen lobes extend from the lateral edges of the anterior sclerite, and have been excavated to reveal that they lie ventral to the tergum (Figs. 3.1, 4). Their shape is flasklike, being more constricted proximally. No lens structures have been observed, but their position and form is most suggestive of lateral eyes.

In the allied *Skoeldia aldna* (unpublished specimen ELRC 19502), the exoskeleton forms two mounds just posterolateral to the anterior sternite. The mounds are well delimited laterally, anteriorly and posteriorly, but adaxially more weakly separated from the adjacent exoskeleton. These mounds (also Hou and Bergström, 1997, fig. 63, 65A) are in the same relative position as structures interpreted as eyes in *Saperion glumaceum* (Figs. 3.1, 4).

The function of the exoskeletal bulges must be to accommodate the eyes, i.e., to enable the eyes to fit into a corresponding dorsally-directed depression on the ventral side. Because the eyes were stalked at least in *Kuamaia*, and show no reason or

FIGURE 3—1, *Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991. Dorsal view of cephalic region of complete individual ELRC 19500a, locality MQ1, showing anterior sclerite, hypostome, eye lobes, and antennae (see Fig. 4 for camera lucida drawing). Right antenna exposed by preparation. Light from NW,  $\times 3.8$ . 2, *Kuamaia lata* Hou, 1987. Dorsal view of cephalon of ELRC 19584a,  $\times 8.7$ . Dorsal surface of hypostome exposed by preparation, light from NE. Arrow indicates posterior margin of hypostome.

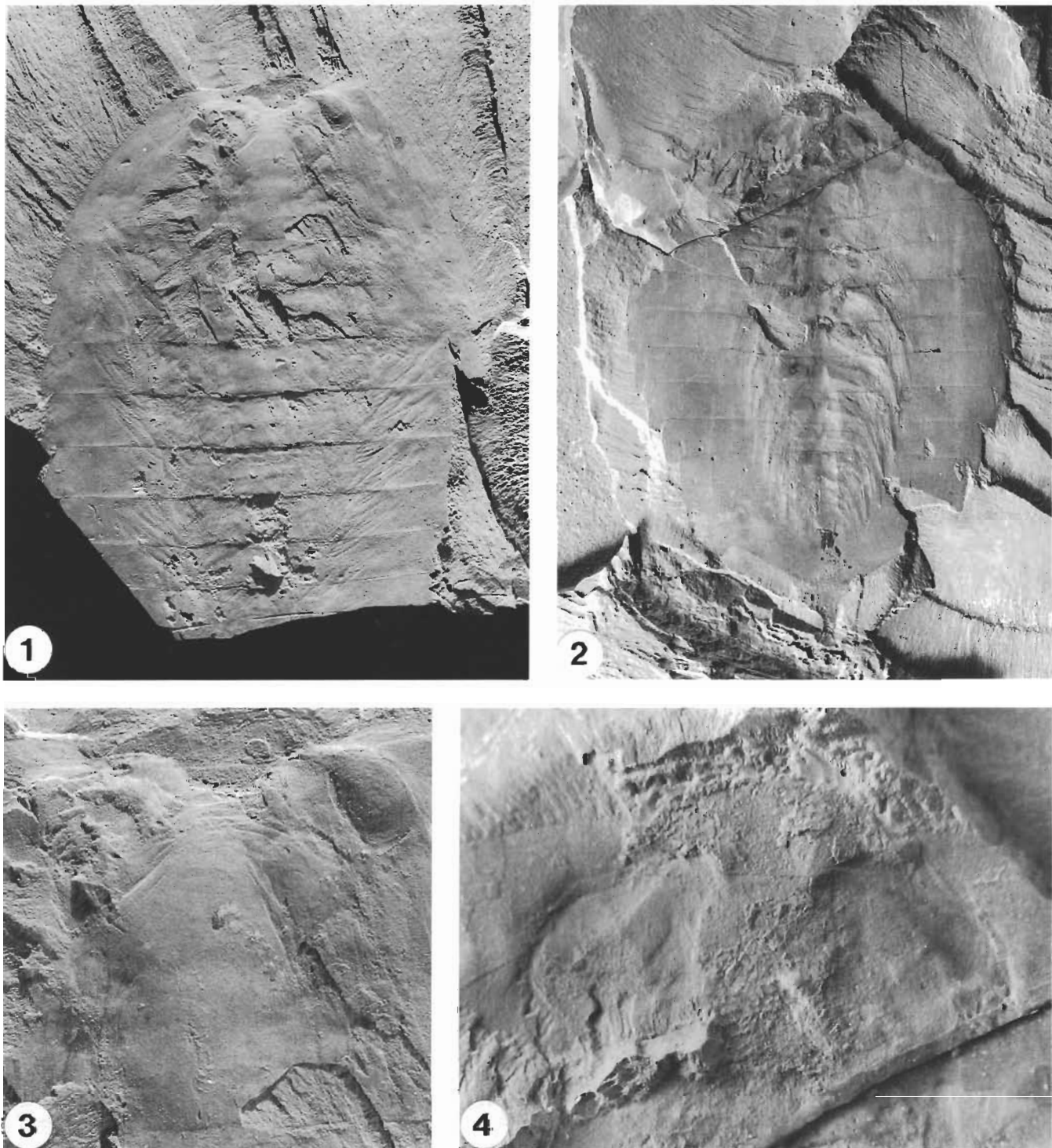


FIGURE 5.—*Kuamaia lata* Hou, 1987. 1, 3, Articulated cephalon and thorax ELRC 19584a; 1, dorsal view, light from NNE,  $\times 2.1$ ; 3, median region of cephalon, before preparation of hypostome, light from NNE (see Fig. 3.2 for preparation),  $\times 5.9$ . 2, 4, Ventral view of complete individual ELRC 19580 (see Fig. 6 for camera lucida drawing); 2, light from NE,  $\times 2.1$ ; 4, detail of cephalon, light from WNW,  $\times 7.7$ .

evidence to the contrary in *Helmetia* or *Saperion*, we interpret them as movable. In other comparable Chengjiang arachnates, the combined thickness of dorsal exoskeleton, soft tissue, and ventral cuticle is small in areas outside the trunk stem, the central area carrying limbs and containing the digestive system. In helmetiids and tegopeltids, the thickness could have been further

reduced in the bulges, to permit light to diffuse through to the eyes immediately below. In that way, the eyes could functionally have been both ventral and dorsal. A comparable situation, although based on a different morphological solution, is present in *Xandarella* (Hou et al., 1991, fig. 3B), where an exoskeletal opening permits dorsal sight to the ventral eyes (see character



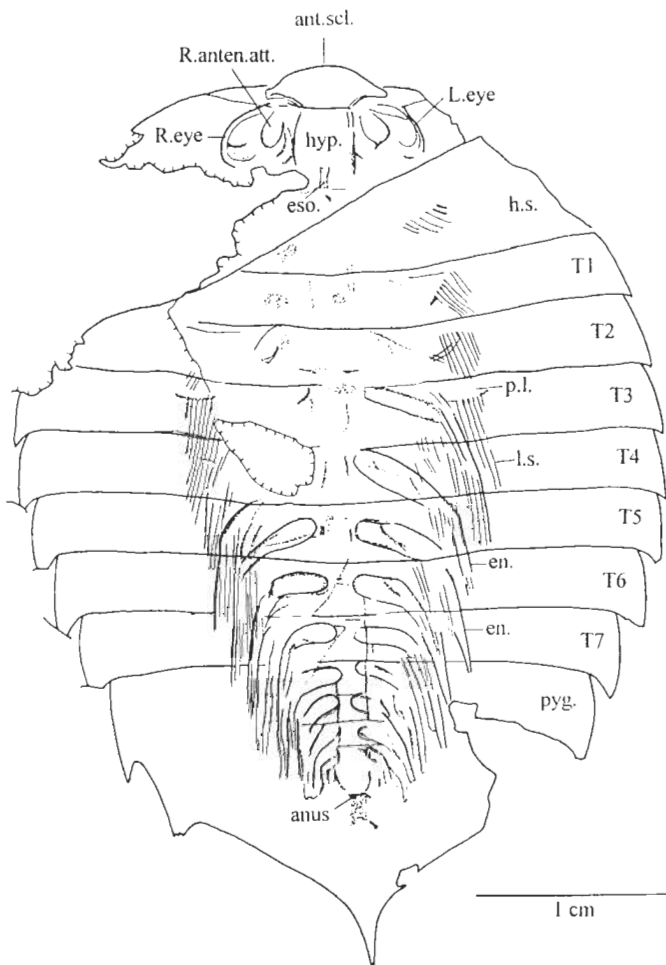


FIGURE 6—*Kuamaia lata* Hou, 1987. Camera lucida drawing of ELRC 19580 (Figs. 5.2, 5.4). Abbreviations as for Fig. 4, with the following additions: ant.att., antennal attachment site; en., endopod; eso., esophagus; h.s., head shield; l.s., lamellar setae on exopod; p.l., proximal lobe of exopod; pyg., pygidium; T, thoracic tergite.

7). Helmetiida show, however, no evidence for an opening through the exoskeletal bulge. Another function of the bulges might have been protective, in that the animals were able to move the eyes into the bulges during activity on the substrate.

Another Chengjiang arachnate apparently showing a similar eye morphology is *Sinoburius lunaris* (Hou et al., 1991, fig. 4). All examined specimens show the raised bulges seen in the holotype (e.g., Chen et al., 1996, fig. 215; Chen and Zhou, 1997, fig. 89). The bulges are teardrop-shaped, distinctly outlined except adaxially where they narrow and fade into the adjacent exoskeletal surface. Specimens exposing the ventral surface of the exoskeleton (Fig. 1.1), such as the holotype, show a rounded patch of material adhering to the ventral side of the bulge. These patches are interpreted here as remains of the eyes. Thus the eyes in *Sinoburius* could be accommodated in dorsal bulges of the cephalic shield.

We conclude that the eyes in *Helmetia*, *Kuamaia*, *Saperion*, and apparently *Sinoburius* are of the same type. They are interpreted as homologous with lateral faceted eyes in other arthropods, in part because more compelling candidates for median eyes have been identified in helmetiids (the reflective spots on the anterior sclerite of *Helmetia*; see character 11). This would

imply that position of the lateral faceted eye (dorsal versus ventral) is rather labile in trilobite-allied arachnates, a point acknowledged by Hou and Bergström (1997).

Whittington (1985) interpreted small, curved reflective patches on the cephalic pleural field of *Tegopelte gigas* as eyes, and possibly dorsal. These structures are positioned approximately opposite to the inferred antennal attachments, and opposite the inferred hypostome. Given that the structures here interpreted as eyes in *Saperion* originate anterior to the antennal attachments and lie largely anterior to the hypostome (Figs. 3.1, 4), they may not be homologous with the supposed eyes of *Tegopelte*. We regard the identity of the reflective curves in *Tegopelte* as uncertain.

7) Eye slits: 0—absent; 1—present.

In *Xandarella spectaculum*, the eye is set in a raised exoskeletal bulge as is indicated by the wrinkles surrounding the eyes. Just outside the visual surface is a circumocular suture or a hole through the exoskeleton. A gap separates the visual surface from the suture or hole, and Hou and Bergström (1997, p. 74) suggested that "the eye is situated on a discrete little round tergite." This observation is incorrect because in the holotype (Hou et al., 1991, fig. 3B), the oval visual surface of the right eye can be seen to extend from a transversely directed eye stalk attaching to its anteromedial part. The eye is thus stalked, based ventrally, and is morphologically similar to the eyes in *Cinderella* and *Sinoburius* (see below). From the posterolateral part of the suture or hole runs a slit or suture transversely to the lateral margin of the head shield, curving posteriorly just before reaching the margin. The slit is much reminiscent in position and course of the posterior part of the facial suture in trilobites. Hou et al. (1991) suggested the slit to represent "a suture or an unfused segmental? boundary," and Hou and Bergström (1997) posit that it is an unfused tergite boundary.

In a reconstruction by Chen et al. (1996, fig. 214), a similar slit was suggested for *Sinoburius lunaris*. The few specimens known are small (8–12 mm long), with less detail preserved than in *Xandarella*. The eyes are prominent, oval, with their long axis parallel to a tangent to the margin closest to the eye, as is also the case in *Xandarella*. In the holotype (Hou et al., 1991, fig. 4; Hou and Bergström, 1997, fig. 77A, B) a curved scarp or suture lies near the adaxial margin of the eye mound, best seen on the individual's right side (left in fig. 4 of Hou et al., 1991). Just inside the scarp is an oval, ventrally convex structure, well delimited except anteromedially where it continues as a band to the small hypostome (anteriorly displaced in this specimen; see Hou and Bergström, 1997, fig. 77C, D for undistorted hypostome position). We interpret this as the ventral surface of a stalked eye very similar to that in *Xandarella*. Two specimens (Chen et al., 1996, fig. 215; Fig. 1.1 herein; Hou and Bergström, 1997, fig. 77D) show the ventral side of the prominent teardrop-shaped eye mounds, with the transversely directed impressions of the eye stalks seen to nearly meet just in front of the hypostome.

The circumocular suture or hole on the adaxial side of the visual surface is present in *Sinoburius* (Fig. 1.2; Chen and Zhou, 1997, fig. 90). From the posterior margin of the suture or hole, a distinct line runs laterally and very slightly anteriorly to the margin of the head shield. The holotype does not preserve any similar lines, but the other ELRC specimen (Chen et al., 1996, fig. 215; Fig. 1.1 herein) shows faint lines in the same position. The interpretation of these lines as slits is strengthened by a specimen figured by Hou and Bergström (1997, fig. 77C–D), in which the first limb pair is seen to extend well beyond the cephalic margin. The limb pair is based near the posterolateral corners of the hypostome, just posterior to the antennal attachments (Hou and Bergström, 1997, figs. 77C–D, 78C). From the

posterolateral corner of the eye lobe to where these limbs extrude from underneath the margin, a deep slit follows the same course (about 30 degrees anteriorly) as the appendage part outside the margin, joining the distal appendage part with the proximal part. Other limbs are outlined as weak furrows in the head shield. Our interpretation why this pair, but no others, would cause slits through the head shield, is that proximal to the shield margin, in this specimen these limbs lie directly underneath the slits, and their collapse during compression caused sediment to follow suite down through a line of weakness, i.e., through already existing slits. We are inclined to interpret these lines as slits or sutures similar to those in *Xandarella*.

The eye slits in *Xandarella* and *Sinoburius* appear to be unique, and we know of no arthropods with closely comparable structures. The superficially similar slit and eye in certain trilobites such as *Loganopeltoidea* (Rasetti, 1948, pl. 7, figs. 1–8) are vestiges of a free cheek, a structure unknown outside the Trilobita. Hou and Bergström's (1997) speculations that eyes associated with an anterior suture in a range of Cambrian arachnates (*Sidneyia*, *Helmetiida*, *Xandarella*) may record a primordial phylotypic stage of cephalization and "eye capture" are intriguing but not well supported.

8) Dorsal facial sutures: 0—absent; 1—present.

The dorsal facial suture in Trilobita (to the exclusion of the "olenellid" grade) is a shared derived character, and has been regarded as a synapomorphy (Lauterbach, 1980, 1983). Geyer (1996) suggested that the dorsal suture arose independently in different groups of "olenellids," such that a taxon based solely on this character is polyphyletic. This scenario requires detailed documentation before it can be endorsed.

9) Head shield overlapping anterior trunk tergite(s): 0—insignificant overlap; 1—head shield covers first thoracic tergite only; 2—head shield covers multiple anterior trunk tergites, with small median area of attachment.

Most of the forms under discussion here have a cephalo-thoracic articulation that is similar to the more posterior articulations. In some forms, the head shield is extended posteriorly to overlap the anterior trunk portion to a larger or smaller extent. Distinctive apomorphic states characterize a liwiine group of naraoiids (state 1 above; documented in discussion of character 18) and a clade including *Sinoburius*, *Xandarella*, and *Cindarella* (state 2, discussed below).

*Xandarella*.—New material (Chen et al., 1996; Hou and Bergström, 1997; Luo et al., 1997) confirms the presence of the small, anterior trunk tergite observed in the two type specimens. Hou et al. (1991) suggested that this tergite was set in a posterior embayment of the cephalic shield. New specimens (Chen et al., 1996, fig. 213) appear to show that no such embayment exists but that the posterior margin of the cephalic shield passes above or slightly behind the posterior edge of the small anterior trunk tergite. A comparison with *Cindarella*, where the attachment of the trunk to the cephalon is known in some detail, makes it likely that the small anterior trunk tergite in *Xandarella* provided the attachment of the trunk to the cephalon, along its rather narrow (transverse) anterior margin.

*Cindarella*.—The anterior six trunk tergites are completely covered by the head shield, and the seventh tergite partly so (see Ramsköld et al., 1997, for details).

*Sinoburius*.—In the holotype (Hou et al., 1991, fig. 4) the seventh tergite from the posterior shield underlies the head, and the sixth tergite is partly overlain. If the lateral margins of the first segment are complete, as they appear to be, then the first trunk tergite is considerably narrower (transversely) than the second one. In ELRC 19550 on the right side (as illustrated in Chen et al. 1996, fig. 215, and Fig. 1.1 herein) the posterior head margin can be followed adaxially, and it passes over the second

(from anterior) tergite. In both specimens, the first tergite has a transverse anterior margin, presumably the line of attachment. In ELRC 19550, a thick layer of matrix between the head shield and the first and second trunk tergites wedges out anteriorly at this transverse line, which supports the interpretation as a small median area of attachment. It thus appears that *Sinoburius* possesses a trunk that is anteriorly tapering and underlying the head shield, as in *Xandarella* and *Cindarella*.

10) Anteromedian margin of cephalon notched, accommodating strongly sclerotised plate: 0—notch and plate absent; 1—notch and plate present.

This character refers to the "rostral plate" of Hou and Bergström (1997), and associated structures (anterior suture and "pararostral plates") that are restricted to *Helmetiida*. We prefer to refer to this plate as an anterior sclerite to avoid confusion with the rostral plate of Trilobita (see discussion under character 11). The anterior sclerite is not known for *Tegopelte*, but the notching of the cephalic margin is the same as is known for *Saperion*, and we have accordingly coded for the apomorphic state in *Tegopelte*.

For *Saperion*, the anterior plate is shown by ELRC 19500 (Figs. 3.1, 4, 7.1), in which it partly underlies the hypostome (see below). Its posterior margin may be exposed as a break in cuticle at about 18 percent of the preserved length of the hypostome (Fig. 4). The lateral and anterior margins of the anterior sclerite are fragmented in ELRC 19500a, but it is presumed to be considerably wider than long.

11) Frontal organs on transversely ovate pre-hypostomal sclerite: 0—absent; 1—present.

*Helmetia* (Walcott, 1931, pl. 23), *Kuamaia* (Hou, 1987, pl. 4, fig. 2, 3; Figs. 3.2, 5, 6 herein) and *Rhombicalvaria* (Hou, 1987, pl. 3, fig. 4) each possess a wide, ovate sclerite partly underlying the anteromedian margin of the head shield. The homology of this structure was obvious to Hou (1987) and Hou and Bergström (1991), who suggested that it is possibly the labrum. Briggs in Conway Morris et al. (1982) forwarded the same interpretation for this sclerite in *Helmetia*, and Delle Cave and Simonetta (1991) reaffirmed it for all *helmetiids*. However, the presence of a hypostome behind the rear margin of the anterior sclerite in *Kuamaia* (Figs. 3.2, 5.4, 6) indicates that the anterior sclerite is not the labrum. The same relationship between the hypostome and a more ventrally-set anterior sclerite is observed in *Saperion* (Figs. 3.1, 4) and in both *saperiids* and *helmetiids* the anterior sclerite projects in front of a median embayment in the cephalic margin.

The strongly sclerotized anterior plate of *Helmetiida* is presumed to be a different structure to the trilobite rostral plate, which is a sector of the cephalic doublure set off by sutures (rostral suture and, usually, connective sutures). A more plausible homology is with the boomerang-shaped sclerotization that lies in front of the median lobe of the hypostome in the naraoiid *Misszhouia longicaudata* (see Chen et al., 1997). This is suggested not only by their shared pre-hypostomal position, but by the presence of a pair of organs on each of these sternites. Chen et al. (1997) interpreted these "frontal organs" in *Misszhouia*, which are preserved in considerable relief, as organs of the median eye complex, and the same interpretation could be extended to the paired reflective spots in *Helmetia*. The fact that *helmetiids* possess clearly identifiable compound eyes as well as frontal organs indicates that the frontal organs cannot be lateral eyes, failing the conjunction test for homology (Patterson, 1982).

Homologues of the frontal organs of *Misszhouia* are preserved in *Sinoburius*. A specimen figured by Hou and Bergström (1997, fig. 77D), shows a lateral pair of swellings and a more anteriorly-positioned median swelling (or pair of swellings?) preserved in strong relief. As for *Helmetia*, they occur in addition

to obvious compound eyes, and are likewise regarded as median eyes.

This character is coded as absent in taxa in which the hypostome abuts the doublure such that a pre-hypostomal field is absent (e.g., *Trilobita*, *Retifacies*, *Sidneyia*, *Emeraldella*).

12) Hypostome attachment: 0—wide attachment, with or without suture; 1—natanant; 2—narrow overlap with pre-hypostomal sclerite; 3—narrow attachment at hypostomal suture.

To clarify the morphology of the hypostome in *Helmetiida*, descriptive remarks upon *Saperion* and *Kuamaia* are required. State 0 is present in many Cambrian arachnates, including the early chelicerate *Kodymirus* (see Chlupáč, 1995, pl. 2, figs. 1–4).

*Saperion*.—The hypostome is not well preserved in ELRC 19500a (Figs. 3.1, 4, 7.1), but its general relationships can be determined. Its (broken) anterior edge overlies the rear margin of the anterior sclerite. The contact between these sclerites is not a functional hypostomal suture of trilobite type (state 3 above). The posterior margin of the hypostome is approximately transverse, and is more strongly defined than the lateral margins. The latter are difficult to distinguish from more or less longitudinal folds which are present on the surface of the hypostome. This folding, along with the ill-defined lateral margin, indicates the weak degree of sclerotization of the hypostome in *Saperion*. Evidence at hand suggests an approximately square hypostomal outline.

*Kuamaia*.—Information on the hypostome is provided in dorsal view by ELRC 19584a (Fig. 3.2) and in ventral view by ELRC 19580 (Figs. 5.2, 5.4, 6). The lateral margins of the hypostome are usually not clearly defined and its degree of sclerotization is less than that of the anterior sclerite. ELRC 19584a indicates that the posterolateral margins of the hypostome are curved, and the posteromedian margin is approximately straight (Fig. 3.2). The hypostome may have lacked significant relief. The lateral margins of the hypostome are convex outward in ELRC 19580 (Fig. 5.4), contributing to a barrel-shaped outline. The posterior edge has been broken off in this specimen, exposing a narrow median band immediately above the hypostome. This band is interpreted as representing the esophagus, and its posterior terminus is regarded as the mouth opening. If so, then the full length of the hypostome can be estimated for this specimen (the mouth opening marking the posterior edge of the hypostome), and is in agreement with the relative lengths of the anterior sclerite and hypostome in ELRC 19584a (Fig. 3.2). Length of the hypostome is about 1.3 times its maximum width.

13) Decoupling of trunk tergites and somites: 0—absent; 1—present.

Ramsköld et al. (1997) provided a description of the decoupling of trunk somites and tergites in xandarellids (*Cindarella* and *Xandarella*). Convincing evidence that *Sinoburius* retains the plesiomorphic state of somites corresponding to tergites is provided by specimens figured by Hou and Bergström (1997).

14) Trunk narrowed anteriorly relative to head shield, widest posteriorly: 0—absent (trunk wider anteriorly or of equal width); 1—present.

All naraoiids share this distinct shape of the tagmata, regardless of whether or not there are free thoracic segments, cited as an apomorphy by Chen et al. (1997).

15) Trunk effacement: 0—trunk with defined (separate or fused) tergite boundaries; 1—trunk tergum completely effaced.

Complete effacement of the trunk is restricted to some naraoiids (*Naraoia* and *Misszhouia*), a group that is unique in the total fusion of the trunk tergites (see character 16). While the possibility exists that fusion of the tergum is a prerequisite for effacement, we are reluctant to aggregate this variation in a single character because several instances of tergite fusion occur

without effacement (see character 17). In *Saperion*, remnants of tergites are indicated in the central area by transverse furrows that weaken or become effaced before reaching the shield margin. *Tegopelte* is smoother than *Saperion*, and if there are transverse furrows, they must be confined to the axial area, in which the exoskeleton is not preserved in the few specimens known. We accordingly code *Tegopelte* as missing data.

16) Trunk tagmosis of pygidium fused to thorax: 0—absent; 1—present, with functional cephalic articulation; 2—present, with fused cephalic articulation.

Although we have employed the pygidium in the definition of this character, it is coded more generally to include taxa lacking a pygidium; state 0 applies to any taxon that possesses functional trunk articulations. The coding employed here recognizes an apomorphic state in some naraoiids (state 1), in which the entire trunk is fused but the cephalic articulation remains functional. The complete fusion (or rather the inhibited development of joints) of the tergum as a single shield (state 2) is shared by *Tegopelte*, *Saperion*, and *Skioldia* (diagnostic of *Tegopeltidae*/*Saperiidae*/*Skioldiidae*). The multistate coding permits a transformation from state 1 to state 2 (by fusing the cephalon to the trunk) at a cost of a single step, and is consistent with the fusion of the pygidium and thorax being homologous in both variants.

Fusion of the tergum in *Saperion* is linked to a unique profile in cross section; the axial region is gently convex, and the distal margins of the tergum are turned up, at least in the large specimens. Considering the 10:1 diagenetic compaction of sediment and specimen, the cross-section of the dorsal shield of *Saperion glumaceum* described a wide and rounded 'W' with deeply troughed pleural areas. This cross-section is made possible by freedom from the usual constraints of tergite articulation.

17) Joints between posterior tergites functional, anterior ones variably fused: 0—absent; 1—present.

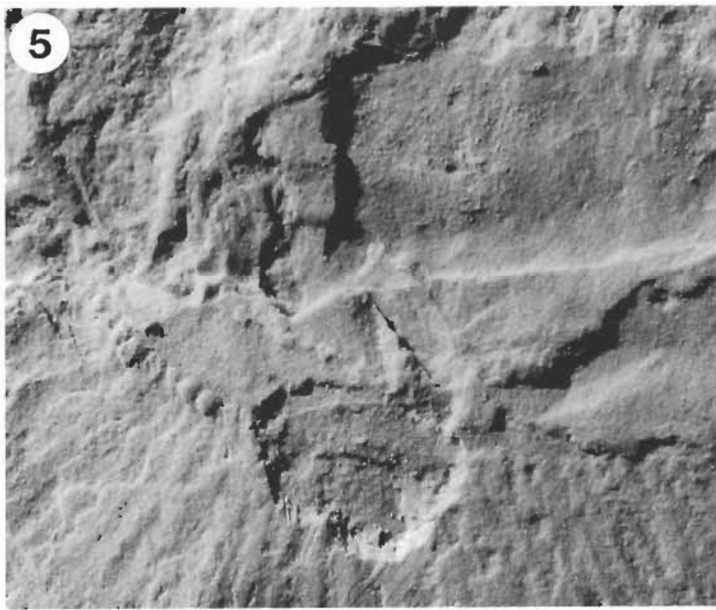
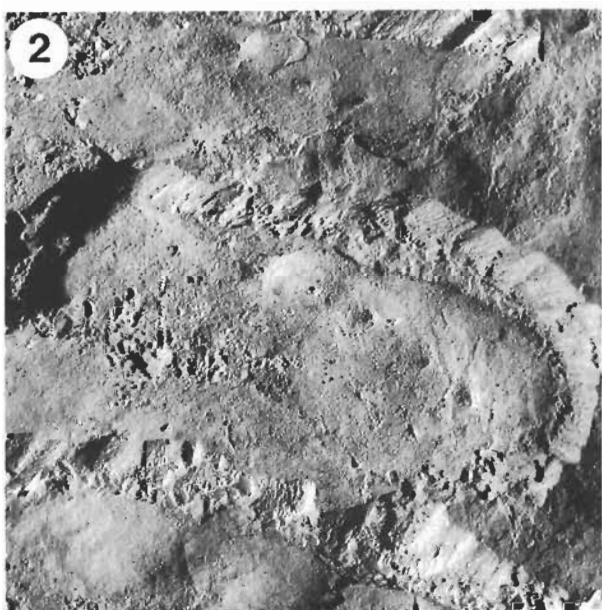
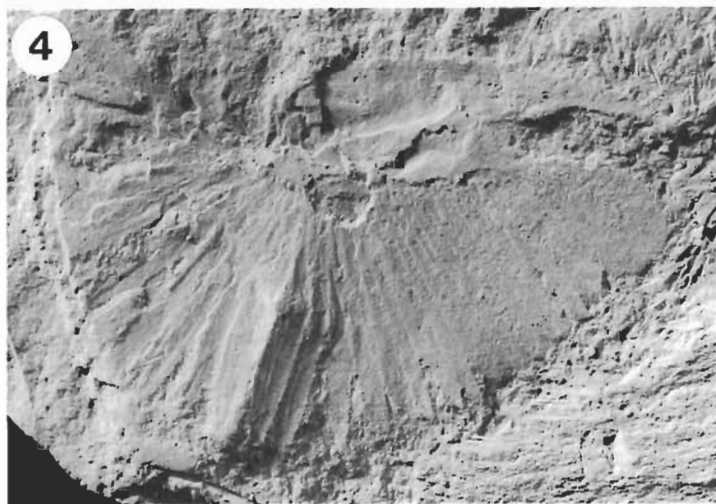
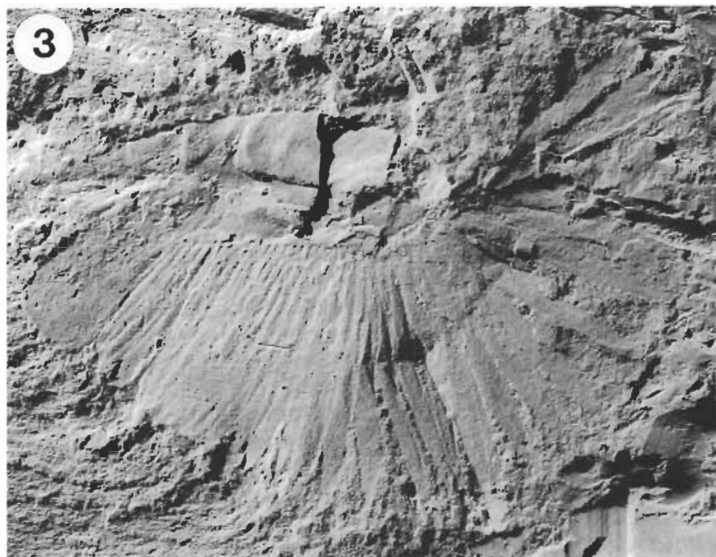
In *Kuamaia*, the articulations between the tergites were clearly functional, providing some flexibility to the exoskeleton. The anterolaterally directed tergite junctions in the anterior part of the trunk would, however, not have permitted much movement between tergites articulating edge-to-edge. *Kuamaia* appears to have been relatively flat, with some convexity in the axial region and with the pleural areas perhaps nearly horizontal. Some kind of flexible folds or articulating half rings were likely present in the axial region, or rotation between tergites would have ruptured the arthroal membrane in that area.

The limited capacity for movement between tergites is taken a step further in *Helmetia*. Tergite boundaries deviate even more anterolaterally from the transverse direction, and there is no indication of functional articulation anterior to the joint between thorax and pygidium (contra the reconstruction of Simonetta and Delle Cave, 1975, pl. 2, fig. 2c). The latter joint is transverse and was clearly functional (Walcott, 1931, pl. 23). *Helmetiids* thus appear to be characterized by functional articulations between posterior trunk tergites but variably fused anterior tergites.

We have coded for the absence of the apomorphic state in taxa for which the posterior tergites are fused, although the character might logically be viewed as inapplicable. The absence coding is more explicit, but carries an implicit assumption that posterior fusion did not result from a helmetiid-like precursor.

18) Tergite articulations: 0—extensive overlap of tergites; 1—edge-to-edge articulations.

This character recognizes a derived state in helmetiids (and saperiids, despite nonfunctional articulations) and trilobites. Tergite margins may be positioned edge-to-edge to either form functional hinge joints, with tergite overlap in the raised axial region only, or when more or less fused, form a weakly radiating



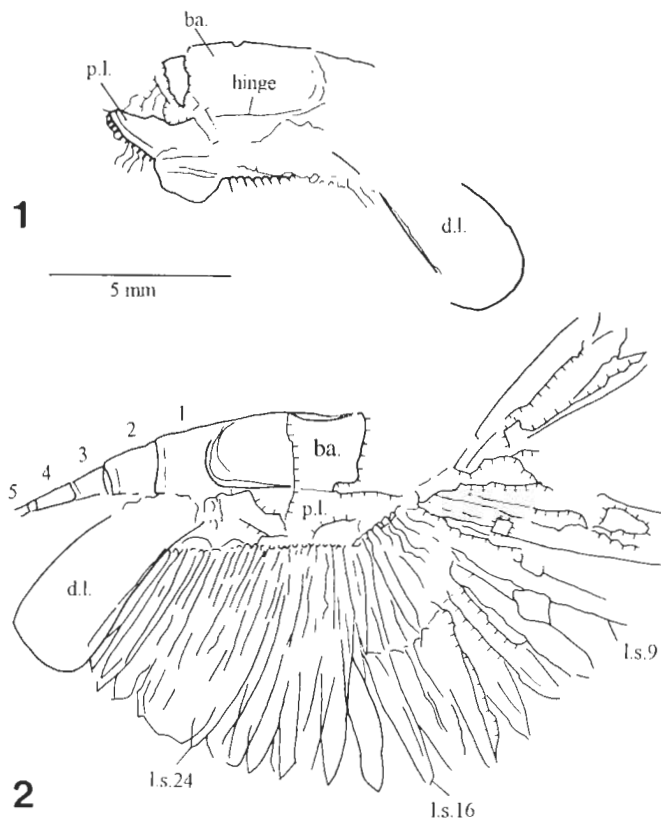


FIGURE 8—*Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991. 1. Camera lucida drawing of disarticulated appendage ELRC 19503b in ventral view (Fig. 7.4, 7.5); 2. camera lucida drawing of ELRC 19503a in dorsal view (Fig. 7.3). Podomeres of endopod numbered 1–5. A few lamellar setae (9, 16, 24) labelled, counting from proximal. Scale bar applies to both figures. Abbreviations as for Figure 3 with the following additions: ba., basis; d.l., distal lobe of exopod; hinge, hinge-like juncture between exopod and basis; l.s., lamellar setae; p.l., proximal lobe of exopod.

pattern of adaxially distinct and laterally variably effaced furrows. We document the plesiomorphic state, extensive overlap of tergites, in naraoiids and several other groups.

*Naraoiidae*.—Naraoiids are quite varied morphologically, but a fundamental structure such as the mode of tergite articulation can be expected to be of the same basic kind throughout the group.

Whittington (1977) illustrated numerous specimens of *Naraoia compacta* that show how the head shield overlaps the posterior shield (Whittington, 1977, figs. 5, 9, 60, 63, 87), and he excavated specimens to show the exact extent of the overlap (Whittington, 1977, figs. 8, 12). Some specimens show the posterior margin of the cephalon coinciding closely with the anterior margin of the trunk shield (Whittington, 1977, fig. 75). However, as shown by specimens preserved in lateral view (Whittington, 1977, fig. 79; Collins, 1986, p. 86 top), this arrangement is an artifact caused by an anteroventral tilt of the head shield. The

overlap in dorsal view, as measured from Whittington's reconstructed life attitude, is 10.5 percent the length of the head shield.

Most specimens of *Misszhouia longicaudata* show the posterior margin of the cephalon coinciding closely with the anterior margin of the trunk shield (Chen et al., 1997, figs. 2a, b, 9b). However, in these specimens the shape of the head shield shows that it is diagenetically shortened due to an anteroventral tilt of the head. An anteroventral tilt of about 30 degrees is the most commonly preserved posture in articulated specimens (Chen et al., 1997, fig. 20a). In specimens preserved with the head shield in the horizontal plane (Zhang and Hou, 1985, pl. 1, fig. 1, 2, pl. 3, fig. 1; Chen et al., 1997, fig. 5a), indicated by the shape and proportions of the shield, the posterior margin of the head is posteriorly convex, not concave as in the distorted specimens. The head shield overlies an anterior spindle-shaped portion of the trunk shield. The overlap amounts to about 7 percent of the head shield (Zhang and Hou, 1985, pl. 1, figs. 1, 2; Chen et al., 1997, fig. 5a).

The holotype of *Liwia plana* (Dzik and Lendzion, 1988, fig. 4a, b) is an articulated, flattened specimen with the tergite edges preserved as a black film. The posteriorly convex margin of the cephalic shield overlies the first thoracic tergite. Adaxially the overlap reaches to the anterior edge of the second thoracic segment and amounts to 12–13 percent of the cephalic length. The relation between the thoracic tergites can be inferred from the black areas interpreted here as overlap between tergites. The shape of these black areas agrees with the shape of overlap of thoracic tergites in arachnates where this feature can be unequivocally observed, such as *Sidneyia*, *Emeraldella*, *Cindarella* and several other Burgess Shale and Chengjiang forms. The overlap in *Liwia* is approximately one-third the length of the tergite both anteriorly and posteriorly, with only the central (sagittal, exsagittal) one-third not overlapping or being overlapped.

In articulated specimens of *Tariccoia arrusensis*, the first thoracic tergite is regularly completely overlapped by the cephalic shield. The thoracic tergites are short (sag., exsag.), with almost transverse anterior and posterior margins. There is a very small apparent overlap between thoracic tergites in the articulated specimens. Two individuals shown in longitudinal section confirm the small length of the tergites (Hammann et al., 1990, pl. 1, fig. 6, pl. 3, fig. 4). The sections through the tergites show that they are evenly convex, with no flanges or other articulating devices. Articulated individuals show that the tergites imbricate without direct contact as shown by the consistent layer of matrix interspersed between the posterior edge of the overlapping tergite and the anterior edge of the one overlapped. The kind of articulation can be described as a loose telescoping of tergites, in which the amount of overlap depends on the angle (in the sagittal plane) between the cephalon and the pygidium.

The three least distorted, articulated individuals of *Soomaspis splendida* Fortey and Theron, 1994, show how the anteriormost thoracic tergite is completely overlapped by the cephalic shield. The tergites possess a very short articulating half ring, and possibly narrow rims acting as articulating flanges. The strong relief would have prohibited telescoping of the thoracic tergites.

FIGURE 7—*Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991. 1. Dorsal view of complete individual ELRC 19500a, locality MQ1 (see Fig. 3.1 for cephalon and Fig. 9 for appendages), light from NNW,  $\times 1.1$ ; 2. detail of proximal parts of two appendages from anterior part of thorax of ELRC 19500a, light from W,  $\times 7.9$ . Note rows of four pits (spines) on limb bases (see Fig. 10.1 for camera lucida drawing). 3–5. Small disarticulated appendage ELRC 19503, from MQ1 (see Fig. 8 for camera lucida drawing). 3. Dorsal view of ELRC 19503a, light from NNW,  $\times 5$ ; 4, 5. ventral view of ELRC 19503b, light from NNW,  $\times 5$ ,  $\times 14.8$ .

*Trilobita and Helmetiidae*.—The general condition in trilobites is that tergites articulate edge-to-edge in the pleural areas (between the axial furrow and the fulcrum). An articulating half ring enables overlap in the axial region. Articulating structures such as flanges, bosses, fulcra, and facets are usually well developed.

The mode of tergite articulation in helmetiids is essentially similar to the trilobite type of articulation. During ontogeny of trilobites, and as we infer also helmetiids, segments were released into the thorax from the pygidium (see character 20). As more tergites were released, the first ones came to occupy a relatively more anterior position. With each moult, some change could take place in the morphology of the released tergites. This well known ontogenetic development explains why anterior thoracic segments are commonly modified relative to posterior ones in trilobites. With this process operating in helmetiids, the posterior thoracic tergites, including their articulation, should be less modified than anterior ones. The material confirms this hypothesis, in that several helmetiids, possibly all, have one or more articulations from the head and posteriorly partly or fully fused (character 17). The further posteriorly, the more transverse, functional, and trilobite-like is the articulation. These circumstances indicate that the fusion of the anterior tergites, and the anteriorly progressively more inclined tergite margins, is a secondary phenomenon, and that the fused joints were transverse and functional earlier in ontogeny.

Tergites may articulate edge-to-edge only if rotation at the joint is around a straight axis, i.e., a hinge-joint. This hinge is formed in the pleural areas which must thus be horizontal between the fulcra (if such are present). A construction of flat pleural areas with hinge articulations is intimately coupled with a raised axis, i.e., some type of trilobation. The raised axis allows the dorsal longitudinal muscles in the trunk stem to be at a more dorsal level than the pleural hinge articulations. This is necessary because with horizontal pleurae, a non-raised axis would prohibit longitudinal extensor musculature. The flexor muscles would then lack antagonists, which in turn would make flexure, i.e., rotation, around the tergite joints impossible, and the joints could not function as such.

To avoid gaps in the axis during flexure, overlap is necessary in a relaxed state. Trilobites possess articulating half rings, and similar structures are present in helmetiids, as exemplified by *Kuamaia*. Well preserved material shows the presence of a spindle-shaped overlap in the raised axial region (Hou and Bergström, 1997, fig. 57A-C, G). The overlap is well defined in lateral extent, posteriorly occupying 20–21 percent of the width between fulcra (Hou and Bergström, 1997, fig. 57C), and anteriorly close to 30 percent (Hou and Bergström, 1997, fig. 57G). Although all specimens are considerably flattened, the axis retains a distinct convexity, and the abrupt change from edge-to-edge articulation in the pleural areas to overlap in the axis indicates that trilobation in *Kuamaia* was conspicuous in life.

*Other arachnates*.—The above described edge-to-edge articulation contrasts with the strong overlap between tergites seen in Cambrian arachnates such as *xandarellids* (Ramsköld et al., 1997), and numerous Burgess Shale arachnates including at least *Sidneyia*, *Emeraldella*, *Leanochoilia*, *Alalcomenaeus*, *Acteus*, *Sarotrocercus*, *Habelia*, and *Molaria*. Tergite articulation is a structurally and functionally complex feature of fundamental importance to other aspects of the body plan. Although a particular kind of articulation certainly may develop independently in different groups, the edge-to-edge articulation in Helmetiida and Trilobita provides a possible synapomorphy for these taxa.

19) Exoskeletal boundaries of anterior trunk segments reflexed anterolaterally: 0—boundaries transverse or reflexed posterolaterally; 1—reflexed anterolaterally.

Helmetiida (Helmetiidae, *Skioldia*, *Saperion*) possess a distinctive configuration of the anterior few thoracic segments. The posterior margin of the head is reflexed anteriorly in its abaxial portion, and an anterolateral course is maintained in the anterior thoracic segments. By the middle of the thorax, the margins of segments/tergites run more or less transversely. This shape is paralleled in some other Palaeozoic arachnates, such as *Chelonellon*, *Duslia*, *Pseudarthron*, and *Triopus* (see Chlupáč, 1988). These taxa have most recently been recognised as comprising a clade close to Chelicerata (Dunlop and Selden, 1997), and the similarity to Helmetiida is certainly convergent.

20) Pygidium: 0—absent; 1—present

The term pygidium has been applied to multisegmental posterior tagma and cited as a synapomorphy for Trilobita (Fortey and Whittington, 1989; Fortey and Theron, 1994) or Eutrlobita (Hahn, 1989). Ramsköld et al. (1997) made a distinction between two fundamentally different types of multisegmental posterior tagma in Arachnata based on their mode of development. One of these, a pygidium, defines a monophyletic group including helmetiids, naraoidids, trilobites (and presumably *Tegopelte*, *Saperion*, and *Skioldia*). In trilobites, naraoidids (e.g., *Liwia*, *Soomaspis*, and *Tariccoia*), and helmetiids the thoracic tergites each correspond to a single somite, whereas the pygidium marks the point at which tergites cease being released anteriorly (from the transitory pygidium) in ontogeny. We code this developmental mode of thoracic/pygidial tagmosis as a putative synapomorphy for Naraoididae, Helmetiida, and Trilobita.

21) Median keel on pygidium: 0—absent; 1—present.

A median keel on the pygidium is shared by *Tariccoia* and *Soomaspis* (Chen et al., 1997). The character is scored as inapplicable (“—”) for those taxa lacking a pygidium.

22) Pygidium with broad-based median spine and two pairs of segmental marginal spines: 0—spines absent; 1—spines present.

As for character 21 we have coded this character as inapplicable for taxa without pygidial tagmosis. *Tegopelte*, *Saperion*, and *Skioldia* are coded as lacking these spines, despite the uncertainty of coding any pygidial characters in these taxa. Certainly the spines are absent on the posterior (pygidial?) part of the tergum in these taxa. Coding the character as missing data for these genera would permit spurious optimizations, such as presence of the spines.

23) Posterior tergite with axial spine: 0—absent; 1—present.

The best preserved specimen of *Sinoburius lunaris* (Luo et al., 1997, pl. 2, fig. 4) shows evidence for a median axial spine similar to those of *Xandarella* and *Cindarella*.

24) Width of doublure: 0—narrow or moderately wide; 1—wide (maximum width more than 30 percent length of head shield or more than 25 percent width of pygidium).

Chen et al. (1997) scored the wide doublures of *Tariccoia* and *Soomaspis* as a shared derived character, an action followed here. In *Soomaspis* the cephalic doublure extends to about 35 percent the length (sag.) of the head shield (Fortey and Theron, 1994, text-fig. 1A), and in *Tariccoia* the pygidial doublure has a width 25–28 percent the width of the pygidium (Hammann et al., 1990, text-fig. 4b). Most taxa grouped in state 0 have narrow doublures, with *Retifacies* providing the upper limit (maximum width of doublure about 18 percent the width of the pygidium).

25) Paired flaps lateral to telson: 0—absent; 1—present.

Hou and Bergström (1997) cited “uropods” as a defining character of their taxon Xenopoda. This homologizes the paired flaps against the telson spine in *Emeraldella* with the flap-like paddles beside the telson in *Sidneyia*. The homology is reasonable (although the usage of the term “uropod,” which has a

precise meaning in Malacostraca, should be discouraged). Possible homologues cannot be identified in other terminals in this analysis.

26) Exopod differentiated into proximal and distal lobes: 0—absent; 1—present.

Ramsköld and Edgecombe (1996) described a division of the exopod into proximal and distal lobes in trilobites and naraoiids, as well as hinging of the exopod along the length of the basis (see Ramsköld et al., 1997, for xandarellids). These characters are not pan-arachnatan in their distributions. A distal lobe is lacking in *Retifacies* (Hou and Bergström, 1997, and our study of ELRC 19259, illustrated by Chen and Zhou, 1997, fig. 70), and does not appear to be present in *Sidneyia*. We document their expression in saperiids/tegopeltids in the following descriptive account of *Saperion glumaceum*, along with comparison to *Tegopelte*, and present a new interpretation of *Emeraldella* that recognizes proximal and distal lobes.

*Saperion*.—Several thoracic exopods have been exposed in ELRC 19500a (Figs. 7.1, 9, 10), revealing their bilobate structure (proximal and distal lobes). The exopod covers a very large surface area, chiefly due to a fan of long lamellar setae, and most of the pleural field is underlain by exopods. The setae extend back to such an extent that a fan in the anterior part of the trunk covers parts of the following three or possibly even four limbs. Setae of similar proportions are exposed in the presumed cephalic region of the same specimen (Fig. 7.1), such that exopods do not vary significantly from the cephalon through the thorax. Appendages narrow evenly in the posterior part of the trunk of the possibly conspecific ELRC 19501 (Chen et al., 1996, fig. 216; Chen and Zhou, 1997, fig. 73), and the crowding of the “pygidial” limbs described by Whittington (1985) for *Tegopelte* applies to *Saperion* as well (see decreasing distance between segmental structures behind last fold across pleurae in ELRC 19500b; Chen et al., 1996, fig. 217B; Ramsköld et al., 1996, fig. 1A).

The proximal lobe of the exopod, to which the setae articulate, is large and flat. Its posterior margin is flexed backwards, although significant sectors are approximately straight (Figs. 9, 10). The outer edge of the proximal lobe, its point of articulation with the distal lobe, is straight. The distal lobe is of similar surface area to the proximal lobe, but is more or less clavate in outline. The attachment of the exopod to the basis is ambiguous in ELRC 19500a (Figs. 9, 10), but is more clearly shown by isolated appendage ELRC 19503a (Figs. 7.3–7.5, 8). A straight line delimits the contact between the basis and the proximal lobe, and this line extends along the entire length of the basis. We accordingly interpret the exopod attachment as the sort of “hinge” seen in naraoiids and trilobites (Ramsköld and Edgecombe, 1996), as also documented for helmetiids (*Kuamaia*) and *Retifacies* by Hou and Bergström (1997).

The configuration of lamellar setae on the proximal lobe is best displayed by ELRC 19503a (Figs. 7.3–7.5, 8), in which the proximal setae are fanned out to reveal their margins. The setae are lanceolate in outline, but tapering distally to a pointed tip. They imbricate with each seta partly underlying its proximal neighbour. The inner edge of the distal lobe of the exopod is overlapped by one or two lamellar setae, a condition that has been observed in various other trilobite-allied Cambrian arachnates (Chen et al., 1997; Ramsköld et al., 1997). Setae articulate along the entire length of the proximal lobe, extending inwards to the most proximal part of the exopod. The distal lobe of the exopod does not bear any setae, nor have bristles been observed along its margins.

The morphology of the exopod in *Saperion* differs strikingly

from that interpreted for *Tegopelte gigas* in prior work (Simonetta and Delle Cave, 1975; Whittington, 1985). Bilobate structure has not been confirmed for *Tegopelte*; rather, the exopod has been reconstructed as a relatively short (exsagittal) undivided ramus with lamellar setae splaying off along its length (Whittington, 1985, fig. 17). This contrasts with the presence of a long, flattened inner lobe with a well marked line of setal articulation and pronounced outer lobe in *Saperion*. Given the close similarity of exoskeletal morphology between the two taxa, it would be surprising that exopod form would differ so dramatically between closely related taxa, particularly in light of the structure of *Saperion* being closely mirrored by helmetiids (e.g., *Kuamaia*; Hou and Bergström, 1997). This would suggest that the exopod of *Helmetiida* is conservative, and ingroup lability is less probable. Until better material is available for *Tegopelte*, we are uncertain to what degree the apparent differences between *Tegopelte* and *Saperion* reflect preservational ambiguities of the former, rather than real morphological differences. *Tegopelte gigas* at least appears to possess a lobate exopod shaft. Although Whittington (1985, fig. 17) reconstructed the shaft of the exopod as slender, he noted (1985, p. 1261) that it appeared to be lobate proximally, an observation confirmed by his photographs (especially limb 1 in figs. 7, 8, 10, 12, 13). The posteriorly curved edge to which the lamellar setae articulate on this exopod is suggestive of the edge of the proximal lobe in *Saperion glumaceum*. The apparent articulation of lamellar setae to the distal part of this exopod in *Tegopelte* (Whittington, 1985, figs. 7, 12) is difficult to reconcile with the clear lack of setae on the distal lobe in *Saperion* (and other Cambrian arachnates; see Chen et al., 1997) and we suspect that these setae may originate on a proximal lobe.

*Emeraldella*.—The interpretation of the biramous limbs of *Emeraldella brocki* given by Bruton and Whittington (1983) showed a unique, complex exopod (“gill branch”) that changed shape along the trunk. Hou and Bergström (1997, fig. 86) reinterpreted two detached exopods (Bruton and Whittington, 1983, figs. 43–45, 47, 49) as being folded over themselves to produce the apparent subdivision of the “gill branch” into two parts. This interpretation would explain some of the apparent discrepancy sometimes seen between the shape of isolated limbs and those preserved in situ in some specimens. However, we disagree with the Hou and Bergström interpretation and here give an alternative that shows the *Emeraldella* limb to be of the same general construction as in most of the groups included in this study, with a separate, articulated distal lobe.

Some of the complete *Emeraldella* specimens show limbs that agree with the shape seen in the isolated appendages. Particularly clear is USNM 136442, which shows several appendages (Bruton and Whittington, 1983, figs. 22, 23, 25–27). All of these are in the same shape and orientation, and are clearly preserved without folding. A few appendages show both endopod and exopod, the best of these preserving almost as much as the most complete of the isolated appendages. The basis (“coxa”) is partly exposed and the four proximal podomeres are very well preserved. Posterior to these are the exopod, showing an oblique articulation between the proximal and distal lobes. The middle of the third podomere lies adjacent to the articulation. Also in the isolated limb (Bruton and Whittington, 1983, fig. 44), the articulation is adjacent to the middle of the third podomere. In both specimens, as in the second isolated limb (Bruton and Whittington, 1983, fig. 45), the line of articulation between proximal and distal lobes is directed anterolaterally when the appendage is oriented with the endopod extended laterally. That this line is a real feature and not an artifact of folding is proven by USNM 136440 (Bruton and Whittington, 1983, fig. 11) and USNM 144928 (Bruton and Whittington, 1983, fig. 36). In these





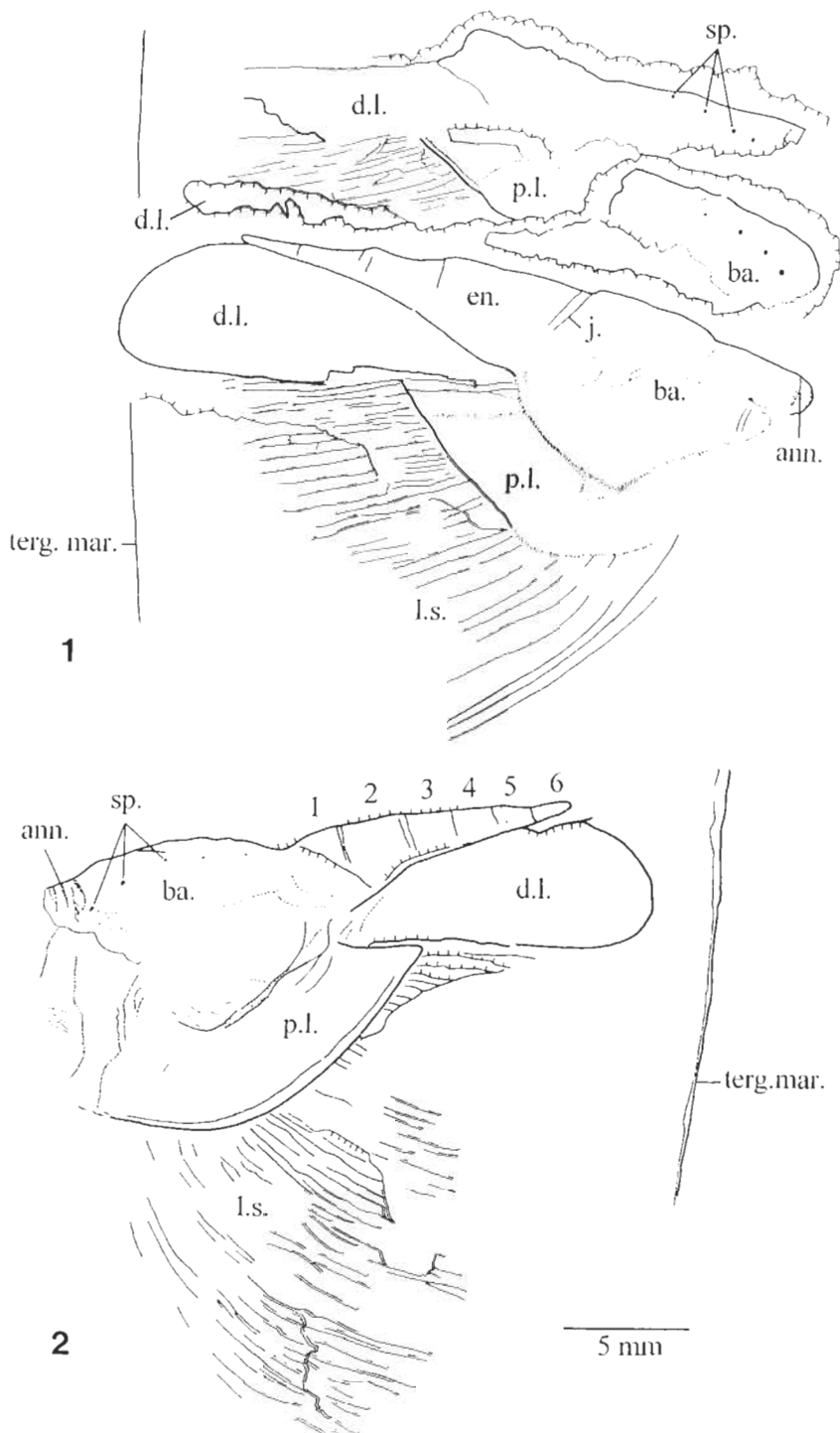


FIGURE 10—1, 2. *Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991. Camera lucida drawings of thoracic appendages of ELRC 19500a. 1, See Figure 9.1; 2, see Figure 9.2. Podomeres of endopod numbered 1–6. Scale bar applies to both figures. Abbreviations as for Figure 6 with the following additions: ann., annulated cornus at leg attachment; ba., basis; d.l., distal lobe of exopod; j., joint between basis and endopod; sp., spinule on basis; terg.mar., margin of tergum.

FIGURE 9—1–3. *Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991. Dorsal views of thoracic appendages of ELRC 19500a, locality MQ1 (see Fig. 7.1 for complete specimen). 1, Appendages on left side of anterior part of thorax (see Fig. 10.1 for camera lucida drawing), light from NW,  $\times 4.7$ ; 2, appendages on right side of anterior part of thorax (see Fig. 10.2 for camera lucida drawing), light from W,  $\times 6.2$ ; 3, detail of lamellar setae articulating to proximal lobe of exopod, low light from NE,  $\times 6.2$ .

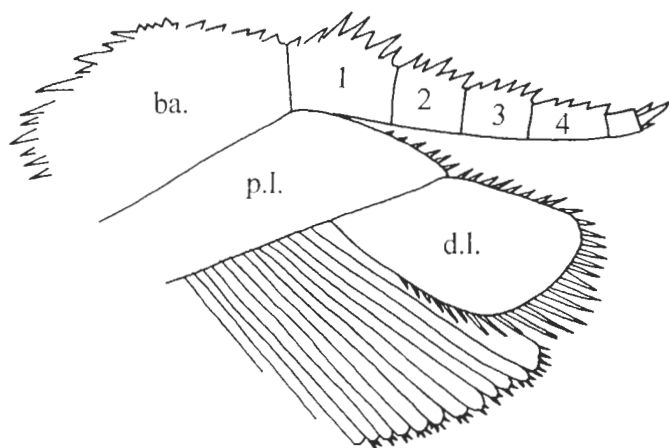


FIGURE 11—*Emeraldella brocki* Walcott, 1912. Reconstruction of an isolated limb in common preservational aspect (not life position). See discussion of character 26 for evidence for exopod attachment and lobation. Abbreviations: ba., basis; d.l., distal lobe of exopod; p.l., proximal lobe of exopod; 1–4, first four podomeres of endopod.

specimens, the limbs are rotated around their axis to be oriented with the endopod posterior to the exopod, a rotation that is common in other Burgess Shale and Chengjiang arachnates. In USNM 136440, Limb 13 on the left side has been prepared to show the proximal and distal exopod lobes. The junction between these lobes is oblique in the opposite direction to the previously discussed specimens. In USNM 144928, an exopod on the posterior left side also shows this junction, and it is in the same orientation. This shows that the oblique line is present on both the dorsal and ventral sides of the exopod, and that its position and direction are consistent both in isolated limbs and in situ whether overturned or not.

The hinge between the basis and the exopod proximal lobe is preserved as the line of rupture in one specimen (Bruton and Whittington, 1983, fig. 45). In the two specimens preserving the basis and exopod together, the fusion can be seen to end at the joint between the basis and podomere 1 (Bruton and Whittington, 1983, figs. 22, 44), because the matrix separating the endopod from the exopod ends at this point. The adaxial direction of the hinge is indicated by the line of rupture in USNM 250228, which is the same as the conspicuous line seen in USNM 155636. The detailed shape of the basis is not known, but the proximal end of the exopod is apparently preserved in USNM 250228.

Most of the above specimens show rather short, sturdy endopods, but USNM 144928 is of the type with strikingly different limbs, with long endopodal podomeres. The difference is in part due to the longitudinal position of the limb, posterior limbs being shorter than anterior ones, and since both types of specimens show the same construction of the exopod lobes, the question of conspecificity of these specimens is not considered here.

On the basis of the above observations, a new interpretation of the limb of *Emeraldella* is given (Fig. 11), and forms the basis for codings.

27) Proximal section of exopod: 0—lobe; 1—shaft.

The naraoiids *Naraoia* and *Misszhouia* and the xandarellid *Xandarella* differ from most other taxa under consideration in that the exopodal setae articulate to a relatively slender shaft rather than to a large, flattened lobe. The state of this character is unknown for the other naraoiids, for which limbs are unpreserved. Hou and Bergström (1997) regarded the naraoiid state as plesiomorphic, apparently influenced by outgroup comparison

TABLE 1—Twenty-nine characters used in the phylogenetic analysis. “?” indicates missing data. “-” indicates inapplicability. Note that characters 2 and 4 are polymorphic for Marrellomorpha (“states 6 and 7”) whereas character 4 is partially uncertain for *Tariccoia* and *Soomaspis* (“either state 0 or 2, but not 1”).

Marrellomorpha	0602?	00000	00000	00??0	--0-0	02-0
<i>Sidneyia</i>	00100	00000	00000	00000	--001	02-0
<i>Emeraldella</i>	0402?	00000	00000	00000	--001	1000
<i>Cindarella</i>	03000	00020	01100	00000	--100	1001
<i>Xandarella</i>	05000	01020	01100	00000	--100	1100
<i>Sinoburius</i>	03000	11020	11000	00001	01100	???
<i>Rettifacies</i>	01000	00000	00000	00001	00000	00-0
<i>Kuamaia</i>	02000	10001	22000	01111	01000	1010
<i>Helmetia</i>	02200	20001	12000	01111	01000	???
<i>Skioldia</i>	02200	10001	22-00	2021?	-0000	???
<i>Saperion</i>	02200	10001	22-00	2011?	-0000	1011
<i>Tegopelte</i>	02020	20001	??-0?	201??	-0000	2021
<i>Livia</i>	021??	??010	??210	00001	00020	???
<i>Tariccoia</i>	0220?	00010	??210	00001	10010	???
<i>Soomaspis</i>	0220?	00010	??210	00001	10010	???
<i>Misszhouia</i>	0202?	00000	11-11	10001	00000	1100
<i>Naraoia</i>	0212?	00000	21-11	10001	00000	1100
<i>Eoredlichia</i>	12011	00100	03000	00101	00000	1000
<i>Olenoides</i>	12011	00100	03000	00101	00000	1000

with marrellomorphs, although the homology is dubious given the lack of differentiation into proximal and distal segments in marrellomorphs.

28) Shape and articulation of distal lobe of exopod: 0—small to moderate sized flap, with short to moderately long attachment to proximal lobe; 1—large, teardrop shaped, with long attachment to proximal lobe.

State 1 recognizes a similarity between the exopods of *Kuamaia* and *Saperion* (see description under character 26; Figs. 9.1, 9.2, 10). We acknowledge that state 0 lumps considerable variation within which additional states may be recognized. Hou and Bergström (1997) reconstructed the distal lobe in *Kuamaia* as composed of two elements. The critical specimen (Hou and Bergström, 1997, fig. 57B) has a wide, low ridge in this position, not a thin line. The ridge is most likely an impression of an overlying structure, caused by compaction, and we regard the distal lobe of *Kuamaia* to be more similar to that of *Saperion* than is shown in the Hou and Bergström interpretation.

29) Gnathobase on basis and prominent endites on endopod: 0—present; 1—absent.

The absence of major endites on the endopod and lack of gnathobases on the basis is shared by *Saperion* (documented in the following account of the limb base and endopod), *Tegopelte*, and *Cindarella* (see Chen et al., 1997, for documentation). Presence is coded when endites and gnathobases are observed on any limbs (e.g., on the trunk limbs of *Triarthrus*, for which endites are lacking on cephalic limbs fide Whittington and Almond, 1987).

*Saperion*.—The limb base (homologized with the crustacean basis, following Walossek, 1993) has been exposed in several thoracic appendages (Figs. 9, 10). It is large and robust and, where most accurately measured (Fig. 10.1), more than 70 percent the length of the endopod. This extreme length of the basis begs the question of whether one or more endopodal podomeres may be fused to it but are undetected. Several successive appendages in the anterior part of the trunk reveal a line of up to four pits in the upper surface of the basis (Figs. 7.2, 10). These are interpreted as small spines that project ventrally. Otherwise, there is no evidence for endites on the basis and definitely no gnathobasic lobe. The appendages in ELRC 19500 rotated with the exopods lying posterior to the endopods. The exopods are

in their undisturbed, dorsal-up position. When limbs of Chengjiang arthropods with gnathobases, such as the naraoiid *Misszhouia longicaudata* (Chen et al., 1997) or the trilobite *Eoredlichia intermedia* (Ramsköld and Edgecombe, 1996), rotate into this position (endopod anterior to exopod), the gnathobase is seen to project anteriorly. No projections from the (anterior, as preserved) margin of the basis are present in ELRC 19500. That the row of pits (spines) lies towards the preserved anterior edge of the basis indicates that it is approximately ventral.

The basis of *Saperion* is considerably larger in cross-section than that reconstructed for *Tegopelte* but several conspicuous similarities are observed that strengthen Whittington's (1985, fig. 17.3) interpretation. Both taxa are characterized by the absence of either medially or ventrally directed gnathobases, and endites on the basis are either absent or represented by very small spines.

The endopod of *Saperion* is relatively short, terminating well inward of the exoskeletal margin (by contrast, the outer edge of the exopod extends to the exoskeletal margin). The juncture between the basis and the presumed first podomere of the endopod is not marked by a strong articulation in any specimens, but is represented by a rather weak, possibly incomplete joint (j in Fig. 10.1). Podomere counts are imprecise for most of the preserved endopods. The maximal number of podomeres that can be identified in any endopod is six in the anterior trunk limb in Figs. 9.2 and 10.2, although the contact between the basis and the endopod is not marked (we assume that the endopod commences opposite the juncture between the proximal and distal lobes of the exopod, as is the case in other nearby limbs; cf. Fig. 10.1). The podomeres show a progressive shortening distally. None have endites, and the endopod appears to terminate with a stout point. Five podomeres are defined in the endopod of ELRC 19503a (Figs. 7.3, 8.2), although this limb is not complete distally. It confirms observations from ELRC 19500a that the endopod tapers rapidly distally, and no endites or accessory spines are developed on any of the podomeres.

Endopods in *Saperion* differ in a number of respects from those of *Tegopelte*. The thoracic endopods of *Tegopelte gigas* are considerably longer and more slender. When fully extended they project outside the margin of the tergum (Whittington, 1985, fig. 8.1). The pronounced taper of the endopods of *Saperion* is not seen in *Tegopelte*, which displays a greater similarity to outgroup taxa such as trilobites.

#### LIMB ATTACHMENT

Limb attachments marked by several concentric folds or annulations of arthroal membrane are known for *Kuamaia lata* (Hou and Bergström, 1997, fig. 58B) and a specimen that possibly represents *Saperion glumaceum* (Chen et al., 1996, fig. 216; Chen and Zhou, 1997, fig. 73). This construction is the same as that described for the naraoiid *Misszhouia longicaudata* by Chen et al. (1997). In *Kuamaia* and *Misszhouia*, the annulated cornus is seen to originate at the edges of an hourglass-shaped sternite. Hou and Bergström (1997) identified the annulated cornus in *Retifacies*, and proposed that it is a synapomorphy for Nectopleura (*Retifaciida* + *Nectaspidida*). This is curious given that they (1997, p. 63) observed "curved lines similar to those of *Naraoia* and *Retifacies* and indicating the soft cornus of the appendage" in *Kuamaia*. We agree with their interpretation of these structures, having likewise observed four or five annulate folds at the limb base in specimens of *Kuamaia lata*, but this more general distribution in *Helmetiida* refutes the value of this character as a "nectopleuran" synapomorphy.

Furthermore, as Chen et al. (1997) noted, the attachment of

the basis to annulated arthroal membrane in Cambrian arachnates is similar to leg attachments in stem-lineage crustaceans (Walossek and Müller, 1990). This is beautifully illustrated for *Martinssonina* by Walossek and Szaniawski (1991, fig. 7D). Rather than serving as a "nectopleuran" synapomorphy, we recognize this morphology as part of the groundpattern for the schizoramous arthropods, and have accordingly not used an annulate cornus as a character in our analysis. Within the framework of atelocerate arthropods being a clade, arrangements in which the leg base articulates to the body at a condyle (e.g., the coxa/sternum condyle of myriapods or the coxa/pleuron condyle of hexapods) must be regarded as derived relative to the similar state of folded arthroal membrane at the leg base in early arachnates and crustaceans.

#### PRIMARY AND SECONDARY CHARACTERS

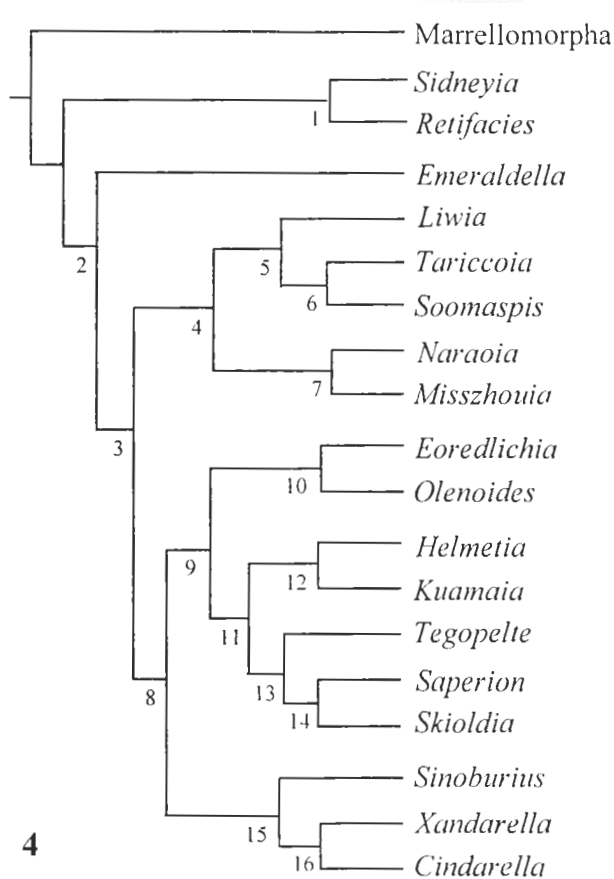
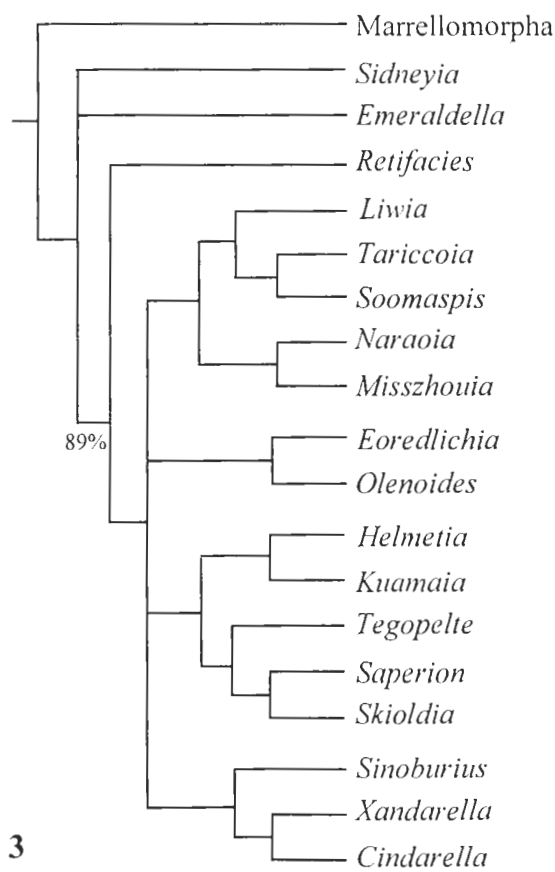
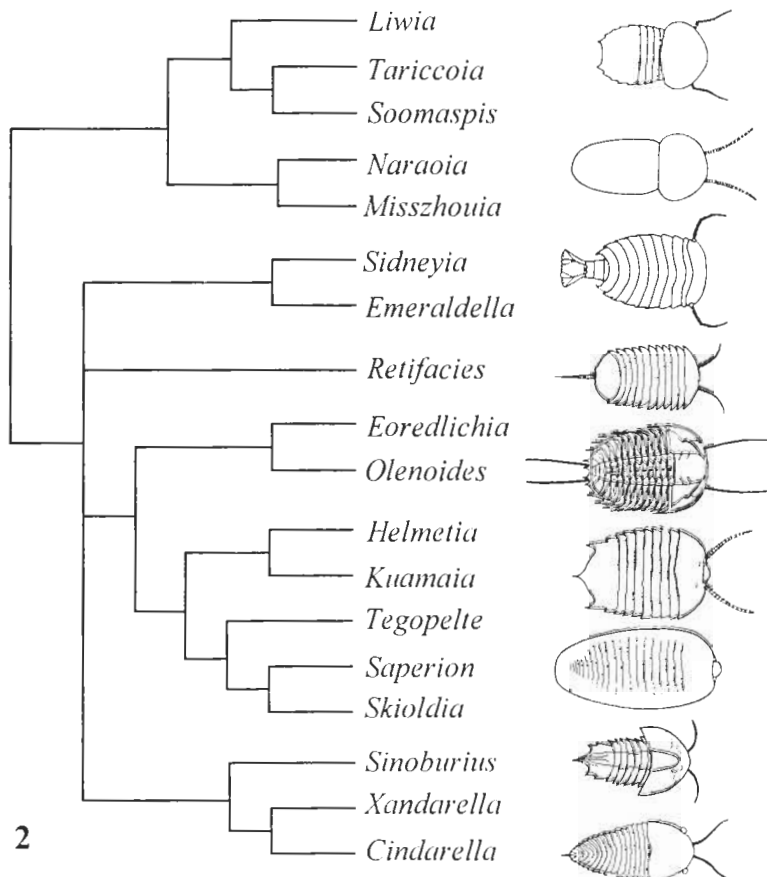
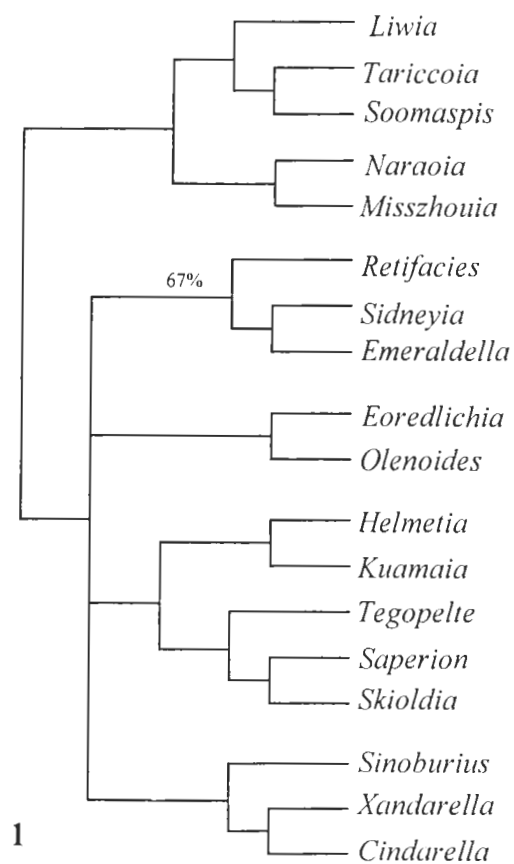
We have endeavored to use characters that can be directly observed in the fossil material. These bases for comparison are what we would call primary characters. Subsequent to observation of primary characters, evidence from these characters may be inferred to indicate aspects of morphology or function. Such inferred conditions form a special category, here termed secondary characters.

Some of the key characters employed by Hou and Bergström (1997) fall into this category of secondary characters. Among these are the distinction between semi-pendent and laterally-splayed appendages, their character "Stance of ventral appendages," and the mode of feeding (see "Deposit feeding" below).

*Limb stance.*—The limb stance in fossil material can be directly observed only in virtually undistorted material, such as three-dimensionally preserved, phosphatic specimens. From the Upper Cambrian orsten material, original limb stance can be directly observed in, among others, the arthropods *Agnostus* (Müller and Walossek, 1987) and *Rehbachella* (Walossek, 1993). In all other types of preservation, the limb stance must be inferred from flattened and more or less distorted material. Some information may be gained from constraints to possible limb stances, such as the shape of the exoskeleton. Obviously limbs must somehow fit inside a carapace or bivalved exoskeleton. In taxa with a strongly vaulted exoskeleton, the limbs must by necessity be held hanging down from the trunk (the pendent or semipendent state of Hou and Bergström, 1997). Proponents of the view that limb stance is an overriding character might reverse this correlation and propose that in taxa with pendent limbs, the exoskeleton will be strongly vaulted. The overall shape of the exoskeleton tends to be conservative within clades, and a listing of preserved orientation of Chengjiang arthropod specimens (Hou et al., 1991, Table 1) shows a general agreement within each of the major arthropod groups.

In this study, however, most of the taxa concerned have a broad, rather flat exoskeleton. This gives full freedom to the limbs to spread out nearly horizontally or to hang down vertically, or any intermediates. Most commonly, the limbs are spread out under the exoskeleton, but in some specimens, the stance is pendent, such as in the *Kuamaia lata* specimen ELRC 19580 (Fig. 5.2). It is impossible to say whether the spread out or the hanging stance was the "original" one, since the animal's death struggle during entombment may have produced an atypical limb stance that was not generally held under normal conditions. Observation of preserved limb stance alone is not sufficient to determine the situation in life.

The construction of the limb attachment and the podomere joints may indicate limits to possible limb stances, but even in well preserved material we should be careful to infer how much flexibility the joints permitted. These difficulties, combined with the lack of suitable material, have led to the nature of limb



attachment in Cambrian arthropods having not yet been studied for even a single species. We can, however, be certain that the limb stance varied due to the requirements for the moment: swimming, walking, resting and other activities demanded different limb stances. Until the nature and constraints of the limb attachments and podomere joints have been studied in detail in a number of taxa, limb stance has little substance as a character, and should not be used as a basis for phylogenetic conclusions.

**Deposit feeding.**—Another secondary character used by Hou and Bergström (1997) is the feeding strategy (their character "Mode of feeding," also discussed by them under "Intestine").

Some Burgess Shale arthropods have been described as regularly having a mud-filled gut, e.g., *Naraoia* (Whittington, 1977). This condition is better seen in the Chengjiang material, where mud in the gut is three-dimensionally preserved, is structurally indistinguishable from the mudstone matrix, and where the shape of the gut is often cast in fine detail. In some taxa, such as *Naraoia spinosa*, most specimens have a mud filled digestive system that includes numerous diverticulae in the head (Chen et al., 1997, figs. 16a, c, 18b). Some *N. spinosa* specimens have a mud filled gut but lack mud in the diverticulae (Chen et al., 1996, fig. 229; Chen et al., 1997, fig. 16b), and some lack mud altogether (Chen et al., 1996, fig. 230). In the naraoiid *Misszhouia longicaudata*, most specimens lack mud in the gut, while some have the esophagus and the ventricle-like expansion in the head filled with mud (Chen et al., 1997, fig. 9b; Hou and Bergström, 1997, fig. 39A), and some exhibit a completely mud filled digestive system (Chen et al., 1997, fig. 18a; Hou and Bergström, 1997, fig. 39D), sometimes with mud that has also penetrated the diverticulae in the head and trunk (Chen et al., 1997, fig. 2a).

In *Naraoia spinosa*, the strongly developed cephalic diverticulae may be indicative of an adaptation for mud-eating, but what about the closely related *Misszhouia longicaudata*? Most specimens lack mud-filling in the gut, so can the minority that shows presence of mud be taken to indicate that the animal was a mud-feeder? Had *M. longicaudata* been a rare species known from just a few individuals, the situation with many of the taxa under consideration here, these would statistically be specimens lacking mud in the gut. Some light is shed on this problem by a comparison with the situation in animals that were not mud-eaters, the onychophorans. The Cambrian lobopodians show a morphology adapted for climbing, living in symbiosis with (or perhaps feeding on) sponges, *Eldonia*, and other organisms. Their limbs are unsuitable for walking on a muddy substrate, and when found as fossils, they are frequently directly associated with their host organisms. The gut is usually well preserved, forming a dark band showing that it was filled with organic contents. However, occasionally the gut has some mud-fill, as in rare specimens of *Microdictyon sinicum* (Chen et al., 1995, pl. 7, fig. 2) and *Hallucigenia fortis* (Ramsköld and Chen, 1998, figs. 3.3A, D). A reasonable explanation for this is that during entombment and death struggle, these individuals involuntarily ingested mud. The mud-fills are located at different places along the gut, indicating that peristaltic waves transported the mud to

its final place. A hypothesis of passively introduced mud is refuted by the localized sections of the mud-fill; had mud been passively introduced into the gut, it should be concentrated near the anterior end (and perhaps the posterior), which is not the case. We conclude that in these animals, mud was actively ingested during burial, whereas in normal life, mud was not part of the diet.

Sometimes morphological evidence contradicts the gut contents. In small individuals of *Fuxianhuia*, the gut is completely filled with mud (Chen et al., 1995), whereas adults very rarely show a mud-filling. Furthermore, *Fuxianhuia* possesses a pair of subchelate appendages in the head, showing a position and morphology well adapted for handling food particles and moving them to the mouth. Chen et al. (1995, p. 1341) suggested that perhaps juveniles were deposit feeders while adults were predators. These conflicting pieces of evidence were interpreted by Hou and Bergström (1997, p. 19) thus: "the mud commonly contains black grains which may be phosphatic and indicate remains of engulfed prey. We suggest that the appendages were used for shuffling in sediment and prey in the mouth without full discrimination." This attempt to combine conflicting data is heroic but we reject it and maintain that a shift from mud-eating to predation took place before the adult stage was reached.

In summary, the evidence from the gut contents is commonly ambiguous. There is some good indication, in particular from the diverticulae but also from preservational attitude (Chen et al., 1997), that *Naraoia spinosa* was a mud-eater, but we also know that many *spinosa* specimens have no mud at all in the digestive system. Other animals may have ingested mud during burial, or for that matter may have defaecated during burial, so that the gut appears empty in the fossil. In our view, presence or absence of deposit feeding can only be inferred with reasonable certainty when dealing with *Naraoia* and a few other very common species.

We conclude that these secondary characters are too ambiguous to include in phylogenetic analyses. The primary characters on which they are based may or may not be of use. In the case of feeding habits, the primary character would be "gut with mud contents," which would be of little utility since it would be coded as polymorphic for nearly all taxa. In the case of limb stance, some taxa would be polymorphic, and for others it would be impossible to know if an aberrant, post mortem stance were coded instead of the life attitude. For these and related reasons, we caution against the use of secondary characters.

#### CLADISTIC ANALYSIS

Codings for the 29 characters described above are shown in Table 1. Most parsimonious trees for these data were calculated using PAUP version 3.1 (Swofford, 1993). In all iterations, multistate characters were treated as non-additive. Tree lengths implied by alternative topologies and character optimizations were examined using MacClade version 3.04 (Maddison and Maddison, 1993).

With the number of terminal taxa scored in Table 1 (maximum

FIGURE 12—Networks and cladograms. 1, Majority rules consensus of 12 shortest trees (51 steps) for character data in Table 1, excluding Marrellomorpha. All nodes are in the strict consensus except one indicated (in 67 percent of trees). Networks are rooted between naraoiids and the remainder of the ingroup (cf. Hou and Bergström, 1997); 2, strict consensus of four shortest trees (329 steps) with successive approximations weighting using the rescaled consistency index (base weight of 10). Network is rooted as in Figure 12.1. Reconstructions, from top to bottom, are *Liwia*, *Misszhouia*, *Sidneyia*, *Retifacies*, *Olenoides*, *Kuamaia*, *Saperion*, *Sinoburtius*, and *Cindarella*; 3, majority rules consensus of 18 shortest cladograms (56 steps) rooted on Marrellomorpha. All nodes are in strict consensus except one indicated (in 89 percent of trees); 4, single shortest cladogram (390 steps) using reweighted characters, selected from the set of 18 cladograms based on equally weighted characters. Synapomorphies at numbered nodes are indicated in Table 2.

TABLE 2—Synapomorphies for nodes in Figure 12.4, optimized using accelerated transformation (ACCTRAN). Apomorphies that are equivocal are indicated by asterisk.

Node	Taxon	Synapomorphies
1		4(0)
2		26(1)
3		2(2), 11(1)*, 12(1), 20(1)
4	Naroiidae	3(1)*, 14(1), 27(1)*
5	Liwiinae	9(1), 24(1)
6		21(1)
7		15(1), 16(1)
8		4(0)
9		18(1)
10	Trilobita	1(1), 4(1), 5(1), 8(1), 12(3)
11	Helmetiida	6(1), 10(1), 12(2), 19(1), 28(1)
12	Helmetiidae	17(1), 22(1)
13		16(2), 29(1)
14		3(2)
15	Petalopleura	2(3), 7(1)*, 9(2), 23(1)
16	Xandarellida	13(1), 20(0)

of 19), it was possible to use the exact, Branch and Bound algorithm, this being done with the "furthest" taxon addition sequence, setting the upper bound to a length determined by a heuristic search using random stepwise addition. Successive approximations weighting used the rescaled consistency index, with a base weight of 10.

The initial runs were unrooted networks for the ingroup alone. We subsequently coded an outgroup, Marrellomorpha, to root the trees. The choice of marrellomorpha (coding *Marrella* and *Mimetaster*) as outgroup is based on the sister group relationship between this taxon and the arachnate ingroup in the phylogenetic trees of Hou and Bergström (1997). Marrellomorpha are one node removed from the arachnates in the cladistic analysis of Wills et al. (1998), also suggesting their appropriateness for rooting.

## RESULTS

Analysis of all ingroup taxa, using the analytical parameters described above, yields 12 shortest cladograms of 51 steps (consistency index 0.765; retention index 0.812). Figure 12.1 is a majority rules consensus of these 12 trees. For illustrative purposes we have drafted the network with a root between the naroiids and the remainder of the ingroup (to conform to the hypothesis of Hou and Bergström, 1997 that a "nectopleuran" group including naroiids is basal for the ingroup), but the reader is cautioned that this is a purely graphical convention. Linkages in all networks include Naroiidae, a liwiine subclade including *Tariccoia* + *Soomaspis*, *Naraoia* and *Misszhouia*, *Sidneyia* and *Emeraldella*, Trilobita, Helmetiida [with the ingroup resolution (Helmetiidae (Tegopeltidae (Saperiidae + Skioldiidae)))]], Petalopleura, and Xandarellida. Nectopleura sensu Hou and Bergström is not represented in any of the 12 shortest trees; one or two extra steps are required to unite *Retifacies* with the naroiid clade. We note that none of the shortest trees unite naroiids with Trilobita (*Eoredlichia* + *Olenoides*), this resolution also forcing an extra step. Successive weighting decreases the number of shortest trees to four (see Fig. 12.2 for strict consensus of these). Trilobites are most closely allied to Helmetiida, a relationship supported by edge-to-edge trunk articulations (character 18).

To root the trees, the coding for Marrellomorpha shown in Table 1 was activated. A few characters possess novel conditions in marrellomorpha, demanding that new states be added to the

character list, and comments are required for some other codings. Character 2 has distinct states in *Marrella* (A+1) and *Mimetaster* (A+2), these being coded as new states 6 and 7, respectively, and polymorphic for Marrellomorpha. Character 4 is also polymorphic, *Marrella* coding with state 2 (lateral eyes absent) and *Mimetaster* possessing a unique state of stalked dorsal eyes (scored as state 3 in the matrix). We consider it erroneous to code this as equivalent to the dorsal eyes of trilobites, which penetrate the dorsal surface of the head shield. These polymorphic codings were treated by PAUP as polymorphisms (rather than as missing). Codings for characters involving trunk tergites (13, 15–18) accept the interpretation of Stürmer and Bergström (1976) that *Mimetaster* bears small tergites. Character 27 receives a novel state for Marrellomorpha, a slender annulated shaft. We are less convinced than were Hou and Bergström (1997) that this condition should be regarded as the same as that in naroiids (proximal lobe of the exopod a shaft). Character 29 is coded in marrellomorpha with emphasis on the presence of endites on the posterior trunk endopods. Comparison with other relevant outgroups, such as stem-lineage crustaceans (Walossek and Müller, 1990), confirm the presence of endites and gnathobases at the base of the ingroup.

Reanalyzing the data with Marrellomorpha as outgroup (ingroup monophyly constrained) yields 18 shortest trees of 56 steps (consistency index 0.768; retention index 0.809). The majority rules consensus of these is shown in Figure 12.3, again featuring a substantial measure of irresolution between major ingroup lineages. As in the analysis without marrellomorpha, none of the shortest cladograms support Nectopleura (*Retifacies* + Naroiidae) nor a naroiid sister group to the Trilobita. Two or three steps must be added to the shortest trees to unite *Retifacies* and naroiids, three or four steps to place "Nectopleura" at the base of the ingroup, and one or two steps to force naroiids to be sister group to trilobites. "Xenopoda" is of uncertain status (*Sidneyia* and *Emeraldella* are not sister taxa in most trees), and this clade or grade lies stemward of most of the ingroup.

Reweighting the characters based on their fits to these trees yields a single shortest cladogram of 390 steps (consistency index 0.882; retention index 0.913), with a more explicit hypothesis of relationships than in the other analyses (Fig. 12.4). Synapomorphies under ACCTRAN optimization are listed in Table 2. Some of these optimizations should differ if analysis included additional outgroup taxa, such as Crustacea. The optimizations of character 4 (eye position) are particularly suspect. Including Crustacea as an another outgroup suggests that anteroventral eyes (state 1) are plesiomorphic for the ingroup, rather than the lack of lateral eyes that optimizes basally when Marrellomorpha is used as sole outgroup.

## DISCUSSION

Despite our attempts to analyze all well understood characters relevant to the "trilobitomorpha" and the wealth of new data provided by the Chengjiang fauna, a glaring conclusion from the cladograms (Fig. 12) is that relationships between major groups remain ambiguous. Nonetheless, several major clades have emerged and have stable patterns of ingroup relationships (e.g., Petalopleura, Xandarellida, Helmetiida, Naroiidae), even if inter-relationships between these taxa and Trilobita are confounded by conflicting characters. The discovery that naroiids are a well-supported monophyletic group requires that ideas that they are a grade of "soft-bodied trilobite" ancestors (e.g., Shu et al., 1995, fig. 20B) be abandoned.

In spite of considerable ambiguity, our results indicate that some recently advanced groupings find support, whereas others are suboptimal. The sister group relationship between *Sinoburium*

and Xandarellida, comprising the taxon *Petalopleura* Hou and Bergström, 1997, is endorsed, although we cite completely different characters as synapomorphies (e.g., overlap of the anterior trunk segments by the head shield; axial spine on the posterior trunk tergite). None of the “petalopleuran” characters listed by Hou and Bergström (1997, p. 73) are regarded by us as synapomorphies at that level. Grouping of naraoiids and *Retifacies* as a clade (*Nectopleura sensu* Hou and Bergström, 1997) requires extra steps and is rejected as unparsimonious. Hou and Bergström’s diagnostic characters for this group were as follow: large tail shield; semipendent limbs with wrinkled proximal cornus; compound eyes in original ventral position, and; feeding through mud ingestion. The semi-pendant limb stance and ventral eyes were admitted by Hou and Bergström (1997) to be symplesiomorphies. We concur, but thus reject them as evidence for grouping. As noted above, we regard the annulate cornus as another symplesiomorphy, and reject the presence of compound eyes in naraoiids. “Feeding through mud ingestion” is well documented for certain naraoiids (see “Secondary characters” above), but is not well corroborated as a general character for the group, rendering this character ambiguous at best. In any event it was regarded by Hou and Bergström (1997) as a symplesiomorphy. Finally, the “large pygidium” is a most dubious synapomorphy, given that Hou and Bergström (1997) (reasonably) considered *Squamacula clypeata* to be a probable retifaciid. The fact that this taxon possesses a tiny pygidium makes it clear that size of the pygidium in this group is unreliable.

“Nectopleura” was resolved by Hou and Bergström (1997) as sister group to the rest of Lamellipedia (another explicitly paraphyletic group) and Chelicerata. Naraoiids and retifaciids were excluded based on the absence of three derived characters (Hou and Bergström, 1997, fig. 87): lateral deflection of appendages, a flat exopod blade, and well-developed pleura. Characters 1 and 3 have a correlation in this group in that taxa with laterally splayed appendages have wide pleurae; the converse is not necessarily true, however. We do not understand how retifaciids and naraoiids can be claimed to lack well-developed pleurae (even Hou and Bergström, 1997, p. 43, acknowledge wide pleural folds in *Naraoia*). Hou and Bergström (1997) were inconsistent in their treatment of this character (nodes o and E in their figs. 87, 88, respectively, optimize wide pleurae at different levels; we agree with the latter figure, rendering this character uninformative for the group considered here). Concerning limb stance, we can see no rationale for coding *Kuamaia* or *Saperion* (allegedly laterally-splayed) as different from *Misszhouia* and *Retifacies* (semi-pendent). These empirical problems must be added to our philosophical objection to “secondary characters,” discussed above. Their character 2, the flat exopod blade, has been included in our analysis (as character 27).

An especially close relationship between naraoiids and trilobites is opposed by our results. A taxon composed exclusively of these two clades is not present in any of the minimal length trees generated in this study. We can see no rationale for broadening “Trilobita” to include naraoiids because a monophyletic group including these clades also includes, at least, *Helmetiida* (and in some equally parsimonious trees, various other taxa, such as *Sinoburius* and *Xandarellida*). This deviates radically from conventional understanding of “trilobites.” Our concept of Trilobita (Ramsköld and Edgecombe, 1991) differs little from the traditional usage since the erection of the taxon by Walch in 1771. Exclusion of naraoiids from Trilobita is followed by Hou and Bergström (1997), who provide further arguments that we fully endorse. Based on evidence at hand, *Helmetiida* are the best supported candidate for sister group of Trilobita, this resolution being present in the reweighted ingroup networks (Fig.

12.2) as well as the cladogram rooted on marrellomorphs after successive weighting (Fig. 12.4).

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