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THE EARLY DEVONIAN ARMOURED AGNATHANS OF PODOLIA, UKRAINE

(PANCERNE BEZSZCZĘKOWCE WCZESNEGO DEWONU PODOLA)

BY

VICTOR VOICHYSHYN

(WITH 105 TEXT-FIGURES)

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In the marine Přidolian to early Lochkovian environments of Podolia, vertebrates were represented almost exclusively by thelodonts and acanthodians. Starting from the mid Lochkovian (Chortkiv Formation), the heterostracans increased their abundance and diversity. Diverse macroscopic remains of the cyathaspidid heterostracans, the first small-size pteraspidids and osteostracans appeared in the late Lochkovian (Ivanie Formation). The Old Red-type ecosystem of Podolia gradually emerged with retreat of the sea. Simultaneously, various agnathans, with ecological preferences to brackish or fresh waters, appeared. At the transition to the Pragian (red-bed Dniester Formation), when coarse terrigenous quartz sand gradually replaced fine carbonate silt and clay, the armoured vertebrate community reached its peak diversity, especially regarding the osteostracans and pteraspidid heterostracans. Many local lineages developed but some ties of the heterostracan faunas with those of western European and the osteostracan faunas with Spitsbergen ones are traceable. Most evolutionary series recognised show increase in body size, both regarding the heterostracans and osteostracans. Taxonomic diversity decreased with coarsening of the sandy sediment and increase of sedimentation rate, culminating in complete disappearance of fish fossils before the Emsian. The sensory line system of the pteraspidids, with supraorbital commissures developed on the rostral plate and arrangement of dorsomedial canals on the dorsal shield, is proposed to have high diagnostic value. Some 33 species, belonging to 20 genera of the heterostracans and 16 species of 9 genera of the osteostracans, are described. *Althaspis tarloi* sp. n., *Djurinaspis secunda* sp. n., *Palanasaspis chekhivensis* gen. et sp. n., *Podolaspis danieli* sp. n., *Semipodolaspis slobodensis* gen. et sp. n., and *Zenaspis kasymyri* sp. n. are proposed.

Key words: Vertebrates, Agnatha, taxonomy, taphonomy, morphology, fossil assemblages, Podolia, Early Devonian.

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INTRODUCTION

In the Early Palaeozoic, two unrelated groups of agnathans developed a stiff carapace built of more or less tightly fused dermal bony plates; the advanced heterostracans classified in the orders Cyathaspidiformes Kiaer, 1930, and Pteraspidiformes Berg, 1940, and the osteostracans. The unique features of these heterostracans is the histology of their plates, with externally located dentine ridges or ribs, aspidine-built middle honeycomb and basal lamellar layers, a single common branchial opening on each side of the body, and a mostly hypocercal tail fin. In the osteostracans, the branchial openings were separate, which is a plesiomorphic feature, but what distinguishes them from other agnathans is the presence of cellular bone in their mineralised dermal skeleton and presence of a heterocercal tail fin. Both groups inhabited mostly near-shore marine environments with sandy bottom and possibly also estuaries or even fresh waters. Such conditions developed near the end of the Silurian and continued for some part of the Early Devonian in Podolia, Ukraine. This region is among the classic sources of information on the armoured agnathans.

The Early Palaeozoic agnathans are of crucial importance for understanding the phylogeny of vertebrates. They offer anatomical information from geological epochs close in time to the ancestry of major clades of the vertebrates, including the gnathostomes (Forey and Janvier 1993; Forey 1995; Janvier 1996, 2008; Donoghue and Sansom 2002; Hou *et al*. 2002; Novitskaya 2006). Their phyletic evolution is of much value for refining the stratigraphic correlation between regions and provides a basis for zonation of strata devoid of other guide fossils. Because the occurrence of armoured agnathans is restricted to specific shallow marine or fresh-water environments, it is possible to use them as highly sensitive palaeoecological indicators. The virtually worldwide distribution of diverse faunas of the Early Devonian agnathans allows one to define biogeographic subdivisions, estimate degree of the endemism, and trace connections between marine basins (see discussions in Blieck and Janvier 1991; Janvier and Blieck 1993; Sansom 2009b).

In Ukraine, fossil remains of the Palaeozoic agnathans occur in marly and coarse clastic continental deposits of the Early Devonian of Podolia. As a result of more than a hundred years of study, 99 localities with these fossils have been discovered on the banks of the Dniester River and its tributaries in the Ternopil', Ivano-Frankivs'k and Chernivtsi oblasts (see Voichyshyn 2001a). In the present publication, the fossil agnathan morphology, taxonomy, taphonomy, and stratigraphic distribution are discussed on the basis of material that has been accumulated during the last eighty years in the collection of the State Museum of Natural History, National Academy of Sciences of Ukraine, in L'viv.

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HISTORY OF STUDIES ON THE PODOLIAN AGNATHANS

The study of Podolian fossil agnathans began with the publication by **Rudolf Kner** (1847) who described, under the name *Pteraspis*, a pteraspidid ventral shield found by himself. The figured specimen is now the lectotype of *Larnovaspis kneri* (Lankester, 1868).

Alois von Alth (1874, 1884, 1886a, b) described diverse and numerous material that, however, was mostly poorly preserved, at the best by moulds of the carapace dorsal side with unclear margins of the plates. This material mainly represents pteraspidids. Among the Podolian heterostracans, he distinguished three genera: *Cyathaspis*, *Pteraspis*, and *Scaphaspis*. The latter taxon was based on ventral shields belonging to *Pteraspis*. Alth (1874) distinguished the new species *Pteraspis podolicus*, now classified as *Podolaspis podolica* (Alth, 1874), as well as *Pteraspis angustatus* (now "*P.*" *angustata*), *P. major* [*Larnovaspis kneri* (Lankester, 1868)], and *Cyathaspis sturi*. All the names except for the third one remain valid. He also initiated studies on the Podolian osteostracans based on fragments that were referred to *Auchenaspis* Egerton, 1857. Unfortunately, the present location of Alth's collection, with two lectotypes, is unknown (Voichyshyn 2006c).

Some remains of the Devonian agnathans (cyathaspidids, pteraspidids, cephalaspidids) from Podolia, in particular species distinguished by Alth, were mentioned in the work of **Józef Siemiradzki** (1906) which was devoted to the Palaeozoic strata of Podolia. He provided species names along with location of about 15 finds but gave no descriptions or pictures.

The first comprehensive study on the Early Devonian ichthyofauna of Podolia was attempted by **Władysław Zych** (1927b, 1931, 1937), who considerably extended the previous geographical and stratigraphic limits of research on the agnathans in the region. By 1927, he had collected about 300 shields representing all the earlier known genera (Zych 1927a). He described four morphological varieties of *Pteraspis sturi* (Alth, 1874) and *P. lerichei* Zych, 1927, named by him "mutations", asserting that each "mutation" characterises one of eight horizons of the Podolian Old Red distinguished by him. The second, fourth and seventh of these horizons differed also by the presence of five varieties of *Cephalaspis* Agassiz, 1835 (Osteostraci). Thus, Zych was the first who appreciated the value of heterostracans and osteostracans for the stratigraphic subdivision of the Podolian Early Devonian. At the first stage of his research on the pteraspidids, he distinguished two species, *Pteraspis sturi* and *P. lerichei*, the latter different in a greater width of the carapace, its straight posterior margin, and wide, flipper-like cornual plates. Their subdivision into "mutations" was rather artificial, although it stimulated subsequent erection of several new species and genera.

The distinctions indicated by Zych often expressed rather the state of preservation of the posterior margin of the carapace and artificial rather than biological differences. In a number of cases, Zych was undecided in classifying heterostracan specimens. However, in spite of these imperfections, the first classification of Podolian pteraspidids was an important step in the search for criteria in the taxonomy of early agnathans.

Zych (1931) further developed his views on the agnathan taxonomy. In captions to figures in a work devoted to the morphology of the Podolian heterostracans, he proposed the name *Podolaspis* for all the Podolian pteraspidids, probably to highlight their distinction from the West European pteraspidids known by that time. The names *Althaspis* and *Lericheaspis* were probably meant as sub-genera. An important step forward was dropping the former subdivision of all the Podolian pteraspidids into only two species (the names *P. sturi* and *P. lerichei* were not even mentioned in his work) and giving species rank to some "mutations" (*Podolaspis rostrata*, *P. major*, *P. elongata*, *P. longirostra*). In addition, Zych offered a classification of all the heterostracans, proposed the family Pteraspidae (*recte* Pteraspididae), in which he distinguished subfamilies Podolaspinae, Belgicaspinae, and Rostraspinae. Zych planned a taxonomic work with detailed classification of fossil agnathans of Podolia, but it has never been published because meanwhile a number of Brotzen's papers also devoted to this problem have appeared (Zych 1937).

Zych (1931) paid considerable attention to comparative morphology of the heterostracans, as well as to the ontogeny and phylogeny of the Podolian agnathans. Of special interest is his research on the sensory lateral line system of the heterostracans and his interpretation of the origin and mode of development of the armour of these animals. Zych's subsequent (1937) work was devoted to the Podolian osteostracans. He offered a description and reconstruction of the anatomy of *Ukrainaspis kozlowskii* (Zych, 1937).

A revision of the Podolian fossil fish fauna was conducted by **Franz Brotzen** (1933a, 1933b, 1934, 1936). Unlike Zych, he did not specialise in the osteostracans, but gave a lot of attention to the classification of all the heterostracans and early gnathostome fishes. He proposed several new taxa of the heterostracans: *Poraspis pompeckji*, *P. simplex*, *Pteraspis zychi* (now *Podolaspis zychi*), *P. iwaniensis* (*Larnovaspis iwaniensis*), *P. magnipinealis* (*Alaeckaspis magnipinealis*), *Brachipteraspis heintzi* (*Zascinaspis heintzi*), *B. bryanti* (*Zascinaspis bryanti*), *Protaspis arnelli* (*Europrotaspis arnelli*), and *Weigeltaspis alta*. In a number of cases Brotzen offered more precise description of species established earlier by Zych. He also outlined the phylogeny of the Podolian pteraspidids, and proposed biostratigraphic subdivision of the Old Red deposits into three zones.

Theodor Văscăuţanu, in his work (1931) devoted to the geology of the right Bukovinian bank of the Dniester River, mentioned a few new species names of the Palaeozoic agnathans. **Mircea Paucă** (1941) described the collection of Văscăuţanu under species names *Palaeaspis bucovinensis* Văscăuţanu, 1931, *P. simionescui* Văscăuţanu, 1931, *Pteraspis kneri*, *P. lerichei*, *P. lerichei* var. *plana* Brotzen, 1933, *P. latissima* Zych, 1927, *P. major*, *Cephalaspis* aff. *heintzi* Stensiö, 1927, and *C. bucovinensis* Văscăuţanu, 1931. The material was poorly preserved, superficially described and not referred to specific localities, which complicates appropriate use in taxonomic studies. Among the newly introduced taxa, only *Cephalaspis bucovinensis* (now *Zychaspis bucovinensis*) has been accepted as valid (Janvier 1988; Voichyshyn 1998).

Pavlo Balabai (1959b, 1961a) undertook studies on the Podolian armoured agnathans and critically reviewed works of his predecessors. He came to the conclusion that, in the Early Devonian Dniester Formation (Old Red) of Podolia, six species should be distinguished: *Pteraspis lerichei*, *P. major*, *P. elongata* Zych, 1927, *P. longirostra* Zych, 1927, *Brachipteraspis heintzi* Brotzen, 1936, and *B. latissima* Zych, 1927 (*sic!*). According to his opinion, *Pteraspis podolica*, *P. kneri*, *P. zychi*, *P. iwaniensis*, and *Brachipteraspis bryanti* Brotzen, 1936 are characteristic for the Late Silurian (now the Early Devonian Chortkiv and Ivanie Stages). Unfortunately, the criteria applied to species identification in these works are rather vague and influenced by the state of preservation of the fossil material. Specimens of *Larnovaspis major*, for example, were often identified as *Althaspis elongata*, and *vice versa*. As a result, that author (Balabai 1959b) came to the incorrect conclusion that the stratigraphic distribution of these species is the same in almost all sections of the Podolian Old Red. Balabai (1957, 1959a, 1961b; Balabai and Opalatenko 1957) distinguished three heterostracan zones in the Podolian Old Red, not well supported because of deficient taxonomy. In a paper devoted to the Podolian osteostracans (Balabai 1962), he described four new species (*Cephalaspis major*, *C. podolica*, *C. djurinensis*, and *C. microlepidota*) and other determined earlier by Zych in that collection. Insufficient descriptions, poor illustrations and a number of mistakes in the text make these papers difficult to use without a revision of the material (Janvier 1985b; Afanassieva and Voichyshyn 1991; Voichyshyn 2006b).

In the works of **Erik Stensiö** (1958, 1964), the founder of the Stockholm School of vertebrate palaeontology (Schultze 2009), a few new pteraspidid taxa were described on the basis of the Podolian material collected by Zych and by Stensiö himself in 1934 and now housed in Stockholm. The morphology of the oral region of the carapace and the ventral surface of rostrum were used as the main taxonomic criteria. These works represent a fundamental contribution to recognition of morphology and anatomy of fossil agnathans. Concerning the Podolian species, it has to be noted, however, that new taxa were established without diagnoses and indication of the type specimens, which resulted in subsequent proliferation of synonyms and taxonomic misinterpretations (Voichyshyn 2001c).

Tor Ørvig (1961) in an article devoted to the drepanaspidids, described from Zych's collection kept in Stockholm a plate fragment referred to as Drepanaspidida gen. et sp. indet., collected at Jagilnytsia Stara. This specimen became the type for *Tesseraspis orvigi* Tarlo, 1964.

Lambert Beverly Tarlo (Halstead) (1961) undertook some actions concerning the taxonomy of the Podolian pteraspidids. In particular, he chose the type specimens for *Podolaspis lerichei* and the type species for *Mylopteraspis* (*M. robusta* Stensiö, 1958). In addition, he proposed the generic name *Loricopteraspis* and the new name *Althaspis samsonowiczi* instead of *A. elongata*, but the last action was not supported by majority of subsequent researchers. In addition, he added his new species *Weigeltaspis brotzeni* and *Tesseraspis orvigi* to the Podolian fauna (Tarlo 1964, 1965).

Dmitrij Obruchev (1964) in the reference book *Osnovy Paleontologii* (*Fundamentals of Palaeontology*) summarised information on the taxonomy of armoured agnathans at the generic and higher levels. For the Podolian pteraspidids, he offered the generic name *Glossoidaspis* (junior synonym of *Europrotaspis* White, 1961), and put *Brachipteraspis* Brotzen, 1936 and *Parapteraspis* Stensiö, 1958 in the synonymy of *Pteraspis* Kner, 1847, an action that was not accepted by subsequent researchers.

Larissa Novitskaya (1975, 1983, 1986, 2004) made a considerable contribution to knowledge of morphology, distribution, and classification of the Podolian heterostracans. She gave much taxonomic value to the morphology of the orbito-pineal belt, the shape of large plates of the carapace, morphology of the branchial region, location of dorsal spine, morphology of the ventral side of the rostrum, general size, and proportions of carapace. This resulted in a revision of the group, with introduction of a number of new generic and family-level taxa (*Dnestraspis*, *Djurinaspis*, Podolaspididae, and Rhinopteraspididae). Diagnoses were given for many Podolian taxa. New species were among the Podolian cyathaspidids *Irregulareaspis seretensis* and *I. skalskiensis*, among pteraspidids *Dnestraspis firma*, *Djurinaspis prima*, and *Althaspis sapovensis*. Improvement in the Podolian heterostracan taxonomy allowed definition of species assemblages, characteristic for particular stratigraphic units of the region, although some proposals remain controversial (Voichyshyn 2001b). In a work devoted to heterostracan morphology (Novitskaya 1983), discussion on the cyathaspidids and pteraspidids was based mainly on the Podolian material. This refers especially to the types of the orbito-pineal belt in the pteraspidids.

Alain Blieck (1984) summarised information on pteraspidids from all localities of the northern hemisphere known at that time. He paid considerable attention to the questions of their phylogeny, stratigraphic distribution, and biogeography. The Podolian pteraspidids were studied by him in Zych's collection, parts of which are kept in London and Stockholm. The classification was based on features of the rostrum, orbito-pineal and branchio-cornual regions, and also on the lateral line system. In diagnosing the taxa, the latter was restricted to the location of the "pineal canal" behind or within the limits of the pineal plate. As a result of revision of the English and Podolian species, Blieck (1984) established the new genera *Mylopteraspidella*, *Errivaspis*, and *Larnovaspis*, as well as the species *Parapteraspis djurinensis* and *Larnovaspis mogielnensis* that, however, did not find unanimous support from subsequent researchers (Novitskaya 1986, 2004; Voichyshyn 2001c).

Philippe Janvier (1985b, 1988), in his research on the anatomy, morphology, and taxonomy of the Osteostraci, studied the Podolian osteostracans in the collections of Zych kept in London, Stockholm, and Warsaw. Based on these materials and also on the publication of Balabai (1962), he listed 16 species of the regional fauna belonging to the scolenaspidids and cephalaspidids (Janvier 1985b). New species (*Zychaspis siemiradzkii*, *Stensiopelta pustulata*, and *Mimetaspis glazewskii*) were established. The Podolian deposits of the Early Devonian were correlated with the upper part of the Red Bay Group of Spitsbergen and with the Dittonian-II of Wales. Later, Janvier (1988) described another Podolian form ("*Cephalaspis*" *dniestrensis*), and also suggested to transfer "*Cephalaspis*" *bucovinensis* Văscăuţanu, 1931, to *Zychaspis*. In another article, Belles-Isles and Janvier (1984) described new species of genera new for Podolia: *Benneviaspis whitei*, *B. polonica* (considered here as *Citharaspis polonica*), and *Tegaspis waengsjoei*.

Podolian osteostracans found important place in the research of **Olga Afanassieva** (1989, 1990, 1991, 2004). She proposed complexes of features to define taxa of higher rank and developed a classification for their Podolian representatives. She erected new Podolian genera *Citharaspis* and *Heraspis* and species *Benneviaspis zychi*, *B. talimaae*, *Citharaspis junia*, *Diademaspis stensioei*, and *Parameteoraspis dobrovlensis*, and discussed their stratigraphic distribution. She also proposed *Tremataspis*-like and *Cephalaspis*-like morpho-ecological types of the osteostracans (Afanassieva 1991, 1992), with a number of species, including those from Podolia, belonging to an intermediate type.

Questions concerning taxonomy and morphology of the armoured Podolian agnathans, as well as the distribution of their remains in fossil assemblages of the Podolian Early Devonian sections, were examined in the works by myself (Voichyshyn 1990, 1994, 1997, 1998, 1999, 2001a–c, 2006a–c, 2010; Voichyshyn and Solodkyi 2004). The Devonian fossil fish collection, on which these studies were based, was more than twice as large as the material of the preceding workers due to collecting of fossils during field work in 1986–1992, 1994–1995, and 2001–2004. Some new taxa, both heterostracan and osteostracan, were introduced: genera *Alaeckaspis*, *Pavloaspis*, and *Wladysagitta*, and species *Alaeckaspis ustetchkiensis*, *A. verbivciensis*, *Mimetaspis concordis*, *Pavloaspis pasternaki*, *Wladysagitta janvieri*, *Zenaspis dzieduszyckii*, *Zychaspis concinna*, and *Z. granulata*.

The collection of T. Văscăuţanu mentioned above was reinvestigated by **Mihai Dumbrava** and Alain Blieck (2005). This poorly preserved material allowed determination of two forms only, namely *Podolaspis lerichei* and *Brachipteraspis* sp. cf. *B. latissima*. The latter identification may not be correct, and one is dealing with remains of *Larnovaspis kneri*.

Anders Carlsson and **Henning Blom** (2008) described the new genus and species *Victoraspis longicornualis* based on Zych's material kept in Uppsala, characterised by the longest cornual process among the Podolian osteostracans. A phylogenetic analysis of its systematic position within related forms (*Stensiopelta* and *Zychaspis*) was performed.

Robert Sansom (2009a), in a paper on the phylogeny and classification of the Osteostraci, proposed the new generic name *Ukrainaspis* for the Podolian *Heraspis kozlowskii* (Zych, 1937) because of homonymy.

GEOLOGICAL SETTING

Lithological units of the Devonian of Podolia, their spatial distribution and age have been studied and discussed beginning from the last decades of the 19th century (Alth and Bieniasz 1887; Teisseyre 1900; Łomnicki 1901; Zych 1927a, b; Kozłowski 1929; Văscăuţanu 1931; Brovkov 1955; Dikenshtein 1957; Balabai 1961b; Nikiforova *et al.* 1972; Narbutas 1984; Drygant 1988, 2000, 2003, 2010; Małkowski *et al.* 2009). The subdivision varied from author to author and changed according to different methodological approaches to stratigraphy by successive geological teams. As a result, some nomenclatorial inconsistency developed and most divisions remain informal. In this Chapter, the regional lithostratigraphic scheme proposed by Drygant (2000, 2003, 2010) and Małkowski *et al.* (2009) is used with slight modifications making it consistent with internationally used stratigraphic terminology.

PALAEOGEOGRAPHY OF PODOLIA IN THE EARLY DEVONIAN

The region of Podolia was situated in the Late Silurian–Early Devonian in the Southern Hemisphere between about 10° S and 20° S, at the S or SE margin of the Baltica continent (Fig. 1; see also Blieck and Janvier 1991; Blieck and Tarrant 2001; Blieck *et al*. 2002; Kozłowski 2003). Westward, it was limited by the Teisseyre-Törnquist (Trans-European) Suture Zone, which runs under the North Sea, southern Denmark, northern Germany and Poland. The suture developed in the Late Ordovician, about 450 million years ago, with the disappearing of the Törnquist sea (Torsvik and Rehnström 2003) as a result of the collision between Avalonia and Baltica.

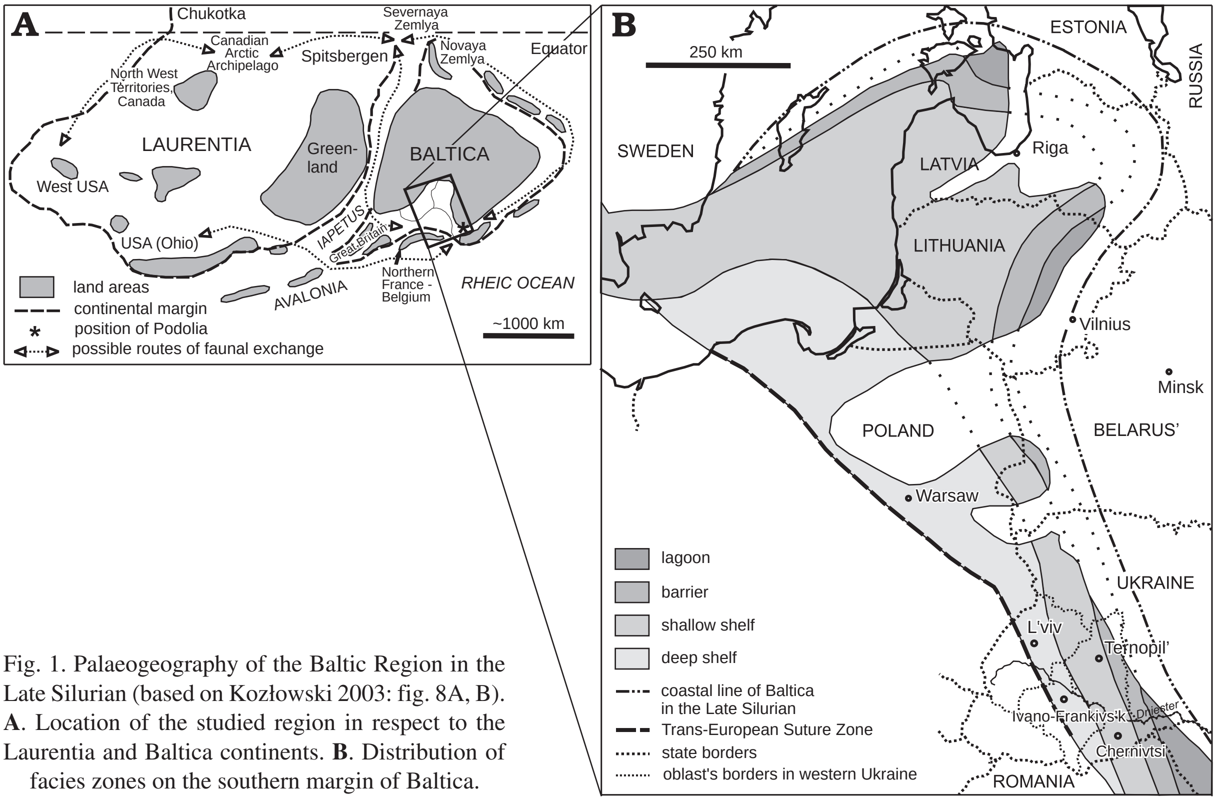

Fig. 1. Palaeogeography of the Baltic Region in the Late Silurian (based on Kozłowski 2003: fig. 8A, B). **A**. Location of the studied region in respect to the Laurentia and Baltica continents. **B**. Distribution of facies zones on the southern margin of Baltica.

In the Silurian, Volyno-Podolia was a shelf area of a vast ocean that spread west- and south-westward of the East European platform. At the end of the Silurian (Skala time), a considerable shallowing of the sea took place as a result of local tectonic movements in Podolia (Pomianovs'ka and Khyzhniakov 1974). The subsequent rise at the end of the Silurian was over with an almost sudden considerable deepening that was compensated by deposition during almost all the Borshchiv time. The sea with normal salinity was inhabited by a rich brachiopod fauna with species of wide geographical distribution.

The exchange of fauna continued to the Early Devonian, when the disappearing sea of Volyno-Podolia lost its connection with the Baltic basin, after a long common history dating from the Cambrian. With the end of Borshchiv time, deposition prevailed over deepening and as a result the sea gradually shallowed (Pomianovs'ka and Khyzhniakov 1974). The water salinity in shoals decreased as a result of dilution with fresh waters from the land, and terrigenous red-coloured argillaceous-silt and sand replaced the limy mud.

The conditions of sedimentation in Podolia during Dniester time remain a matter of dispute. Zych (1927) and Văscăuțanu (1931) considered the "Babin sandstone beds" as an aeolian lacustrine sediment of arid climate, deposited near seashore. Brovkov (1955) considered these deposits alluvial, deposited in a deltaic environment, in riverbeds, back-waters, and a delta. Narbutas (1984) proposed that in Dniester time the sedimentary conditions gradually changed from basinal to alluvial deltaic. According to him, the Dniester Formation consists of tripartite sedimentary cycles. The basal part of each of them consists of main stream, channel deposits, the middle part is represented by lateral channel deposits or a drying up river-bed, and the upper part originated in a bayou, lake, or poorly drained reservoir. Drygant (2003) pointed out that the vast extension of particular beds and their gradual lateral substitutions with different facies do not agree with their fluvial origin. Such wide extent of uniform development of the argillaceous-silt fine-grained sandstones was explained by Narbutas (1984) as a result of transport by wind.

After deposition of the Smerkliv beds, Podolia became a dry land, but sedimentation of the Old Red Sandstone continued in an up to 50 km wide basin along the Teisseyre-Törnquist Fault Zone (Drygant 2000, 2010).

Biogeography of the "Old Red Continent". — Most of the data on the Late Silurian to Early Devonian agnathans come from localities in Great Britain, Canada, Spitsbergen, and Ukraine. In the Early Palaeozoic, these areas were located on different continents with changing areas and relationships (Cocks and Fortey 1990).

The Silurian began with a sea-level rise, presumably a result of melting of the continental ice sheets in the African and South American portions of Gondwana. Until the mid Silurian, shallow epicontinental seas reached extend rarely achieved in the Phanerozoic (Ziegler *et al.* 1973). It is believed that most the Silurian vertebrates were marine (Halstead 1973; Blieck and Janvier 1991) and there were no barriers to their migration between coasts of the narrowing Iapetus Ocean (Fig. 1A), as shown by distribution of the *Protopteraspis* species (see Blieck and Tarrant 2001). Also thelodonts, which are considered to be pelagic animals (Märss 1986; Blieck and Janvier 1991), show wide distribution in the Late Silurian and Early Devonian, presumably colonizing various marine environments (from lagoonal to the shelf slope).

The closure of the Iapetus Ocean, separating Laurentia from Baltica, continued to the Early–mid-Silurian continental collision (Torsvik *et al.* 1996; Gee *et al.* 2008). A mountain chain developed that extended across the new "Old Red Continent" (Euramerica or Laurussia) from what is now Scandinavia through Scotland to the Catskill Mountains in the present-day North America (Barclay 2005). Erosion of the mountain belt supplied sediments to the Old Red Sandstone intramontane basins (Barclay 2005; see also Janvier and Blieck 1993: fig. 4.1, Blieck and Tarrant 2001: text-fig. 9). Many of the back arc basins behind the western Baltica island arc remained after the collision and major depositional basins were formed. Among them, the Orcadian Basin of the Orkneys, Shetlands and northern mainland Scotland, and the Anglo-Welsh Basin offer the classic lacustrine successions with rich and well-preserved fossil fish assemblages. The fish fauna migrations and exchange were influenced by these changing conditions (see also Blieck and Janvier 1991: p. 375).

Presumably the presence of island arcs or archipelagos supported dispersion of the agnathans (Blieck *et al.* 2002). Among the heterostracans, the cyathaspidids diversify rapidly in the Late Silurian but become rare by the end of the Early Devonian (Janvier and Blieck 1993, Novitskaya 2007). They probably inhabited marine or brackish shallow waters (for Podolian data see Table 1) and this may explain their wide distribution in North America, Greenland, Europe and Severnaya Zemlya, although these small animals could hardly be active migrants (Novitskaya 2007).

Isolation of the Podolian basin from the British one progressed during the Early Devonian, and eventually the sea of Volyno-Podolia lost connection with the South Baltic basin (Pomianovs'ka and Khyzhniakov 1974). The pteraspidids substituted for the cyathaspidids to some extent (Janvier and Blieck 1993), especially in low salinity or fresh waters. Their carapace was somewhat more streamlined (Novitskaya 2007) but probably they did not belong to especially active nekton (see above; Blieck 1984). The osteostracans, with their flat ventral body surface, were apparently near-bottom animals (Afanassieva 1992; Voichyshyn and Solodkyi 2004), confined to brackish or even fresh-water environments. Nevertheless, both these groups are no less widespread geographically than the cyathaspidids.

Allen and Tarlo (1963) suggested that the British Dittonian agnathans known also from Canada, Spitsbergen, and Ukraine could survive marine conditions in their early ontogeny, later being adapted to more restricted environments. However, in the opinion of Blieck and Janvier (1991; Janvier and Blieck 1993; Janvier 1996; Blieck *et al.* 2002), proximal marine environments frequently developed in the Old Red basins, since strontium isotope ratios yielded a typical marine signal in the fish localities, especially in Podolia (see also Janvier 1996: p. 294). The question of ecological preferences of the Early Devonian agnathans remains thus controversial.

LITHOLOGICAL UNITS OF THE LOWER DEVONIAN OF PODOLIA

The mostly calcareous, Upper Silurian Trubchyn and Dzvenygorod Stages form the upper part of the **Skala Formation** (Fig. 2). Dark, fossiliferous, nodular limestone, 19 m thick, predominates in the topmost interval, and contains characteristic Silurian brachiopods, trilobites, and conodonts (Małkowski *et al.* 2009). There are also chitinozoans, stromatoporoids, corals, bivalves, nautiloids, bryozoans, ostracods, crinoids, and plant remains (Paris and Grahn 1996).

The Lower Devonian of the Volyno-Podolia is in depositional continuity with the Silurian. A regressive basin, which gradually shallowed and narrowed (Drygant 2010), developed there, delimited from the west by the mobile Trans-European Suture Zone (Teisseyre-Törnquist Fault Zone). The sea regression is expressed in displacement of coastal facies westward, an increase in contribution of terrigenous material to the sediment, and extinction of reef-building and bioherm-forming organisms (Drygant 2010).

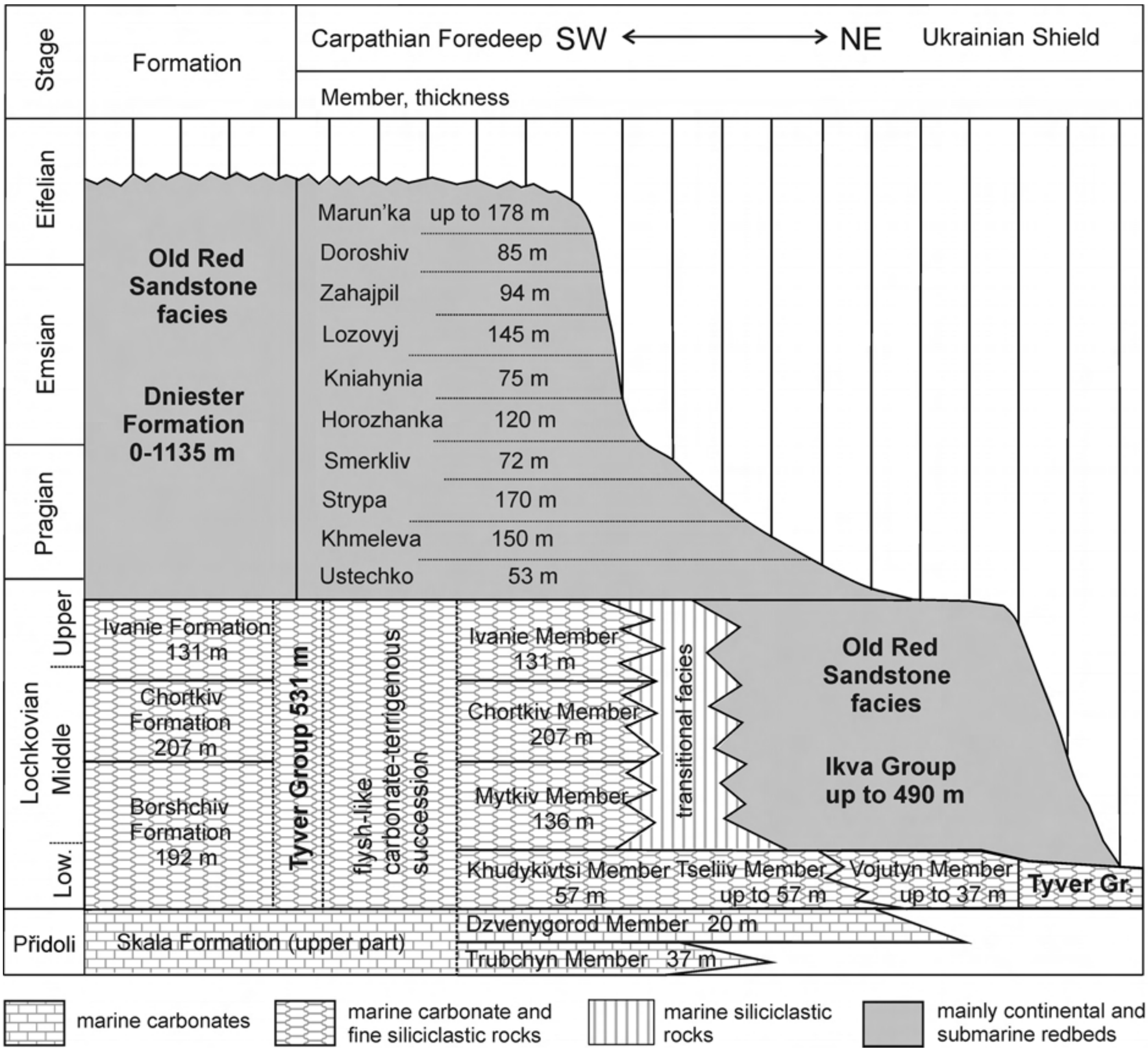

Fig. 2. Lithologic units of the Upper Silurian–Lower Devonian strata on the southwestern margin of the East European Platform (after Drygant 2003, 2010; Małkowski *et al*. 2009).

Within the Lower Devonian of Podolia, there are two successive major lithostratigraphic units, differentiated by their facies (Figs 2–4). The lower part is an open-marine argillaceous-calcareous sequence with abundant brachiopod, ostracod, and tentaculitid fossils, referred to as the **Tyver Group** (up to 530 m thick), which is subdivided into three well-known Borshchiv, Chortkiv, and Ivanie Formations (Alth 1874; Kozłowski 1929; Drygant 2010). Laterally northwestward, it is gradually replaced by dolomitic and siliciclastic continental "Old Red Sandstone" strata of the isochronous Ikva Group (Drygant 2003, 2010). The upper part of the Lower Devonian succession in Podolia is in the Old Red Sandstone units of the area, earlier known as the "Terebovlia beds", "Podolian Old Red", "Babyn sandstones", has been included into the Dniester Formation (Narbutas 1984). It is up to 1800 m thick near the Trans-European Suture Zone, elsewhere representing coastal-continental facies with fossil remains limited to numerous agnathan fish (Drygant 2003; Małkowski *et al.* 2009).

The **Borshchiv Formation** is about 192–194 m thick (Drygant 2010). It is characterised by platy limestone and variably interbedded dark grey argillaceous shale, marl, and marly to micritic limestone, intercalated with rare bioclastic limestone beds (mostly encrinite) in the higher part. The upper part of the formation is a thick succession of dark grey argillaceous shale with rare and thin intercalations and lenticles (up to 1–6 cm) of grey marly or biodetrital limestone, frequently represented by brachiopod coquinas (Małkowski *et al.* 2009; Drygant 2010). Well-preserved fossils of diverse exclusively marine invertebrates, including graptolites, chitinozoans,

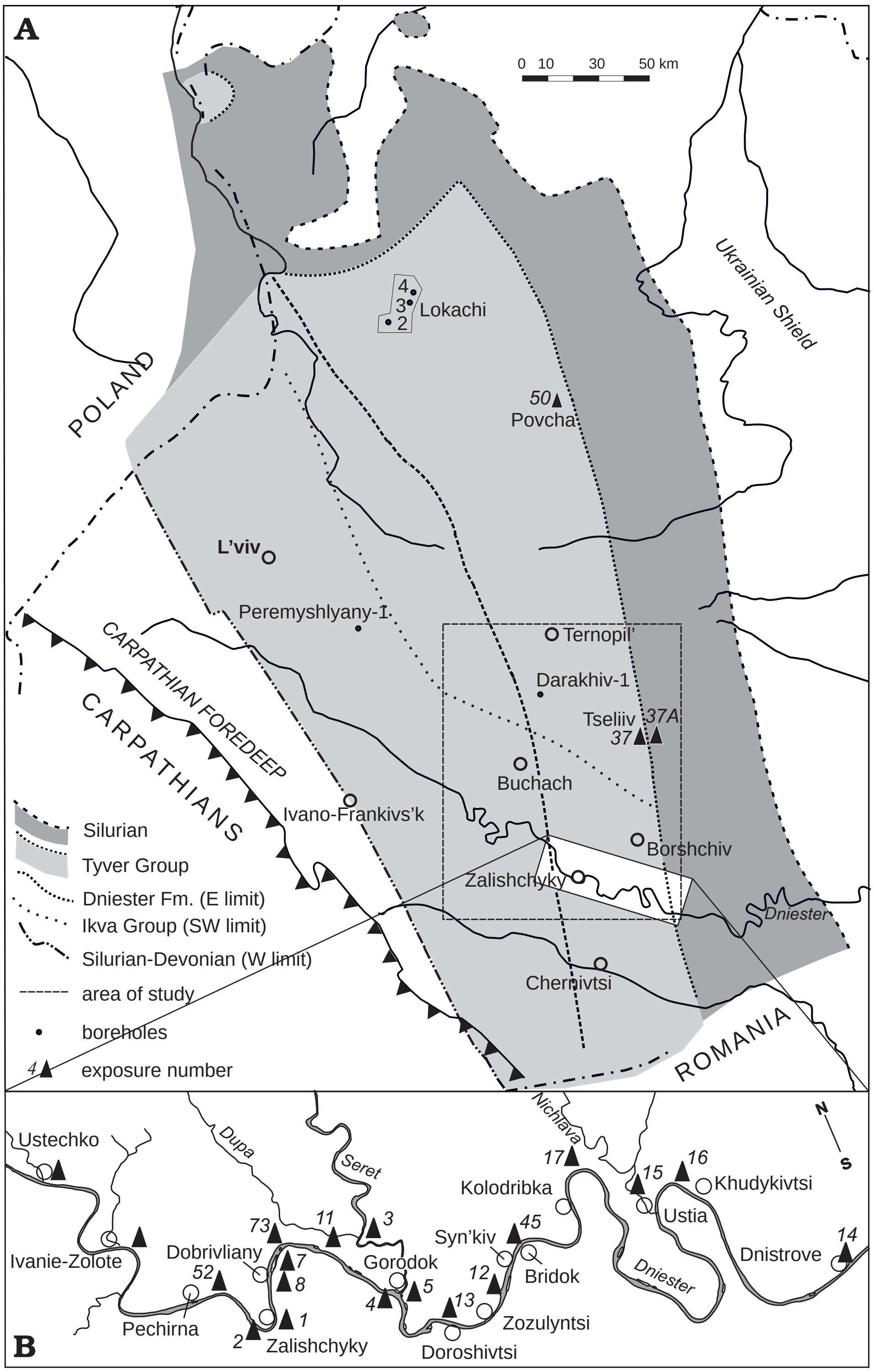

Fig. 3. **A**. Subsurface distribution of the Upper Silurian–Lower Devonian lithological units in western Ukraine with locations and boreholes with microremains of fossil fish fauna (after Drygant 2010: fig. 1.8). **B**. Outcrops along the Dniester with fish fossil microremains (after Drygant 2010: fig. 1.8, modified).

corals, bivalves, nautiloids, bryozoans, brachiopods, ostracods, trilobites, and crinoids, as well as conodonts, rare agnathan and fish microremains have been described from the Borshchiv deposits (Karatajūtė-Talimaa 1978; Paris and Grahn 1996; Karatajūtė-Talimaa and Märss 2004; Drygant 2010).

The **Chortkiv Formation**, more than 200 m thick, is represented by alternating dark grey argillaceous shale and thin-bedded (1–10 cm, rarely up to 20 cm) fine-grained limestone. In the upper, more carbonate-rich part, brownish and reddish claystones up to 3 m thick appear for the first time in the Podolian succession. The fossil assemblages are very diverse in the limestone and not so in the shale. In addition to abundant marine invertebrate fossils similar to those of the Borshchiv Formation, numerous agnathan remains occur (Obruchev and Karatajūtė-Talimaa 1968; Karatajūtė-Talimaa 1978; Karatajūtė-Talimaa and Märss 2004; Małkowski *et al.* 2009; Drygant 2010). Ostracodes, bivalves and tentaculites often form coquinas. The Chortkiv beds crop out extensively along the Dniester, the Seret and the Dupa rivers, in the vicinities of Kolodribka, Bridok, Syn'kiv, Zozulyntsi, Gorodok, Kasperivtsi, Jagilnytsia, and Chortkiv (Nikiforova *et al.* 1972; Paris and Grahn 1996; Drygant 2010).

The **Ivanie Formation**, up to 131 m thick, comprises dark, variably silty shale, with intercalations of thin-bedded, nodular, biodetrital limestone. The lower part (about 60 m thick) is a rhythmic alternation of shale and siltstone with thin intercalations and lenticles of nodular, biodetrital (mainly ostracods) limestone. The upper part (about 70 m) is dominated by siltstone beds (bioturbated grey to yellowish-green siltstone, upward red siltstone and limestone alternating with grey, bioturbated siltstone), containing scarce fossil assemblages that include agnathans, ostracods, brachiopods, and eurypterids (Paris and Grahn 1996; Małkowski *et al.* 2009; Drygant 2010). The transition into the overlying Old Red Sandstone facies is marked by the appearance of thick-bedded red sandstone and sandy shale with siltstone admixtures (Narbutas 1984), representing inshore lagoonal to fluvial-estuarine regimes (Uchman *et al.* 2004). The Ivanie beds crop out along the Dniester River, in the vicinities of Dobrivliany, Zalishchyky, Ivanie-Zolote, and Ustechko. Except for ostracodes, the fossils are similar to those of the underlying Chortkiv Horizon. The fossil remains occur in almost all rock types, but are less diverse than in the underlying beds. These are often endemic species, dominated by brachiopods *Mutationella podolica* Kozłowski, 1929 and ostracods *Leperditia tyraica* F. Schmidt, 1873, shells of which locally form coquinas, associated with corals, bivalves, nautiloids, tentaculitids, crinoids, and fish remains (Paris and Grahn 1996). The calcic siltstone of the Ivanie beds is characterised by undulated texture and traces of detritophages (Narbutas 1984). Fish fossils consist of micro- and macroremains of all major agnathan and gnathostome groups known up to date from the Podolian Lower Devonian section (Table 1; Obruchev and Karatajūtė-Talimaa 1968; Voichyshyn 2001b; Karatajūtė-Talimaa and Märss 2004). Conodonts *Zieglerodina serrula* (Drygant, 1974), *Caudicriodus serus* (Drygant, 1974) are common in the lower part of the unit; eurypterids have also been reported from the Ivanie beds (Alth 1874; Nikiforova *et al.* 1972; Drygant 2010).

The boundary between the Ivanie Formation and the Old Red Sandstone facies is marked by the disappearence of grey carbonate and siliciclastic rocks with marine fossils and their replacement by monotonous red beds (Narbutas 1984). This change can be observed in the basin of the Bila River and farther north- and northwestward along the Seret and Perejma rivers. Traces of crawling organisms and desiccation fissures are often preserved on the siltstone surface (Drygant 2010).

The thickness of the Old Red Sandstone facies strata gradually rises from none on the NE to more than 1100 m in the Carpathian Foredeep. The succession is subdivided into two series: the Ikva Group, which is a continental equivalent of the marine Tyver Group, and the Dniester Formation, overlying both these units (Fig. 2).

The **Ikva Group** includes the oldest strata of the Old Red Sandstone facies in the north-eastern part of the region (Fig. 2). The total thickness of the Ikva Group is up to 490 m. It is composed of light-grey or red fine-grained quartz sandstone intercalated with multicoloured siltstone and shale. In Podolia, deposits of this kind may contribute to the Ivanie Formation in its northern part near Terebovlia, exposed in outcrops and quarries on banks of the Seret and Gnizna Rivers. Intercalations of red-coloured thick layers of sandstone (of 0.3–2.0 m) with shale and sandy siltstone occur there. Fossils are represented by sporadic mollusks, ostracods, and agnathans (Drygant 2000, 2010).

The **Dniester Formation** is represented by exclusively continental red terrigenous sandstone, siltstone, and mudstone. Desiccation fissures and ripple marks are common (Paris and Grahn 1996). The thickness of the Dniester Formation increases from none in the NE to 1135 m in the Carpathian Foredeep (Fig. 2). Its subdivision into members (corresponding to local "stages") is based on differences in proportions of particular rock types. Only the first four among the ten stages, the Ustechko (53 m), Khmeleva (150 m), Strypa (170 m), and Smerkliv (72 m) ones, are represented by deposits exposed in Podolia. Others are known only from boreholes near the Trans-European Suture Zone (Drygant 2000, 2010).

Table 1. Distribution of fossil vertebrate remains in the Mid Palaeozoic deposits of Podolia.

Period	Silurian	Devonian								
Age	Pridoli	Lochkovian				↔	Pragian			
Ma (Williams *et al.* 2000)	from 419	418				413.5				to 409.5
Formation [Series]	Skala	Tyver			Ikva	Dniester				
Stage [Member]	sk3	bch	ch	iv		ust		khm1	khm2-3	str
Old Red faunal zones						I			II	III
Deposits	marine				continental					
Facies / Species	open-sea	near shore		littoral	lower salinity to fresh-water					
					lagoon-delta			lake		channel
Benneviaspis zychi										■
B. talimaae						■				
B. whitei						■		■		
“*Cephalaspis*” *djurinensis*							■?			
“*C.*” *microlepidota*						■				
Citharaspis junia										■
C. polonica										■
Diademaspis stensioei						■				
Machairaspis sp.						■				
Mimetaspis concordis							■	■		
M. glazewskii						■	■			
Osteostraci indet.			■		■					
Parameteoraspis dobrovlensis				■						
Pattenaspis rogalai					■	■	■	■	■	
Stensiopelta pustulata						■		■	■	
Tegaspis waengsjoei					■					
T.? sp. 1							■?			
Ukrainaspis kozlowskii				■		■	■			
Victoraspis longicornualis						■?				■?
Wladysagitta janvieri	Cephalaspidiformes							■		
Zenaspis dzieduszyckii							■			
Z. kasymyri sp. n.							■			
Z. major							■			
Z. podolica						■		■	■	
Zychaspis concinna						■				
Z. elegans									■	
Z. granulata							■?	■		
Z. siemiradzkii						■		■		
Alaeckaspis? *depressa*			■							
A. magnipinealis				■						
A. ustetchkiensis								■		
A. verbivciensis					■					
Althaspis elongata										■
A. longirostra										■
A. sapovensis										■
A. tarloi sp. n.						■?				
A.? *spathulirostris*										■
?*Belgicaspis crouchi*					■			■		
Brachipteraspis latissima										■
Djurinaspis prima						■				
D. secunda sp. n.					■					
Dnestraspis firma								■		
Europrotaspis arnelli										■
Larnovaspis iwaniensis				■					Pteraspidiformes	
L. kneri			■	■						
L. major				■		■				
L. mogielnensis					■	■				
Mylopteraspis robusta						■?				
Mylopteraspidella gracilis						■				

Palanasaspis chekhivensis sp. n.										■
Parapteraspis lata				■		■				
P. plana						■		■		
Pavloaspis pasternaki							■			
Podolaspis danieli sp. n.							■			
P. lerichei				■	■	■				
P. podolica					■	■	■			
P. zychi				■		■				
"*Pteraspis*" *angustata*						■		■		
Semipodolaspis slobodensis sp. n.			?	■?						
Zascinaspis bryanti				■						
Z. heintzi					■	■	■	■	■	
Ctenaspis kiaeri				■						
Irregulareaspis seretensis				■						
I. skalskiensis	■									
I. stensioei				■						
I. sp.				▲						
Poraspis pompeckji				■	Cyathaspidiformes					
P. siemiradzkii				■						
P. simplex				■						
P. sturi			■	■		■	■	■?		
P. sp.			▲	▲■						
P. sp. 1							■			
Seretaspis zychi			■							
Corvaspis kingi			▲	▲■			other Heterostraci			
C. sp.			▲	▲						
"*Lepidaspis*" sp.			▲	▲						
Tesseraspis orvigi				▲						
Weigeltaspis alta				■		■		■		
W. brotzeni				■		?		■		
W. sp. 1 and 2								■		
Apalolepis brotzeni				▲						
A. obruchevi			▲	▲						
Gampsolepis insueta			▲							
Nikolivia balabayi			▲					Thelodonti		
N. elongata			▲	▲		?				
N. oervigi				▲						
Turinia pagei	?	▲	▲	▲		▲				
T. polita			▲	▲		▲				
Ericaspis zychi					■	■		■	■	
Kujdanowiaspis podolica	Placodermi					■		■	■	
K. buczacziensis									?	■
Tyriolepis radiata			▲							
Erriwacanthus falcatus								Acanthodii		■
"*Gomphodus*" sp.	▲	▲	▲	▲						
Nostolepis sp.	▲	▲	▲	▲		?				
Onchus sp.		▲	▲			?				
Ptomacanthus sp.				■						
Altholepis composite			▲	▲		?				
Ivanelepis costulata			▲	▲						
Knerialepis mashkovae			▲	▲			Chondrichthyes			
Polymerolepis whitei			▲	▲						
Seretolepis elegans				▲						

▲ – microremains
■ – macroremains
■? – uncertain stratigraphic location
? – probable occurrence
↔ – uncertain correlation with the boundary of international units (Drygant, pers. comm.)

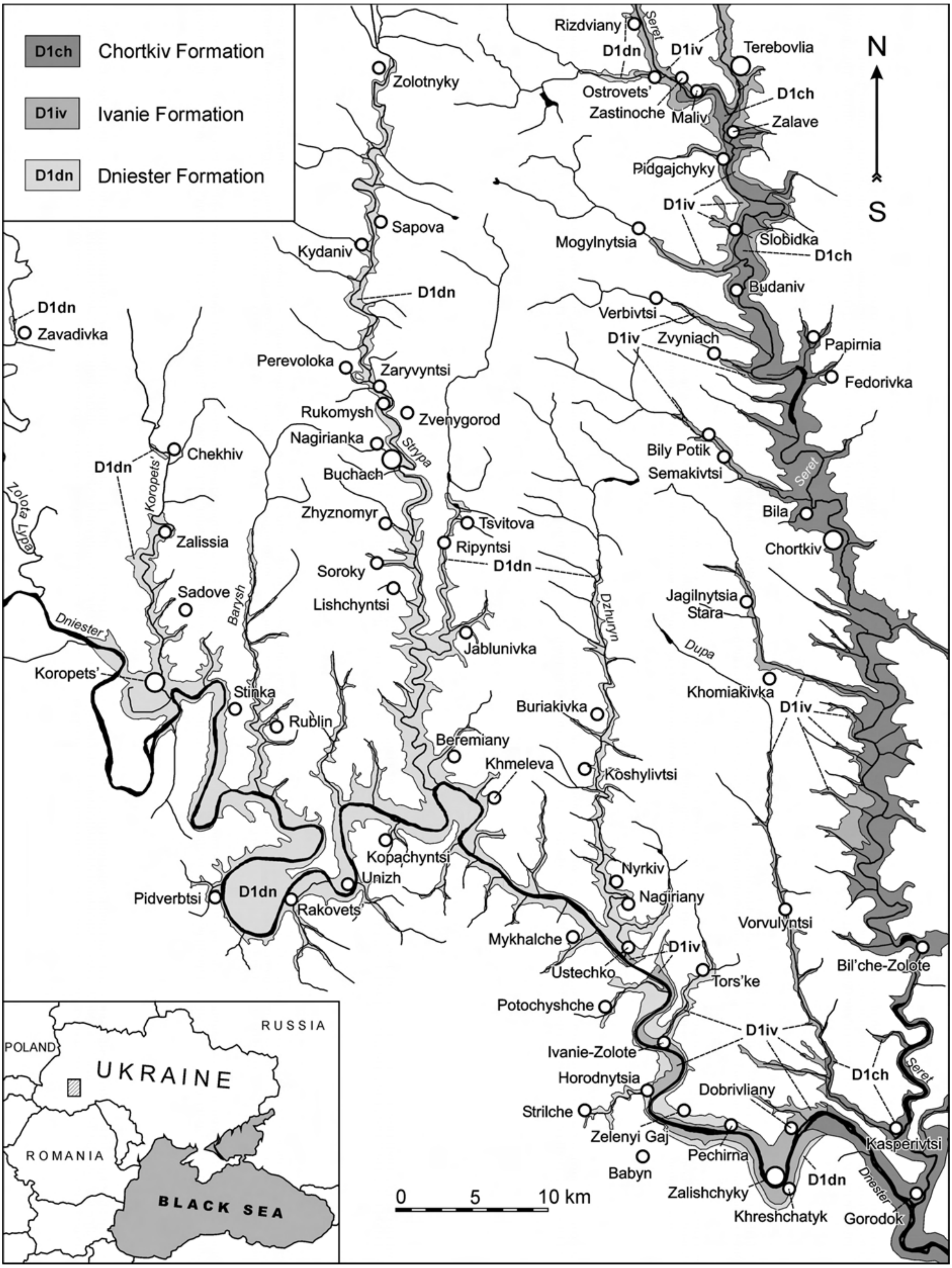

Fig. 4. Lower Devonian exposures in Podolia (compiled after Alth and Bieniasz 1887; Teisseyre 1900; Łomnicki 1901; Nikiforova *et al*. 1972) and localities with fish fossils (after Voichyshyn 2001a), mentioned in the text.

The extent of the Dniester Formation is not easily determinable because of limitations of both the palaeontological data and stratigraphic correlation methods available. Sedimentary cycles from sandstone to fine-grained siltstone and shale have been identified within the succession (Narbutas 1984). All divisions of

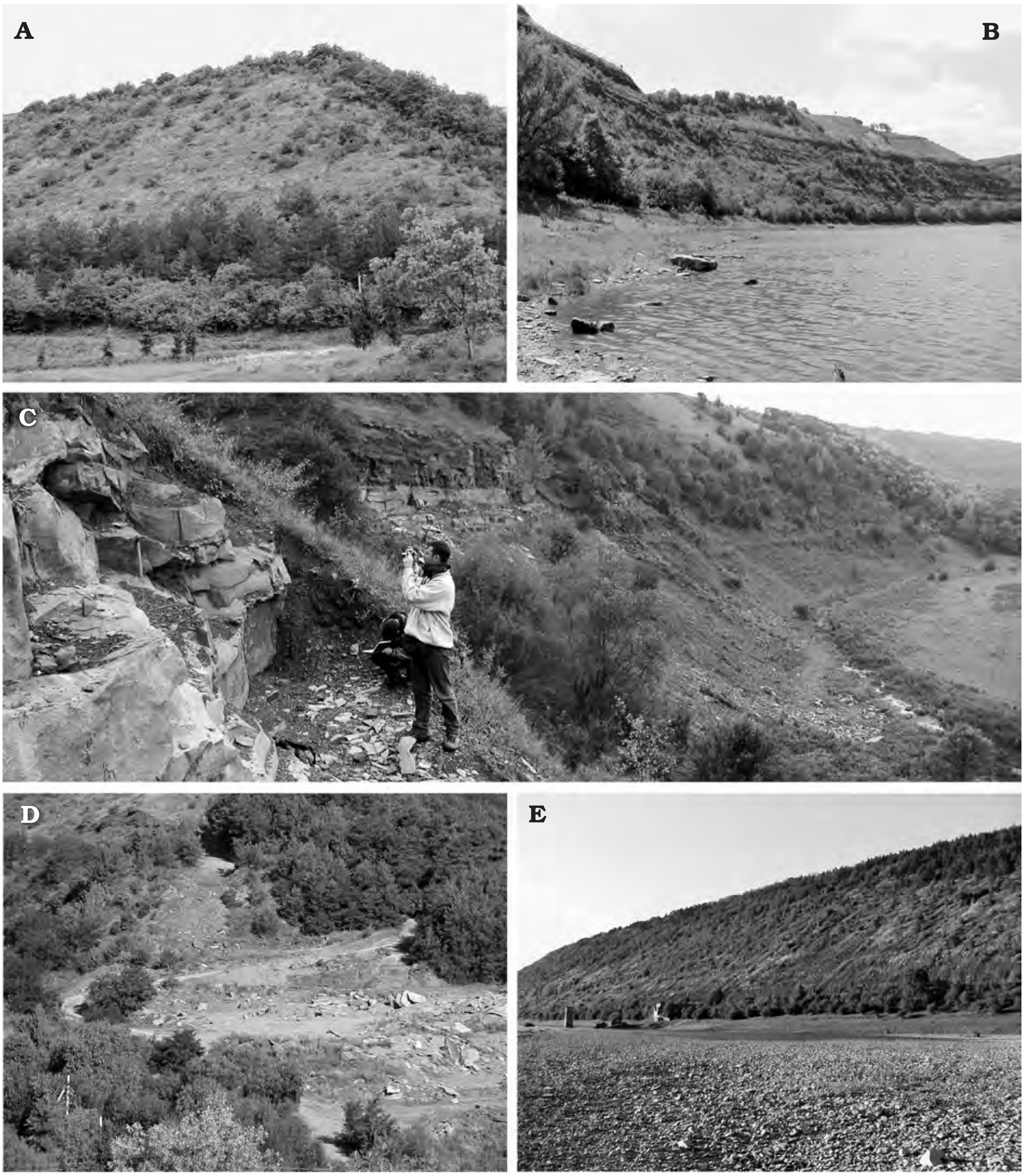

Fig. 5. Agnathan localities in Podolia. **A**. Exposure of the lower part of Ivanie Member of the Tyver Formation in the left bank of the Dniester River eastward of Dobrivliany. **B**. Exposure of the upper part of the Ivanie Member of the Tyver Formation at the right bank of the Dniester River opposite to Zalishchyky. **C**. Exposure of the Ustechko or lower part of Khmeleva Member of the Dniester Formation on SE slope of the Dzhuryn River bank near Nagiriany (photo taken in September 2002; in the foreground standing Vincent Dupret and sitting Vincent Pernègre). **D**. One of the quarries of the Ustechko or lower part of Khmeleva Member of the Dniester Formation SW of Horodnytsia. **E**. Main exposure of the uppermost part of the Ustechko Member to lower part of Khmeleva Member of the Dniester Formation on the left bank of Dniester River NW Ustechko near destroyed old bridge.

the formation show alternation of red-coloured, more rarely greenish-grey siltstone and shale with grey, fine-grained, thick-bedded quartz sandstone. Faunal remains are known from the Ustechko, Khmeleva, and Strypa Stages (Voichyshyn 2001; Drygant 2010). Deposits of the Smerkliv Stage contain a rich plant assemblage (Ishchenko 1972).

Apart from specific lithology and dominantly red colouration, the Dniester Formation deposits, especially sandstones and siltstones, show cross bedding, convolution, traces of waves and currents, underwater erosion, desiccation fissures, and traces of crawling of benthic organisms. Marine invertebrate fossils are lacking (Drygant 2000, 2010). Rocks of the lower part of the Dniester Series share with the Ivanie beds the abundance of arthropod and worm trace fossils (Narbutas 1984). A rich agnathan fossil assemblage occurs in the basal beds and gradually disappears upwards the section.

TAPHONOMY OF PODOLIAN FISH ASSEMBLAGES

To be preserved as fossils, skeletal remains of the Podolian agnathans had to be protected against scavengers, mechanical fragmentation, bacterial decomposition, and chemical dissolution (e.g., Obruchev 1972). The best protection against organisms is contamination of the bottom environment with hydrogen sulphide. Such protection is especially important in the case of vertebrate skeletons, built of calcium phosphate that in most environments is in short supply for organisms demanding phosphate ions. The simplest way to protect such skeletons from environmental destructive factors is to cover them with sediment quickly enough that the sediment in not penetrable by infaunal organisms. A high rate of sedimentation may result, however, in dilution of fossils in a great volume of the rock, unless high biological productivity guarantees a steady supply of great quantities of cadavers.

In Podolia, agnathan skeletons are best preserved in marine carbonate rocks of the Chortkiv and Ivanie Stages of the Tyver Formation. The alkaline environment of the rock protected their calcium phosphate tissues

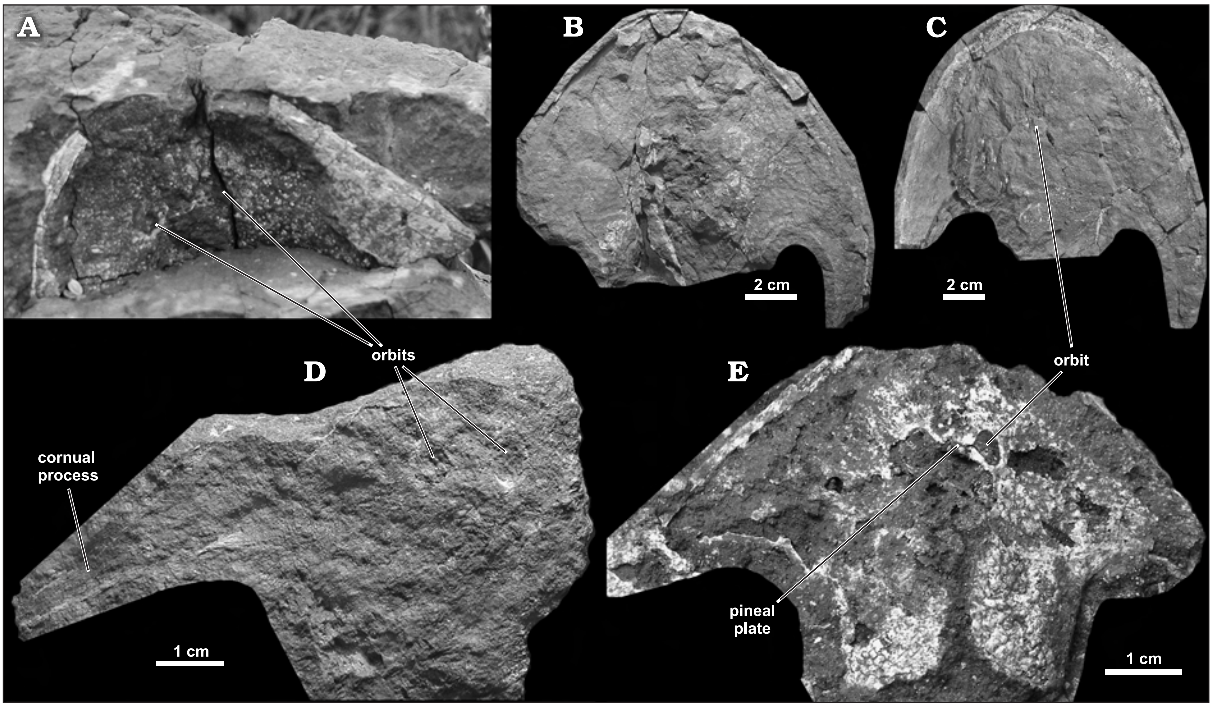

Fig. 6. Preservation of armoured agnathans in Podolia. **A**. Zenaspididae gen. indet., partial headshield imprint photographed *in situ* at the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **B**. *Zenaspis podolica* (Balabai, 1962), imprint of crushed headshield SMNH BP.29 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, dorsal view. **C**. Same species, mould of crushed headshield SMNH BP.28 from the Horodnytsia old quarry talus, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view. **D**. *Stensiopelta*? *pustulata* Janvier, 1985, eroded mould of partial headshield SMNH BP.1273 from Khmeleva, left bank of Dniester River at river water level, Khmeleva Member of the Dniester Formation, dorsal view. **E**. *Stensiopelta pustulata* Janvier, 1985, eroded mould of headshield IGP (unnumbered) from Ustechko, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view.

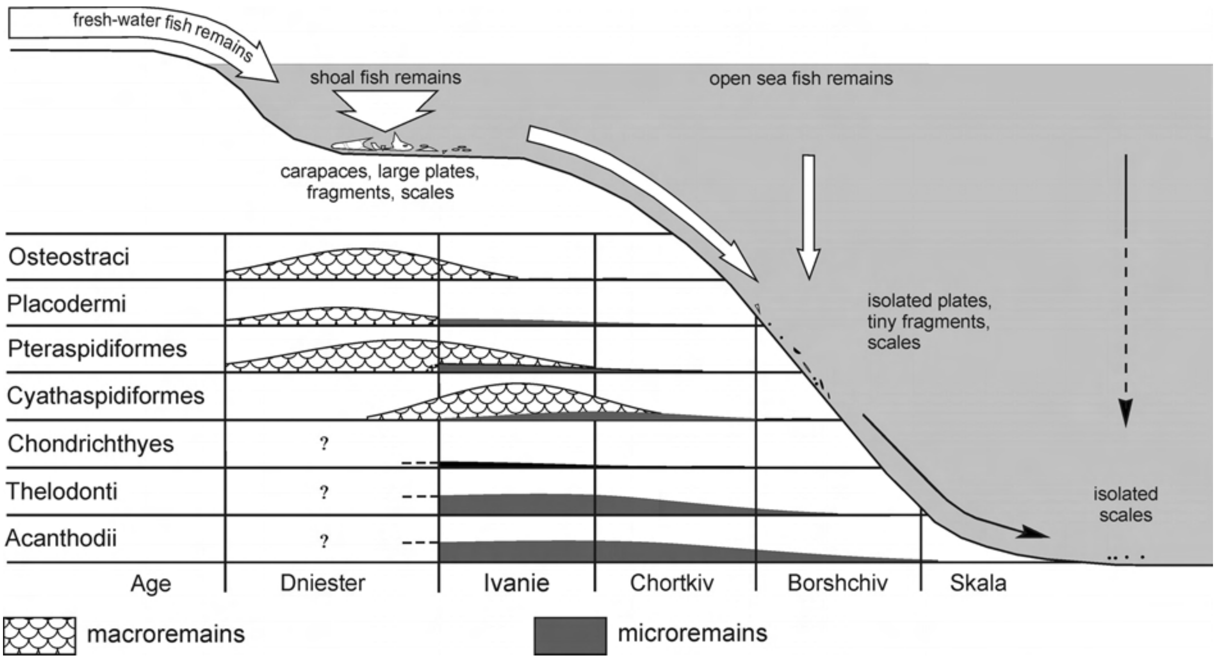

Fig. 7. Proposed interpretation of taphonomic history of the Early Devonian fish fossil assemblages of Podolia and changes in distribution of source environments over geological time (after Voichyshyn 2001b).

against dissolution during early and late diagenesis and, after they were enclosed by fine-grained sediment, against scavengers and bacterial decay. Unfortunately, before this happened, the cadavers and elements of the skeleton were exposed to activity of bottom organisms of rich and productive marine communities flourishing at that time. As a result, skeletal remains of agnathans are not numerous there and represented mostly by separated plates of the armour (Fig. 34), their fragments, scales and tesserae (Figs 7, 15, 17, 28, 29, 80).

Classification of the Podolian fossil agnathans (except for thelodonts) is based on morphology of their macroremains (carapaces, shields and their parts). Usually, fossil material does not allow studies of macro- and microremains of the same specimen. Therefore, microremains of armoured agnathans, as a rule, are difficult to determine at the family and lower taxonomical levels.

More or less articulated pteraspidid carapaces and entire osteostracan shields, with different degrees of the dermal skeleton damage, occur in the lower part of the Dniester Formation (ranging from the Ustechko Stage to the lower part of the Khmeleva Stage). These remains were buried in clay deposits (argillites) mainly. In this case, fast sedimentation was the main protective factor, but geochemical conditions within the rock were unfavorable for the calcium phosphate skeleton, which is poorly preserved and practically defies microscopic studies. Despite these obstacles, such specimens can be identified to species. This material by virtue of its taxonomic identification enables estimation of richness of the fish fauna during time of formation of deposits of the lower part of the Dniester Formation. There are specimens with state of preservation good enough to permit preparation of canals of the lateral line system (Figs 31A, D, 32A, E, 67A).

In the upper part of the succession (Khmeleva and Strypa Stages of the Dniester Formation), bone-bearing horizons occur mostly in sandstone. Such coarse terrigenous material was apparently transported into the basin from the neighboring land area with high-energy water. Agnathan remains are presented by eroded moulds of carapace or separate plates (Figs 73A, B, 75D, 77B, C). It remains unknown whether this is a result of transport of skeletal remains together with the sediment from possibly fresh-water environments or abrasion developed at the place of sedimentation. Because of poor preservation, fossils usually can be determined only at the generic level. Anyway, the fossil assemblages from this part of the Podolian Early Devonian are of low taxonomic diversity although the morphology of some members of the fauna suggests ecological specialization.

There is a clear correlation between the size of carapaces and degree of their damage in the Devonian fish fauna. Strongly convex shields of large osteostracans, for example species of *Zenaspis*, occur very rarely in undamaged state with the original shape preserved (Fig. 93B; Voichyshyn 2006b). Often, they are crushed (Figs 6A–C, 92C, 93A, C). This is less expressed in the shields of *Pattenaspis rogalai* or *Stensiopelta* *pustulata* of considerably smaller size (Figs 6D, E, 85A, 90A, 91B). As for the shields of the smallest (30 mm in length), among the Podolian osteostracans, *Mimetaspis concordis*, they are almost never damaged in a way distorting its original shape (Figs 83E, 84A, C). The same refers to the pteraspidids. The largest Podolian pteraspidids of *Althaspis* (Figs 74D, 75A, D) and *Larnovaspis mogielnensis* (Fig. 61B, D, F) are preserved as poorly as the zenaspidids.

MATERIAL AND METHODS

The material used for this study mainly belongs to the fossil fish collection (prefixed BP) of the section Palaeozoology: Vertebrates in the palaeontological division of the State Museum of Natural History, L'viv, Ukraine (Voichyshyn 2009). At present, the fossil fish collection accommodates 1357 units of storage representing remains of the Early Devonian fish fauna from Podolia. It contains among others the material collected by Władysław Zych (in 1924–1940), Pavlo Balabai (in 1948–1959), and myself (in 1986–1992, 1994–1995, and 2002–2004). In addition, I examined the collection of the Geological Museum, L'viv State University, containing some specimens from Zych's old collection and specimens collected by university students, the collection of Podolian osteostracans housed at the Palaeontological Institute, Russian Academy of Sciences, Moscow, the collection of the Muzeum of Earth, Polish Academy of Sciences, Warsaw, the collection of the Institute of Geology of Warsaw University, and the collection of the State Geological Institute, Warsaw.

All the material was mechanically cleaned, if necessary, then measured, photographed and studied under optical microscope. Photographs were taken by the author with Olympus C-2100 camera and Panasonic DMC-FZ50 camera, with macro convertors. Microscopic-sized specimens were photographed by Andrzej Baliński (Institute of Paleobiology PAS) using a Fujifilm FinePix S2 pro camera.

The SEM photographs were taken at the Institute of Paleobiology PAS, Warsaw using a Philips XL-20 scanning electron microscope. Microremains (ichthyoliths) were mounted on stubs and coated with gold for SEM examination.

All the photographs were recorded in high-resolution TIF files, which were used to prepare the figures using Adobe Photoshop 7.0, CorelDraw 11, and PhotoZoomPro 2 software.

Abbreviations. — Abbreviations for the sensory line system of heterostracans (Fig. 8A, B, E, F; after Denison 1964 and Novitskaya 1986): cm.dl, dorsolateral commissure; cm.dm, dorsomedial commissure; cm.so, supraorbital commissure; cm.v, ventral commissure; ifc, infraorbital canal; ldl, dorsolateral canal; lvl, ventrolateral canal; mdl, dorsomedial canal; poc, postoral canal; soc, supraorbital canal; vm, ventromedial canal.

Abbreviations for plates and other aspects of the pteraspidid carapace (Fig. 8E, F; after Blieck 1984 and Novitskaya 1986): Br, branchial; C, cornual; D, dorsal shield; L, lateral; O, orbital; OL, oralolateral; Or, oral; P, pineal; POr, postoral; R, rostral; V, ventral shield; br.o., branchial opening; d.n., notch for dorsal spine; orb., orbit.

Abbreviations for the osteostracan headshield (Fig. 8C, D; after Denison 1951 and Afanassieva 1991): co, cornual process (cornu); df, dorsal field; lf, lateral field; nh, nasohypophyseal opening; orb, orbit; pin, pineal plate.

Measurements used in description of the dorsal shield of Cyathaspidiformes follow those of Denison (1964) and Novitskaya (1986) (Fig. 8A, B): ML, maximum length; OL, orbital length: distance between the middle of anterior margin of the shield and orbit level; OW, orbital width: width of the shield on the orbital level; PL, pineal length: distance between the middle of anterior margin of the shield and middle of the pineal spot; PBL, postbranchial length: distance between posterior margin of the branchial notch and posterior margin of the shield; W, maximum width.

Measurements used in description of the carapace of Pteraspidiformes are taken from Blieck (1984) (Fig. 8E, F): CL, length of the cornual plate; CW, width of the cornual plate; DL, length of the dorsal shield; DW, width of the dorsal shield; PL, length of the pineal plate; PW, width of the pineal plate; RL, length of the rostral plate; RW, width of the rostral plate; tL, total length of the carapace (from anterior margin of the rostral plate to posterior margin of the dorsal shield); VL, length of the ventral plate; VW, width of the ventral plate.

Measurements used in description of the headshield of Osteostraci follow those of Denison (1951) and Afanassieva (1991) with some additions (Fig. 8C, D): A, distance between the pineal foramen and the posterior margin of the median dorsal field; B, pre-pineal length of shield: distance between the anterior margin of the

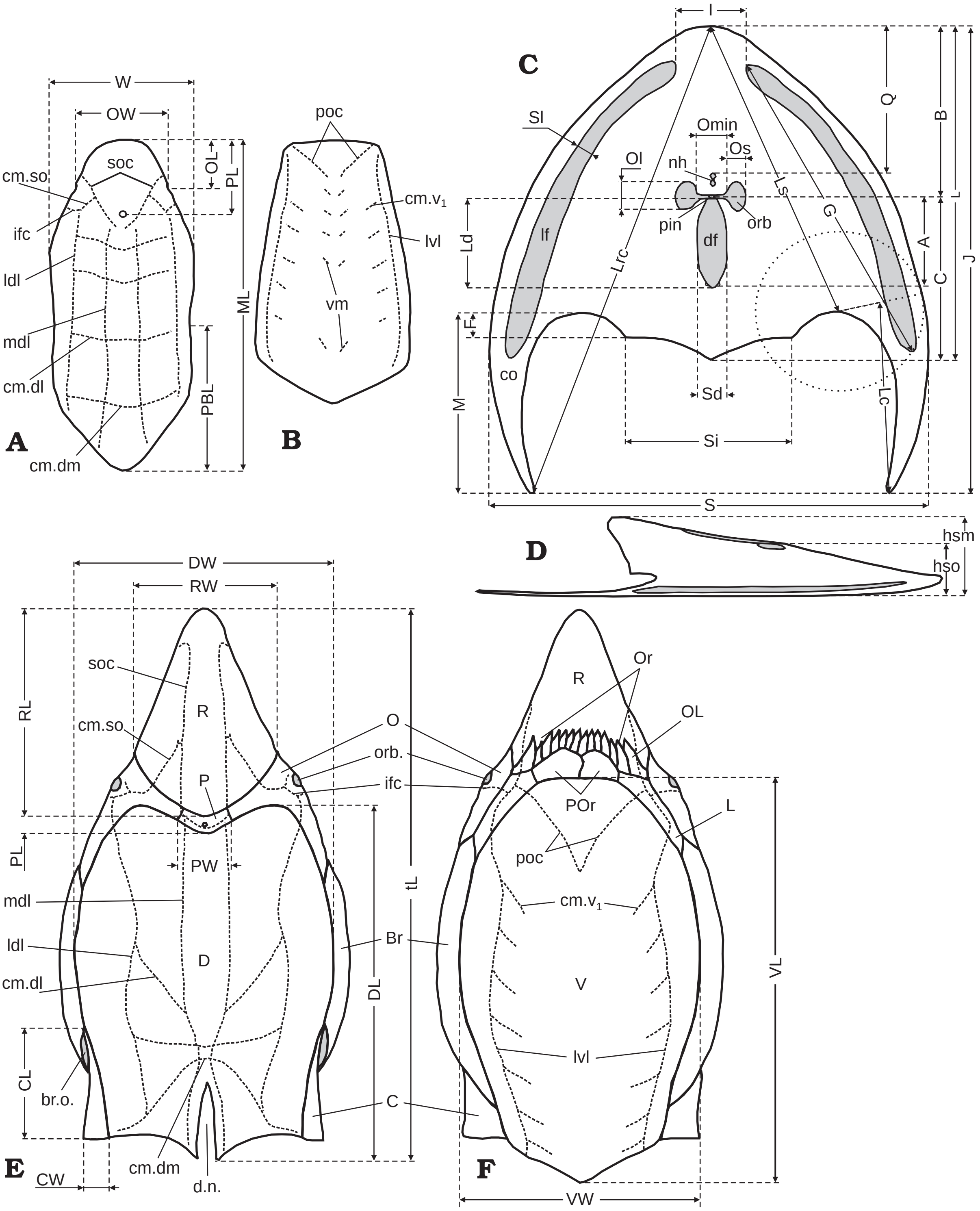

Fig. 8. Measured aspects of a cyathaspidid dorsal (**A**) and ventral (**B**) shields (after Novitskaya 1986), an osteostracan headshield from dorsal (**C**) and lateral (**D**) sides (after Denison 1951 and Afanassieva 1991, modified), and a pteraspidid carapace from dorsal (**E**) and ventral (**F**) sides (after Blieck 1984, modified).

shield and the pineal foramen; C, post-pineal length of shield: distance between the pineal foramen and the posterior margin of the shield; F, depth of pectoral sinus: distance between line connected the tips of pectoral sinuses and line connected posterolateral corners of abdominal division of the shield; G, maximum length of lateral field: distance between the anterior and posterior margins of the lateral field; hsm, maximum height of the shield: distance between the highest elevation of the shield (tip of the dorsal crest, if preserved) and the shield ventral plane; hso, orbital height: distance between the level of orbits and the shield ventral plane; I, distance between anterior ends of the lateral fields; J, distance between the anterior margin of the shield and the line connecting posterior tips of cornual processes; L, maximum length of the shield: distance between the anterior margin of the shield and posterior margin of its abdominal part; Lc, length of cornual processes: distance between the middle of the shortest line connecting the tip of the pectoral sinus to the lateral margin of the shield and the tip of the cornual process; Ld, maximum length of median dorsal field; Lrc, distance between the anterior margin of the shield (without rostral process) and the tip of the cornual process; Ls, distance between the anterior margin of the shield (without rostral process) and the tip of the pectoral sinus; M, comparative length of the cornual processes: distance between line connected the tips of pectoral sinuses and line connected posterior ends of the cornual processes; Ol, orbit length: distance between anterior and posterior margins of the orbit; Omin, minimum distance between orbits; Os, orbit width: distance between lateral margins of the orbits; Q, distance between the anterior margin of the shield and the nasohypophyseal opening; S, maximum width of shield; Sd, maximum width of median dorsal field; Si, width of the abdominal part of the shield.

Institutional abbreviations: BM(NH), The Natural History Museum (London, Great Britain), previously British Museum of Natural History; GI (previously TAGI), Geoloogia Instituut, Tallinn University of Technology (Tallinn, Estonia); GMLSU, Geological Museum of L’viv State University, Department of Geology (L’viv, Ukraine); IGP, Institute of Basic Geology, Warsaw University (Warsaw, Poland); LIG, Institute of Geology and Geography (Vilnius, Lithuania); MNG, National Geological Museum (Bucharest, Romania); MNHN, Muséum National d’Histoire Naturelle (Paris, France); MZ, Muzeum Ziemi PAS (Warsaw, Poland); NHRM, Naturhistoriska Riksmuseet (Stockholm, Sweden); PIG, Polish Geological Institute (Warsaw, Poland); PIN, Palaeontological Institute, Russian Academy of Sciences (Moscow, Russia); PMU, Museum of Evolution, Palaeontological collections (Uppsala, Sweden); SMNH, State Museum of Natural History, National Academy of Sciences of Ukraine (L’viv, Ukraine).

Names of Podolian fossil fish localities

English transcription	**Ukrainian name**	**Earlier used names**
Babyn	Бабин	Babin
Bazar	Базар	Bazar
Bedrykivtsi	Бедриківці	Bedrykowce
Beremiany	Берем’яни	Beremiany
Bila	Біла	Biała
Bilche-Zolote	Білъче-Золоте	Bilcze
Bily Potik	Білий Потік	Potok Biały
Birky Velyki	Бірки Великі	Borki Wielkie
Buchach	Бучач	Buczacz
Budaniv	Буданів	Budzanów
Buriakivka	Буряківка	Burakówka
Butsniv	Буцнів	Bucniow
Chekhiv	Чехів	Czechów
Chervonograd	Червоноград	Czerwonogród
Dnistrove (former Vovkivtsi)	Дністрове (кол. Вовківці)	?Wołkowce
Dobrivliany	Добрівляни	Dobrowlany
Doroshivtsi	Дорошівці	Doroszoutz (Romania)
Fedorivka	Федорівка	Tudorów
Gorodok	Городок	Gródek
Horodnytsia	Городниця	Horodnica
Ivanie-Zolote	Іванє-Золоте	Iwanie
Jablunivka	Яблунівка	Jazłowiec
Jagilnytsia	Ягільниця	Jagielnica
Jagilnytsia Stara	Ягільниця Стара	Jagielnica Stara
Kaptury	Каптури	Kaptury
Kapustyntsi	Капустинці	Kapuścińce
Kasperivtsi	Касперівці	Kasperowce
Khmeleva	Хмелева	Chmielowa
Khomiakivka	Хом’яківка (now unified with Nagirianka)	Chomiakówka
Khreshchatyk	Хрещатик	Kryszczatek
Kopachyntsi	Копачинці	Kopaczyńce
Koropets’	Коропець	Koropiec
Koshylivtsi	Кошилівці	Koszyłowce
Kovalivka	Ковалівка	Kowalówka

English transcription	**Ukrainian name**	**Earlier used names**
Krovinka	Кровінка	Krowinka
Krynytsia	Криниця	?
Kryvche	Кривче	Krzywki
Kydaniv	Киданів	Kujdanów
Lishchyntsi	Ліщинці	Leszczańce
Luka	Лука	Luka
Lysivtsi	Лисівці	Lisowce
Maliv	Малів	Małów
Mazurivka	Мазурівка	Mazurówka
Mogyl’nytsia	Могильниця	Mogielnica
Mykhalche	Михальче	Michalcze
Myshkivtsi	Мишківці	Myszkowce
Nagirianka	Нагірянка	Nagórzanka
Nagiriany	Нагіряни	Nagórzany
Nyrkiv	Нирків	Nyrków
Ostrovets’	Островець	Ostrowczyk
Papirnia	Папірня	Papiernia
Pechirna	Печірна	Pieczarna
Perevoloka	Переволока	Przewłoka
Pidgajchyky	Підгайчики	Podhajczyki
Pidverbtsi	Підвербці	Podwerbce
Potochyshche	Поточище	Potoczyska
Rakovets’	Раковець	Rakowiec
Ripyntsi	Ріпинці	Rzepińce
Rizdviany	Різдв’яни	Ruzdwiany
Rublin	Рублін	?
Rukhotyn	Рухотин	?
Rukomysh	Рукомиш	Rukomysz
Rusyliv	Русилів	Rusiłów
Sadove	Садове	Nowosiołka Koropiecka
Sapova	Сапова	Sapowa
Semakivtsi	Семаківці	Siemakowce
Slobidka	Слобідка (Янівська)	Słobódka
Slobidka Strusivs’ka	Слобідка Струсівська (now Kamianka)	Słobódka Strusowska
Smykivtsi	Смиківці	Smykowce
Soroky	Сороки	Soroki
Stephaneshty	Стефанешти	?
Stinka	Стінка	Ścianka
Strilche	Стрілче	Strzylce
Strusiv	Струсів	Strusów
Terebovlia	Теребовля	Trembowla
Tors’ke	Торське	Torskie
Tovstolug	Товстолуг	Toustoług
Tseliiv	Целіїв	Celejów
Tsvitova	Цвітова	Cwitowa
Unizh	Уніж	Uniż
Ustechko	Устечко	Uścieczko
Varvarivtsi	Варварівці	Warwaryńce
Vasyliv	Василів	Wasileu (Romania)
Verbivtsi	Вербівці	Wierzbowiec
Vorvulyntsi	Ворвулинці	Worwulińce
Vynogradiv	Виноградів	Kościelniki
Zalave	Залаве	Załawie
Zalishchyky	Заліщики	Zaleszczyki
Zalissia	Залісся	Ẓalesie
Zaryvyntsi	Заривинці	Żurawińce
Zastinka	Застінка	Zaścianka
Zastinoche	Застіноче	Zaścinocze
Zavadivka	Завадівка	Ẓawadówka
Zelenyj Gaj	Зелений Гай (Жежава)	Żeżawa
Zhyznomyr	Жизномир	Zyźnomierz
Zolotnyky	Золотники	Złotniki
Zozulyntsi	Зозулинці	Zazulińce
Zvenygorod	Звенигород	Dźwinogród
Zvyniach	Звиняч	Zwiniacz

MORPHOLOGY OF THE PODOLIAN ARMOURED AGNATHANS

In morphologic descriptions of the Podolian agnathans, the structure of their armour, its external sculpture, sensory lateral line system, internal organs (visceral skeleton, brain cavity), and also the ontogenetic development of the armour is taken into account. Below, an overview of the most characteristic features of the family rank groups, the cyathaspidids, corvaspidids, pteraspidids, and cephalaspidids, is given.

CYATHASPIDIFORM HETEROSTRACANS

Large unpaired dorsal and ventral shields made most of the armour of the cyathaspidids (Fig. 8A, B). On the lateral sides, there were paired branchial plates (among Podolian genera, in *Poraspis*), with few exceptions (among Podolian forms, in *Ctenaspis*). Several small (usually paired) oral, lateral, and suborbital plates covered the region of mouth opening and orbits in the fore part of armour.

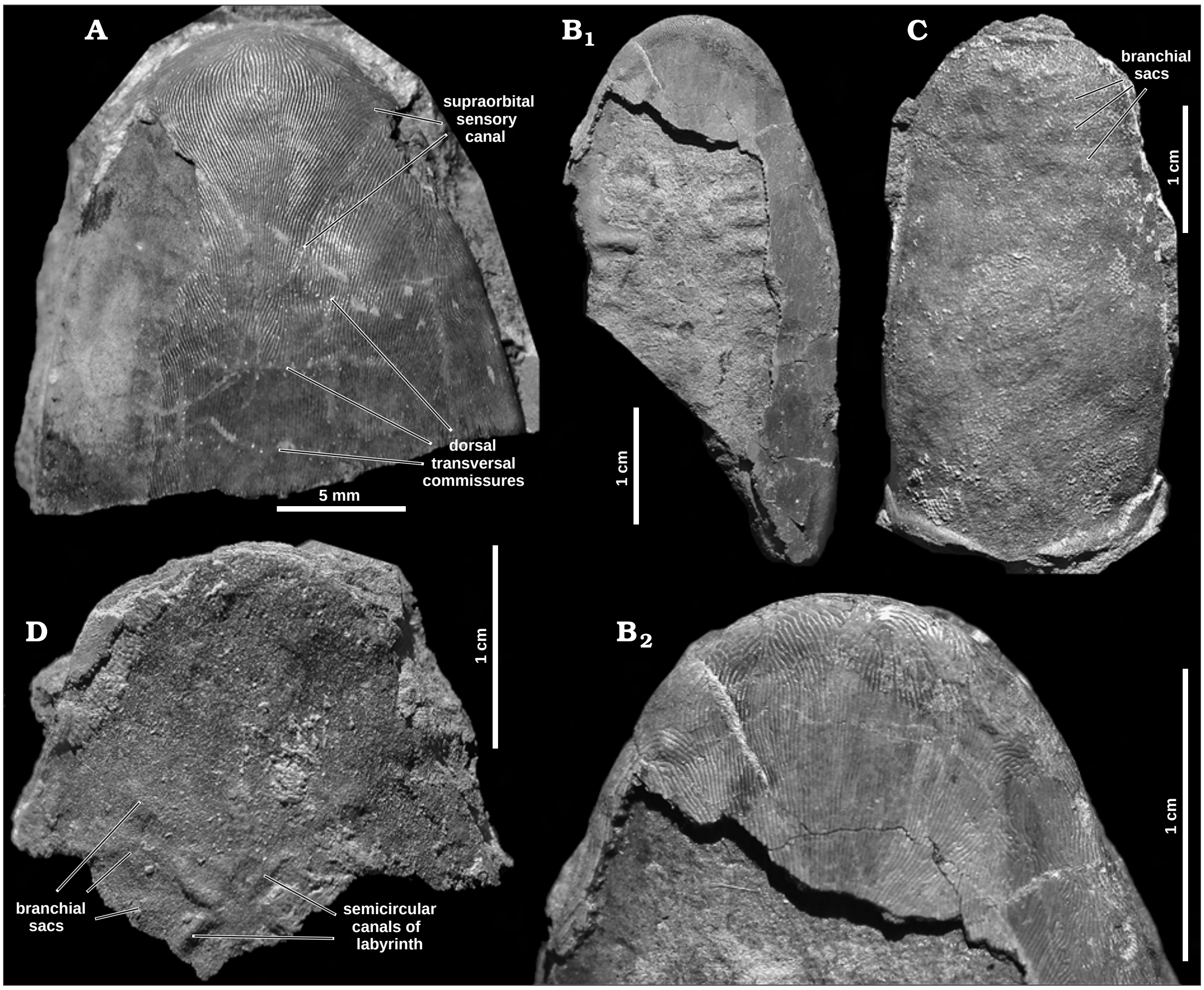

Fig. 9. Carapace morphology of undetermined species of the poraspidid *Poraspis*. **A**. Anterior part of the dorsal shield SMNH BP.461 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **B**. Fragmentary dorsal shield SMNH BP.428 from Zalishchyky, upper part of Ivanie Member of the Tyver Formation, dorsal view, also enlarged portion of the specimen. **C**. Mould of the ventral shield SMNH BP.436 from Ustechko, left bank of the Dniester River, uppermost part of the Ivanie Member of the Tyver Formation, dorsal view. **D**. Mould of anterior part of dorsal shield SMNH BP.367 from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member of the Tyver Formation, dorsal view.

Fig. 10. Carapace morphology of the poraspidid *Poraspis*. **A**. *Poraspis* sp., fragmentary dorsal shield SMNH BP.372 from Zalave, right bank of Seret River, upper part of Chortkiv or lower part of Ivanie Member of the Tyver Formation, frontal and dorsal view, anterior part of the same specimen in dorsal view and its partial imprint in dorsal view, respectively. **B**. *Poraspis* sp.,

→

anterior part of the dorsal shield SMNH BP.413 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation seen from inside. **C**. *Poraspis* sp., anterior part of the dorsal shield SMNH BP.416 from the same locality in dorsal view. **D**. *Poraspis*? *sturi* (Alth, 1874), mould of the dorsal shield SMNH BP.378 with remains of armour from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, dorsal view. **E**. *Poraspis siemiradzkii* (Zych, 1931), abraded mould of the dorsal shield SMNH BP.445 with remains of armour from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorso-lateral (left side) view. **F**. Another specimen SMNH BP.469 (see also Fig. 43E) of the same species from the same locality, frontal view. **G**. *Poraspis siemiradzkii* (Zych, 1931), dorsal shield SMNH BP.467 (see also Fig. 43A) from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, frontal view. **H**. *Poraspis* sp., imprint of anterior end of the dorsal shield SMNH BP.391 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, dorsal view.

The dorsal shield covered the head-and-trunk part on the dorsal side from anterior margin to the base of scaly flexible abdomen-tail unit. The abdominal side was covered with the ventral shield that anteriorly joined the lateral and oral or post-oral plates. The branchial plates were inserted in-between the dorsal and ventral shields from the orbital area, in *Poraspis* joining the suborbital and lateral plates, to the base of the abdomen-tail. Occasionally, in particular in *Ctenaspis*, the branchial plates were incorporated in the dorsal shield and the latter directly contacted the ventral plate.

According to Novitskaya (1983), among the representatives of the order, the smallest mature shields characterise *Anglaspis* (20–25 mm) and the largest *Allocryptaspis utahensis* (110 mm). Among the Podolian cyathaspidids, length of the dorsal shield of *Poraspis* ranges (after material of SMNH collection) within the limit of 45–59 mm. In *Irregulareaspis stensioei*, it is 26–31 mm, in *Ctenaspis kiaeri* it equals 21–30 mm, and in *Seretaspis zychi* (according to Stensiö 1958) the length of the dorsal shield amounts about 30 mm.

Margins of the dorsal shield curve downward except for its posterior region and the orbital and branchial notches (Figs 13A, C, 38D, 39E, 43A, E, 45F, 46A, E, 47D, E). The anterior margin of the dorsal shield (frontal zone, see below) is usually ornamented with dentine ridges parallel to the shield margin (*Irregulareaspis*, *Poraspis*; Figs 10A, E–G, 11E, F, 13C), but in one case in *Poraspis* the anterior margin has an unusual appearance (Fig. 13A) as if it would be a strip of overlapping by another plate of carapace. A narrow maxillary rim can be distinguished along the anterior margin from the ventral side bearing also parallel dentine ridges (*Poraspis*; Figs 12A, 13F, 42C). Probably, this strip corresponds to the area of overlap with the oral and lateral plates. On the lateral sides of the dorsal shield, the preorbital processes are significantly curved downward (gently and gradually in *Poraspis* and *Irregulareaspis*: Figs 13A, C, 38D, 43E); strongly and abruptly in *Ctenaspis*: Figs 46A, E, 47D, E), and delimit the orbital notches on their anterior side. The orbits are bordered from below by the suborbital plate, and behind by the bent downward lateral margins of the dorsal shield.

In *Ctenaspis*, in which the branchial plates are unified with the dorsal one, they extend to the ventral side. Lateral margins of the dorsal armour viewed from above are arched in *Ctenaspis*, and the branchial openings are marked by notches behind (Figs 46A, 47B). In *Poraspis*, lateral margins of the dorsal shield between orbital and branchial notches are bowed, and behind the branchial opening they form postbranchial blades that in the Podolian species occupy from 1/3 to 2/5 the length of the armour (Fig. 43E). Viewed from above, the anterior margin of the dorsal shield of the Podolian cyathaspidids is more or less widely rounded and the locations of the orbital, and in some *Poraspis* also branchial, notches are visible (Figs 10D, 11B, 43A, 44B).

The armour usually reaches its maximum width between the orbits and the branchial openings, where its margins are most convex. The posterior margin of the dorsal shield forms a medial ledge, which can take a more or less widely angular shape or a lobe (Figs 10D, 11A, B, G, 13D, E, 41A, D, E, 42B, C, 43B, 44A, B). No dorsal spine or crest is present. The posterior margin of the shield of *Ctenaspis* forms three clearly distinguishable regions. The lateral ones can be transverse or inclined, and they may correspond to the branchial openings. Between them, there is a small medial ledge with obtuse (120°) angular tip, ornamented with longitudinal ridges that in shape resemble a reverse herringbone pattern (Figs 46A, B, D, 47B, C). Borders between the medial ledge and the lateral areas in *Ctenaspis* run at some distance deep into the dorsal shield, probably delimiting the branchial channel. Possibly, the lateral prebranchial areas delimited in this way are homologues of the posterior part of the lateral border of the amphiaspidids.

The dorsal shield of many cyathaspidids is subdivided into epitega (Novitskaya 1983) but they are lacking in the Podolian species, except for *Seretaspis zychi* (Novitskaya 1986).

The ventral shield usually is more convex than the dorsal one, which seems to correspond to its function. Namely, on the forward movement of the animal, the difference in convexity of ventral and dorsal sides resulted in creation of an upwardly directed force, which lifted the body above the bottom (Aleev 1963; Novitskaya 2000). Among the Podolian cyathaspidids, the ventral plates are known only in *Poraspis* and *Irregulareaspis* (Figs 9C, 12C–F, 38F, 39C, D, F, G, 42D, 45A, B–E). The anterior margin of the ventral shield in these genera is more or less straight and the anterolateral corners are rounded. The lateral margins are usually also straight and, as a rule, to some extent diverge backward, although not in all species, in such a manner that the maximum width of the ventral shield is at the level of the posterolateral corners. The lateral margins of the shield are turned up slightly anteriorly and more apparently near the posterolateral corners, the tips of which are rounded. The posterior margin of the shield has a small medial ledge in *Poraspis* (Figs 12E, 42D, 45A–E); in *Irregulareaspis* the ledge is angular (Fig. 39D, G). No overlap with the branchial plate is

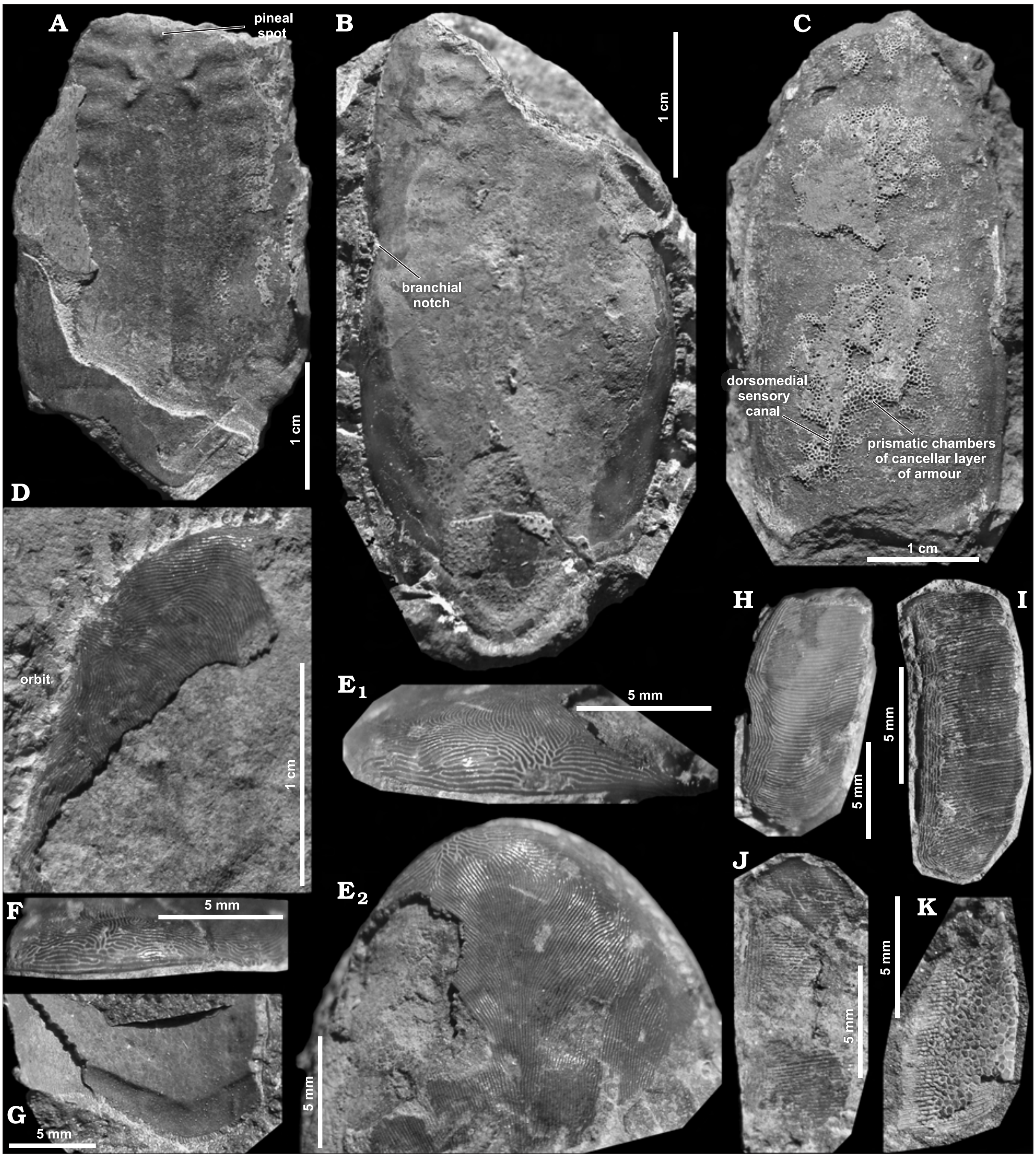

Fig. 11. Carapace morphology of the poraspidid *Poraspis*. **A**. Fragmentary mould of the dorsal shield SMNH BP.430 with remains of armour from Zalishchyky, upper part of Ivanie Member of the Tyver Formation, dorsal view. **B**. Mould of dorsal shield SMNH BP.371 lacking anterior part in dorsal view from Zalishchyky, upper part of Ivanie Member of the Tyver Formation. **C**. Mould of dorsal shield SMNH BP.403 with remains of armour from Ustechko, left bank of the Dniester River, uppermost part of Ustechko Member of the Dniester Formation, dorsal view. **D**. Fragment of dorsal shield SMNH BP.562/2 from around left orbit from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **E**. Anterior part of dorsal shield SMNH BP.417 from the same locality, antero-lateral (left side) and dorsal views. **F**. Partial dorsal shield SMNH BP.439/1, same locality, frontal view. **G**. Posterior margin of dorsal shield SMNH BP.424/2, same locality, inside view. **H**. Lateral scale of the trunk SMNH BP.369 from the same locality. **I**. Lateral scale SMNH BP.919/3, same locality. **J**. Fragmentary lateral scale SMNH BP.1188/2, same locality. **K**. Scale SMNH BP.426/2 from Ustechko, left bank of Dniester River, uppermost part of Ustechko beds, inside view.

distinguishable in the studied material. No differentiation in ornamentation on the ventral shields of the Podolian cyathaspidids was observed.

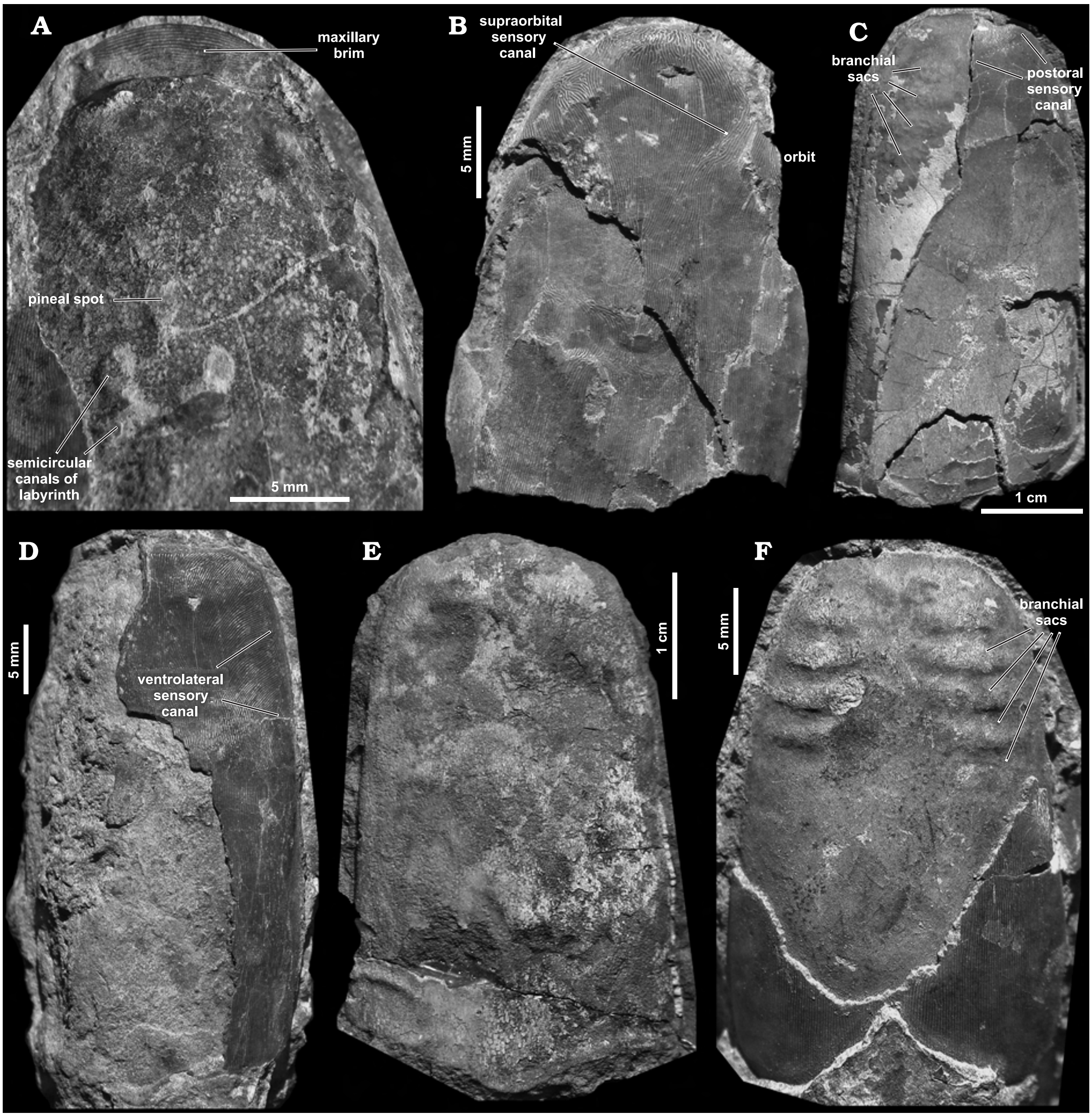

Fig. 12. Carapace morphology of the poraspidid *Poraspis*. **A**. Anterior part of dorsal shield SMNH BP.1152 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, inside view. **B**. Fragmentary anterior parts of two dorsal shields one over another SMNH BP.914/2 from the same locality, dorsal view. **C**. Distorted mould of ventral shield SMNH BP.376 with remains of armour from Zalishchyky, upper part of Ivanie Member of the Tyver Formation, dorsal view. **D**. Partial ventral shield SMNH BP.486 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **E**. Mould of ventral shield SMNH BP.408 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, dorsal view. **F**. Mould of ventral shield SMNH BP.496/1 with remains of armour from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view.

No other plates of cyathaspidid armour are represented in the studied material. Few finds of such plates are known for all the Cyathaspidiformes [Novitskaya 1983; see e.g., Blieck and Heintz (1983: figs 4B, C and 9A, B) for this part of the carapace of *Irregulareaspis hoeli* (Kiaer, 1932) and *Poraspis polaris* Kiaer, 1930]. According to them, it is known that suborbital plates of very small size delimited the orbital openings from below, being in contact with the preorbital processes of the dorsal shield, lateral plate, anterior end of branchial plate and the lower margin of the dorsal shield behind the orbit. Plates of the oral region seem to represent different sets, probably depending on the degree of mobility of elements of the oral area specialised in gathering food. The oral opening was closed by oral plates (Novitskaya 1983) that probably contacted the maxillary border of the anterior margin of the dorsal shield. Laterally, they adjoined to the lateral plates, and posteriorly to the ventral shield. Lateral plates (one from each side) adjoined the preorbital processes of the

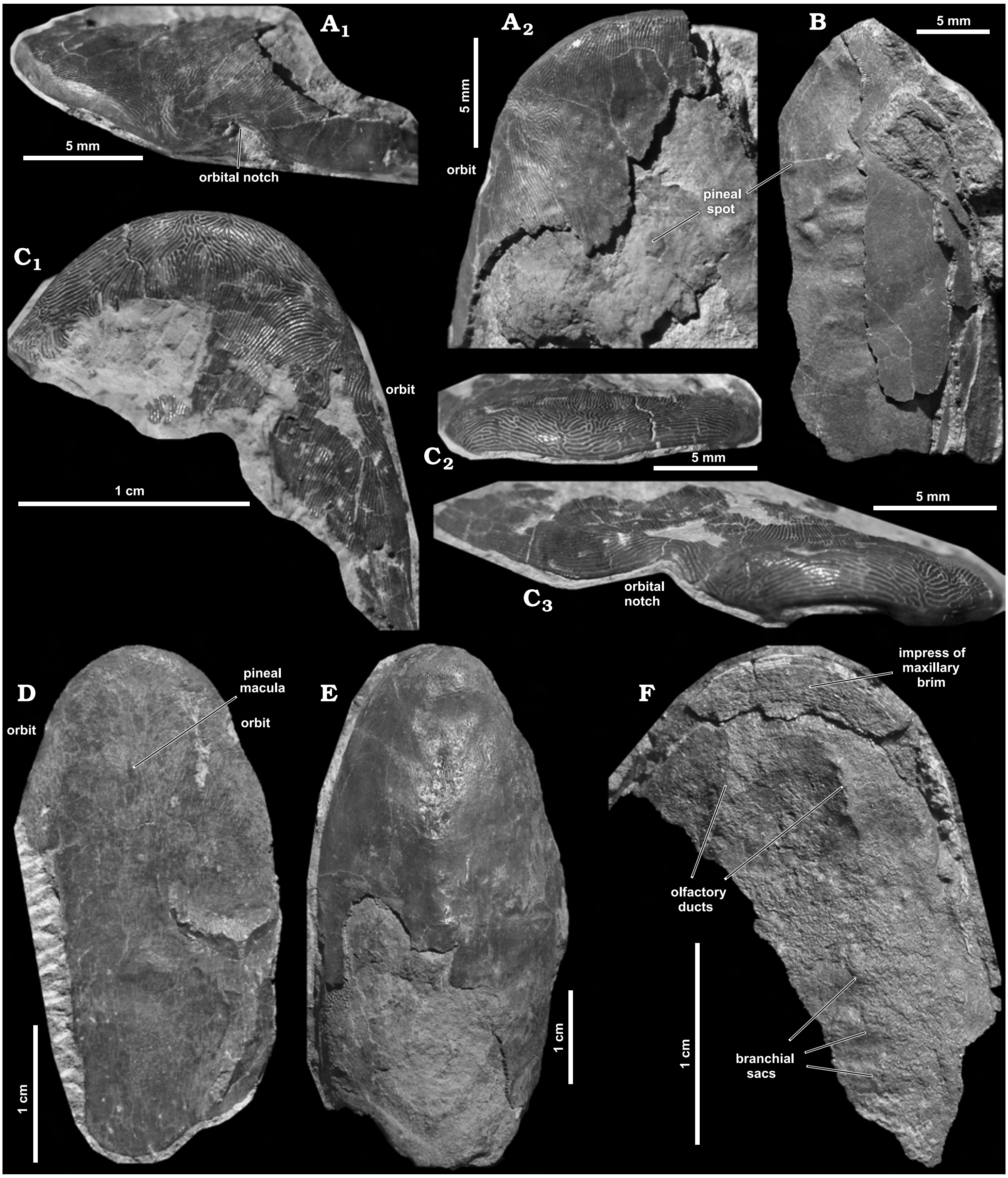

Fig. 13. Carapace morphology of the poraspidid *Poraspis*. **A**. *Poraspis* sp., anterior and left part of dorsal shield SMNH BP.418 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorso-lateral (left side) and dorsal view. **B**. Partial mould of anterior part of dorsal shield SMNH BP.452/1 with remains of armour from the same locality in dorsal view. **C**. *Poraspis* sp., anterior part of dorsal shield SMNH BP.919/2, same locality, dorsal, frontal, and antero-lateral (right side) views. **D**. Partial dorsal shield SMNH BP.434, same locality, dorsal view. **E**. Partial dorsal shield and its mould SMNH BP.466, same locality, dorsal view. **F**. *Poraspis*? *sturi* (Alth, 1874), partial mould of anterior part of the dorsal shield SMNH BP.399 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member of the Dniester Formation, dorsal view.

dorsal shield, the oral plates, the anterolateral corners of ventral shield, the anterior margin of the branchial plate, and the lower margin of the suborbital plate (Novitskaya 1983). Narrow and elongated branchial plates located on each side of the armour between the shields were anteriorly adjoined to the suborbital and lateral plates, and behind they faced the abdomen-tail.

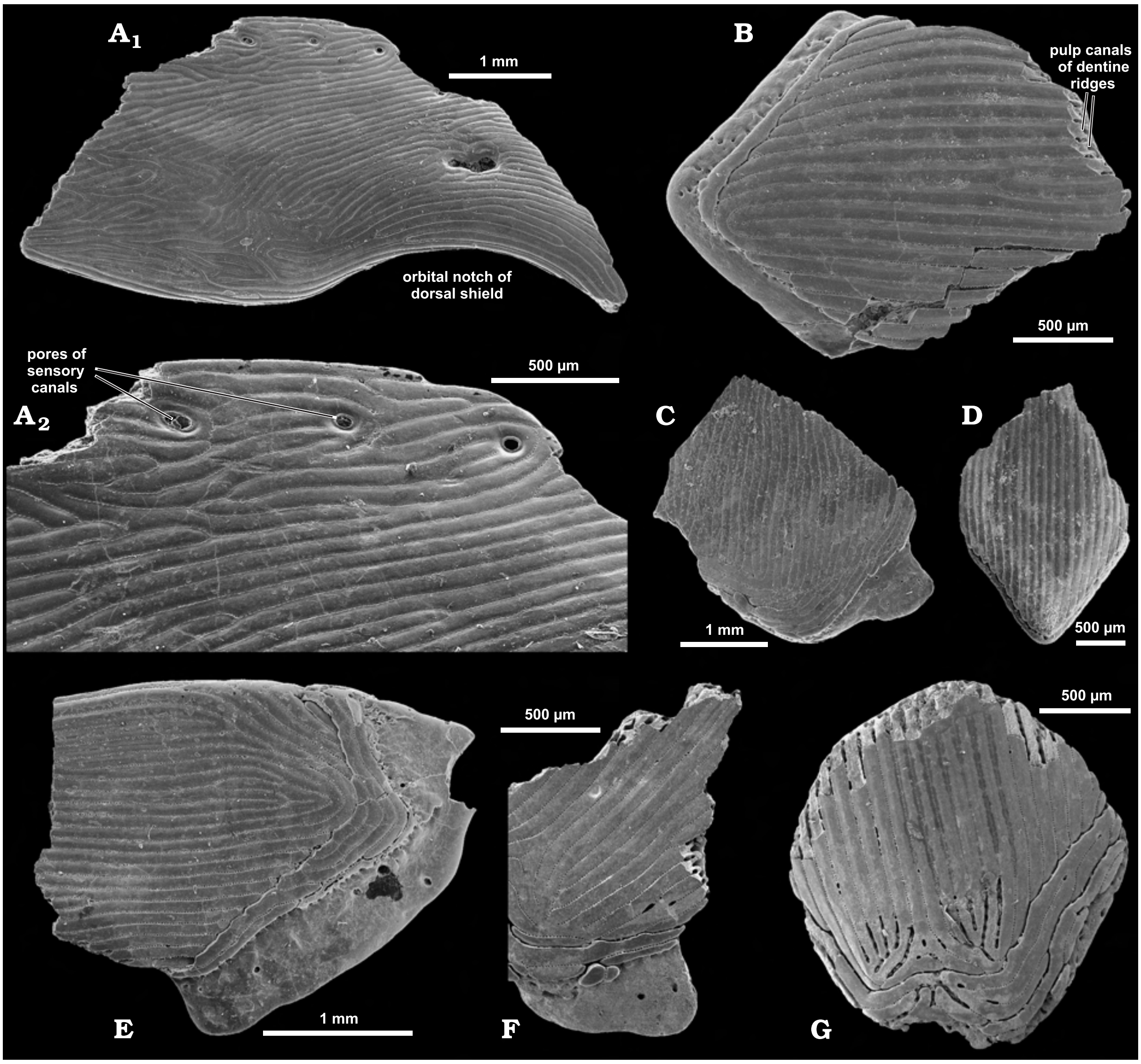

Fig. 14. Micromorphology of the irregularaeaspid *Irregulareaspis*. **A**. Piece of armour SMNH BP.1548/4 (see also Fig. 16A) from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member of the Tyver Formation, also enlarged. **B**. Scale SMNH BP.1543/8 (see also Fig. 16E) from outcrop 11 (Fig. 3B) on left bank of Dniester River, upper part of Chortkiv Member of the Tyver Formation. **C**. Lateral scale SMNH BP.1543/1 from the same locality. **D**. Scale SMNH BP.1547/14 from Gorodok, left bank of Dniester River, Chortkiv Member of the Tyver Formation. **E**. Fragmentary scale SMNH BP.1544/4 from Zalishchyky. **F**. Fragmentary scale SMNH BP.1550/13 from outcrop 11. **G**. Scale SMNH BP.1550/10, same locality.

The abdomen-tail part of the body was covered with scales (Figs 11K, 14E–G, 15B, D, E) of morphologies dependent on the location. As the only mobile part of the body, it served as the locomotory organ of the cyathaspidids. The trunk armour consisted of rings of scales, generally formed by dorsal median, ventral median, and pairs of dorsolateral and ventrolateral elongated scales (Janvier 1996: chevron-shaped flange scales) (Fig. 11H–J). The caudal fin or, at least, its lobes were covered by smaller lozenge-shaped scales (Figs 14B–D, 15C). Hypocercal tails were believed to be characteristic of irregulareaspidid cyathaspidiform and most heterostracan agnathans (Pellèrin and Wilson 1995; Helfman *et al.* 2009) but Pellèrin and Wilson (1995) have shown that heterostracan tails may be nearly symmetrical and forked, with lobes supporting a fin web.

Structure of dermal skeleton of the cyathaspidiforms. — The external (sculptured) surface of the armour of the Cyathaspidiformes (as well as Pteraspidiformes) was made of dentine that corresponds to the superficial layer of dermal bone. Underneath, the reticular, cancellar, and basal layers formed by aspidin were present (Fig. 15A). In *Ctenaspis*, as an exception, the dentine is absent and the sculpture consists of aspidin tubercles (Figs 46A, B, 47C). The unique elements of the armour ornamentation of the Podolian cya-

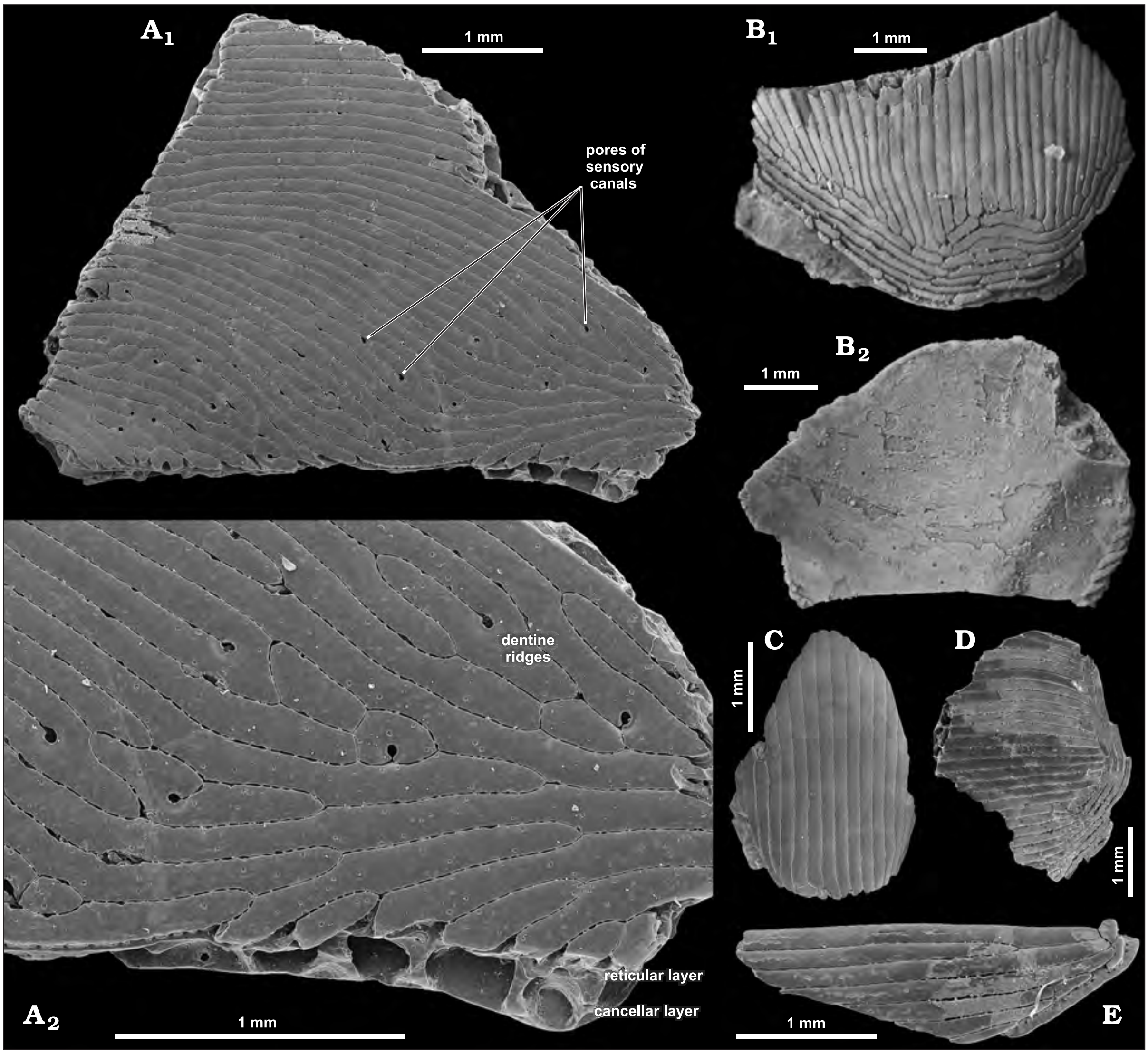

Fig. 15. Micromorphology of the poraspidid *Poraspis*. **A**. Piece of armour SMNH BP.1541/5 (see also Fig. 16B) from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member of the Tyver Formation, also enlarged. **B**. Fragmentary scale SMNH BP.1561/1 from Zalishchyky, upper part of Ivanie Member of the Tyver Formation, from outside and inside. **C**. Scale SMNH BP.1541/6 from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member of the Tyver Formation. **D**. Fragmentary scale SMNH BP.1547/7 from Gorodok, left bank of Dniester River, Chortkiv Member of the Tyver Formation. **E**. Fragmentary scale SMNH BP.1547/2 (see also Fig. 16D) from the same locality.

thaspidids (except for *Ctenaspis*) are dentine ridges separated by aspidin grooves (Fig. 15A, E). They were laid on a thin reticular layer containing a system of canals. Round or elongated openings were arranged in a regular interval along the grooves in *Irregulareaspis*. They are formed by juts of adjoining dentine ridges (Figs 14B, 16E). Probably, they connected the grooves with pulp canals. The arrangement and size of the openings vary in scales of *Irregulareaspis*; they might be about 4–8 µm in diameter and 8–12 µm apart (Fig. 16E). In the orbital region of the dorsal shield of *Irregulareaspis*, these values are 4.5–6 µm and 7.5–12 µm, respectively (Figs 14A, 16A). Such regular perforations along borders of the dentine ridges have not be observed on the armour surface of *Poraspis* (Fig. 16B–D). The cancellar layer located below consists of large (as a rule across all the layer thickness) prismatic chambers (Figs 11C, K, 38A, 42C, D). The lowermost thin basal layer, as well as the reticular one, is also pierced by the system of canals (Novitskaya 1983, 2004). The general thickness of the armour in *Irregulareaspis* is about 0.2 mm, in *Ctenaspis* about 0.3 mm, and in *Poraspis* it is 0.25–0.4 mm (thickening from the center of the dorsal shield towards its lateral margin). The dentine ridges are slightly convex (*Poraspis*, *Irregulareaspis*) and of different widths: 6–9 crests per millimeter in *Poraspis*, 8–9 in *Seretaspis* (Novitskaya 1986), 10–13 in *Irregulareaspis*. Width of the ridges may vary slightly; along the shield margins they are usually narrower, and at the posterior margin of the shield they are wider than in the central part of the armour. Several zones with different dentine ridge arrangements can be distinguished in the dorsal shield of *Poraspis*. At the anterior margin of the shield, there is a frontal zone of dentine ridges parallel to the shield margin. A narrow transitional zone is developed behind the frontal one, characterised by chaotically arranged dentine ridges, usually wider than in other shield areas (Figs 10C, F, H, 13C, 43A). Sometimes, the transitional zone is lacking (Figs 11D, 13A). An interorbital zone (between orbits, pineal spot and the transitional zone) follows backward, with ridges fan-shaped or parallel to the body axis (Figs 9A, B, 10A, 11E, 43A). Over the rest of the dorsal shield and the whole ventral one, dentine ridges are mostly parallel to the body axis (Figs 12B, 13C, 43A, B, 45A–E). In *Irregulareaspis*, they are chaotic in distribution (Figs 14A, 38C, E, 39A, D), but in the posterior part of the shields they are parallel to the body axis. All the Podolian species have dentine ridges near the lateral margins of the shield parallel to the margins. On the pineal spot, the armour is thinner, and its lamella is built of dentine in *Irregulareaspis* and *Poraspis* and of aspidin in *Ctenaspis* (Figs 10C, 43C, 46B).

Some plates in *Poraspis* bear traces of biotic invasion. It is not clear whether these marks were made during the animal's life or *post mortem*. These are fossulae in dentine ridges with uneven surface, different depth, and, in general, irregular rounded shape. In some cases, they are singular, roughly rounded, about 8–20 µm in diameter (Fig. 16C) or sparsely distributed (Fig. 16B). Only on one scale (Fig. 16D), they are abundant, of chaotic shape and about 2–42 µm in diameter. Their origin remains enigmatic. They are too small to represent drilling of a metazoan predator (Brett and Walker 2002) or parasite (Lukševičs *et al.* 2009). Remarkably, no other agnathan in the SMNH collection shows such traces.

Lateral line system of the cyathaspidiforms. — The suggestion by Novitskaya (2006) that well developed sensory line system compensated poor eyesight in the agnathans applies well to the cyathaspids. Pores of the sensory lateral line system over the surface of the armour of *Poraspis*, *Irregulareaspis*, and *Seretaspis* are well visible. In *Poraspis*, they are connected with the interridge grooves by a thin canal (Figs 15A, 16B, C), but in *Irregulareaspis* there are no such connections (Figs 14A, 16A). Their distribution reflects the course of canals. Outlets of sensory pores in *Poraspis* are usually accompanied by local disturbances in the distribution of dentine ridges (Figs 12B, 15A).

The distribution of lateral line canals on the dorsal shield of the Podolian cyathaspidids strictly corresponds to the scheme inherent for representatives of the order (Fig. 8A, B): along the body axis there is a pair of dorsomedial and a pair of dorsolateral canals, which were united by four dorsomedial and dorsolateral transverse commissures (Figs 10C, 38A, 42C, 46C). The dorsolateral canals (on the anterior part of the shield) pass into the infraorbital ones, which run behind the orbits (Figs 9A, 12B). The dorsomedial canals approach the supraorbital canals, which often meet behind the pineal macula. Such scheme is characteristic in particular for *Poraspis* and *Ctenaspis*. In *Irregulareaspis*, it is complicated by the appearance of additional ramifications, which together form a dense network of canals (Fig. 38A). And, if in *Poraspis* it is possible to track the course of sensory canals by exits of pores on the surface of skeleton, in *Irregulareaspis* it is prevented by their high number and dense distribution over the carapace.

The sensory lateral line system on the ventral shield of the cyathaspidids from the SMNH collection is known only for *Poraspis* (Figs 12C, D, 45A, C–E). It consists of continuous ventrolateral canals passing at a small distance from the lateral margins of the shield. A V-shaped pair of postoral canals departs from the anterolateral corners of the shield obliquely in posteromedial direction. In a similar mode, a number of isolated V-shaped ventromedial canals occur behind them along the body axis, backward to posterior end of the shield. Lateral ventral transverse commissures pass medially from ventrolateral canals as short separate units. The ventral shield of *Irregulareaspis* contains a dense network of canals. Outlets of lateral line pores on the ventral shields of *Poraspis* and *Irregulareaspis* (Fig. 39C, G) are similar to those on the dorsal shields.

Internal anatomy of the cyathaspidiforms. — Imprints of internal anatomical structures are rather well visible on moulds of shields and on their inner surface in the cyathaspidids (Figs 9B, 10A, B, 11A, 12F, 13B, 38A, 41E, 44A, B–F, 47A, B). It is explained (Novitskaya 1983) by a small thickness of the cartilaginous visceral skeleton which was located immediately under the dermal skeleton, adjusting its internal surface to the internal organs. As a result, the outline of the brain and visceral organs is rather accurately represented on the inner surface of the dorsal shield. The pineal organ is believed to have been light sensitive in larvae without armour by analogy with the lamprey; but when covered by the dermal skeleton its function possibly changed

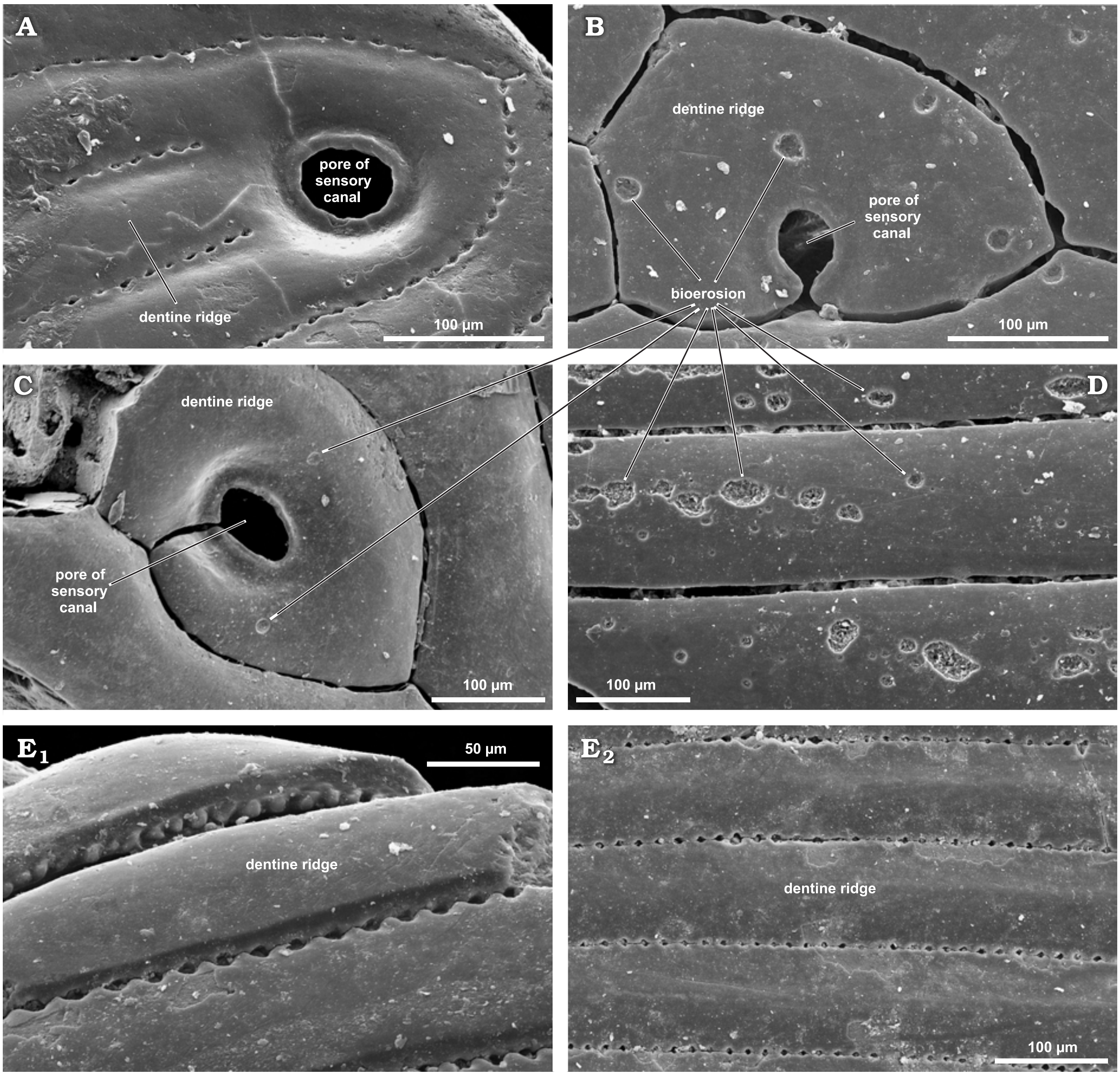

Fig. 16. Micromorphology of mostly unidentified poraspids and irregulareaspids. **A**. Armour around pore of sensory canal in specimen SMNH BP.1548/4 (see also Fig. 14A) from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member of the Tyver Formation. **B**. Armour around pore of sensory canal in specimen SMNH BP.1541/5 (see also Fig. 15A) from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member of the Tyver Formation. **C**. *Poraspis* sp., armour around pore of sensory canal in specimen SMNH BP.1550/33 from outcrop 11 (Fig. 3B), left bank of Dniester River, upper part of Chortkiv Member of the Tyver Formation. **D**. Scale SMNH BP.1547/2 (see also Fig. 15E) from Gorodok, left bank of Dniester River, Chortkiv Member of the Tyver Formation, portion enlarged. **E**. Scale 1543/8 (see also Fig. 14B), margin and central part enlarged.

(Novitskaya 2004). Often, some distance behind the pineal macula on moulds of the dorsal shield, imprints of the anterior and posterior pairs of the vertical semicircular canals of the labyrinth are represented (Figs 9D, 10B, 11A, 12A, 13B, 38A, B, 41E, 44A, D, E, 46A, 47A). On each side of them, it is often possible to see traces of seven pairs of branchial pouches (sacs) (Figs 9B, 10A, 11B, 13B, 41A, E, 44D, E, 47B). The semicircular canals were located approximately at the level of the pineal macula (and the second pair of branchial pouches) and extended for two pairs of branchial arches, to between the third and fourth branchial pouch. Laterally to the branchial sacs, arch-shaped casts are sometimes visible (Figs 38D, 43C, 44D–F), interpreted as traces of individual efferent ducts of the branchial pouches (Novitskaya 1983), which then joined the extrabranchial duct leading to a branchial opening.

Traces of the mesencephalon, myelencephalon and fossa rhomboidalis are less apparent (Figs 11A, 44C, D). The exact form of the middle brain (mesencephalon) is known only in *Poraspis pompeckji* (Novitskaya

1983). Traces of nasal capsules and olfactory ducts are discernible on some dorsal shield moulds of *Poraspis* sp. from the SMNH collection (Figs 13F, 44B, E, 47A).

Casts of four pairs of branchial pouches are discernible in the anterior part of moulds of the ventral shield of *Poraspis* (Figs 9C, 12C, F, 45A). In front of them, a trace of a V-shaped structure of unknown identity is well visible along the body axis (Figs 9C, 12F).

Data on the internal anatomy are restricted to *Poraspis*. In *Ctenaspis*, these structures are poorly represented in the fossil material and in *Irregulareaspis* only the semicircular canals can be trace in the studied material.

Ontogeny of the cyathaspidiform carapace. — It was believed that the carapace in the majority of cyathaspidids mineralised after the growth of the animals was terminated (Obruchev 1945; Novitskaya 1977, 1983). One of the main arguments in favour of this interpretation is the difficulty with augmentation of the shield without disturbing the lateral line system, canals of which were enclosed within the armour. However, unlike the pteraspidids, in which the dentine ridges of the skeleton coincide with growth increments of particular plates of the carapace enabling identification of their primordial regions and directions of growth, in the majority of cyathaspidids, the vector of ossification of the dermal skeleton remains unknown. Novitskaya (2004) hypothesized that cyathaspids with longitudinal dentine ridges on the dorsal and ventral shields had no armour as juveniles. Their carapace, composed of layers of thin dentine (on ridges) and aspidine (in grooves between the ridges), apparently mineralised simultaneously over all its area after the animal reached its final size. During subsequent growth, the layers thickened gradually. This may refer to the Podolian poraspids and irregulareaspids.

However, Greeniaus and Wilson (2003) showed that the cyathaspids *Dinaspidella elizabethae* Blieck *et* Heintz, 1983 and *Nahanniaspis mackenziei* Dineley *et* Loeffler, 1976 from the Northwest Territories, Canada, began bone formation before being 60% or 70% of adult size, perhaps even earlier. The dorsal and ventral shields in these species, as well as the trunk median scales, developed as a primordium located in the posterior region of the shield or scale. Posterior margins of shields and scales completed their growth first, and all parts of the carapace show posterior-to-anterior growth polarity. Juvenile specimens of both species have only the superficial and reticular layers of dermal bone developed.

CORVASPIDID HETEROSTRACANS

Of the two corvaspidid genera known (Blieck and Karatajūtė-Talimaa 2001), in Podolia, only remains of *Corvaspis kingi* Woodward, 1934 have been found.

The corvaspidid carapace may have consisted of only (?) the dorsal and ventral shields or an assemblage of separate plates: unpaired rostral, pineal, median dorsal and median ventral plates; paired orbital, dorsolateral, and branchial plates; possibly also oral, postoral and/or orolateral platelets occurred (Blieck and Karatajūtė-Talimaa 2001). The abdomen-tail was, as in other heterostracans, covered with rhombic scales (Fig. 17D, F, I). A distinctive feature of the corvaspidid dermal skeleton is that the carapace plates did not

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Fig. 17. Micromorphology of armor of the corvaspidid *Corvaspis*. **A**. *Corvaspis kingi* Woodward, 1934, piece of armour (one and part of a tesseriform units) SMNH BP.1560 from outcrop 8 (Fig. 3B), right bank of Dniester River, lower to middle part of Ivanie Member of the Tyver Formation, dorsal view. **B**. *Corvaspis* sp., partial tesseriform unit SMNH BP.1550/11 from outcrop 11 (Fig. 3B), left bank of Dniester River, upper part of Chortkiv Member of the Tyver Formation, dorsal view. **C**. *Corvaspis* sp., piece of armour SMNH BP.1038/2 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation. **D**. *Corvaspis kingi* Woodward, 1934, fragmentary tesseriform unit of scale SMNH BP.1543/7 from outcrop 11. **E**. Same species, fragment of tesseriform unit SMNH BP.1543/2 from the same locality and its two enlarged portions. **F**. Same species, fragmentary scale SMNH BP.1545/16 from outcrop 8. **G**. *Corvaspis* sp., tesseriform unit SMNH BP.1545/15 from outcrop 11. **H**. *Corvaspis kingi* Woodward, 1934, fragmentary tesseriform unit SMNH BP.1550/25 from outcrop 7 (Fig. 3B), right bank of Dniester River, uppermost part of Chortkiv Member of the Tyver Formation, dorso-lateral view. **I**. *Corvaspis* sp., scale SMNH BP.1544/10 from Gorodok, left bank of Dniester River, Chortkiv Member of the Tyver Formation. **J**. *Corvaspis* sp., tesseriform unit SMNH BP.1550/9 from outcrop 11. **K**. *Corvaspis* sp., fragmentary tesseriform unit SMNH BP.1550/15 from the same locality. **L**. *Corvaspis* sp., piece of tesseriform unit SMNH BP.1546/13, same locality. **M**. *Corvaspis kingi* Woodward, 1934, fragmentary tesseriform unit SMNH BP.1562/1, same locality, dorsal and inside views. **N**. Same species, fragmentary tesseriform unit SMNH BP.1562/3, dorsal and inside views. **O**. Same species, carapace SMNH BP.568 from outcrop east of Dobrivliany, lower part of Ivanie Member of the Tyver Formation, central part of median plate and its entire dorsal view.

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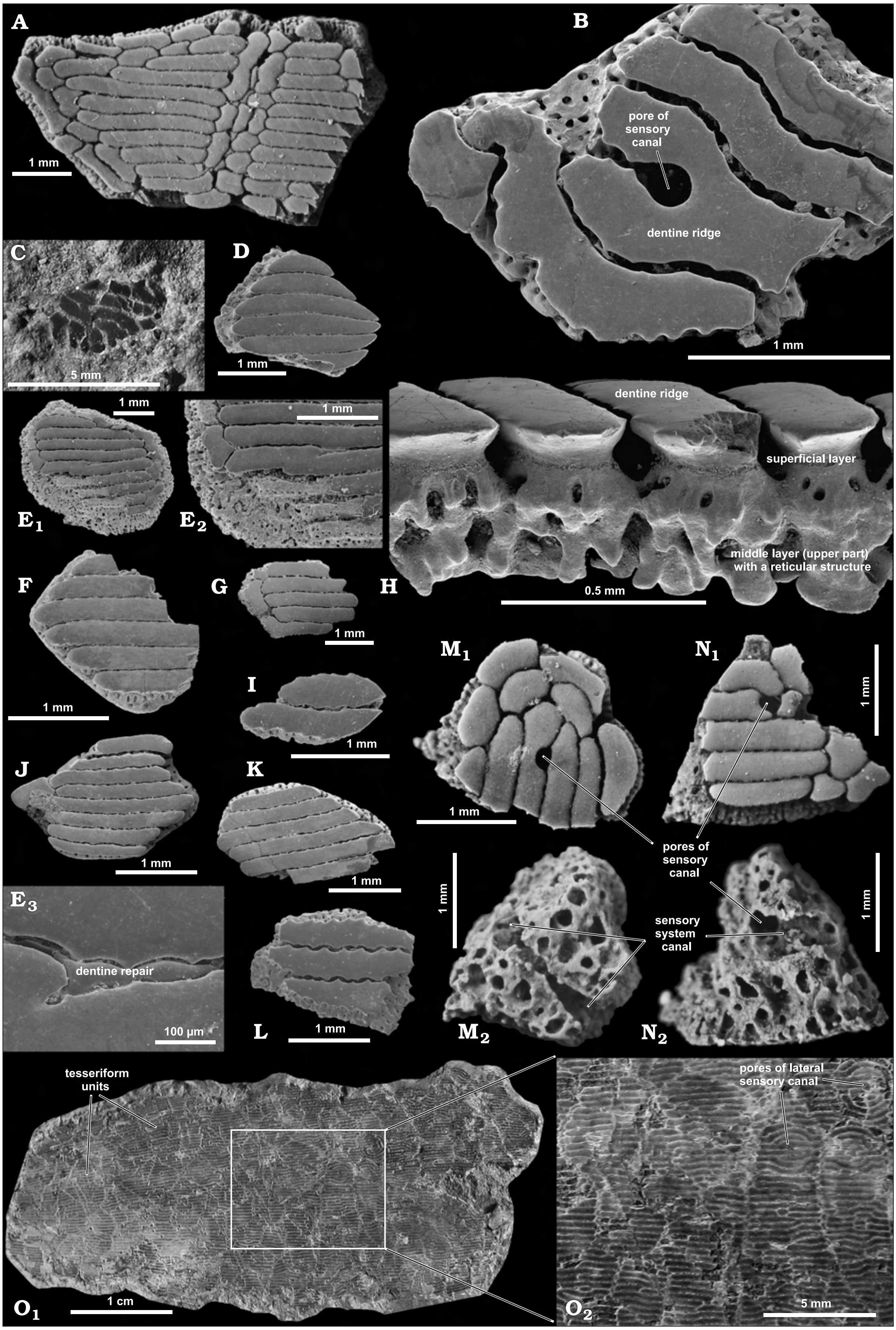
A
1 mm
B
pore of sensory canal
dentine ridge
1 mm
C
5 mm
D
1 mm
E1
1 mm
E2
1 mm
dentine ridge
superficial layer
middle layer (upper part) with a reticular structure
0.5 mm
F
1 mm
G
1 mm
H
I
1 mm
J
1 mm
K
1 mm
M1
1 mm
N1
1 mm
pores of sensory canal
E3
dentine repair
100 µm
L
1 mm
1 mm
sensory system canal
1 mm
M2
N2
tesseriform units
pores of lateral sensory canal
O1
1 cm
O2
5 mm

contact directly one with another, but have been surrounded by a sort of buffer zone of more or less rounded tubercles (tesserae). This probably was the cause of the median plate's contour being rather irregular, as Tarlo (1965) noticed (Fig. 17O). The general shape of the flat plate can be described as elongated-oval (not less than 60 mm in length and ~30 mm in width).

No other plates of *Corvaspis* carapace are represented in my material. In the literature (Tarlo 1965), also orbital and branchial plates are described. It has to be mentioned that, according to Tarlo (1965), the flatness of the large orbital plate indicates that the whole carapace was of such shape, and that the orbits were more likely located on the dorsal side than laterally. The branchial plates of *C. kingi* were approximately oval, extending backward and bent (Tarlo 1965). Tarlo (1965) proposed to consider one of the plates (BM(NH) P.42843) as a pineal, based on its similarity to such an element in *Drepanaspis*.

The sculpture of the median plate consists of flat synchronomorial tesseriform units (see Blieck and Karatajūtė-Talimaa 2001) or "tesserae" which have been divided by narrow grooves or arranged in 1–2 rows of tubercles (Fig. 17A, B, H, O). The units were formed by short (1–3 mm in length), wide (3 per 1 mm), flat, smooth dentine ridges which in general are parallel to the body axis. In the posterior part of the plate, ridges are placed cyclomorially on several tesseriform units (Fig. 17O), probably around pores of sensory canals (Fig. 17B), although in other cases (Fig. 17M, N) such arrangement is not observed. The interridge grooves were opened in the pores (Fig. 17B), but, in contrast with *Poraspis*, they can be more than one per pore (Fig. 17M, N). Tubercles represent very short (0.2–0.3 mm) dentine ridges that, except for their dimensions, do not differ from ridges on the units (Fig. 17A, M, N). Size of the units fluctuates from 2–2.5 mm to 3 mm; their shape is irregular.

The ornamentation of the carapace of *Corvaspis kingi* in the Tarlo's (1965) material is more variable than in the SMNH collection. It ranges from separate tesserae surrounded by groups of tubercles, through a stage when the tesserae are delimited by narrow grooves (as at BP.568 from the SMNH collection), then through another morphology with separate ridges of adjacent tesserae merging each other, and to a variant in which dentine ridges stretch almost continuously over considerable distance, sometimes along all the length of the plate. The orbits are surrounded by concentric ridges on the orbital plates, while margins of the plates themselves are in the zone of small rounded tubercles (Tarlo 1965). The orbit of *Corveolepis elgae* Blieck *et* Karatajūtė-Talimaa, 2001 is almost circular (Blieck and Karatajūtė-Talimaa 2001: fig. 4C).

The sensory lateral line system of *Corvaspis* is known incompletely. Tarlo (1965) mentioned four sensory pores on the orbital plate "each of them being surrounded by concentric dentine rings" (cf. Fig. 17O). Sensory pores on the branchial plate have the same rings (Tarlo 1965: p. 17). Dentine ridges surrounding the pores of sensory canals sometimes are sinuous (Fig. 17B, probably also Fig. 17O), but in other cases they are not (Fig. 17M, N). External pores of the right lateral dorsal line (sensory canal) have been recognised in the holotype of *Corveolepis elgae* (Blieck and Karatajūtė-Talimaa 2001: fig. 3B).

One of the fragmental tesserae from the SMNH collection demonstrates a possibly damaged dentine ridge repaired by dentine "intercalations" (Fig. 17E).

Internal anatomy of the corvaspidids remains practically unknown. The holotype of *Corveolepis elgae* shows an impression of the myelencephalon on the mould of a dorsal shield (Blieck and Karatajūtė-Talimaa 2001: fig. 4B).

PTERASPIDIFORM HETEROSTRACANS

The Podolian pteraspidids have a stable (apart from small plates of the oral region) set of carapace plates (Fig. 8E, F). The main ones are unpaired rostral, pineal, dorsal, and ventral plates and paired orbital, branchial, and cornual ones. The dorsal spine was attached to the posteromedian part of the dorsal plate. The anteriorly located mouth opening was delimited from its anterior side by the rostral plate, and posteriorly by a row of oral plates, which joined to the anterior margin of the ventral plate. In a more complex variant, postoral plates are situated between the oral and ventral ones.

Lengths of carapaces of Podolian pteraspidids range within wide limits: from 45–50 mm in mature individuals of *Zascinaspis bryanti* (Figs 24G, 70B) to 160 mm in *Larnovaspis mogielnensis* (cf. Fig. 60C), and 180 mm in *Althaspis longirostra* (Balabai 1959b: pl. 3, fig. 3).

The rostral plate occupied the anterior end of the carapace. Generally, its shape, as seen from the dorsal side, is triangular, with lateral sides of the plate meeting anteromedially up to the rounded tip (Figs 19E, 49A,

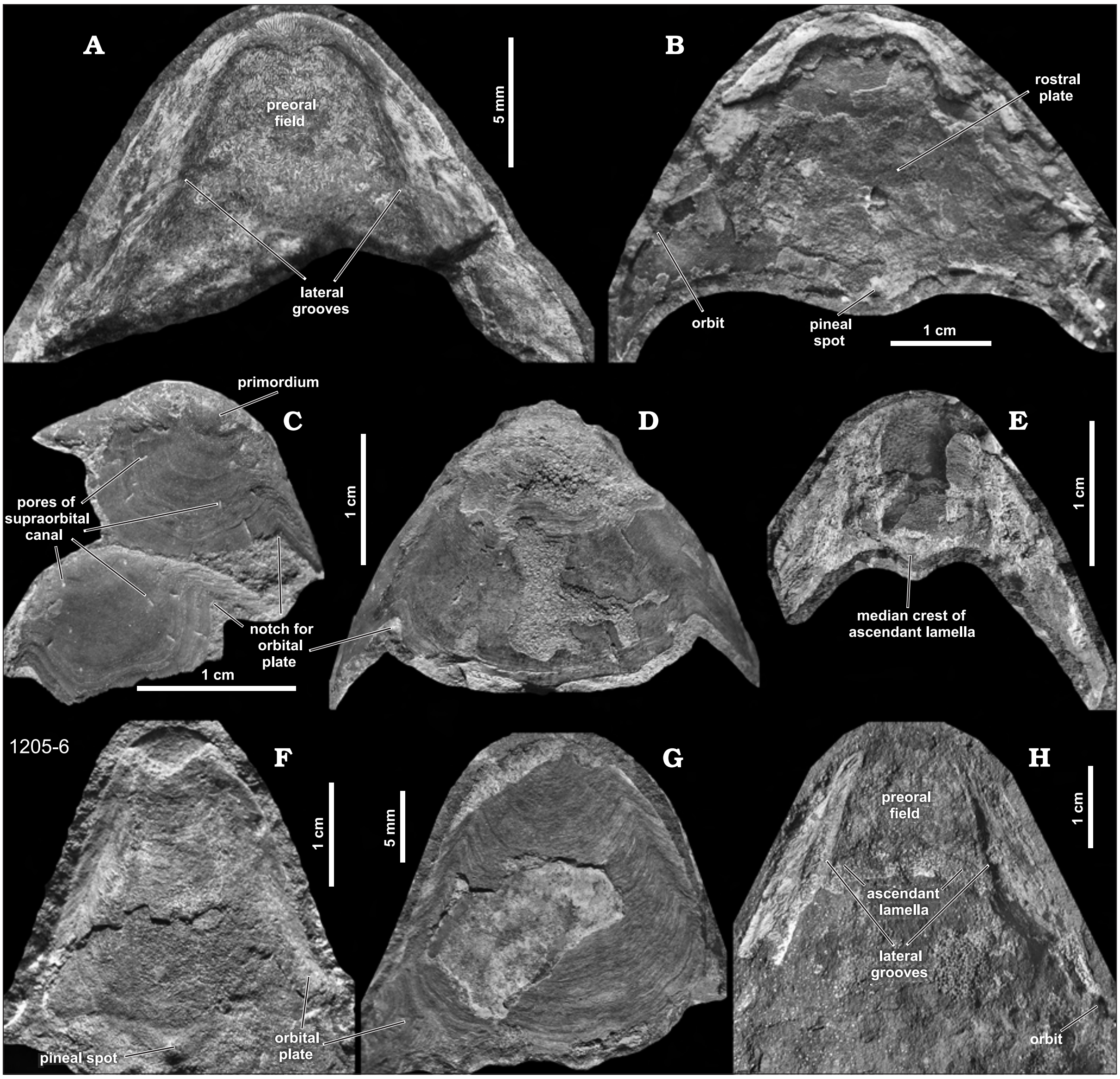

Fig. 18. Morphology of the pteraspidid heterostracans. **A**. Pteraspidoidei indet., partial rostral plate SMNH BP.330/2 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member of the Dniester Formation, ventral view. **B**. *Zascinaspis heintzi* (Brotzen, 1936), imprint of rostral plate and orbito-pineal belt SMNH BP.1468/1 from the same locality, dorsal view with parts of rostral plate in ventral view. **C**. Pteraspidoidei indet., rostral plates of juvenile individuals SMNH BP.515 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **D**. Pteraspidoidei indet., partial rostral plate SMNH BP.1205 from the same locality, dorsal view. **E**. Pteraspidoidei indet., fragments of rostral plate SMNH BP.201/2 (see also Fig. 101F) from Ustechko, ventral view. **F**. Pteraspidoidei indet., fragmentary rostral plate and mould of orbito-pineal belt SMNH BP.580 from the Mogylnytsia quarry (lower part), Ivanie Member, dorsal view. **G**. Pteraspidoidei indet., fragmentary rostral plate and left orbital plate SMNH BP.1239 from Ustechko, dorsal view. **H**. *Larnovaspis mogielnensis* Blieck, 1984, partial rostral plate SMNH BP.1095 (see also Fig. 61B) from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, ventral view.

51C, 59A). Lateral margins of the plate may be more or less straight, convex or concave (Figs 18C, D, F, G). The posterior margin of the rostral plate has a more complex course and only roughly can be described as the posterior side of the triangle. Usually, this margin has two symmetrically placed notches that housed anterior processes of the orbital plates (Figs 18C, D, 21D, 56E, 65C, 70E, F). The notches may be shallower or deeper (the extreme shapes are observed in *Alaeckaspis*? *depressa* and *Zascinaspis heintzi*), their tips are usually sharply angular, and on occasion they are gently rounded to a degree that the posterior margin of the rostral plate is sinusoidal in shape (*Zascinaspis*; Fig. 69G). In some pteraspidids (*Belgicaspis*, *Brachipteraspis, Althaspis*, and *Europrotaspis*), notches are invisible in dorsal view and this gives an impression that the rostral plate is held laterally by orbital ones (Figs 71A, B, D, 73A, B, 75E, 77A). The lack of material pre-

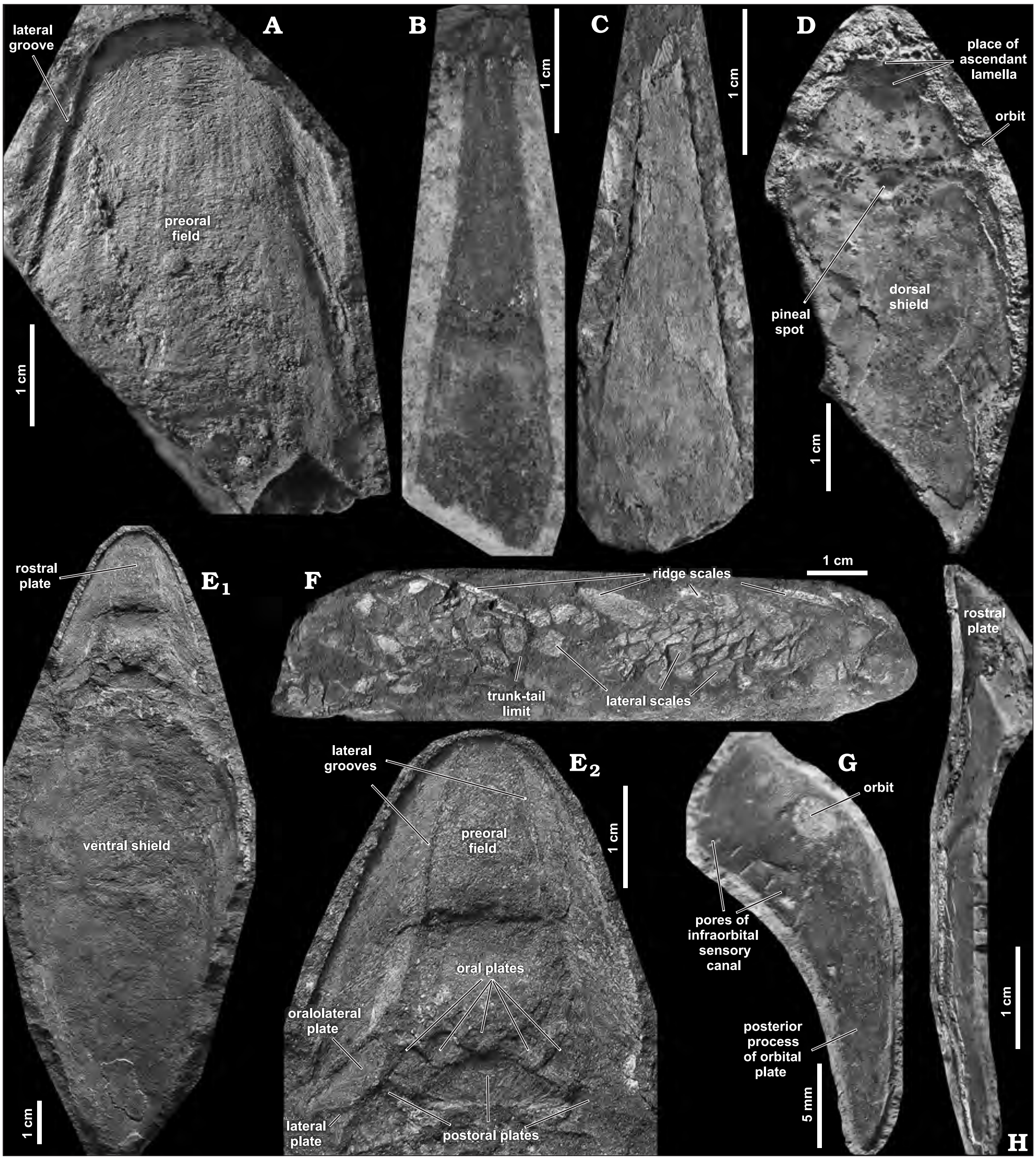

Fig. 19. Morphology of the pteraspidid heterostracans. **A**. *Palanasaspis chekhivensis* gen. et sp. n., holotype partial imprint of ventral surface of rostral plate SMNH BP.197 from Chekhiv, quarry, Strypa Member of the Dniester Formation. **B**. ?*Belgicaspis crouchi* (Lankester, 1868), partial rostral plate SMNH BP.1186 from the Verbivtsi quarry, Ivanie Member of the Tyver Formation, dorsal view. **C**. Same species, partial rostral plate SMNH BP.1232 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view. **D**. ?*Podolaspis* sp., partial carapace (rostral, pineal, orbital plates and part of dorsal shield) SMNH BP.266 from Zalishchyky, upper part of Ivanie Member, inside dorsal view. **E**. *Larnovaspis* sp., partial imprint of carapace ventral side SMNH BP.233 from Buriakivka, most probably Ustechko Member, and its oro-rostral region. **F**. Pteraspidoidei indet., trunk squamation and part of caudal fin SMNH BP.1449/2 probably from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, lateral (right side) view. **G**. Pteraspidoidei indet., right orbital plate of juvenile individual SMNH BP.565/1 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **H**. ?*Larnovaspis kneri* (Lankester, 1868), lateral (right side) section of partial carapace SMNH BP.1440 from outcrop east of Dobrivliany, lower part of Ivanie Member of the Tyver Formation.

served well enough does not allow a decision as to whether this is a real feature of morphology, or the edges of rostral plate are broken. The posterior margin of the plate between the notches in a simpler variant is more

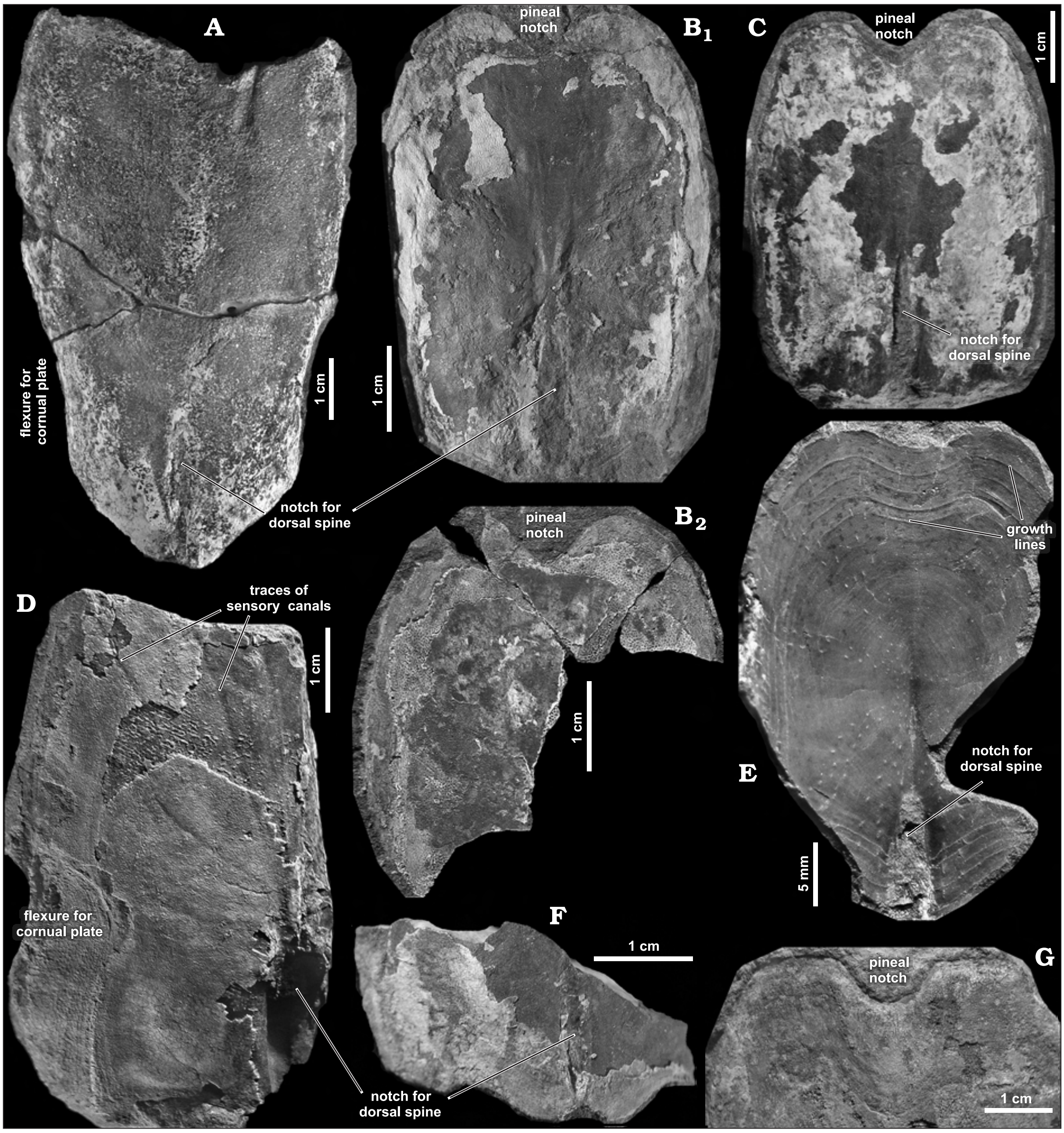

Fig. 20. Morphology of the pteraspidid heterostracans. **A**. *Larnovaspis* sp., mould of dorsal shield SMNH BP.1356 from Buriakivka, most probably Ustechko Member of the Dniester Formation, dorsal view. **B**. ?Podolaspididae indet., mould of dorsal shield SMNH BP.1097 from Ustechko, right bank of Dzhuryn River, 2nd ravine, talus on slope, probably Ustechko Member, and its partial imprint in dorsal view. **C**. Pteraspidoidei indet., mould of dorsal shield SMNH BP.319 from unknown locality in Podolia, probably Ustechko or Khmeleva Member of the Dniester Formation, dorsal view. **D**. Podolaspididae indet., partial dorsal shield SMNH BP.189 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member, dorso-lateral (left side) view. **E**. Pteraspidoidei indet., partial imprint of juvenile dorsal shield SMNH BP.916/5 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **F**. Pteraspidoidei indet., posterior part of dorsal shield mould SMNH BP.1249 from Ustechko, dorsal view. **G**. Pteraspidoidei indet., anterior part of dorsal shield SMNH BP.1305 from Ivanie-Zolote, left bank of Dniester River, lower part of Ustechko Member, dorsal view.

or less convex (*Larnovaspis*, *Brachipteraspis*, *Zascinaspis*, *Althaspis*, and *Europrotaspis*), sometimes almost straight (*Podolaspis*) or has something that looks like a notch for the pineal plate in the central part (*Parapteraspis*, some representatives of *Larnovaspis* and *Alaeckaspis*).

The shape of the rostral plate approaches an equilateral triangle with more or less obtuse anterior tip characteristic for the Podolaspididae, Protaspididae, and some representatives of the Larnovaspididae (Fig. 18D, F,

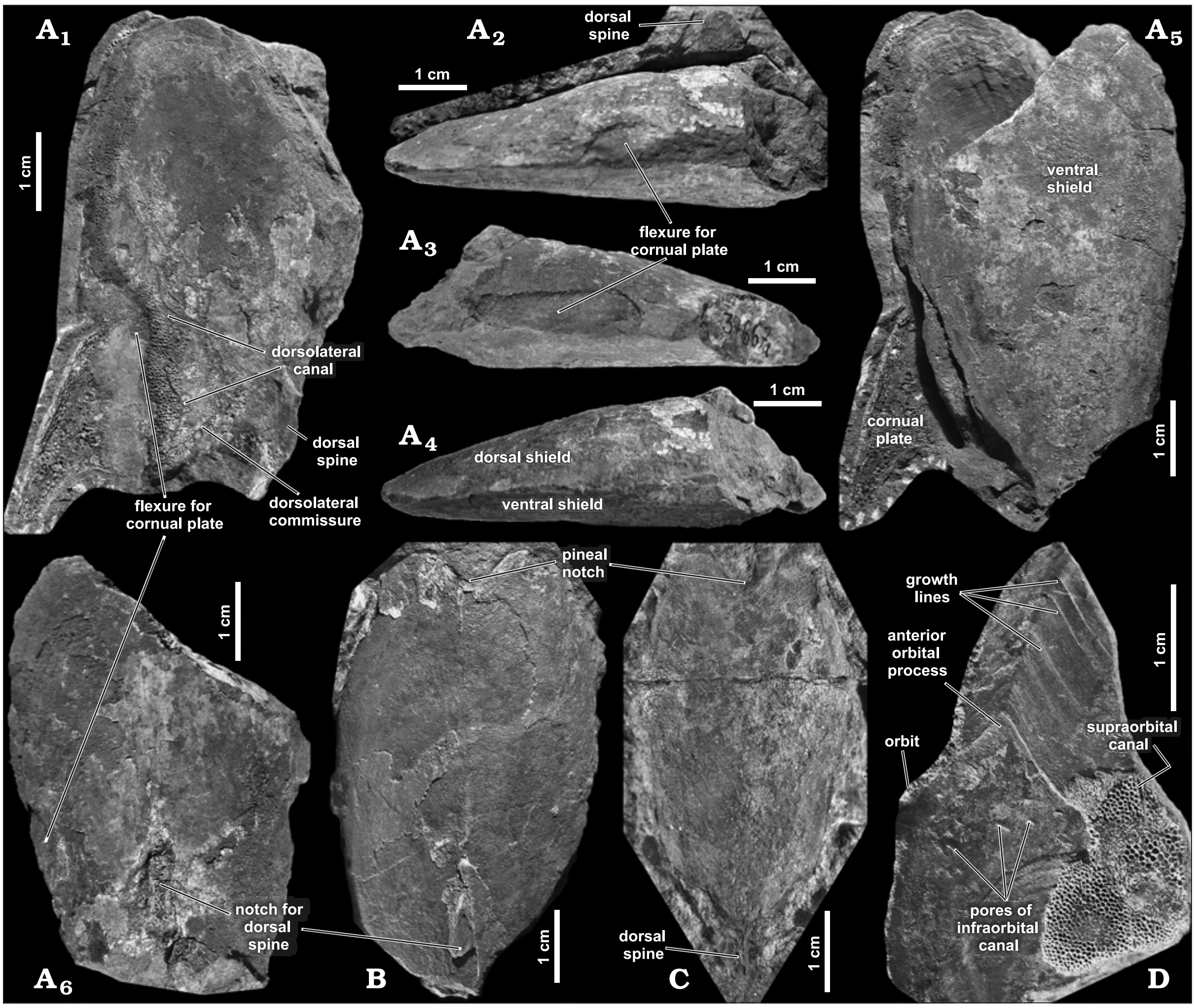

Fig. 21. Morphology of the pteraspidid heterostracans. **A**. Podolaspididae gen. indet., partial imprint of dorsal side carapace and mould of ventral shield SMNH BP.586 from Ustechko, left bank of Dzhuryn River, Ustechko Member of the Dniester Formation, dorsal, lateral (left and right side) views. **B**. "*Pteraspis*" *angustata* Alth, 1874, almost complete dorsal shield SMNH BP.181 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view. **C**. Same species, dorsal shield SMNH BP.184 from the same locality, dorsal view. **D**. ?*Larnovaspis* sp., part of carapace surrounding left orbit SMNH BP.193 from unknown locality in Podolia, probably Ustechko or Khmeleva Member, dorsal view.

H). Other larnovaspidids have either a narrow pivot-shaped rostral plate with protuberant base (*Belgicaspis*; Fig. 19B, C) or a very wide and rounded one (*Zascinaspis*; Figs 18B, 67A, 68B, 70B). An elongate rostral plate with wide anterior margin is characteristic of *Palanasaspis* gen. n. (Fig. 19A). The shape of the plate in *Althaspis* is close to a much lengthened isosceles triangle (Figs 72A, B, 75A, D).

The ventral side of the rostral plate is shorter than the dorsal one and more complexly built (Figs 18A, H, 31B, 62A). The ratio between its ventral and rostral lengths is small in wide-snouted pteraspidids (0.3 in *Zascinaspis heintzi*). It increases in species with rostral plate approaching an equilateral triangle (0.4–0.5 in *Larnovaspis kneri*), and achieves its maximum value in long-snouted pteraspidids (0.7 in *Althaspis longirostra*). This part of the carapace is rarely preserved well enough in the Podolian material (Figs 18A, E, H, 19A,

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Fig. 22. Morphology of the pteraspidid heterostracans. **A**. ?Podolaspididae indet., dorsal shield SMNH BP.273 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, inside view and dorsal spine in lateral (left side) view. **B**. Podolaspididae indet., imprint of associated dorsal spine and dorsal shield SMNH BP.268/1 from Ustechko, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation dorsal and lateral (left side) views. **C**. ?Podolaspididae indet., imprint of associated damaged dorsal spine and dorsal shield SMNH BP.1238 from the Verbivtsi quarry, Ivanie Member of the Tyver Formation, lateral (left side) view. **D**. Podolaspididae indet., dorsal spine SMNH BP.1069 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, lateral (right side) view. **E**. *Zascinaspis heintzi*

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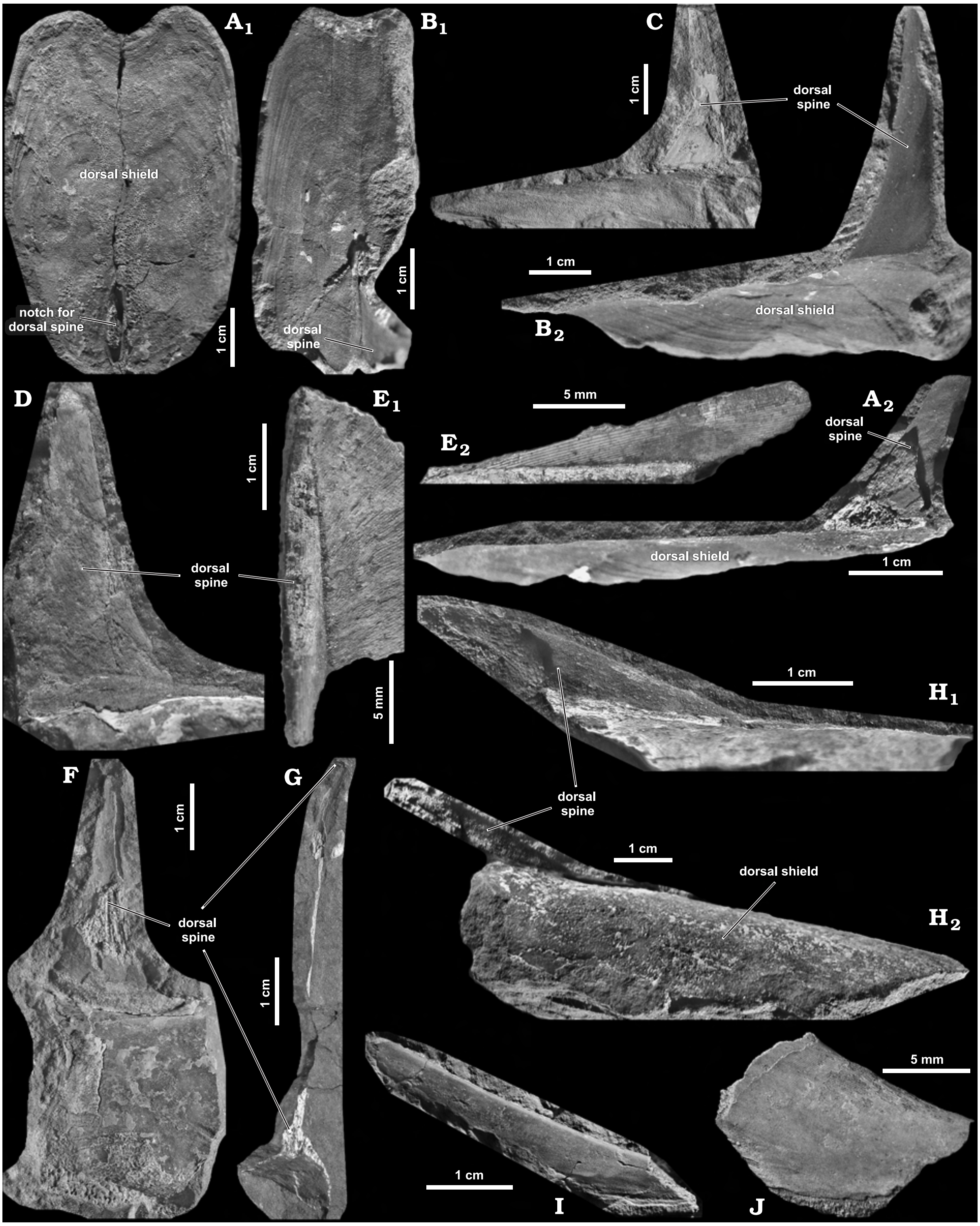


(Brotzen, 1936), dorsal spine SMNH BP.348 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, dorsal and lateral (left side) views. **F**. Podolaspididae indet., partial dorsal spine and dorsal shield SMNH BP.1244 from Ustechko, left bank of Dniester River, 2nd ravine W of the village, lower part of Khmeleva Member, lateral (right side) view. **G**. Podolaspididae indet., fragmentary dorsal spine SMNH BP.1229 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member, antero-lateral view. **H**. ?Larnovaspididae indet., dorsal spine SMNH BP.637 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, lateral (right side) view and mould of dorsal shield associated with partial dorsal spine in lateral (right side) view. **I**. ?Larnovaspididae, partial dorsal spine SMNH BP.1156 from Ustechko, left bank of Dzhuryn River, Ustechko Member, lateral (right side) view. **J**. Pteraspidoidei indet., basal part of dorsal spine SMNH BP.1329 from outcrop east of Dobrivliany, lower part of Ivanie Member, lateral (right side) view.

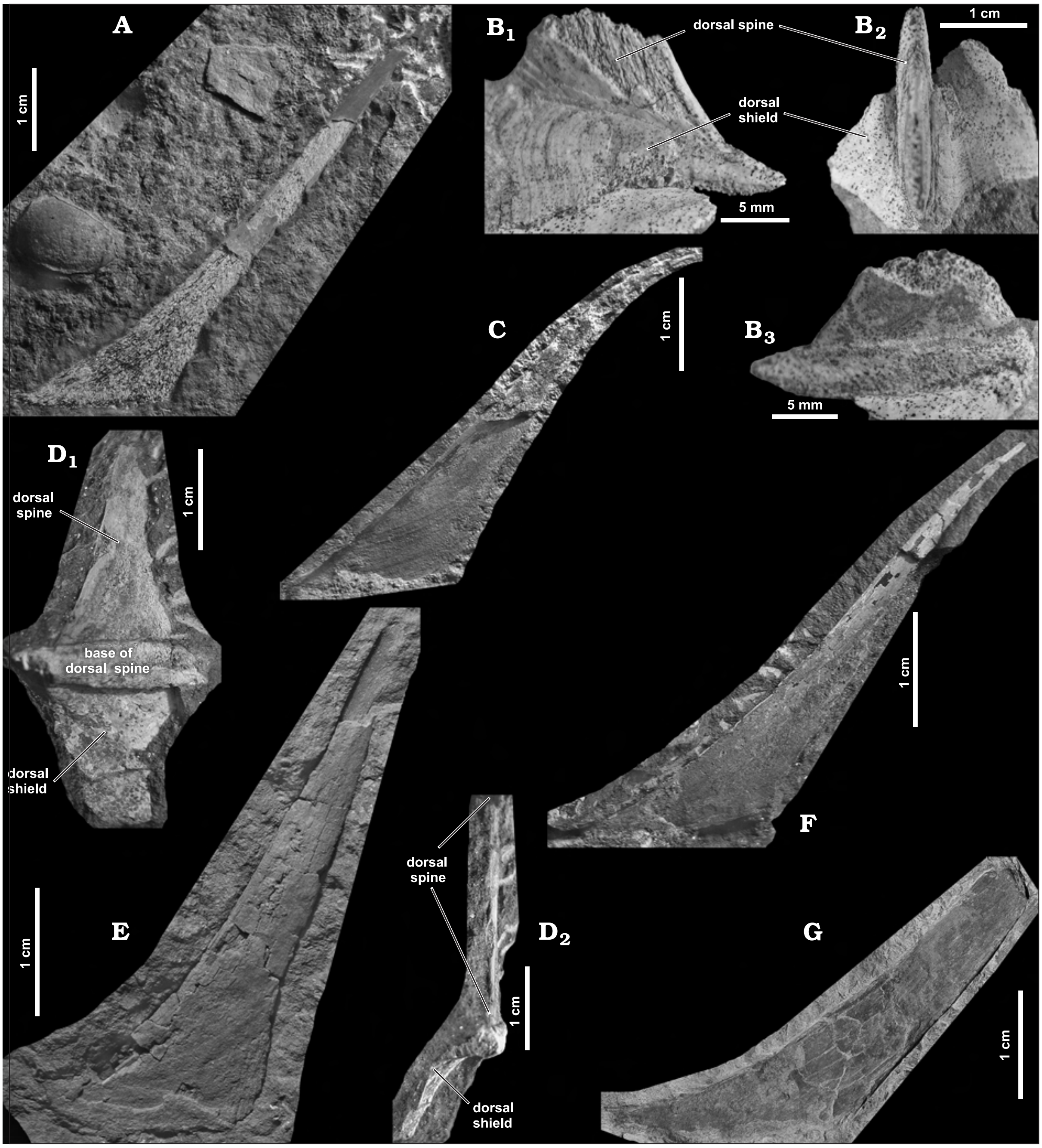


Fig. 23. Morphology of the pteraspidid heterostracans. **A**. Pteraspidoidei indet., partial dorsal spine SMNH BP.1066 with ostracode shell mould from outcrop east of Dobrivliany, lower part of Ivanie Member of the Tyver Formation, lateral (left side) view. **B**. Pteraspidoidei indet., base of dorsal spine with associated part of dorsal shield SMNH BP.969 from unknown locality in Podolia, lower part of the Dniester Formation, lateral (right side), dorsal and lateral (left side) views. **C**. Pteraspidoidei indet., partial dorsal spine SMNH BP.178/2 from the Horodnytsia quarry, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, lateral (left side) view. **D**. Podolaspididae indet., partial dorsal spine and fragment of dorsal shield SMNH BP.1230 from the same locality, ventro-lateral and anterior views. **E**. Podolaspididae indet., partial dorsal spine SMNH BP.1237 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member, lateral (left side) view. **F**. Pteraspidoidei indet., partial dorsal spine SMNH BP.1269/2 from the Horodnytsia quarry, lateral (left side) view. **G**. Podolaspididae indet., basal part of dorsal spine SMNH BP.1188/1 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, lateral (left side) view.

E, 72E). It was, however, possible to offer a precise description of it in *Podolaspis* sp. (Zych 1931: fig. 20) and *Larnovaspis kneri* (Novitskaya 1983: pl. 27, fig. 3). Important, although fragmentary, material from Podolia was at the disposal of Stensiö (1958, 1964). The morphology of the ventral side of the rostral plate has already been described in detail, and also for the Podolian pteraspidids (Novitskaya 1983); therefore, this discussion is

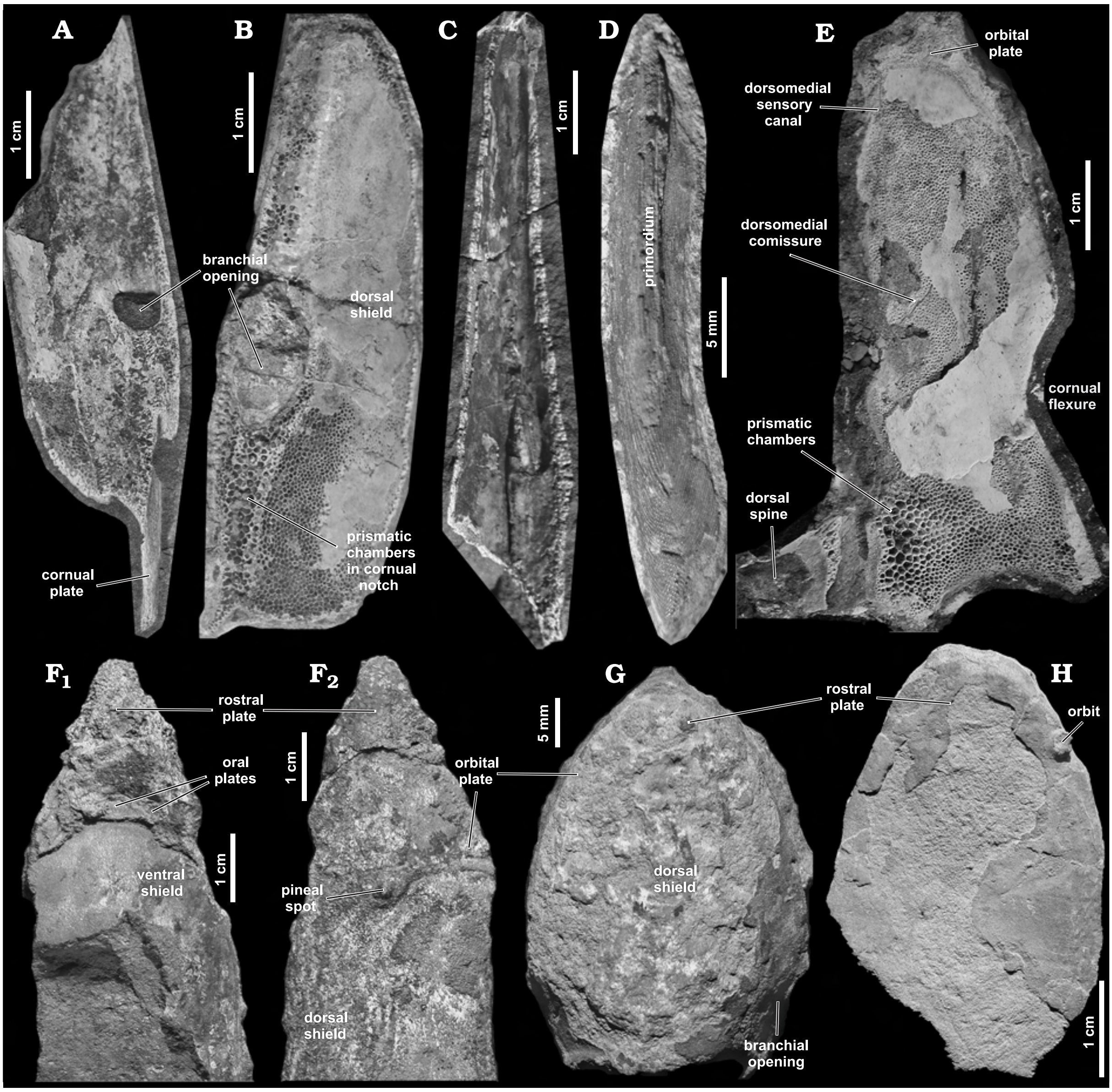


Fig. 24. Morphology of the pteraspidid heterostracans. **A**. Pteraspidoidei indet., branchio-cornual region of carapace IGP (unnumbered) from Ustechko, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, inside view. **B**. Pteraspidoidei indet., partial dorsal shield SMNH BP.1296 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member of the Tyver Formation, inside view. **C**. Pteraspidoidei indet., partial branchial plate SMNH BP.1187/1 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member or lowermost part of Khmeleva Member, inside view. **D**. Pteraspidoidei indet., branchial plate SMNH BP.548/1 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation. **E**. Pteraspidoidei indet., partial left part of carapace IGP (unnumbered) from Ustechko, Ustechko Member or lower part of Khmeleva Member, inside view. **F**. Larnovaspididae gen. indet., mould of anterior part of carapace SMNH BP.234 from the Horodnytsia quarry, Ustechko Member or lower part of Khmeleva Member, ventral and dorsal views. **G**. ?*Zascinaspis bryanti* (Brotzen, 1936), abraded mould of complete carapace SMNH BP.563 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **H**. Same species, abraded mould of juvenile carapace SMNH BP.1180 from the same locality, dorsal view.

limited to determination of only its basic aspects, the preoral field and the ascending plate (lamella). The preoral field most authors understand as an area with a sculpture (of dentine ridges or tubercles), limited laterally by longitudinal (lateral) grooves of the oral-to-nasal furrows, and posteriorly by the ascending plate (a more or less wide terminal bar, turning back into the oral cavity) (Figs 18A, E, H, 19A, D, E).

In the evolution of rostral plate (particularly for Podolian pteraspidids), there is a tendency to increase its size by considerable lengthening or expansion, that is, towards change from the shape of a more or less equilateral triangle to more complex shapes.

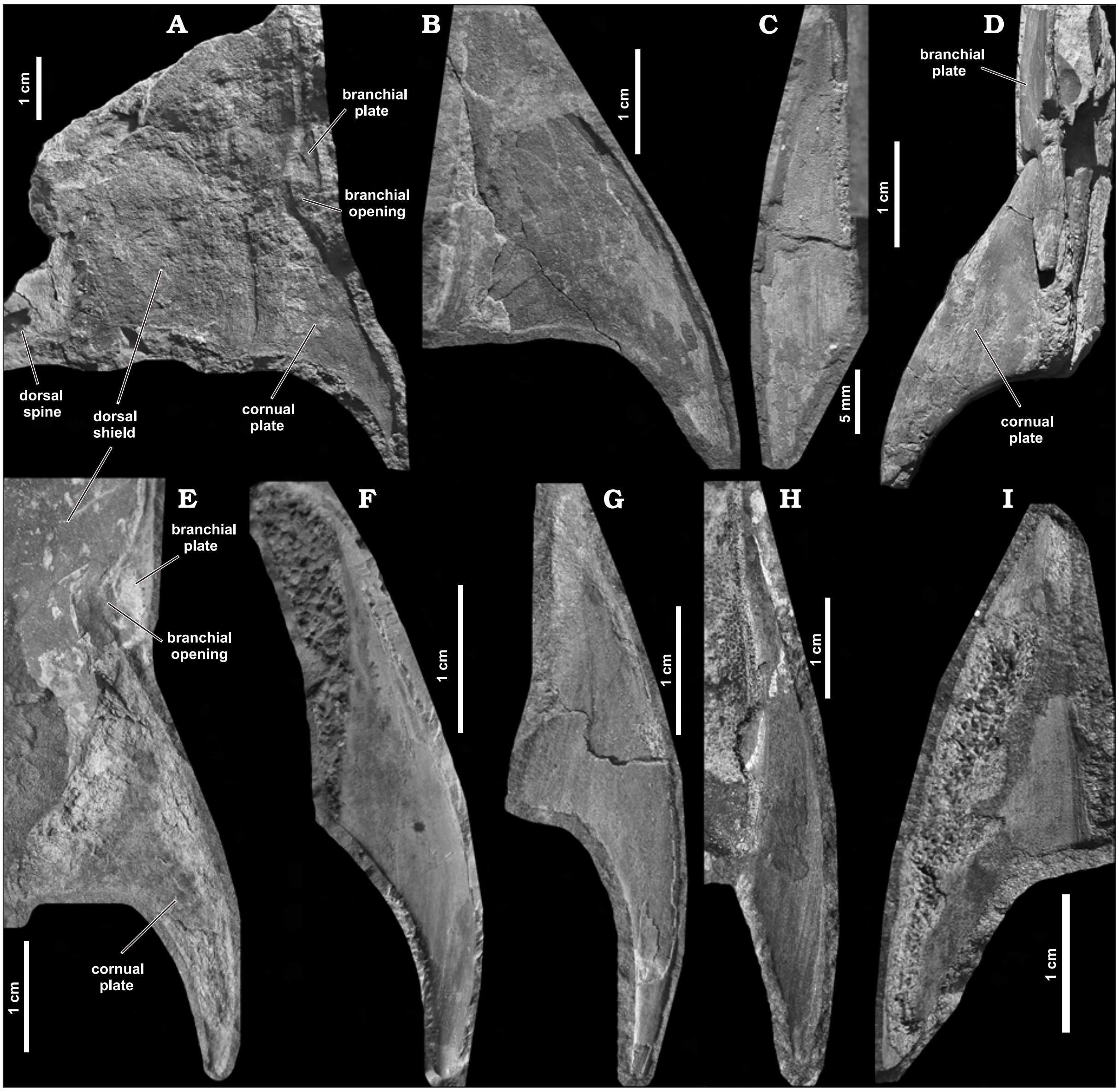


Fig. 25. Morphology of the pteraspidid heterostracans. **A**. Podolaspididae indet., imprint of posterior left part of carapace SMNH BP.213 from Ustechko, left bank of Dniester River, talus, lowermost part of Khmeleva Member of the Dniester Formation. **B**. Podolaspididae indet., imprint of cornual plate SMNH BP.1400 from Ustechko, talus, Ustechko Member or lower part of Khmeleva Member. **C**. Larnovaspididae indet., partial cornual plate SMNH BP.1235 from Ivanie-Zolote, left bank of Dniester River, lower part of Ustechko Member of the Dniester Formation. **D**. Podolaspididae indet., branchio-cornual region of carapace SMNH BP.558 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation. **E**. Podolaspididae indet., branchio-cornual region of carapace SMNH BP.1246 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member, dorsal view. **F**. Pteraspidoidei indet., cornual plate SMNH BP.1067 from outcrop east of Dobrivliany, lower part of Ivanie Member. **G**. Pteraspidoidei indet., cornual plate SMNH BP.1234 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member. **H**. *Larnovaspis* sp., cornual plate SMNH BP.231 from Ustechko, left bank of Dniester River, Ustechko Member or lower part of Khmeleva Member. **I**. Pteraspidoidei indet., partial cornual plate SMNH BP.1335 fom Horodnytsia, talus, Ustechko Member or lower part of Khmeleva Member.

The morphology of the orbito-pineal belt, which consists of a pair of orbital (Fig. 19G) and pineal plates situated between them (Figs 24F, 59C, D, F), is believed to have a substantial value in diagnosing pteraspidids genera and families (Novitskaya 1975, 1983, 1986; Blieck 1984; Voichyshyn 2001c). The belt can be discontinuous when the pineal plate does not touch the orbital ones and its component elements are apart at more or less considerable distance (*Dnestraspis*, *Pavloaspis*, separate cases in *Podolaspis* and *Parapteraspis*; Figs 50E, 52B, 54B, 57C, D, 78A). These plates may touch each other at one point (partly in *Podolaspis*; Figs 49A, B,

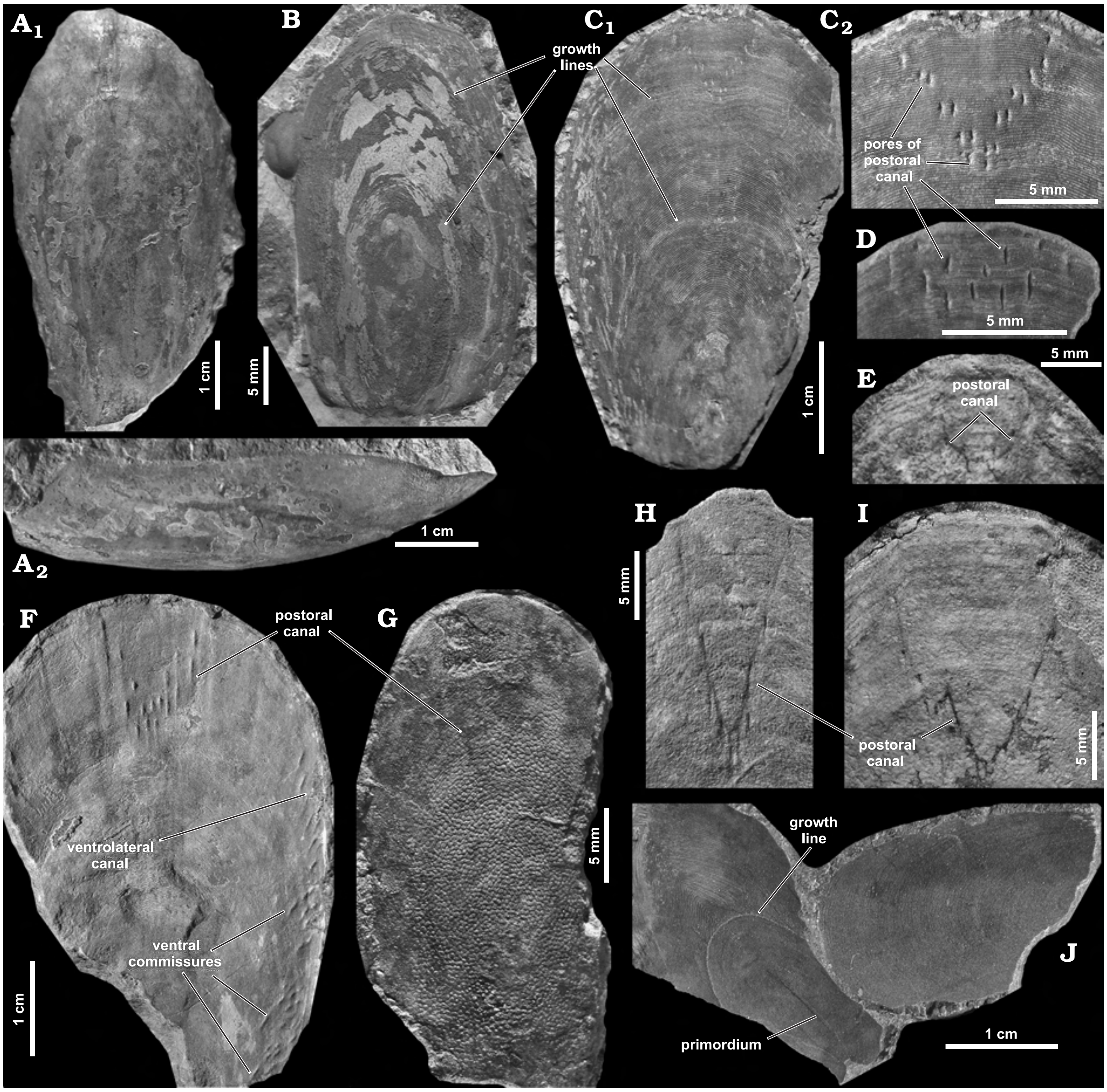


Fig. 26. Morphology of the undetermined pteraspidoideans. **A**. Mould of ventral shield SMNH BP.635 from Gorodok, left bank of Dniester River, Chortkiv Member of the Tyver Formation, ventral and lateral (right side) views. **B**. Mould of ventral shield SMNH BP.541 with ostracode shell mould from unknown locality on left bank of Dniester River, upper third of Chortkiv Member of the Tyver Formation, ventral view. **C**. Anterior part of juvenile ventral shield SMNH BP.540 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, ventral views. **D**. Ventral shield SMNH BP.551 (see also Fig. 27B) from same locality, ventral view. **E**. Anterior part of ventral shield SMNH BP.305 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member of the Dniester Formation, ventral view. **F**. Imprint of partial ventral shield SMNH BP.591 from Ustechko, left bank of Dniester River, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, ventral view. **G**. Partial juvenile ventral shield SMNH BP.676 from Kydaniv, Strypa Member of the Dniester Formation, ventral view. **H**. Anterior part of ventral shield SMNH BP.296 with a trace of postoral canal from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member, ventral view. **I**. Anterior part of ventral shield SMNH BP.1461 with trace of postoral canal from the same locality, ventral view. **J**. Partial imprint of ventral shields SMNH BP.521 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, ventral view.

50C, D, 52A). In such a case, their contact ends are sharpened (medial processes of the orbital plates and lateral ends of the pineal). The contact may be more extensive and the orbito-pineal belt achieves the shape of a more or less wide ribbon (this type of belt occurs in the majority of taxa; it is identified in the Podolian pteraspidids of families Larnovaspididae, Rhinopteraspididae, and Protaspididae; Figs 59A, B, E, 60A, C, 62E, 65C, 67C, 68B, 69B, F, 70C, E, 71A, B, 75B, 77A). Each of the mentioned variants of the belt has a number of varieties in shape, size and proportions of the plates and also contact between them or between the rostral and dorsal plates.

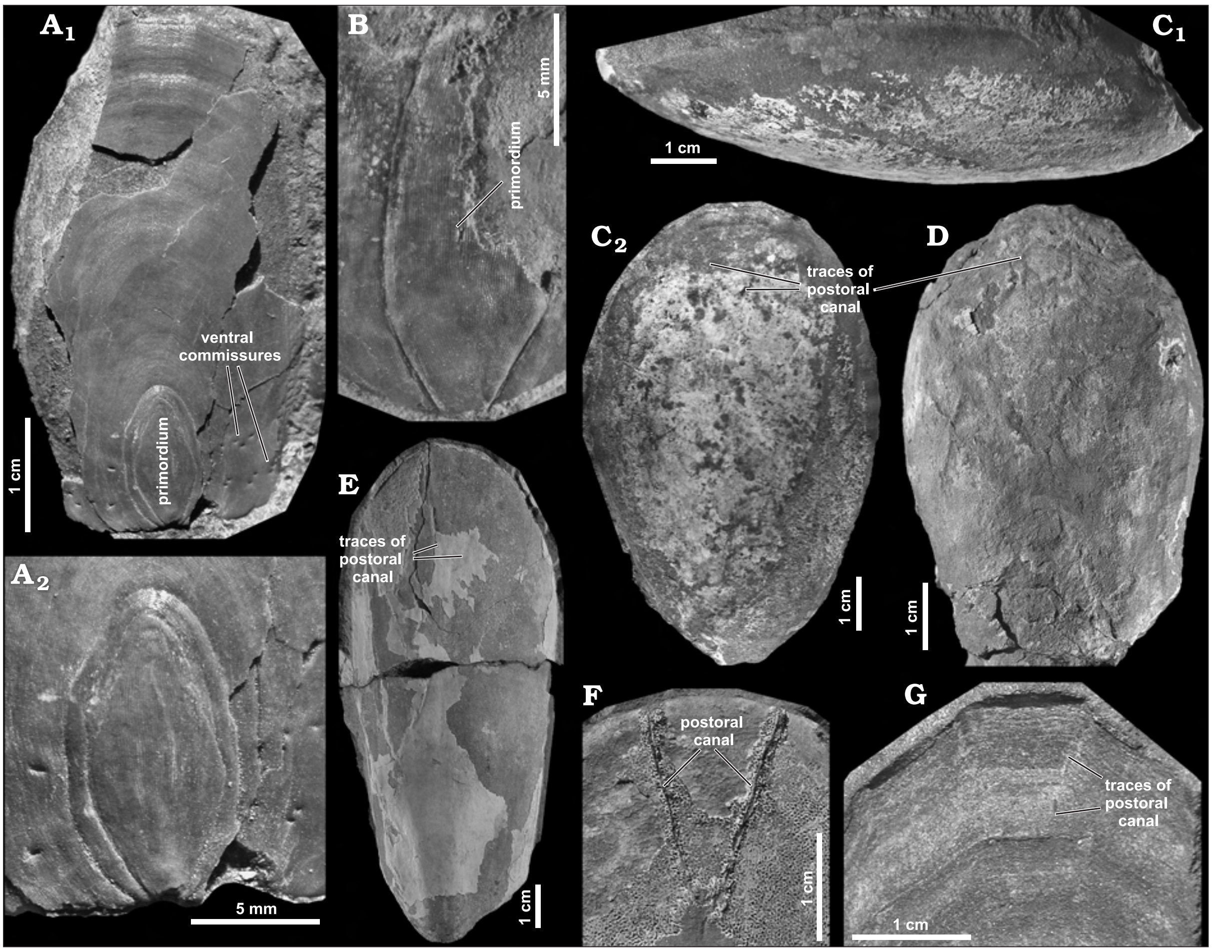
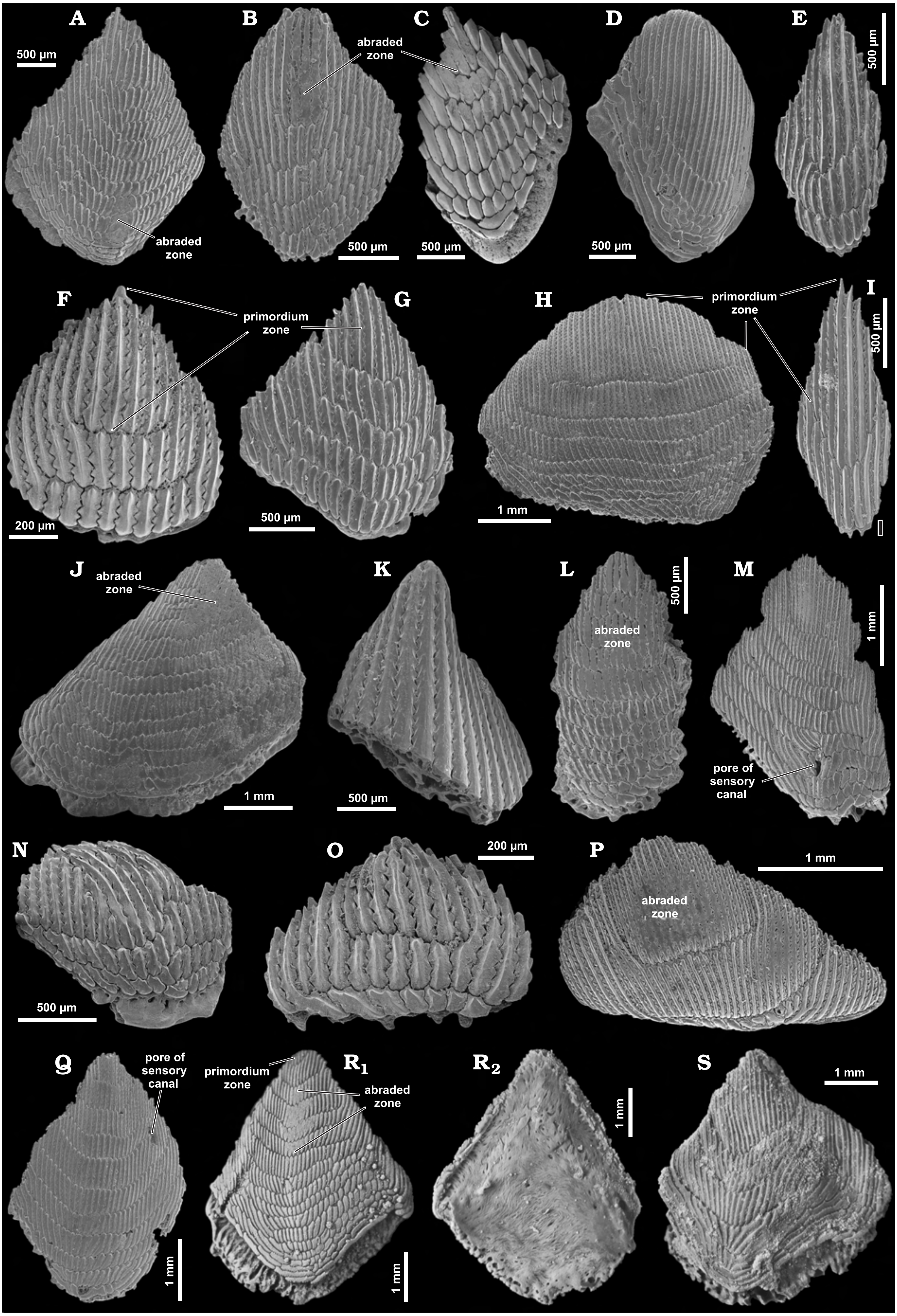


Fig. 27. Morphology of the pteraspidid heterostracans. **A**. Pteraspidoidei indet., partial ventral shield SMNH BP.546 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, ventral view and primordium zone. **B**. Pteraspidoidei indet., primordium zone of ventral shield SMNH BP.551 (see also Fig. 26D) from the same locality, ventral view. **C**. ?*Zascinaspis heintzi* (Brotzen, 1936), mould of ventral shield SMNH BP.614 from probably Horodnytsia, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, ventral and lateral (left side) views. **D**. Same species, ventral shield SMNH BP.1163 from Ustechko, left bank of Dniester River, lowermost part of Khmeleva Member of the Dniester Formation. **E**. *Larnovaspis* sp., mould of ventral shield SMNH BP.1099 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, ventral view. **F**. Pteraspidoidei indet., anterior part of inside of ventral shield SMNH BP.1100 with prepared postoral canal from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member or lowermost part of Khmeleva Member. **G**. Pteraspidoidei indet., imprint of anterior part of ventral shield SMNH BP.1068 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member.

Fig. 28. Morphology of scales of unidentified pteraspidoids. **A**. Lateral scale SMNH BP.1544/6 from Gorodok, left bank of Dniester River, Chortkiv Member of the Tyver Formation. **B**. Lateral scale SMNH BP.1539/12 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member of the Tyver Formation. **C**. Lateral scale SMNH BP.1550/16 from Dobrivliany, lower part of Ivanie Member. **D**. Lateral scale SMNH BP.1545/20 (see also Fig. 30C) from outcrop 1 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member. **E**. Scale SMNH BP.1549/12 from outcrop 2 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member. **F**. Juvenile lateral scale SMNH BP.1550/5 from the same locality. **G**. Lateral scale SMNH BP.1548/18 from Dobrivliany, lower part of Ivanie Member. **H**. Mature lateral scale SMNH BP.1541/9 (see also Fig. 30G) from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member. **I**. Scale SMNH BP.1545/12 from outcrop 8 (Fig. 3B), right bank of Dniester River, lower to middle part of Ivanie Member. **J**. Mature lateral scale SMNH BP.1544/8 from Gorodok. **K**. Terminal part of ridge scale SMNH BP.1545/7 from outcrop 1. **L**. Mature lateral scale with very abraded surface (specimen lost) from Ustechko. **M**. Lateral scale SMNH BP.1547/4 with sensory canal pore from Gorodok. **N**. Scale SMNH BP.1550/32 from outcrop 1. **O**. Juvenile lateral scale SMNH BP.1550/18 from outcrop 2. **P**. Lateral scale SMNH BP.1547/3 from Gorodok. **Q**. Scale SMNH BP.1544/14, same locality. **R**. Lateral scale SMNH BP.1557, same locality, also inside view. **S**. Scale SMNH BP.1561/2 from Zalishchyky, upper part of Ivanie Member. →


A
500 µm
abraded zone
B
abraded zone
500 µm
C
500 µm
D
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E
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F
primordium zone
200 µm
G
500 µm
H
primordium zone
1 mm
I
500 µm
J
abraded zone
1 mm
K
500 µm
L
500 µm
abraded zone
M
1 mm
pore of sensory canal
N
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pore of sensory canal
1 mm
primordium zone
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So, for the first variant, in *Dnestraspis*, the suture between rostral and dorsal plates notably bends anteriorward (Fig. 54B, C), whereas in *Pavloaspis* the pineal plate is large, rounded in shape (Fig. 78A), and in *Podolaspis* and *Semipodolaspis* gen. n. it takes the shape of a laterally expanded part-moon (Figs 49A, B, 50C, 52A, B, 54A). Another variant is represented by different shapes and width of the pineal plate (*Parapteraspis*, to some degree *Mylopteraspidella* and other podolaspidids; Figs 18F, 56A, B, E, 57C, 58A, C). Much variation in appearance was achieved by the third, ribbon-like variant of the orbito-pineal belt. If in previously considered variants the shape and relative size of the orbital plates changes in a limited range, in the latter variant its aspect is often distinctive. The shape and size of the pineal plate as well as character of its contact with the orbital are especially important. The width of the orbital medial processes and the extent of the pineal plate along the body axis at the place of contact may correspond to each other, which is a distinctive feature of the equal-contact ribbon-shaped belt in *Althaspis*, and also some species of *Larnovaspis*. In other cases, the pineal plate extends farther than the corresponding part of orbital processes, characteristic of the non-equal-contact wedge-shaped belt (in some species of *Larnovaspis* and *Zascinaspis*; Fig. 69E, G). It may be of interest to note that the inverse relationship, with the pineal being shorter, has never been observed. An unusual variant of the orbito-pineal belt is represented by *Woodfjordaspis felixi* Pernègre, 2006 from the Early Devonian of Spitsbergen. Presumably the acute orbital medial processes are almost in contact, and the moon-shaped pineal plate is anterior to them (Pernègre 2006: fig. 5A).

The dorsal plate or shield (Figs 8E, 19D, 21A, 22A, 51B, 54A, 56E, 59F, 74E, 77A), being the largest component element of armour cover of pteraspidids, borders anteriorly the plates of the orbito-pineal belt, and in the case when the last is discontinuous, also partly with the posterior margin of the rostral plate. Pineal notches may have the appearance of just a concavity at the anterior margin of the dorsal shield or a clear, more or less deep three-cornered or rounded notch ("*Pteraspis*" *angustata, Podolaspis, Djurinaspis, Pavloaspis, Alaeckaspis*; Figs 20B, C, G, 21B, 22A, 50C, 62D, 66B, 78A). The first variant is characteristic for pteraspidids with the wide-contact orbito-pineal belt, in which the notch holds also a part of the medial orbital process and is not exclusively "pineal" (Figs 69F, 77A). In the second variant, it fits the pineal plate only. A special case is *Dnestraspis* that has a large notch holding the pineal plate and a part of the rostral plate (Fig. 54B). The deep and wide notch in the anterior margin of the shield in *Althaspis* makes a separate case. It holds a considerable part of the narrow ribbon-shaped orbito-pineal belt and merges with the posterior margin of the rostral plate (Figs 73A, 75A, B, E). The anterior margin of the dorsal shield in *Podolaspis danieli* sp. n. is unusual in having two symmetrical depressions on both sides of the pineal notch (Fig. 52B).

The lateral sides of the dorsal shield abut upon the posterior processes of orbital plates, branchial and cornual plates. In the posterior third of the dorsal shield in mature individuals of some pteraspidids, lateral margins form a flexure in front of branchial openings, where the suture of cornual plates enters (majority of the Podolaspididae, some *Larnovaspis*, possibly *Brachipteraspis* and *Althaspis*; Figs 20A, D, 21A, 24E, 49A, 50B, D, 51A, C, D, 56E, 57D, 58A, 59E). The presence of flexure usually depends on the degree of development of cornual plates (except for *Althaspis*; Fig. 73F). It is practically absent in pteraspidids with narrow or poorly developed cornual plates (*Alaeckaspis*, *Pavloaspis*, *Belgicaspis*, and *Zascinaspis*). The lateral margins of the dorsal shield may have a small branchial notch also in the region of the branchial openings (for example, in *Pavloaspis*; Fig. 78A), which is a component of the cornual flexure (*Podolaspis*).

The posterior margin of the dorsal shield of pteraspidids abuts upon the scales of the abdomen-tail (Fig. 34F). *Europrotaspis* makes an exception (in the Podolian fauna), in which the branchial area was displaced there, and the posterior margin of the dorsal shield not only contacts small cornual plates but also serves, according to Brotzen (1936), as a part of the branchial openings. As a rule, the posterior margin of the shield stretches into a median ledge, more or less rounded or angular (*Larnovaspis*, *Zascinaspis*, *Althaspis*, etc.; Figs 20A, 21C, 50F, 59E, F, 60B, 61E, 62C, 67D, 68D, 71D, 74B, C, 77A). This may be complicated by notches at both sides of the medial ledge, and as a result the margin assumes a sinusoidal course (for example, in *Parapteraspis plana*; Figs 20F, 57B). But in some cases, as in *Podolaspis lerichei*, the posterior margin may be roughly straight (Fig. 51A).

The notch holding the dorsal spine, which according to Janvier (2003) is a modified dorsal median ridge scale, may be more or less elongated on the dorsal shield (Figs 20E, 33C, 49B, 50B, D, 57A, D, 60B, 74A), but its anterior margin does not extend forward farther than to the level of branchial openings (Figs 20A, D, 62C), whereas the posterior one, extends to the posterior margin of the dorsal shield (Figs 20F, 51A, 52B, 54B, 58A, 67D, 68D, 72D, F, 73E) or, possibly, behind it (Figs 21C, 75C). The shape of the spine is variable

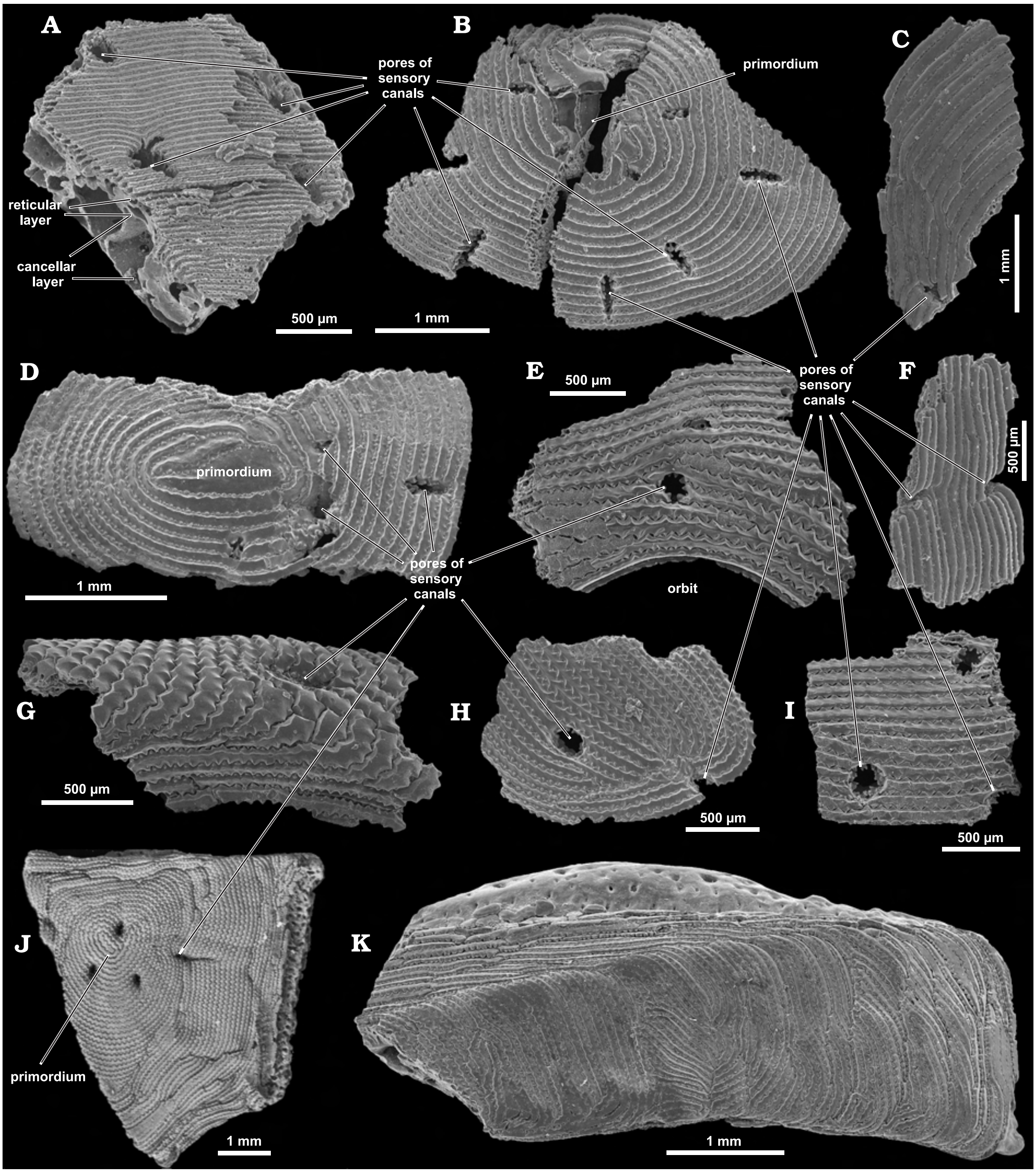

Fig. 29. Micromorphology of armour of unidentified pteraspidoids. **A**. Piece of armour SMNH BP.1542/6 (see also Fig. 30A) from outcrop 11 (Fig. 3B), left bank of Dniester River, upper part of Chortkiv Member of the Tyver Formation. **B**. Central part of pineal plate SMNH BP.1549/35 (see also Fig. 30D) from outcrop 2 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member of the Tyver Formation. **C**. Piece of armour SMNH BP.1542/4 from outcrop 11. **D**. Central part of pineal plate SMNH BP.1548/8 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member. **E**. Probable piece of orbital plate SMNH BP.1547/18 from Gorodok, left bank of Dniester River, Chortkiv Member. **F**. Piece of armour SMNH BP.1542/5 from outcrop 11. **G**. Piece of armour SMNH BP.1542/8, same locality. **H**. Piece of armour SMNH BP.1533/17 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member. **I**. Piece of armour SMNH BP.1549/13 (see also Fig. 30E) with sensory pores from outcrop 2. **J**. Partial pineal plate SMNH BP.1558 from Dobrivliany, lower part of Ivanie Member of the Tyver Formation, dorsal view. **K**. Part of undetermined plate SMNH BP.1544/1 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member.

in the Podolian pteraspidids. It may be long, directed upward and a few backwards or ahead (*Podolaspis* and, probably, other podolaspidids; Figs 21A, 22A–D, F, G, 23B, D, E, 24E, 49C, 50C, E, 52B, 56D, 58A), very

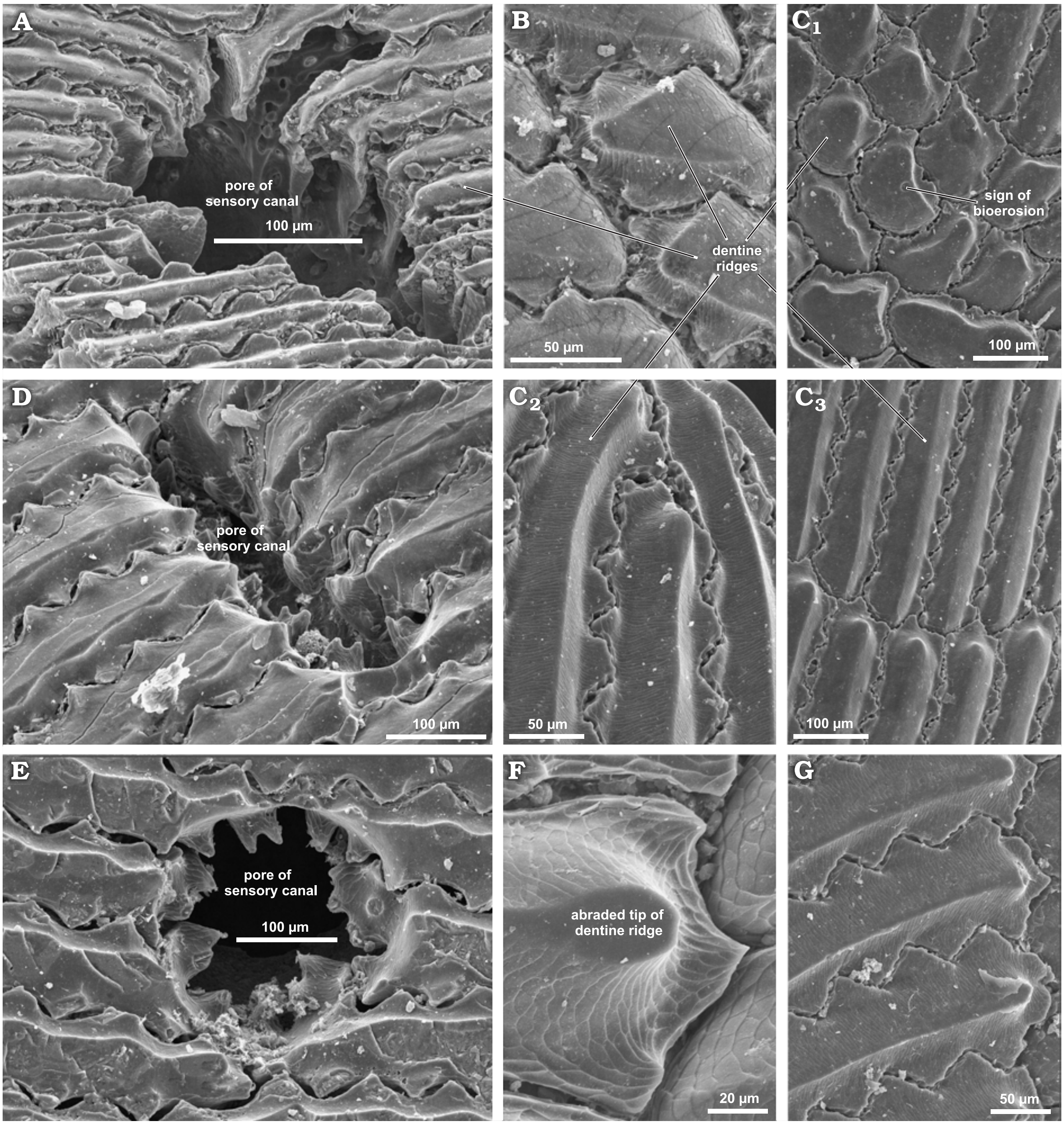

Fig. 30. Micromorphology of armour of unidentified pteraspidoids. **A**. Pore of sensory canal in piece of armour SMNH BP.1542/6 (see also Fig. 29A) from outcrop 11 (Fig. 3B), left bank of Dniester River, upper part of Chortkiv Member of the Tyver Formation. **B**. Dentine ridges at the base of lateral scale SMNH BP.1543/6 from outcrop 52 (Fig. 3B), left bank of Dniester River, Ivanie Member of the Tyver Formation. **C**. Dentine ridges at the base, top and in middle of lateral scale SMNH BP.1545/20 (see also Fig. 28D) from outcrop 1 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member. **D**. Pore of the "pineal" sensory canal of pineal plate SMNH BP.1549/35 (see also Fig. 29B) from outcrop 2 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member of the Tyver Formation. **E**. Pore of sensory canal in a piece of armour SMNH BP.1549/13 (see also Fig. 29I), same locality. **F**. End of dentine ridge on scale SMNH BP.1540/9 from Dobrivliany, lower part of Ivanie Member. **G**. Dentine ridges on middle part of mature lateral scale SMNH BP.1541/9 (see also Fig. 28H) from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member.

long, narrow, directed backwards under a small angle (*Althaspis*; Figs 72F, 73D, E, 74B–E), or low, comparatively wide and declined backwards under the angle of 9–10° (*Zascinaspis*; Figs 22E, 67D, 68E). In *Djurinaspis*, *Semipodolaspis* gen. n., as well as in *Larnovaspis*, the dorsal spine is also declined backwards (Figs 22H, I, J, 54A, 64A). The dorsal spine pattern does not seem to characterise any specific clade (Fig. 23A, C, F, G). Long (high) and prominent dorsal spine, as well as similar processes in other ostracoderms, may have been protective against predators.

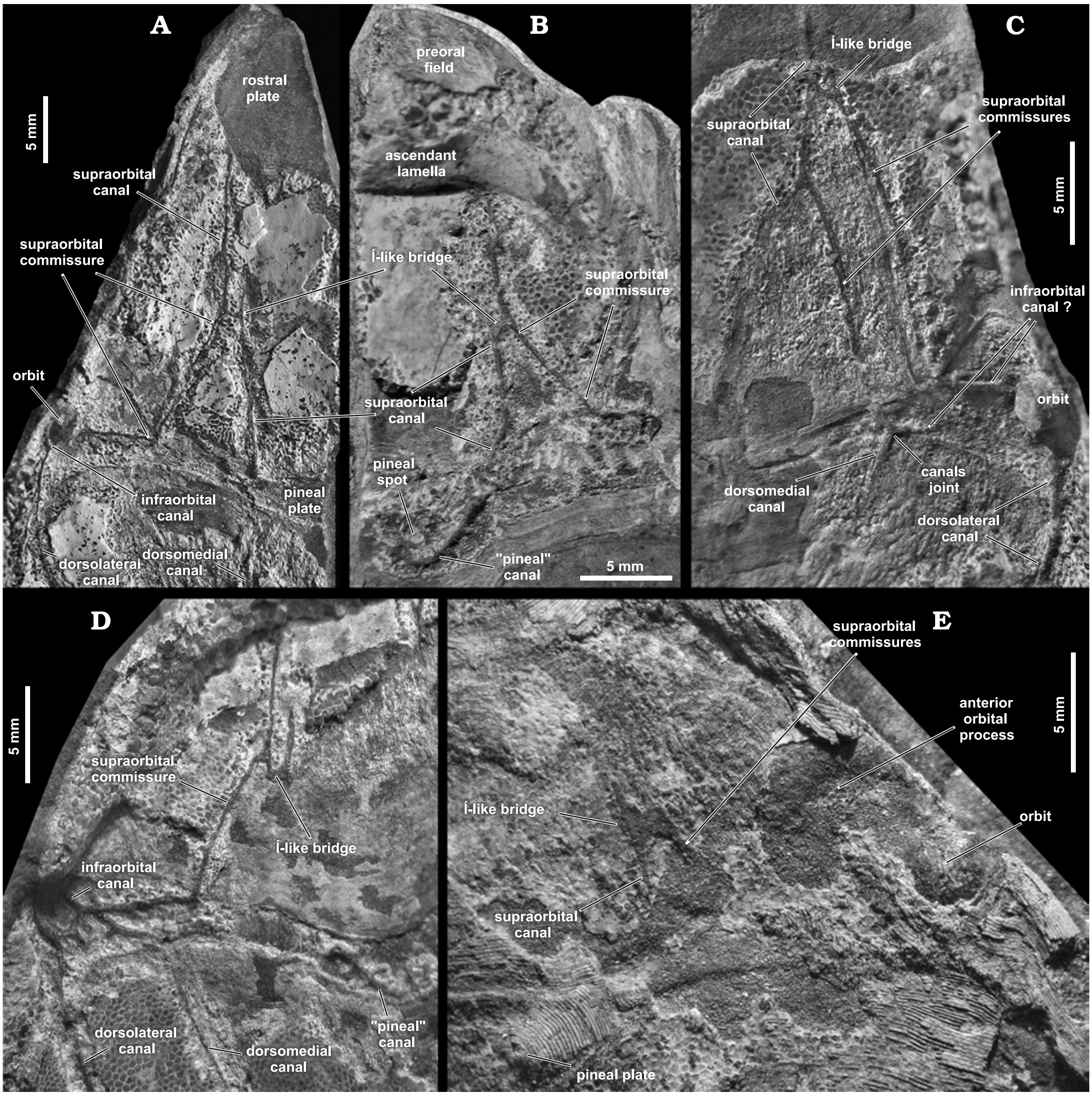

Fig. 31. Morphology of the pteraspidid heterostracans. **A**. *Larnovaspis* sp., inside of anterior right part of carapace SMNH BP.176 with prepared sensory canals from the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **B**. *Larnovaspis kneri* (Lankester, 1868), inside of anterior part of carapace SMNH BP.243 (see also Fig. 62A) with sensory canal remains from Zalishchyky, right bank of Dniester River, talus, upper part of Ivanie Member of the Tyver Formation. **C**. *Larnovaspis* sp., inside of partial rostral plate SMNH BP.174 showing supraorbital commissures from the Horodnytsia quarry talus. **D**. Same species, inside of part of rostral plate and orbito-pineal belt SMNH BP.173 with prepared sensory canals, same locality. **E**. *Zascinaspis ?heintzi* (Brotzen, 1936), mould of orbital region of carapace SMNH BP.603 (see also Fig. 68A) showing H-like bridge from Ustechko, left bank of Dniester River, lower part of Khmeleva Member.

A bulge on the dorsal shield of pteraspidids may extend as far as from the anterior margin, sometimes from the middle of the shield, to the edge of the dorsal spine, and also from the lateral margins to the edge (Figs 21A, 49A, B, 50A, 51A, C, D, 52A, 57D, 58A, D, 61F, 62D, 66E, 71D, 75C, F, 78A). In some pteraspidids (especially those narrow-shielded; *Podolaspis*, *Althaspis*), height of the posterior part of the dorsal shield exceeds its width in the same region. In wide, flattened pteraspidids (*Brachipteraspis*, *Zascinaspis*), this value does not exceed 1/5 of the width.

Branchial plates have an appearance of long and narrow, poorly bent ribbons (Figs 24C, D, 65A), contacting anteriorly with the orbital, possibly rostral (Novitskaya 1983: text-fig. 86), and lateral plates, dorsally with the dorsal (up to the beginning of cornual flexure), and ventrally with the ventral shield. They limit the lower margin of the branchial opening, behind which they adjoin with cornual plates dorsally (Figs 25D, 54A, 59D, 61D, 62C, 64A, 66D, F, 73F), and their posterior margins, possibly, contact the abdomen-tail scales. In wide-shielded, presumably near-bottom-living pteraspidids (*Europrotaspis*), the branchial plates have a considerable width in their dorso-ventral extent and they serve as a continuation of lateral margins of the dorsal shield, covering their posterolateral corners, where the branchial openings are located.

The cornual plates are located in the postero-lateral regions of the carapace, approximately in the plane of the dorsal shield (Fig. 50A), assuming shapes from wide aliform or falcate triangles, oriented antero-laterally, to more or less narrow wedge- or fin-shaped ribbons, directed backwards (Figs 25C, F–I, 49A, 66F, 66G). The base (medial margin) of cornual plates is attached to the cornual flexure of the dorsal shield, such that seen from above the plates abut upon the latter, and from below upon the branchial plate and serve as the overhead margin of the branchial opening (Figs 24A, B, 25A, E). In the Podolaspididae, the contour of the antero-lateral margin of the cornual plates is sinusoidal; thus, a shallow notch changes backwards into a convexity which at the posterior margin of the plates ends as a sharp angulation (Figs 25B, 49A). Beginning from it and up to the contact with the dorsal shield, the contour of the posterior margin of the cornual plate is similar to the antero-lateral one. If for the podolaspidids the ratio CL/CW is close to 1.6 (*Podolaspis podolica*, Fig. 49A), in many representatives of Larnovaspididae the length of the cornual plates exceeds its width considerably. For example, in *Djurinaspis secunda* sp. n. (Fig. 64A) the plate is 16 times longer than wide, in *Alaeckaspis verbivciensis* (Fig. 66F) 10 times, in *Larnovaspis* sp. (Fig. 25H) 8.6 times, and in ?*Zascinaspis bryanti* (Fig. 70B) about 6 times longer. The rhinopteraspidids have also narrow ribbon-like cornual plates with CL/CW ratio about 10 (Fig. 73F). The geometry of plate contours changes accordingly. Their posterior margin becomes considerably shorter than medial and anterolateral ones. In *Europrotaspis*, the cornual plates are very small, narrow and short, displaced to the posterior margin of the dorsal shield.

Shape of the cornual plates seems to be correlated with size and orientation of the dorsal spine. Pteraspidids with wide, falcate cornual plates have a long, elevated dorsal spine (*Podolaspis*). The dorsal spine also deviates posteriorly in species with cornual plates relatively narrow and directed backwards (*Larnovaspis*, *Djurinaspis*). If this list is supplemented with wide-shielded *Zascinaspis* and narrow-shielded, elongated *Belgicaspis* and *Althaspis* the complete spectrum of hydrodynamic types of the Podolian pteraspidids is represented. The role of the well-developed dorsal spine as stabilizing direction of motion and large cornual plates as a hydrofoil of nectonic pteraspidids has been already forwarded in the literature (Novitskaya 1983, 2007). However, the dorsal spines of, for example, *Althaspis* and *Podolaspis*, have a substantially different orientation in spite of closely similar size. The cornual plates of these species considerably differ in size and probably configuration of their surfaces. Apparently, all this testifies for distinctions in the modes of motion of different species.

Ventral shields of the Pteraspidoidei are generally oval, with varying elongation (Figs 8F, 19E, 21A, 27C, E, 72C). The anterior margin of the ventral plate is, as a rule, rounded (Figs 26C, F, G, 27D). In some early pteraspidids, especially those from the Ivanie Stage, it was truncated anteriorly (SMNH BP.593; Fig. 27G). Outline of the posterior margin may be roughly straight (Figs 26B, 27A), or angular (Figs 68F, 77C, D). There is a small, elongated median depression of unknown function on the posterior end of the ventral shield in *Althaspis* (Fig. 73C). A similar depression occurs also in *Pteraspis* (*Belgicaspis*) *crouchi* (Novitskaya 1983). A bulge of the ventral shield is well developed, being similar to the dorsal one but often more prominent (Figs 21A, 26A, 27C, 77B–D). Because ventral shields are rarely articulated with other carapace plates, their taxonomic identification within Pteraspidoidei remains problematic. This has been achieved in *Zascinaspis heintzi* (Fig. 69C), Podolaspididae gen. indet. (Fig. 21A), or Larnovaspididae gen. indet. (Fig. 24F). In the case of *Althaspis* (Fig. 77D), generic identification of shields in the Podolian material seems rather secure, as in the 3rd Old Red zone strata no other pteraspidid with elongated carapace is known. The wide-shielded ventral plates of *Brachipteraspis* and *Europrotaspis* from the same strata cannot be matched with dorsal ones so easily, especially because of rare and fragmentary finds (Fig. 77B, C). In the 1st Old Red zone, the ventral plates of *Zascinaspis* can be identified due to their considerable width (Fig. 68F) and this applies to a certain extent also to *Larnovaspis* with plates of remarkable size (Fig. 19E). No criteria for recognition of the Podolaspididae and most of the plates of Larnovaspididae are available.

The abdomen-tail of pteraspidids, similarly as in the cyathaspidids, was covered with scales (Figs 19F, 28B, C, D, N, Q–S). The shape and probably sculpture of the scales depends on the area of the trunk or tail, as in thelodonts. There are several kinds of scales, ranging from minute and elongated (Fig. 28E, I) to comparatively

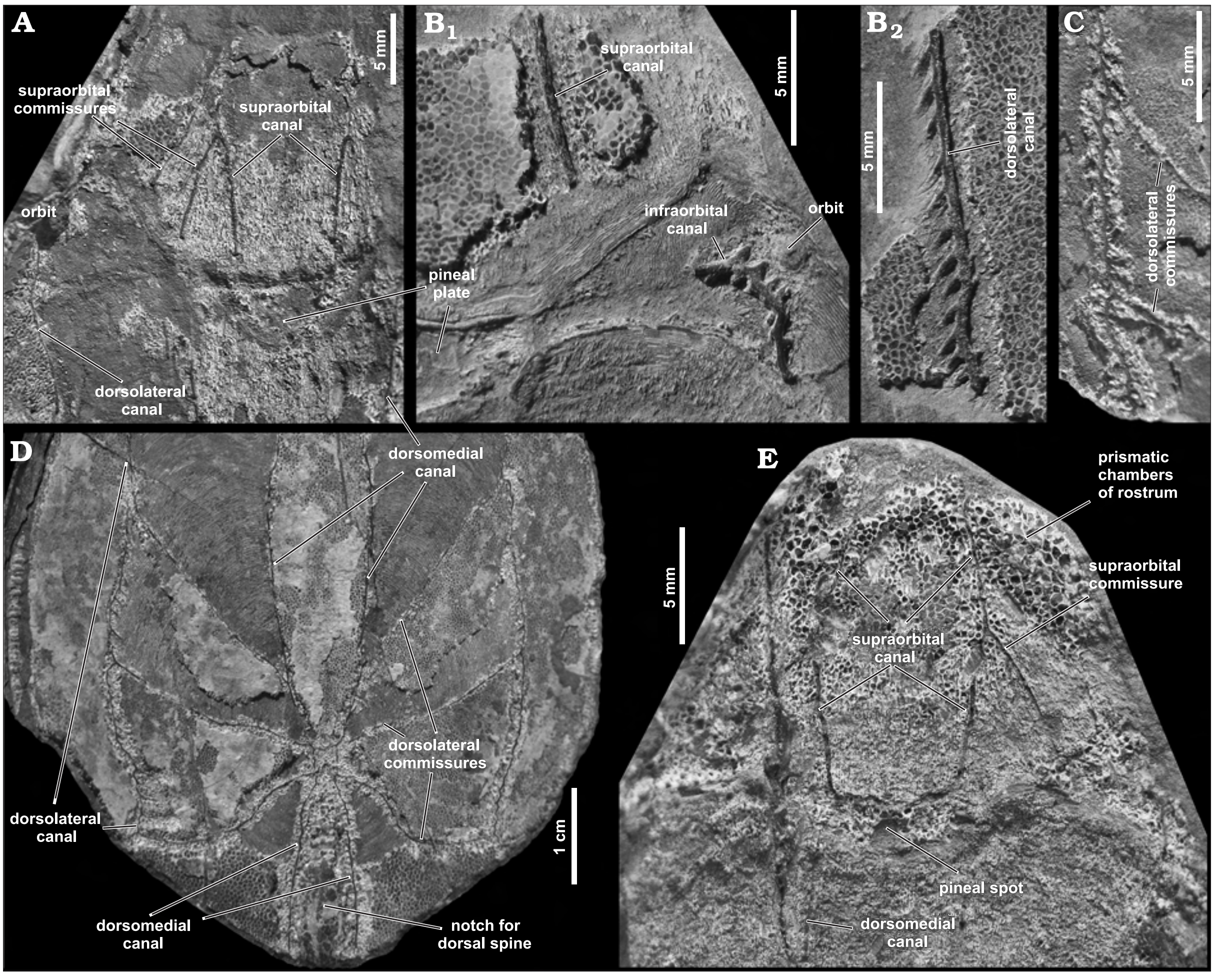

Fig. 32. Morphology of the pteraspidid heterostracans. **A**. *Podolaspis* sp., inside of anterior part of carapace SMNH BP.175 (see also Fig. 48A) with prepared sensory canals from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation. **B**. *Larnovaspis* sp., inside of anterior part of carapace SMNH BP.239 with sensory canal remains from Zalishchyky, right bank of Dniester River, talus, upper part of Ivanie Member of the Tyver Formation, also part of dorsolateral canal. **C**. *Podolaspis podolica* (Alth, 1874), part of dorsolateral canal in carapace SMNH BP.172 (see also Fig. 49B) from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member. **D**. *Zascinaspis heintzi* (Brotzen, 1936), inside of dorsal shield SMNH BP.327 (see also Fig. 67A) with prepared sensory canals, same locality. **E**. *Parapteraspis plana* Stensiö, 1958, inside of anterior part of carapace SMNH BP.295 (see also Figs 48B, 57B) with prepared sensory canals, same locality.

large and short (Fig. 28H, J, P). Size of scales from SMNH collection varies from 0.5 mm to about 3.5 mm in length and from about 1 mm to 4 mm in width (Fig. 28F, J, O). The trunk part consists of dorsal and ventral median scale ridges (Fig. 28K); between them the body is covered by mainly rhombic lateral scales (Fig. 28A, G, S). The same pattern is in the tail part, but the scales gradually diminish in size posteriorly (Fig. 19F). Protuberant parts of large scales often are abraded (Figs 28A–C, J, L, P, R, 30F). At least in one case, a sign of dentine ridge bioerosion similar to that in *Poraspis* has been identified on the pteraspidid scale (Fig. 30C).

Structure of the dermal skeleton of the pteraspidiforms. — The pteraspid armour is of structure similar to that of the cyathaspid one, with the external (sculptured) layer built of dentine and the aspidine reticular, cancellar and basal layers underneath (Fig. 29A). The cancellar layer is similar to those of cyathaspidids in having prismatic chambers well developed in protruding parts of the pteraspidid carapace, where they are gradually replaced distally with the sponge tissue (the distal part of the rostrum, proximal part of cornual plates, part of dorsal shield surrounding the notches for dorsal spine and cornual plates; Figs 24B, E, 32E, 49A, C, 62A, B, 67A, 69B, 71C, 72E, 75B). The prismatic chambers occur also in the weigeltaspids (Fig. 81B).

The dermal skeleton ornamentation in the pteraspidids seems rather uniform, and consists only of dentine ridges (Figs 28C, F, 29C, F, K, 30B, C, G, 67C, 70C). But under SEM different types of dentine ridge morphology can be recognized (Figs 28C, G, 29F–H). Perhaps, morphology of the dentine ridges may serve as an additional species diagnostic feature. The dentine ridges which are located on the salient elements of armour (cornual plates, dorsal spine, scales) are parallel or at an angle to one of the plate margins (see their arrangement on cornual plates, Fig. 25F, H, and the dorsal spine, Figs 22E, 23E–G, 67D). On all other carapace plates, dentine ridges are arranged in a concentric manner, around the primary center of growth (primordium; Figs 18C, 27A, 34A, C, G, I, J). The primordium usually consists of parallel dentine ridges (Figs 24D, 26J, 27A, B). The pineal plate initiated its growth from the area around the pineal spot; the primordium comprised several expanded dentine ridges (Fig. 29B), a single ridge-platelet (Figs 29D, 70A, B), or a spiral-like ridge of normal width (Fig. 29J). Possibly these are species. The primary centre of growth in scales is located on their tip (primordium zone; Fig. 28–H). Proximally, it was supplemented by subsequent-generation dentine ridges. Their number ranges from one (Fig. 28I) to at least twelve (Fig. 28R).

Usually, there are from 5 (in the primordial areas of dorsal and ventral shields) to 13 (on periphery of the plates) dentine ridges at 1 mm. On the ventral surface of the supposed rostral plate (at its anterior end) of ?*Belgicaspis crouchi*, only three ridges per millimetre were counted (Fig. 19B, C).

Some pteraspidid specimens from Jagilnytsia Stara had their armour damaged during life (Fig. 33A, D). The damaged areas in the antero-central part of the dorsal and ventral shields were repaired. Possibly, these are results of predation.

Lateral line system of the pteraspidiforms. — The sensory lateral line system of the Podolian pteraspidids (Figs 8E, F, 49A, 57B, 67A, 72H) was commented on by a number of authors (Zych 1931; Brotzen 1936; Novitskaya 1983; Blieck 1984). Its basic pattern was recognised by E. White in 1935 in *Pteraspis rostrata* (Agassiz, 1835) (Blieck 1984: fig. 38A) and has been accepted as a typical one for all, at least Podolian, pteraspidids (Novitskaya 1983).

On the dorsal surface of rostral plates, a pair of supraorbital canals is disposed (Fig. 33F), extending posteriorly to the pineal plate, crossing its anterior margin and uniting with each other behind the pineal spot. A separate case is made by the location of the supraorbital canals in *Zascinaspis heintzi* where they run outside the rostrum not on the pineal, but on the medial processes of the orbital plates (see presumable crossing of anterior margin of the medial orbital process by supraorbital canal on Fig. 31E, and pore(s) of this canal on the distal end of the process in Novitskaya 1983: pl. 31, fig. 3). The supraorbital canals unite with the infraorbital ones (Figs 19G, 21D, 32B) through supraorbital commissures near the orbits (Fig. 31A, C, D).

It is believed (Novitskaya 1983, 2004; Blieck 1984) that the supraorbital commissures in the pteraspidids (in particular the Podolian representatives of the group) run strictly parallel to the orbito-pineal belt and, as a rule, within the limits of orbital medial processes. Probably, this has resulted from the reconstructions being based mainly on the location of pores of sensory canals on the armour (as was probably the case in *Zascinaspis heintzi* PIN 3592/22; see Novitskaya 1983: pl. 31, fig. 3 and text-fig. 45a), instead of actual canals. This was already noticed by Zych (1931) in his comment on earlier works. But in all known cases, based on prepared canals, the supraorbital commissures branch off the supraorbital canals approximately in the central part of the rostral plate at the level of the anterior ends of the orbital plates or higher, and run posterolaterally to the base of the medial orbital processes, where they unite with the infraorbital canals (Fig. 8E). This pattern, described already by Zych (1931), is characteristic of *Podolaspis* (Figs 32A, 48A, 49A, 52B; Zych 1931: fig. 14), *Parapteraspis* (Figs 32E, 48B), *Dnestraspis* (Fig. 54B), *Larnovaspis* (Figs 31A–D, 60A; Zych 1931: fig. 23), *Zascinaspis* (Figs 31E, 70A), *Althaspis* (Fig. 71B, D; Zych 1931: figs 41, 49), probably *Pavloaspis* (Fig. 78A), possibly *Semipodolaspis* (Fig. 54A), and seems to be plesiomorphic. Traces of sensory canal on the specimen NHRM C1558 of *Parapteraspis plana* (in my interpretation), which Blieck (1984: fig. 10B) identified as the supraorbital canal (*soc*), may belong rather to the supraorbital commissure. Sometimes, at least in *Podolaspis*, *Larnovaspis* (Figs 31C, 32A), probably *Dnestraspis* (Fig. 54B), not one but two parallel supraorbital commissures occur. The lower commissure contacts the infraorbital (?) and dorsomedial canals (Fig. 31C) or at least the last one (Fig. 32A) in one point, and the upper commissure probably unites only with the infraorbital one. Unlike the representatives of the Podolaspididae (*Podolaspis, Parapteraspis*; Figs 32A, E, 49A), in *Larnovaspis* (Figs 31A–D, 60A), *Zascinaspis* (Figs 31E, 71B) and, judging from the figures of Zych (1931: figs 41, 49), in *Althaspis*, there are H-like bridges in the place of departure of the supraorbital commissures from the supraorbital canals. They may serve as diagnostic features at the level of family.

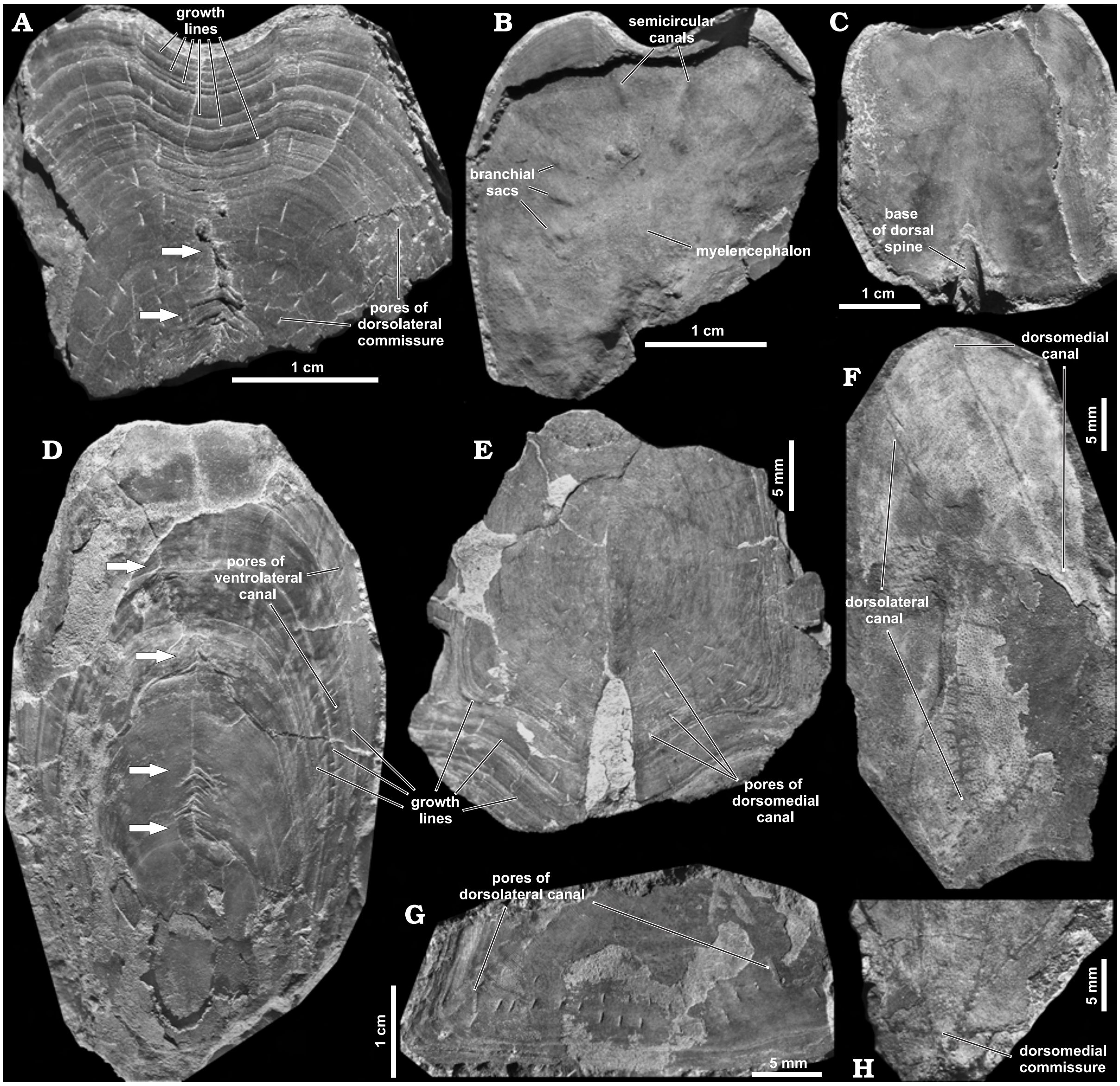

Fig. 33. Morphology of undetermined pteraspidids. **A**. Anterior part of dorsal shield SMNH BP.564 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, with signs of damaging and repairing of armour (white arrows). **B**. Anterior part of mould of dorsal shield SMNH BP.547 from the same locality with signs of internal structures. **C**. Partial dorsal shield SMNH BP.549 from the same locality, inside view. **D**. Partial ventral shield SMNH BP.1204 from same locality with signs of damaging and repairing of armour (white arrows). **E**. Partial dorsal shield SMNH BP.1477 from Dobrivliany, lower part of Ivanie Member. **F**. Left portion of dorsal shield SMNH BP.1241 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation. **G**. Right posterolateral part of dorsal shield SMNH BP.1476 from Dobrivliany. **H**. Central part of dorsal shield SMNH BP.1254 from the Horodnytsia quarry, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, with traces of sensory canals.

This pattern confirms that details of the arrangement of the sensory line system (at least, within the mentioned pteraspidid families) are of little adaptive importance. If this were not the case, variants of the arrangement would be more numerous. Such arrangement of supraorbital commissures has been observed in various cyathaspidids, *Liliaspis philippovae* Novitskaya, 1972 (see Novitskaya 1983: text-fig. 30a), *Poraspis polaris* Kiaer, 1930 (Novitskaya 1983: text-fig. 30b), and *Poraspis* sp. (Novitskaya 1983: text-fig. 36). This seems consistent with the probable descent of the pteraspidids from cyathaspidids. In *Tuberculaspis elyensis* Ilyes *et* Elliott, 1994 and *Lamiaspis longiripa* Ilyes *et* Elliott, 1994 from the Early Devonian of Nevada, supraorbital canals (if these are not commissures) are located in the same place as the supraorbital commissures in the Podolian pteraspidids (Ilyes and Elliott 1994: figs 2-4 and 6-1, respectively).

The lateral line system of the pteraspidids on the dorsal shield is represented by two pairs of longitudinal canals, dorsomedial (mdl) in the centre of the shield and dorsolateral (ldl) at some distance from its lateral sides (Figs 8E, 49A, 67A). Lateral and medial canals are connected by three pairs of transverse dorsolateral commissures which, except for the first pair, unite between themeselves in the primordial area of the shield by a corresponding dorsomedial commissure (Figs 33H, 34D, H, 54B, 72H). Such pattern, as far as it is known, is characteristic for all representatives of the suborder Pteraspidoidei. Dorsomedial canals are stretched out from the posterior margin of the shield along the notch for the dorsal spine (Figs 32D, 33E). On leaving from the primordial area, they diverge more or less, directed to lateral parts of the pineal plate (parallel type; Figs 31A, 32E, 57A, 58A, 67A, 70A) or to the basis of medial processes of the orbital plates (radial type; Figs 31C, D, 49A, 56C, 60A, 78A). Intermediate variants are also known; probably this depends on the lateral extent of the pineal plate (but see Blieck 1984: figs 17D and 42A for *Mylopteraspidella gracilis*). Nevertheless, all pteraspidids known to date possessed one of the two mentioned types of disposition of dorsomedial canals (see, e.g., Blieck 1984). The most abundant Podolian pteraspidid, *Zascinaspis heintzi*, demonstrates that the parallel type of the mdl canals is stable within the species (Figs 67A, C, 69B; Brotzen 1936: text-fig. 16; Blieck 1984: fig. 28B). Presumably, it refers also to other pteraspidids. This may mean two possibilities: (1) mentioned types of dorsomedial sensory canals are of little adaptive importance and randomly develop in various pteraspidids or (2) they developed convergently under strong selection pressure in different monophyletic groups of the pteraspidids. To solve the problem the functional significance of the described sensory canal arrangements has to be disclosed.

Within limits of the orbito-pineal belt, the medial canals unite with the pineal part of the supraorbital canal, or a "pineal" (inter-orbital; Figs 31B, D, 52B) canal according to some authors (concerning terminology see discussion in Novitskaya 2004: pp. 76–78) (*Parapteraspis*, *Zascinaspis*), or with the supraorbital commissure and infraorbital canal (*Podolaspis*, *Larnovaspis*, *Pavloaspis*). In the primordial area, at the level of contact with the second and third pairs of dorsolateral commissures, medial canals unite between themseves through transverse dorsomedial commissures.

The laterally inclined anterior part of the dorsomedial canals in the anchipteraspidids (Elliott 1983b: text-figs 2B, 5G, 7A, and 8A) and the radial type of these canals in *Protopteraspis* species (Blieck 1984: fig. 30), as in the most primitive representatives of the Pteraspidiformes, suggest that the radial type of the mdl canals in pteraspidids developed first. But already in relatively underived British *Pteraspis*, the mdl canals are of the parallel type (Blieck 1984: figs 5E, 38A, D).

All the mentioned taxa (except for *Pteraspis*) as well as *Canadapteraspis alocostomata* Dineley *et* Loeffler, 1976 (Northwest Territories, Canada; Blieck 1984: fig. 31A) share also the presence of the "pineal" sensory canal on the dorsal shield behind the pineal plate. Such a condition, but with the mdl canals of parallel type, is known in *Miltaspis anatirostrata* (Blieck, 1981) from Spitsbergen, *Stegobranchiaspis baringensis* Elliott, 1983 (Blieck 1984: figs 32A and 33B, respectively), and, possibly, *Unarkaspis schultzei* Elliott, 1983 (Blieck 1984: fig. 34A; Elliott 1983a: fig. 8C, D), both from the Northwest Territories, Canada. As far as it is known now, all other pteraspidids have the "pineal" canal within the limits of the pineal plate. In this connection an enigmatic case is the "pineal" canal that stretched almost to middle part of the dorsal shield in probable *Zascinaspis heintzi* (Fig. 68C). Incomplete preservation of this structure (and the entire specimen) prevents its more specific interpretation.

Based on the "pineal" canal position, Blieck (1984) proposed diagnoses of two families, the Protopteraspididae, with "pineal" canal behind the pineal plate, and the Pteraspididae with "pineal" canal within the pineal plate. Probably, the type of mdl canals is of not less significance. Unfortunately, the literature sources are contradictory, even in respect to the same species. For instance, according to Blieck (1984: fig. 41E following Brotzen 1933: fig. 4a, b) *Podolaspis podolica* has dorsomedial sensory canals of parallel type, whereas specimens PIN 3592/43a (Novitskaya 2004: text-fig. 69) and SMNH BP.170 (Fig. 49A) of the species show canals of radial type. Similar discrepancies are in data on *Parapteraspis plana* (compare Blieck 1984: figs 10A, 11A, and Figs 32E, 57A) and *Mylopteraspidella gracilis* (compare Blieck 1984: figs 17D, C, 42, and Fig. 56C, also Novitskaya 2004: text-fig. 73, pl. 10, fig. 7).

Dorsolateral canals, each on left and right parts of the shield, pass from the posterolateral corners of the dorsal shield (Figs 32D, 33F, G, 34E, 49B, 57B, 64A, 72H, 78A) along its lateral margins (on some distance from them) to the base of posterior processes of the orbital plates. There, they unite with the infraorbital canals. The dorsolateral canals, unlike dorsomedial ones, have numerous short simple branches (*Podolaspis*,

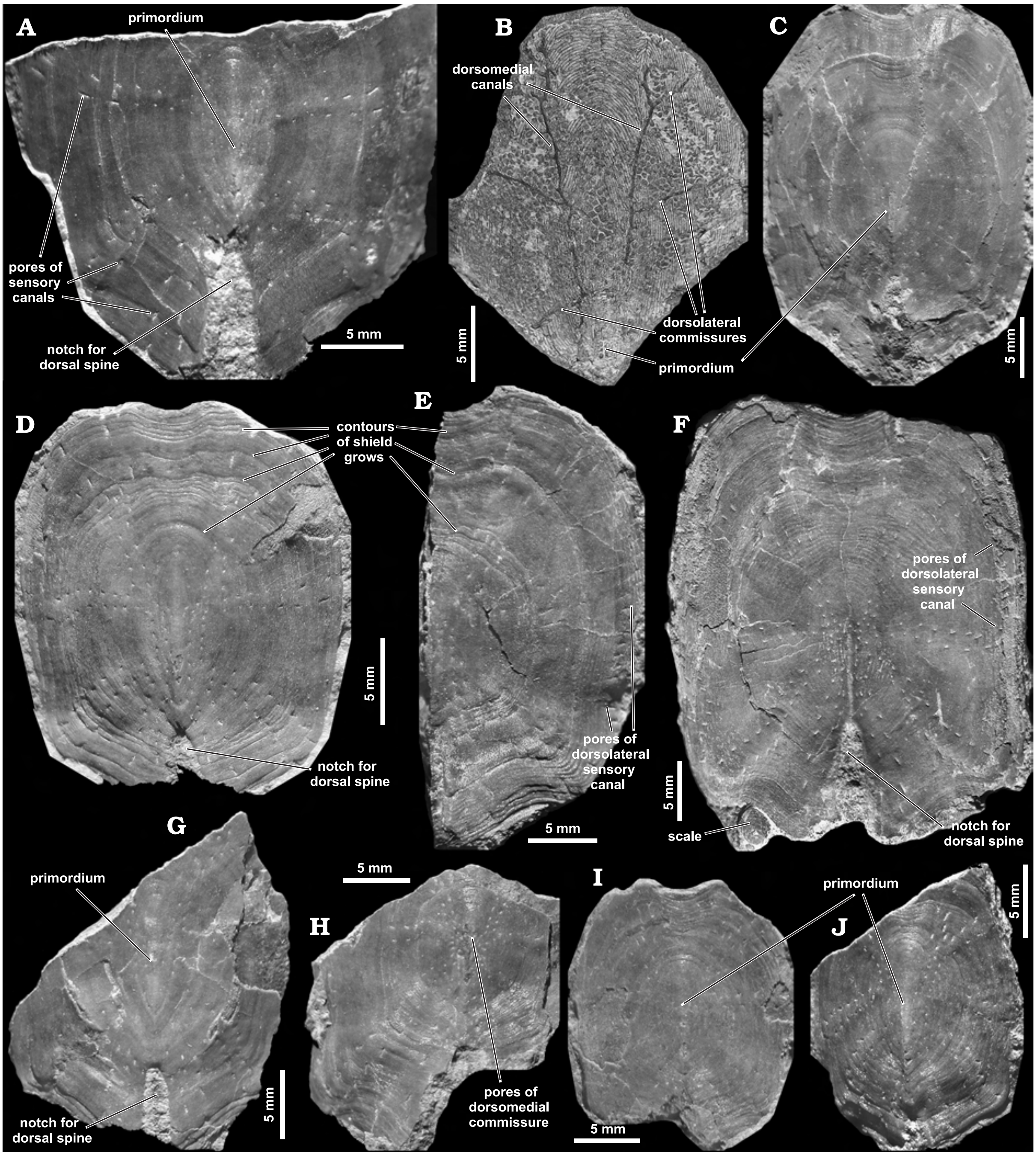

Fig. 34. Juvenile specimens of undetermined pteraspidids. **A**. Posterior part of dorsal shield SMNH BP.510/1 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation. **B**. Partial dorsal shield SMNH BP.570 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation with traces of sensory canals. **C**. Dorsal shield SMNH BP.1331 from Jagilnytsia Stara. **D**. Dorsal shield SMNH BP.566 from the same locality. **E**. Right part of dorsal shield SMNH BP.1208, same locality. **F**. Dorsal shield and lateral scale SMNH BP.535, same locality. **G**. Partial dorsal shield SMNH BP.518, same locality. **H**. Partial dorsal shield SMNH BP.517, same locality. **I**. Dorsal shield SMNH BP.522, same locality. **J**. Partial dorsal shield SMNH BP.511, same locality.

Larnovaspis; from tenths of a milimetre to 3 mm in *Zascinaspis heintzi*; Figs 32B–D, 33F). Similar branches may occur also in dorsolateral commissures (Fig. 62C).

Transverse dorsolateral commissures in general disperse radially from the primordial area: the first pair in the anterolateral, the second in the (antero-) lateral, and the third in the posterolateral direction (Fig. 34A–D).

On the ventral shield of the pteraspidids, the lateral line system is represented by the V-shaped postoral canal (Figs 8F, poc; 26C–I, 27C–G, 68F, 72C) and by a pair of longitudinal ventrolateral canals at some distance from its lateral sides (Fig. 8F, lvl). In addition, there is a set of short ventral commissures along the ventrolateral canals (Fig. 26F), as in the cyathaspidid *Poraspis*, but there are no ventromedial canals.

Longitudinal sensory canals are developed also on the trunk, at least one per body side. Their pores penetrate lateral scales (Fig. 28M, Q). Pores of sensory canals are at least of two kinds. Those located on the pineal plates, scales and other parts of armour are elongate (Figs 29A–C, F, G, J, 30A, D). Others, found on indeterminable carapace fragments (orbital plate?), are rounded; that may mean that these specimens represent different species (Fig. 29E, H, I). Dentine ridge ends at the pore margin possess a number of short obtuse outward-directed spines (Fig. 30D, E), presumably of protective function.

Internal anatomy of the pteraspidiforms. — Internal anatomy of the pteraspidids is less completely known than in the cyathaspidids. This is probably because the dorsal cartilaginous skeleton of the pteraspidid internal organs was thick and, except for the antero-dorsal part of the rostrum and the pineal organ, made these organs too distant from the carapace shields to leave an imprint on their interior surface (Novitskaya 1983). Only in the anchipteraspidids, the closest relatives of the cyathaspidids, the internal anatomy is visible well enough (Elliott 1983b: pl. 22, fig. 3, 6, pl. 23, fig. 1, pl. 24, fig. 6).

Nevertheless, traces of paired cartilages covering the nasal capsules (Figs 50B, 56B, 75D), and also the whole dorsal cartilage above them (Fig. 56B) are recognizable in some Podolian specimens. In rare cases, it is possible to see traces of four branchial pouches (probably, from the 3rd to the 6th ones), semicircular canals and myelencephalon on the mould of a pteraspidid dorsal shield from Jagilnytsia Stara (Fig. 33B). Impressions of semicircular canals of the labyrinth are also represented in the specimen of *Podolaspis ?lerichei* LIG 5-512 (Novitskaya 1983: pl. 22, fig. 3).

Possibly, the presence or absence of traces of internal organs in pteraspidid fossils is related to individual age of the animal. In younger individuals, a relatively thin cartilaginous skeleton gave more chance for the internal organs to be imprinted.

Ontogeny and evolution of the pteraspidiform armour. — The cyathaspidids were, probably, basal to the pteraspidids (Obruchev 1945; Denison 1964). Novitskaya (1983) proposed the evolutionary transition *Archegonaspis* (primitive cyathaspidid) → *Protopteraspis* (early pteraspidid). In addition to numerous homologies that support such phylogeny, also the arrangement of dentine ridges on the rostral plate of ?*Protopteraspis* sp. (Novitskaya 1983: text-fig. 43, pl. 22, fig. 2) testifies in favor of this interpretation. They are parallel to the body axis in the central part of the plate, which is characteristic for this area in many cyathaspidids, but not in advanced pteraspidids. This has been further strengthened with description of the anchipteraspidids (five species of *Anchipteraspis*, *Ulutitaspis*, and *Rhachiaspis*), primitive pteraspidomorph heterostracans from the Late Silurian and Early Devonian of the Canadian Arctic. They are similar to the cyathaspidids in having a single fused orbito-cornual plate and a pineal plate that is still totally enclosed by the dorsal shield (Elliott 1983b), and in arrangement of the sensory line system canals on the dorsal shield (Janvier 1996: fig. 4.7.B). Their pattern is closely similar to the condition in *Protopteraspis*. Other pteraspidiform features of the anchipteraspidids are the presence of a separate dorsal spine, the concentric arrangement of the dentine ridges in armour ornamentation, and the mode of dorsal shield growth (Elliott 1983b; Janvier 1996).

If the pteraspidids did evolve from primitive cyathaspidids, how did their carapace originate? According to Obruchev (1945), formation of the armour in the pteraspidids was initiated in earlier stages of the ontogeny than in the cyathaspidids. This resulted in the appearance of numerous centres of ossification. Each plate of the carapace, regardless of its final size, developed from an oval centre of plate cyclomorial growth. Usually, the primordium is located in the middle of the plate and it can be easily identified (for example, on the dorsal shield: Fig. 34A, D, G–J; on the rostral plate, Fig. 19G; on the ventral shield, Fig. 27A; on the oral plates, Fig. 19E). In the case of plates located outside the trunk, branchial and cornual plates, and the dorsal spine, the primordia were located on their apices (Figs 24D, 25F).

At a certain stage of ontogeny, plates of the carapace met. Their further growth was carried out at close contact and zones of growth developed at boundaries between them. As a result, the sutures between plates took characteristic shapes. There are orbital indentations on the posterior margin of the rostral plate, pineal indentation at the anterior margin of the dorsal shield, etc.

Finds of dorsal shields that are without traces of dorsolateral sensory canals (presumably they did not develop yet) (Fig. 34B, D, H, J; see also for comparison Fig. 34E, F) but with developed pineal notch testify that plates of the carapace did not close up simultaneously. Probably, the rate of growth differed not only in whole plates but also they grew with different rates in various directions.

The sensory system of pteraspidids probably developed from that of early cyathaspidids (Novitskaya 1983), in which transversal commissures were more or less evenly distributed along the dorsal shield. In the evolution of the Pteraspidoidei, the commissures were displaced backwards to the base of the dorsal spine. A primitive arrangement of the commissures close to the cyathaspidian one was identified only in the anchipteraspidids and *Protopteraspis* (possibly, also in *Pteraspis*? *dixoni* (White, 1938)). In all other representatives of the suborder with known lateral line system, the commissures are more or less displaced towards the basis of the dorsal spine. This tendency reached extremes in the late wide-shielded pteraspidids (*Brachipteraspis*, *Europrotaspis*, etc.).

The ancestral pteraspidid probably had a small club-shaped orbital plate, with rounded anterior end (lacking any differentiation of the anterior and medial processes) and the posterior process somewhat elongated and sharp-ending. Its pineal plate was small and had triangle-rounded or oval outline. Such morphology is represented in the early ontogeny of advanced pteraspidids (Fig. 19G; Novitskaya 1983: text-figs 11, 12) and in mature individuals of the geologically oldest member of the group, *Protopteraspis* (Blieck 1984: fig. 30). In Podolia, however, such adult forms have not been encountered.

The next stage in the evolution of the orbito-pineal belt seems to be represented by the state when short and, as a rule, sharpened anterior and medial processes developed in the orbital plates (Podolaspididae, *Pavloaspis*; Figs 50C, 52A, 54A, 56A, E, 58C, 78A). As has been already indicated, the belt with orbital plates discontinuous (or contacting in one point) is rather conservative in its shape and proportions. The pineal plate develops various shapes there.

In a subsequent stage of evolution, plates of the orbito-pineal belt enlarged (with the leading role of the median processes of the orbital plates) and the belt becomes continuous, of ribbon-like shape. In some varieties, the shape of the anterior orbital processes changed. They became massive and expanded, changing curvature of their lateral margins (*Larnovaspis iwaniensis, Belgicaspis, Alaeckaspis*; Figs 65B, C, 66B).

Although these evolutionary trends of development of the orbito-pineal belt are rather apparent, in Podolia pteraspidids with different types of the belt coexisted for a long time. Species with the first (discontinuous) or second (one-point-contact) types of the belt have not been found only in the third Old Red zone (after Brotzen 1936), and only species with the first type of the belt (*Podolaspis*) occur for certain in the most ancient deposits with pteraspidid remains (from upper part of the Chortkiv Stage).

In taxonomy of the pteraspidids, the following carapace components seem to be of special value: (1) rostrum, (2) orbito-pineal belt, (3) dorsal shield, (4) branchio-cornual region of the carapace and corresponding plates, (5) dorsal spine (or, in special cases, its notch), (6) sensory line system, (7) sculpture of dermal skeleton (dentine ridges). Morphometric indices of length to width ratios of separate carapace plates (RL/RW, DW/DL) also appear useful. The morphology of the ventral surface of the rostral plate may be taxonomically useful, but it is poorly represented in the available material. The ventral shield morphology is too poorly known to base taxonomic decision on it, with the exception of “wide” pteraspidids *Zascinaspis*, *Brachipteraspis*, *Europrotaspis*, and elongated *Althaspis*. Despite its simple outline, the ventral plate may offer other taxonomically instructive aspects of its morphology, for instance its shape in anterior and lateral views (Figs 26A, 27C, 77D) and its height. Also, location of the V-shaped postoral sensory canals has some diagnostic potential.

OSTEOSTRACANS

The completely fused headshield of the osteostracans (Fig. 8C, D) bore nasohypophyseal, pineal and (for both sides from the last) orbital openings on the elevated central part of the dorsal side. The oralobranchial cavity (Figs 35A, C, 83A) is opened on the flattened ventral side of the shield at the oralobranchial fenestra, which is covered by minute scales (dermal denticles) or larger plates (not preserved in the Podolian material). The mouth opened anteriorly along the margin of the oralobranchial fenestra and laterally. There is a number of branchial openings along its margin. The shield had in general a horseshoe-like shape due to the wide semicircular anterior margin and the paired lateral extensions usually directed latero-caudally: the cornual processes (*cornua*). Sometimes, the internal margin of the cornual processes was serrate (Figs 84A, 85B). A pair of fins, that are very rarely fossilized and unknown in the Podolian material, was located in pectoral sinuses between the cornual processes and the abdominal portion of the shield. Dorsal and lateral sensory fields which, as is assumed by Forey and Janvier (1993), served as detectors of vibrations in the water, occupied the area behind the orbito-pineal region in the central part of the shield, and along the lateral margins of the shield. Many osteostracans had a dorsomedial crest (spine) on the abdominal part of the shield behind the dorsal field. It may be rudimentary (Fig. 84C) or of considerable size (Figs 85D, F, G, 93B). The abdomen-tail part of the body was covered with scaly trunk segments (Figs 90A, 94A, B).

Janvier (unpublished manuscript) has noted that the body length of the Late Silurian and Early Devonian osteostracans ranges from 50 mm to 300 mm. The largest known shields are known in *Trewinia magnifica* (Traquair, 1893) from the Mid Devonian of Scotland (Janvier and Newman 2004) and in the osteostracan genera *Parameteoraspis* (Janvier 1985a, pls. 5, 6) and *Diademaspis* (Janvier 1985a, pl. 2) from the Early Devonian of Spitsbergen. They reach up to 330 mm in width. It is noteworthy that *Parameteoraspis* and *Diademaspis* species from Podolia are of much smaller sizes than their relatives from Spitsbergen (Afanassieva 1991; Voichyshyn 2006a). The Early Devonian vertebrate fauna of Spitsbergen is remarkable also for the most minute osteostracan shields, for example, *Acrotomaspis instabilis* with a width of 11.0 mm and length of 13.5 mm. The benneviaspidid osteostracan *Hapilaspis apheles* Mark-Kurik *et* Janvier, 1995, from the Early Devonian of Severnaya Zemlya, has its headshield of about 17 mm width and 12 mm length (Mark-Kurik and Janvier 1995: fig. 10). The largest shields of Podolian osteostracans belong to *Zenaspis*. That of *Z. major* is of 180 mm in width and about 120 mm in length. The smallest known Podolian osteostracan is *Mimetaspis concordis* with a shield width of 27 mm and length of 20 mm.

Finds of articulated osteostracans, which allow measuring body length and estimate headshield to trunk proportions, are very rare in Podolia. In those available, for example *Zychaspis* sp. (Fig. 88B), length of the trunk-caudal part of body takes about 54% of the total body length, which equals approximately 150 mm (Voichyshyn and Solodkyi 2004).

Shapes of the osteostracan headshield. — The shape of the headshield is one of the important diagnostic features in taxonomy of the Osteostraci. The anterior (rostral) margin of the headshield of the Podolian osteostracans may be widely arched in *Parameteoraspis dobrovlensis* (Afanassieva 1991: text-fig. 12b), species of *Mimetaspis* (Fig. 83B, C, E; Janvier 1985b: fig. 17A) and especially *Benneviaspis* (Figs 1A and 86A; Belles-Isles and Janvier 1984; Afanassieva 1989: text-fig. 1a), species of *Citharaspis* (Belles-Isles and Janvier 1984: fig. 2A; Afanassieva 1989: text-fig. 1b), *Ukrainaspis kozlowskii* (Fig. 86B, C; Afanassieva 1991: text-fig. 15a), species of *Zenaspis* (Voichyshyn 2006b: fig. 2C–E), and perhaps also in *Diademaspis stensioei* (Afanassieva 1989: text-fig. 3). *Benneviaspis whitei* has two widely rounded angular extensions on sides of the shield, which delimit the boundary between anterior and lateral shield margins (Fig. 86A; Belles-Isles and Janvier 1984: fig. 1A), while *Benneviaspis talimaae* is remarkable in having two lateral lobes and a rostral one, all of them sharply pointed (Afanassieva 1990: fig. 1a). Some species show a constriction in the anterior part of the shield that modifies the rostral contour, as it is in "*Cephalaspis*" *microlepidota* (Afanassieva and Voichyshyn 1991: fig. 3). *Zenaspis kasymyri* sp. n. represents an intermediate variant (Fig. 96E). Several forms, such as *Pattenaspis rogalai* (Fig. 85A, D) and especially *Stensiopelta pustulata* (Figs 35E, 90C), all *Zychaspis* species (Figs 87B, D, 88A–C) and various related scolenaspidian forms (Figs 35A, 91C) have a more or less developed rostral lobe. *Wladysagitta janvieri* shows a rostral ledge of appearance similar to a true rostrum (Fig. 99B, C).

In general, the Podolian cephalaspidids and zenaspidids possess a gently rounded rostral margin of the headshield, whereas scolenaspidids and related forms show angularities, extensions, or lobes expressed to different degrees.

The headshield of *Benneviaspis talimaae* is unique among the osteostracans, in that its lateral margins are separated by a depression in the shield contour from cornual processes, resulting in the cornual processes projecting laterally (Afanassieva 1990: fig. 1a, b). Among other osteostracans, some irregularity in the lateral margin curvature seems correlated with size of massive cornual processes, in such large forms as *Tegaspis waengsjoei* (Belles-Isles and Janvier 1984: fig. 3), *T.*? sp. 1 (Fig. 35F), and, possibly, *Zenaspis podolica* (Fig. 93B).

The cornual processes of the Podolian osteostracans differ in size, ranging from being relatively short in *Parameteoraspis* and *Benneviaspis* species, and *Zenaspis dzieduszyckii* (Figs 35D, 86A, 95A, B; Afanassieva 2004: text-fig. 23) to long and very long in *Stensiopelta* and *Victoraspis* (Figs 35E, 91B; Carlsson and Blom 2008: fig. 1B). They curve more or less caudally or latero-caudally (Fig. 35A–C). Such condition is

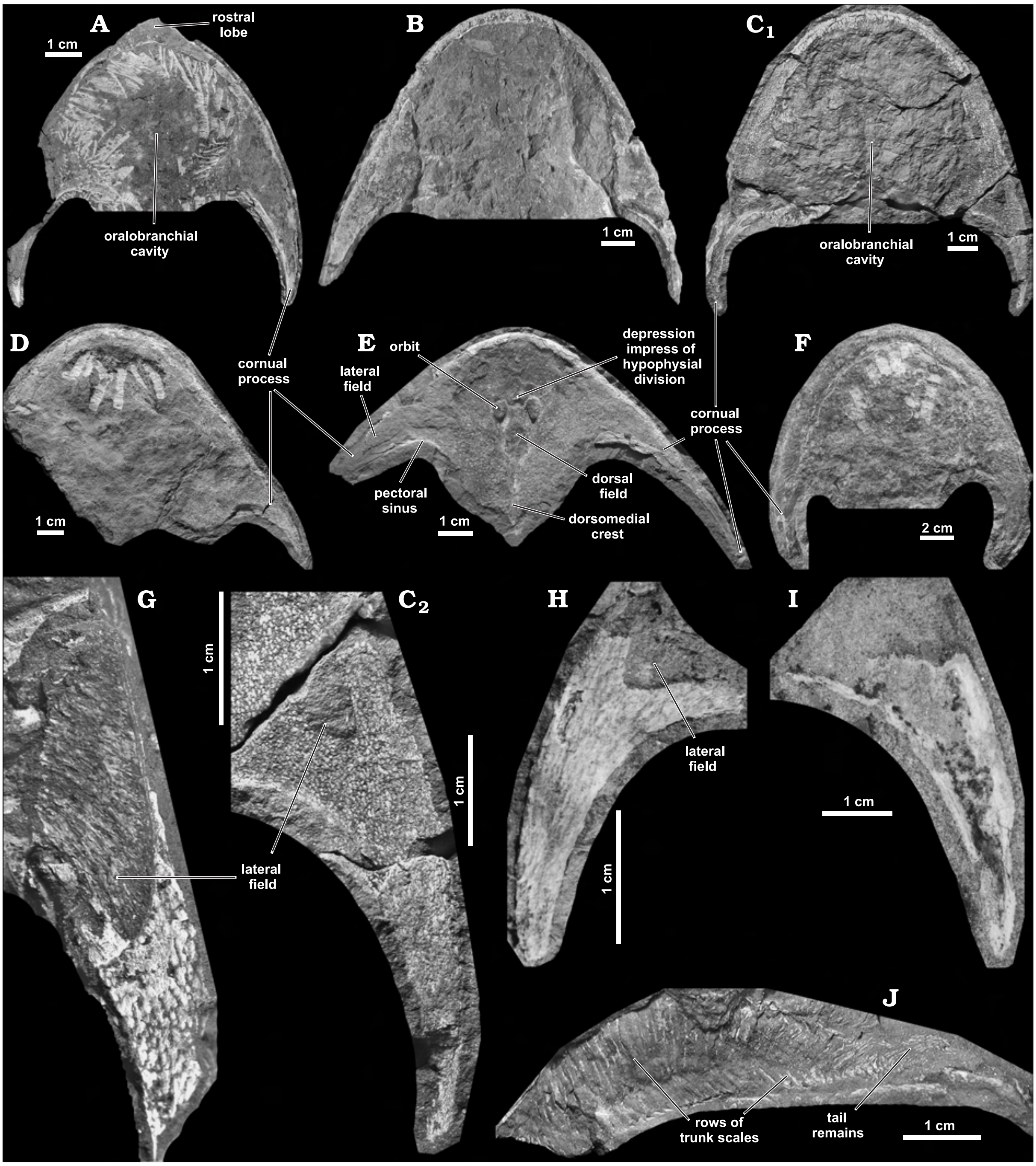

Fig. 35. Morphology of the osteostracans. **A**. Scolenaspididae gen. indet., fragmentary headshield SMNH BP.109 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, ventral view. **B**. Scolenaspididae gen. indet., headshield margin SMNH BP.106 from the same locality, ventral view. **C**. Scolenaspididae gen. indet., headshield margin SMNH BP.901/9 from the same locality, ventral view and imprint of cornual process. **D**. *Zenaspis dzieduszyckii* Voichyshyn, 2006, partial headshield margin SMNH BP.1215 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, ventral view. **E**. *Stensiopelta pustulata* Janvier, 1985, imprint of headshield SMNH BP.5 (lacking distal part of right cornual process) from unknown locality in Podolia, probably Ustechko or Khmeleva Member, dorsal view. **F**. *Tegaspis*? sp. 1, margin of headshield SMNH BP.53 from Nagiriany W (probably slope of Dzhuryn River), Ustechko Member or lower part of Khmeleva Member, ventral view. **G**. Scolenaspididae gen. indet., posterior end of lateral field SMNH BP.201/3 (see also Fig. 101F) from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation. **H**. Scolenaspididae gen. indet., cornual process SMNH BP.935/1 from the same locality. **I**. Cephalaspidiformes indet., distal part of cornual process SMNH BP.51 from Budaniv W, 2nd quarry, talus, upper part of Chortkiv or lower part of Ivanie Member. **J**. ?*Stensiopelta* sp., imprint of trunk-tail part SMNH BP.901/10 from Nagiriany, slab from talus at SE slope of Dzhuryn River, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation.

characteristic for the Zenaspididae and cephalaspidids, except for the *Parameteoraspis*. The curvature of the cornual processes is strong in *Zenaspis podolica*, *Zychaspis siemiradzkii*, *Victoraspis* and, especially, in *Zenaspis kasymyri* sp. n. and *T.*? sp. 1 (Figs 35F, 92C, 93B, 96E). On the contrary, *Stensiopelta*, *Parameteoraspis*, and benneviaspidids have cornual processes that tend to project laterally (to greatest degree in *Benneviaspis talimaae*). The greatest relative length of the cornual processes of Podolian osteostracans is observed in *Victoraspis longicornualis* (Lrc/Ls 2.25). Denticles on the inner margin of the cornual processes are present in species of *Mimetaspis* and *Pattenaspis* (Figs 84A, 85B). The cornual processes disappeared in *Citharaspis* species (Belles-Isles and Janvier 1984: fig. 2A; Afanassieva 1989: text-fig. 1b) where only lateral or "cornual" corners are developed.

The outline of the abdominal division, as a part of the shield contour, depends on the shape of the pectoral sinuses. A shallow pectoral sinus results in a short and indistinct abdominal part of the shield (as in the Podolian species of *Mimetaspis*). The longest abdominal division is demonstrated by "*Cephalaspis*" *microlepidota*, where the abdominal division begins behind the level of the external openings of the endolymphatic ducts (Fig. 91C), as well as *Stensiopelta* (Figs 35E, 90A, D, 91A) and, probably, *Victoraspis*. All these osteostracans, except for "*Cephalaspis*" *microlepidota*, show more or less expressed posterior narrowing of this part of the shield. The same is observed in *Tegaspis waengsjoei* (Belles-Isles and Janvier 1984: fig. 3). A very wide and extremely short abdominal division is seen in *Benneviaspis* and *Citharaspis*, as the pectoral sinus in the former is wide and shallow (Fig. 86A), being virtually lacking in the latter. Sometimes, the pectoral sinus is asymmetric, with its tip closer to the axis of the body (*Mimetaspis*, *Pattenaspis*, *Wladysagitta*, *Stensiopelta*, and *Zenaspis podolica*). In all Podolian osteostracans, the abdominal division (its interzonal part) bears a more or less expressed medial projection projecting caudaly. A dorsomedial crest or spine may develop there. It is prominent in such large forms as *Zenaspis podolica* (Figs 93B, 94A), and possibly in other zenaspidids (Fig. 96C), but it is very low in Zenaspididae gen. indet. (Fig. 92B) and in *Ukrainaspis kozlowskii* (Afanassieva 2004: pl. 13, fig. 3). It was relatively large also in *Pattenaspis rogalai* (Fig. 85D, F, G). In species of *Mimetaspis* and *Zychaspis*, the median dorsal crest is very small and hardly visible (Fig. 84C). In *Stensiopelta*, it is low and small, but in contrast with other Podolian osteostracans with a median dorsal crest, it is displaced forward from the posterior margin of the shield (Figs 37A, 90A, B, D, 91A). It is not clear whether the medial dorsal spine was developed in any Podolian osteostracan. Possibly, it was present in *Machairaspis* sp. (Janvier 1985b: fig. 15) or in "*Cephalaspis*" *microlepidota* (Fig. 91C) but it has been broken off in both the specimens. Benneviaspidids and citharaspidids do not have any dorsal median crest.

The trunk division of the osteostracans was covered with rows of elongated scales usually extending transversely to the body axis. This part of the body is rarely represented in the Podolian material (Figs 35J, 90A, 91B; Carlsson and Blom 2008: fig. 1A, B). Several specimens of *Zenaspis podolica* with a dorsal ridge row of scales articulated with the headshield were found (Fig. 94A, B). Generally, articulated osteostracans are extremely rare in Podolia (Fig. 88B).

Sensory organs. — A pair of orbits was situated in the central part of the shield (in the orbito-pineal zone). They are usually oval (rarely, more rounded) in shape; their longitudinal axes may be inclined to the body axis. Size of the orbits may be relatively small (*Benneviaspis*, *Ukrainaspis kozlowskii*) or large (*Mimetaspis*, *Pattenaspis*, *Zenaspis dzieduszyckii*). Some species show a circumborbital thickening surrounding the orbits (Fig. 36B–E). Usually, it was covered with small tubercles.

The pineal plate is placed between the orbits. It is transversely extended in *Pattenaspis rogalai* (Fig. 85A). In several forms (*Mimetaspis*, *Benneviaspis*, and *Citharaspis* species, and *Parameteoraspis dobrovlensis*), the pineal plate is lacking (Fig. 84C, D) or fused with the dorsal field (*Zychaspis granulata*, Fig. 36C). It is reduced or absent also in *Diademaspis* (Fig. 96C). The pineal foramen, oval or round in shape, is situated between the orbits and in the centre of the pineal plate, if developed.

There is a nasohypophyseal opening in front of the pineal foramen (Figs 36A–D, F, 91A). Usually, it is key-hole shaped, nasal and hypophyseal divisions being more or less of the same size and shape (Figs 36C, F, 86C). In the Benneviaspididae, the nasohypophyseal opening is elongated and narrow (Fig. 86A). In the Zenaspididae, the hypophyseal division is, as a rule (and especially in *Diademaspis*; Figs 36B, 96C), larger than the nasal division. The hypophyseal division was located in a triangular or oval depression (Figs 36B, D, 85F, 90A, B, D, 92E), while the nasal one on an elevation (Figs 36A, 84C, 85C, D).

The dorsal (median) field is situated in the central part of the shield between the pineal plate and the median dorsal crest, or the abdominal division of the shield. It comes in a variety of shapes. Usually, it is elongated axi-

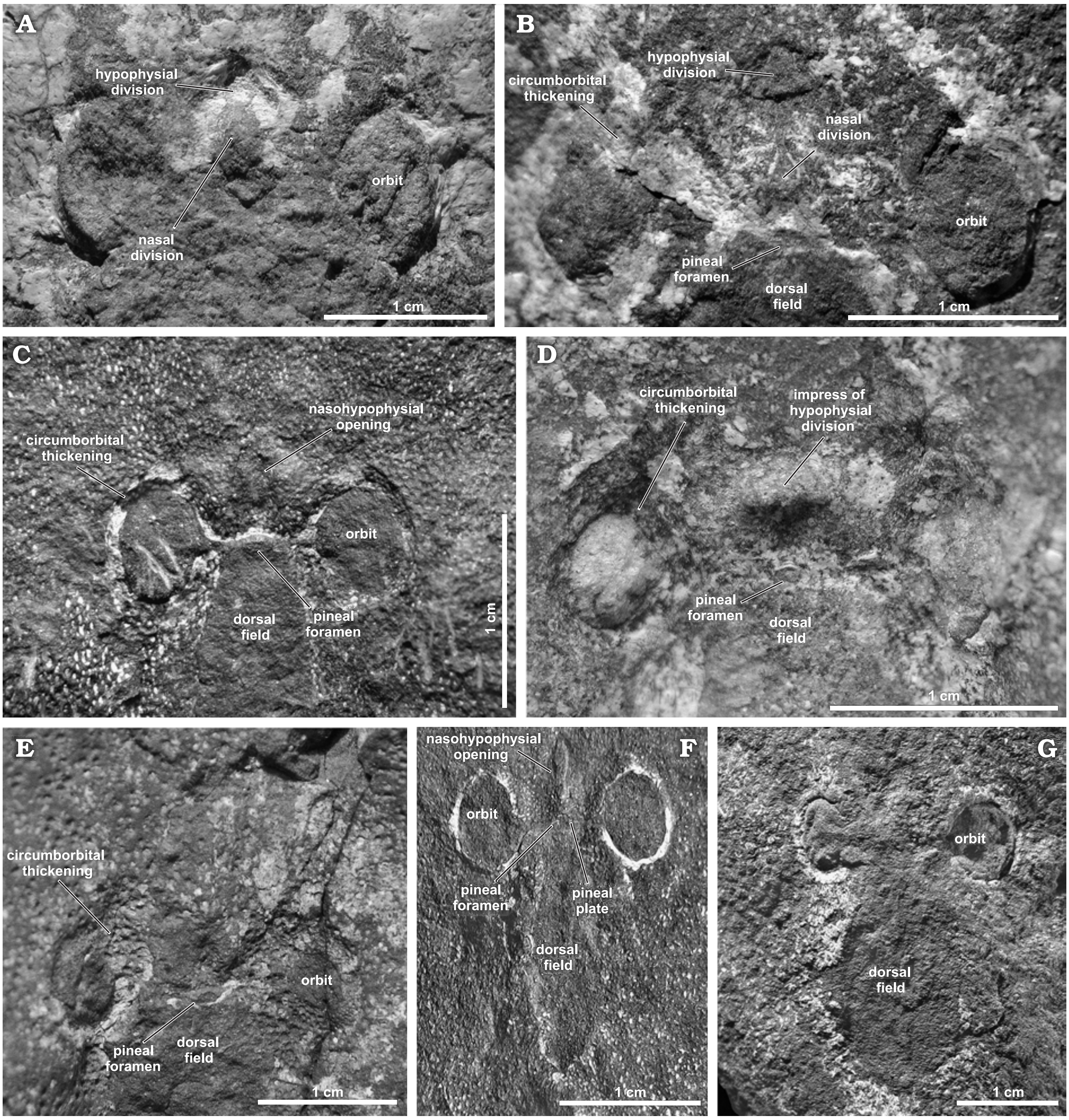

Fig. 36. Morphology of the osteostracans. **A**. Zenaspididae gen. indet., nasohypophyseal and orbito-pineal zone of headshield SMNH BP.86 (see also Fig. 92B) from Ustechko, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **B**. *Zenaspis podolica* (Balabai, 1962), nasohypophyseal and orbito-pineal zone of headshield SMNH BP.36 (see also Fig. 93C) from the same locality, talus. **C**. *Zychaspis granulata* Voichyshyn, 1998, central part of imprint of headshield SMNH BP.49 (see also Figs 87A, 88C) from Ustechko, lower part of Khmeleva Member. **D**. *Zenaspis dzieduszyckii* Voichyshyn, 2006, nasohypophyseal and orbito-pineal zone of headshield SMNH BP.103 (see also Figs 93D, 95A) from the Horodnytsia old quarry talus, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **E**. *Diademaspis stensioei* Afanassieva, 1989, nasohypophyseal and orbito-pineal zone of headshield SMNH BP.945 (see also Figs 95A, 96D,) from the Horodnytsia new quarry, talus. **F**. *Zychaspis concinna* Voichyshyn *et* Solodkyi, 2004, central part of the holotype headshield SMNH BP.966/1 (see also Fig. 87D) from the Horodnytsia quarry. **G**. *Ukrainaspis kozlowskii* (Zych, 1937), central part of headshield mould SMNH BP.62 from Ustechko, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation.

ally and moderately broad in *Mimetaspis*, *Pattenaspis*, and many representatives of the Scolenaspididae (Figs 86C, 91A, 92A). In *Parameteoraspis*, it narrows caudally (Afanassieva 2004: pl. 10, fig. 5). In the species of Zenaspididae, it was considerably wider (Figs 92B, 93B, 94A, 95A, 96C). The anterior part of the field is often narrowed (*Mimetaspis concordis*, *Stensiopelta*, "*Cephalaspis*" *microlepidota*, etc.). The posterior margin is slightly pointed (*Stensiopelta*), rounded (*Mimetaspis*), or has two clear ledges (*Diademaspis* sp. 1, probably

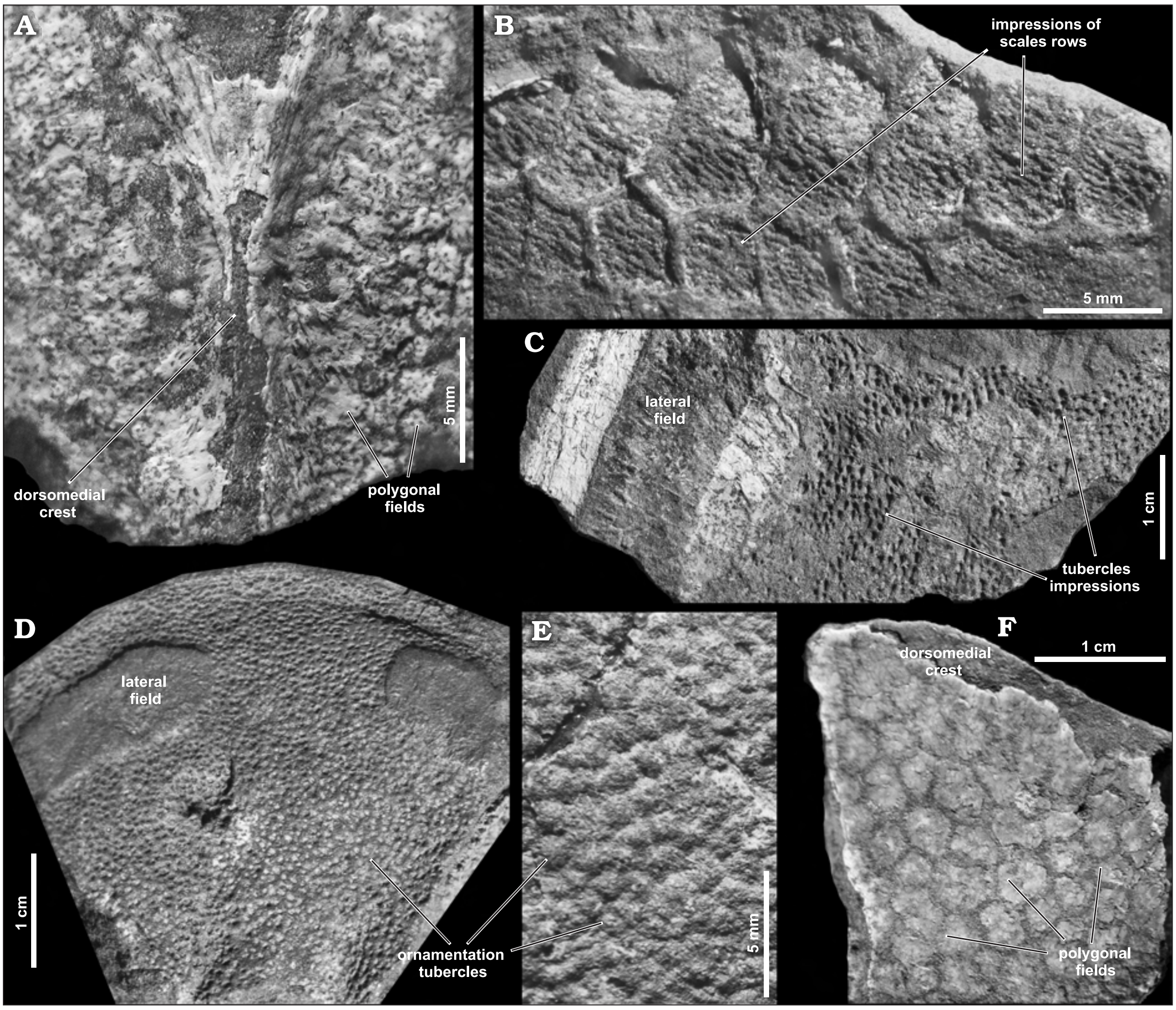

Fig. 37. Morphology of the osteostracans. **A**. *Stensiopelta pustulata* Janvier, 1985, interzonal part of headshield SMNH BP.8 (see also Figs 90B, 91A) from the Horodnytsia old quarry, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **B**. *Zenaspis podolica* (Balabai, 1962), enlarged impint of the trunk SMNH BP.30 (see also Fig. 94B) from Ivanie-Zolote, lower part of Ustechko Member of the Dniester Formation. **C**. ?*Diademaspis* sp., fragmentary imprint of headshield SMNH BP.1124 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, in dorsal view. **D**. Zenaspididae gen. indet., imprint of anterior part of headshield SMNH BP.968 from an unknown locality in Podolia, lower part of the Dniester Formation, dorsal view. **E**. *Ukrainaspis kozlowskii* (Zych, 1937), sculpture of headshield SMNH BP.17 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member. **F**. *Zenaspis podolica* (Balabai, 1962), part of headshield around dorsomedial crest SMNH BP.26 from Ustechko, left bank of Dniester River, Ustechko Member or lower part of Khmeleva Member, lateral (right side) view.

“*Cephalaspis*” *microlepidota*). In the Benneviaspididae, the dorsal field is swollen and was as a rule wider than longer (Afanassieva 2004: pl. 11, fig. 3).

The lateral fields stretched along (and parallel to) the lateral margins of the shield, approaching anteriorly the rostral shield region, and extending posteriorly from the proximal part of the cornual processes (Zenaspididae and most Scolenaspididae; Figs 35C, G, H, 95A, 96A, B, E) to their distal ends (*Mimetaspis*; Fig. 83C–E). In the Benneviaspididae, the lateral fields reach the proximal part of the cornual processes. They extend then to the abdominal division of the shield bordering the pectoral sinus (Afanassieva 2004: pl. 11, fig. 3). The anterior part of the fields is sometimes rather broad, as in *Ukrainaspis* (Afanassieva 2004: pl. 8, figs 1, 2; Fig. 86C) or *Diademaspis* sp. (Fig. 37D). The posterior part is often widened if it enters the proximal part of the cornual processes (Zenaspididae; Figs 35G, 95A, 96B, E). *Tegaspis* shows a unique shape, having the fields with a posteromedial ledge (Belles-Isles and Janvier 1984: pl. 27, fig. 3), which developed further in *Benneviaspis* and *Citharaspis*. In the Zenaspididae, the position of the posterior end of the lateral fields relatively to the margins of the shield may be characteristic of genera (Voichyshyn 2006a). In *Pattenaspis* *rogalai* and *Zychaspis siemiradzkii*, the lateral fields are of more or less equal width along their extent, except for the ends (Figs 85B, E, 88A). Usually, the lateral fields lay close to the lateral margins of the shield, except for *Tegaspis waengsjoei* (Belles-Isles and Janvier 1984: fig. 3).

Structure of the osteostracan dermal skeleton. — The mineralized skeleton of the osteostracans is characterised by the presence of true bone, with osteocytes incorporated into the mineral tissue. Its ossification began before the animal reached one fifth of its mature size (Hawthorn *et al.* 2008). The dermal skeletal structures usually consist of three layers, superficial (formed with mesodentine), middle (built of bone tissue), and basal (formed with isopedine) (Afanassieva 1991). The surface of armour of some osteostracans (suborder Scolenaspidoidei) is covered by tubercles of different size and shape (Figs 35C, H, 36C, E–G, 37A, C–E). Besides lateral-line system canals, a network of canals outlining the polygonal fields was developed in the middle layer of the dermal skeleton (Figs 37F, 92B, F, 94A, B, 96E). It is believed that this network is related to the sensory lateral line system (Obruchev 1964; Afanassieva 1991). Probably, the polygons of the middle layer developed at an early stage of the ontogeny as isolated units and later, supported by the basal layer, accreted into the consolidated shield (Obruchev 1945).

Lateral line system and internal organs of the osteostracans. — Canals of the sensory line system of the osteostracans look like narrow grooves, lined with elongated tubercles on the shield surface, "sensory" tubercles, or ridges (Janvier unpublished manuscript; Afanassieva 2004). They are not preserved in material at my disposal. Infraorbital, postorbital and supratemporal canals, which are marked on the surface of the dermal skeleton by paired lengthened tubercles, are known in *Diademaspis stensioei* (Afanassieva 1989).

Internal organs are represented by traces of semicircular canals in *Mimetaspis concordis* (Fig. 84C), with the sel$_1$–sel$_5$ canals running from the vestibular cavity approaching the lateral fields in *M. concordis* and *Pattenaspis rogalai* (Fig. 85B, E), and also by the canals of the circulatory and nervous systems in *Zychaspis siemiradzkii* and *Stensiopelta* sp. (Figs 88A, 90D). The point of bifurcation of the sel$_1$ canal in *Pattenaspis rogalai*, located near the orbit (Fig. 85D, E), confirms its cephalaspidoidean nature.

Principles of taxonomy of the osteostracans, unlike heterostracans, are based not only on morphology of the dermal skeleton, but also on the internal anatomy that is widely accessible for studies due to perichondral ossification of the skull (Stensiö 1958; Afanassieva 1991, 2004). However, in Podolian material, as a rule, endoskeleton is not preserved. Therefore, comparative morphology of the head-trunk shield still remains a basic criterion for classification of Podolian osteostracans.

TAXONOMY

Class **PTERASPIDOMORPHI** Goodrich, 1909

Subclass **HETEROSTRACI** Lankester, 1868 (Pteraspides)

Order **Cyathaspidiformes** Kiaer, 1930

Family **Cyathaspididae** Kiaer, 1932

Genus *Seretaspis* Stensiö, 1958

1958. *Seretaspis*; Stensiö 1958: pp. 314–316, 318, 366, 371, 384, 386, 387, 391, 393.
1964. *Seretaspis*; Denison 1964: p. 366.
1964. *Seretaspis*; Stensiö 1964: pp. 250–252, 323, 326–328, 367.
1964. *Seretaspis*; Obruchev 1964: p. 59.
1986. *Seretaspis*; Novitskaya 1986: pp. 13–14.
2004. *Seretaspis*; Novitskaya 2004: p. 102.

Type species: *Seretaspis zychi* Stensiö, 1958; Early Devonian (Chortkiv Stage) of Podolia.

Diagnosis. — Dorsal shield is oval, relatively wide, with maximum width at its posterior third. The length of the shield ranges 25–30 mm. Anterior margin of the shield is widely rounded, the lateral margins are convex. There are epitega and postrostral field. Dentine ridges of the ornamentation are thin (8–9 cr/mm), parallel to margins of the shield and fan-like at the rostral epitegum.

Remarks. —The incompleteness of the single known specimen of the type species provoked different interpretations of relationship of *Seretaspis*. Stensiö (1958) proposed it was related to *Anglaspis*, but, as it has been shown by Denison (1964), this was based on conjectural interpretation of the posterior part of the shield. Denison himself (1964) considered *Seretaspis* similar to *Archegonaspis*. *Seretaspis* differs from *Archegonaspis* in having thinner dentine ridges (8–9 cr/mm against 4–6 cr/mm), relatively larger pores of sensory canals, and rather small shield (see Novitskaya 2004).

Species included. — Only type species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Seretaspis zychi Stensiö, 1958

1958. *Seretaspis zychi*; Stensiö 1958: p. 366, fig. 204.
1964. *Seretaspis zychi*; Denison 1964: pp. 366–367.
1964. *Seretaspis zychi*; Stensiö 1964: p. 323, fig. 109.
1986. *Seretaspis zychi*; Novitskaya 1986: p. 14, synoptic table, p. 137, fig. 2.
2004. *Seretaspis zychi*; Novitskaya 2004: p. 102.

Type specimen: Holotype (by monotypy) NHRM C1618 (according to Stensiö 1958: p. 204; or C1608a, b according to Denison 1964: p. 366), dorsal shield lacking its posterior part.

Localities and age. — Locality is unknown; Lochkovian (most probably Chortkiv or Ivanie Stage of the Tyver formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Family **Irregulareaspididae** Denison, 1964

Genus *Irregulareaspis* Zych, 1931

1931. *Irregulareaspis*; Zych 1931: pp. 83–84.
1964. *Irregulareaspis*; Denison 1964: pp. 401–402.
1964. *Irregulareaspis*; Obruchev 1964: p. 58.
1982. *Irregulareaspis*; Blieck 1982: p. 34.
1983. *Irregulareaspis*; Blieck and Heintz 1983: p. 52.
1986. *Irregulareaspis*; Novitskaya 1986: p. 18.
2004. *Irregulareaspis*; Novitskaya 2004: p. 105.

Type species: *Irregulareaspis stensioei* Zych, 1931; Early Devonian (Ivanie Stage) of Podolia.

Diagnosis. — The dorsal shield is small, oval, slightly elongated, from about 30 mm to 70 mm in length. Its anterior margin is widely rounded; the posterior one has a medial ledge. Preorbital processes are developed. Postbranchial blades are small. The ventral shield is of pentagonal shape, its width gradually expands approximately from the anterolateral corners to posterolateral ones. The anterior margin of the ventral shield is straight. The sensory line system is represented by a dense network of canals. Its minute pores are distributed densely at more or less regular intervals on the carapace surface. Dentine ridges are thin (8–13 cr/mm). In the central part of shields, their orientation is chaotic.

Species included. — Besides the type species: *I. seretensis* Novitskaya, 1983, Early Devonian, Ivanie Stage of Podolia; *I. skalskiensis* Novitskaya, 1983, Late Silurian, Skala Stage of Podolia; *I. hoeli* Kiaer, 1932 nom. nudum, Early Devonian, Red Bay Series of Spitsbergen; *I. complicata* Kiaer, 1932 nom. nudum, Early Devonian of Spitsbergen. *Irregulareaspis* sp. has been identified also in the Pod'emnaya Formation of Severnaya Zemlya (Blieck *et al.* 2002).

Occurrence. — From the Late Silurian to Early Devonian of Podolia (Ukraine); Early Devonian of Spitsbergen (Norway) and Severnaya Zemlya (Russia).

Irregulareaspis stensioei Zych, 1931

(Figs 38A–F, 39A–G)

1931. *Irregulareaspis stensiöi*; Zych 1931: pp. 83–84, 46–47, figs 5–7.
1964. *Irregulareaspis stensioi*; Denison 1964: p. 402.
1964. *Irregulareaspis stensioi*; Obruchev 1964: p. 58, fig. 17.
1983. *Irregulareaspis stensioei*; Blieck and Heintz 1983: p. 52.
1986. *Irregulareaspis stensioi*; Novitskaya 1986: p. 19, synoptic table, p. 137, fig. 5.

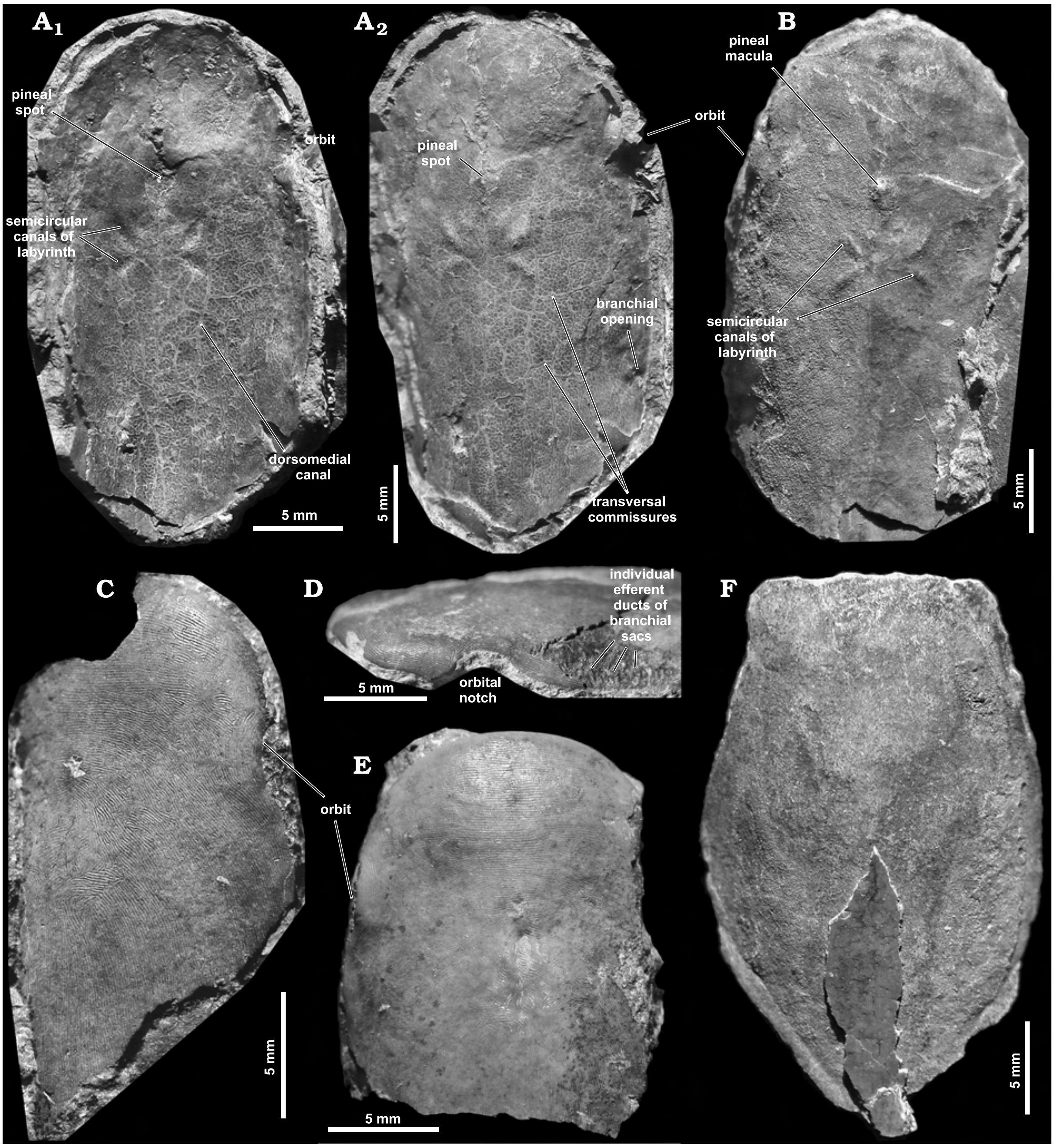

Fig. 38. Irregulareaspidid *Irregulareaspis stensioei* Zych, 1931 from Jagilnytsia Stara, the Ivanie Member of the Tyver Formation, Podolia. **A**. Partial dorsal shield SMNH BP.910/1, inside view. **B**. Partial mould of dorsal shield SMNH BP.912/1, dorsal view. **C**. Fragmentary imprint of anterior part of dorsal shield SMNH BP.507/2. **D**. Anterior part of dorsal shield SMNH BP.905 (see also Fig. 39A), lateral (left side) view. **E**. Anterior part of dorsal shield SMNH BP.504 (see also Fig. 39E), dorsal view. **F**. Mould of ventral shield SMNH BP.911/1.

2004. *Irregulareaspis stensioei*; Novitskaya 2004: p. 105.

Type specimen: Holotype (Zych 1931: figs 46, 47), dorsal shield; Jagilnytsia Stara, Chortkiv rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Referred material. — Fragments of dorsal and ventral shields SMNH BP.504, 507, 903/1, 904/1, 905, 906, 907, 909, 910/1, 911/1, 912/1–2, 913 and 914/1.

Diagnosis. — Relatively small-size *Irregulareaspis* with posterior margin of the shield extended into a blunt corner.

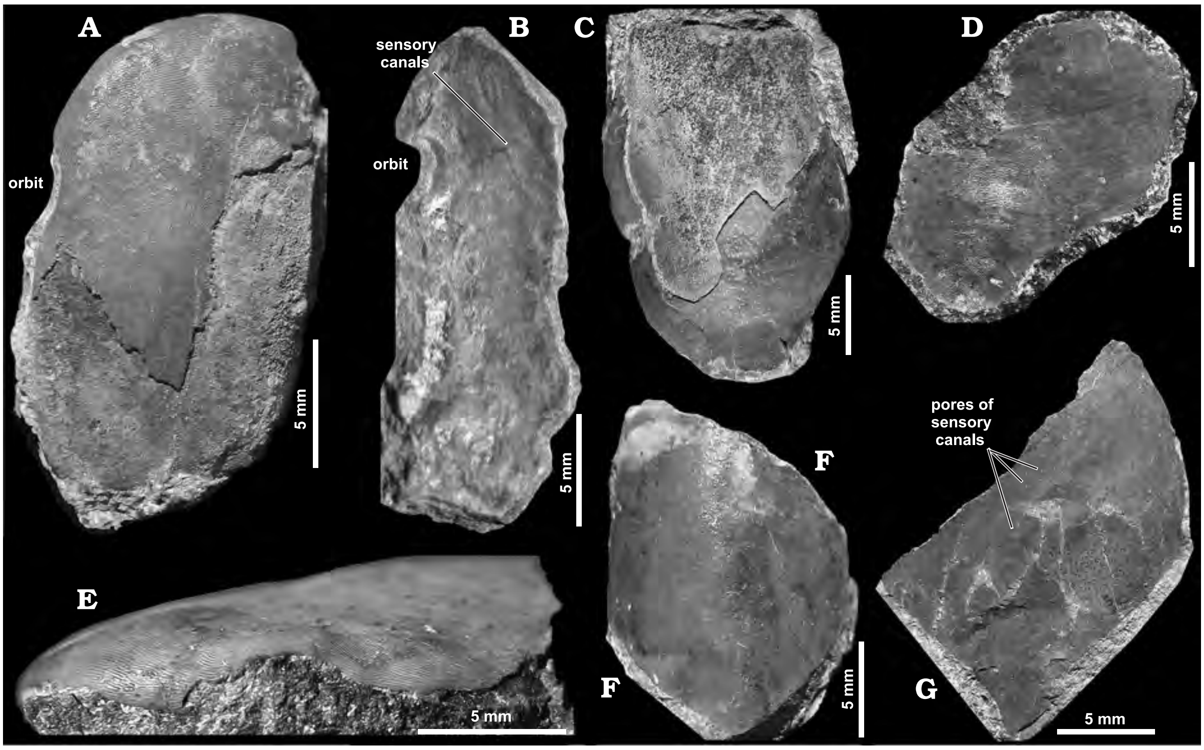

Fig. 39. Irregulareaspidid *Irregulareaspis stensioei* Zych, 1931 from Jagilnytsia Stara, the Ivanie Member of the Tyver Formation, Podolia. **A**. Fragmentary anterior part of dorsal shield SMNH BP.905 (see also Fig. 38D), dorsal view. **B**. Fragmentary dorsal shield SMNH BP.903/1, inside view. **C**. Mould of ventral shield SMNH BP.904/1 with fragments of armour. **D**. Fragmentary posterior part of ventral (?) shield SMNH BP.507/1. **E**. Anterior part of dorsal shield SMNH BP.504 (see also Fig. 38E), lateral (left side) view. **F**. Partial ventral (?) shield SMNH BP.906. **G**. Partial ventral (?) shield SMNH BP.907.

Description. — The dorsal shield is small, of 26–31 mm, but according to Zych (1931) up to 37 mm in length. W is about 17–22 mm, OW is 11.5–15.5 mm. The anterior margin of the dorsal shield is widely rounded. In the ventral shield, it is almost straight, with well-developed anterolateral corners. The posterior margin forms a corner at 108–113° angle in the dorsal and 90–100° in ventral shield. The orbital notches are visible from above. Dentine ridges (usually 10 cr/mm, at the posterior margin of the dorsal shield SMNH BP.909 8 cr/mm, in some ventral shields up to 13 cr/mm) are parallel to the anterior and lateral margins near them. In the central parts of the shields, beginning approximately from the level of orbits, their arrangement is chaotic. Dentine ridges are parallel to body axis at posterior part of the shields.

Comparison. — In contrast with this species, *I. complicata* has a different shape of the anterior (with preorbital processes) and the posterior (extended as a small ledge, instead of a blunt angle) margins of the dorsal shield. *Irregulareaspis hoeli* has longer and narrower ventral shield, relatively larger distance between antero- and posterolateral corners, and greater distinction in width of a shield at levels of the antero- and posterolateral corners. *Irregulareaspis seretensis* is generally of larger size. In size and shape of its holotype, *I. skalskiensis* is quite similar to specimens of *I. stensioei*. The significant age difference between these species is currently the only basis for their separation (see remarks on *I. skalskiensis*).

Localities and age. — Jagilnytsia Stara, also (Novitskaya 1986) Dobrivliany is specified; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine).

Irregulareaspis seretensis Novitskaya, 1983

1983. *Irregulareaspis seretensis*; Novitskaya 1983: p. 178, pl. 2, figs 6, 7.

1986. *Irregulareaspis seretensis*; Novitskaya 1986: p. 19, pl. 2, fig. 4.

2004. *Irregulareaspis seretensis*; Novitskaya 2004: pp. 105–106, pl. 1, figs 5, 6.

Type specimen: Holotype LIG 140/30, an almost complete ventral shield (Novitskaya 2004); north of Zvyniach, right bank of Seret River, Chortkiv rayon, Ternopil’ oblast’ (Podolia).

Remarks. —This is a large irregulareaspid. The ventral shield of the only known specimen, lacking the anterior end, is 53 mm long (Novitskaya 2004: pl. 1, fig. 5). Its maximum width (30 mm) is probably at the posterior third of the shield. Its posterior margin forms a corner at about 95° angle. The cr/mm index (8–10) and densely set pores of sensory canals (cf. with Fig. 39G) make it similar to *I. stensioei*, but in size (Novitskaya 2004) it is twice as large.

Localities and age. — Only the type locality; Lochkovian (Ivanie Stage of the Tyver formation). No similar material is known in the SMNH collection.

Irregulareaspis skalskiensis Novitskaya, 1983

1964. *Irregulareaspis*? sp.; Obruchev 1964: p. 58, pl. 1, fig. 5.
1983. *Irregulareaspis skalskiensis*; Novitskaya 1983: p. 178, pl. 2, figs 4, 5.
1986. *Irregulareaspis skalskiensis*; Novitskaya 1986: p. 20, pl. 3, figs 2–4.
2004. *Irregulareaspis skalskiensis*; Novitskaya 2004: p. 106, pl. 2, figs 1, 2.

Type specimen: Holotype PIN 2828/1, rostral part of dorsal shield (Novitskaya 1983); Dnistrove, Borshchiv rayon, Ternopil' oblast' (Podolia).

Remarks. —The type specimen is an anterior margin of a small irregulareaspid shield. Its contour is quite similar to that of *I. stensioei* (cf. Novitskaya 2004: pl. 2, figs 1, 2, and Figs 38A–C, E, 39A). Orbital width (OW) of *I. skalskiensis* is somewhat larger (16 mm) than of *I. stensioei* (13.5 mm), but in the latter species it may reach 15.5 mm. Probable complete length of the shield of 30 mm and dentine ridges of 8/10 cr/mm (Novitskaya 2004: p. 106) are similar to *I. stensioei*.

Localities and age. — Dnistrove (Fig. 3B); Late Pridolian (Dzvenygorod beds of the Skala Formation) of Podolia (Ukraine). This is the only Podolian armoured agnathan found in Late Silurian rocks. No similar material is represented in the SMNH collection.

Family **Poraspididae** Kiaer, 1932

Genus *Poraspis* Kiaer, 1930

1873. *Holaspis*; Lankester 1873: pp. 242–243.
1874. *Cyathaspis*; Alth 1874: p. 46 (pars).
1930. *Poraspis*; Kiaer 1930: p. 4.
1931. *Palaeaspis*; Zych 1931: p. 84.
1933. *Palaeaspis*; Brotzen 1933a: pp. 431–432.
1952. *Poraspis*; Wängsjö 1952: p. 562.
1953. *Poraspis*; Denison 1953: pp. 293, 296, 303–304.
1964. *Poraspis*; Denison 1964: pp. 403–404.
1964. *Poraspis*; Obruchev 1964: p. 58.
1972. *Poraspis*; Novitskaya 1972: p. 112.
1983. *Poraspis*; Blieck and Heintz 1983: p. 55.
1986. *Poraspis*; Novitskaya 1986: pp. 21–22.
1998. *Poraspis*; Elliott *et al*. 1998: p. 361.
2004. *Poraspis*; Novitskaya 2004: p. 106.

Type species: *Holaspis sericeus* Lankester, 1873; Early Devonian ("Grey Cornstone" near Abergavenny) of Wales (Elliott *et al*. 1998).

Diagnosis. — The dorsal shield is very small to large, usually elongated, 10–85 mm in length. The preorbital margin of the shield is rounded, and frequently narrowed. Its lateral margins are more or less convex and the posterior one has a medial ledge forming a corner (at angle ~90°) or lobe. Preorbital processes are developed. The branchial notches are visible or not. The anterior margin of the ventral shield is straight, and the posterior forms a corner with an obtuse angle. Dentine ridges (6–11 cr/mm) are mainly parallel to the body axis.

Species included. — Besides the type species: *Poraspis sturi* (Alth, 1874), *P. pompeckji* (Brotzen, 1933), *P. simplex* (Brotzen, 1933), *P. siemiradzkii* (Zych, 1931), and *P.* sp. 1, all from the Early Devonian of Podolia; *P. polaris* Kiaer, 1930, *P. brevis* Kiaer *et* Heintz, 1935, *P. rostrata* Kiaer *et* Heintz, 1935, all from the Early Devonian (Red Bay Series) of Spitsbergen; *P. barroisi* (Leriche, 1906), Early Devonian of France; *P. heintzae* Elliott, Loeffler *et* Liu, 1998, *P. cracens* Elliott, Loeffler *et* Liu, 1998, *P. thules* Elliott, Loeffler *et*

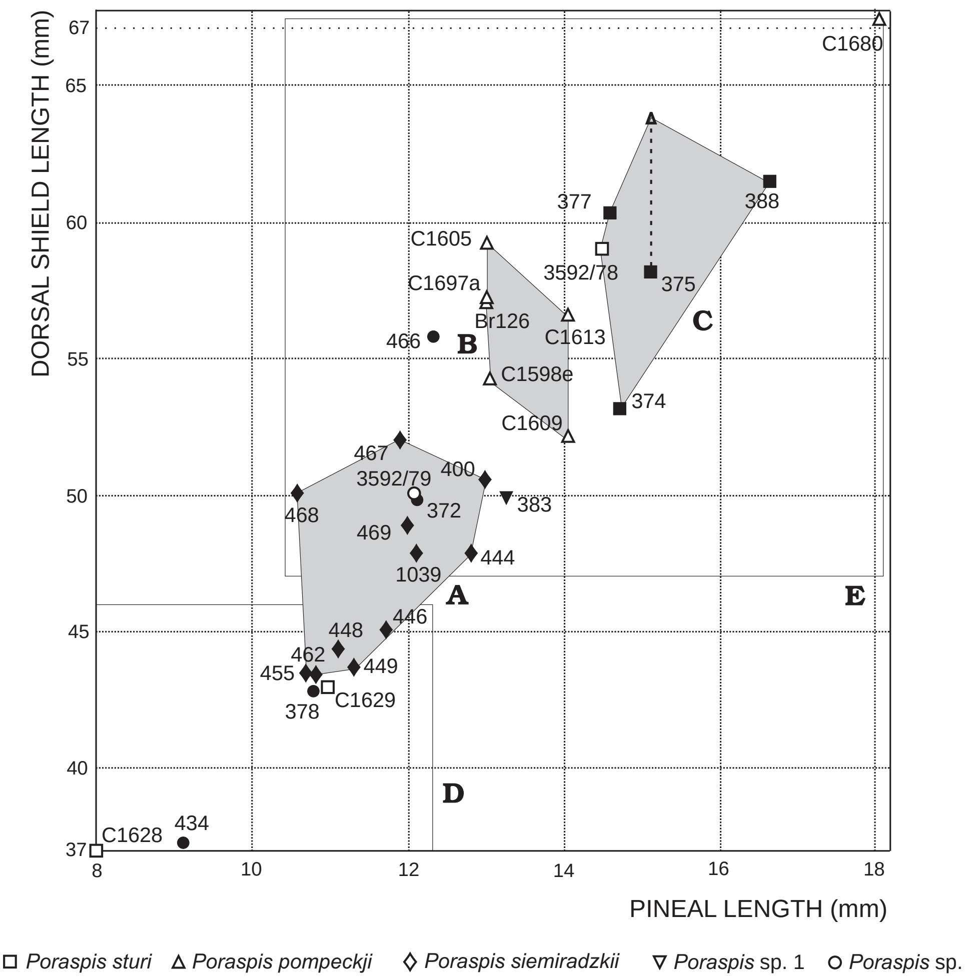

Fig. 40. Relationship between the pineal length (PL) and the complete length of the dorsal shield (ML) in Podolian specimens of *Poraspis* from the SMNH (black dots) and other (white dots) collections. Clusters of *Poraspis siemiradzkii* (**A**), *Poraspis pompeckji* (**B**), and *Poraspis sturi* (**C**). Shown also ranges of variability for *Poraspis polaris* (*P. sturi*) (**D**) and of *Poraspis rostrata* (*P. pompeckji*) (**E**) proposed by Blieck and Heintz (1983: fig. 11B, C). Measured specimens: *Poraspis sturi* (SMNH BP 374, 375, 377, 388; PIN 3592/78 from Novitskaya 2004: fig. 3B6; NHRM C1628, C1629 from Blieck and Heintz 1983: fig. 11); *Poraspis pompeckji* (NHRM C1598e, C1605, C1609, C1613, C1680, C1697a from Blieck and Heintz 1983: fig. 11; n126 from Brotzen (1933a); *Poraspis siemiradzkii* (SMNH BP.400, 444, 446, 448, 449, 455, 467, 468, 469, 1039); *P*. sp. (SMNH BP.372, 378, 434, 466; PIN 3592/79 after Novitskaya 2004: pl. 2, fig. 4); *P*. sp. 1 (SMNH BP.383).

Liu, 1998, and *P. parmula* Elliott, Loeffler *et* Liu, 1998, all from the Late Silurian to Early Devonian of the Northwest Territories of Canada. *Poraspis* cf. *Poraspis polaris* has been indicated also in deposits of Pod'emnaya and Spokoinaya Formations of Severnaya Zemlya (Blieck *et al.* 2002).

Remarks. — Classification of *Poraspis* species, especially Podolian, is difficult because of rather generalised morphology of their dorsal shield and possible post-mortem deformation. Blieck and Heintz (1983) revised poraspids from Spitsbergen using morphometric parametres, that is combination of total length of the dorsal shield (LoT; ML in this work) and pineal length (LoP; PL here). As a result, some Spitsbergen species were connected with Podolian ones (Blieck and Heintz 1983: fig. 11). *Poraspis barroisi*, partly *P. elongata*, *P. rostrata* and *P. cylindrica*, together with *P. sturi* from Podolia were connected with *P. polaris*. *P. magna*, partly *P. rostrata* and *P. cylindrica*, also *P. pompeckji* from Podolia were synonymised with *P. rostrata*. Similar relationships were proposed for other Podolian specimens of *Poraspis* (Fig. 40). Extension of this approach to the Podolian species, neglecting stratigraphic and geographic distribution, as well as other possibly diagnostic features, seems too simplistic. Nevertheless, it is quite clear that at least three Podolian species of *Poraspis* can be distinguished.

Occurrence. — Early Devonian of Great Britain, Spitsbergen (Norway), Podolia (Ukraine), France, Canada, and Severnaya Zemlya (Russia).

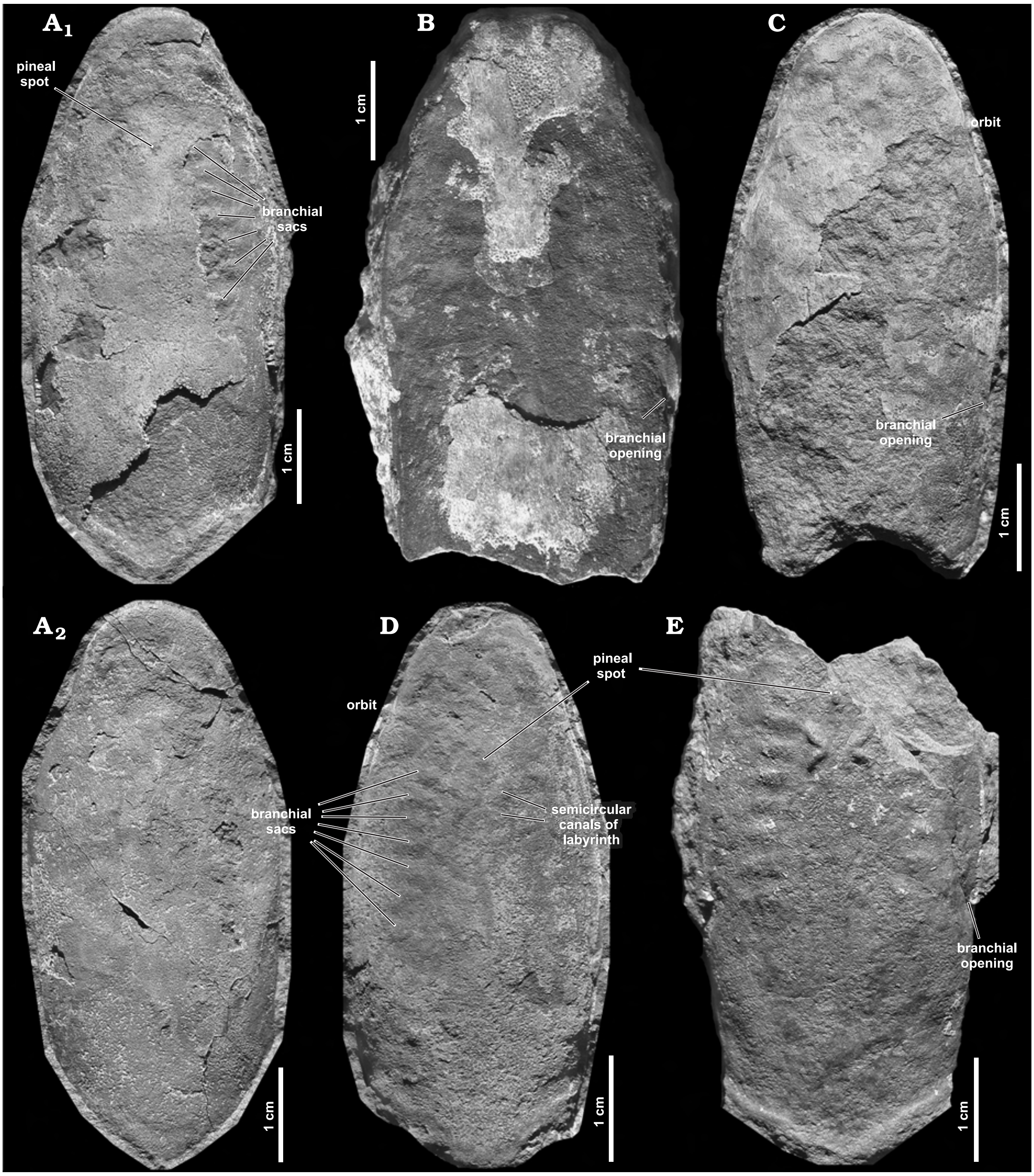

Fig. 41. Poraspid *Poraspis sturi* (Alth, 1874) from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, Podolia. **A**. Mould and imprint of dorsal shield SMNH BP.377 with armour remains dorsal view. **B**. *Poraspis* sp. (*sturi*?), mould of dorsal shield SMNH BP.375 lacking posterior part from left bank of Dzhuryn River, Ustechko Member of the Dniester Formation, dorsal view. **C**. Mould of dorsal shield SMNH BP.389 with remains of armour lacking posterior end, dorsal view. **D**. Dorsal shield SMNH BP.374, dorsal view. **E**. Mould of the dorsal shield SMNH BP.385 lacking anterior part, from lowermost part of Khmeleva Member of the Dniester Formation, dorsal view.

Poraspis sturi (Alth, 1874)
(Figs 13F, 41A–E, 42A, B)

1874. *Cyathaspis sturi*; Alth 1874: p. 46, pl. 5, figs 1, 2.

1927. "*Pteraspis*" (*Cyathaspis*) *sturi*; Zych 1927: p. 52, pl. 2, figs 1, 2.

1964. *Poraspis sturi*; Denison 1964: pp. 409–410.

1983. *Poraspis sturi*; Novitskaya 1983: p. 178, pl. 3, fig. 3.

Fig. 42. Poraspid *Poraspis sturi* (Alth, 1874) and related form from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, Podolia. **A**. Mould of the dorsal shield SMNH BP.388 with remains of armour, dorsal view. **B**. Mould of dorsal shield SMNH BP.379, dorsal view. **C**. *Poraspis* sp. 1, mould of dorsal shield SMNH BP.383/1 and partial internal side of dorsal shield dorsal view. **D**. *Poraspis* sp. 1, partial ventral shield IGP (unnumbered), part and counterpart.

1986. *Poraspis sturi*; Novitskaya 1986: pp. 22–24, text-fig. 2, pl. 2, fig. 5, synoptic table, p. 137, fig. 8.

2004. *Poraspis sturi*; Novitskaya 2004: pp. 106–107, fig. 36.

Type specimen: Lectotype (Alth 1874: pl. V, figs 1, 2), mould and imprint of dorsal shield; Doroshivtsi, Zastavna rayon, Chernivtsi oblast' (Podolia).

Referred material. — Moulds of dorsal shield SMNH BP.374, 377, 379, 385, 388, 389 and 393; probably also BP.399 and 375, possibly BP.378.

Diagnosis. — Relatively large *Poraspis* species with almost straight lateral margins of the dorsal shield.

Description. — The dorsal shield is narrow and elongated. Its length is 55–60 mm (possibly up to 65 mm, as in BP.375) and width (maximal in the middle of the length) is 24–28 mm. Ratio W/ML equals 0.42–0.47, OL/ML 0.21, OW/OL 1.5–1.7 (possibly up to 1.9, as in BP.375), OW/ML 0.32–0.36, PL/ML 0.24–0.28 (after Zych (1927) 0.22), PBL/ML 0.33–0.42. The preorbital part of the shield is rounded and appreciably narrowed. Lateral margins of the shield from first third of its extent to the posterolateral corners are almost straight. An insignificant narrowing of the shield in caudal direction may develop. The posterior margin of the dorsal shield looks like a narrow blade or obtuse angle corner. The notches of the branchial openings are recognizable on moulds of the shield, but are imperceptible on its surface. The ventral shield is elongated, relatively narrow, and gradually widens backward. The anterior margin of the shield is almost straight, with rounded anterolateral corners. Dentine ridges (7–8 cr/mm) between the orbits are fan-like or longitudinal. At the anterior margin, they are transverse.

Comparison. — In comparison with this species, *Poraspis siemiradzkii* has wider preorbital and postbranchial parts of the dorsal shield and smaller size, and greater value of the OW/OL index. *Poraspis pompeckji* differs in wider preorbital part and not straight lateral margins. *Poraspis simplex* has more obtuse posterior end of the shield, besides (as well as *P. polaris*, *P. brevis*, *P. rostrata*, *P. heintzae*, *P. cracens*, *P. thules*, and *P. parmula*) smaller size. *Poraspis brevis* has wider shield, while *P. polaris* differs by visible branchial notches. *Poraspis sericea* is of larger size, has wider anterior part of the shield, and more pointed blade at its posterior margin.

Remarks. — Two specimens of probable *Poraspis sturi* (Figs 13F, 41E) were found in the beds on the left bank of Dniester in Ustechko, which may belong to the lowest part of Khmeleva Stage of the Dniester Formation. They are associated with *Weigeltaspis alta* and *Kujdanowiaspis* sp.

The large size (W about 31 mm and ML approximately up to 64 mm) specimen BP.375 (Fig. 41B) from the talus on the slope of the 1st (eastern) ravine on the left bank of Dzhuryn, in Ustechko exceeds the size usual for the species (Fig. 40). Its early Ustechko age suggests that it may belong to a separate population of the species with greater body size, or to a new chronospecies.

Localities and age. — Doroshivtsi, Ustechko; according to Novitskaya (1986) also Zozulyntsi; from late Lochkovian to early Pragian (from the Ivanie Stage to the upper part of the Ustechko Stage or, possibly, even the lowermost part of the Khmeleva Stage) of the Dniester Formation of Podolia (Ukraine).

Poraspis siemiradzkii (Zych, 1931)

(Figs 10E–G, 43A–D, 44A–F, 45A–F)

1931. *Palaeaspis* (*Poraspis*) *siemiradzkii*; Zych 1931: figs 37–39.
1931. *Poraspis siemiradzkii*; Zych 1931: figs 3, 4.
1936. *Palaeaspis* (*Poraspis*) *siemiradzkii*; Brotzen 1936: p. 6.
1964. *Poraspis siemiradzkii*; Denison 1964: p. 410.
1986. *Poraspis siemiradzkii*; Novitskaya 1986: pp. 26–27, synoptic table, p. 137, fig. 11.
2004. *Poraspis siemiradzkii*; Novitskaya 2004: p. 109.

Type specimen: Lectotype (Zych 1931: fig. 4), mould of dorsal shield with a fragment of armour covering; Jagilnytsia Stara, Chortkiv rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Referred material. — Partial dorsal and ventral shields or their moulds SMNH BP.400, 431, 435, 439, 443, 444, 445, 446, 448, 449, 450, 455, 460, 462, 467, 468, 469, 478, 479, 481 and 1039.

Diagnosis. — Medium-size *Poraspis* species with wide preorbital and postbranchial parts of the dorsal shield.

Description. — Maximum width of the dorsal shield equals 22–25 mm and falls at its pre- or postbranchial part, near the branchial notch. The length of the dorsal shield is 43–52 mm. Values of shield indices are: W/ML 0.44–0.52, OL/ML 0.18–0.21, OW/OL 1.9–2.2, OW/ML 0.36–0.41, PL/ML 0.21–0.28, PBL/ML 0.34–0.46. Anterior margin of the dorsal shield in its preorbital part is rather widely rounded, and narrows very little. Branchial notches on the mould of the dorsal shield are clearly outlined, deep and well seen from above, but they are poorly visible under the armour cover. Breadth of the prebranchial part of the shield is somewhat less than, or equal to, the postbranchial one. Dentine ridges (6–7 cr/mm) are parallel to lateral margins of the shield. The outline of posterior margin of the shield looks as the same as in *P. sturi*, although the medial angulation of the margin may be shorter.

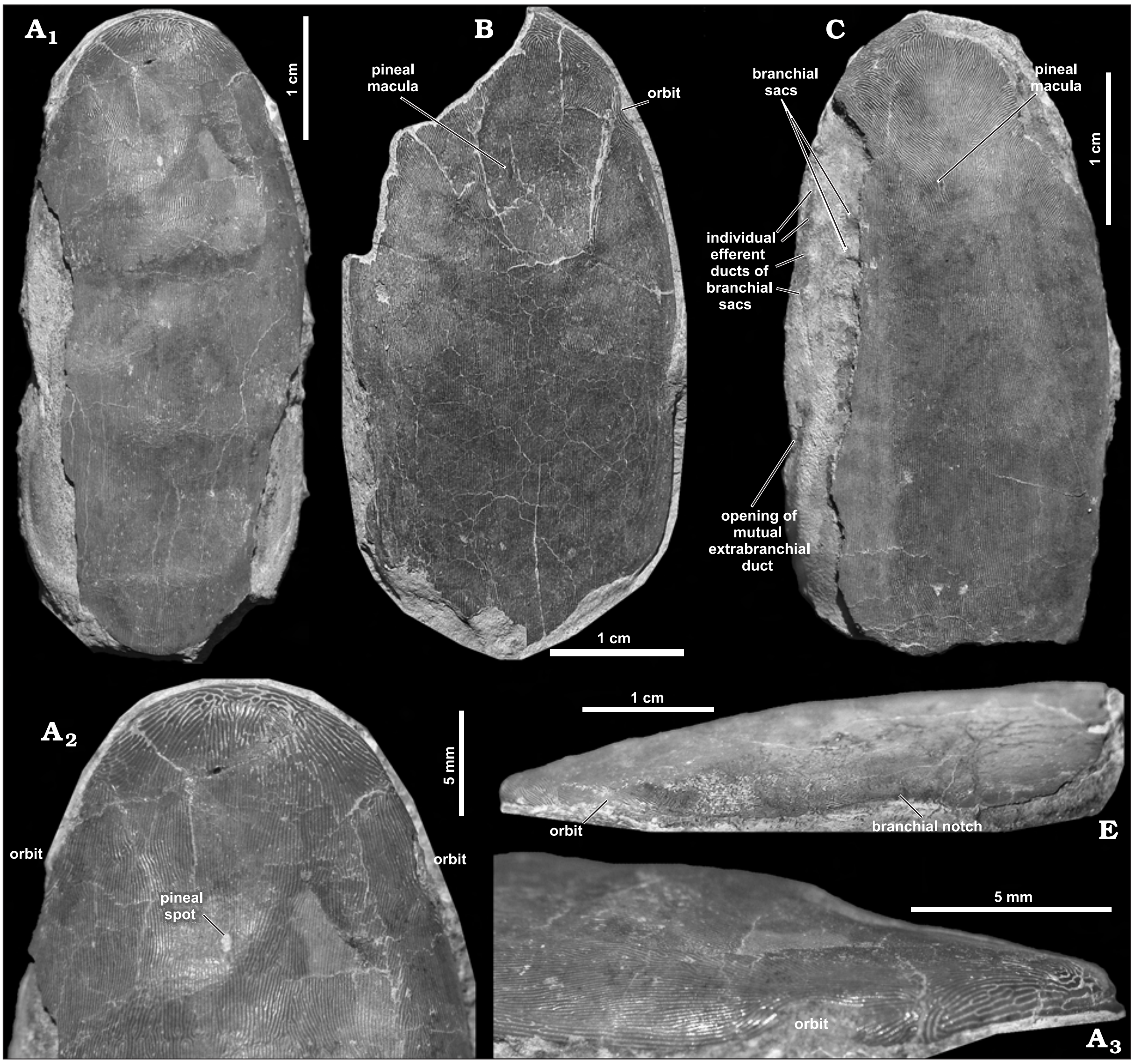

Fig. 43. Poraspid *Poraspis siemiradzkii* (Zych, 1931), Jagilnytsia Stara, Ivanie Member of the Tyver Formation, Podolia. **A**. Fragmentary dorsal shield SMNH BP.467 (see also Fig. 10G), dorsal view and its anterior part dorsal and lateral (right side) views. **B**. Fragmentary dorsal shield SMNH BP.1039, dorsal view. **C**. Fragmentary dorsal shield SMNH BP.449, dorsal view. **D**. Partial dorsal shield SMNH BP.469 (see also Fig. 10F), lateral (left side) view.

Comparison. — The species differs from *Poraspis pompeckji* and *P. simplex* by lack of the narrowing of the postbranchial part of the shield, deeper branchial notches, and from *P. simplex* besides, by wider preorbital part of the shield. In comparison with this species, *P. polaris*, *P. brevis*, *P. barroisi* are of smaller size. Besides, *Poraspis brevis* has narrower shield and *P. barroisi* relatively shorter postbranchial part of the shield. *Poraspis polaris* and *P. sericea* have narrower preorbital part of the shield and longer its posterior margin. *Poraspis sericea* is also of larger size. *Poraspis heintzae*, *P. cracens*, *P. thules*, and *P. parmula* are significantly smaller. Comparison with *Poraspis sturi* is given above in the description of this species.

Remarks. — While introducing this species Zych (1931) presented a schematic reconstruction of the dorsal shield and several photographs of the same specimen. Although no one among studied specimens demonstrates the widening of postbranchial part of the shield to such degree as the lectotype, they most likely belong to *Poraspis siemiradzkii*. The characteristic features of the species are wide enough preorbital part of the shield, deep branchial notches, and lack of any narrowing of the shield in its postbranchial part. These aspects of the species, which is known from numerous specimens from Jagilnytsia Stara, make it different from all other species of the genus. This is supported by parametres ML and PL (Fig. 40).

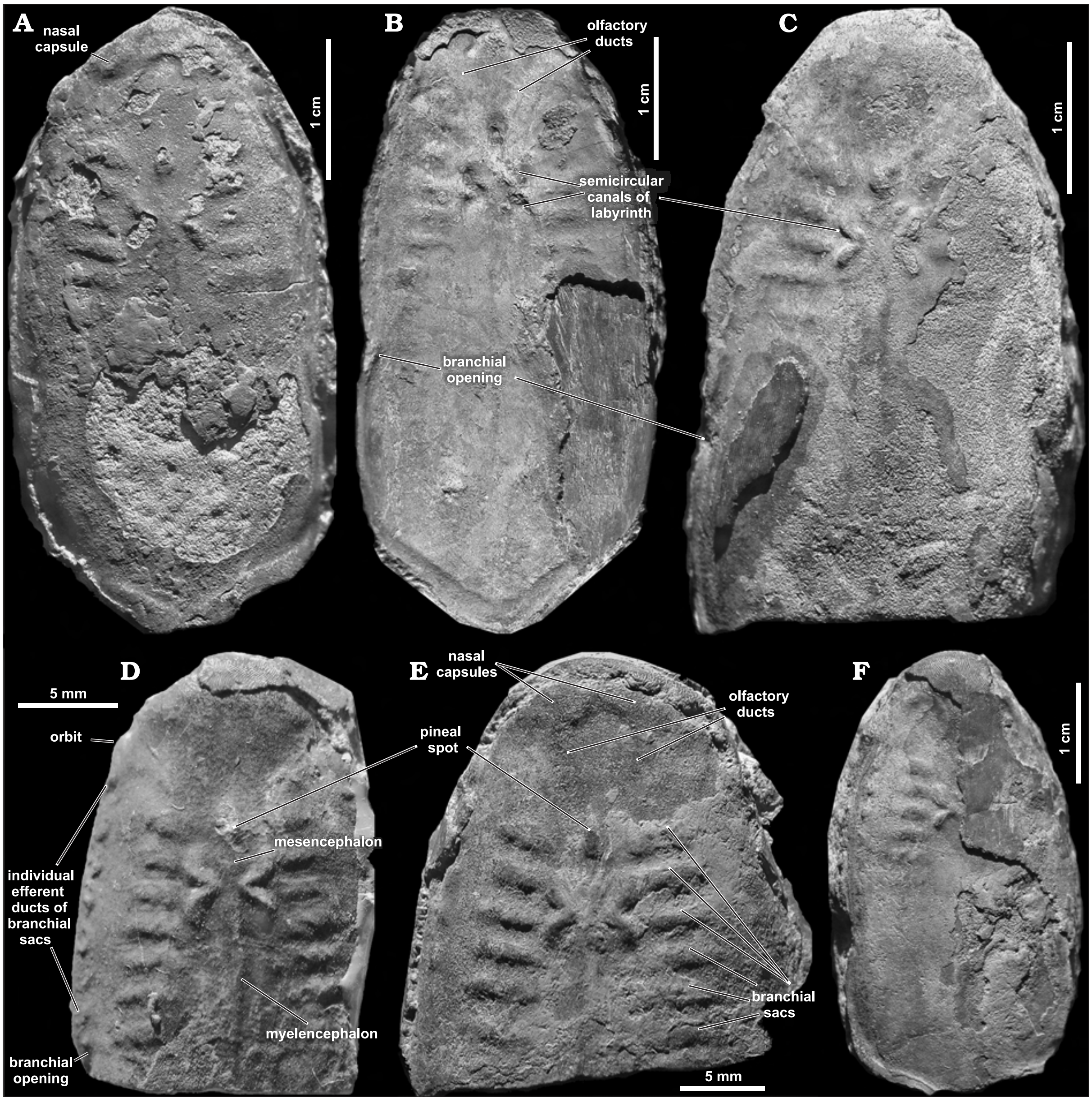

Fig. 44. Poraspid *Poraspis siemiradzkii* (Zych, 1931), Jagilnytsia Stara, Ivanie Member of the Tyver Formation, Podolia. **A**. Mould of dorsal shield SMNH BP.448, dorsal view. **B**. Mould of dorsal shield SMNH BP.468, dorsal view. **C**. Mould of dorsal shield SMNH BP.443 lacking posterior end, dorsal view. **D**. Mould of dorsal shield SMNH BP.460 lacking its posterior third, dorsal view. **E**. Mould of dorsal shield SMNH BP.435 lacking posterior part, dorsal view. **F**. Mould of dorsal shield SMNH BP.446, dorsal view.

Although considerably different in size (Fig. 40), specimens BP.434 and 466 (Fig. 13D, E) from the type locality of the species demonstrate some of its features and may appear conspecific.

Localities and age. — Jagilnytsia Stara; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine).

Poraspis pompeckji (Brotzen, 1933)

1933. *Palaeaspis pompeckji*; Brotzen 1933a: pp. 433–435, fig. 2, pl. 24, figs 1, 2, 4.
1964. *Poraspis pompeckji*; Denison 1964: p. 410.
1983. *Poraspis pompeckji*; Novitskaya 1983: p. 178, pl. 4, figs 1–3.
1986. *Poraspis pompeckji*; Novitskaya 1986: pp. 24–25, text-fig. 3, pl. 3, fig. 1, synoptic table, p. 137, fig. 9.
2004. *Poraspis pompeckji*; Novitskaya 2004: pp. 107–108, figs 25b, 26, 37.

Fig. 45. Poraspid *Poraspis siemiradzkii* (Zych, 1931), Jagilnytsia Stara, Ivanie Member of the Tyver Formation, Podolia. **A**. Partial ventral shield SMNH BP.481 and its mould, ventral view. **B**. Partial ventral shield SMNH BP.439/2, ventral view. **C**. Partial ventral shield SMNH BP.479, ventral view. **D**. Ventral shield SMNH BP.450, ventral view. **E**. Ventral shield SMNH BP.478, ventral view. **F**. Partial dorsal shield SMNH BP.444 lacking posterior end, dorsal view.

Type specimen: Neotype PIN 2172/3 (Novitskaya 1986, 2004), dorsal shield; Zalishchyky, Zalishchyky rayon, Ternopil' oblast' (Podolia). All the type series (one specimen figured by Brotzen 1933a: pl. 24, fig. 2) probably lost.

Remarks. — Judging from available data (Brotzen 1933a; Novitskaya 1983, 1986, 2004), the species is characterised by two narrowings of dorsal shield (at orbital and branchial levels) with a wider part separating them. The presence of a posteromedial blade on the posterior shield margin distinguishes *Poraspis pompeckji* from the more slender *P. simplex*. This is probably the smallest size Podolian poraspid, although its specimens' size is not much smaller than of other species, except for *P. sturi*.

Localities and age. — Zalishchyky, Ivanie-Zolote and Ustechko; probably late Lochkovian (from Ivanie Stage of the Tyver formation to Ustechko Stage of the Dniester Formation) of Podolia (Ukraine). No similar material seems to be represented in the SMNH collection.

Poraspis simplex (Brotzen, 1933)

1933. *Palaeaspis simplex*; Brotzen 1933a: p. 432, pl. 24, fig. 3.

1936. *Palaeaspis simplex*; Brotzen 1936: p. 6.

1964. *Poraspis simplex*; Denison 1964: p. 409.

1983. *Poraspis simplex*; Novitskaya 1983: p. 178, pl. 3, figs 1, 2.

1986. *Poraspis simplex*; Novitskaya 1986: pp. 25–26, text-fig. 4, pl. 4, figs 2–4, synoptic table, p. 137, fig. 10.

2004. *Poraspis simplex*; Novitskaya 2004: pp. 108–109, fig. 38, pl. 2, fig. 3.

Type specimen: Holotype (by monotypy) figured by Brotzen (1933a: pl. 24, fig. 3), mould of dorsal shield; Zalishchyky, Zalishchyky rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown. Novitskaya (1986) identified specimen LIG 5-556 from Dobrivliany as belonging to this species.

Remarks. — Only two specimens of the species have been been identified up to date and the holotype is probably lost. The dorsal shield is slender and its posterior margin forms a short, obtuse corner at about 135° angle (Brotzen 1933a: pl. 24, fig. 3). No one of the other Podolian species has similar features.

Localities and age. — Dobrivliany and Zalishchyky; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Poraspis sp. 1

(Fig. 42C, D)

Referred material. — Specimen SMNH BP.383, mould and imprint of dorsal shield, and partial mould and imprint of ventral shield from the IGP collection without number.

Description. — Length of the dorsal shield is 49.9 mm and its maximum width (at the 2/3 of the length) is 25.2 mm. Ratio W/ML equals 0.51, OL/ML 0.20, OW/OL 1.8, OW/ML 0.38, PL/ML 0.27, PBL/ML 0.41. Preorbital part of the shield is rounded and slightly narrowed. Lateral margins of the shield from first third of its extent to the posterolateral corners are almost straight. Slight narrowing of the shield in caudal direction is observed. Posterior margin of the dorsal shield formed medial angle with regularly and faintly concave lateral sides. The notches of the branchial openings are hardly recognizable. The ventral shield is 41.5 mm in length and 23.5 mm in width. It widens backward very feebly. Anterior margin of the shield has a convex outline, with rounded anterolateral corners, while posterior margin looks as that in the dorsal shield (Fig. 42D). There are 7 cr/mm on the dorsal and 6–7 cr/mm on the ventral shield.

Comparison. — *Poraspis siemiradzkii* has wider preorbital and postbranchial parts of the dorsal shield and smaller size. *Poraspis pompeckji* differs by wider preorbital part and not straight lateral margins. *Poraspis simplex* has narrower shield. *Poraspis polaris*, *P. brevis*, *P. rostrata*, *P. heintzae*, *P. cracens*, *P. thules*, and *P. parmula* is smaller in size. *Poraspis brevis* has wider shield, while *P. polaris* differs by visible branchial notches. *Poraspis sericea* is of considerably larger size.

Remarks. — Being found in the same layer as several specimens of *Poraspis sturi* the specimen BP.383 may belong to the group *sturi*, as the specimen BP.375 mentioned in description of *P. sturi*, see above, but it is of somewhat smaller size and has a shorter shield, relatively less narrowing in its anterior part and shorter median blade on its posterior margin (cf. Fig. 42C and Fig. 42A, B). Both dorsal and ventral shields have been found in the same locality that fit each other in size and outline of the posterior margin.

Localities and age. — Ustechko; early Pragian (uppermost part of Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Family **Ctenaspididae** Kiaer, 1930

Genus *Ctenaspis* Kiaer, 1930

1930. *Ctenaspis*; Kiaer 1930: pp. 3–5.

1953. *Ctenaspis*; Denison 1953: p. 293.

1964. *Ctenaspis*; Denison 1964: pp. 438–440.

1964. *Ctenaspis*; Obruchev 1964: p. 60.

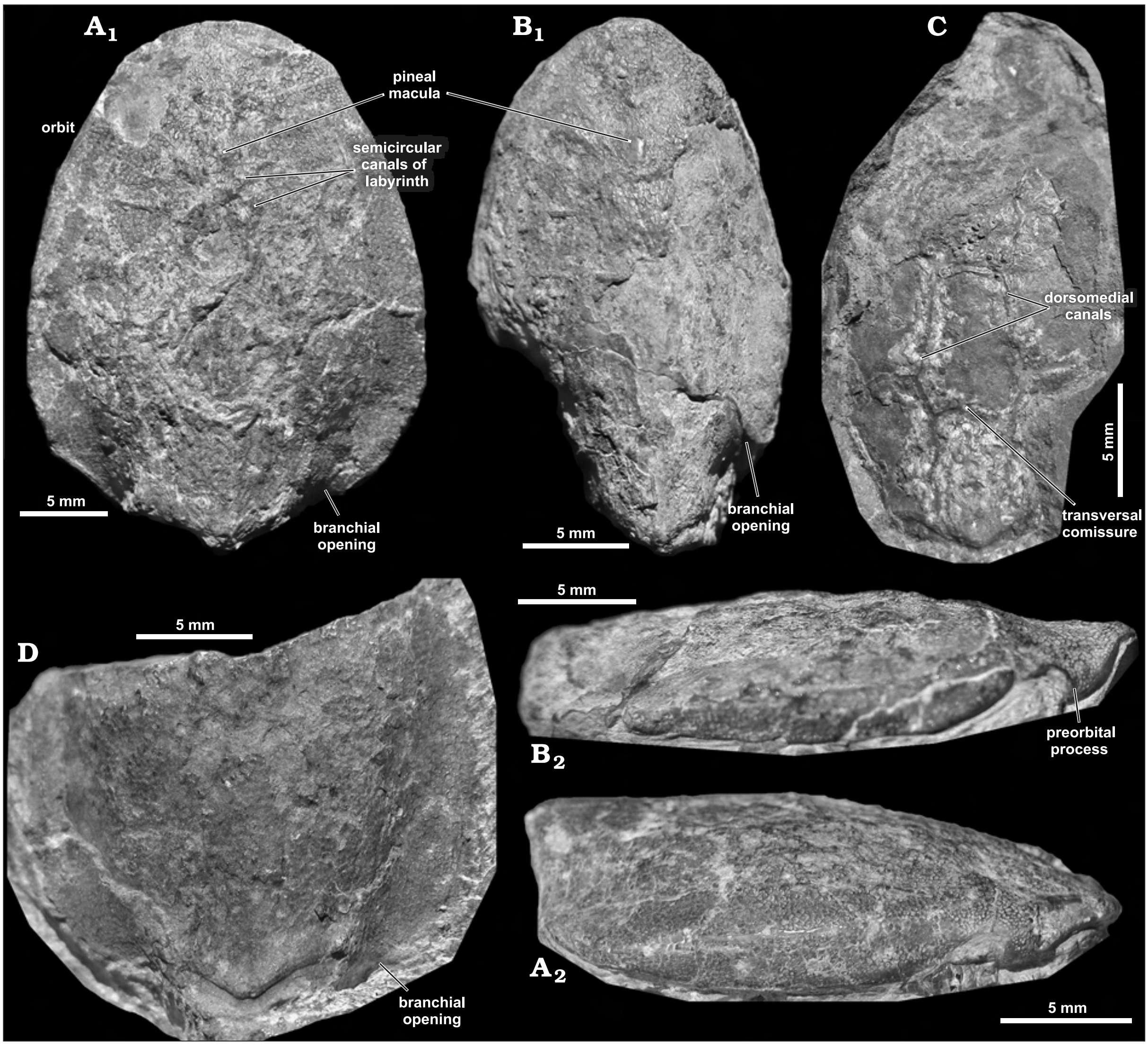

Fig. 46. Ctenaspidid *Ctenaspis kiaeri* Zych, 1931 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, Podolia. **A**. Dorsal shield SMNH BP.918 (see also Fig. 47D), dorsal and right side views. **B**. Dorsal shield SMNH BP.924 (see also Fig. 47E), dorsal and right side views. **C**. Partial dorsal shield SMNH BP.916/3 (see also Fig. 101A), inside view. **D**. Posterior part of mould of dorsal shield SMNH BP.916/2 (see also Fig. 101A), dorsal view.

1964. *Bothriaspis*; Obruchev 1964: p. 60.
1986. *Ctenaspis*; Novitskaya 1986: pp. 29–30.
2004. *Ctenaspis*; Novitskaya 2004: p. 113.

Type species: *Ctenaspis dentata* Kiaer, 1930; Early Devonian (upper part of the Red Bay Series) of Spitsbergen.

Diagnosis. — The carapace is approximately oval, with some expansion in its posterior part (length of the carapace ranges 23–60 mm). Anterior margin of the dorsal shield is rounded. There are preorbital processes. Posterior margin of the shield has a medial ledge. The branchial openings are usually displaced to the posterior margin of the carapace, postbranchial blades are absent. The dorsal shield is merged with the branchial plates. Ornamentation consists of aspidine tubercles and a network of ridges.

Species included. — Besides the type species: *Ctenaspis cancellata* Kiaer, 1930, Red Bay Formation of Spitsbergen; *C. kiaeri* Zych, 1931, Ivanie Stage of Podolia, *C. obruchevi* Dineley, 1976, *C. russelli* Dineley, 1976, and *C. ornata* Dineley, 1976. All three species are from the Early Devonian of Canada. *Ctenaspis* sp. has been identified also in deposits of Pod'emnaya Formation of Severnaya Zemlya (Blieck *et al.* 2002).

Occurrence. — Early Devonian of Podolia (Ukraine), Spitsbergen, Canada, and Severnaya Zemlya (Russia).

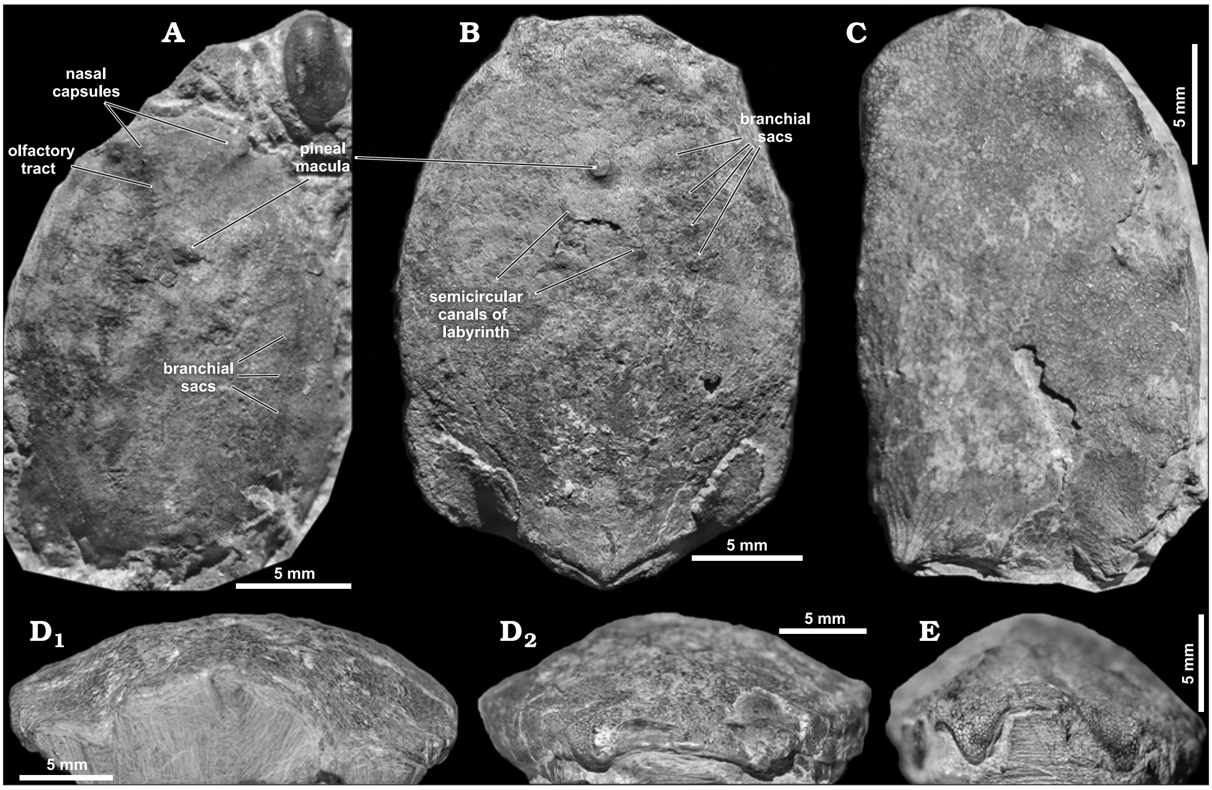

Fig. 47. Ctenaspidid *Ctenaspis kiaeri* Zych, 1931 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, Podolia. **A**. Mould of dorsal shield SMNH BP.508/1 with ostracod shell mould, dorsal view. **B**. Mould of dorsal shield SMNH BP.920, dorsal view. **C**. partial dorsal shield SMNH BP.919/1, dorsal/right side view. **D**. Dorsal shield SMNH BP.918 (see also Fig. 46A), back and frontal view. **E**. Distorted dorsal shield SMNH BP.924 (see also Fig. 46B), frontal view.

Ctenaspis kiaeri Zych, 1931
(Figs 46A–D, 47A–E, 101A, D)

1931. *Ctenaspis kiaeri*; Zych 1931: pp. 86–87, figs 11, 45a–e.
1936. *Ctenaspis kiaeri*; Brotzen 1936: p. 6.
1958. *Ctenaspis zychi*; Stensiö 1958: p. 295, fig. 176.
1958. *Ctenaspis zychi* (nom. nud.); Stensiö 1958: p. 295, fig. 178A.
1961. *Ctenaspis kiaeri*; Balabai 1961a: p. 5, fig. 3.
1964. *Ctenaspis kiaeri*; Denison 1964: pp. 441–442.
1964. *Ctenaspis zychi*; Stensiö 1964: fig. 80.
1986. *Ctenaspis kiaeri*; Novitskaya 1986: pp. 30–31, text-fig. 6, synoptic table, p. 138, fig. 13.
2004. *Ctenaspis kiaeri*; Novitskaya 2004: pp. 113–114, text-fig. 42.

Type specimen: Lectotype NHRM C1616 selected by Denison (1964) in Stensiö (1958), who identified this specimen as the holotype of *Ctenaspis zychi* (Novitskaya 2004), dorsal shield; Jagilnytsia Stara, Chortkiv rayon, Ternopil' oblast' (Podolia).

Referred material. — Dorsal shields, their moulds and imprints or fragments of different state of preservation, SMNH BP.439/4, 508/1, 565/2, 915/1–3, 916/1–3, 917, 918, 919/1, 920, 921, 922, 923/1, 924, 925, 926, 927, 928, 929, 930, 931, 932, 933, 934, 1038/1, 1045, 1046, and 1206.

Diagnosis. — Relatively small sized *Ctenaspis* species with a network of ridges as the dermal skeleton ornamentation.

Description. — Dorsal shield is oval in shape, with some narrowing in anterior part and expansion in posterior part. The shield length is 24–31 mm, maximum width (in the posterior third) ~20 mm. Values of the shield indices: W/ML 68–77, OL/ML 7–12, PL/ML 25–29, OW/ML 40–48. Anterior margin of the shield is rounded and a little bit narrowed. Posterior margin has a medial angular ledge (115–126°). The armour surface of the dorsal shield looks like a network of ridges (with mesh about 0.2–0.3 mm), on which background, in particular in the central and posterior parts of the shield, elongated tubercles are discernible. Sizes of the latter increase from 0.5 to 1.0 mm while approaching posterior margin of the shield. The posterior medial ledge is ornamented with longitudinal ridges developing lateral branches forming herringbone pattern.

Comparison. — In contrast with this species, *C. cancellata* carapace is wider, *C. dentata* differs by other ornamentation of the exoskeleton, while *C. obruchevi*, *C. russelli*, and *C. ornata* are larger in size.

Localities and age. — Jagilnytsia Stara; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine).

Order **Tesseraspidiformes** Halstead, 1962

Family **Tesseraspididae** Berg, 1940

Genus *Tesseraspis* Wills, 1935

1935. *Tesseraspis*; Wills 1935: p. 435.
1964. *Tesseraspis*; Obruchev 1964: p. 56.
1964. *Tesseraspis*; Tarlo 1964: pp. 24–25.
1965. *Tesseraspis*; Tarlo 1965: p. 2.
2004. *Tesseraspis*; Novitskaya 2004: p. 196.

Type species: *Tesseraspis tesselata* Wills, 1935; Early Devonian (early Lochkovian) of Great Britain.

Diagnosis. — Tesseraspidids with elongated carapace with thick marginal tesserae, even thicker median tesserae, and a zone of thinner tesserae between them.

Species included. — Besides the type species: *Tesseraspis toombsi* Tarlo, 1964, *T. mutabilis* (Brotzen, 1934), *T. orvigi* Tarlo, 1964, *T. denisoni* Tarlo, 1964, and *T. talimaae* Tarlo, 1965.

Remarks. — Single Podolian tesseraspidid species still is known after the tessera fragment figured by Ørvig (1961).

Occurrence. — Early Devonian (Lochkovian) of Great Britain, Podolia (Ukraine), Germany, Lithuania, and Canada.

Tesseraspis orvigi Tarlo, 1964

1961. Drepanaspida gen. et sp. indet.; Ørvig 1961: pp. 523–524, text-fig. 4.
1964. *Tesseraspis orvigi*; Tarlo 1964: p. 110.
1965. *Tesseraspis orvigi*; Tarlo 1965: pp. 7–8.
2004. *Tesseraspis orvigi*; Novitskaya 2004: p. 197.

Type specimen: Holotype NHRM C1727, fragment of tessera has been collected in Jagilnytsia Stara, Chortkiv rayon, Ternopil' oblast' (Podolia).

Localities and age. — Jagilnytsia Stara; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Order **Corvaspidiformes** Stensiö, 1964

Family **Corvaspididae** Dineley, 1955

Genus *Corvaspis* Woodward, 1934

1934. *Corvaspis*; Woodward 1934: p. 566.
1964. *Corvaspis*; Obruchev 1964: p. 59.
1965. *Corvaspis*; Tarlo 1965: p. 15.
1982. *Corvaspis*; Blieck 1982: p. 46.
2004. *Corvaspis*; Novitskaya 2004: pp. 197–198.

Type species: *Corvaspis kingi* Woodward, 1934; Early Devonian (*Traquairaspis symondsi* Zone) of Great Britain.

Diagnosis. — The carapace includes the dorsal and ventral median plates, as well as orbital, branchial and postorbital (?) ones. The ornamentation consists of short longitudinal dentine ridges forming synchronomorial tesseriform units, which may be separated by dentine tubercles. Dentine tubercles form peripheral zones in plates of the carapace.

Species included. — Besides the type species: *C. graticulata* Dineley, 1953, Early Devonian (Ben Nevis Formation) of Spitsbergen; *C. karatajuteae* Tarlo, 1965, Early Devonian (Tilze Stage) of Lithuania.

Remarks. — *Corvaspis graticulata* Dineley, 1953 is now considered to be a species of *Corveolepis*? (Blieck and Karatajūtė-Talimaa 2001).

Occurrence. — Early Devonian of Great Britain, Podolia (Ukraine), Spitsbergen, Lithuania, and Canada (see Loeffler and Dineley 1976).

Corvaspis kingi Woodward, 1934
(Fig. 17A, D–F, H, M–O)

1960. *Corvaspis kingi*; Woodward 1934: pp. 566–567, pl. 19, figs 1–3.
1960. *Corvaspis kingi*; Tarlo 1960: pls 37, 38.
1964. *Corvaspis kingi*; Obruchev 1964: text-figs. 9, 20, 21, pl. 5, fig. 5.
1965. *Corvaspis kingi*; Tarlo 1965: pp. 16–18, pl. 3.
2004. *Corvaspis kingi*; Novitskaya 2004: p. 198.
2010. *Corvaspis kingi*; Voichyshyn 2010: pl. 2, fig. 1.

Type specimen: Holotype BM(NH) P.16446, part of the median plate; Earnstrey Hall, Shropshire, Great Britain.

Referred material. — Median plate SMNH BP.568; fragments of tesseriform units in collection of microremains (ichthyoliths) BP.1543/2, 1543/7, 1545/16, 1550/25, 1560, 1562/1, and 1562/3.

Diagnosis. — *Corvaspis* species with wide dentine ridges and narrow grooves at borders between tesserae.

Description. — Median plate is elongated (length ~60 mm), relatively wide (width ~30 mm), and flat. The exact shape of the plate is unknown; roughly it is oval. Ornamentation of the carapace consists of flat tesseriform units of synchronomorial type, which are divided by narrow grooves. The units are formed by short, wide (3 cr/mm), flat and smooth dentine ridges, which are mostly parallel to the body axis. There are several cyclomorial units in the posterior part of the plate. Ridges on these units probably surround pores of the lateral line canals. Size of the tesseriform units fluctuates from 2 mm to 3 mm, their shape is angular or irregular.

Comparison. — The species differs from *C. graticulata* by character of borders between the tesseriform units (in *C. graticulata* there is a double series of small rounded tubercles), and also by wider dentine ridges. In *C. karatajuteae*, borders between the units are poorly recognizable.

Remarks. — Several tesseriform unit fragments from Gorodok (BP.1544/10) and outcrop no. 11 (BP.1545/15, 1546/13, 1550/11, 1550/12, 1550/14, and 1550/27; Fig. 17B, G, I, L) show wider dentine ridges (about 2.5–2.7 cr/mm; even 2 cr/mm in BP.1038/2) than it is typical for the species (Fig. 17C). In other specimens, ridges are as dense as to 4–5 cr/mm (Fig. 17J, K). It is likely due to variability of the *Corvaspis kingi* armour. According to Blieck and Karatajūtė-Talimaa (2001), the width of dentine ridges in *Corveolepis elgae* equals 4–6 cr/mm. This parametre varies also in another tessellate heterostracan, *Oniscolepis dentata* Pander, 1856, depending on location on the body, and it is 3–10 cr/mm (see Märss and Karatajūtė-Talimaa 2009). However, the possibility that these are remains of another species cannot be exluded.

Tarlo (1960) noted that Stensiö in 1944 "recorded *Corvaspis* from the Czortkow Series of Podolia". Novitskaya (2004) also mentioned "fragments of plates and tesserae from localities in Podolia, Chortkiv Horizon".

Localities and age. — East of Dobrivliany on both the banks of Dniester River; Lochkovian (from upper part of the Chortkiv Stage to lower part of Ivanie Stage of the Tyver formation) of Podolia (Ukraine).

Order **Pteraspidiformes** Berg, 1940
Suborder **Pteraspidoidei** Berg, 1940
Family **Podolaspididae** Novitskaya, 1983
Genus *Podolaspis* Zych, 1931

1927. *Pteraspis*; Zych 1927: pp. 52–54 (pars).
1931. *Podolaspis*; Zych 1931: pp. 89–91 (pars).
1933. *Pteraspis*; Brotzen 1933a: p. 445 (pars).
1959. *Pteraspis*; Balabai 1959b: p. 6 (pars).
1961. *Podolaspis*; Tarlo 1961: pp. 380–381.
1964. *Podolaspis*; Obruchev 1964: p. 65.
1975. *Podolaspis*; Novitskaya 1975: p. 81.
1984. *Podolaspis*; Blieck 1984: p. 40 (pars).

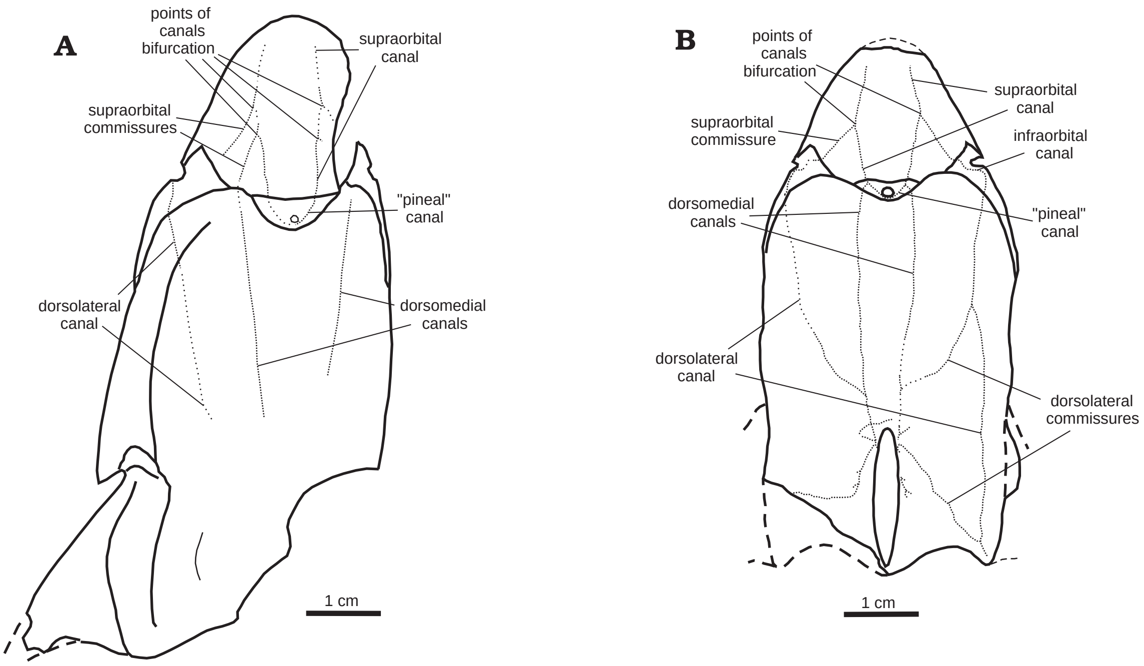

Fig. 48. Arrangement of sensory line system on dorsal carapace surface of Podolaspididae. **A**. *Podolaspis* sp., specimen SMNH BP.175 (see also Fig. 32A). **B**. *Parapteraspis plana* Stensiö, 1958, specimen SMNH BP.295 (see also Figs 32E, 57B).

1986. *Podolaspis*; Novitskaya 1986: pp. 77–78.
2001. *Podolaspis*; Voichyshyn 2001c: pp. 28–30, 35–36.
2004. *Podolaspis*; Novitskaya 2004: pp. 144–145.

Type species: *Pteraspis lerichei* mut. *rostrata* Zych, 1927; Early Devonian (Ivanie Stage, lower part of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized pteraspidids. The carapace is elongated (tL 70–120 mm), rather narrow and convex. Index RL/RW is 0.8–1.1. Orbital processes are short and pointed. The pineal plate has a part-moon shape with pointed lateral tips that are in contact with the medial orbital processes, or not. DW/DL ~0.5–0.65. Dorsal spine is large and almost vertical. The cornual plates are wide, triangular or crescent in shape. Mdl canals are of radial type (the type of divergence is not known for all the species).

Species included. — Besides the type species: *Podolaspis podolica* (Alth, 1874), *P. zychi* (Brotzen, 1933), and *P. danieli* sp. n., all from the Early Devonian of Podolia.

Remarks. — Species distinction of *Podolaspis gracilis* (Stensiö, 1958), which has been excluded from the genus *Parapteraspis* by Novitskaya (1986), does not seem substantiated well enough. She indicated a similarity between *Podolaspis gracilis* and *P. lerichei* and indicated the lack of preorogonial corners and wider carapace of the former as the differences. Preorogonial corners are one of the elements of morphology of the ventral side of the rostral plate which characterise (Novitskaya 1986) the lectotype of *P. gracilis*, NHRM C1558, which according to Stensiö (1958) and Blieck (1984: fig. 10A–C) represents *Parapteraspis*. The specimen PIN 3592/47, on which Novitskaya (1986: text-fig. 34, pl. 17, fig. 1) based her concept of *P. gracilis*, hardly falls outside the limits of variability of the *P. podolica*–*P. lerichei* group.

Occurrence. — Early Devonian of Podolia (Ukraine).

Podolaspis podolica (Alth, 1874)
(Figs 32C, 49A–C, 50A–G)

1874. *Pteraspis podolicus*; Alth 1874: p. 42, pl. 1, figs 5–10.
1927. *Pteraspis sturi* Alth, mut. *rostrata*; Zych 1927: p. 161, pl. 2, fig. 6.
1931. *Podolaspis rostrata*; Zych 1931: p. 90, fig. 14.
1933. *Pteraspis podolica*; Brotzen 1933a: pp. 439–442, figs 4, 5.
1933. *Pteraspis podolica* Alth var. *haueri*; Brotzen 1933a: p. 441, fig. 6.
1959. *Pteraspis lerichei*; Balabai 1959b: pl. 1, figs 2, 3 (pars).

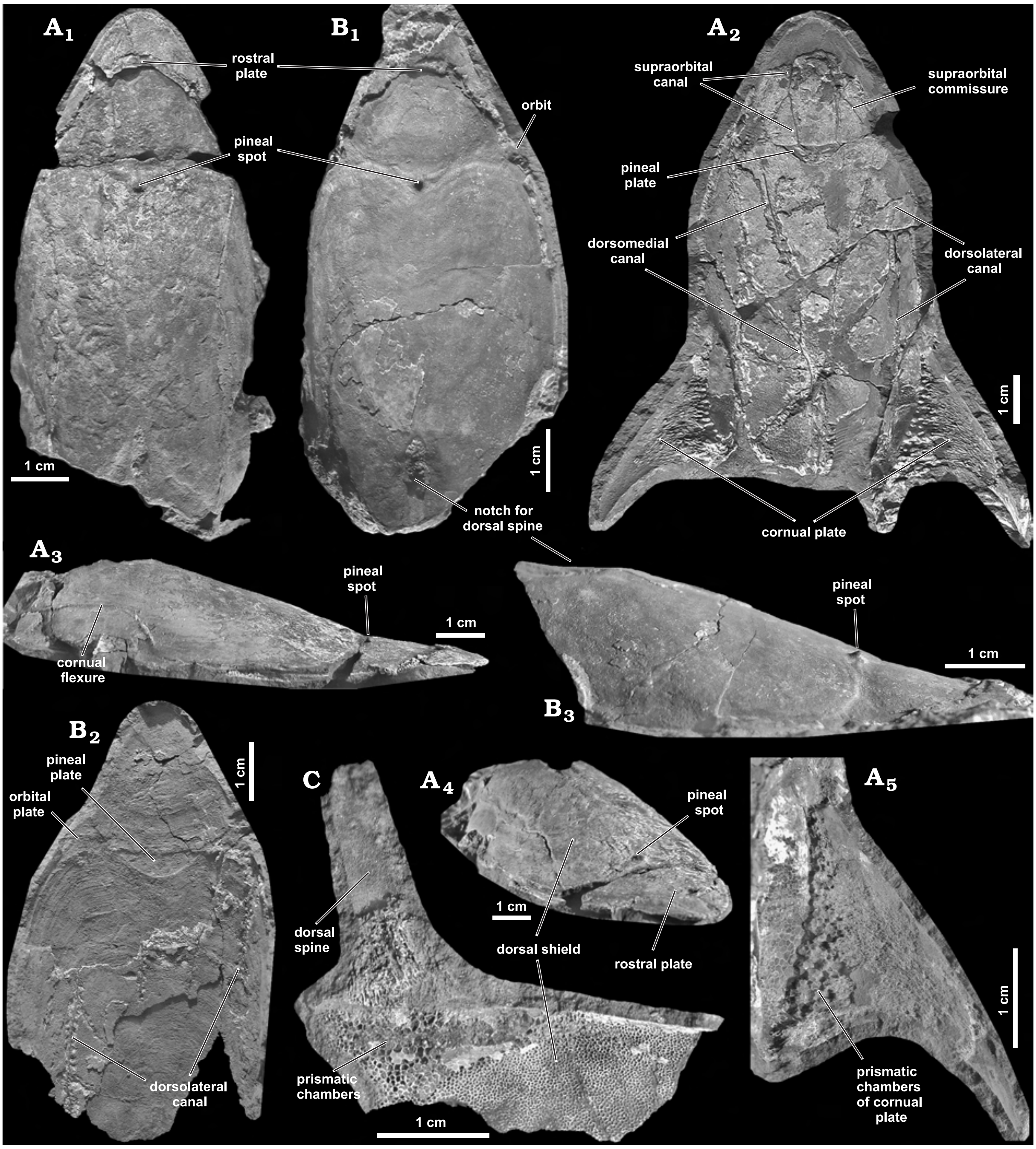

Fig. 49. Podolaspidid *Podolaspis podolica* (Alth, 1874) from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation, Podolia. **A**. Mould of carapace SMNH BP.170/1, dorsal, inside and lateral (right side), antero-lateral views and cornual plate. **B**. Mould of partial dorsal carapace SMNH BP.172 (see also Fig. 32C) and imprint of its anterior part, dorsal and lateral (right side) views. **C**. Partial dorsal spine and dorsal shield SMNH BP.170/2, lateral view.

1961. *Pteraspis podolica*; Balabai 1961b: pp. 5–6, figs 4, 5.

1975. *Podolaspis podolica*; Novitskaya 1975: p. 82.

1983. *Podolaspis podolica*; Novitskaya 1983: pl. 24, figs 3, 4.

1984. *Podolaspis podolica*; Blieck 1984: p. 43.

1986. *Podolaspis podolica*; Novitskaya 1986: pp. 81–82, text-fig. 31, 32, pl. 16, figs 4, 5, synoptic table, p. 143, fig. 39.

2004. *Podolaspis podolica*; Novitskaya 2004: pp. 146–147, text-figs 68, 69, pl. 10, figs 3, 4.

Type specimen: Lectotype selected by Brotzen (1933a) in Alth (1874: pl. 1, fig. 5), dorsal shield; vicinities of Zalishchyky, Zalishchyky rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

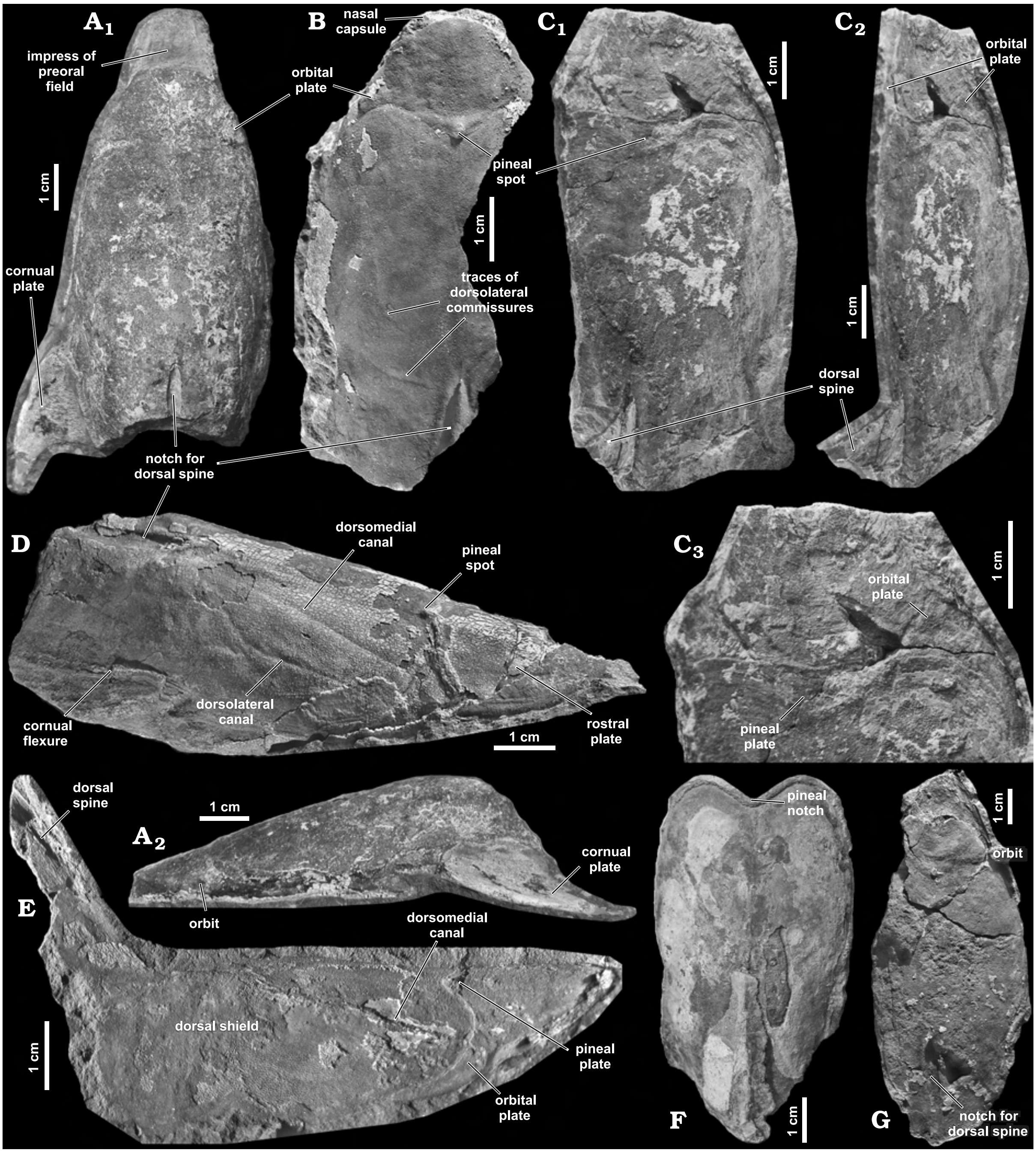

Fig. 50. Podolaspidid *Podolaspis podolica* (Alth, 1874) from various localities of the Dniester Formation in Podolia. **A**. Carapace MZ V III Vp-187 of questionable species identity lacking right cornual plate from Chervonograd, near castle (“przy zamku”), Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal and lateral (left side) views. **B**. Mainly left portion of carapace mould SMNH BP.217 lacking cornual and branchial plates from Ustechko, left bank of Dniester River, talus, lower part of Khmeleva Member, dorsal view. **C**. Partial imprint of carapace SMNH BP.303 from Potochyshche N, Ustechko Member or lower part of Khmeleva Member, dorsal and lateral (right side) views, also enlarged orbito-pineal belt zone. **D**. Partial mould of carapace SMNH BP.254 from Ustechko, left bank of Dzhuryn River, 1st ravine, Ustechko Member, dorso-lateral (right side) view. **E**. Imprint of carapace left part SMNH BP.204 of questionable species identity from Ustechko, lateral (right side) view. **F**. Mould of carapace MZ V III Vp-177 of questionable species identity lacking right cornual plate from Dobrivliany (“Dobrowlany na N od Strzelnicy”), lower part of Ivanie Member of the Tyver Formation, dorsal view. **G**. Partial abraded mould of carapace SMNH BP.203 from Ustechko, left bank of Dniester River, 1st ravine W of the village, lower part of Khmeleva Member, dorsal view.

Referred material. — Specimens SMNH BP.170/1, 170/2, 172, 216, 217, 254 and 303; possibly also SMNH BP.191, 203, 204, MZ V III Vp-177, and V III Vp-187.

Diagnosis. — Medium sized *Podolaspis* species with narrowing of the dorsal shield in its posterobranchial part and extended medial ledge of its posterior margin.

Description. — The carapace is moderately wide; tL 90–100 mm. Index RL/RW is 0.8–0.9. The anterior margin of the pineal plate is slightly concave, while the posterior one is convex and rounded. The orbital plates are small. The medial orbital processes may be in contact with lateral tips of the pineal plate. The dorsal shield (DW/DL ~0.6–0.65) appreciably narrows in its postbranchial part. The posterior margin of the shield has a significant medial ledge. The notch of the dorsal spine begins at the level of cornual flexures. The dorsal spine is high and almost vertical. The cornual plates are large, crescent, and posterolaterally directed. Mdl canals are of radial type.

Comparison. — The species differs from *Podolaspis lerichei* by a narrowing of the dorsal shield in its posterobranchial part and wider (in general) dorsal shield and by extended medial ledge of its posterior margin. Novitskaya (1986) also indicated as a difference a longitudinal excess of the branchial plates in *P. podolica*. *P. zychi* has more elongated pineal plate, with more convex posterior margin, narrower dorsal shield and is of larger general size. Comparison with *P. danieli* sp. n. is given in its description.

Remarks. — The posterior margin of the pineal plate in *P. podolica* is gently rounded rather than forming a sharp angle (Figs 49A, B, 50C; Brotzen 1933a: fig. 4b) and in this respect it virtually does not differ from that in *P. lerichei* (Zych 1927: pl. 3, fig. 3).

Localities and age. — Potochyshche, Ustechko, Zalishchyky, according Novitskaya (2004) also Khreshchatyk and Zastinoche; from Lochkovian to early Pragian (from Ivanie Stage of the Tyver formation to the lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Podolaspis lerichei (Zych, 1927)

(Fig. 51A–D)

1927. *Pteraspis lerichei* sp. n., mut. *rostrata* n. mut.; Zych 1927: p. 54, text-fig. 5, pl. 2, fig. 7, 9, pl. 3, fig. 3.
1933. *Pteraspis lerichei*; Brotzen 1933a: pp. 445–447, fig. 9.
1941. *Pteraspis lerichei*; Pauča 1941: pp. 25–26, pl. 2, fig. 2.
1941. *Pteraspis lerichei* var. *plana*; Pauča 1941: p. 27, pl. 2, fig. 3.
1958. *Plesiopteraspis* sp.; Stensiö 1958: pp. 269, 271, figs 146A, 148.
1959. *Pteraspis lerichei*; Balabai 1959b: p. 6, pl. 1, fig. 1.
1961. *Podolaspis lerichei*; Tarlo 1961: p. 380, fig. 8.
1964. *Podolaspis lerichei*; Obruchev 1964: p. 65, pl. 6, fig. 8, text-figs 33, 34.
1983. *Podolaspis lerichei*; Novitskaya 1983: pl. 23, figs 1–5, pl. 24, figs 1, 2, pl. 26, fig. 4.
1984. *Podolaspis lerichei*; Blieck 1984: pp. 40, 42–43, fig. 41C.
1986. *Podolaspis lerichei*; Novitskaya 1986: pp. 78–81, text-figs 29, 30, pl. 16, figs 1, 2, synoptic table, p. 143, fig. 38.
2001. *Podolaspis lerichei*; Voichyshyn 2001c: p. 28, fig. 1.
2004. *Podolaspis lerichei*; Novitskaya 2004: pp. 145–146, text-fig. 66, pl. 10, figs 1, 2.
2005. *Podolaspis lerichei*; Dumbrava and Blieck 2005: pp. 165–166, fig. 3, pl. 1, figs 10, 11.

Type specimen: Lectotype selected by Tarlo (1961) in Zych (1927: pl. 3, fig. 3), anterior part of carapace in dorsal view; Mogyl'nytsia, Terebovlia rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Referred material. — Moulds or imprints of carapace SMNH BP. 214/1 and 588; possibly also SMNH BP.206, 208, and IGP A-22.

Diagnosis. — Small to medium sized *Podolaspis* species with approximately straight posterior margin of the dorsal shield, and without narrowing of the dorsal shield in its posterobranchial part.

Description. — The length of the carapace is ~80 mm. Index RL/RW is in limits of 0.85–1.1. The shape and proportions of the orbito-pineal belt are as at the previous species. Sometimes, the pineal plate is a little bit longer (Novitskaya 1986: pl. 16, fig. 1). The dorsal shield (DW/DL ~0.54) insignificantly narrowed on an anterior margin and at the postbranchial part. Posterior margin of the shield in general is straight or a little concave, and has a small medial ledge. Shape, proportions and orientation of the dorsal spine, the notch holding it on the dorsal shield, and the cornual plates are the same as of *P. podolica*. Mdl canals are probably of radial type (Fig. 51C), but Blieck (1984: fig. 41B, C) showed parallel type of them based, evidently, on Brotzen's figure (1933a: fig. 9a).

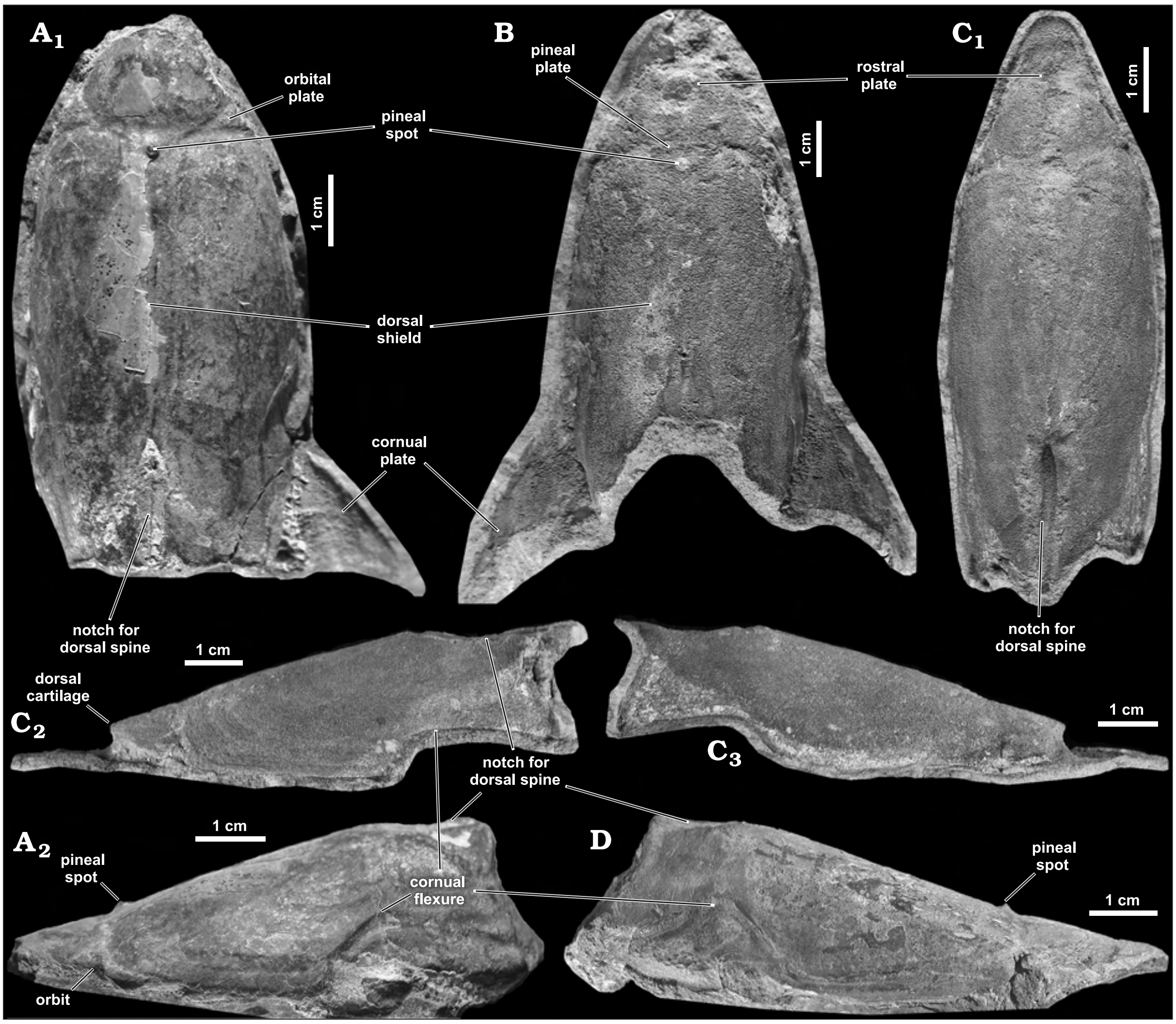

Fig. 51. Podolaspidid *Podolaspis lerichei* (Zych, 1927) from various localities of the Tyver Formation in Podolia. **A**. Mould of carapace SMNH BP.588 lacking left cornual plate from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member, dorsal and lateral (left side) views. **B**. Mould of carapace SMNH BP.214/1 lacking posterior part of dorsal shield from the Verbivtsi quarry, Ivanie Member, dorsal view. **C**. Mould of carapace IGP (unnumbered) of questionable species identity from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, lacking branchial and cornual plates, dorsal and lateral (left and right side) views. **D**. Mould of carapace SMNH BP.208 of questionable species identity from Zalishchyky, right bank of Dniester River, talus, upper part of Ivanie Member, lateral (right side) view.

Comparison. — *Podolaspis zychi* has longer pineal plate, larger general size, and twisted branchial plates, according to Novitskaya 1986. The differences from *P. podolica* and *P. danieli* sp. n. are listed in their descriptions.

Localities and age. — Zalishchyky, Ustechko, Verbivtsi, Mogyl’nytsia; Lochkovian (from Ivanie Stage of the Tyver formation to the lower part of the Dniester Formation) of Podolia (Ukraine).

Podolaspis zychi (Brotzen, 1933)
(Fig. 52A)

1933. *Pteraspis zychi*; Brotzen 1933a: pp. 448–450, fig. 11.
1984. *Podolaspis*? *zychi*; Blieck 1984: pp. 43–44, fig. 41F.
1986. *Podolaspis zychi*; Novitskaya 1986: pp. 82–83, text-fig. 33.
2004. *Podolaspis zychi*; Novitskaya 2004: pp. 147–148, text-fig. 80.

Type specimen: Lectotype was figured by Brotzen (1933a: fig. 11), carapace in dorsal view; Zelenyj Gaj, Zalishchyky rayon, Ternopil’ oblast’ (Podolia). The location of the specimen is unknown.

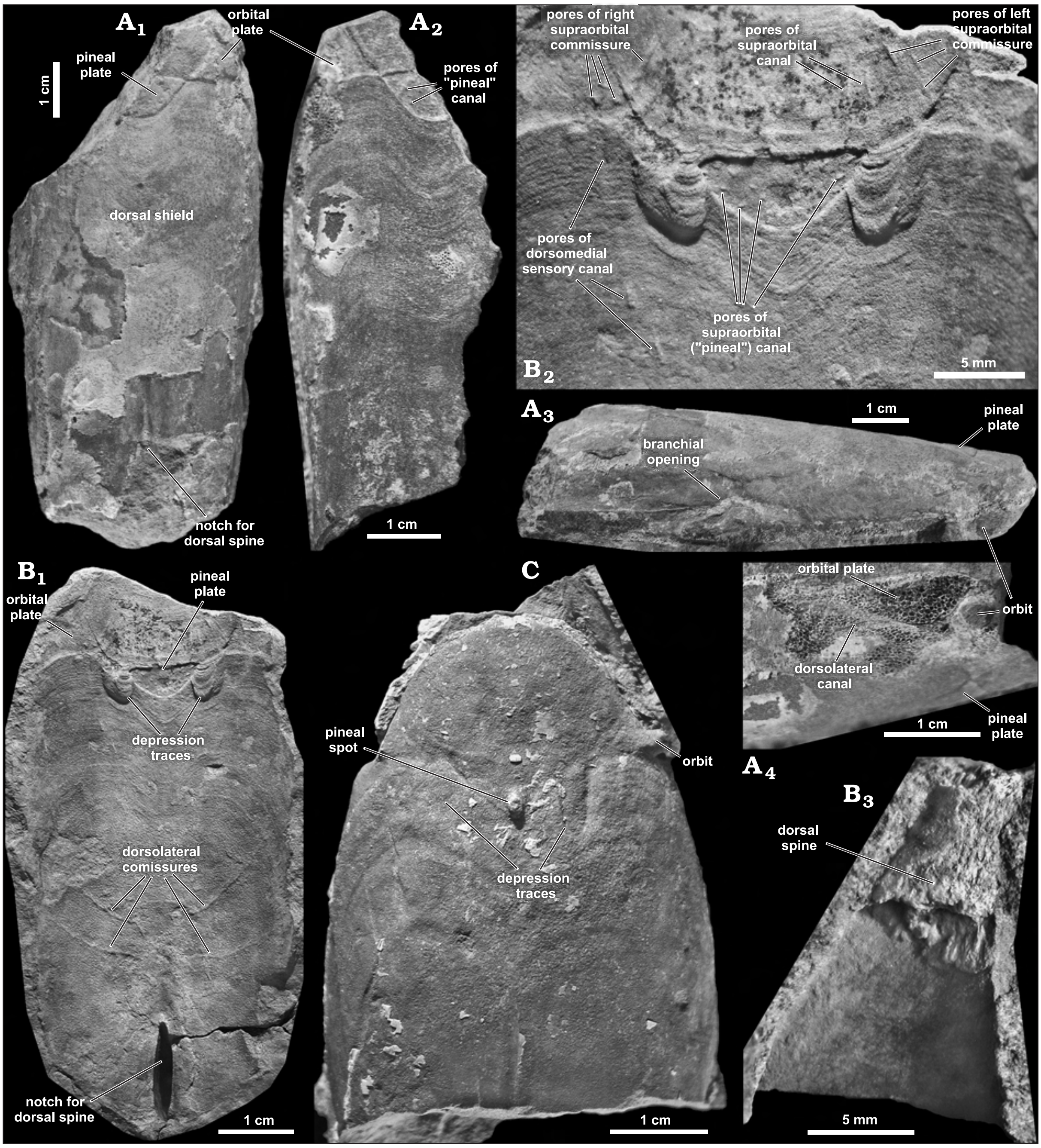

Fig. 52. Podolaspidids from the Dniester Formation at Ustechko. **A**. *Podolaspis zychi* (Brotzen, 1933), partial mould of carapace SMNH BP.302 from left bank of Dniester River, Ustechko Member or lower part of Khmeleva Member, dorsal and lateral (right side) view of carapace and its imprint, also enlarged anterior part. **B**. *Podolaspis danieli* sp. n., the holotype incomplete imprint of carapace SMNH BP.262 from the Ustechko Member, dorsal view, imprint of orbito-pineal belt region and proximal part of dorsal spine and its imprint. **C**. Same species, anterior part of carapace mould SMNH BP.274 from talus on slope of left bank of Dzhuryn River, 3rd ravine, Ustechko Member, dorsal view.

Referred material. — Partial mould and imprint of the carapace (mainly its right part) SMNH BP.302.

Diagnosis. — Large sized *Podolaspis* species with large elongated pineal plate.

Description. — The carapace is of length ranging from 110 mm (after Novitskaya 1986) up to 120–130 mm. Index RL/RW is 1.0–1.1. Anterior orbital processes are robust. The pineal plate is large (PL 7 mm, PW 14 mm), with straight anterior and convex posterior margins. Pointed lateral corners of the plate touch tips of the medial orbital processes. The dorsal shield is narrowed (DW/DL 0.50–0.53), convex in all its extent, with the maximum width approximately in the middle of the shield in the prebranchial part. The postbranchial part of the shield is slightly narrowed, with straight lateral margins. According to Blieck (1984: fig. 41F, citing Brotzen 1933: fig. 11b), the mdl canals are of the parallel type.

Comparison. — See descriptions of other *Podolaspis* species.

Localities and age. — Dobrivliany, Ustechko, and Zelenyj Gaj; Lochkovian (from the Ivanie Stage of the Tyver formation to the lower part of the Dniester Formation) of Podolia (Ukraine).

Podolaspis danieli sp. n.
(Figs 52B, C, 53)

Derivation of the name: In honour of Dr Daniel Drygant (SMNH).

Type specimen: Holotype SMNH BP.262, carapace imprint in dorsal view lacking anterior part of the rostral plate and lateral margins of the dorsal shield; Ustechko, left bank of the Dzhuryn River (lower part of Ustechko Stage of the Dniester Formation), Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Besides the holotype, specimen SMNH BP.274, mould of anterior part of carapace from talus in the 3rd ravine on the left bank of Dzhuryn River.

Diagnosis. — Small to medium sized *Podolaspis* species with discontinuous orbito-pineal belt and pressed down antero-median parts of dorsal shield.

Description. — Length of the carapace in the holotype is estimately at 80 mm. Length of the preserved part of rostral plate is 13–15 mm (estimated full length 22 mm); RW 29 mm. The pineal plate (PL 3.8 mm, PW 10 mm) is moon-like in shape, with roundly convex posterior margins. The anterior margin of the pineal plate is almost straight or little concave, but rather oblique laterally. Pineal spot is large, 1.4 mm in diameter. Anterior and medial orbital processes are short, the latter with sharp medial ends. The shape of orbito-pineal belt is characteristic for the genus. The belt is discontinuous. The distance between lateral corners of the pineal plate and medial ends of median orbital processes is from 1/3 to almost 1/2 of PW (3.2 mm on left and 4.8 mm on right side of the holotype). The dorsal shield is probably of medium width (DL 62 mm, DW about 40 mm; DW/DL about 0.65, what corresponds to *P. podolica*). The posterior margin of the shield is the same as in *P. lerichei*. Depressions of the dorsal shield on both sides of the pineal plate are 3.5×2.3 mm (on right side) and 4.6×2.9 mm (on left one). The notch of the dorsal spine is 13 mm in length, and 2.5 mm in width. Dorsal spine is strong and massive at its base (Fig. 52B) probably high and orientation close to vertical. The branchial and cornual plates are not preserved in the studied material. There are 12 cr/mm on anterior part of the dorsal shield. Mdl canals are of radial type.

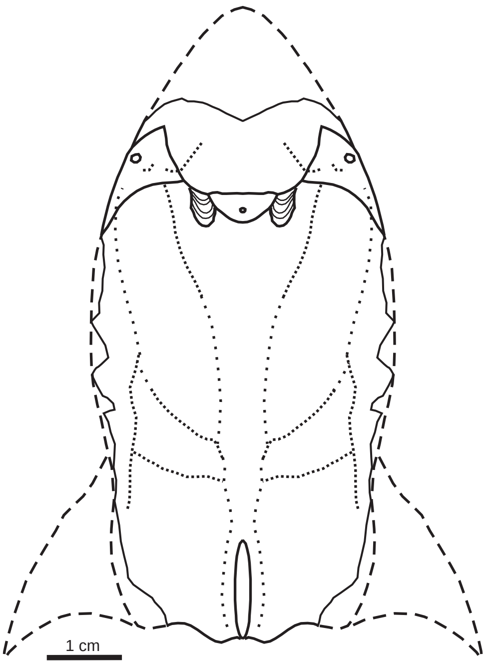

Fig. 53. *Podolaspis danieli* sp. n., reconstruction of the carapace dorsal view.

Comparison. — The new form differs from all other species of the genus in having depressions on anterior part of the dorsal shield, larger distance between lateral corners of the pineal plate and medial ends of median orbital processes, and, probably, smaller index RL/RW. Besides, the specimens are smaller than in *P. podolica* and *P. zychi*, and have wider dorsal shields than *P. lerichei* and *P. zychi*.

Remarks. — Two depressions on the anterior margin of dorsal shield are considered here the distinctive feature of the new species. Their semmetrical disposition suggests that these are not chance anomalies.

Localities and age. — Ustechko; late Lochkovian (lower part of the Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Genus *Semipodolaspis* gen. n.

Derivation of the name: Prefix *semi* refers to incomplete *Podolaspis* characteristic of the type species.

Type species: *Semipodolaspis slobodensis* sp. n.; Early Devonian (most probably, Ivanie Stage of the Tyver formation) of Podolia.

Diagnosis. — Rather large sized pteraspidids. The carapace is elongated (tL 110–120 mm) and rather narrow and convex. Index RL/RW is about 0.9. Orbital processes are short and pointed. The pineal plate has a

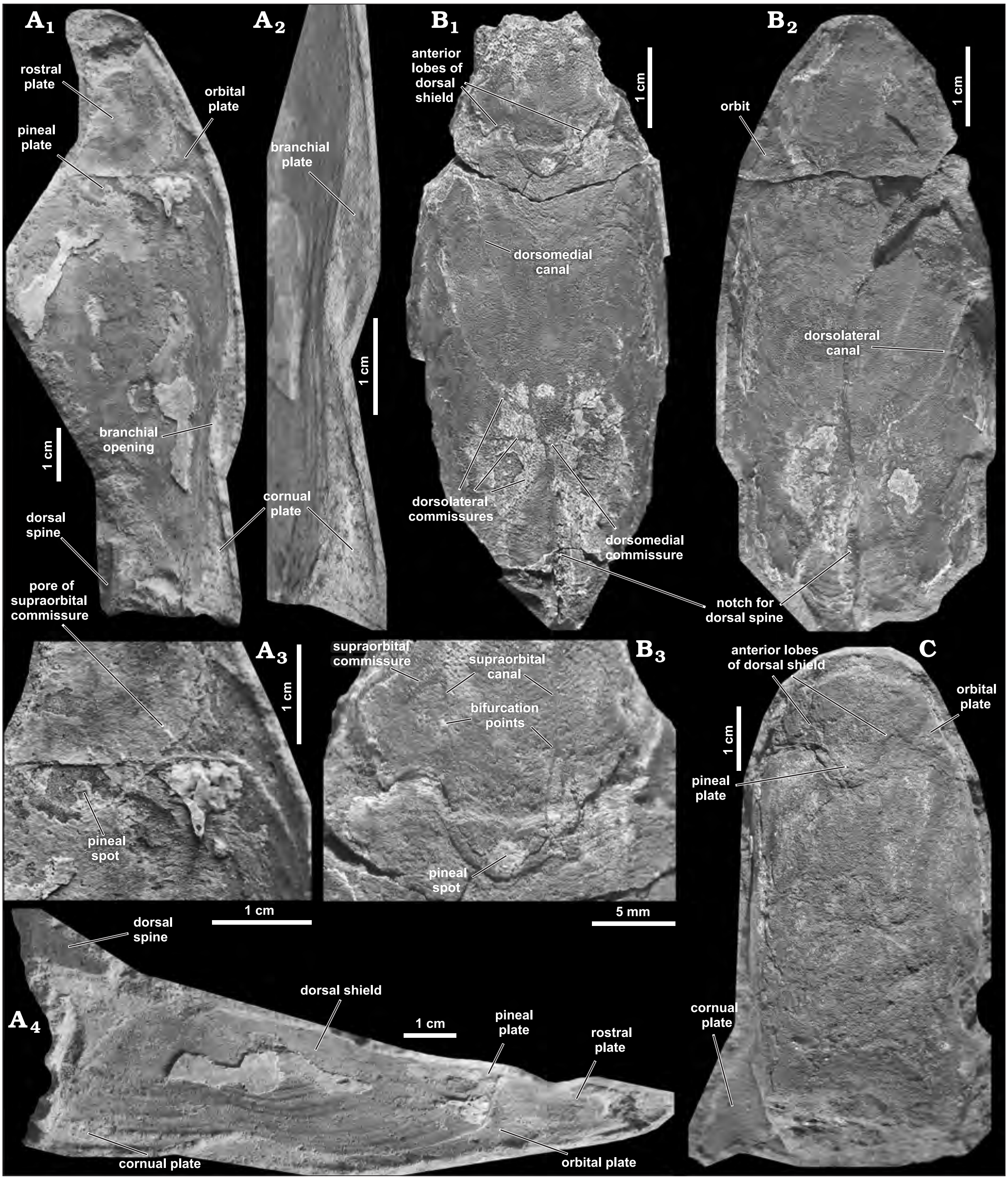

Fig. 54. Podolaspidids from Podolia. **A**. *Semipodolaspis slobodensis* gen. et sp. n., imprint of branchio-cornual zone of the holotype carapace SMNH BP.1211 from Slobidka, Chortkiv Member or Ivanie Member of the Tyver Formation, imprint of left part of carapace, complete specimen dorsal and lateral views, also enlarged orbito-pineal zone. **B**. *Dnestraspis firma* Novitskaya, 1983, partial mould of carapace SMNH BP.171 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view, also partial imprint dorsal view and orbito-pineal belt dorsal view. **C**. *Dnestraspis firma* Novitskaya, 1983, partial mould of carapace SMNH BP.1062 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view.

part-moon shape with pointed lateral tips that almost are in contact with the medial orbital processes. DW/DL 0.6. The dorsal spine is probably large and inclined backwards. The cornual plates are narrow and elongated, possibly triangular in shape.

Species included. — Only the type species.

Comparison. — The type species resembles *Podolaspis* species, especially in morphology of the orbito-pineal belt, but in the shape and orientation of the cornual processes and dorsal spine it is similar rather to *Larnovaspis* (compare the branchio-cornual zone of the new taxon, Fig. 54A, with that of *Larnovaspis mogielnensis*, Fig. 61D). As these features interfere with important diagnostic characteristics of the genus *Podolaspis*, the new genus is proposed for the species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Semipodolaspis slobodensis sp. n.
(Figs 54A, 55)

Derivation of the name: After the type locality name.

Type specimen: Holotype, SMNH BP.1211; impression of carapace right part; Slobidka, Terebovlia rayon, Ternopil' oblast' (Podolia).

Referred material. — Only the holotype.

Diagnosis. — Same as for the genus.

Description. — Carapace is 115 mm of length. The rostral plate is of typical for Podolaspididae shape and proportions (RL 30 mm, RW 32.4 mm). The pineal plate is part-moon shaped and wide. Its anterior margin is straight, while the posterior one is gently convex and rather deep, as in *Podolaspis podolica* (PL 5 mm, PW 15 mm). The pineal spot is large (2 mm in diameter). The length of anterior and medial orbital processes is approximately the same. The posterior processes are three and part times longer. All the orbital plate processes are pointed. The median ones narrow rapidly and almost in contact with the lateral ends of the pineal plate. The space between the pineal and orbital plates is about 0.5 mm wide. The dorsal shield is elongated (DL 83 mm, DW 50 mm) with clear but not deep cornual flexures. Maximum width of the shield falls on prebranchial part. In the postbranchial one, it is much narrower (about 37 mm). The length of dorsal spine notch is more than 17 mm. The spine is inclined backwards at the angle of thirty degrees, and its projection exceeds the posterior margin of the dorsal shield. The branchial plate is 48 mm, and branchial opening is almost 13 mm in length. The cornual plates are elongated (CL ≥ 33 mm) and narrow (CW 8 mm), what makes the differences between the species and those of *Podolaspis*. The posterior part of cornual plates remains unknown. There are 9–10 cr/mm on the posterior part of the rostral plate and 8–9 cr/mm on the anterior part of the dorsal shield. The type specimen preserves no traces of the mdl sensory canals. Imprints of pores of dorsolateral canal and commissure are visible on the part of dorsal shield adjoining the cornual plate. The supraorbital commissure is represented on the rostral plate near the medial orbital process (Fig. 54A).

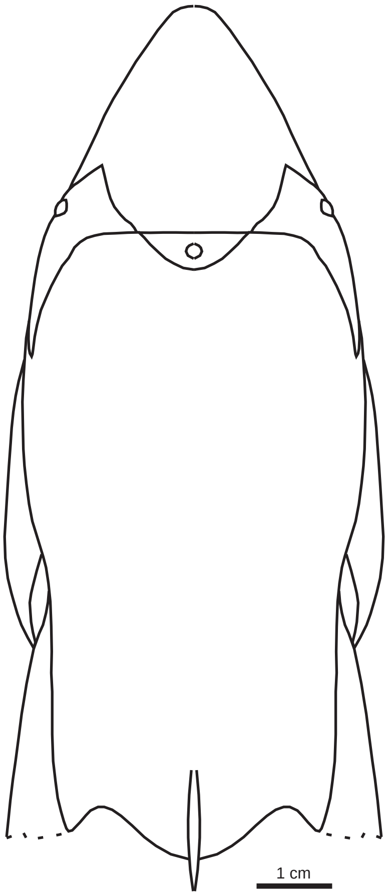

Fig. 55. Podolaspidid *Semipodolaspis slobodensis* gen. et sp. n., reconstruction of the carapace dorsal view.

Remarks. — Owing to preservation of the original shape of the cornual plates and dorsal spine reconstruction of the carapace can be attempted (Fig. 55).

Localities and age. — Slobidka; Lochkovian (possibly Chortkiv Stage, but most probably Ivanie Stage of the Tyver formation) of Podolia (Ukraine).

Genus *Dnestraspis* Novitskaya, 1983

1983. *Dnestraspis*; Novitskaya 1983: pp. 160–161.
1986. *Dnestraspis*; Novitskaya 1986: p. 84.
2001. *Dnestraspis*; Voichyshyn 2001c: p. 36.
2004. *Dnestraspis*; Novitskaya 2004: p. 149.

Type species: *Dnestraspis firma* Novitskaya, 1983; Early Devonian (lower part of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized podolaspids. The carapace is elongated (tL is 70–80 mm), narrow and convex. The rostral plate in front is narrowed. The configuration of its posterior margin is complicated. On both sides at the boundary with the pineal plate, there are notches where processes of the dorsal shield enter. Index RL/RW equals 0.9–0.95. Anterior and medial orbital processes are short. The pineal plate is of part-moon shape with obtuse lateral tips separated from the orbital plates by processes of the dorsal shield. The cornual plates are crescentic. Mdl canals are of radial type.

Species included. — Type species only.

Occurrence. — Early Devonian of Podolia (Ukraine).

Dnestraspis firma Novitskaya, 1983
(Fig. 54B, C)

1983. *Dnestraspis firma*; Novitskaya 1983: p. 181, pl. 25, fig. 2.

1986. *Dnestraspis firma*; Novitskaya 1986: p. 85, text-fig. 35, pl. 17, fig. 2, synoptic table, p. 143, fig. 42.

2004. *Dnestraspis firma*; Novitskaya 2004: p. 149, text-fig. 72.

Type specimen: Holotype PIN 3592/48, anterior part of carapace in dorsal view; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Mould and imprint of the carapace SMNH BP.171, and partial mould of carapace BP.1062.

Diagnosis. — Medium sized podolaspidid species with the pineal plate separated from medial orbital processes by two small lobes on the anterior margin of the dorsal shield.

Description. — The carapace is of 74–87 mm length. The rostral plate is small (RL 18.5 mm, RW 20 mm). The anterior margin of the pineal plate is relatively straight, while the posterior one is widely convex (PL 3.5 mm, PW 7 mm). Anterior orbital processes are pointed, the medial ones are widely wedge-shaped and very short. The dorsal shield is not wide (DW/DL 0.50–0.56) and on its anterior margin are two small lobes that separate the pineal plate from medial orbital processes. The shield is a little bit narrowed at the level of the branchial openings, then again restores its width. The posterior margin of the shield has a median ledge. The notch of the dorsal spine is 13 mm in length and 2 mm in width. The cornual plates are crescent in shape, but seem smaller than those of *Podolaspis podolica*. They are not less than 20 mm in length and 15 mm in width in SMNH BP.1062. The mould of rostral plate in SMNH BP.171 shows fragments of supraorbital sensory canal group, including supraorbital canal proper, left supraorbital commissure, and below two points of bifurcation of additional supraorbital commissure from the right and left canal branches (Fig. 54B). Levels of the bifurcation are different on the right and left supraorbital canal branches.

Localities and age. — Ustechko, Horodnytsia; early Pragian (Ustechko Stage or lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Genus *Mylopteraspis* Stensiö, 1958 (sensu Blieck, 1984)

1958. *Mylopteraspis*; Stensiö 1958: pp. 258, 263, 280 (pars).

1961. *Mylopteraspis*; Tarlo 1961: pp. 383–384 (pars).

1964. *Mylopteraspis*; Stensiö 1964: pp. 192, 197, 215 (pars).

1964. *Mylopteraspis*; Obruchev 1964: p. 67 (pars).

1975. *Mylopteraspis*; Novitskaya 1975: p. 82 (pars).

1984. *Mylopteraspis*; Blieck 1984: pp. 46–47.

1986. *Mylopteraspis*; Novitskaya 1986: p. 86 (pars).

2001. *Mylopteraspis*; Voichyshyn 2001c: p. 32.

2004. *Mylopteraspis*; Novitskaya 2004: pp. 149–150 (pars).

Type species: *Mylopteraspis robusta* Stensiö, 1958; Early Devonian of Podolia.

Diagnosis. — Medium sized pteraspidids. Preoral field is elongated, trapeziform, and covered by randomly arranged dentine ridges. Medial crest of the ascending plate is indistinct. Preorogonial corners in a form of short ledges. Postoral plates are present.

Species included. — Only type species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Mylopteraspis robusta Stensiö, 1958

1958. *Mylopteraspis robusta*; Stensiö 1958: p. 263, 280, figs 142, 156.
1961. *Mylopteraspis robusta*; Tarlo 1961: p. 383.
1964. *Mylopteraspis robusta*; Stensiö 1964: p. 197, figs 44, 58.
1964. *Mylopteraspis robusta*; Obruchev 1964: pp. 66–67, fig. 39.
1984. *Mylopteraspis robusta*; Blieck 1984: p. 47, figs 18, 42C.
1986. *Mylopteraspis robusta*; Novitskaya 1986: p. 86, pl. 17, fig. 5, synoptic table, p. 143, fig. 43.
2004. *Mylopteraspis robusta*; Novitskaya 2004: p. 150, pl. 10, fig. 6.

Type specimen: Lectotype NHRM C1546, rostral region of carapace in ventral view; locality unknown.

Remarks. — The original specimen, of unknown provenance, represents a rostral plate visible from its ventral side (Stensiö 1958). Novitskaya (1986: pl. 17, fig. 5) figured a rostral plate from Ustechko that, in her opinion, belongs to this species.

Localities and age. —Ustechko; late Lochkovian or early Pragian (probably Ustechko Stage or the lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Genus *Mylopteraspidella* Blieck, 1984

1958. *Mylopteraspis*; Stensiö 1958: pp. 258, 263, 280 (pars).
1961. *Mylopteraspis*; Tarlo 1961: pp. 383–384 (pars).
1964. *Mylopteraspis*; Stensiö 1964: pp. 192, 197, 215 (pars).
1964. *Mylopteraspis*; Obruchev 1964: p. 67 (pars).
1975. *Mylopteraspis*; Novitskaya 1975: p. 82 (pars).
1984. *Mylopteraspidella*; Blieck 1984: p. 45.
1986. *Mylopteraspis*; Novitskaya 1986: p. 86 (pars).
2001. *Mylopteraspidella*; Voichyshyn 2001c: p. 36.
2004. *Mylopteraspis*; Novitskaya 2004: pp. 149–150 (pars).

Type species: *Mylopteraspis gracilis* Stensiö, 1958; Early Devonian (lower part of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized pteraspidids. The carapace is elongated, moderately wide, and a little narrowed in the postbranchial part. Index RL/RW is 1–1.2. The anterior and medial processes of the orbital plates are short and usually dull, while the posterior ones are of moderate length. The pineal plate is of part-moon shape. Its width makes more than half of the orbito-pineal belt. The cornual plates are wide and crescent-shaped.

Species included. — Only type species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Mylopteraspidella gracilis (Stensiö, 1958)

(Figs 56A–E, 57E, 58B, D)

1958. *Mylopteraspis gracilis*; Stensiö 1958: p. 258, fig. 139.
1964. *Mylopteraspis gracilis*; Stensiö 1964: p. 192, fig. 41.
1961. *Mylopteraspis gracilis*; Tarlo 1961: p. 384, fig. 11.
1983. *Mylopteraspis gracilis*; Novitskaya 1983: text-fig. 45b, pl. 25, figs 3, 4.
1984. *Mylopteraspidella gracilis*; Blieck 1984: pp. 45–46, fig. 17.
1986. *Mylopteraspis gracilis*; Novitskaya 1986: pp. 87–88, text-figs 36, 37, pl. 17, fig. 3, synoptic table, p. 143, fig. 44.
2004. *Mylopteraspis gracilis*; Novitskaya 2004: pp. 150–151, text-figs 73, 74, pl. 10, fig. 7.

Type specimen: Lectotype NHRM C 1547, anterior part of the carapace in ventral view; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.190, 196, 284, 287, 301, 315, 1178, 1257, and 1443.

Diagnosis. — The same as for the genus (by monotypy).

Description. — The value tL equals 90–100 mm. The pineal plate is V-shaped, short (5 mm) and wide (15.5 mm). The anterior margin of the pineal plate is almost straight (it is little concave), the posterior one is widely rounded. The lateral ends of the pineal plate are widely or narrowly wedge-shaped, and contact with very short and dull medial orbital processes. The anterior orbital processes are short and obtuse (or pointed), while the posterior ones are somewhat elongated. Large pores of sensory line system are charac-

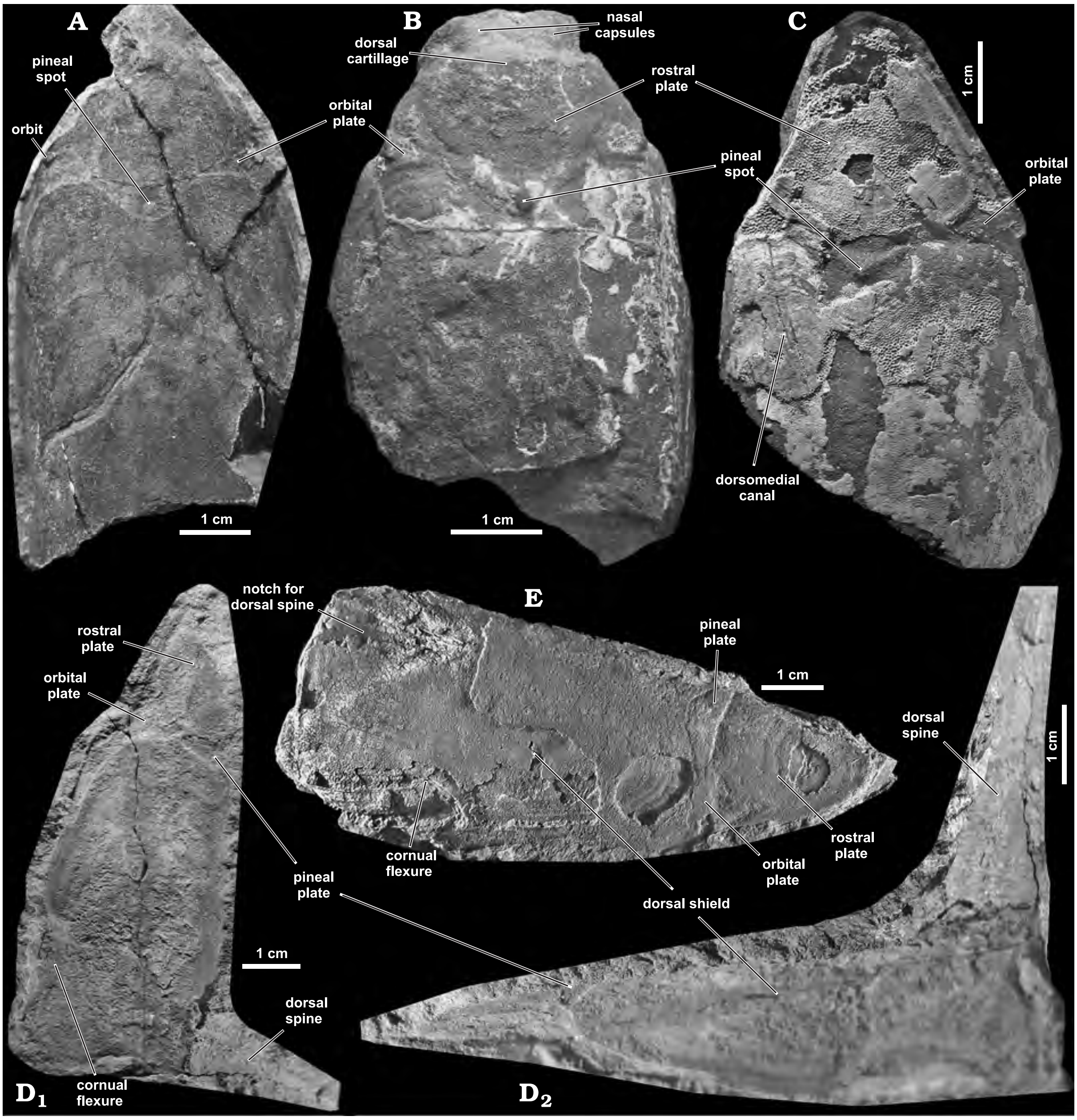

Fig. 56. Podolaspidid *Mylopteraspidella gracilis* (Stensiö, 1958) from various localities of the Dniester Formation in Podolia. **A**. Partial imprint of carapace SMNH BP.301 from Ustechko, left bank of Dniester River, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. Partial mould of carapace SMNH BP.284 from Potochyshche N, Ustechko Member or lower part of Khmeleva Member, dorsal view. **C**. Partial mould of carapace SMNH BP.196 from Ustechko, dorsal view. **D**. Partial imprint of carapace SMNH BP.1178 lacking cornual plate from Ustechko, dorso-lateral and lateral views. **E**. Partial carapace SMNH BP.190 lacking cornual plate from Ustechko, left bank of Dzhuryn River, 1st ravine, Ustechko Member, dorso-lateral (right side) view.

teristic for plates of the orbito-pineal belt. The notch for the dorsal spine reaches the level of branchial openings. The dorsal spine is long, almost vertical and projected somewhat backwards. Dentine ridges 13 cr/mm have been recorded on the anterior margin of the rostrum. According to data presented by Blick (1984: figs 17D, C, 42), the dorsomedial canals of lateral line system are of parallel type, but see their traces in the specimens PIN 3592/50 (Novitskaya 2004: text-fig. 73, pl. 10, fig. 7) and SMNH BP.196 (Fig. 56C).

Localities and age. — Ustechko, Verbivtsi, Potochyshche; late Lochkovian (from Ivanie Stage of the Tyver formation to lower part of the Dniester Formation) of Podolia (Ukraine).

Genus *Parapteraspis* Stensiö, 1958

1958. *Parapteraspis*; Stensiö 1958: pp. 265, 279 (pars).
1964. *Parapteraspis*; Stensiö 1964: pp. 198, 213 (pars).
1964. *Pteraspis*; Obruchev 1964: p. 67 (pars).
1975. *Parapteraspis*; Novitskaya 1975: p. 83.
1984. *Parapteraspis*; Blieck 1984: p. 34 (pars).
1984. *Podolaspis*?; Blieck 1984: p. 40 (pars).
1986. *Parapteraspis*; Novitskaya 1986: pp. 88–89.
2001. *Parapteraspis*; Voichyshyn 2001c: pp. 30–31, 36.
2004. *Parapteraspis*; Novitskaya 2004: pp. 151–152.

Type species: *Parapteraspis plana* Stensiö, 1958; Early Devonian (lower part of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized pteraspidids. The carapace is elongated, with moderate width and without appreciable narrowing in the postbranchial part. The rostral plate is more or less widely rounded. Index RL/RW 0.7–0.9. Anterior and medial orbital processes are short and pointed, while the posterior ones are longer. The pineal plate is V-shaped, with oblique lateral margins, and without contact with the orbital plates. The cornual plates are triangular and relatively wide.

Species included. — Besides the type species, *Parapteraspis lata* (Stensiö, 1958), Early Devonian of Podolia.

Remarks. — Blieck (1984) included the British species *Pteraspis jackana* White, 1935 in the genus *Parapteraspis*, but this is contradicted some features of this species: *P. jackana* has a different proportion of the rostral plate (index RL/RW is 0.6), and the pineal plate is of part-moon shape (Blieck 1984: fig. 12A, B, D).

Occurrence. — Early Devonian of Podolia (Ukraine).

Parapteraspis plana Stensiö, 1958
(Figs 32E, 48B, 57A–D)

1958. *Parapteraspis plana*?; Stensiö 1958: pp. 265, 279, figs 143B, 154B.
1964. *Parapteraspis plana*?; Stensiö 1964: pp. 198, 213, figs 45B, 56B.
1983. *Parapteraspis plana*; Novitskaya 1983: p. 182, pl. 26, fig. 1.
1984. *Parapteraspis gracilis*; Blieck 1984: pp. 34–35, fig. 10.
1984. *Parapteraspis djurinensis*; Blieck 1984: pp. 35–36, fig. 11.
1986. *Parapteraspis plana*; Novitskaya 1986: pp. 89–90, text-fig. 38, pl. 18, fig. 1, synoptic table, p. 144, fig. 45.
2004. *Parapteraspis plana*; Novitskaya 2004: p. 152, text-fig. 75, pl. 11, fig. 1.

Type specimen: Lectotype NHRM C1548, partial carapace in dorsal view; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.205, 295, 297, 300, and 306, probably, also BP.202 and 308.

Diagnosis. — *Parapteraspis* species with a gap between the orbital median processes and the pineal plate.

Description. — The length of the carapace is 70–80 mm, according to Novitskaya (1986) it equals 80–95 mm. The length of the rostral plate makes ~27% of the total length of the carapace. The pineal plate is V-shaped, with a little bit concave anterior margin. Posterior margin merges at obtuse angle. The lateral margins are oblique. The orbital processes are short and pointed, while the medial ones are relatively wide, not contacting the pineal plate. The dorsal shield is rather wide (DW/DL 0.64) and little narrowed at its postbranchial part. The notch of the dorsal spine is wide and reaches the level of branchial openings. Probably the dorsomedial canals of lateral line system are of parallel type.

Comparison. — This species differs from *Parapteraspis lata* by presence of a gap between the orbital and the pineal plates, and also (after Novitskaya 1986) by longer and narrower rostrum.

Remarks. — The dorsomedial canals of sensory line system of parallel type are characteristic for the material at my disposal (Fig. 57A, B) in contrast with specimens from the NHRM (Blieck 1984: figs 10A, 11A). Probably they represent different species.

Localities and age. — Horodnytsia and Ustechko; early Pragian (lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

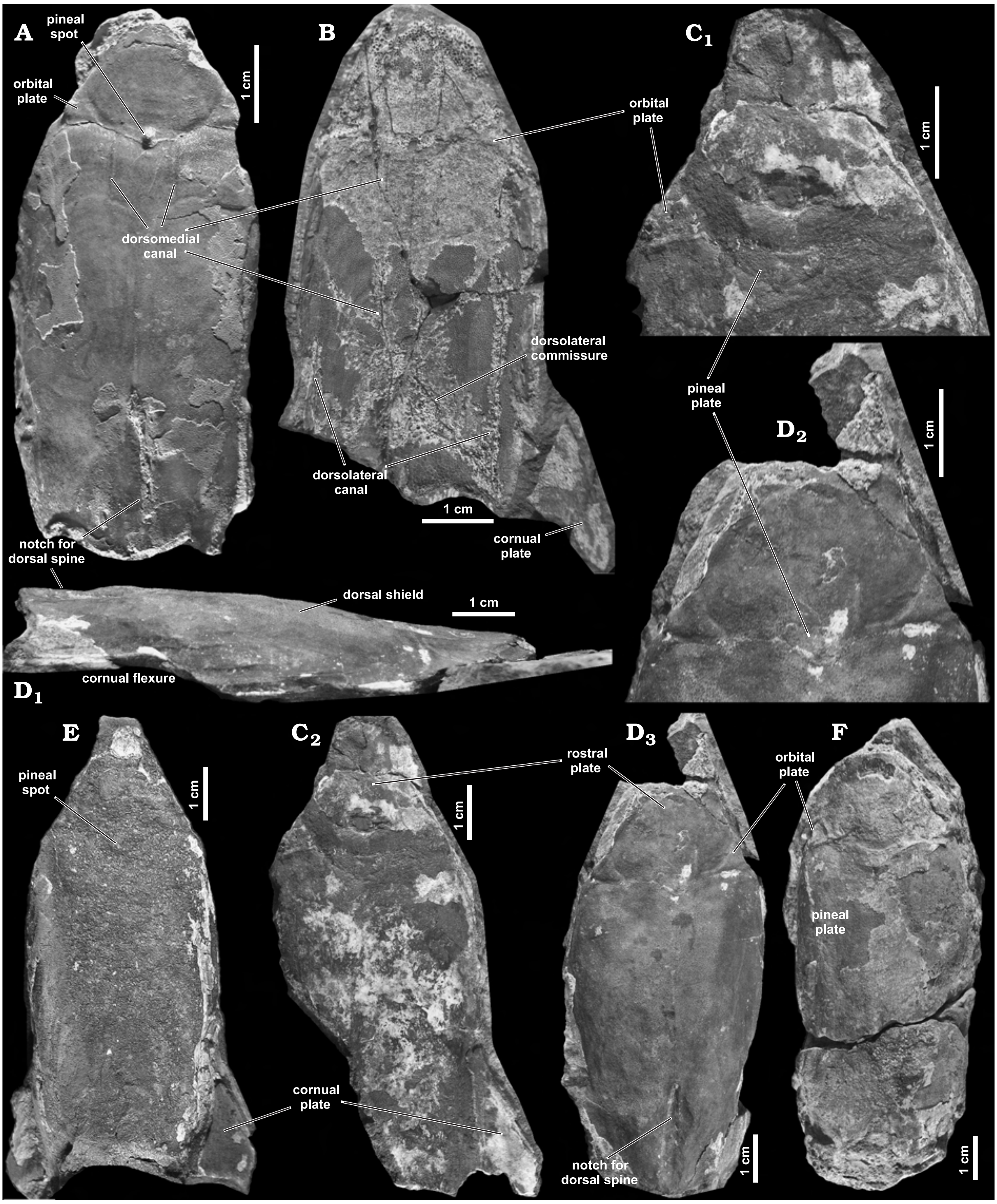

Fig. 57. Podolaspidids from various localities of the Dniester Formation in Podolia. **A**. *Parapteraspis plana* Stensiö, 1958, mould of carapace SMNH BP.297 lacking cornual plates from unknown locality, probably Ustechko or Khmeleva Member, dorsal view. **B**. Same species, inside of carapace SMNH BP.295 (see also Figs 32E, 48B) from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member, dorsal view. **C**. Same species, partial mould of carapace SMNH BP.300 lacking left cornual plate from the same locality, lower part of Khmeleva Member, dorsal view, also enlarged anterior part. **D**. Same species, partial mould of carapace SMNH BP.306 lacking cornual plates from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorsal and lateral (right side) views, also enlarged anterior part. **E**. *Mylopteraspidella gracilis* (Stensiö, 1958), partial mould of carapace SMNH BP.1443 (see also Fig. 58D) from Ustechko, left bank of Dniester River, talus on slope, lower part of Khmeleva Member, dorsal view. **F**. *Parapteraspis lata* (Stensiö, 1958), partial mould of carapace SMNH BP.298 (see also Fig. 58C) lacking cornual plates from Ivanie-Zolote, left bank of Dniester River, lower part of Ustechko Member, dorsal view.

Parapteraspis lata (Stensiö, 1958)

(Figs 57F, 58A, C)

1958. *Plesiopteraspis*? *lata*; Stensiö 1958: p. 257, fig. 138.
1964. *Plesiopteraspis*? *lata*; Stensiö 1964: p. 191, fig. 40.
1983. *Parapteraspis lata*; Novitskaya 1983: p. 182, pl. 26, figs 2, 3.
1984. *Podolaspis*? *lata*; Blieck 1984: pp. 44–45, figs 16, 41G.
1986. *Parapteraspis lata*; Novitskaya 1986: pp. 90–91, text-fig. 39, pl. 17, fig. 4, synoptic table, p. 144, fig. 46.
2004. *Parapteraspis lata*; Novitskaya 2004: pp. 152–153, text-fig. 76, pl. 11, fig. 2.

Type specimen: Lectotype NHRM C1540, partial (except for right side part) carapace in dorsal view; Jagilnytsia Stara, Chortkiv rayon, Ternopil' oblast' (Podolia).

Referred material. — Fragmentary mould of carapace SMNH BP.207 and 298.

Diagnosis. — *Parapteraspis* species with very short gap between the orbital median processes and the pineal plate.

Description. — The carapace from Ivanie-Zolote is more than 100 mm in length (Novitskaya 1986 reported 75 mm). The rostral plate is about 30 mm in length. Index RL/RW is ~0.9. Pineal plate looks like that of *Parapteraspis plana*, but extends more to sides and takes about part of the extent of orbito-pineal belt. The medial orbital processes are wide and short and almost touch the pineal plate. The anterior orbital processes are wide and short as well. Dorsal shield (DL 75 mm, DW ~38 mm; DW/DL 0.51) seems slightly elongated and shows no appreciable narrowing in its postbranchial part, in contrast with data of Novitskaya (1986, 2004). The notch for dorsal spine extends a bit in front of the level of posterolateral corners of the dorsal shield. Judging from materials studied by Blieck (1984: figs 16E, 41G) and from traces in studied specimen, the mdl canals are of parallel type.

Remarks. — The species is restricted to the Ivanie Stage, and nowhere co-occurs with *P. plana*.

Localities and age. — Ivanie-Zolote, Zalishchyky, Jagilnytsia Stara; Lochkovian (from Ivanie Stage of the Tyver formation to, probably, the lower part of the Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Family **Larnovaspididae** Halstead *in* Novitskaya 2004

Genus *Larnovaspis* Blieck, 1984

1927. *Pteraspis*; Zych 1927: pp. 50–56 (pars).
1933. *Pteraspis*; Brotzen 1933a: pp. 435–462 (pars).
1959. *Pteraspis*; Balabai 1959b: p. 6 (pars).
1961. *Pteraspis*; Tarlo 1961: p. 383 (pars).
1964. *Pteraspis*; Obruchev 1964: p. 67 (pars).
1975. *Pteraspis*; Novitskaya 1975: p. 79.
1984. *Larnovaspis*; Blieck 1984: pp. 52–53.
1986. *Larnovaspis*; Novitskaya 1986: pp. 92–93.
2001. *Larnovaspis*; Voichyshyn 2001c: p. 36.
2004. *Larnovaspis*; Novitskaya 2004: pp. 153–154.

Type species: *Pteraspis stensioei* White, 1935; Early Devonian of Great Britain.

Diagnosis. — Medium or large sized pteraspidids (tL is 80–160 mm). Index RL/RW equals 0.7–1.2. The anterior orbital processes are short, pointed and wide, while the medial ones are ribbon-shaped or wedge-shaped. The pineal plate is quadrangular. Its corners are not rounded or rounded insignificantly. The anterior margin of the pineal plate is slightly concave, while the posterior one is more or less convex and the lateral ones are straight. The orbito-pineal belt is of equal-contact or non-equal-contact type. The dorsal shield is more or less wide (DW/DL is 0.54–0.77). The dorsal spine has a wide basis and is inclined backwards. The cornual plates are usually elongated, narrow and oriented caudally or wide, triangular in shape and directed laterocaudally.

Species included. — Besides the type species: *Larnovaspis goujeti* (Blieck, 1982), Early Devonian of Spitsbergen, *L. kneri* (Lankester, 1868), *L. iwaniensis* (Brotzen, 1933), *L. major* (Zych, 1927), *L. mogielnensis* Blieck, 1984; all four species are from Early Devonian of Podolia.

Remarks. — The Podolian species of the genus need to be revised. Prominent carapace parts (cornual plates in this case) of large specimens have little chance to be preserved and this precludes adequate defini-

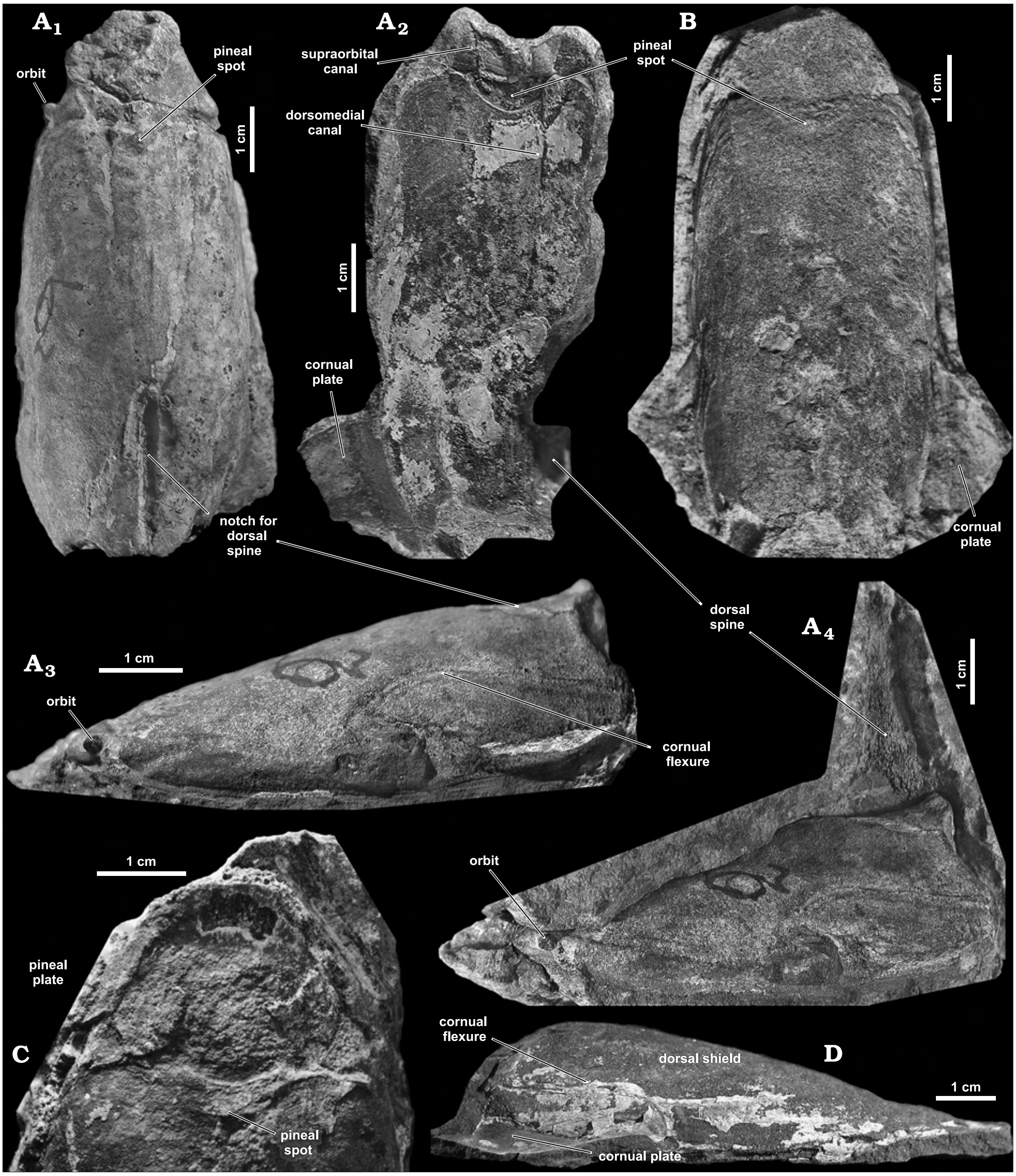

Fig. 58. Podolaspidids from various localities of the Dniester Formation in Podolia. **A**. *Parapteraspis lata* (Stensiö, 1958), partial mould of carapace SMNH BP.207 from Zalishchyky, right bank of Dniester River, talus, upper part of Ivanie Member of the Tyver Formation, dorsal and lateral (left side with adjoining imprint of dorsal spine) views, also partial imprint of carapace dorsal and lateral (left side) views. **B**. *Mylopteraspidella gracilis* (Stensiö, 1958), partial mould of carapace SMNH BP.315 lacking distal parts of rostral and cornual plates from the Verbivtsi quarry, Ivanie Member, dorsal view. **C**. *Parapteraspis lata* (Stensiö, 1958), partial mould of carapace SMNH BP.298 (see also Fig. 57F) lacking cornual plates from Ivanie-Zolote, left bank of Dniester River, lower part of Ustechko Member, anterior part. **D**. *Mylopteraspidella gracilis* (Stensiö, 1958), partial mould of carapace SMNH BP.1443 (see also Fig. 57E) from Ustechko, left bank of Dniester River, talus on slope, lower part of Khmeleva Member of the Dniester Formation, lateral (right side) view.

tion and comparison. This is one of the reasons of dispute regarding *L. mogielnensis*. Also, diagnostic features of *L. major* remain poorly known.

Occurrence. — Early Devonian of Podolia (Ukraine), Great Britain, and Spitsbergen (Norway).

Larnovaspis major (Zych, 1927)

(Figs 59A–G, 60A, D)

1927. *Pteraspis lerichei*, mut. *major*; Zych 1927: pp. 19, 54 (pars), pl. 2, fig. 8, text-fig. 6a, b.

1931. *Podolaspis major*; Zych, 1931: photo 23.

1933. *Pteraspis major*; Brotzen 1933a: pp. 451–453, fig. 13.

1959. *Pteraspis elongata*; Balabai 1959b: pp. 9–12 (pars), pl. 2, fig. 4b, pl. 3, fig. 1.

1983. *Pteraspis major*; Novitskaya 1983: p. 182, text-fig. 11b, pl. 28, figs 1, 2.

1984. *Larnovaspis major*; Blieck 1984: p. 55, fig. 44D.

1986. *Larnovaspis major*; Novitskaya 1986: pp. 95–96, text-figs 41, 42, pl. 19, figs 1, 2, synoptic table, p. 144, fig. 48.

2004. *Larnovaspis major*; Novitskaya 2004: pp. 155–156, text-figs 78, 79, pl. 11, figs 4, 5.

Type specimen: Lectotype (Zych 1927: pl. 2, fig. 8) designated by Blieck (1984: p. 55), carapace in dorsal view; Mogyl'nytsia, Terebovlia rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Referred material. — Specimens SMNH BP.236, 237, 244, 247, 970, 1202, 1469, and MZ V III Vp-203. Although there are many more specimens in the SMNH collection referrable to the species *sensu* Novitskaya (1984, 2004), only those listed fit diagnosis proposed below.

Diagnosis. — Medium sized *Larnovaspis* species with crescent-shaped cornual plates directed latero-caudally and lateral margins of the pineal plate wider than the medial orbital processes at the place of contact.

Description. — The length of the carapace is 100–130 mm. The rostral plate is robust and slightly convex at lateral margins. Index RL/RW (according to different authors) equals 0.8–1.1. The anterior orbital processes are short and massive, while the medial ones are relatively long, narrow and ribbon-shaped. At the place of contact, they are narrower than lateral margins of the pineal plate. The latter is rounded quadrangular. The dorsal shield is rather wide and somewhat narrows in the postbranchial part. The posterior margin of the shield is slightly concave between posterolateral corners and medial ledge, which are placed approximately on the same level. The notch of the dorsal extends a little bit before the level of branchial openings. Mdl canals are of radial type (Fig. 59E).

Comparison. — This species differs from *Larnovaspis stensioei*, *L. kneri*, *L. iwaniensis*, and *L. goujeti* by the morphology of the orbito-pineal belt. Besides, *L. stensioei* has a shorter rostral plate, more convex lateral margins of the orbital plates, other arrangement of the notch of the dorsal spine, more obtuse tips of the cornual plates and parallel arrangement of the mdl canals. *Larnovaspis kneri* is of smaller size, while *Larnovaspis iwaniensis* has more massive anterior orbital processes and narrower dorsal shield. *Larnovaspis goujeti* has more rounded outer margin of the rostrum, better developed anterior orbital processes, wider pineal plate, as well as *Larnovaspis mogielnensis*, other shape and orientation of the cornual plates. Moreover, *L. mogielnensis* has narrower postbranchial part of the dorsal shield and it is of larger mature size.

Remarks. — Except for the photo of the lectotype, there are no figures of the cornual plates (triangular, of the “podolaspidid” type) of this species in the literature. The cornual plates, attributed to this species by Brotzen (1933a: fig. 13b), are appreciably thinner and more backward directed. Long enough, rather narrow, more or less elongated in caudal direction cornual plates are characteristic for the larnovaspidids. The shape of these plates is practically the only distinction between *Larnovaspis major* and *L. mogielnensis*, so more that there are differences in interpretation of these species. For example, the lectotype of *Larnovaspis major* has elongated dorsal shield (DW/DL is 0.53), the notch for the dorsal spine extending up to the level of arrangement of the branchial openings and posterior margin of the shield, judging by size of the notch, is generally concave and similar to that of *L. stensioei*. On the other hand, Brotzen’s (1933a) specimen shows wide dorsal shield (DW/DL 0.73) and the notch of the dorsal spine, which extends much further forward.

The lectotype preservation does not allow one to discern the orbito-pineal belt on the photograph given by Zych (1927: pl. 2, fig. 8), and a possibility remains that it was podolaspidid-like; see for comparison specimen PIN 3592/31 of *Podolaspis podolica* in Novitskaya (2004: text-fig. 68) or SMNH BP.170 (Fig. 49A). If this is the case, all discrepancies mentioned above would find an explanation. Such a conclusion is contradicted by the reconstruction of the lectotype by Zych (1927: text-fig. 6a), who noted that “… 2 tarcze oczne i środkowa – jak u [two orbital plates and median one are the same as in] *Pteraspis Sturi* mut. *major*”. Possibly the reconstruction and description of the orbito-pineal belt were based on another specimen attributed by

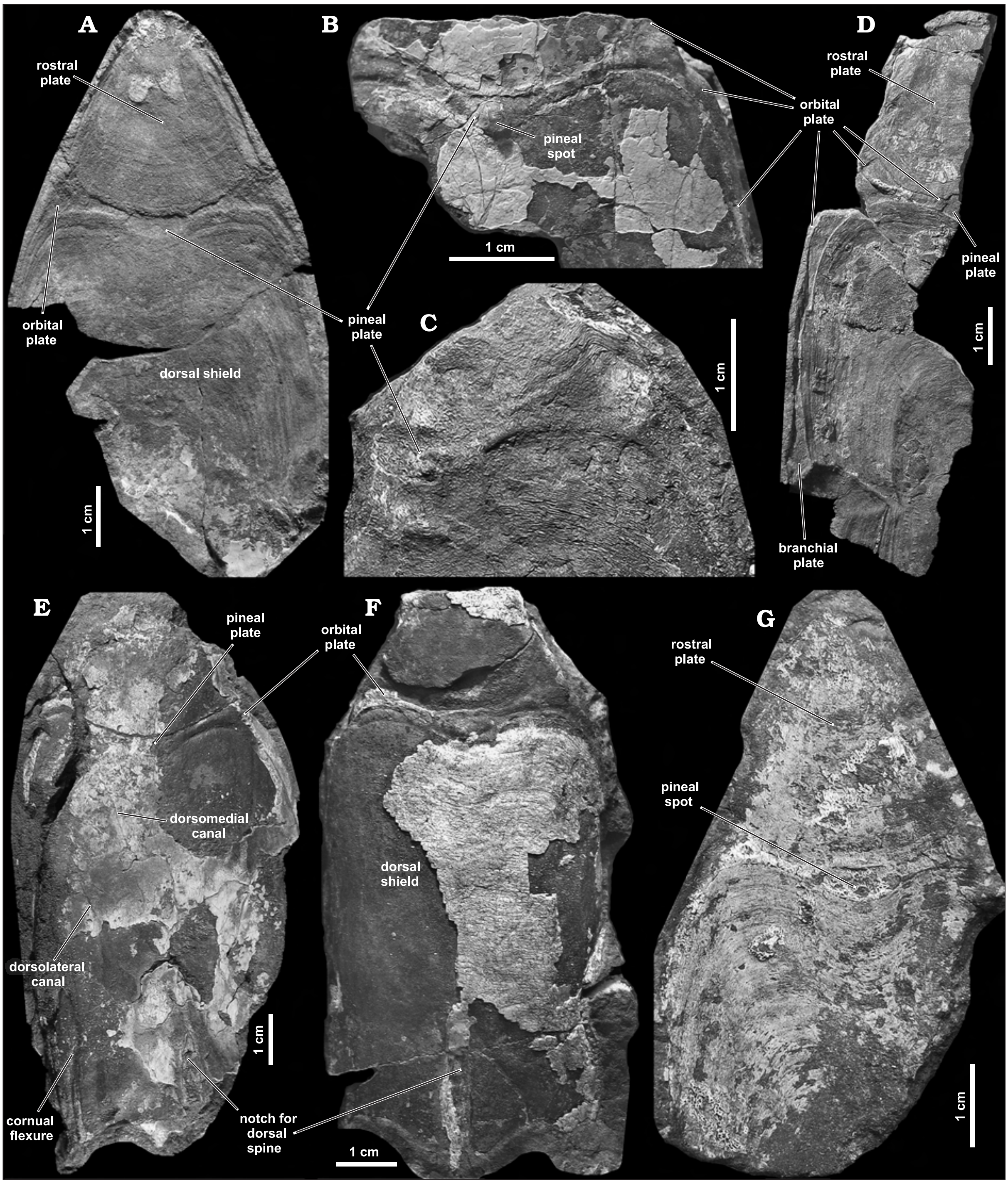

Fig. 59. Larnovaspidid *Larnovaspis major* (Zych, 1927) from various localities of the Dniester Formation in Podolia. **A**. Partial imprint of carapace SMNH BP.247 from unknown locality on left bank of Dzhuryn River, Ustechko Member, dorsal view. **B**. Partial mould of orbito-pineal zone SMNH BP.970 from unknown locality, lower part of the Dniester Formation, dorsal view. **C**. Partial imprint of orbito-pineal zone SMNH BP.1469 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member, dorsal view. **D**. Partial imprint of right part of carapace SMNH BP.236 (see also Fig. 60A) from the same locality and horizon, talus on slope, dorsal view. **E**. Partial mould of carapace SMNH BP.244 from Nyrkiv, Ustechko Member or lower part of Khmeleva Member, dorsal view. **F**. Partial mould of carapace SMNH BP.1202 lacking branchial and cornual plates probably from Ustechko, lower part of the Dniester Formation, dorsal view. **G**. Imprint of carapace anterior part MZ V III Vp-203 from Ustechko, at the old destroyed bridge ("przy moście"), lower part of the Dniester Formation, dorsal view.

Zych to *Pteraspis lerichei* mut. *major* (Zych 1927: pl. 3, fig. 2). Two plaster casts of this specimen in the collection of IGP (Fig. 60C) give an impression that this was truly the case.

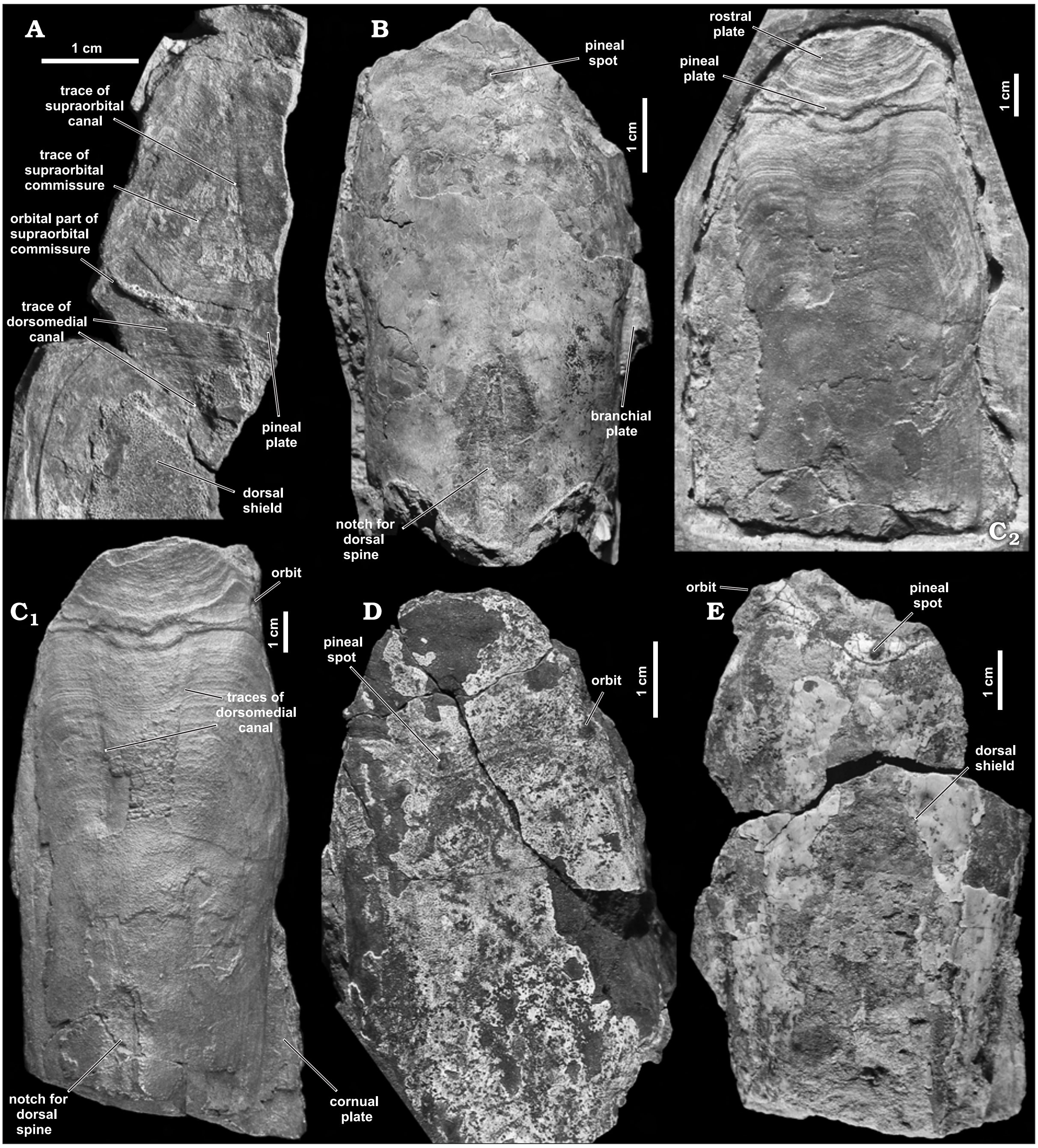

Fig. 60. Larnovaspidids from various localities in Podolia. **A**. *Larnovaspis major* (Zych, 1927), partial imprint of right part of carapace SMNH BP.236 (see also Fig. 59D) from Ustechko, talus on slope, lower part of Khmeleva Member of the Dniester Formation, enlarged anterior part (see also Fig. 57D). **B**. *Larnovaspis* sp., mould of dorsal shield and pineal plate SMNH BP.1189 from unknown locality, lower part of the Dniester Formation, dorsal view. **C**. *Larnovaspis mogielnensis* Blieck, 1984, plaster-cast copies IGP 03909 and IGP A-25 of the partial carapace figured by W.Zych (1927: pl. 3, fig. 2) from Mogylnytsia, Ivanie Member of the Tyver Formation, dorsal views. **D**. *Larnovaspis major* (Zych, 1927), partial mould of carapace SMNH BP.237 from the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view. **E**. *Larnovaspis ?mogielnensis* Blieck, 1984, partial mould of carapace SMNH BP.240 from Buriakivka, left bank of Dzhuryn River, probably Ustechko Member, dorsal view.

Localities and age. — Ustechko, Mogyl’nytsia, Nyrkiv, Horodnytsia, Zalishchyky; from Lochkovian to early Pragian (from upper part of the Ivanie Stage to lower part of the Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Larnovaspis iwaniensis (Brotzen, 1933)

1933. *Pteraspis iwaniensis*; Brotzen 1933a: pp. 450–451, fig. 12.
1975. *Pteraspis iwaniensis*; Novitskaya 1975: p. 79.
1983. *Pteraspis iwaniensis*; Novitskaya 1983: p. 182, pl. 28, fig. 3.
1984. *Larnovaspis iwaniensis*; Blieck 1984: pp. 54–55.
1986. *Larnovaspis iwaniensis*; Novitskaya 1986: pp. 96–97, text-fig. 43, pl. 19, fig. 3, synoptic table, p. 144, fig. 49.
2004. *Larnovaspis iwaniensis*; Novitskaya 2004: pp. 156–157, text-fig. 80.

Type specimen: Lectotype figured by Brotzen (1933a: fig. 12), carapace in dorsal view; Ivanie Zolote, Zalishchyky rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Remarks. — Except for the lectotype, which is probably lost, the species is known from a mould of the carapace PIN 3592/59, lacking anterior and posterior parts (Novitskaya 1986: text-fig. 43, pl. 19, fig. 3, 2004: text-fig. 80). This is a rather small-sized slender larnovaspid species with an equal-contact ribbon-shaped orbito-pineal belt and massive orbital plates.

Localities and age. — Ivanie-Zolote (Brotzen 1933a; Novitskaya 1986); late Lochkovian (Ivanie Stage of the Tyver formation or lower part of Ustechko Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is kept in the SMNH collection.

Larnovaspis mogielnensis Blieck, 1984

(Figs 18H, 60C, E, 61A–D)

1927. *Pteraspis sturi* Alth mut. *major*; Zych 1927: pp. 16–17, pl. 3, fig. 1, text fig. 4.
1927. *Pteraspis lerichei* mut. *major*; Zych 1927: pl. 3, fig. 2.
1984. *Larnovaspis mogielnensis*; Blieck 1984: pp. 55–57, figs 24A–C, 44H.
1986. *Larnovaspis major*; Novitskaya 1986: pp. 95–96 (pars).
2004. *Larnovaspis major*; Novitskaya 2004: pp. 155–156 (pars).

Type specimen: Lectotype (Zych 1927: pl. 3, fig. 1), almost complete mould of the carapace in dorsal view; Mogyl'nytsia, Terebovlia rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown. At least two plaster-cast copies of syntype of *Pteraspis lerichei* mut. *major* figured by Zych (1927: pl. 3, fig. 2) and regarded here as belonged to *Larnovaspis mogielnensis* are kept in the IGP collection (Voichyshyn 2006c; Fig. 60C).

Referred material. — Fragmentary moulds of carapaces SMNH BP.238, 240, 289, 291, 292/1, 293, and 1095, also possibly, BP.240.

Diagnosis. — Large sized *Larnovaspis* species with relatively wide and ribbon-shaped medial orbital processes and large, long, narrow and caudally directed cornual plates.

Description. — The length of carapace is 120–150 mm (up to 160 mm according to Zych 1927; the length of dorsal shield of the specimen IGP 03909 is not less than 120 mm). Rostral plate is massive. Index RL/RW equals 0.8–1.1. The anterior orbital processes are short, wide and acutely angular, while the medial ones are more or less elongated, relatively wide and ribbon-shaped. The pineal plate is rectangular in shape. Its anterior margin is rather concave. The posterior one is slightly convex, while the lateral ones are straight and slightly oblique. The orbito-pineal belt is equal or unequal at contact. The dorsal shield is elongated, massive, not especially wide (DW/DL 0.54–0.63), with maximum width approximately at the middle of the prebranchial part. It is somewhat narrowed in the postbranchial part. The notch of the dorsal spine is large. The dorsal spine (at least at its base) is inclinated backwards at angle of 18° to the surface of the shield. The cornual plates are large, elongated (50–70 mm), narrow and of directed caudally. According to Blieck (1984: figs 24A–C, 44H), the mdl canals of this species are of radial type.

Comparison. — The species differs from *L. stensioei* by longer rostral plate, less convex lateral sides of the orbital plates, narrower dorsal shield (DW/DL of *mogielnensis* is 0.54–0.63, the index of s*tensioei* equals 0.77), less apparent narrowing of the postbranchial part of the dorsal shield, narrower and longer cornual plates, the type of arrangement of the mdl canals, and larger size. Unlike this species, *L. goujeti*, *L. iwaniensis* and *L. kneri* have a wider postbranchial part of the dorsal shield. Besides, *L. goujeti* has a wider anterior margin of the rostrum, wider pineal plate, parallel mdl canals, considerably smaller size, while *L. iwaniensis* has more massive anterior and shorter medial orbital processes, smaller (and of other shape) cornual plates and adult size. *Larnovaspis kneri* is essentially of smaller size. Comparison with *L. major* is given in its description.

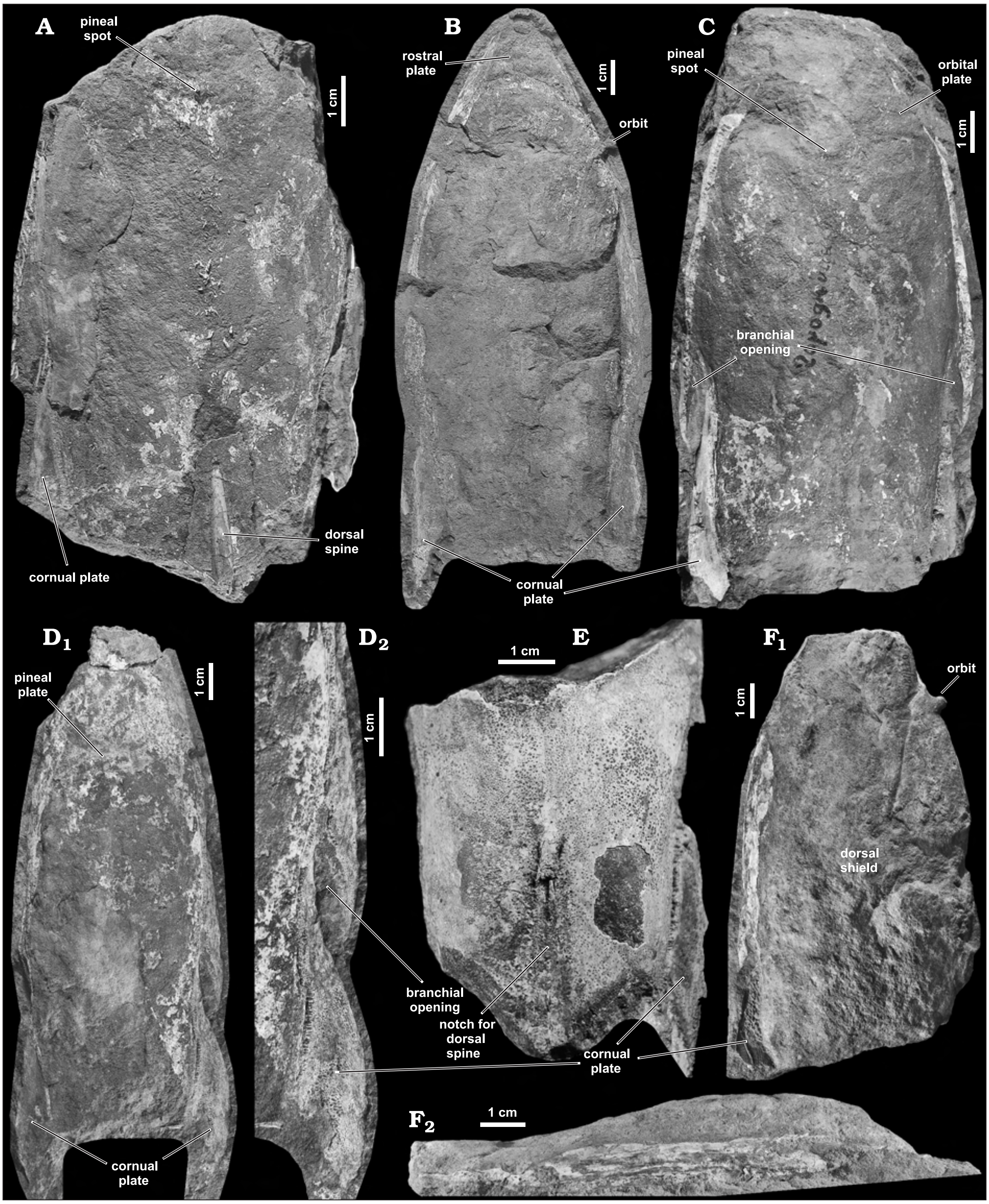

Fig. 61. Larnovaspidids from various localities of the Dniester Formation in Podolia. **A**. *Larnovaspis mogielnensis* Blieck, 1984, partial mould of carapace SMNH BP.238 from the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. Same species, abraded mould of carapace SMNH BP.1095 (see also Fig. 18H), same locality, dorsal view. **C**. Same species, partial mould of carapace SMNH BP.289 from same locality, dorsal view. **D**. Same species, partial mould of carapace SMNH BP.292/1, same locality, dorsal view and enlarged branchio-cornual zone. **E**. *Larnovaspis* sp., partial mould of posterior carapace part SMNH BP.241, same locality, dorsal view. **F**. *Larnovaspis* sp., partial abraded mould of carapace SMNH BP.313 from unknown locality on bank of Krynytsia River, lower part of the Dniester Formation, dorsal and lateral (left side) views.

Remarks. — The SMNH specimens of *L. mogielnensis*, in contrast with ones studied by Blieck (1984), have equal-contact (see Morphology Chapter) orbito-pineal belt, clearly rectangular pineal plate, more stable ratio DW/DL (0.57–0.58) and not so narrow rostral plate with index RL/RW 0.78. One of the specimen figured by Blieck (1984: fig. 24A) has the index 0.79. However, general size and proportion of the dorsal shield, and also the degree of development of cornual plates in both the collections, are similar.

Localities and age. — Mogyl'nytsia, Buriakivka, Horodnytsia, Chervonograd, Potochyshche; from Lochkovian to early Pragian (from the Ivanie Stage of the Tyver formation to lower part of the Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Larnovaspis kneri (Lankester, 1868)

(Figs 19H, 31B, 62A, B, E)

1868. *Scaphaspis kneri*; Lankester 1868: pp. 19–20, fig. 9.
1874. *Pteraspis major* m.; Alth 1874: pp. 44–45 (pars), pl. 1, figs 1, 2.
1933. *Pteraspis kneri*; Brotzen 1933a: pp. 442–444, fig. 7.
1941. *Pteraspis kneri*; Pauča 1941: pp. 24–25 (pars), pl. 2, figs 4–6.
1983. *Pteraspis kneri*; Novitskaya 1983: p. 182, pl. 27, figs 1–3.
1984. *Larnovaspis* gen. n. *kneri*; Blieck 1984: pp. 53–54, figs 23, 44B.
1986. *Larnovaspis kneri*; Novitskaya 1986: pp. 93–95, text-fig. 40, pl. 18, figs 2, 3, synoptic table, p. 144, fig. 47.
2004. *Larnovaspis kneri*; Novitskaya 2004: pp. 154–155, text-fig. 77, pl. 11, fig. 3.
2005. *Brachipteraspis* sp. cf. *B. latissima*; Dumbrava and Blieck 2005: pp. 166–167 (pars), fig. 4a, pl. 1, fig. 12.
2009. *Larnovaspis kneri*; Lebedev *et al.* 2009: pp. 345–346, fig. 1.

Type specimen: Lectotype (Lankester 1868: fig. 9), ventral shield; vicinities of Zalishchyky, Podolia. (Novitskaya 1986) considered the figure in Brotzen (1933a: fig. 7) as the reference. The location of the specimen is unknown.

Referred material. — Fragmentary moulds of anterior part of carapace SMNH BP.194 and 245; carapace fragments BP.246 and 1440, probably, partial moulds of carapace lacking cornual plates BP.576 and 1256.

Diagnosis. — Small sized *Larnovaspis* species with relatively wide dorsal shield and orbito-pineal belt.

Description. — The value tL generally does not exceed 90 mm (less than 80 mm in specimen LIG 5-800 but up to 93 mm in BP.1256). Index RL/RW is mostly 0.7–0.8 (up to 0.9 in BP.1256). Ratio of length of ventral side of the rostrum to dorsal one is ~0.4–0.5: 0.375 in material of Novitskaya (1986), 0.388–0.480 in my specimens, and ~0.5 in specimen LIG 5-800. The preoral field is covered with transverse ridges. The ascending plate is wide (~4 mm), sharply bent inside of the mouth. The medial crest is small and rounded. The pineal plate is rectangular (PL 4–5 mm, PW 7–8.6 mm), with straight anterior, hardly oblique lateral and convex posterior margin. The lateral margins of the plate are in full contact with ribbon-wedge-shaped medial orbital processes. Soc canals cross the anterior margin of the pineal plate near its anterolateral corners. Supraorbital comissures branch off from soc almost at the level of anterior ends of the orbital plates or a little bit higher. In the place of branching, an H-shaped crosspiece is observed (Fig. 31B). The prebranchial part of the dorsal shield seems to be wider than the postbranchial one, but narrower in specimen LIG 5-800. DL 65 mm, DW 32 mm, DW/DL is 0.49 (in BP.1256). The posterior margin of the shield bears a median ledge. The notch for the dorsal spine is 22 mm long and takes about 30% of the total length of the dorsal shield in BP.1256. In specimen LIG 5-800, these values are 16 mm and about 20%. Density of dentine ribs is 10 cr/mm over the rostral plate and 8–9 cr/mm on the dorsal one. The type of mdl sensory canals remains unknown.

Comparison. — In contrast with this species, *L. stensioei* has narrower orbito-pineal belt and smaller pineal plate as well as the dorsal shield in the postbranchial part. *Larnovaspis goujeti* has a wider pineal plate and different shape of the orbital plates, while *L. iwaniensis* has a narrower dorsal shield and pineal plate, and more robust orbital plates. Comparison with other species of the genus is given in their description.

Remarks. — The part of a pteraspid carapace MNG I (V) 0031, including partial rostral plate and orbito-pineal belt, collected by Theodor Văscăuțanu at Babyn on the Bukovinian (right) bank of Dniester River and attributed by Dumbrava and Blieck (2005) to *Brachipteraspis* sp. cf. *B. latissima*, almost certainly belongs to *Larnovaspis kneri* (cf., Blieck 1984: fig. 44B; Novitskaya 2004: fig. 77). These authors based their identification only on a photograph of the specimen (Dumbrava and Blieck 2005: p. 167), at which the orbito-pineal belt looks as a ribbon (Dumbrava and Blieck 2005: pl. 1, fig. 12) wider than on its drawing (Dumbrava and Blieck 2005: fig. 4a).

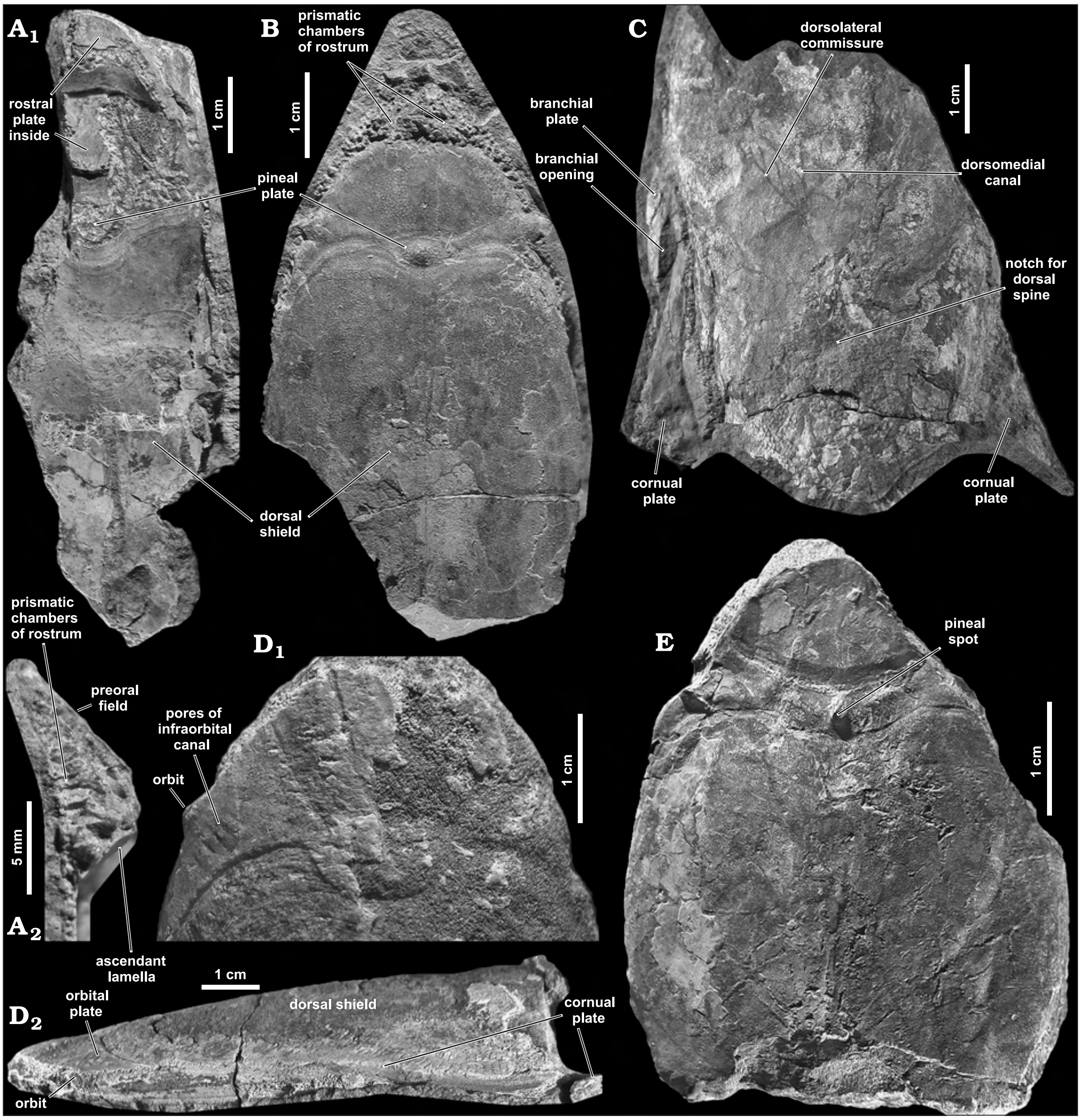

Fig. 62. Larnovaspidids from various localities in Podolia. **A**. *Larnovaspis kneri* (Lankester, 1868), partial carapace SMNH BP.246 (see also Fig. 31B) from Zalishchyky, upper part of Ivanie Member of the Tyver Formation, inside and lateral (right side) views of the anterior part. **B**. Same species mould of anterior carapace part SMNH BP.576 from the same locality. **C**. *Larnovaspis* sp., mould of carapace posterior part SMNH BP.242 from Ivanie-Zolote, left bank of Dniester River, lower part of Ustechko Member of the Dniester Formation, dorsal view. **D**. *Djurinaspis secunda* sp. n., mould of the holotype carapace SMNH BP.166 (see also Fig. 64) from vicinity of Bily Potik, Ivanie Member of the Tyver Formation, anterior part and lateral (left side) view. **E**. *Larnovaspis kneri* (Lankester, 1868), partial mould of carapace SMNH BP.194 from Zalishchyky, dorsal view.

Specimen LIG 5-800 (Blieck 1984, fig. 23; Lebedev *et al.* 2009: fig. 1), found at Gorodok, representing complete articulated carapace, with only posterior parts of the cornual plates and the dorsal spine are. It is the best preserved in all the material referred to the species. The specimen is remarkable in having a large bite mark, about 5 mm in diameter, in the left posterior quarter of the dorsal shield, which is probably the oldest predation trace on any vertebrate remain known up-to-date (Lebedev *et al.* 2009). The predator could be a sarcopterygian or acanthodian fish, or perhaps an eurypterid. The specimen in question demonstrates rather parallel type of mdl canals (Blieck 1984: fig. 23A).

Localities and age. — Ivanie-Zolote, Gorodok, Zastinoche, Zalishchyky, Babyn; Lochkovian (Ivanie Stage) of Podolia (Ukraine).

Genus *Belgicaspis* Zych, 1931

1931. *Belgicaspis*; Zych 1931: p. 89.
1964. *Belgicaspis*; Obruchev 1964: p. 67.
1975. *Belgicaspis*; Novitskaya 1975: p. 84.
1984. *Rhinopteraspis*; Blieck 1984: pp. 34, 68 (pars).
1986. *Belgicaspis*; Novitskaya 1986: p. 98.
2001. *Belgicaspis*; Voichyshyn 2001c: p. 36.
2004. *Belgicaspis*; Novitskaya 2004: pp. 157–158.

Type species: *Pteraspis crouchi* Lankester, 1868; Early Devonian of Great Britain.

Diagnosis. — Medium sized pteraspidids (tL is 100–140 mm). The rostral plate is narrow, long, pivot-shaped, with lateral margins that are concave at the base of the plate (RL/RW is 2.8). The orbital plates are massive, with convex lateral margins. Their anterior processes are pointed, while the medial ones are wedge-ribbon-shaped. The pineal plate is small, rectangular, with straight lateral margins. The dorsal shield (DW/DL is 0.65) has poorly convex lateral margins. The dorsal spine is developed. The cornual plates are small and narrow. Mdl canals are of radial type.

Species included. — Only type species.

Remarks. — Novitskaya (1986) noticed that *Belgicaspis* is known in Podolia from “rare finds”. In opinion of this author, “with most confidence, it is possible to attribute to this species a rostral plate” from Pechirna (specimen PIN 2828/2). However, this plate is fragmentary and there can not be safely determined as belonging to *Belgicaspis*. Actually, the same can be said about my own material referred to this taxon.

Occurrence. — Early Devonian of Great Britain, France, Belgium, and possibly Podolia (Ukraine).

?*Belgicaspis crouchi* (Lankester, 1868)
(Fig. 19B, C)

1868. *Pteraspis crouchi*; Lankester 1868: p. 30, pl. 3, figs 5, 6, 8.
1931. *Pteraspis* (*Belgicaspis*); Zych 1931: p. 89, fig. 40.
1964. *Belgicaspis crouchi*; Obruchev 1964: p. 67, pl. 2, fig. 3.
1983. *Belgicaspis crouchi*; Novitskaya 1983: p. 182, pl. 27, figs 4, 5.
1984. *Rhinopteraspis crouchi*; Blieck 1984: pp. 34, 68 (pars), fig. 37C, D.
1986. *Belgicaspis crouchi*; Novitskaya 1986: pp. 98–99, text-fig. 44, pl. 19, fig. 4, pl. 21, fig. 3, synoptic table, p. 145, fig. 51.
2004. *Belgicaspis crouchi*; Novitskaya 2004: p. 158, text-fig. 81, pl. 11, figs 6, 7.
2009. *Rhinopteraspis crouchi*; Thirion and Blieck 2009: pp. 34–36, fig. 5, pl. 1, pl. 2, figs B–D.
2010. *Belgicaspis*(?) *crouchi*; Voichyshyn 2010: pl. 3, fig. 2.

Type specimen: Lectotype depicted by Lankester (Novitskaya 2004), mould of dorsal shield and fragmentary rostrum; England. The location of the specimen is unknown.

Referred material. — Fragmentary (lacking posterior parts) rostral plates SMNH BP.1186 and 1232.

Diagnosis. — The same as for the genus (by monotypy).

Description. — The rostral plate is pivot-shaped and considerably elongated (RL > 40 mm, RW > 10 mm). Dentine ridges show density of 3–4 cr/mm on the ventral surface of the plate (at the anterior end) and 5–8 cr/mm on the dorsal one, over the whole visible area.

Remarks. — The species was described from the Early Devonian rocks of Britain. From Podolia, it was reported only after deformed rostral plates from Pechirna (Novitskaya 1986: text-fig. 44; PIN 2828/2), Verbivtsi and Ustechko. It is possible that the dorsal shields, considered here as belonging to “*Pteraspis*” *angustata*, are actually parts of the carapace of *Belgicaspis crouchi*, despite differences listed below. Unfortunately, articulated carapaces that could demonstrate identity of particular plates are lacking.

Specimens from the SMNH collection probably belonging to the species, show almost straight lateral margins of the supposed rostral plates. Thus, they differ from those from Belgium (cf. Thirion and Blieck 2009: fig. 5e, f, pl. 2, fig. B). The reconstruction by Blieck (1984: fig. 37C, D) is more similar to the SMNH specimens.

Localities and age. — Pechirna, Ustechko and Verbivtsi; from Lochkovian to early Pragian (from the Ivanie Stage of the Tyver formation to lower part of the Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Genus *Djurinaspis* Novitskaya, 1983

1983. *Djurinaspis*; Novitskaya 1983: pp. 160–161, 164.
1986. *Djurinaspis*; Novitskaya 1986: pp. 99–100.
2001. *Djurinaspis*; Voichyshyn 2001c: p. 36.
2004. *Djurinaspis*; Novitskaya 2004: pp. 158–159.

Type species: *Djurinaspis prima* Novitskaya, 1983; Early Devonian (Ustechko Stage and lower? part of Khmeleva Stage of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized larnovaspidids. Carapace is elongated (tL is about 90–110 mm), not wide, convex. Index RL/RW equals 0.8–0.9. The pineal plate is wide, taking not less than one third of the length of the orbito-pineal belt, short (PW/PL 2.0–3.0), laterally elongated and rounded. Orbital plates bear short, massive, and pointed anterior and wedge-shaped medial processes. The latter are narrower than the lateral margins of the pineal plate at the place of contact. The cornual plates are elongated and narrow, caudally directed, extending behind the posterior margin of the shield. The dorsal spine is well developed and inclined backwards.

Species included. — Besides type species, *Djurinaspis secunda* sp. n. from the Early Devonian of Podolia (Ukraine).

Occurrence. — Early Devonian of Podolia (Ukraine).

Djurinaspis prima Novitskaya, 1983

1983. *Djurinaspis prima*; Novitskaya 1983: p. 182, pl. 28, fig. 4.
1986. *Djurinaspis prima*; Novitskaya 1986: p. 100, text-fig. 45, pl. 20, fig. 1, synoptic table, p. 145, fig. 52.
2004. *Djurinaspis prima*; Novitskaya 2004: p. 159, text-fig. 82, pl. 12, fig. 1.

Type specimen: Holotype PIN 3592/71, almost complete inside of carapace in dorsal view; Ustechko (right bank of the Dzhuryn River), Zalishchyky rayon, Ternopil' oblast' (Podolia).

Remarks. — The dorsal shield has a narrowing at the level of branchial openings (Novitskaya 1986: text-fig. 45, pl. 20, fig. 1).

Localities and age. — Ustechko; probably late Lochkovian (Ustechko Stage of the Dniester Formation) of Podolia (Ukraine). No material that might be referred to the species is kept in SMNH collection.

Djurinaspis secunda sp. n.
(Figs 62D, 63, 64A)

Derivation of the name: Referring to the species name *Djurinaspis prima* by Novitskaya (1983: p. 182), as the second Podolian species of the genus.

Type specimen: Holotype SMNH BP.166, mould and imprint of the left part of carapace; vicinity of Bily Potik (Lochkovian, Ivanie Stage of the Tyver formation), Chortkiv rayon, Ternopil' oblast' (Podolia).

Referred material. — The holotype only.

Diagnosis. — Medium to large sized *Djurinaspis* species with relatively long and large pineal plate.

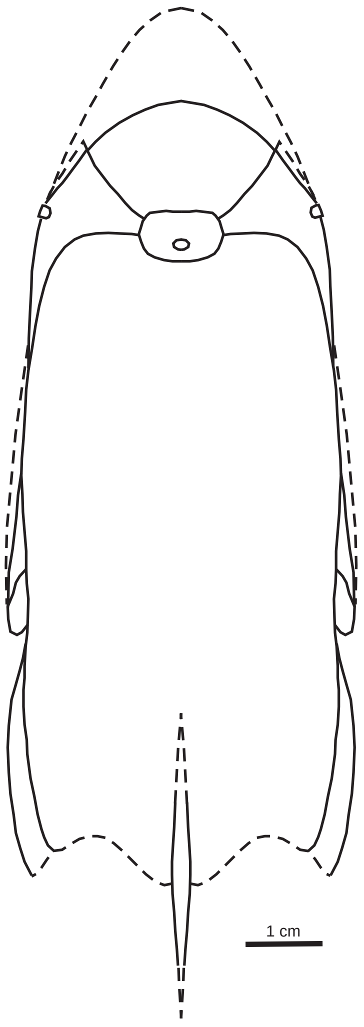

Fig. 63. Larnovaspidid *Djurinaspis secunda* sp. n., reconstruction of the carapace in dorsal view.

Description. — Carapace of the only known specimen is slender (tL is about 114 mm). Rostral plate is not preserved completely, and has been represented by a mould of supranasal cartilage (of 15 mm in length along the body axis). Usually, the rostral plate is at least about one-third longer than the anterior limit of supranasal cartilage, that is about 22–23 mm in length; RW 27 mm, RL/RW ~0.85). Anterior (rather massive) and medial (wedge-shaped) orbital processes are short. The pineal plate is wide (PL 6.8 mm, PW 12.9 mm; PW/PL ~2.0), rounded-rectangular in shape. Its anterior margin is straight, the posterior one is slightly convex and the lateral ones are oblique. The dorsal shield is elongated, somewhat narrowed at the level of the branchial openings, equally wide in pre- and postbranchial

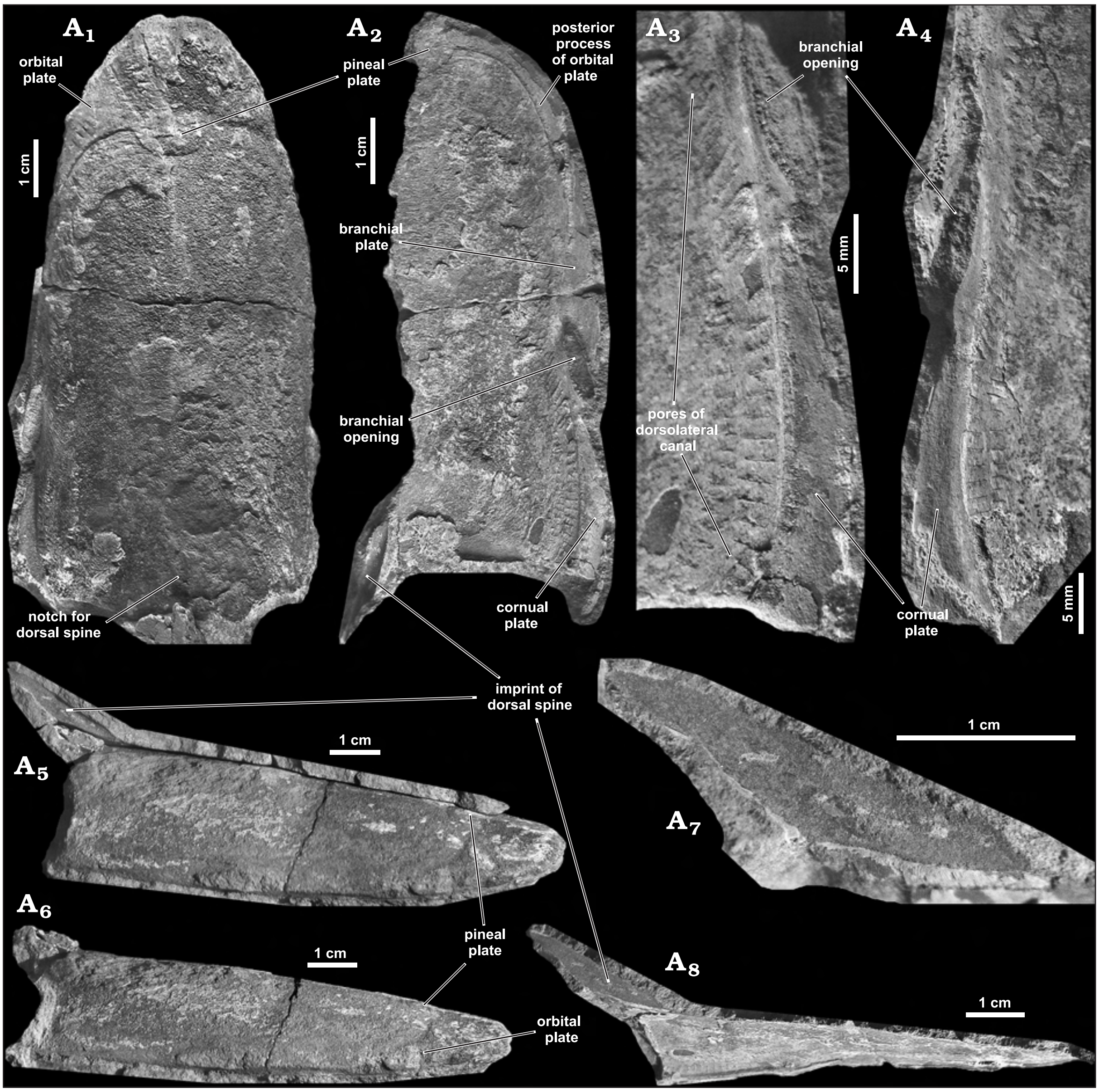

Fig. 64. Larnovaspidid *Djurinaspis secunda* sp. n., holotype SMNH BP.166 (see also Fig. 62D) from vicinity of Bily Potik, Ivanie Member of the Tyver Formation, the carapace dorsal view, imprint of left part and left cornual region in dorsal view, left branchio-cornual region, mould of the carapace and imprint of dorsal spine, in lateral (right side) view, carapace in lateral (right side) view, dorsal spine in lateral (left side) view and imprint of left part of carapace in lateral view, respectively.

parts (DW/DL is 0.55). The dorsal spine is rather small (length along its axis is ~25 mm and height ~12 mm), inclined backwards. The angle between its anterior margin and the dorsal shield reaches 25°. The cornual plates are long (40 mm) and narrow (2.5 mm at its middle part). Dentine ridges are of density 5 cr/mm in the anterior and 6 cr/mm in the posterior parts of the dorsal shield, around the notch for the dorsal spine.

Comparison. — The new species differs from *Djurinaspis prima* by generally greater mature size, longer (and more massive) pineal plate (with index PW/PL 2.0 in contrast with 3.0 in *D. prima*), and less narrow dorsal shield in the region of branchial openings. At the same time, it shares a number of features with the type species of the genus, namely the general type of orbito-pineal belt, morphology of branchio-cornual region, and similar (as far as can be judged) shape of the cornual plates.

Remarks. — Remains of the species come from terrigenous deposits of Ivanie Stage of the Tyver formation, whereas the type species is known from similar deposits of the lower part of the Dniester Formation.

Localities and age. — Bily Potik; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine).

Genus *Alaeckaspis* Voichyshyn, 1999

1933. *Pteraspis*; Brotzen 1933a: pp. 454–455 (pars).
1984. *Errivaspis*; Blieck 1984: pp. 47–48, 83 (pars).
1999. *Alaeckaspis*; Voichyshyn 1999: pp. 48–49.
2001. *Alaeckaspis*; Voichyshyn 2001c: p. 36.

Type species: *Alaeckaspis verbivciensis* Voichyshyn, 1999; Early Devonian (lower part of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized pteraspidids (tL is 95–130 mm). Carapace is fairly slender. Index RL/RW equals 0.8. The orbito-pineal belt is wide and its components may contact each other. Orbital plates are massive, with noticeably developed anterior processes and rather short, wide and wedge-shaped medial ones. The pineal plate is large, with convex posterior margin, and amounts about 1/3 of the orbito-pineal belt extent. The dorsal shield is not wide (DW/DL is 0.53–0.61). The cornual plates are narrow and elongated. Dorsomedial sensory canals are of parallel type.

Species included. — Besides the type species: *A. ustetchkiensis* Voichyshyn, 1999, *A. magnipinealis* (Brotzen, 1933), and, perhaps, *A.*? *depressa* (Stensiö, 1958), all from the Early Devonian of Podolia.

Remarks. — In contrast with this genus, *Larnovaspis* has orbital plates that are not so massive, and in particular, anterior orbital processes that are not so well developed, a much smaller pineal plate, and wider and larger cornual plates. *Errivaspis* has a wider carapace, smaller pineal plate, longer medial orbital processes and appreciably less developed anterior ones. *Belgicaspis* shows a different shape of the rostral and pineal plates and smaller size of the latter. *Brachipteraspis* has a wider carapace, smaller elements of the orbito-pineal belt, greater branchial plates, and dorsomedial sensory canals of radial type. *Zascinaspis* has a different shape of the rostral, orbital and dorsal plates. By general shape of the carapace, rostral, dorsal and, probably, cornual plates *Alaeckaspis* is most similar to *Djurinaspis*, but differs from it by larger orbital plates (with more developed anterior and wider medial processes) and (longer) pineal one.

The antero-lateral (orbital?) notches, which developed at the anterior margin of dorsal shield in juvenils, have been found in the holotypes of the both *Alaeckaspis* species described below. It is unclear whether this phenomenon is a feature of the genus.

Some specimens belonging to *Errivaspis waynensis* (White, 1935) (e.g., "*Pteraspis rostrata* var. *toombsi* White, 1935"; see Blieck 1984: fig. 19D–F), the type species of the genus, have large orbital plates, which are fairly like the plates of *Alaeckaspis*. Possibly these represent limits of within-species variability. Blieck (1984: fig. 43A) did not included these peculiarities in his reconstruction of *E. waynensis*.

Occurrence. — Early Devonian of Podolia (Ukraine).

Alaeckaspis verbivciensis Voichyshyn, 1999
(Figs 65B, C, 66A–F)

1999. *Alaeckaspis verbivciensis*; Voichyshyn 1999: pp. 49–51, figs 1, 2.
2006. *Alaeckaspis verbivciensis*; Voichyshyn 2006c: pp. 28–29, pl. 1, fig. 2.

Type specimen: Holotype SMNH BP.167/1, mould of carapace; Verbivtsi, Terebovlia rayon, Ternopil' oblast' (Podolia).

Referred material. — Variably preserved carapace moulds SMNH BP.167/2–3, 168, 180, 187, 188, 218, 219, 220, 221, 222, 224, 226/1, 645, and 1258.

Diagnosis. — Medium sized *Alaeckaspis* species with large rounded pineal plate and very narrow cornual plates stretched backwards.

Description. — The carapace length equals 100–120 mm. The rostral plate is with rather widely rounded anterior margin and little convex lateral ones. The anterior orbital processes are robust, fairly elongated and pointed, while the median ones are wedge-shaped and noticeably narrowed at the contact with lateral margins of the pineal plate. The pineal plate is large (in holotype its length is PL 9.9 mm and PW is 13.6 mm; PW/PL 1.37), slightly extended laterally, rounded, with convex margins. It covers up 29–30% of the orbito-pineal belt extent. The dorsal shield is widest in the prebranchial part and narrows in the postbranchial one (DW/DL is 0.53–0.56). The cornual plates are very narrow, about 40–45 mm in length and 5 mm in

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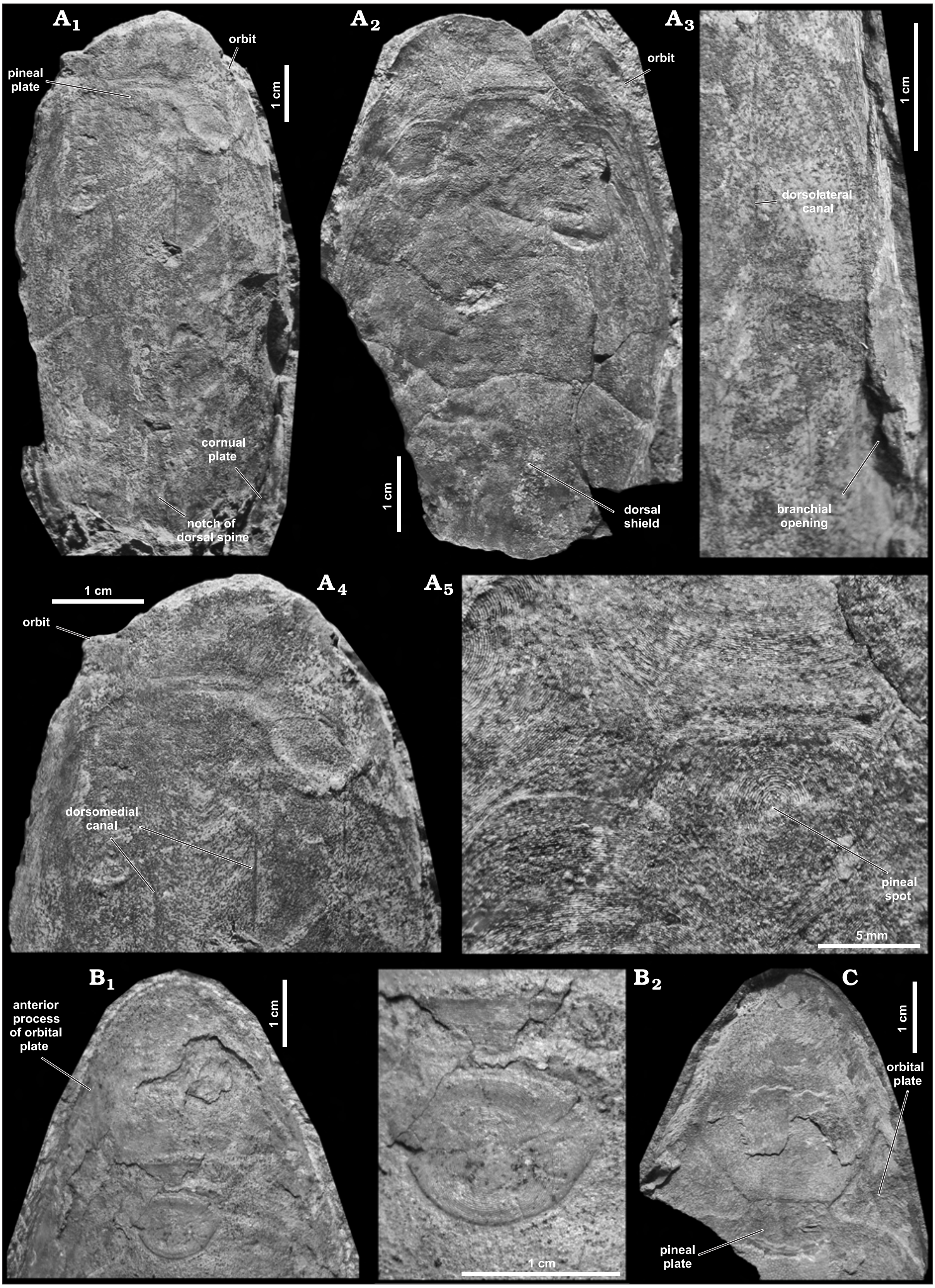
Fig. 65. Larnovaspidids *Alaeckaspis* from various localities in Podolia. **A**. *Alaeckaspis ustetchkiensis* Voichyshyn, 1999, mould of the holotype carapace SMNH BP.168 (see also Fig. 66G) lacking rostral part from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view of the carapace, its incomplete imprint, right branchial →



plate, anterior part of carapace mould, and imprint of pineal plate and adjacent parts, respectively. **B**. *Alaeckaspis verbivciensis* Voichyshyn, 1999, almost complete holotype carapace SMNH BP.167/1 (see also Fig. 66A) from the Verbivtsi quarry, Ivanie Member of the Tyver Formation, dorsal view of the anterior part and enlarged pineal plate. **C**. Same species, imprint of anterior part of carapace SMNH BP.226/1 from the same locality, dorsal view.

width, with elongated and sharp posterior end, that is directed backwards and slightly sideways, reaching far behind the posterior margin of dorsal shield. The considerable stretching of the posterior margin of cornual plate is its characteristic feature. Dorsomedial sensory canals are directed towards lateral parts of the pineal plate. Dentine ridges of the dermal skeleton ornamentation are of different width. Their density is 4.5 cr/mm in the primordium zone, 5.5 cr/mm in the centre, 7 cr/mm at the anterior margin of the ventral shield, 5–6 cr/mm in the primordium area, 7 cr/mm at the anterior margin, and up to 11 cr/mm over the branchio-cornual region of the dorsal shield.

Comparison. — The taxon differs from other species of the genus by the shape of the pineal and cornual plates. Furthermore, *A. ustetchkiensis* has less massive orbital plates, with shorter anterior processes, and a not so narrow dorsal shield in the postbranchial part. *Alaeckaspis magnipinealis* has considerably wider, and comparatively shorter anteriorly, orbital processes. *Alaeckaspis*? *depressa* has less massive orbital plates.

Localities and age. — Verbivtsi; Lochkovian (Ivanie Stage of the Tyver Formation) of Podolia (Ukraine).

Alaeckaspis ustetchkiensis Voichyshyn, 1999
(Figs 65A, 66G)

1999. *Alaeckaspis ustetchkiensis*; Voichyshyn 1999: pp. 51–52, fig. 3.

2006. *Alaeckaspis ustetchkiensis*; Voichyshyn 2006c: p. 28, pl. 1, fig. 1.

Type specimen: Holotype SMNH BP.168, mould and imprint of carapace lacking rostral part; Ustechko at the left bank of the Dniester River, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Only the holotype.

Diagnosis. — Medium sized *Alaeckaspis* species with very convex and rounded posterior margin of the pineal plate and narrow cornual plates, stretched backwards not further than to the posterior margin of dorsal shield.

Description. — Length of the only known carapace is ~105 mm. The pineal plate comparatively large (PL 8 mm, PW 11 mm) and takes up 32 % of the orbito-pineal belt length. The plate has straight anterior and lateral margins which are in full contact with relatively short and wide medial orbital processes. Posterior margin of the pineal plate is very convex and rounded. The anterior orbital processes are short, wide and pointed, while posterior ones are long. Ratio DW/DL is 0.57. Anterior margin of the dorsal shield has deep pineal hollow, while the posterior one has a small medial projection. Groove at the base of the dorsal process is relatively narrow, 20 mm in length. The cornual plates are narrow, 25 mm long. Dorsomedial sensory canals are directed to the tops of the medial orbital processes. Density of dentine ridges is 5 cr/mm in the primordial zone of the dorsal shield, 6 cr/mm on the pineal plate, 7 cr/mm over the dorsal and branchial plates, and 7–8 cr/mm on the rostral plate.

Comparison. — This species differs from *A. magnipinealis* by smaller width and size, different shape of the elements of orbito-pineal belt, and contour of the anterior margin of the dorsal shield. It differs from *A.*? *depressa* by shorter and wider medial orbital processes and noticeably shorter anterior ones, moreover, by larger pineal plate, with considerably convex posterior margin. Distinctions from *A. verbivciensis* are given in its description.

Remarks. — *Alaeckaspis ustetchkiensis* bears resemblance to specimen PIN 3592/28 (Novitskaya 1986: text-fig. 52, pl. 22, fig. 2), identified by Novitskaya as *Zascinaspis bryanti*. Similarities between these specimens concern morphology of the orbito-pineal belt, especially in the shape of pineal plate and mode of its contact with orbital ones. They differ in that the posterior margin of the pineal plate stretches drop-like and the pineal spot is considerably smaller. Among different morphological features of the orbito-pineal belt is also the shape of anterior orbital processes, the antero-medial margin of the orbital plates, and greater width of the medial processes.

Localities and age. — Ustechko; early Pragian (lower part of the Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Alaeckaspis magnipinealis (Brotzen, 1933a)

1933. *Pteraspis magnipinealis*; Brotzen 1933a: pp. 454–456, fig. 14a.

1984. *Errivaspis magnipinealis*; Blieck 1984: pp. 50–51, fig. 43D.

1986. *Zascinaspis heintzi*; Novitskaya 1986: pp. 103–104, 106 (pars).

1999. *Alaeckaspis magnipinealis*; Voichyshyn 1999: p. 49.

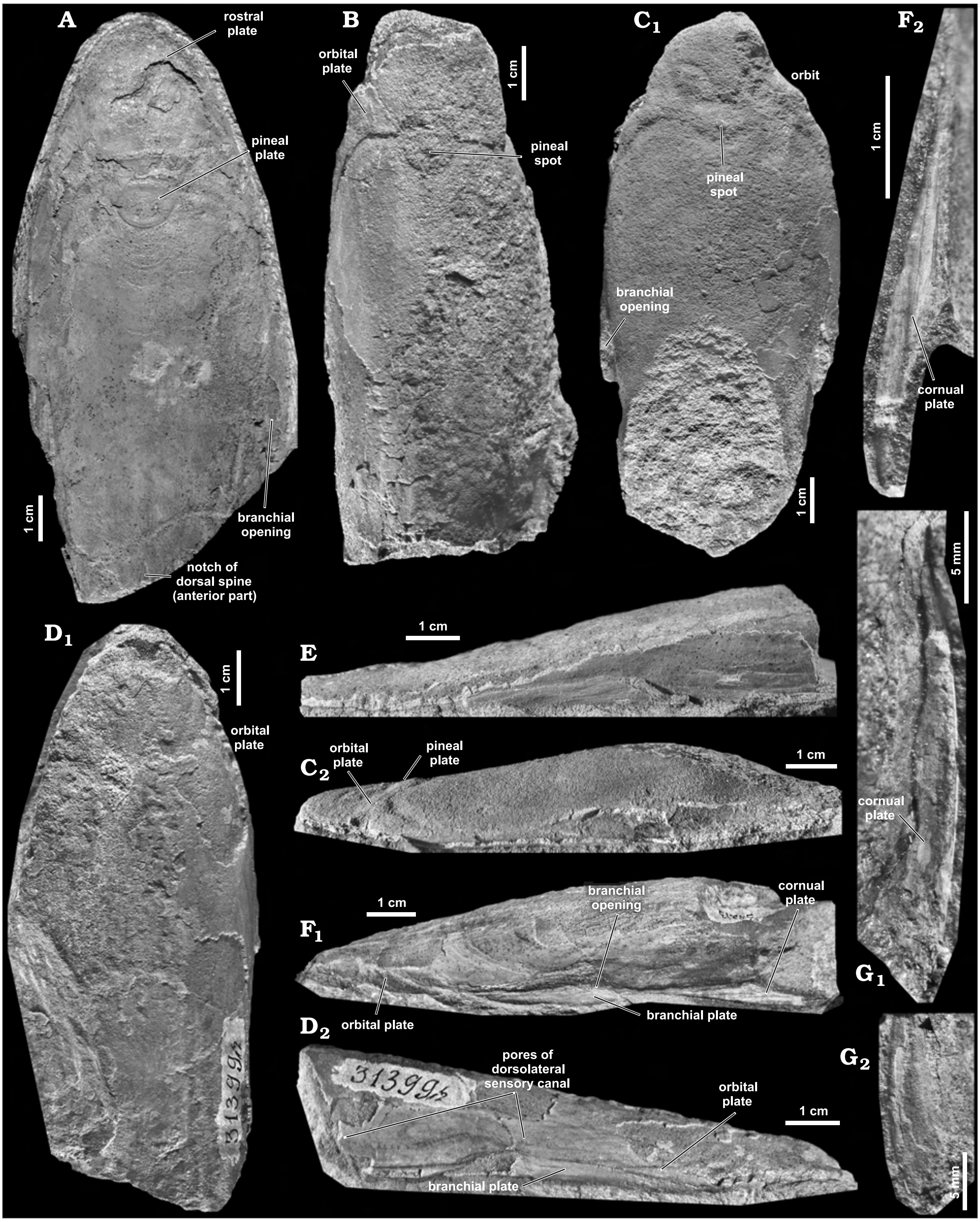


Fig. 66. Larnovaspidids *Alaeckaspis* from various localities in Podolia. **A**. *Alaeckaspis verbivciensis* Voichyshyn, 1999 from the Verbivtsi quarry, Ivanie Member of the Tyver Formation. almost complete holotype carapace SMNH BP.167/1 (see also Fig. 65B), dorsal view. **B**. Same species, partial mould of carapace SMNH BP.180, same locality, dorsal view. **C**. Same species, incomplete mould of carapace SMNH BP.188, same locality, dorsal and lateral (left side) views. **D**. Same species, partial carapace SMNH BP.167/2, same locality, dorsal and lateral (right side) views. **E**. Same species, partial carapace SMNH BP.220, same locality, lateral (left side) view. **F**. Same species, carapace SMNH BP.167/3, same locality, lateral (left side) and left (incomplete) cornual plate. **G**. *Alaeckaspis ustetchkiensis* Voichyshyn, 1999, holotype carapace SMNH BP.168 (see also Fig. 65A) from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, right cornual plate and fragmentary left cornual plate.

Type specimen: Holotype (by monotypy) (Brotzen 1933a: fig. 14a), almost complete carapace in dorsal view; Ivanie-Zolote, Zalishchyky rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Remarks. — According to Brotzen (1933a), the following features are characteristic for the species. Length of the carapace equals ~110 mm. The orbito-pineal belt is very wide, all its elements are massive and large. The anterior orbital processes are pointed and very wide, the medial ones are wide-wedge-shaped and short. Lateral margins of the orbital plates are convex. The pineal plate is pentagonal in shape, with more or less straight anterior and lateral margins which are in full contact with corresponding suture of the orbital plates. The dorsal shield maximum width is in its prebranchial part. The branchial notches are visible. The cornual plates are narrow and elongated.

Novitskaya (1986: p. 106) pointed out that "*Pteraspis*" *magnipinealis* virtually does not differ from large *Zascinaspis heintzi* specimens (PIN 3592/27 and 3592/72) in shape of the plates of orbito-pineal belt and therefore she put it into synonymy of this species. Specimen PIN 3592/27 was illustrated with only photograph of the rostral plate ornament (Novitskaya 1986: pl. 22, figs 1, 5) and is difficult to compare it with Brotzen's specimen. Specimen PIN 3592/72 (Novitskaya 1983: pl. 30, fig. 2) truly has a wide ribbon-like orbito-pineal belt, but, apart from superficial resemblance, its shape and size, as well as those of its separate plates, noticeably differ from "*P.*" *magnipinealis*. Pineal and orbital plates of the latter are more massive. Anterior orbital processes are pointed and stretched forward much farther than those of PIN specimen (and of *Z. heintzi*, as a whole), medial processes are shorter and wider, and the pineal plate is also larger (covers about 1/3 of the belt length in "*P.*" *magnipinealis* against 1/5 of this in *Z. heintzi*). Besides these distinctions there are others of no less importance: the rostral plate of "*P.*" *magnipinealis* is narrower (RL/RW from 0.8 to 0.5–0.6 in *Z. heintzi*) and dorsal shield is more slender (DW/DL is from 0.61 to 0.77–0.91 in *Z. heintzi*). Thus, Brotzen's (1933a) taxonomic decision is supported.

Localities and age. — Ivanie-Zolote; late Lochkovian (Ivanie Stage of the Tyver formation or lower part of Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Alaeckaspis? *depressa* (Stensiö, 1958)

1958. *Plesiopteraspis*? *depressa*; Stensiö 1958: pp. 256, 268, 278, fig. 137.
1964. *Plesiopteraspis*? *depressa*; Stensiö 1964: p. 190, figs 39, 55.
1984. *Errivaspis depressa*; Blieck 1984: p. 50, figs 21, 43C.
1986. *Larnovaspis depressa*; Novitskaya 1986: p. 97, synoptic table, p. 144, fig. 50.
1999. *Alaeckaspis*? *depressa*; Voichyshyn 1999: p. 49.
2004. *Larnovaspis depressa*; Novitskaya 2004: p. 157.

Type specimen: Holotype NHRM C1538, poorly preserved carapace in dorsal view; Kasperivtsi, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Remarks. — "*Plesiopteraspis*?" *depressa* was included by Novitskaya (1986) in *Larnovaspis*, but it differs from other species of this genus in a series of features that are shared with *Alaeckaspis*. The most problematic is considerable size of anterior orbital processes and very narrow cornual plates. Besides, carapace is narrower than that of *Larnovaspis*. Blieck (1984) attributed "*P.*?" *depressa* to *Errivaspis* based on rather narrow dorsal shield, V-like pineal plate, and narrow cornual plates. But, the type species, *E. waynensis* has wider and shorter dorsal shield (DW/DL 0.71) than "*P.*?" *depressa* (DW/DL 0.52) and also excessive development of the latter's anterior orbital processes was apparently ignored. The difference between both species in this aspect is quite clear in their reconstruction (Blieck 1984: fig. 43A, C), although it is not apparent in case of some specimens of *E. waynensis* and the lectotype of "*P.*?" *depressa* (Blieck 1984: figs 19D–F, 21A). At the same time, the small size of the pineal plate prevents attribution of this species to *Alaeckaspis* with certainty. Judging from figure of the only known specimen (Blieck 1984: fig. 21A), the pineal plate is not preserved and its reconstruction is conjectural.

Localities and age. — Kasperivtsi; Lochkovian (Chortkiv Stage of the Tyver formation) of Podolia (Ukraine).

Genus *Brachipteraspis* Brotzen, 1936

1927. *Pteraspis*; Zych 1927: p. 55 (pars).
1933. *Pteraspis*; Brotzen 1933a: p. 460.
1936. *Brachipteraspis*; Brotzen 1936: pp. 31–35 (pars).
1958. *Brachipteraspis*; Stensiö 1958: p. 271.

1964. *Brachipteraspis*; Stensiö 1964: pp. 204–205.
1964. *Pteraspis*; Obruchev 1964: p. 67 (pars).
1975. *Brachipteraspis*; Novitskaya 1975: p. 80.
1984. *Brachipteraspis*; Blieck 1984: p. 59.
1986. *Brachipteraspis*; Novitskaya 1986: pp. 100–101.
2001. *Brachipteraspis*; Voichyshyn 2001c: p. 36.
2004. *Brachipteraspis*; Novitskaya 2004: pp. 159–160.

Type species: *Pteraspis lerichei* mut. *latissima* Zych, 1927; Early Devonian (Strypa Stage of the Dniester Formation) of Podolia.

Diagnosis. — Large sized pteraspidids, tL according to Brotzen (1936) and Zych (1927) is 130–170 mm. The rostral plate strongly narrows forward. Index RL/RW is about 0.9. The anterior and posterior orbital processes are relatively short, and wide, while medial ones are long and ribbon-shaped. The pineal plate is almost rectangular in shape. Its width exceeds its length twice. The lateral margins of the pineal plate fully contact with the medial orbital processes. The dorsal shield is flattened, wide (DW/DL is 0.8–0.9), with the greatest width approximately in the middle. The notch for the dorsal spine is short. The branchial and cornual plates are wide, long and massive. Mdl canals are of radial type.

Species included. — Only type species.

Remarks. — Novitskaya (1986, 2004) doubted whether the British *Brachipteraspis monmouthensis* (White, 1935) sensu Blieck (1984) from the Early Devonian (Dittonian, *Pteraspis leathensis* Zone) belongs to the genus. The differences between *Brachipteraspis latissima* and *B. monmouthensis* (see Novitskaya 2004: p. 160) truly support such conclusion. A separate genus should be erected for *Pteraspis rostrata* var. *monmouthensis*, although probably related to *Brachipteraspis*.

Occurrence. — Early Devonian of Podolia (Ukraine) and Great Britain.

Brachipteraspis latissima (Zych, 1927)

1927. *Pteraspis lerichei* sp. n., mut. *latissima* m. n.; Zych 1927: pp. 55–56, pl. 6, figs 1–3, 5, text-fig. 8a–c (pars).
1933. *Pteraspis latissima*; Brotzen 1933a: pp. 460–462, fig. 18a–d.
1936. *Brachipteraspis latissima*; Brotzen 1936: pp. 35–42, pl. 5, fig. 1, pl. 5, pl. 6, figs 1, 2, pl. 7, figs 1, 2, 4, text-figs 10–13.
1958. *Brachipteraspis latissima*; Stensiö 1958: pp. 270–271, fig. 147B.
1964. *Brachipteraspis latissima*; Stensiö 1964: p. 205, fig. 49B.
1984. *Brachipteraspis latissima*; Blieck 1984: pp. 59–60, fig. 45A.
1986. *Brachipteraspis latissima*; Novitskaya 1986: pp. 101–102 (pars), synoptic table, p. 145, fig. 53.
2004. *Brachipteraspis latissima*; Novitskaya 2004: p. 160 (pars).

Type specimen: Lectotype (Zych 1927: pl. 6, fig. 5) chosen by Brotzen (1936), mould of carapace; Sapova, Terebovlia rayon, Ternopil' oblast' (Podolia). The location of the specimen is unknown.

Remarks. — The material of Zych (1927: pl. 6, fig. 5) and Brotzen (1936: p. 41, figs 11, 14) shows the ratio DW/DL of 0.81–0.93. The same index for *Zascinaspis heintzi* (18 specimens from the SMNH collection) equals 0.77–0.91 (lectotype ~0.86). They do not differ in this respect. They differ in the shape of the rostral plate (*B. latissima* has index RL/RW 0.84–0.94, while *Z. heintzi* 0.52–0.63), in shape of anterior orbital processes, and in orientation of mdl canals. However, it is difficult to distinguish these species after dorsal shields only. They seem to differ somewhat in the contour of posterior margin of the shield, and also in the maximum width of the shield in adult individuals of *Z. heintzi* being located backwards. However, shields from Ustechko, which, based on the arrangement of mdl canals, are identified as small, probably juvenile *Z. heintzi*, have the maximum width approximately in the midlength as in SMNH BP.245).

Brotzen (1936) noticed that *B. latissima* occurs in beds with "*Rhinopteraspis*" *elongata* (now *Althaspis elongata*). All his as well as Zych's specimens came from the third zone (apparently Strypa Stage of the Dniester Formation) of the Podolian Old Red. This is in conflict with the finding of *Brachipteraspis latissima* in Ustechko. Although the Ustechko agnathan assemblage is very rich, it does not come from strata with *A. elongata*. Novitskaya (1986: text-fig. 46, pl. 22, fig. 4 and text-fig. 47, pl. 21, fig. 2) attributed to *B. latissima* two dorsal shields from Ustechko lacking posterior margin. As shown above, proportions of the dorsal shield of this species almost coinciding with those of *Z. heintzi* cannot serve as a convincing argument for her identification. Moreover, one of the figured moulds of the shield (Novitskaya 1986: text-fig. 46) shows traces of the point of junction of the dorsomedial canal with the first dorsolateral comissure of lateral line system, in

Brachipteraspis displaced backwards almost to the basis of the dorsal spine, but this is not the case with this specimen. Besides, the shields from Ustechko are smaller than typical for *B. latissima*. In SMNH collection, there is a mould of the dorsal shield (Fig. 67D), which very much reminds the material studied by Novitskaya (1986). It has been found in Ustechko at the level with a mass burial of *Z. heintzi*. The contour of its posterior margin reminds that of *Zascinaspis*, although the maximum width is situated at the same level as in *Brachipteraspis*. Ratio DW/DL of this specimen equals 0.88. Thus, taking all into account, all specimens from Ustechko seem to belong to *Z. heintzi*.

Localities and age. — Kydaniv, Sapova, Perevoloka and Buchach (Zych 1927; Brotzen 1936); Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Genus *Zascinaspis* Stensiö, 1958

1936. *Brachipteraspis*; Brotzen 1936: p. 31.
1958. *Zascinaspis*; Stensiö 1958: pp. 264–265, 338–339.
1961. *Zascinaspis*; Tarlo 1961: p. 378.
1964. *Zascinaspis*; Obruchev 1964: p. 65.
1975. *Zascinaspis*; Novitskaya 1975: p. 81.
1983. *Zascinaspis*; Blieck and Goujet 1983: pp. 45–46.
1984. *Zascinaspis*; Blieck 1984: p. 61.
1986. *Zascinaspis*; Novitskaya 1986: pp. 102–103.
2001. *Zascinaspis*; Voichyshyn 2001c: pp. 32–36.
2004. *Zascinaspis*; Novitskaya 2004: pp. 160–161.

Type species: *Brachipteraspis heintzi* Brotzen, 1936; Early Devonian (Ivanie Stage to lower part of the Dniester Formation) of Podolia.

Emended diagnosis. — Pteraspidids of various sizes. Carapace is wide and flattened. The rostral plate is very wide, with widely rounded anterior margin. Index RL/RW equals 0.4–0.6. The anterior orbital processes are short, rounded or oblique. The medial ones are more or less wide, ribbon-shaped and in contact with the pineal plate. The pineal plate is rectangular or pentagonal in shape, with rounded posterior margin. The dorsal shield is wide, widest in front of the branchial openings. Posterior margin of the shield forms a rounded medial ledge. DW/DL is in limits of 0.77–0.94 (probably, up to 1.0 in *Z. bryanti*). The branchial plates are long and a little bit bent. The cornual plates are rather narrow and short. Mdl canals are of parallel type.

Species included. — Besides the type species: *Zascinaspis bryanti* (Brotzen, 1936), Ivanie Stage of Podolia; *Z. carmani* (Denison, 1960), Early Devonian of Ohio, USA; possibly *Z. laticephala* Blieck and Goujet, 1983, Early Devonian of Spitsbergen.

Remarks. — *Zascinaspis laticephala* from the Early Devonian of Spitsbergen differs from other species of the genus by (1) morphology of branchio-cornual region, especially by very thin branchial plates, and very wide (wider than longer) cornual plates, (2) arrangement of the ldl canals of sensory line system, where they are extremely displaced laterally, probably also by (3) ventral plate which is relatively small as compared with the dorsal shield, and (4) generally large size. The shape of the carapace is similar rather to that of *Xylaspis prima* (Pernègre, 2003) than of *Zascinaspis* (cf. Blieck 1984: fig. 46F and Pernègre 2003: fig. 7; Pernègre 2004), although a number of features clearly separate these taxa. It is very probable that *Z. laticephala* represents a separate genus.

Occurrence. — Early Devonian of Podolia (Ukraine), possibly Spitsbergen, and Ohio.

Zascinaspis heintzi (Brotzen, 1936)
(Figs 18B, 22E, 27C, D, 31E, 32D, 67A–D, 68A–F, 69A–C, E–G, 70E, F)

1936. *Brachipteraspis heintzi*; Brotzen 1936: pp. 46–47, text-fig. 16, pl. 7, fig. 3.
1936. *Brachipteraspis grossi*; Brotzen 1936: pp. 47–48, text-fig. 17, pl. 8, fig. 1.
1958. *Zascinaspis heintzi*; Stensiö 1958: pp. 255, 339, fig. 189.
1958. *Zascinaspis obtusirostrata*; Stensiö 1958: pp. 339, fig. 189.
1958. *Zascinaspis* sp.; Stensiö 1964: p. 254, fig. 136C.
1964. *Zascinaspis* sp.; Stensiö 1964: p. 189, figs 38C, D, 45A.
1964. *Zascinaspis heintzi*; Obruchev 1964: p. 65, pl. 6, fig. 4, text-figs 35, 36.

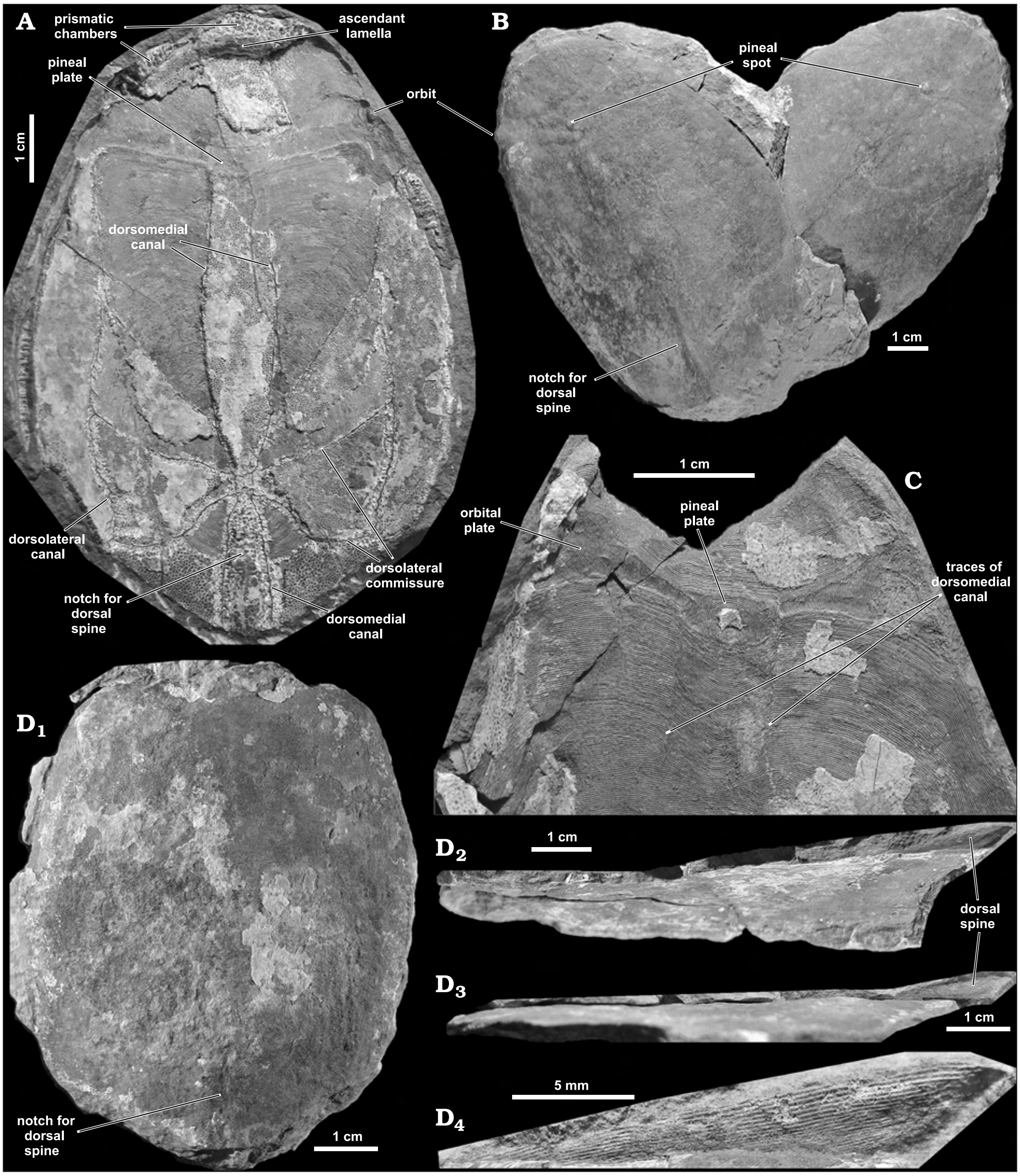


Fig. 67. Larnovaspidid *Zascinaspis heintzi* (Brotzen, 1936) from the Dniester Formation in left bank of Dniester River at Ustechko. **A**. Carapace inside SMNH BP.327 (see also Fig. 32D) with prepared sensory canals, uppermost part of Ustechko Member. **B**. Two moulds of carapace SMNH BP.328/1-2 from 1st ravine W of the village, lower part of Khmeleva Member, dorsal view. **C**. Imprint of anterior carapace SMNH BP.360 (see also Fig. 69C) part from lower part of Khmeleva Member, dorsal view. **D**. Partial mould and imprint of carapace SMNH BP.336 from 1st ravine W of the village, dorsal, lateral (left side) views and enlarged imprint of dorsal spine in lateral (left side) view.

1983. *Zascinaspis heintzi*; Novitskaya 1983: p. 182, text-figs 11a, 12, 45a, pl. 29, figs 3, 4, pl. 30, figs 1, 2, pl. 31, figs 1–4.

1984. *Zascinaspis heintzi*; Blieck 1984: pp. 61–63, fig. 28.

1986. *Zascinaspis heintzi*; Novitskaya 1986: pp. 103–106 (pars), text-figs 48–51, pl. 20, figs 2, 3, pl. 22, figs 1, 5, synoptic table, p. 145, fig. 54.

1986. *Brachipteraspis latissima*; Novitskaya 1986: pp. 101–102 (pars), text-figs 46, 47, pl. 21, fig. 2, pl. 22, fig. 4.

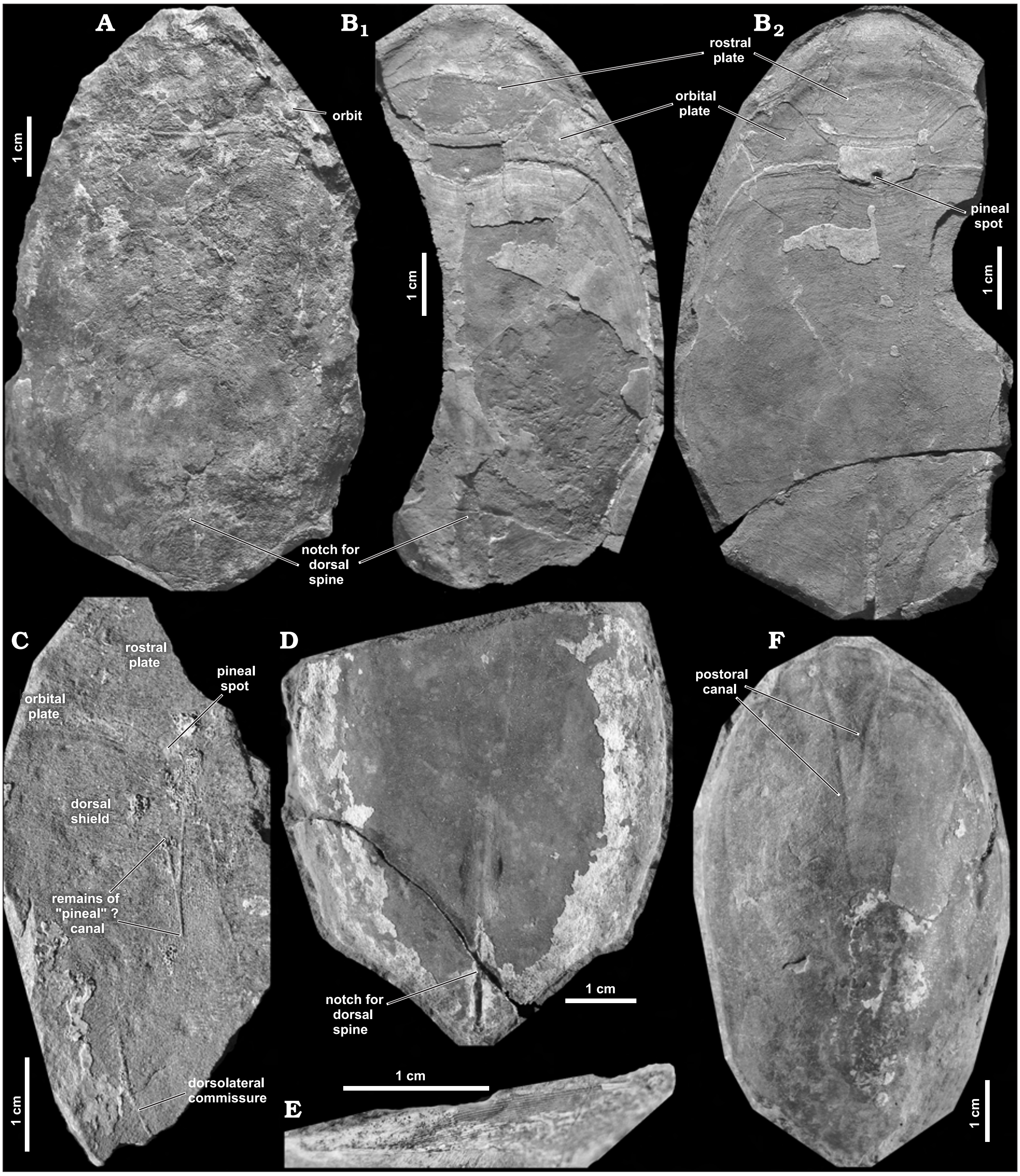


Fig. 68. Larnovaspidid *Zascinaspis heintzi* (Brotzen, 1936) from the Dniester Formation in left bank of Dniester River at Ustechko. **A**. Carapace SMNH BP.603 (see also Fig. 31E) of uncertain species identity from lower part of Khmeleva Member, dorsal view. **B**. Mainly right part mould of carapace SMNH BP.361 (see also Fig. 69G) with partially preserved armour from lower part of Khmeleva Member, dorsal view of part and counterpart. **C**. Imprint of central carapace part SMNH BP.364 of uncertain species identity from 1st ravine W of the village, lower part of Khmeleva Member, dorsal view. **D**. Mould of dorsal shield SMNH BP.600 lacking anterior part from uppermost part of Ustechko Member or lower part of Khmeleva Member, dorsal view. **E**. Imprint of dorsal spine of specimen SMNH BP.329 (see also Fig. 69A) from 1st ravine W of the village, lateral (left side) view. **F**. Mould of ventral shield SMNH BP.363 of uncertain species identity from Ustechko Member or lower part of Khmeleva Member.

2001. *Zascinaspis heintzi*; Voichyshyn 2001c: pp. 33, 35, figs 3, 5.

2004. *Zascinaspis heintzi*; Novitskaya 2004: pp. 161–162, text-figs 84, 85, pl. 12, fig. 3.

2004. *Brachipteraspis latissima*; Novitskaya 2004: p. 160 (pars), text-fig. 83, pl. 12, fig. 2.

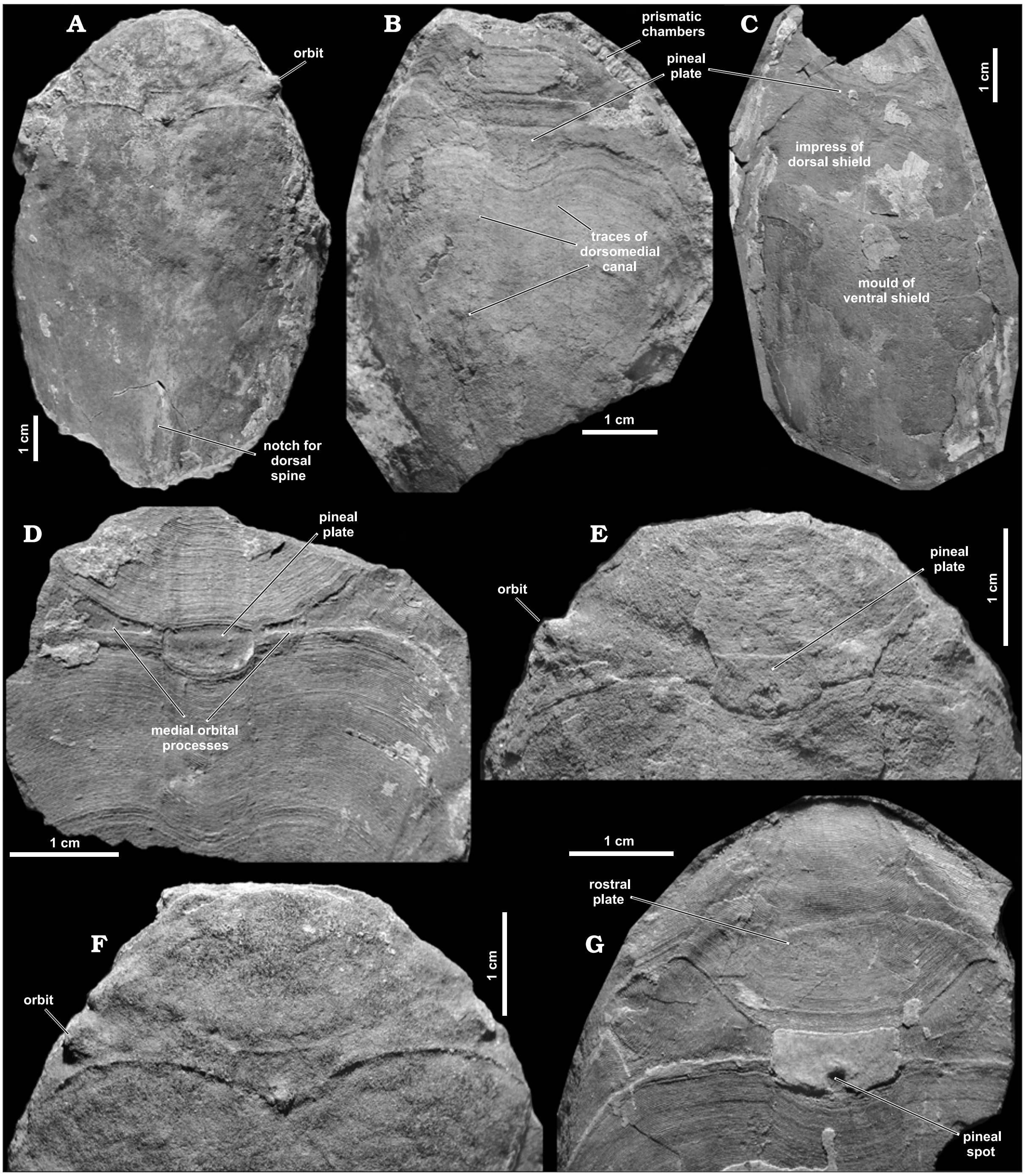


Fig. 69. Larnovaspidid *Zascinaspis heintzi* (Brotzen, 1936) from the Dniester Formation in left bank of Dniester River at Ustechko. **A**. Mould of carapace SMNH BP.329 (see also Fig. 68E) from 1st ravine W of the village, lower part of Khmeleva Member of the Dniester Formation, dorsal view. **B**. Partial carapace SMNH BP.332 from Ustechko Member or lower part of Khmeleva Member, dorsal view. **C**. Associated partial imprint of carapace and mould of ventral shield SMNH BP.360 (see also Fig. 67C) from lower part of Khmeleva Member. **D**. Species undeterminable imprint of orbito-pineal zone SMNH BP.1079 from lower part of Khmeleva Member, dorsal view. **E**. Mould of orbito-pineal zone SMNH BP.365 from same horizon, dorsal view. **F**. Mould of anterior carapace part SMNH BP.601 from 1st ravine W of the village, dorsal view. **G**. Carapace SMNH BP.361 (see also Fig. 68B) from lower part of Khmeleva Member, enlarged anterior part in dorsal view.

Type specimen: Holotype NHRM 1824, right part of carapace without branchial and cornual plates; Rizdviany, Terebovlia rayon, Ternopil' oblast' (Podolia).

Referred material. — Carapaces, their moulds, and separate fragments SMNH BP.110/2, 223, 268/2, 307, 326, 327, 328/1–2, 329, 330/1, 331, 332, 333, 334, 341, 346, 348, 350, 351, 352, 354, 359, 360, 361, 365, 366, 597, 598, 599, 601, 604, 608, 610, 1101, 1310, 1437, 1462, 1464, 1465, 1466, 1468/1, 1469, and 1470, probably, BP.600, and 603, possibly, BP.364, 614, and 1163.

Diagnosis. — Medium sized *Zascinaspis* species with antero-lateral position of the orbits within the orbital plates.

Description. — Carapace is oval, with rather oblique sides of the posterior margin, about 100 mm in length, with maximum width in its posterior third. Posterior margin of the rostral plate is somewhat sinusoidal owing to rounded orbital notches. Index RL/RW equals 0.5–0.6. The pineal plate is from moderate up to rather large size, rectangular or pentagonal in shape. Its anterior margin is straight or slightly concave, while the lateral ones are straight, sometimes rather oblique, and the posterior one is slightly convex and rounded. Anterior processes of the orbital plates are short, rounded or incised, while the medial ones are rather wide and the posterior ones are pointed and not long. The dorsal spine is low, long, points backwards under angle of 9–10°.

Comparison. — The species differs from *Z. bryanti* by proportions of the dorsal shield and by twice as large size. Other species of the genus have larger and wider dorsal shield. Besides, *Z. carmani* has other position of the orbits and posterior ends of the ldl canals of the sensory line system, while *Z. laticephala* has larger rostral, orbital and pineal plates, different shape of the cornual plates, as well as position of the mdl canals and transversal comissures.

Remarks. — Several specimens of the species from Ustechko (Fig. 69D) have the medial orbital processes which are considerably narrowed, although still ribbon-like (see Voichyshyn 2001c). Probably, this is a different variety of *Zascinaspis*.

Localities and age. — Ustechko, Ivanie-Zolote, Horodnytsia, Rizdviany, Terebovlia, Verbivtsi; Novitskaya (1986: p. 106) listed also Zastinoche and Mogyl'nytsia; late Lochkovian (from Ivanie Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Zascinaspis bryanti (Brotzen, 1936)

(Figs 24G, H, 70A–D, G)

1936. *Brachipteraspis* (?) *bryanti*; Brotzen 1936: pp. 44–46, pl. 8, fig. 2, text-fig. 15.

1984. *Zascinaspis bryanti*; Blieck 1984: pp. 63–64, figs 29, 46C.

2001. *Zascinaspis bryanti*; Voichyshyn 2001c: p. 32, fig. 2b.

2001. *Zascinaspis* (?) sp.; Voichyshyn 2001c: p. 33, fig. 4.

Type specimen: Holotype NHRM C1825, partial carapace (right part); east of Dobrivliany, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Partial carapaces and imprints of carapace SMNH BP.531, 532, 561 and 562/1; possibly also BP.530 and eroded moulds of carapace BP.563 and 1180; all from Jagilnytsia Stara.

Diagnosis. — Small sized *Zascinaspis* with oval carapace and very wide dorsal shield (index DW/DL tends to 1.0).

Description. — Carapace generally is oval in shape, tL is about 40–50 mm. Maximum width of the dorsal shield is in its posterior third (about 30–40 mm), sometimes between middle and posterior third of the shield. The rostral plate is distinctive for *Zascinaspis* (RL 8–11 mm, RW 16–22 mm). The anterior orbital processes seem to be oblique and very short, while the median ones are ribbon-like and narrowing towards the pineal plate. The posterior orbital processes are narrowing, pointed out at caudal end, and one and part as long as medial ones. The pineal plate is short (PL 2–3 mm) and more or less wide (PW 5 mm, and up to 7 mm in specimen BP.532). Index PW/PL ranges from 1.6 to 3.5. The dorsal shield is flattened and very wide. DL is 2.9–3.5, DW 2.5–3.5, and DW/DL 0.8–0.86 and seems to be higher in the holotype. The branchial plates are ribbon-like and narrow. Its largest width in posterior third is about 2.5 mm (in BP.530). The cornual plates (in BP.530) are narrow, about 1 mm wide, and elongated about 10 mm along the plate axis.

Comparison. — Differs from all other species referred to the genus by its small mature size.

Remarks. — The species was based on a single incomplete specimen that shows enough information about its shape except for the posterior part. In Brotzen (1936: pl. 8, fig. 2), magnification of the photograph of the holotype was erroneously indicated as 1/1. According to Blieck (1984), who examined the specimen, its complete length was not more than 50 mm, while the width of its dorsal shield was about 36 mm and almost equal to the shield length. Novitskaya (1986: p. 106) describes one more specimen (PIN 3592/28) collected at Ivanie-Zolote as *Z. bryanti*. It is represented by an "almost complete mould of the dorsal side of the

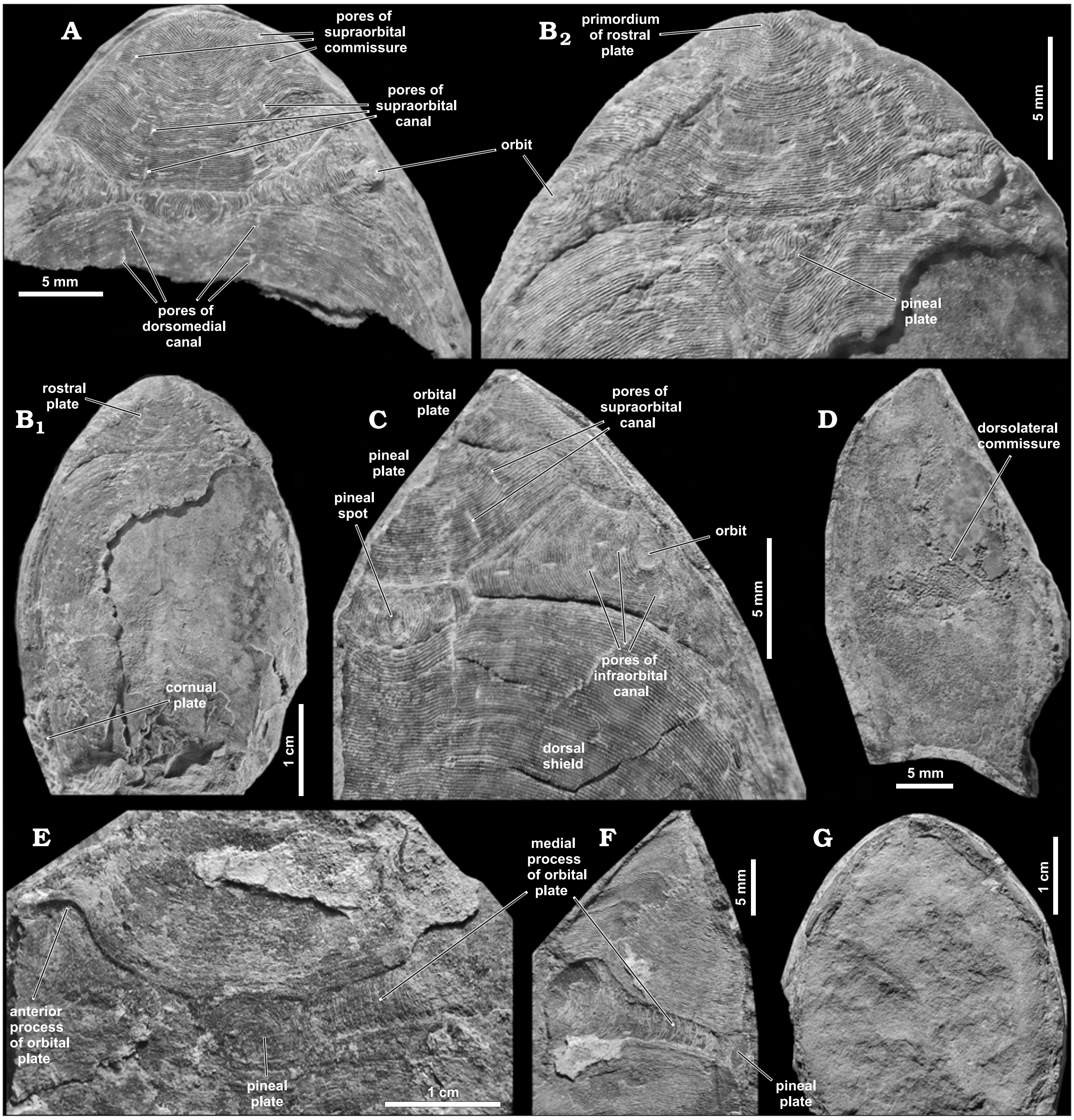


Fig. 70. Larnovaspidids *Zascinaspis* from various localities in Podolia. **A**. *Zascinaspis bryanti* (Brotzen, 1936), anterior part of carapace SMNH BP.532 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view. **B**. Probably same species, partial carapace/mould SMNH BP.530, same locality, dorsal view and enlarged anterior part. **C**. Same species anterior part of carapace SMNH BP.531, same locality, dorsal view. **D**. Same species, partial interior of dorsal shield SMNH BP.561, same locality. **E**. *Zascinaspis heintzi* (Brotzen, 1936), imprint of right part of orbito-pineal belt SMNH BP.599 from the Horodnytsia old quarry, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **F**. Same species, imprint of right part of orbito-pineal belt SMNH BP.351 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member. **G**. *Zascinaspis bryanti* (Brotzen, 1936), margin of carapace SMNH BP.562/1 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation, dorsal view.

carapace" where "the edges of rostral, dorsal, pineal, and orbital plates are seen". But, it is difficult to ascertain the anterior margin of the rostral plate from the photograph (Novitskaya 1986: pl. 22, fig. 2). The drawing of the same specimen indicates that the rostral plate might be longer than it is characteristic for *Zascinaspis*. The anterior processes of the orbital plates seem also not to be rounded and resemble those of *Larnovaspis* or *Alaeckaspis*. As a whole, this carapace is more elongated and slender, than it is typical of *Zascinaspis* (e.g., Novitskaya 2004: text-fig. 86 and Blieck 1984: fig. 46B; Fig. 67A, B), with proportions distant from those of the holotype of *Z. bryanti*. Brotzen (1936: p. 46) wrote in his description: "the small, very wide and flattened shape [of the shield] sufficiently distinguishes [this species] from others." The holotype is about half as large as specimen PIN 3592/28.

Balabai (1961a: fig. 10) reported a finding of two specimens of "*Brachipteraspis*" *bryanti* at Zalishchyky, and published a figure of one of them. Remains of the rostrum in that specimen are limited to moulds of the supranasal cartilage. Hence, the rostral plate was originally about one-third longer. The imprints of the sutures between the rostral and orbital plates indicate more development of the anterior orbital processes than it is characteristic of *Zascinaspis*, and the dorsal shield is actually longer than what is shown in the figure. It is mentioned in the same work (Balabai 1961) that a large number of specimens of "*B.*" *bryanti* was collected by Zych at Jagilnytsia Stara.

Among specimens, which were collected by Zych at Jagilnytsia Stara and kept at the SMNH collection, there is one (BP.530; Fig. 70B) that has to be referred to *Zascinaspis*, based on the general shape and proportions of the carapace as well as the shapes of the rostral, orbital (except for the medial processes), dorsal, branchial, and cornual plates. The half-moon-shaped pineal plate and lack of its contact with the sharp medial orbital processes in this specimen are of "*Podolaspis* type". It is remarkable because, according to the original description (Brotzen 1936: p. 44), the orbital plates of *Z. bryanti* "reach the pineal plate to become considerably narrow, and it is difficult to see that they touch it. The pineal plate has a half-moon shape…" This description fits better the characteristics of the orbito-pineal belt type found in the genus *Podolaspis*. However, in contradiction to the description, the illustrations in Brotzen (1936: text-fig. 15, pl. 8, fig. 2) indicate that the specimen does belong to *Zascinaspis*. Very small size of the Zych's specimen (carapace is 45 mm long and 33 mm wide) suggests that it is a juvenile, but the orbits seem not as in juveniles. Thus, a number of features including the proportions and exact size of the dorsal shield suggest that the specimen is closely related to *Z. bryanti*, despite peculiar orbito-pineal belt. Remains of the other specimens of the species demonstrate some variability of this feature in *Zascinaspis*. A similar range of variability has been reported for *Z. heintzi* too (Voichyshyn 2001c), and this is why specimen SMNH BP.530 is provisionally classified in *Z. bryanti*.

Localities and age. — Dobrivliany and Jagilnytsia Stara; Lochkovian (Ivanie Stage of the Tyver Formation) of Podolia (Ukraine).

Family **Rhinopteraspididae** Novitskaya, 1983

Genus *Althaspis* Zych, 1931

1927. *Pteraspis*; Zych 1927: p. 55 (pars).
1931. *Althaspis*; Zych 1931: p. 89.
1933. *Pteraspis*; Brotzen 1933a: pp. 456–459 (pars).
1959. *Pteraspis*; Balabai 1959b: p. 12 (pars).
1961. *Althaspis*; Tarlo 1961: p. 379.
1964. *Althaspis*; Stensiö 1964: p. 362.
1964. *Althaspis*; Obruchev 1964: pp. 67–68.
1975. *Althaspis*; Novitskaya 1975: pp. 77–78.
1984. *Althaspis*; Blieck 1984: p. 31.
1986. *Althaspis*; Novitskaya 1986: pp. 108–109.
2001. *Althaspis*; Voichyshyn 2001c: p. 36.
2004. *Althaspis*; Novitskaya 2004: pp. 163–164.

Type species: *Pteraspis lerichei* mut. *elongata* Zych, 1927; Early Devonian of Podolia.

Diagnosis. — Large sized pteraspidids (tL is 130–260 mm). The carapace is narrow and convex. The rostral plate is elongated (DL/RL not more than 2). Index RL/RW equals 1.2–2.4. Ventral surface of the rostral plate is covered by transverse dentine ridges. The preoral field is absent except for extreme cases. The orbito-pineal belt is of uniform width, relatively narrow, and equal in contact. The anterior orbital processes are short and pointed and the medial ones are long and ribbon-like. The pineal plate is rectangular, V-shape bent, with straight lateral margins. The dorsal shield is elongated and narrow (DW/DL is 0.46–0.51). The dorsal spine is very long, with a massive base, considerably inclined backwards. The mdl canals are probably of parallel type (Voichyshyn 2001c).

Species included. — Besides the type species: *A. longirostra* (Zych, 1927), *A. sapovensis* Novitskaya, 1986, *A. tarloi* sp. n., all three from the Early Devonian of Podolia; *A. leachi* (White, 1938), Early Devonian

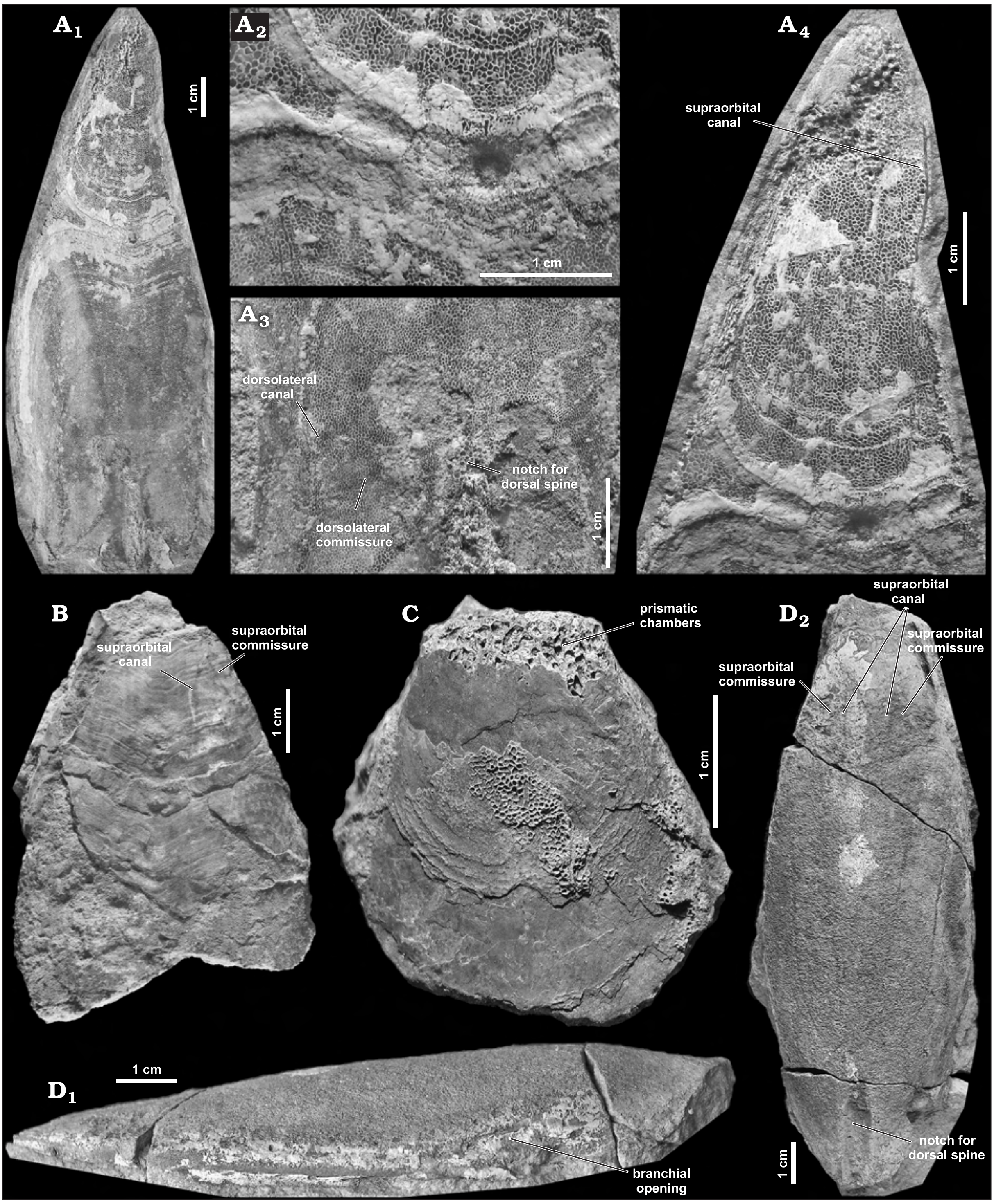


Fig. 71. Rhinopteraspidid *Althaspis elongata* (Zych, 1927) from various localities of Strypa Member of the Dniester Formation in Podolia. **A**. Partial carapace SMNH BP.1203 from Buchach, internal side dorsal view, enlarged pineal plate and adjacent parts of carapace, notch of dorsal spine and adjacent parts of carapace, and anterior part of carapace, respectively. **B**. Anterior part of carapace SMNH BP.628 from Sapova, dorsal view. **C**. Partial rostral plate SMNH BP.1458/1 with uncertain species identity from Rublin, right bank of Barysh River, dorsal view. **D**. Mould of carapace PIG (unnumbered) from Sapova, dorsal and lateral (left side) views.

of Britain, France and Belgium; *A. vimiensis* White, 1960, Early Devonian of France and Belgium; *A. senniensis* Loeffler *et* Thomas, 1980, Early Devonian of Wales; possibly *A.*? *spathulirostris* (Stensiö, 1958), Early Devonian of Podolia.

Remarks. — *Althaspis*? *spathulirostris* has the orbito-pineal belt, which is characteristic for the genus (Blieck 1984: fig. 7A). It differs from other species of the genus by the shape of the rostral plates and, probably, by morphology of its ventral side. However, to specify these differences additional material is necessary. Blieck attributed *A*.? *spathulirostris* to *Miltaspis* on the basis of similarity of the rostrum shape, but this is hardly justified. Probably this species deserves separate genus.

Occurrence. — Early Devonian of Podolia (Ukraine), Great Britain, France, and Belgium.

Althaspis elongata (Zych, 1927)
(Figs 71A–D, 72E, G, 74E, 75E)

1927. *Pteraspis lerichei* mut. *elongata*; Zych 1927: pp. 20, 55, text-fig. 7, pl. 5, figs 2, 3.

1931. *Podolaspis* (*Althaspis*) *elongata*; Zych 1931: p. 89, figs 41, 50.

1936. *Rhinopteraspis elongata*; Brotzen 1936: pp. 5, 7, 14, fig. 2.

1959. *Pteraspis elongata*; Balabai 1959b: pp. 12–15 (pars), pl. 3, fig. 2.

1964. *Althaspis elongata*; Stensiö 1964: p. 200, fig. 46.

1964. *Althaspis samsonowiczi*; Obruchev 1964: pp. 67–68, text-figs 40, 41.

1983. *Althaspis elongata*; Novitskaya 1983: p. 182, text-figs 9, 10, pl. 32, figs 1–5.

1984. *Althaspis elongata*; Blieck 1984: pp. 31–32, 68, figs 7B–E, 8, 9, 36A, B.

1986. *Althaspis elongata*; Novitskaya 1986: pp. 109–112, text-figs 53, 54, 55a, pl. 20, fig. 4, pl. 21, fig. 1 (left specimen), synoptic table, p. 146, fig. 56.

2004. *Althaspis elongata*; Novitskaya 2004: pp. 164–165, text-figs 87, 88, 90a, pl. 12, figs 5–7.

Type specimen: Lectotype (Zych 1927: pl. 5, fig. 2) chosen by Tarlo (1961), incomplete carapace in dorsal view; Zvenygorod, Buchach rayon, Ternopil’ oblast’ (Podolia). The location of the specimen is unknown.

Referred material. — Specimens SMNH BP.286, 290, 618, 625, 628, 1203, and PIG without register number, possibly also SMNH BP.1458/1 and 1458/2.

Diagnosis. — Relatively small to medium sized *Althaspis* species, with relatively short rostral plate and thin dentine ridges on the ventral side of the rostrum.

Description. — Length of the carapace is up to 150–180 mm (Zych 1927). In SMNH BP.618, it is 150 mm, but with the articulated dorsal spine it amounts 226 mm. For specimen SMNH BP.1203: length of carapace is 143 mm, RL 55 mm, RW ~46 mm, PL 4.5 mm, PW 13 mm, DL 88 mm, DW ~58 mm (DW at the level of branchial openings ~47 mm), length of notch of dorsal spine (which begins somewhat below the level of branchial openings) equals 23 mm. Specimen PIG from Sapova: tL >132 mm, DL 104 mm, DW 51 mm, RW 35 mm, PW ~11 mm, heigth of dorsal shield ~19 mm. The rostral plate has a rather convex lateral margins (RL in SMNH BP.618 equals 63 mm). Index RL/RW range is 1.2–1.7. The orbito-pineal belt and the dorsal shield are typical for the genus. The dorsal spine is low, inclined backwards, narrow and very long. Its length makes more than half the length of the shield. In SMNH BP.618, it equals 90 mm. Judging from the Zych (1931: fig. 49) data, mdl canals are of parallel type.

Comparison. — The species in focus differs from *A. longirostra* by shorter rostral plate and thinner dentine ridges on the ventral side of the rostrum (10–12 cr/mm in *A. elongata* after Novitskaya (1986), contrary 6–7 cr/mm in *A. longirostra* after my data). In contrast with *A. elongata*, *A. sapovensis* has concaved lateral margins of the rostral plate, *A. tarloi* sp. n. has lesser size and shorter rostral plate, *A. leachi* has the preoral field, larger size, and relatively longer rostrum. *Althaspis vimiensis* has wider dentine ridges on the ventral side of the rostrum (8 cr/mm after Novitskaya 1986, contrary 10–12 cr/mm in *A. elongata*) and *A. senniensis* has narrower in the basis rostral plate, other value of RL/RW (2 in *A. senniensis*, contrary 1.3–1.7 in *A. elongata*).

Localities and age. — Buchach, Koropets’, Kydaniv, Perevoloka, Rublin, Rukomysh, Sapova, Zalissia, and Zvenygorod; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine).

Althaspis longirostra (Zych, 1927)
(Figs 72A, B, 73B)

1927. *Pteraspis lerichei* mut. *longirostra*; Zych 1927: pp. 20, 55, pl.5, fig. 1.

1933. *Pteraspis longirostrata*; Brotzen 1933a: pp. 459–460, fig. 17.

1959. *Pteraspis longirostra*; Balabai 1959b: pp. 15–16, pl. 3, fig. 3.

1986. *Althaspis longirostra*; Novitskaya 1986: pp. 112–113, text-fig. 56, pl. 13, figs 5, 6, synoptic table, p. 146, fig. 57.

2004. *Althaspis longirostra*; Novitskaya 2004: p. 166, text-fig. 89, pl. 12, fig. 8.

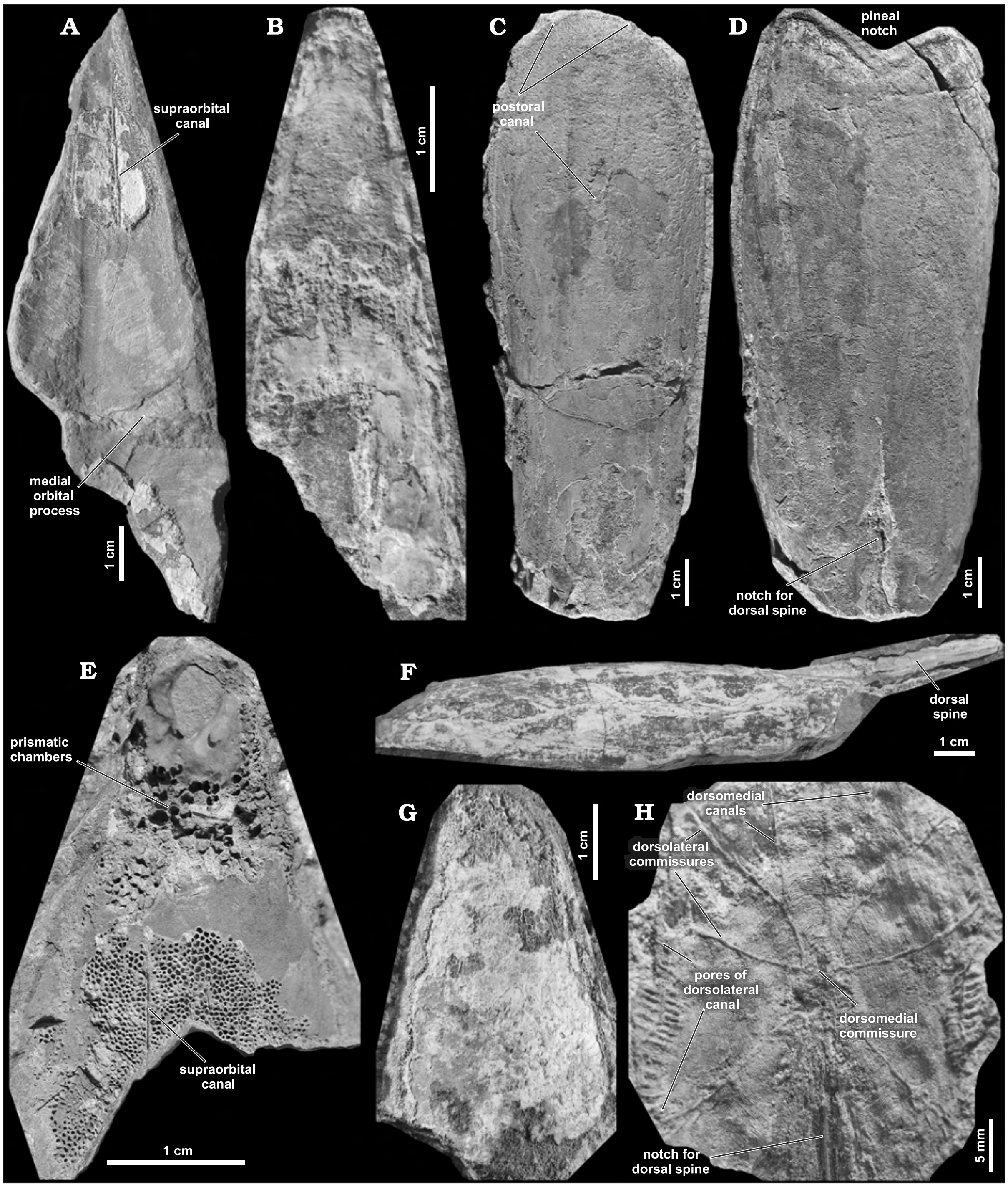


Fig. 72. Rhinopteraspidid *Althaspis* from various localities of Strypa Member of the Dniester Formation in Podolia. **A**. *Althaspis longirostra* (Zych, 1927), partial imprint of rostral plate SMNH BP.581 from Koropets', left bank of Dniester River, dorsal view. **B**. Same species, ventral surface of fragmentary rostral plate SMNH BP.304 from the same locality. **C**. *Althaspis* sp., mould of ventral shield SMNH BP.1420 from Rukomysh, quarry, dorsal view. **D**. *Althaspis* sp., mould of dorsal shield SMNH BP.595/1 (see also Fig. 75F) from the Zaryvyntsi quarry, dorsal view. **E**. ?*Althaspis elongata* (Zych, 1927), partial rostral plate SMNH BP.1458/2 from Rublin, right bank of Barysh River, internal view. **F**. *Althaspis elongata* (Zych, 1927), specimen SMNH BP.619 (see also Figs 73F, 74C) from unknown locality, lateral (left side) view. **G**. Same species, partial mould of rostral plate SMNH BP.286 from Zalissia, dorsal view. **H**. *Althaspis* sp., partial imprint of dorsal shield SMNH BP.617 (see also Fig. 73D) from Zhyznomyr with sensory system canals, enlarged central part. The oldest specimen from Zych collection (1924) in SMNH.

Type specimen: Holotype (Zych 1927: pl. 5, fig. 1), partial mould of carapace in dorsal view; Kopachyntsi, Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia). The location of the specimen is unknown.

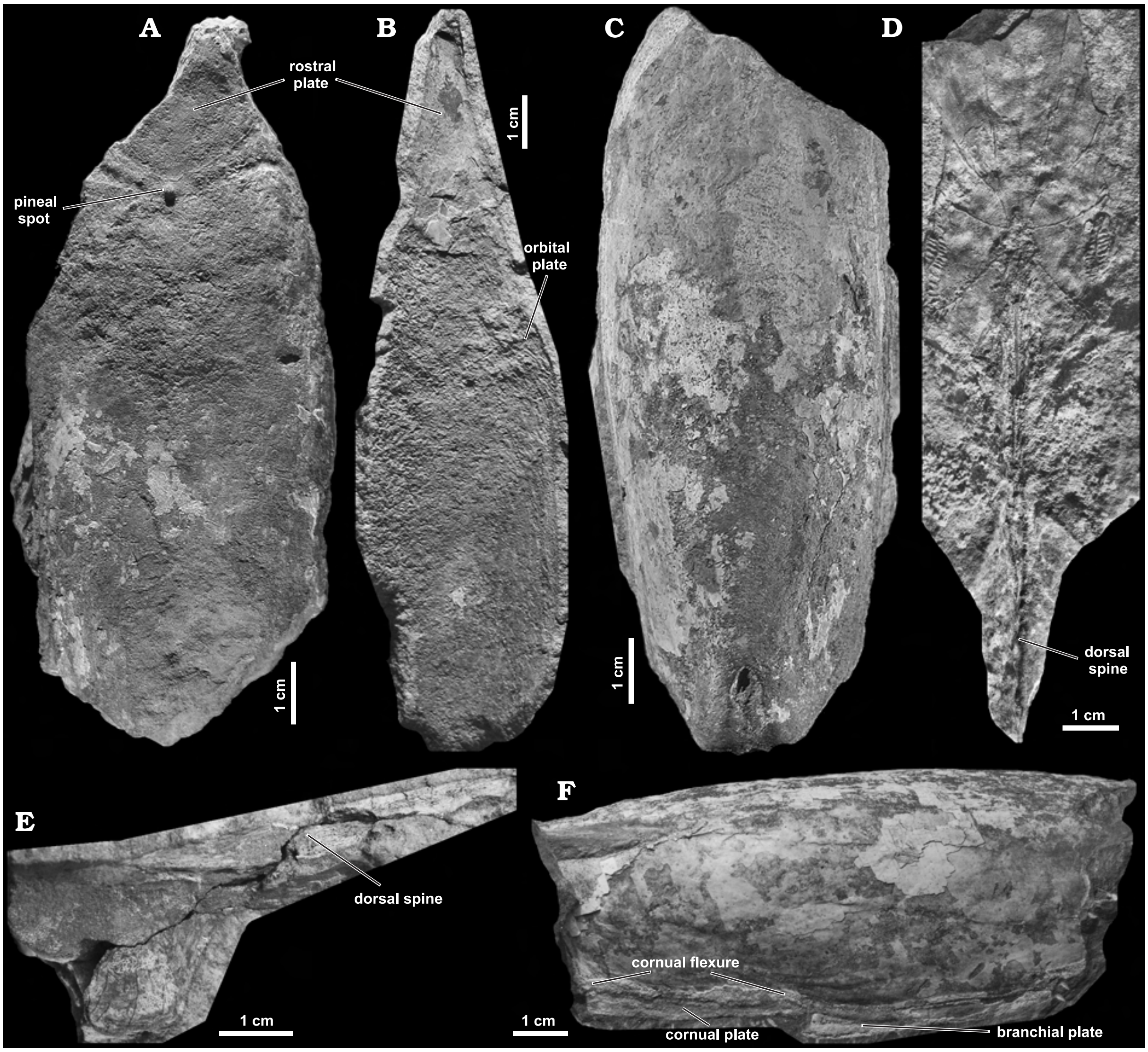


Fig. 73. Rhinopteraspidid *Althaspis* from various localities of Strypa Member of the Dniester Formation in Podolia. **A**. *Althaspis* sp., partial mould of carapace SMNH BP.1417 lacking anterior and posterior ends from Stinka, left bank of Barysh River, dorsal view. **B**. ?*Althaspis longirostra* (Zych, 1927), partial imprint of left part of carapace SMNH BP.1416 from the Rukomysh quarry, dorsal view. **C**. *Althaspis* sp., mould of ventral shield SMNH BP.1423 lacking anterior part from the Zaryvyntsi quarry, dorsal view. **D**. *Althaspis* sp., partial imprint of dorsal shield SMNH BP.617 (see also Fig. 72H) from Zhyznomyr with sensory system canals and dorsal spine, dorsal view. **E**. *Althaspis* sp., partial imprint of dorsal spine and adjacent part of dorsal shield SMNH BP.626 from the lower part of Zaryvyntsi quarry, lateral (left side) view. **F**. *Althaspis* sp., mould of carapace SMNH BP.619 (see also Figs 72F, 74C) from unknown locality lacking anterior part, dorso-lateral (right side) view.

Referred material. — Fragmentary rostral plate SMNH BP.304 exposed from below, fragmentary impression of anterior part of the carapace BP.581, possibly also partial impression of the carapace BP.1416.

Diagnosis. — Medium sized *Althaspis* species with very long rostral plate and relatively wide dentine ridges on the ventral side of the rostrum.

Description. — According to Balabai (1959b) and Zych (1927) length of the carapace is up to 180 mm. Length of the rostral plate is up to 75 mm (Balabai 1959b), and thus not much less than the dorsal shield. Index RL/RW equals 2.1–2.4. In specimen SMNH BP.581, RL is not less than 73 mm, RW is about 36 mm, RL/RW 2.0. Another specimen, BP.1416 has parametral values RL 66.4 mm, RW about 31.8 mm, RL/RW about 2.1, and tL more than 138 mm. Dentine ridges density is from 7 cr/mm (in proximal region) to 6 cr/mm (distally) on the ventral surface of the rostrum, but it is 8 cr/mm on the dorsal surface of rostral plate in BP.581.

Comparison. — All other Podolian species of the genus have shorter rostral plate. Besides, *A. sapovensis* has concave lateral margins of the rostrum, *A. tarloi* sp. n. is of smaller size. *Althaspis longirostra* is similar

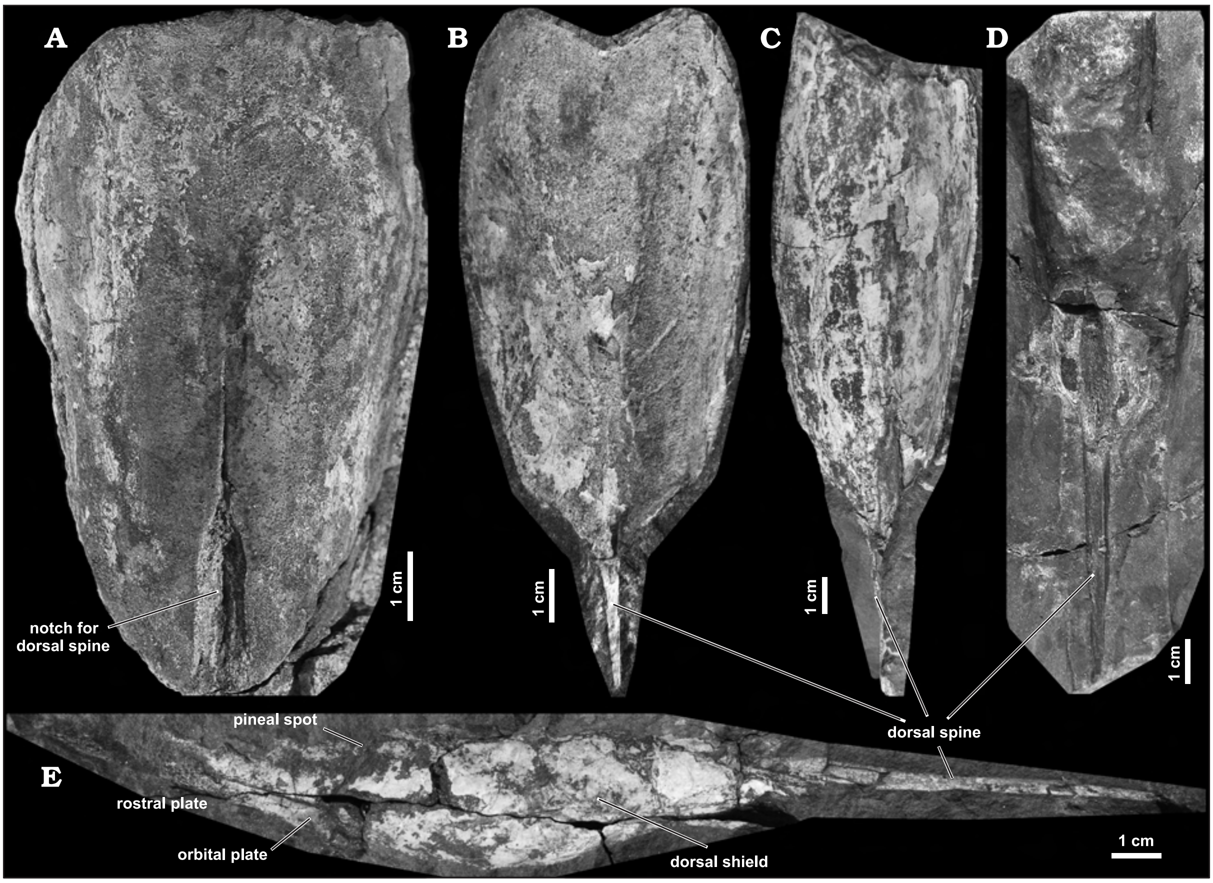


Fig. 74. Rhinopteraspidid *Althaspis* from various localities of Strypa Member of the Dniester Formation in Podolia. **A**. *Althaspis* sp., partial mould of dorsal shield SMNH BP.1422 from the Zaryvyntsi quarry, dorsal view. **B**. *Althaspis* sp., imprint of dorsal shield SMNH BP.621 with part of dorsal spine from Sapova, dorsal view. **C**. *Althaspis* sp., mould of carapace SMNH BP.619 (see also Figs 72F, 73F) from unknown locality lacking anterior part, dorsal view. **D**. *Althaspis* sp., fragment of dorsal shield mould SMNH BP.584 and partial imprint of dorsal spine from Koropets', left bank of Dniester River. **E**. *Althaspis elongata* (Zych, 1927), partial imprint of carapace SMNH BP.618, same locality, dorsal view.

to *A. leachi* by proportions of the plates of the carapace, but differs from it by smaller size and lack of the preoral field. *Althaspis vimiensis* has a wider rostral plate and narrower dentine ridges on its ventral surface, while *A. senniensis* has a shorter rostrum. The differences from *A. elongata* are given in its description.

Remarks. — A number of localities, where the species allegedly occur, were mentioned in the literature (e.g., Balabai 1959b: Koropets', Beremiany, Unizh), but unless rostral plates were found, identification was not possible with certainty. Actually, only the lectotype has the carapace preserved, figured by Zych (1927) and then by Balabai (1959b; unlike Zych, that author provided specimen's magnification, apparently examining it). All other, although very rare specimens of the species, are more or less complete rostral plates.

Although incomplete, specimens SMNH BP.581 and 1416 show proportions of the rostral plate close to those of the species and they are provisionally classified as such.

Localities and age. — Perevoloka, Kopachyntsi, Koropets', Kydaniv, Rukomysh, Sapova; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine).

Althaspis sapovensis Novitskaya, 1986

(Fig. 75D)

1933. *Pteraspis elongata*; Brotzen 1933a: fig. 16.

1986. *Althaspis sapovensis*; Novitskaya 1986: p. 113 (pars), text-fig. 55b, pl. 21, fig. 1 (on the right), pl. 22, fig. 3, pl. 23, figs 1–4.

2004. *Althaspis sapovensis*; Novitskaya 2004: pp. 166–167 (pars), text-fig. 90b, pl. 12, figs 9, 10.

2010. *Althaspis sapovensis*; Voichyshyn 2010: pl. 4, fig. 1.

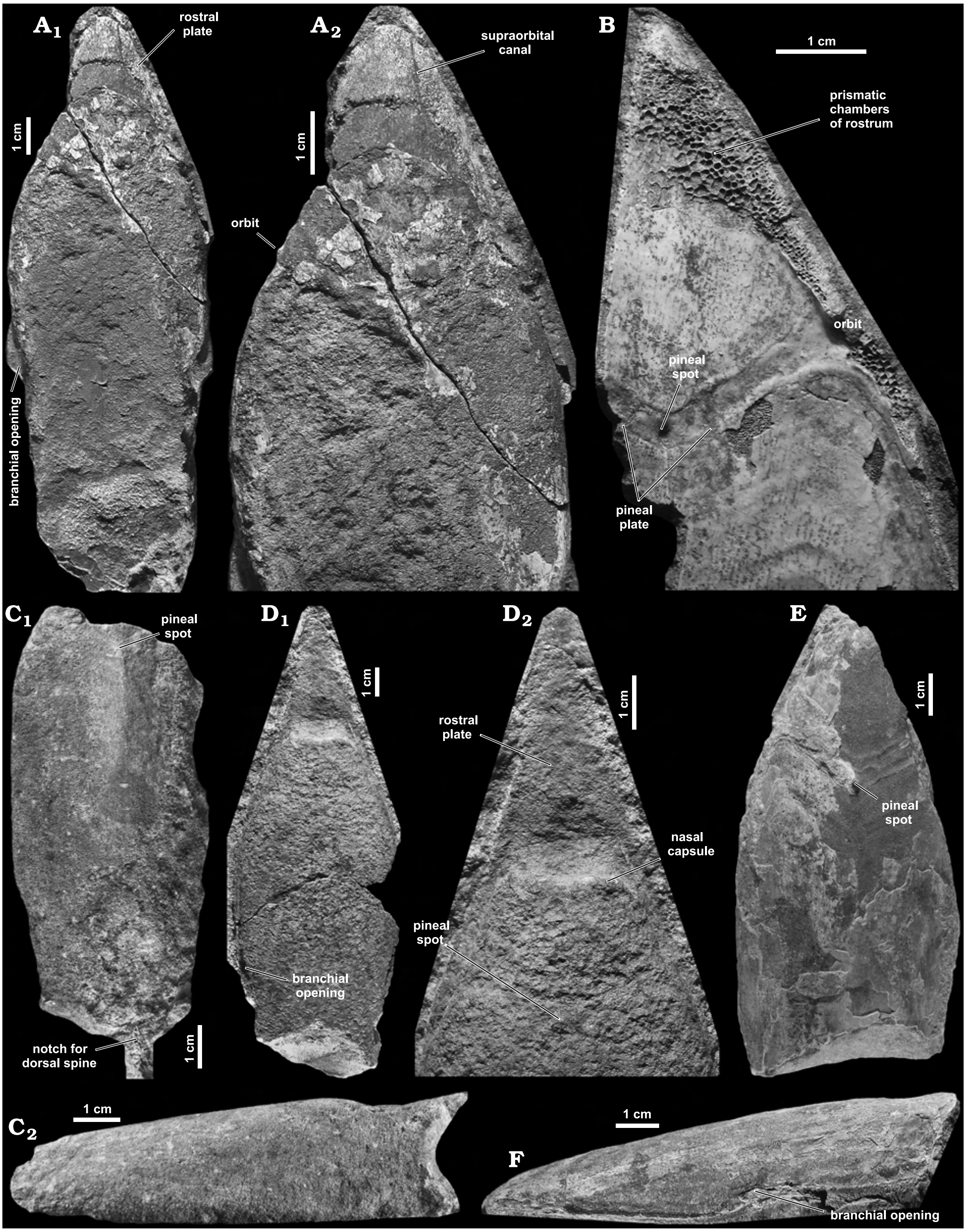


Fig. 75. Rhinopteraspidid *Althaspis* from various localities of the Dniester Formation in Podolia. **A**. *Althaspis tarloi* sp. n., carapace mould of holotype SMNH BP.227 lacking posterior part from Potochyshche, right bank of Dniester River, Ustechko Member, dorsal view, also enlarged anterior part. **B**. Same species, anterior part of left part of carapace SMNH BP.578, same locality, dorsal view of inner surface. **C**. Same species, partial mould of carapace SMNH BP.228, same locality, dorsal and lateral (left side) view. **D**. *Althaspis sapovensis* Novitskaya, 1986, partial abraded mould of carapace SMNH BP.582 from the Zaryvyntsi quarry, Strypa Member of the Dniester Formation, dorsal view and enlarged anterior part. **E**. *Althaspis elongata* (Zych, 1927), carapace SMNH BP.625 lacking posterior part, same locality, dorsal view. **F**. *Althaspis* sp., mould of dorsal shield SMNH BP.595/1 (see also Fig. 72D), same locality, lateral (left side) view.

Type specimen: Holotype, PIN 3592/2b, anterior part of carapace mould in dorsal view; Kydaniv, quarry on the right bank of the Strypa River (Novitskaya 2004), Buchach rayon, Ternopil' oblast' (Podolia).

Referred material. —Abraded mould of carapace SMNH BP.582 and mould of the rostral plate BP.629.

Diagnosis. — Medium sized *Althaspis* species with slightly concave lateral margins of the rostral plate.

Description. — Length of the carapace is 140–170 mm (more than 168 mm or about 175 mm in specimen SMNH BP.582). The rostral plate (RL equals 55 mm, RW 35 mm) has concave lateral margins. Index RL/RW is 1.6–1.8. The shape of the orbito-pineal belt and the dorsal shield is the same as in the type species (Pl 5.6 mm, PW ~11 mm; DW 52 mm).

Comparison. — In contrast with this species, all Western European species of the genus have more massive rostral plate. *Althaspis tarloi* sp. n. has shorter and wider rostrum. Comparison with other Podolian althaspidids is given in their descriptions.

Localities and age. — Zaryvyntsi, also (according to Novitskaya 2004) Kydaniv, Sapova, Perevoloka, and Rukomysh; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine).

Althaspis tarloi sp. n.
(Figs 75A–C, 76)

Derivation of the name: In honour of the late Dr Lambert Beverly Tarlo (Halstead) (1933–1991).

Type specimen: Holotype SMNH BP.227, carapace mould lacking posterior part; Potochyshche, right bank of the Dniester River (lower part of the “Old Red”, Ustechko Stage of the Dniester Formation), Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia).

Referred material. — Besides the holotype, partial mould of carapace SMNH BP.228 and anterior part of left part of carapace exposed from its ventral side BP.578; all from the type locality.

Diagnosis. — Relatively small sized *Althaspis* species with short and wide rostral plate.

Description. — Length of the carapace in the holotype is 130 mm. Lateral margins of the rostral plate are straight and rather convex (RL 42–43 mm, RW 33–35 mm, RL/RW equals 1.2–1.3). The shape of orbito-pineal belt is the same as in the type species. The pineal plate (PL is 4 mm, PW ~10 mm) is rectangular in shape, with equally concave anterior and convex posterior margins. The medial orbital processes are of equal width (3–4 mm), long and ribbon-like. The dorsal shield is elongated, widest in its prebranchial part (DW/DL ~0.5–0.6). Its posterior margin extends into an appreciable ledge. The notch for the dorsal spine is long (29 mm) and narrow (2–3 mm).

Comparison. — The species differs from other representatives of *Althaspis* by smaller size and shorter rostral plate. In the shape of rostrum, the species reminds *A. elongata*, but in *A. tarloi* sp. n., it is not so narrow and long.

Remarks. — Morphology of the ventral surface of the rostral plate, as well as shape and size of dorsal spine, are unknown in this species. Nevertheless, its inclusion in *Althaspis* is rather certain. In Western Europe, *Althaspis* is present across the Lochkovian–Pragian boundary (Blieck 1984; Dupret and Blieck 2009), whereas in Podolia until now it was known only from the Pragian. As the new species is geologically older than other, more derived species of the genus, it is of rather small size and shows some plesiomorphic althaspid features(ratio RL/RW). It can be considered as close to the ancestral form of the *Althaspis* lineage.

Localities and age. — Potochyshche; late Lochkovian or early Pragian (lower part of the Dniester Formation) of Podolia (Ukraine).

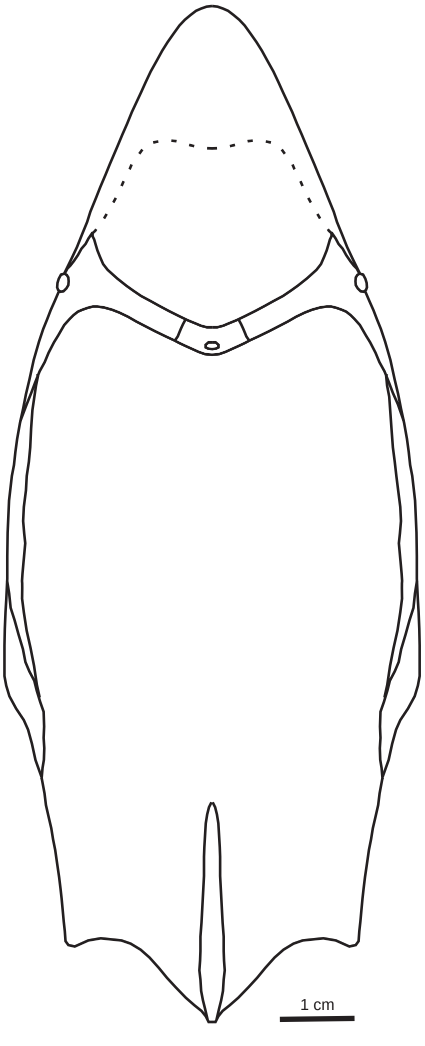


Fig. 76. Rhinopteraspidid *Althaspis tarloi* sp. n., reconstruction of the carapace dorsal view, based on all available specimens.

Althaspis? *spathulirostris* (Stensiö, 1958)

1958. *Pseudopteraspis* ? *spathulirostris* Stensiö, 1958: fig. 187.

1964. *Althaspis*? *spathulirostris*; Stensiö, 1964: fig. 90.

1984. *Miltaspis*? *spathulirostrata*; Blieck 1984: pp. 29–30, fig. 7A.

Type specimen: Holotype NHRM C1560, fragmental mould of anterior part of the carapace; Soroky, Buchach rayon, Ternopil' oblast' (Podolia).

Remarks. — Type, single specimen of the species demonstrates concave lateral margin of the rostral plate. This feature, unless it is not a preservational artifact, together with some pecularities of ventral rostral morphology, makes it different from all other *Althaspis* representatives. At the same time, judging from figure 7A in Blieck (1984), the orbito-pineal belt is of the *Althaspis* type (see also Blieck 1984: p. 31), contrary to its restoration (Blieck 1984: fig. 32C). Anyway, this form seems more closely related to *Althaspis* than to *Miltaspis* (Blieck 1984: fig. 32A). It may represent a separate genus.

Localities and age. — Soroky; Pragian (probably Strypa Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Family **Protaspididae** Bryant, 1933

Genus *Europrotaspis* White, 1961

1936. *Protaspis*; Brotzen 1936: pp. 9–20.

1961. *Protaspis* (*Europrotaspis*); White 1961: pp. 268–270.

1964. *Europrotaspis*; Stensiö 1964: p. 363.

1964. *Glossoidaspis*; Obruchev 1964: p. 68.

1975. *Europrotaspis*; Novitskaya 1975: p. 83.

1984. *Europrotaspis*; Blieck 1984: p. 64.

1986. *Europrotaspis*; Novitskaya 1986: pp. 115–116.

2001. *Europrotaspis*; Voichyshyn 2001c: p. 36.

2004. *Europrotaspis*; Novitskaya 2004: pp. 168–169.

Type species: *Protaspis arnelli* Brotzen, 1936; Early Devonian (Strypa Stage of the Dniester Formation) of Podolia.

Diagnosis. — Medium to large sized pteraspidids. The rostral plate is relatively small. It reaches 1/5 to 1/4 of the total length of the carapace. Index RL/RW is 0.6–0.7. The anterior orbital processes are short and pointed, while the medial ones are ribbon-shaped and elongated, and in full contact with the lateral margins of rectangular pineal plate. The dorsal shield is wide (DW/DL 0.80–0.90), being widest in the posterior third. Posterior margin of the shield has small medial ledge. The notch for dorsal spine is short. The branchial plates are very long, more or less convex, and reach the level of posterior end of the dorsal shield. The cornual plates are very small. The branchial openings are displaced to posterior edge of the carapace, and are placed partly between the branchial and cornual plates. Mdl canals are of radial type, transverse comissures are displaced to the posterior margin of the carapace.

Species included. — Besides the type species, *E. crenulata* (White, 1961) and, possibly, *E.*? *wiheriesiensis* (Brotzen, 1936), Early Devonian of Belgium.

Occurrence. — Early Devonian of Podolia (Ukraine), Great Britain, and possibly Belgium.

Europrotaspis arnelli (Brotzen, 1936)

(Fig. 77A–C)

1936. *Protaspis arnelli*; Brotzen 1936: pp. 20–31, text-fig. 6, pls 1–5.

1964. *Glossoidaspis arnelli*; Obruchev 1964: text-fig. 43.

1984. *Europrotaspis arnelli*; Blieck 1984: pp. 64–65, fig. 47C.

1986. *Europrotaspis arnelli*; Novitskaya 1986: p. 116, text-figs 57–59, pl. 23, fig. 8, 9, synoptic table, p. 146, fig. 60.

2004. *Europrotaspis arnelli*; Novitskaya 2004: p. 169, text-fig. 91.

2010. *Europrotaspis arnelli*; Voichyshyn 2010: pl. 4, fig. 2.

Type specimen: Holotype NHRM C 1792 (P 75, see Novitskaya 2004), incomplete carapace in dorsal view (without rostral plate and orbito-pineal belt); Kydaniv, Buchach rayon, Ternopil' oblast' (Podolia).

Referred material. — Moulds of ventral plates SMNH BP.1414 and 1415 from Sapova; plaster-cast copy of mould of the carapace IGP 03900 from Kydaniv.

Fig. 77. Rhinopteraspidid *Althaspis* and protaspidid *Europrotaspis* from various localities of Strypa Member of the Dniester Formation in Podolia. **A**. *Europrotaspis arnelli* (Brotzen, 1936), plaster-cast copy of mould of carapace IGP 03900 (labelled *Protaspis lata*) lacking branchial and cornual plates from Kydaniv, dorsal view. **B**. Same species, mould of ventral shield SMNH BP.1415 lacking anterior part from Sapova, dorsal, lateral (left side) and posterior views. **C**. Same species, mould of ventral shield SMNH BP.1414 lacking anterior part, same locality back dorsal, posterior and lateral (left side) views. **D**. *Althaspis* sp., complete mould of ventral shield SMNH BP.583 from the Zaryvyntsi quarry, dorsal, lateral (right side), and posterior views.

Diagnosis. — Medium sized *Europrotaspis* species with very wide dorsal shield which considerably narrows in its anterior part.

Description. — Specimen IGP 03900 is relatively small as for the species; tL 95 mm, DL 74 mm, DW 64, RL 21(18) mm, RW 39 mm, PL 3 mm, while its pineal spot is relatively large, 2.5 mm in diameter. Such size of the pineal spot was reported also in specimen PIN 3592/60 (Novitskaya 1986: text-fig. 57, and 2004:

fig. 91). It is probably one of distinctive features of the species. Anterior and posterior orbital processes are very short, the anterior one being half length of the posterior. Median orbital processes are relatively long and ribbon-shaped in the continuous orbito-pineal belt. Their width corresponds to the length of pineal plate (PL). The ventral shield is large, wide in anterior part, appreciably narrowed in caudal direction, and has wide, short and blunt medial ledge at its posterior margin. Maximum width of the shield, approximately at the middle of the shield and closer to the anterior margin, is 65–68 mm; length is more than 100 mm. Central part of the shield is convex. This zone is narrowed and its camber increases backwards.

Comparison. — In contrast with the species in question, *E.*? *wiheriesiensis* has a smaller pineal plate, wider posterior parts of the branchial plates, and mdl canals which come nearer to lateral margins of the dorsal shield.

Remarks. — The holotype (Brotzen 1936: pl. 1, fig. 1) is represented by carapace lacking rostrum and the orbito-pineal belt. However, the specimen shows such features characteristic for the species as very wide, but appreciably narrowed in the anterior part, dorsal shield and more or less equal in width as well as considerably bent in posterior part branchial plates. These features in particular differentiate *E. arnelli* from *E. crenulata* (White, 1961) (cf., Blieck 1984: fig. 47A, C) and argue against their synonymizing by Novitskaya (1986: p. 116, 2004: p. 169). Specimens IGP 03900 and PIN 3592/60 (Novitskaya 1986: text-fig. 57, and 2004: fig. 91) may belong to *E. crenulata* rather than to this species, but they seem to represent younger stages of the carapace development, when shape and proportion (DW/DL) of the dorsal shield still do not reach values demonstrated by the holotype. Actually, Novitskaya (2004) admitted lack of morphological data on ventral surface of the rostral plate and morphology of scales in *E. arnelli*, that makes unification of these species poorly supported.

Localities and age. — Kydaniv, Sapova, and Perevoloka; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine).

Incertae familiae

Genus *Pavloaspis* Voichyshyn, 1999

1999. *Pavloaspis*; Voichyshyn 1999: pp. 52–53.

2001. *Pavloaspis*; Voichyshyn 2001c: p. 36.

Type species: *Pavloaspis pasternaki* Voichyshyn, 1999; Early Devonian (probably near the boundary between Ustechko and Khmeleva Stages of the Dniester Formation) of Podolia.

Diagnosis. — Medium sized pteraspidids. Carapace is elongated, with length of about 100 mm, and massive. The length of the rostral plate is one fourth the whole length of carapace. Index RL/RW equals 0.8. The pineal plate is large and rounded, without any contact with small orbital plates. Anterior and median orbital processes are short and pointed. The cornual plates are elongated and not wide. Dorsomedial sensory canals are of radial type.

Species included. — Only type species.

Remarks. — The genus differs from other representatives of the Pteraspidoidei by morphology of its orbito-pineal belt. An extent of isolation of component belt elements resembles that of Protopteraspididae and Pteraspididae Claypole, 1885. The difference is in shape and size of the plates. Besides, the Protopteraspididae differs in shape of rostral and dorsal plates, different arrangement of the pineal component of supraorbital sensory canals (“pineal” canal), and smaller general size. Pteraspididae differ by shape of the dorsal shield; Podolaspididae by shape of the cornual plates, Rhinopteraspididae by shape of the rostral plate, and Protaspididae by shape of the dorsal, branchial and cornual plates. Shape and size of the dorsal, rostral and cornual plates are similar to those of some Larnovaspididae (*Larnovaspis*, *Djurinaspis*, and *Alaeckaspis*).

Probably a new family should be established for the genus as the third phylogenetic branch of Podolian pteraspidids, along with the Podolaspididae and Larnovaspididae, derived from primitive forms like *Protopteraspis*.

Occurrence. — Early Devonian of Podolia (Ukraine).

Pavloaspis pasternaki Voichyshyn, 1999
(Fig. 78)

1999. *Pavloaspis pasternaki*; Voichyshyn 1999: pp. 53–54, fig. 4.

2006. *Pavloaspis pasternaki*; Voichyshyn 2006c: p. 29, pl. 1, fig. 3.

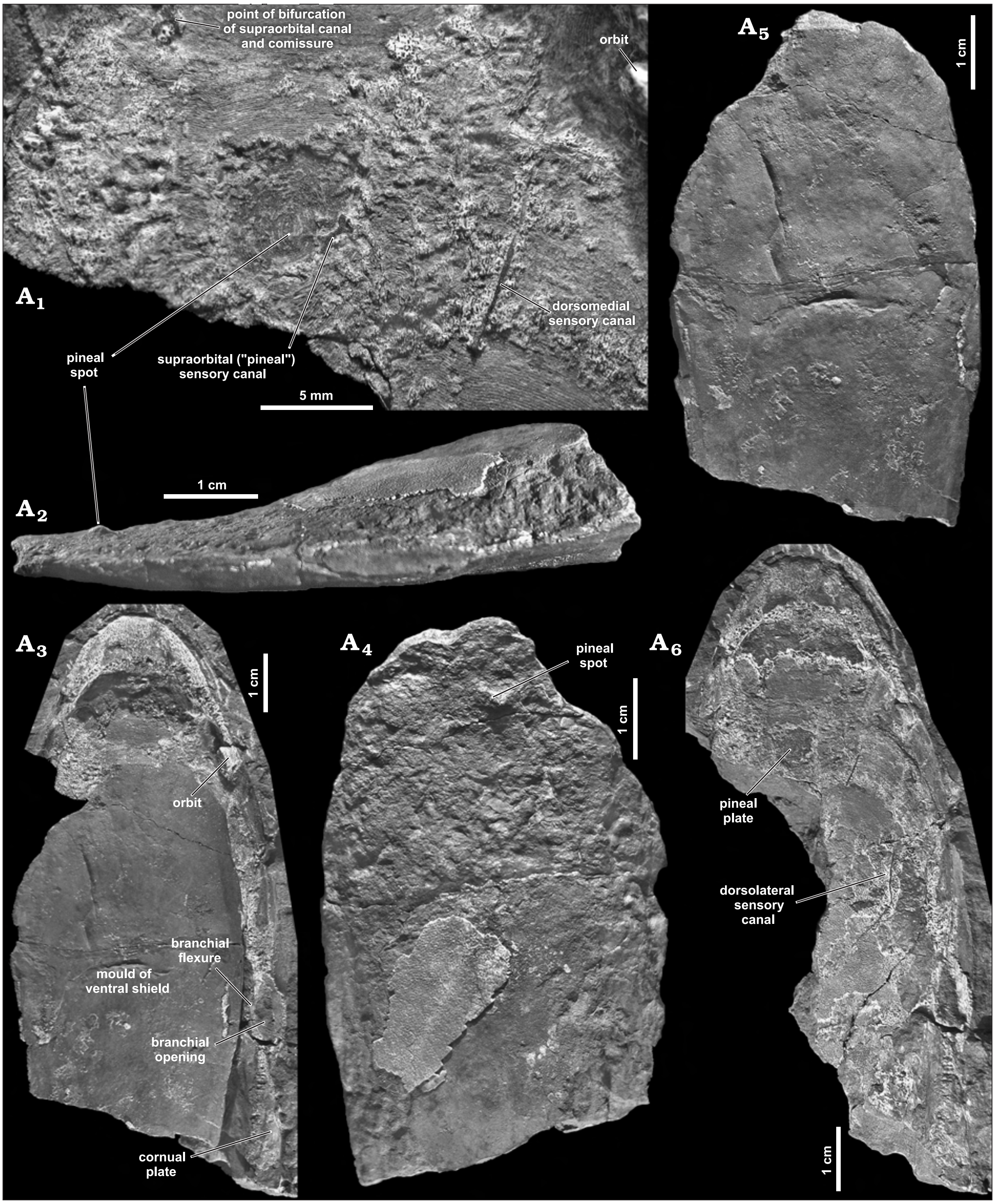


Fig. 78. *Pavloaspis pasternaki* Voichyshyn, 1999, mould of both dorsal and ventral plates and fragmentary imprint of antero-lateral part of carapace SMNH BP.169 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member of the Dniester Formation. Dorsal view of orbito-pineal region of carapace, lateral (left side) view, dorsal view of the carapace, ventral shield in ventral view, and antero-lateral (left side) views, respectively.

Type specimen: Holotype SMNH BP.169a–b, mould of both dorsal and ventral plates and fragmentary impression of antero-lateral part of carapace; Ustechko, left bank of the Dniester River, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Only the holotype.

Diagnosis. — The same as of the genus (by monotypy).

Description. — The carapace of the only known specimen is relatively wide and fairly massive. Ventral length of the rostral plate, from anterior margin to the medial crime, is about half of the dorsal one. The pineal plate is large and nearly round in shape, with approximately the same width and length. It forms poorly visible "hornlets", which are directed laterally and situated at the border between rostral and dorsal plates. The pineal plate takes about 1/5 of the orbito-pineal belt length. The plate is detached from orbital ones by gaps that nearly equal the plate's width. Maximum width of the dorsal shield is in its prebranchial part (DW/DL about 0.6). The shield gets narrow in the region of branchial openings. The branchial plates are relatively short. Branchial openings are fairly long (about 15 mm) and lens-shaped. The cornual plates are elongated and not wide. Supraorbital sensory canals pass the border of the pineal plate in the "hornlets" region. Dorsomedial canals diverge in radial manner to base of the medial orbital processes. Dentine ridges are of density 6 cr/mm over the dorsal shield and the dorsal side of rostral plate, and 9 cr/mm over the ventral side of the latter.

Localities and age. — Ustechko; early Pragian (probably about the boundary between the Ustechko Stage and Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Genus *Loricopteraspis* Tarlo, 1961

1958. *Pteraspis*; Stensiö 1958: p. 277 (pars).
1961. *Loricopteraspis*; Tarlo 1961: pp. 382, 385.
1964. *Loricopteraspis*; Obruchev 1964: p. 67.
1975. *Loricopteraspis*; Novitskaya 1975: p. 82.
1984. *Loricopteraspis*; Blieck 1984: pp. 37–38 (pars).
1986. *Loricopteraspis*; Novitskaya 1986: p. 118.
2004. *Loricopteraspis*; Novitskaya 2004: pp. 169–170.

Type species: *Pteraspis althi* Stensiö, 1958; Early Devonian of Podolia.

Diagnosis. — Small sized pteraspidids with rostral plate slightly narrowed anteriorly. The preoral field is ornamented with longitudinal and transverse dentine ridges. Ascendant lamella is short.

Species included. — Only the type species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Loricopteraspis althi (Stensiö, 1958)

1958. *Pteraspis althi*; Stensiö 1958: p. 277, fig. 152A.
1961. *Loricopteraspis althi*; Tarlo 1961: p. 382, fig. 9.
1984. *Loricopteraspis althi*; Blieck 1984: p. 38 (pars), fig. 13A, B.
1986. *Loricopteraspis althi*; Novitskaya 1986: pp. 118–119.
2004. *Loricopteraspis althi*; Novitskaya 2004: p. 170.

Type specimen: Holotype, NHRM C1559, rostral plate exposed from ventral side; locality unknown, Podolia.

Remarks. — Blieck referred two more specimens from Jagilnytsia and Zastinoche to this species. One of them (NHRM C1691; Blieck 1984: fig. 13E, F) was identified as *L. althi*, on the basis of morphology of the ventral surface of the rostral plate, the other (Blieck 1984: fig. 13C, D; NHRM C2309) on the basis of similarity with the first specimen in morphology of the orbito-pineal belt. In the second specimen, the branchio-cornual region of the carapace is preserved as well. This allowed its reconstruction (Blieck 1984: fig. 40A). However, the orbito-pineal belt of these specimens has as many similarities as differences, making their conspecificity not convincing enough.

Localities and age. — Precise locality is unknown; possibly Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Genus *Palanasaspis* gen. n.

Derivation of the name: Latin *pala*, shovel, and *nasus*, nose, refer to the shovel-shaped rostral plate of the type species.

Type species: *Palanasaspis chekhivensis* sp. n.; Early Devonian (most probably, Strypa Stage of the Dniester Formation) of Podolia.

Diagnosis. — Medium to large sized pteraspidids. The rostral plate is elongated, widely rounded anteriorly and has a trapezoidal shape, with lateral margins probably straight. Preoral field is very wide and it is covered with transversal dentine ridges.

Species included. — Only the type species.

Comparison. — The stretched onward rostral plate and ventral surface ornamentation resemble *Althaspis* but the genus differs in wide anterior plate end, presumed presence of the preoral field, and, probably, in value of index RL/RW. No other known pteraspidid (not only Podolian ones) shows this set of characters.

Occurrence. — Early Devonian of Podolia (Ukraine).

Palanasaspis chekhivensis sp. n.

(Figs 19A, 79)

1999. Pteraspidoidei incertae sedis; Voichyshyn 1999: p. 56, fig. 6.

2010. Pteraspidoidei gen et sp. indet.; Voichyshyn 2010: pl. 4, fig. 4.

Derivation of the name: After the type locality.

Type specimen: Holotype, SMNH BP.197; fragmentary impression of ventral surface of rostral plate; Chekhiv, Monastyrys'ka rayon, Ternopil' oblast' (Podolia).

Referred material. — The holotype only.

Diagnosis. — Same as for the genus.

Description. — The dorsal plate length exceeds its width, which is not less than 45 mm. Its ventral length is 39 mm. Ventral side of the plate shows very wide preoral field, delimited by lateral grooves. It is covered with transversal dentine ridges, which are of uniform width (6 cr/mm). Ascendant lamella seems to be relatively short. The medial crest and paraoral projections are smooth.

Localities and age. — Chekhiv; Pragian (most probably Strypa Stage of the Dniester Formation) of Podolia (Ukraine).

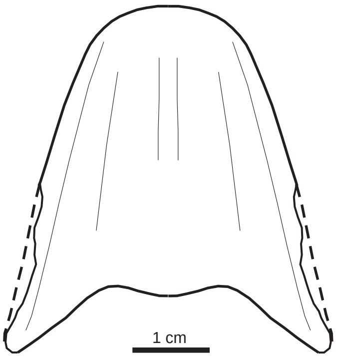


Fig. 79. *Palanasaspis chekhivensis* gen. et sp. n., reconstruction of rostral plate in ventral view.

"*Pteraspis*" *angustata* Alth, 1874

(Fig. 21B, C)

1874. *Pteraspis angustatus*; Alth 1874: p. 45 (pars), pl. 3, figs 6, 7 (only).

1927. *Pteraspis sturi* Alth sp., mut. *rostrata*; Zych 1927: pl. 2, fig. 6.

1933. *Pteraspis concinna*; Brotzen 1933a: pp. 453–454, fig. 14.

1984. *Rhinopteraspis* (= *Belgicaspis*) *crouchi*; Blieck 1984: p. 34.

1999. "*Pteraspis*" *angustata*; Voichyshyn 1999: pp. 54–55, fig. 5.

2010. "*Pteraspis*" *angustata*; Voichyshyn 2010: pl. 3, fig. 3.

Type specimen: Lectotype (Alth 1874: pl. 3, figs 6, 7), incomplete dorsal shield; Khreshchatyk, right bank of the Dniester River (probably the lowest part of the Ustechko Stage of the Dniester Formation), Zastavna rayon, Chernivtsi oblast' (Podolia). The location of the specimen is unknown.

Referred material. — Moulds or impressions of dorsal shields SMNH BP.181, 182, 183, 184, 185, and 186.

Diagnosis. — Relatively small pteraspidids with deep pineal notch in the anterior margin of the dorsal shield, which is narrowed in its posterior part.

Description. — The dorsal shield is small (DL equals 45–60 mm; DW/DL 0.54–0.60), with maximum width in fore-part. The shield gets narrow in the postbranchial part and stretches in acutely angular projection to the caudal end. The notch for the pineal plate in the anterior margin of the dorsal shield is deep and clearly outlined. Notch for the dorsal spine is relatively long and narrow. The dorsal spine in its base gently slopes up backwards. Dorsomedial sensory canals are radial. Dentine ridges of ornamentation are wide (5–6 cr/mm).

Comparison. — "*Pteraspis*" *angustata* is similar to *Rhinopteraspis dunensis* (Roemer, 1855), by contours of anterior and posterior shield margins, but differs from it by considerably smaller size. In contrast with *Belgicaspis crouchi* (Blieck 1984: p. 78, fig. 37C), it has deeper pineal notch in the anterior margin of the dorsal shield, narrower posterior part of the shield (at the level of posterolateral corners), and smaller mature size.

Remarks. — The specimen figured by Zych (1927: pl. 2, fig. 6) belongs to *Podolaspis podolica*, in opinion of Novitskaya (1986: p. 82; but not Brotzen 1933a: p. 441). If true, than it is a juvenile, since mature plate of this species (Novitskaya 1986: text-figs 31, 32) has other shape and larger size. But undoubted juvenile plates of *P. podolica*, for instance specimen PIN 3592/43 (Novitskaya 1986: text-fig. 32), bear no resemblance to Zych's specimen.

Localities and age. — Ustechko and Khreshchatyk; late Lochkovian to early Pragian (from the Ustechko Stage to the lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Incertae ordinis et familiae

Genus *Weigeltaspis* Brotzen, 1933

1933. *Weigeltaspis*; Brotzen 1933: pp. 648–651.
1964. *Weigeltaspis*; Obruchev 1964: p. 63.
1965. *Weigeltaspis*; Tarlo 1965: p. 20.
2004. *Weigeltaspis*; Novitskaya 2004: p. 199.
Type species: *Weigeltaspis alta* Brotzen, 1933; Early Devonian of Podolia.

Diagnosis. — Dorsal median plate is lengthened, relatively narrow, and on its posterior part has rather high medial ridge. Postorbital plate is rectangular, branchial one is convex. The plates are covered with comparatively large and elongated tubercles of oak leaf shape.

Species included. — Besides the type species, *W. brotzeni* Tarlo, 1964, Ustechko Stage of the Dniester Formation of Podolia, probably also *W.* sp. 1 and *W.* sp. 2, both are from the lowest part of Khmeleva Stage of the Dniester Formation of Podolia, *W. godmani* Tarlo, 1964, *Belgicaspis crouchi* Zone of Britain, *W. heintzi* Tarlo, 1964, Red Bay Series of Ben Nevis Formation of Spitsbergen, all from the Early Devonian.

Remarks. — Different types of oak-leaf-like tubercles occur as isolated or in small groups in marine deposits of the Chortkiv Stage (Fig. 80F), as well as in its upper part (Fig. 80A, I), throughout the Ivanie Stage ranging from its lower (Fig. 80H), middle (Fig. 80E), middle to upper (Fig. 80B, G, J, L, M), upper (Fig. 80D, K), and uppermost part (Fig. 80C). In contrast with *Weigeltaspis* ones, they do not merge into larger plates, but form small units of the dermal skeleton. Similar remains were referred by Blieck (1982) to *Lepidaspis*. This genus contains single species *L. serrata* Dineley *et* Loeffler, 1976 from the Early Devonian of the Canadian Arctic, which shows suture traces between separate "tesserae" or "scale-units", even if preserved as continuous carapace, but the degree of fusion of tesserae varies from one individual to other (Janvier 1996: fig. 4.10F1). Since oak-leaf-like tubercles are in general common for so called "tessellate heterostracans" of unknown affinity, the Podolian material is here referred to as "*Lepidaspis*" sp., notwithstanding its morphological diversity. Janvier (1996) considered such remains as belonged to a group of uncertain affinity, the Lepidaspidida.

Occurrence. — Early Devonian of Podolia (Ukraine), Great Britain and Spitsbergen (Norway).

Weigeltaspis alta Brotzen, 1933
(Fig. 81A, C–F)

1933. *Weigeltaspis alta*; Brotzen 1933: pp. 648–649, figs 1, 2.
1964. *Weigeltaspis alta*; Obruchev 1964: p. 63.
1965. *Weigeltaspis alta*; Tarlo 1965: pp. 21–23, text-fig. 2A, pl. 4, figs 3, 4, pl. 5, fig. 1.
2004. *Weigeltaspis alta*; Novitskaya 2004: p. 199.

Type specimen: Lectotype (Brotzen 1933a: fig. 1), dorsal median plate housed in the Geological-Palaeontological Institute, Halle, Germany (Tarlo 1965); Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.111, 114, 117, 118, 121, 125, 126, 151/2, 1126/1, 1212, 1486 and 1487.

Diagnosis. — *Weigeltaspis* species with large and freely distributed tubercles of the dermal oskeleton.

Description. — The complete length of the animal was not less than 250 mm, based on specimen SMNH BP.1212. The length of the carapace is 140 mm or somewhat more. Length of dorsal median plate is about 90 mm. Its width is not less than 38 mm. Height of the median ridge is up to 5 mm. Oak-leaf-like tubercles have wide long bases and five short lateral ledges on both sides. Length of the tubercles is ~1.7–2.7 mm. Distances between them are from 0.3 mm to 2.0 mm. They reach the maximum size on lateral parts of the dorsal median plate. In a strip about 10 mm in width along the median ridge, tubercles are located basically under some angle (20–30°) to it and are finer. Size of orbital plate is about 14 × 22 mm. The plate outline is irregular, roughly beveled anterior and posterior ones, probable medianward is convex whereas lateralward is roughly

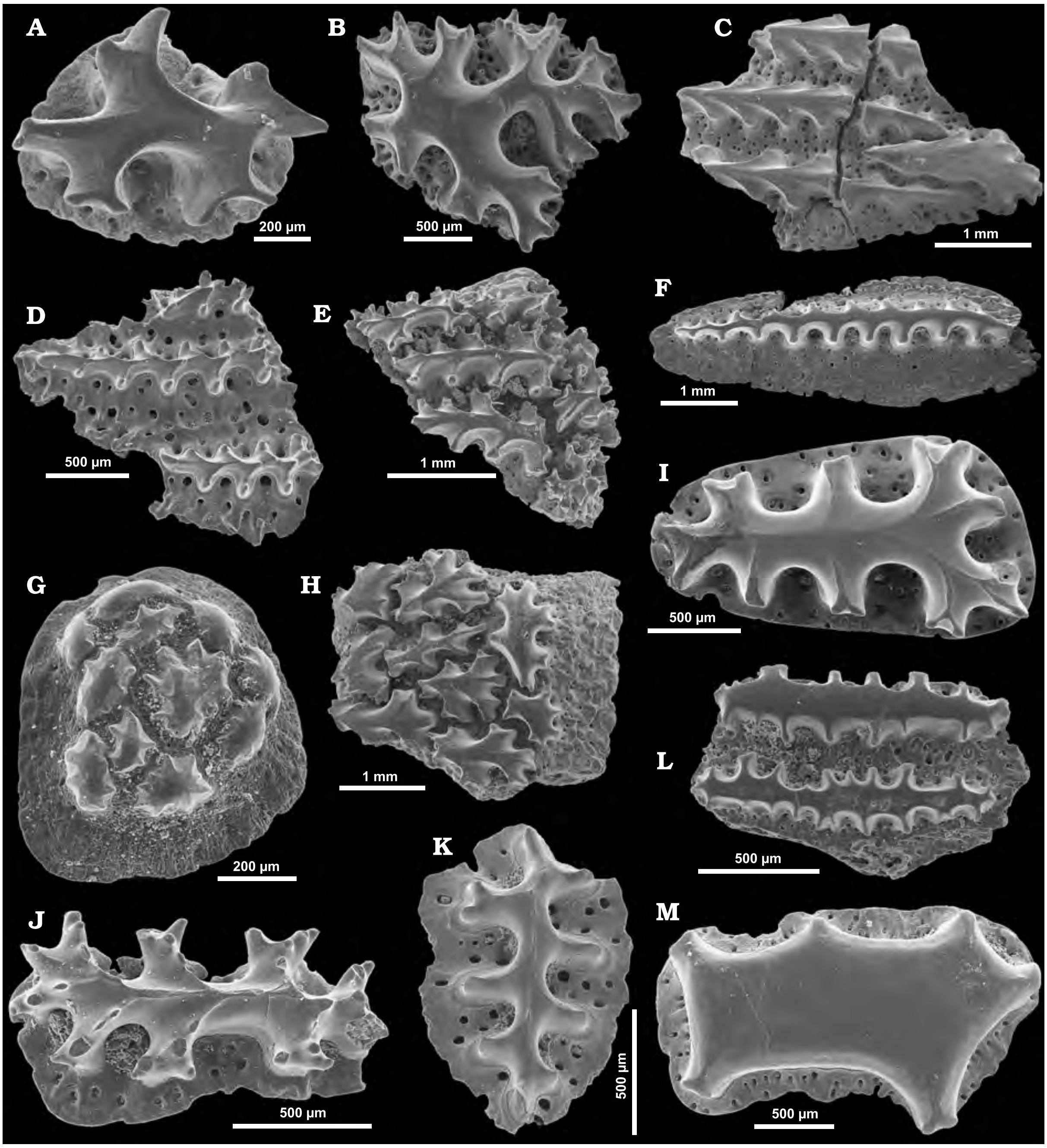


Fig. 80. "*Lepidaspis*" from Podolia. **A**. Tessera SMNH BP.1542/10 from outcrop 11 (Fig. 3B), left bank of Dniester River, upper part of Chortkiv Member of the Tyver Formation. **B**. Tessera SMNH BP.1545/17 from outcrop 1 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member of the Tyver Formation. **C**. Piece of armour (specimen lost) from Ustechko, left bank of Dniester River, uppermost part of Ivanie Member. **D**. Piece of armour SMNH BP.1548/2 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member. **E**. Piece of armour SMNH BP.1546/3 from borehole Peremyshlyany-1 (Fig. 3A), 2135 m, middle part of Ivanie Member. **F**. Tessera SMNH BP.1544/9 from Gorodok, left bank of Dniester River, Chortkiv Member. **G**. Tessera SMNH BP.1549/18 from outcrop 1. **H**. Piece of armour SMNH BP.1540/8 from Dobrivliany, lower part of Ivanie Member. **I**. Tessera SMNH BP.1550/21 from outcrop 11. **J**. Tessera SMNH BP.1545/11 from outcrop 1. **K**. Tessera SMNH BP.1539/13 from Zalishchyky. **L**. Tessera SMNH BP.1546/6 from outcrop 2 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member. **M**. Tessera (specimen lost) from outcrop 1.

concave (Fig. 81D). The orbits are displaced to the convex margin of the plate. They are of about 5 mm in length and 4 mm in width. The tubercles are at different angles to the longitudinal axis of the plate.

Comparison. — The species differs from *W. brotzeni* by almost twice larger and less densely distributed tubercles, from *W. godmani* by narrower and not so rounded tubercles, and from *W. heintzi* by wider tubercles.

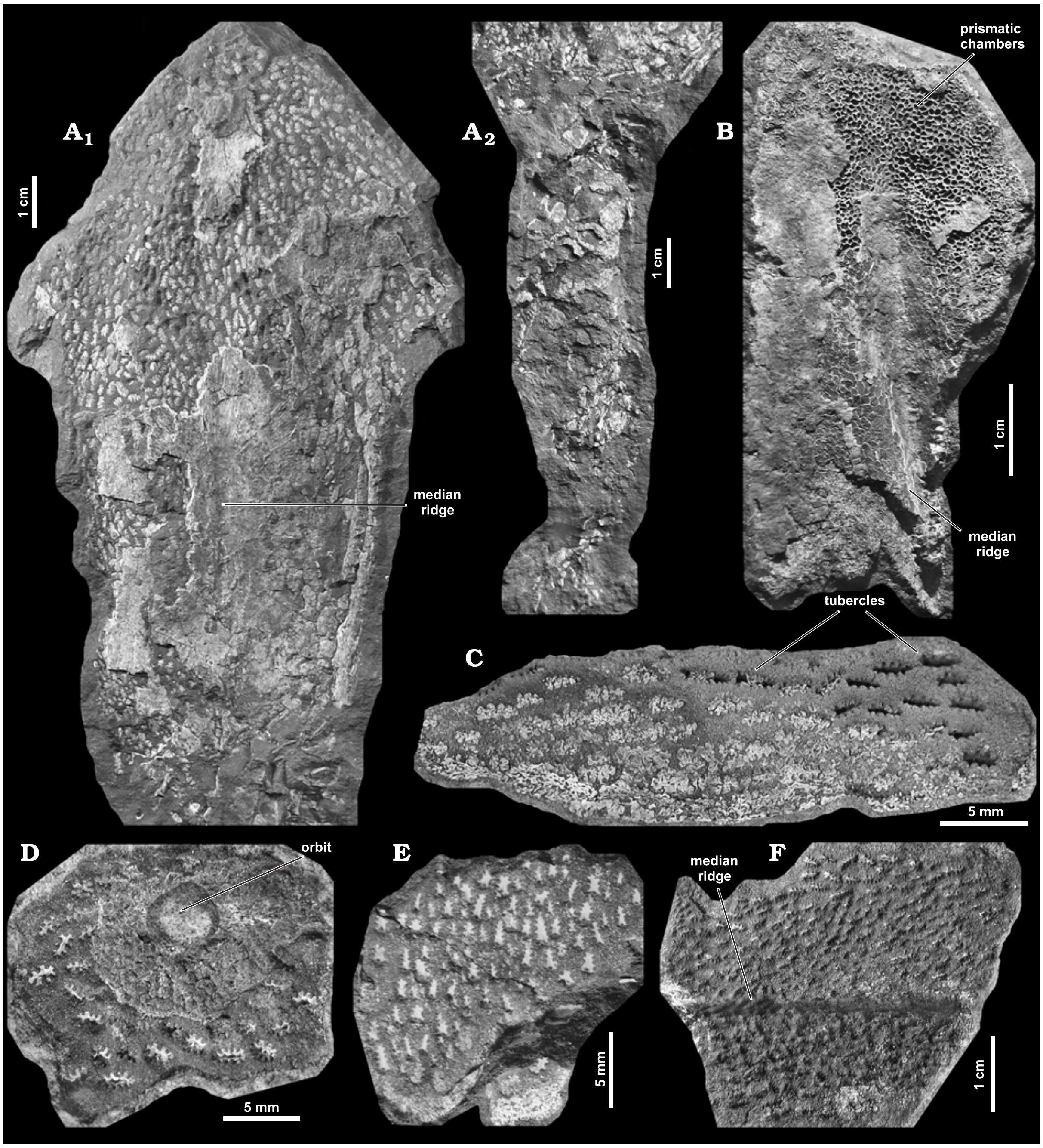


Fig. 81. *Weigeltaspis alta* Brotzen, 1933 from various localities of the Dniester Formation in Podolia. **A**. Pieces of probably dorsal median plate SMNH BP.1212 from Nagiriany, Ustechko Member or lower part of Khmeleva Member, inside view and remains of trunk(-tail). **B**. *Weigeltaspis* sp., partial dorsal median plate SMNH BP.115 from Ustechko, Ustechko Member or lower part of Khmeleva Member, inside view. **C**. Imprint of plate fragment SMNH BP.121 from Ustechko, right bank of Dzhuryn River, probably, Ustechko Member. **D**. Imprint of orbital plate SMNH BP.1126/1 (see also Fig. 101C) from Horodnytsia, Ustechko Member or lower part of Khmeleva Member. **E**. Imprint of plate fragment SMNH BP.125 from the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member. **F**. Imprint of partial dorsal median plate SMNH BP.111 from Ustechko, left bank of Dzhuryn River, Ustechko Member.

Remarks. — Small fragments of plates with “typical sculpture” from Ustechko are in PIN collection (Novitskaya 2004).

Localities and age. — Buriakivka, Horodnytsia, Nagiriany, Potochyshche and Ustechko; Lochkovian to early Pragian (from Ustechko Stage to the lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

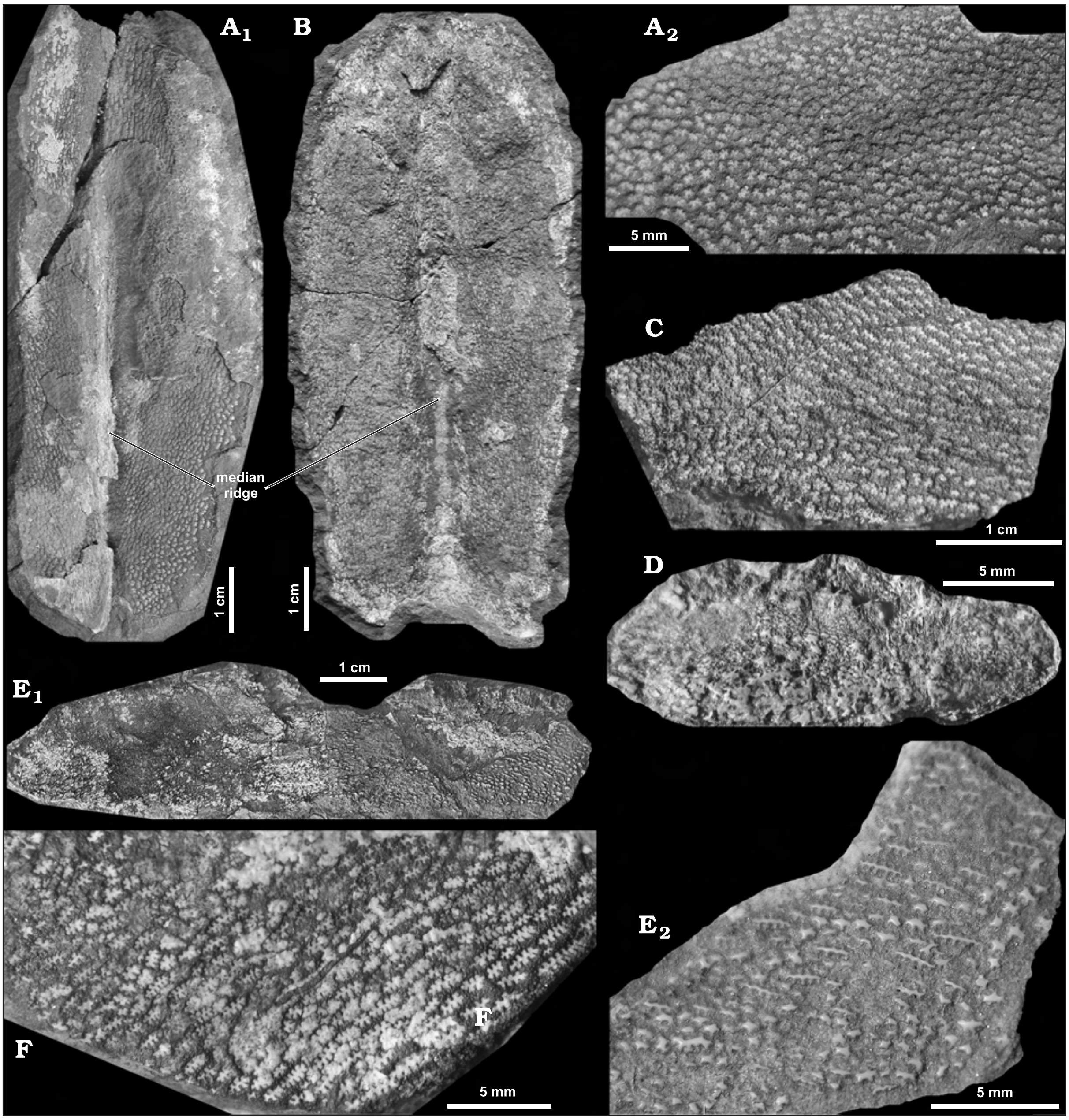


Fig. 82. *Weigeltaspis brotzeni* Tarlo, 1964 and related species from various localities in Podolia. **A**. Partial dorsal median plate SMNH BP.113 from Ustechko, lower part of Khmeleva Member of the Dniester Formation, inside view and imprint of ornamentation. **B**. Dorsal median plate SMNH BP.1200 from Nagiriany, Ustechko Member or lower part of Khmeleva Member, inside view. **C**. Imprint of sculpture SMNH BP.1313 from exposure east of Dobrivliany, lower part of Ivanie Member of the Tyver Formation. **D**. *Weigeltaspis* sp. 2, piece of plate sculpture SMNH BP.201/1 from Ustechko, lower part of Khmeleva Member of the Dniester Formation. **E**. *Weigeltaspis* sp. 1, partial dorsal median plate SMNH BP.116 from Ustechko, the same horizon, dorsal view and enlarged ornamentation. **F**. Imprint of carapace ornamentation SMNH BP.110/1 from Ustechko, the same horizon.

Weigeltaspis brotzeni Tarlo, 1964
(Fig. 82A, B, C, F)

1964. *Weigeltaspis brotzeni*; Tarlo 1964: p. 112.
1965. *Weigeltaspis brotzeni*; Tarlo 1965: pp. 23–24, pl. 5, figs 2, 3.
2004. *Weigeltaspis brotzeni*; Novitskaya 2004: p. 199.
2010. *Weigeltaspis brotzeni*; Voichyshyn 2010: pl. 3, fig. 1.

Type specimen: Holotype BM(NH) P.18266, fragment of the plate; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.110/1, 113, 120/1, 1060, 1200 and 1313.

Diagnosis. — *Weigeltaspis* species with densely distributed tubercles of the dermal oskeleton.

Description. — The dorsal median plate is elongated (~97 mm) and narrow (~40 mm). There is a longitudinal median ridge in its posterior part. Oak-leaf-like tubercles with small narrow bases are dense arranged. Distance between them does not exceed their width. Tubercles are elongated (1.5 mm), narrow (~0.3 mm), and parallel to body axis in anterior part of the plate. At the same time, they are shorter (0.8–1 mm) and wider (~0.5 mm), with two or three lateral ledges in posterior part of the plate, on both sides from the median ridge. Along the ridge, tubercles are oriented under angle of 20–25° to it. The median ridge probably was also ornamented with tubercles.

Comparison. — Other species have tubercles that are distributed less densely.

Localities and age. — Dobrivliany, Horodnytsia, Nagiriany, and Ustechko; Lochkovian to early Pragian (from Ivanie Stage of Tyver formation to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Weigeltaspis sp. 1

(Fig. 82E)

Referred material. — Partial mould of dorsal median plate with fragment of dermal skeleton ornamentation SMNH BP.116, from talus on the slope above old quarry in Ustechko, left bank of the Dniester River.

Description. — Length of the median plate is not less than 80 mm. Ornamentation is preserved in an area at one of the plate ends. It shows a medley of robust and short tubercles, mainly of 0.5–0.7 mm, in a single case up to 1.5 mm in length, and about 0.3–0.35 mm in width, with two or three lateral ledges, together with rare thin and elongate tubercles of 1.0–2.0 mm in length, 0.1–0.2 mm in width, and with four or five lateral ledges. Shape of the tubercles only roughly resembles oak-leaf because of their either robust or delicate appearance. All the tubercles are oriented approximately under angle of about 15° to the plate axis.

Comparison. — General size of median plate seems similar to other Podolian *Weigeltaspis* species, but it differs from all other species of the genus by presence of two different kinds of tubercles. The “lean” tubercles are similar to tubercles of *W. heintzi*, but smaller in size.

Remarks. — The narrow tubercles of this form are very similar to those figured by Ørvig (1961: fig. 2) from the Upper Downton of Shropshire, England, and referred as to *Traquairaspis symondsi* (Lankester, 1868). The figure in his work shows a “scale-area” of the carapace with concentrically arranged tubercles. Instead, narrow tubercles, accompanying the wide ones, are approximately parallel to the body axis in the Podolian form.

Localities and age. — Ustechko; early Pragian (lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Weigeltaspis sp. 2

(Fig. 82D)

Referred material. — Fragment of probably dorsal median plate SMNH BP.201/1; from a slope above old quarry, level “P” in Ustechko, left bank of the Dniester River.

Description. — The plate fragment is 20 mm in length and includes a part of a median ridge. On the top of the ridge, the largest tubercles, of about 1 mm and more in length, merge all together. They show signs of abrasion. Below, there are groups of star-like tubercles (0.4–0.7 mm in length and about 0.4 mm in width), and among these groups there is a lot of minute tubercles (about 0.1–0.2 mm in length and width). All the tubercles regardless of their size are of the same shape, in contrast with condition in previous form of *Weigeltaspis*, and densely arranged. Possibly, this fossil represents a juvenile individual.

Comparison. — Tubercles of such form are similar to robust tubercles of *Weigeltaspis* sp. 1, described above, but they have in general wider lateral ledges. They are also shorter and smaller and have more irregular shapes, with a distant likeness to oak-leaf one, than tubercles of all other *Weigeltaspis* species.

Localities and age. — Ustechko; early Pragian (lower part of the Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Class **CEPHALASPIDOMORPHI** Kiaer *et* Stensiö, 1920

Subclass **OSTEOSTRACI** Lankester, 1868 (Cephalaspides)

Order **Cephalaspidiformes** Halstead Tarlo, 1967

Suborder **Cephalaspidoidei** Halstead Tarlo, 1967

Family **Cephalaspididae** Agassiz, 1843

Genus *Mimetaspis* Stensiö, 1958

1927. *Cephalaspis*; Stensiö 1927: p. 247 (pars).
1932. *Cephalaspis*; Stensiö 1932: pp. 87–90 (pars).
1952. *Cephalaspis*; Wängsjö 1952: pp. 243–252 (pars).
1958. *Mimetaspis*; Stensiö 1958: p. 213.
1964. *Mimetaspis*; Obruchev 1964: p. 103.
1985. *Mimetaspis*; Janvier 1985a: p. 327.
1991. *Mimetaspis*; Afanassieva 1991: pp. 76–77.
2004. *Mimetaspis*; Afanassieva 2004: p. 244.

Type species: *Cephalaspis hoeli* Stensiö, 1927; Early Devonian of Spitsbergen.

Diagnosis. — Osteostracans of small size. Length of the shield is 20–40 mm. Their anterior margin sometimes is rather narrowed. The lateral margins are convex. The cornual processes are not long, with denticles on its inner margin. The abdominal division of the shield is very short, comparatively wide, and has small dorsomedial crest. The nasohypophyseal opening has the identical divisions in size. The pineal plate is lacking. The orbits are large enough. The dorsal field is lengthened and anteriorly narrowed. In front, it is narrowed. The pointed posterior ends of the lateral fields reach the last third or quarter of the cornual processes.

Species included. — Besides the type species, *Mimetaspis exilis* (Wängsjö, 1952) and *M. retusa* (Wängsjö, 1952) are from Early Devonian of Spitsbergen; *M. glazewskii* Janvier, 1985 and *M. concordis* Voichyshyn, 1994, are from Early Devonian of Podolia.

Occurrence. — Early Devonian of Podolia (Ukraine) and Spitsbergen (Norway).

Mimetaspis glazewskii Janvier, 1985

(Fig. 83A–D)

1985. *Mimetaspis glazewskii*; Janvier 1985b: pp. 328–329, figs 17, 18.
1991. *Mimetaspis glazewskii*; Afanassieva 1991: text-fig. 12a, pl. 15, fig. 1.
2004. *Mimetaspis glazewskii*; Afanassieva 2004: pp. 244–245, text-fig. 20, pl. 10, fig. 1.

Type specimen: Holotype BM(NH) P.20958-9, headshield; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.1, 2, 3, 4, 19, 1146/1, and 1433.

Diagnosis. — Large *Mimetaspis* species with relatively broad anterior end of the median dorsal field.

Description. — The shield is not wide (50–60 m) and comparatively short (~40 mm), its anterior margin is rounded. Maximum width of the shield is at the base of the cornual processes. The prepineal part of the shield is shorter than the postpineal one. The cornual processes are wide, relatively short. Their ends are caudally directed. Denticles on the inner margin of the cornual processes in SMNH specimens are not observed, although they have been specified at the holotype reconstruction (Janvier 1985b: fig. 17). The abdominal division of the shield is short and not wide. The dorsomedial crest is small. Pectoral sinuses are very shallow. The nasohypophyseal depression is clear, reminding an equilateral triangle in shape. Orbits are oval, relatively large, located on moderate distance one from another. The dorsal field is long and narrow enough. Its posterior part is fairly pointed, rounded or forms a corner. The lateral fields are long, equal in width. Their anterior ends are rounded and the posterior ones are pointed and enter cornual processes, up to 2/3 or even 3/4 of their length. No ornamentation of the shield is preserved.

Comparison. — *Mimetaspis glazewskii* differs from all other species of the genus by appreciably larger sizes. *Mimetaspis hoeli* has narrower dorsal field, another contour of the posterior margin of abdominal part of the shield. *Mimetaspis exilis* has narrower anterior part of the shield, rounded posterior ends of the lateral fields, that reach the middle of the cornual processes. *Mimetaspis retusa* differs by not so narrow anterior margin of the shield, and by more distant anterior ends of lateral fields, which enter the cornual processes not

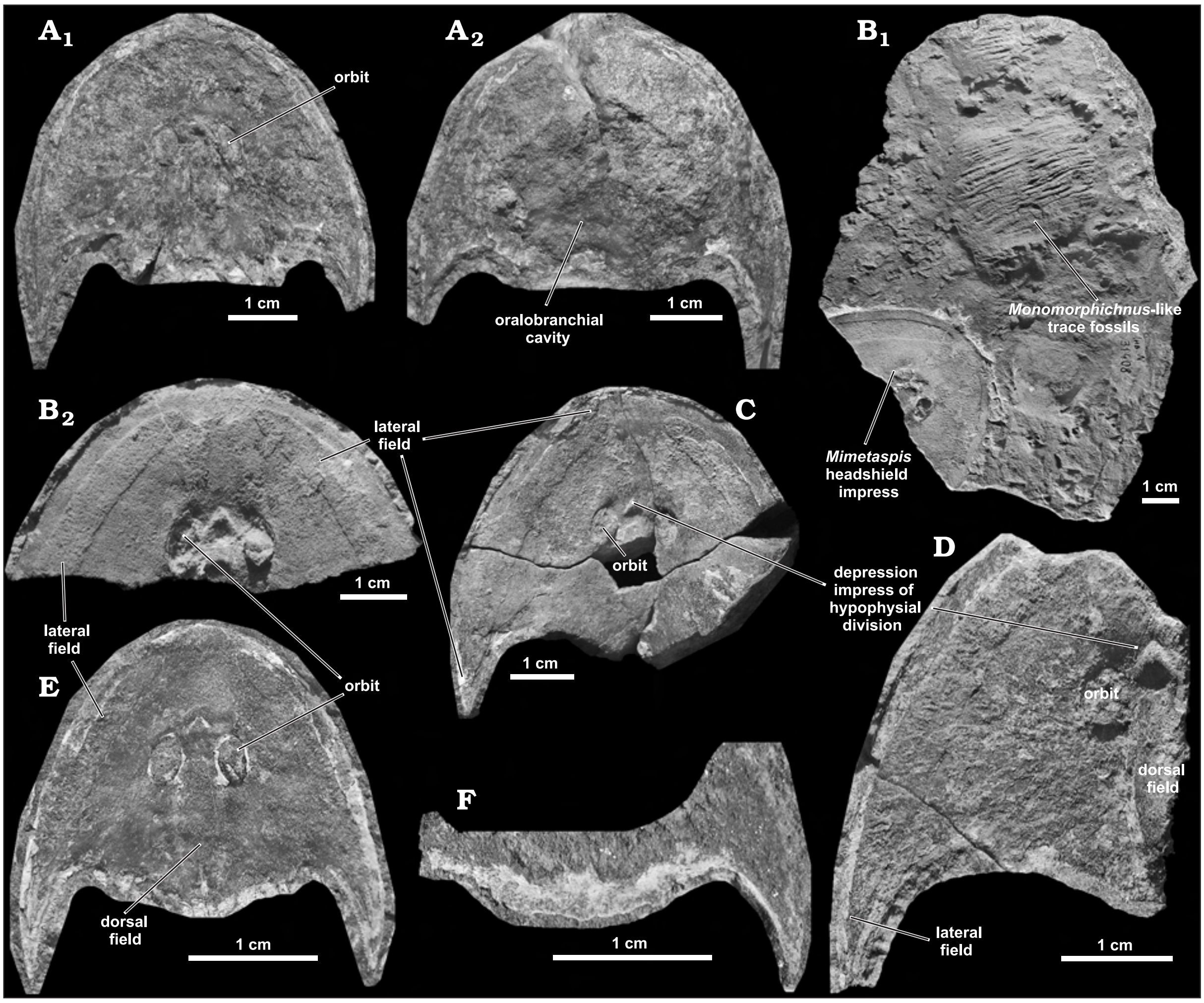


Fig. 83. Cephalaspidids *Mimetaspis* from various localities of the Dniester Formation in Podolia. **A**. *Mimetaspis glazewskii* Janvier, 1985, partial imprint of headshield SMNH BP.1, lacking distal part of left cornual process from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view and partial mould showing posterior part of headshield in ventral view. **B**. Same species, imprint of anterior part of headshield SMNH BP.19 from Horodnytsia S, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, specimen together with *Monomorphichnus*-like trace fossilsand in dorsal view. **C**. Same species, partial imprint of headshield SMNH BP.3 from Ustechko, left bank of Dzhuryn River, top of slope, upper part of Ustechko Member, dorsal view. **D**. Same species, imprint of right part of headshield SMNH BP.2 from the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member, dorsal view. **E**. *Mimetaspis concordis* Voichyshyn, 1994, complete imprint of headshield SMNH BP.983 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member, dorsal view. **F**. Same species, posterior margin of abdominal part of headshield SMNH BP.986 and left cornual process from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, ventral view.

so far. *Mimetaspis concordis* has different shape of the dorsal field, and comparatively larger and close placed orbits.

Localities and age. — Horodnytsia and Ustechko; late Lochkovian (Ustechko Stage and, possibly, lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Mimetaspis concordis Voichyshyn, 1994
(Figs 83E, F, 84A–E)

1994. *Mimetaspis concordis*; Voichyshyn 1994: pp. 20–23, text-figs 1–3, pl. 1, figs 1, 2, 4; pl. 2, figs 1, 2.

1994. *Mimetaspis* aff. *concordis* sp. n.; Voichyshyn 1994: p. 22, text-fig. 4, pl. 1, fig. 3.

2004. *Mimetaspis concordis*; Afanassieva 2004: p. 245, text-fig. 21, pl. 10, fig. 1.

2006. *Mimetaspis concordis*; Voichyshyn 2006c: pp. 29–30, pl. 2, figs 3–5.

2010. *Mimetaspis concordis*; Voichyshyn 2010: pl. 3, fig. 4.

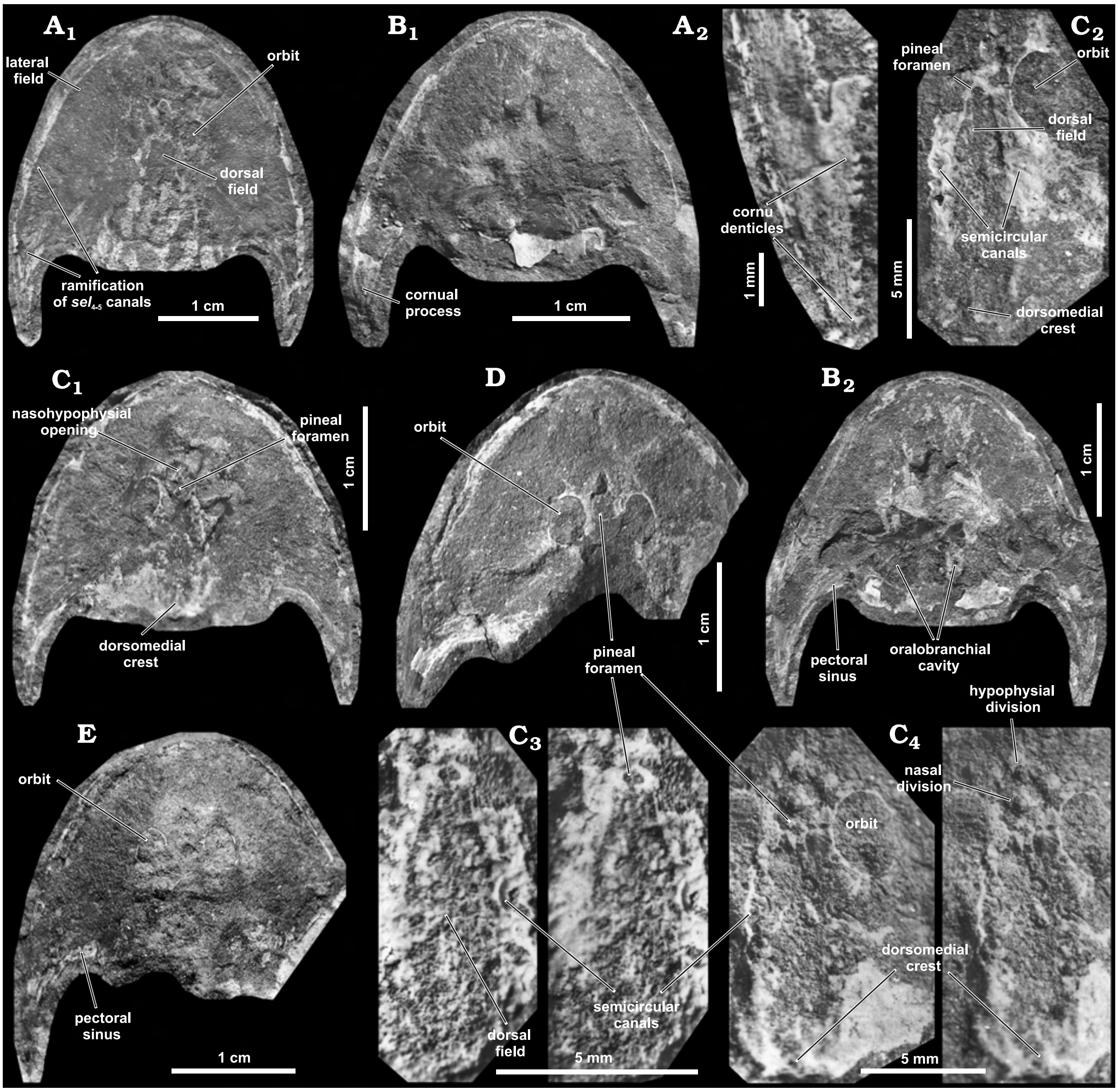


Fig. 84. Cephalaspidid *Mimetaspis concordis* Voichyshyn, 1994 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation. **A**. Imprint of headshield SMNH BP.980, dorsal view and distal part of partial right cornual process in ventral view. **B**. Partial mould/imprint of headshield SMNH BP.981, palimpsest of both dorsal and ventral views. **C**. Imprint of the holotype headshield SMNH BP.982, dorsal view, enlarged central part, otico-occipital and pineal foramen zone, and another portion of central part of headshield. **D**. Partial mould of headshield SMNH BP.985 lacking right cornual process, and of abdominal division, dorsal view. **E**. Partial mould of headshield SMNH BP.984 lacking right cornual process, dorsal view.

Type specimen: Holotype SMNH BP.982, headshield; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Partial moulds or imprints of shields SMNH BP.980, 981, 983, 984, 985, 986, 987, 988, and 1325.

Diagnosis. — Medium sized *Mimetaspis* species with relatively large orbits and very short, relatively wide ledge on the posterior (rougly straight) margin of the shied.

Description. — Shield is not wide (L 20 mm, S 27–28 mm; L/S 0.7), somewhat narrowed in its anterior part, with maximum width at about the middle of the cornual processes. The prepineal part is almost equal to postpineal one. Rostral margin has sometimes a corner. The cornual processes are flattened, not very long, comparatively narrow, rapidly narrow towards their ends, and have caudal orientation. Their outer margin, in distal parts, is parallel to the body axis or very slightly bent medially. Inner margin is slightly concave. It housed set of denticles of elongate-triangular shape (4 per 1 mm), with tips bent antero-medially (Fig. 84A$_2$). The abdominal division of the shield is not wide (Si/A 1.8) and very short. Pectoral sinuses are small. The dorsomedial crest is hardly visible (Fig. 84C$_1$). Its length is 2.7 mm, height 0.4 mm. The nasohypophyseal depression is shallow, triangular in shape, and situated at 7.0–7.9 mm from the rostral margin of the shield. The orbits are oval, of medium size (Ol/A 0.5; Os/A 0.3), and do not approach each other closely (Omin/A 0.4). Their longitudinal axes cross usually at the middle of distance between rostral margin of the shield and the nasohypophyseal depression. The dorsal field is long (L/Ld 2.7; Ld/A 0.9) and narrow (Ld/Sd 3), narrowed anteriorly, and probably rounded posteriorly. The lateral fields are long (G/A 3) and comparatively narrow (Sl/A 0.3), sharp at their ends, and extend on the dorsal surface of the cornual processes up to 2/3 of the latter's length. Surface of the dermal skeleton was probably smooth. Traces of sel canals as well as of vertical semicircular canals of the labyrinth cavity are preserved on the dorsal side of the mould of the holotype.

Comparison. — *Mimetaspis hoeli* is of larger size than *M. concordis* and differs also in having a prominent posteromedial ledge on the posterior margin of the headshield (Wängsjö 1952: fig. 35). *Mimetaspis exilis* is smaller, with different proportions of the shield and lateral margins less convex, the cornual processes shorter and lateral fields longer than dorsal field, larger orbits, and narrower abdominal part of the shield. *Mimetaspis retusa* has different shape of both the shield and the dorsal field, shorter lateral fields, thicker cornual processes, and considerably smaller orbits.

Localities and age. — Ustechko and Horodnytsia; from late Lochkovian to early Pragian (from Ustechko Stage to the lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Family **Parameteoraspididae** Afanassieva, 1991

Genus *Parameteoraspis* (Janvier, 1981)

1952. *Cephalaspis*; Wängsjö 1952: pp. 243–252 (pars).
1981. *Meteoraspis*; Janvier 1981: p. 119.
1985. *Meteoraspis*; Janvier 1985b: p. 200.
1991. *Parameteoraspis*; Afanassieva 1991: pp. 79–80.
2004. *Parameteoraspis*; Afanassieva 2004: p. 246.

Type species: *Cephalaspis gigas* Wängsjö, 1952; Early Devonian of Spitsbergen.

Diagnosis. — Small to very large sized osteostracans (L 40–200 mm). Shield is wide and relatively short. Its anterior margin, as a rule, is widely rounded. The cornual processes are long and proximally wide. The abdominal division of the shield is comparatively narrow. The pineal plate is lacking. The lateral fields are long, almost reaching the caudal ends of the cornual processes.

Species included. — Besides the type species: *Parameteoraspis oblonga* (Stensiö, 1927), *P. lata* (Stensiö, 1927), *P. laticornis* (Stensiö, 1927), *P. lanternaria* (Wängsjö, 1952), *P. moythomasi* (Wängsjö, 1952), *P. semicircularis* (Wängsjö, 1952), *P. menoides* (Wängsjö, 1952), *P. caroli* (Wängsjö, 1952), *P. oberon* (Janvier, 1985b), all from the Early Devonian (Dittonian) of Spitsbergen; *P. dobrovlensis* Afanassieva, 1991, Early Devonian (Ivanie Stage) of Podolia.

Occurrence. — Early Devonian of Spitsbergen and Podolia (Ukraine).

Parameteoraspis dobrovlensis Afanassieva, 1991

1991. *Parameteoraspis dobrovlensis*; Afanassieva 1991: pp. 80–82, text-fig. 12a, pl. 15, figs 2, 3.
2004. *Parameteoraspis dobrovlensis*; Afanassieva 2004: pp. 246–247, text-fig. 23, pl. 10, figs 4, 5.

Type specimen: Holotype (by monotypy) LIG 5-538, part of the headshield mould with fragments of the dermal skeleton; vicinity of Dobrivliany, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Remarks. — This is the geologically one of the oldest species among the Podolian osteostracans. It is also the smallest in size, with shield length of about 45 mm and width about 80 mm, among the species of the genus.

Localities and age. — Dobrivliany; Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Family **Pattenaspididae** Stensiö, 1958

Genus *Pattenaspis* Stensiö, 1958

1927. *Cephalaspis*; Stensiö 1927: p. 246 (pars).
1932. *Cephalaspis*; Stensiö 1932: pp. 87–88 (pars).
1952. *Cephalaspis*; Wängsjö 1952: pp. 243–244 (pars).
1958. *Pattenaspis*; Stensiö 1958: p. 216.
1986. *Pattenaspis*; Friman and Janvier 1986: p. 106.
2004. *Pattenaspis*; Afanassieva 2004: p. 245.

Type species: *Cephalaspis whitei* Stensiö, 1932; Early Devonian of Great Britain.

Diagnosis. — Small to medium sized cephalaspidids (L 20–70 mm). Anterior margin of the shield is usually narrowed and forms a rostral corner or lobe. The cornual processes are elongated, comparatively thin, more or less bent towards the body axis beginning from their middle or on their ends. The inner margin of the cornual processes bears a set of denticles. The abdominal part of the shield is short. The dorsomedial crest is rather high. Orbits are comparatively large. The pineal plate is well developed. The dorsal field is lengthened. The lateral fields are narrow, reaching backwards no far than the middle part of the cornual processes. The shield surface is smooth or covered by very fine tubercles.

Species included. — Besides the type species: *Pattenaspis deltoides* (Wängsjö, 1952), *P. divaricata* (Wängsjö, 1952), *P. eukeraspidoides* (Stensiö, 1927), *P. foyini* (Wängsjö, 1952), *P. eurhynchus* (Wängsjö, 1952), *P. oreas* (Wängsjö, 1952), *P. heintzi* (Stensiö, 1927), *P. pygmaea* (Wängsjö, 1952), all from the Early Devonian of Spitsbergen; *P. woschmidti* (Friman, 1986) and *P. bardenheueri* (Friman, 1986), both from the Early Devonian of Rhineland, Germany; *P. rogalai* (Balabai, 1962), Early Devonian of Podolia.

Remarks. — The genus unites several groups of species. Some similarity in shape and proportions of the shield, its abdominal part, cornual processes, dorsal and lateral fields characterise *P. deltoides* and *P. divaricata*. The shape of cornual processes suggests that they are related with *P. woschmidti* and *P. bardenheueri*. One more group, based on similar shape of the shield, its abdominal part, dorsal field and general size is formed by *P. oreas*, *P. heintzi* and possibly *P. pygmaea*.

Occurrence. — Early Devonian of Great Britain, Spitsbergen, Germany, and Podolia (Ukraine).

Pattenaspis rogalai (Balabai, 1962)
(Fig. 85A–G)

1962. *Cephalaspis rogalai*; Balabai 1962: p. 3, text-fig. 1.
1985. “*Cephalaspis*” *rogalai*; Janvier 1985a: p. 329.
1988. “*Cephalaspis*” *dniestrensis*; Janvier 1988: pp. 357–358, pl. 15, figs 1–3.
1991. *Pattenaspis rogalai*; Afanassieva and Voichyshyn 1991: pp. 67–69, text-figs 1, 2, pl. 9, figs 1, 2.
2006. *Pattenaspis rogalai*; Voichyshyn 2006c: pp. 30–31, pl. 2, fig. 1A, B.

Type specimen: Lectotype SMNH BP.990, fragmentary mould of headshield in dorsal view; Horodnytsia W I, Horodenka rayon, Ivano-Frankivs’k oblast’ (Podolia).

Referred material. — Headshields, their moulds and parts SMNH BP.21, 22, 24, 33, 383/2, 901/2, 902/4, 1019, 1033, 1059, 1167, 1168, 1277, 1278, 1286, 1287, 1291, 1309, 1316, 1320, 1321, 1322, 1323, 1324, 1326, 1359, 1407, 1468/3, and 1472/2.

Diagnosis. — Large *Pattenaspis* species with relatively short cornual processes.

Description. — Shield is moderately wide (L 50–60 mm, S ~60 mm), convex with the maximum width in the middle of the cornual processes. Shield height, up to a level of the dorsal field, equals 8–17 mm. Its prepineal part is of medium in length, and postpineal one is short (B/A ~C/A 1.7–2.0). Rostral part of the shield is narrowed and forms a corner anteriorly. Lateral margins are convex. The cornual processes are flattened, relatively short and wide in its proximal part, and of latero-caudal inclination. Their distal parts are slightly bent to the axis of a body. Denticles occur on the inner margin of the cornual processes (Fig. 85B). The abdominal division of the shield is relatively wide (~25–32 mm, Si/A 2–2.4) and short. The dorsomedial crest is prominent and inclined backwards (Fig. 85D_2, G). Height of the crest from the level of the dorsal field equals 10–14 mm. The nasohypophyseal depression is triangular and large (Q 14–18.5 mm). The nasohypophyseal opening is long, with approximately equal nasal and hypophyseal divisions. The orbits are large and oval (Ol 5.6 mm, Os 4 mm, Omin 5 mm). The pineal plate is narrow and clearly outlined. The dorsal field is

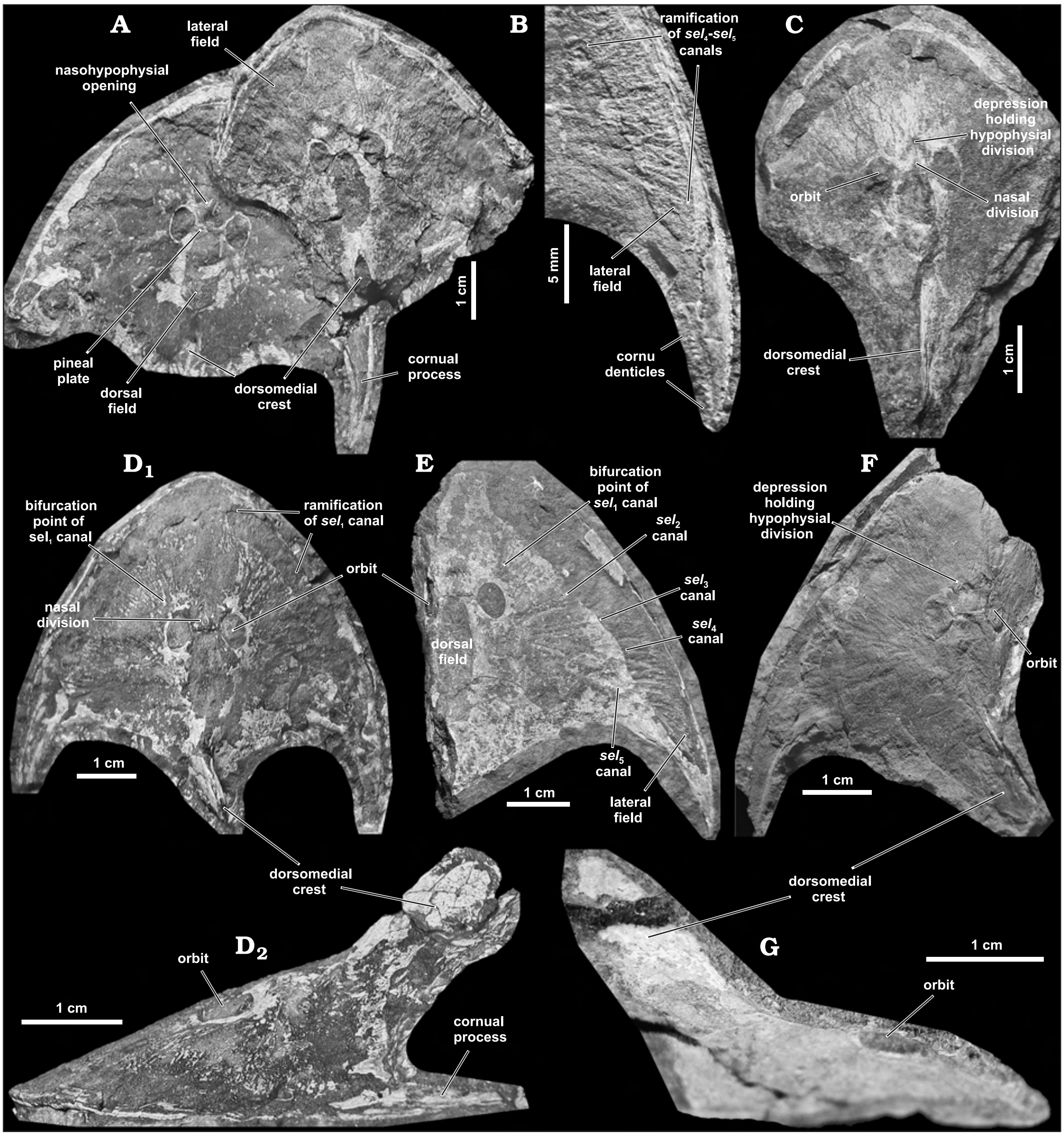


Fig. 85. Pattenaspidid *Pattenaspis rogalai* (Balabai, 1962) from various localities of the Dniester Formation in Podolia. **A**. Partial mould and imprint of headshield SMNH BP.901/7 and 901/8 (see also Fig. 101E) from Nagiriany, slab from talus at SE slope of Dzhuryn River, Ustechko Member or lower part of Khmeleva Member, dorsal views. **B**. Cornual process with adjoining headshield part SMNH BP.1261 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view. **C**. Lectotype partial headshield SMNH BP.990 lacking cornual processes from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorsal view. **D**. Partial headshield SMNH BP.902/1 (see also Fig. 101E) from Nagiriany, slab from talus at SE slope of Dzhuryn River meander, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal and lateral (left side) views. **E**. Complete right part of headshield SMNH BP.383/2 from Ustechko, left bank of Dniester River, uppermost part of Ustechko Member, dorsal view. **F**. Mould of partial (mainly left part) headshield SMNH BP.1278 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member of the Dniester Formation, dorsal view. **G**. Imprint of headshield SMNH BP.1277 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, lateral (right side) view.

long (~12 mm) and narrow (Sd on average 47 mm, Ld/Sd 2.4), and oval in shape. The lateral fields are long (~50 mm), moderately wide (~5 mm), with rounded anterior and posterior ends.

Comparison. — *Pattenaspis rogalai* is of greater size than majority of the *Pattenaspis* species. Besides, *P. whitei* has a different shape of the abdominal division of the shield. *Pattenaspis deltoides*, *P. divaricata*, *P.*

eukeraspidoides, and *P. woschmidti* have considerably longer cornual processes, *P. foyini, P. eurhynchus*, and probably *P. bardencheueri* have no dorsomedial crest and *P. deltoides* has wider shield.

Localities and age. — Ostrovets', Rizdviany, Ustechko, Nagiriany, Khmeleva, and Horodnytsia; Lochkovian to Pragian (from the Ivanie Stage of the Tyver formation to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Order **Benneviaspidiformes** Afanassieva, 1991

Suborder **Benneviaspidoidei** Afanassieva, 1991

Family **Benneviaspididae** Denison, 1951

Genus *Benneviaspis* Stensiö, 1927

1927. *Benneviaspis*; Stensiö 1927: p. 289 (pars).
1932. *Benneviaspis*; Stensiö 1932: pp. 152–153 (pars).
1952. *Benneviaspis*; Wängsjö 1952: pp. 446–447 (pars).
1985. *Benneviaspis*; Janvier 1985b: p. 158 (pars).
1989. *Benneviaspis*; Afanassieva 1989: pp. 52–53.
1991. *Benneviaspis*; Afanassieva 1991: pp. 83–84.
2004. *Benneviaspis*; Afanassieva 2004: pp. 247–248.

Type species: *Benneviaspis holtedahli* Stensiö, 1927; Early Devonian of Spitsbergen.

Diagnosis. — Small to large sized osteostracans. The shield is flattened, wide and short. Rostral margin of the shield is straightened or very widely rounded. The cornual processes are comparatively short, and latero-caudally directed. The abdominal division of the shield is wide, moderately lengthened and lacking any dorsomedial crest or spine. The prepineal part of the shield is longer than the postpineal one. The orbits are small and round. The dorsal field is more or less rounded in shape, with a trilobate posterior margin. The lateral fields merge under angle at the base of the cornual processes and then they follow the lateral margin of the abdominal division of the shield. Surface of the dermal skeleton is without ornamentation.

Species included. — Besides the type species, *Benneviaspis maxima* Wängsjö, 1952, *B. loevgreeni* Wängsjö, 1952, *B. grandis* Wängsjö, 1952, all from the Early Devonian of Spitsbergen, *B. whitei* Belles-Isles *et* Janvier, 1984, *B. zychi* Afanassieva, 1989, and *B. talimaae* Afanassieva, 1990 from the Early Devonian of Podolia, and *B. urvantsevi* Mark-Kurik *et* Janvier, 1995 from the Early Devonian (Pragian) of Severnaya Zemlya (Russia).

Occurrence. — Early Devonian of Spitsbergen, Podolia (Ukraine), and Severnaya Zemlya (Russia).

Benneviaspis whitei Belles-Isles *et* Janvier, 1984

(Fig. 86A)

1984. *Benneviaspis whitei*; Belles-Isles and Janvier 1984: pp. 199–200, text-fig. 1, pl. 27, fig. 1.
1991. *Benneviaspis whitei*; Afanassieva 1991: pp. 86–87.
2004. *Benneviaspis whitei*; Afanassieva 2004: pp. 248–249, text-fig. 24.

Type specimen: Holotype NHRM C2, mould of headshield in dorsal view; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Almost complete mould and imprint of the shield SMNH BP.107.

Diagnosis. — Relatively small *Benneviaspis* species with straightened anterior margin of the shield.

Description. — The shield is comparatively very wide and short (L 35 mm, S 83 mm), and flattened. Its anterior margin forms two symmetric smoothed corners. Rostral margin between these corners is very little convex, while lateral margins of the shield are straightened. Maximum width of the shield is at the tips of cornual processes. The cornual processes are narrow and short, directed latero-caudally. Their outer and inner margins are straightened, and have no denticles. The abdominal division of the shield is very wide and comparatively short. Its posterior margin forms a rounded and smooth ledge between two notches, sinusoidal in shape. The holotype has this ledge pointed out, as it is usual for the benneviaspidids. The pectoral sinuses are not deep. Their axes are parallel to the axis of the shield and the tips of the sinuses are rounded. The nasohypophyseal opening is elongated and located on a significant distance from rostral margin of the shield. The orbits are almost round, relatively small, moderately distant one from another. The pineal plate is not present. Length of the dorsal field equals its width approximately. The lateral fields on material from SMNH collection are not preserved.

Comparison. — This species differs from other *Benneviaspis* species by more straightened anterior margin of the shield. Besides, *B. holtedahli* has wider cornual processes and considerably less developed posterior ledge of the lateral fields. *Benneviaspi maxima* has convex lateral margins of the shield, smaller and more widely disposed orbits, as well as considerably greater size. *Benneviaspis loevgreeni* has convex lateral margins of the shield, greater orbits and dorsal field, *B. grandis* has narrower abdominal division of the shield, considerably widely disposed orbits, different shape of the dorsal field, considerably greater size, while *B. urvantsevi* has headshield of considerably greater size and as much smaller size of orbits. *Benneviaspis talimaae* has a slight lobe on the anterior margin of the shield and is of smaller size and *B. zychi* has as well different contour of the lateral margins of the shield, relatively smaller orbits and larger size.

Localities and age. — Ustechko; early Pragian (lower part of the Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Benneviaspis zychi Afanassieva, 1989

1989. *Benneviaspis zychi*; Afanassieva 1989: pp. 53–54, text-fig. 1a, pl. 4, fig. 1.

1991. *Benneviaspis zychi*; Afanassieva 1991: pp. 85–86, text-fig. 13a, pl. 16.

2004. *Benneviaspis zychi*; Afanassieva 2004: p. 249, text-fig. 25, pl. 11, figs 1–3.

Type specimen: Holotype PIN 3592/88a–b, partial mould and complete imprint of headshield; collected together with several other specimens between Kydaniv and Sapova, on the right bank of the Strypa River, boundary between Buchach and Terebovlia rayons, Ternopil’ oblast’ (Podolia).

Remarks. — This is the largest *Benneviaspis* species in the Podolian fauna, with headshield length of 70 mm and width of about 125 mm (Afanassieva 1989, 1991). It has a relatively large dorsal field and well developed lateral fields. Their lateral ledge enters the proximal part of the cornual processes, and postero-medial part reaches almost the top of the postero-lateral corners of the shield. The shield anterior and lateral margins form a common continuous smooth semicircular outline between the tips of the cornual processes, which are of latero-caudal direction.

Localities and age. — Kydaniv and Sapova; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Benneviaspis talimaae Afanassieva, 1990

1990. *Benneviaspis talimaae*; Afanassieva 1990: pp. 128–131, text-fig. 1.

1991. *Benneviaspis talimaae*; Afanassieva 1991: pp. 87–89, text-fig. 14, pl. 17, fig. 1.

2004. *Benneviaspis talimaae*; Afanassieva 2004: pp. 249–250, text-fig. 26, pl. 11, fig. 4.

Type specimen: Holotype LIG 5-711, anterior part of headshield mould with distal part of left cornual process; quarries SW of Horodnytsia, Horodenka rayon, Ivano-Frankivs’k oblast’ (Podolia).

Remarks. — The headshield of the species shows a pineal furrow, anterolateral angulations and a slight rostral lobe (Afanassieva 1991), which are characteristic of primitive benneviaspidids (Janvier, unpublished manuscript). The dorsal field is not preserved in the single known specimen of the species. In having the shield of about 25 mm long and about 55 mm wide, the species is the smallest among the Podolian Benneviaspididae.

Localities and age. — Horodnytsia; probably late Lochkovian (Ustechko Stage or lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Genus *Citharaspis* Afanassieva, 1989

1984. *Benneviaspis*; Belles-Isles and Janvier 1984: p. 197 (pars).

1989. *Citharaspis*; Afanassieva 1989: p. 54.

1991. *Citharaspis*; Afanassieva 1991: p. 89.

2004. *Citharaspis*; Afanassieva 2004: p. 250.

Type species: *Benneviaspis polonica* Belles-Isles, Janvier, 1984; Early Devoniam (Dniester Formation) of Podolia.

Diagnosis. — Small sized osteostracans (L 40–50 mm). The shield is flattened, with widely rounded anterior margin. Width of the shield exceeds its length a little. There are obtuse lateral triangular ledges instead

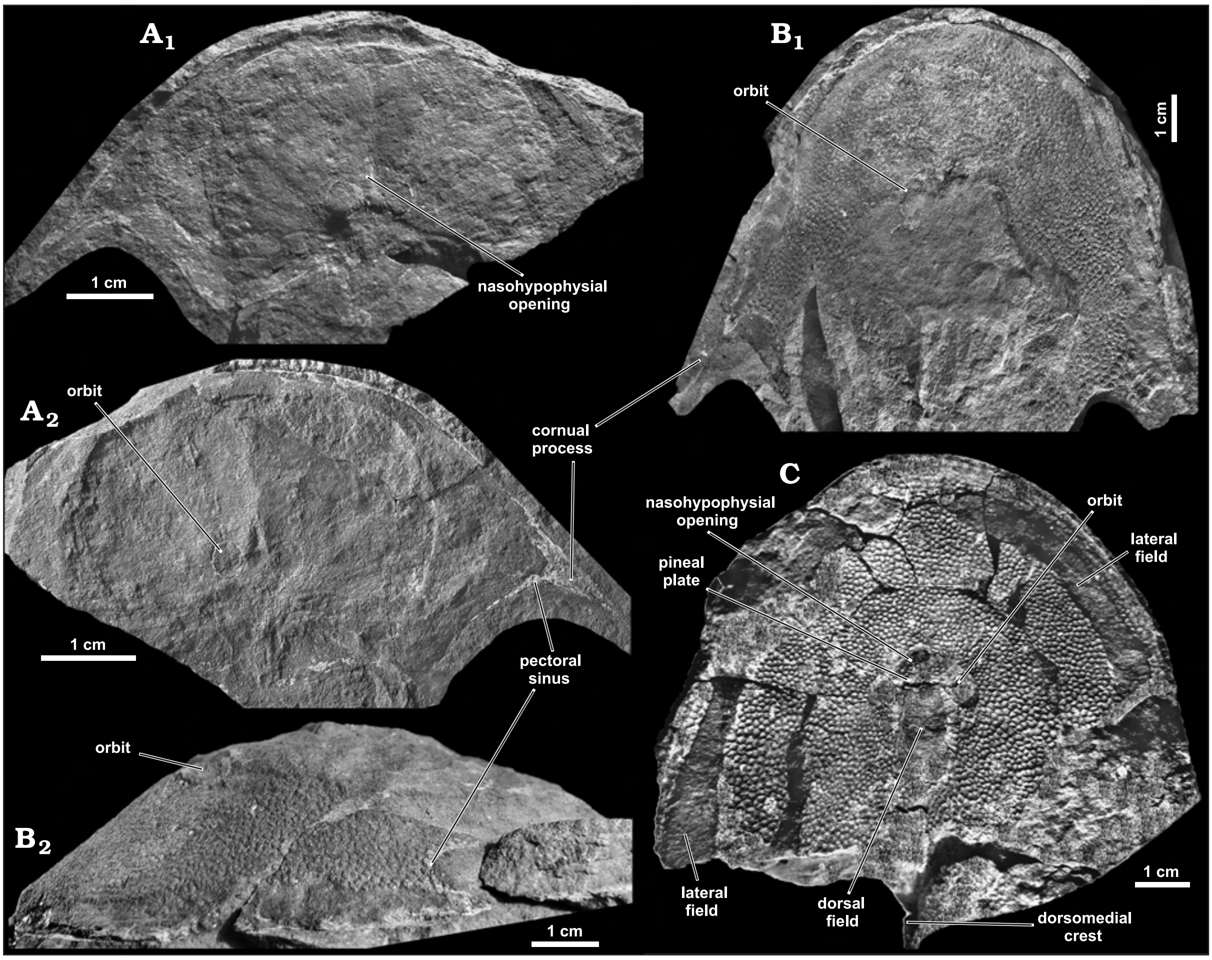


Fig. 86. Benneviaspidid *Benneviaspis* and scolenaspidid *Ukrainaspis* from various localities of the Dniester Formation in Podolia. **A**. *Benneviaspis whitei* Belles-Isles *et* Janvier, 1984, partial mould of headshield SMNH BP.107 lacking right cornual process from Ustechko, lower part of Khmeleva Member of the Dniester Formation, part and counterpart. **B**. *Ukrainaspis kozlowskii* (Zych, 1937), partial headshield SMNH BP.1222 from the Horodnytsia quarry talus, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal and lateral (left side) view. **C**. Same species, imprint of headshield GMLSU 585 lacking cornual processes probably from Ustechko, dorsal view.

of cornual processes. The prepineal part of the shield is longer than the postpineal one. Shape of the abdominal division of the shield, proportions of nasohypophyseal and orbito-pineal regions, as well as shape and relative size of the dorsal field are probably the same as in *Benneviaspis*. The lateral fields have posteromedial ledges. The surface of the skeleton lacks ornamentation.

Species included. — Besides the type species, *C. junia* Afanassieva, 1989, Early Devonian of Podolia.

Remarks. — The broad dorsal field with trilobate posterior margin is characteristic of the genus *Benneviaspis* (Janvier 1985a). This is why the genus *Citharaspis* was not accepted by Mark-Kurik and Janvier (1995; also Sansom 2009a), although its lineage was recognised as "the sister-taxon of *Benneviaspis*". It represents a grade rather than clade (Envall 2008) different from *Benneviaspis* in lacking cornual processes, and, possibly, in having a rather narrower abdominal division of the shield (Afanassieva 1991).

Occurrence. — Early Devonian of Podolia (Ukraine).

Citharaspis polonica (Belles-Isles *et* Janvier, 1984)

1984. *Benneviaspis polonica*; Belles-Isles and Janvier 1984: pp. 200–202, fig. 2, pl. 27, fig. 1.

1991. *Citharaspis polonica*; Afanassieva 1991: pp. 89–90.

2004. *Citharaspis polonica*; Afanassieva 2004: p. 251, text-fig. 28.

Type specimen: Holotype NHRM C3a, mould of headshield in dorsal view; Buchach, Buchach rayon, Ternopil' oblast' (Podolia).

Remarks. — The shape of the dorsal field remains unknown but its was reconstructed based on distal bifurcations of the sel canals (Belles-Isles and Janvier 1984).

Localities and age. — Buchach; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Citharaspis junia Afanassieva, 1989

1989. *Citharaspis junia*; Afanassieva 1989: p. 55, text-fig. 1a, pl. 4, fig. 2.
1991. *Citharaspis junia*; Afanassieva 1991: pp. 90–91, text-fig. 13b, pl. 17, figs 2, 3.
2004. *Citharaspis junia*; Afanassieva 2004: p. 251, text-fig. 29, pl. 12, fig. 1.

Type specimen: Holotype PIN 3592/93a–b, mould and imprint of headshield; together with the paratype probably from the quarry between Kydaniv and Sapova, on the right bank of the Strypa River (Afanassieva 2004), boundary between Buchach and Terebovlia rayons, Ternopil' oblast' (Podolia).

Remarks. — The species differs from *C. polonica* mostly by longer prepineal part of the shield (B/A about 2 against about 1.6).

Localities and age. — Kydaniv and Sapova; Pragian (Strypa Stage of the Dniester Formation) of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Suborder **Scolenaspidoidei** Afanassieva, 1991

Family **Scolenaspididae** Afanassieva, 1991

Emended diagnosis. — Medium sized osteostracans (L ranges from 50 to 120 mm). The headshield is, as a rule, low, but may also be dome-shaped and massive. The abdominal part of the shield has a small median dorsal crest, or it may develop a dorsal spine. The cornual processes are of various length. The hypophysial division of the nasohypophysial opening is approximately equal to, or slightly larger than, the nasal division. The pineal plate is usually well developed. The median dorsal field is rather narrow. The lateral fields are narrow, and may have only a slight widening in their posterior parts, reaching backwards not further than to the proximal part of the dorsal surface of the cornual processes. The ornamentation consists of either tiny, densely set tubercles or of small tesserae covered with minute tubercles.

Included genera. — Besides the type genus, *Stensiopelta* Denison, 1951, *Machairaspis* Janvier, 1985, *Zychaspis* Janvier, 1985, and *Ukrainaspis* Sansom, 2009, possibly, "*Cephalaspis*" *verruculosa* Wängsjö, 1952, and "*C.*" *aarhusi* Wängsjö, 1952, the species which probably represent new genera.

Remarks. — The genera *Ukrainaspis* and *Machairaspis* differ from other scolenaspidids in several aspects, both having a dome-shaped headshield with a prominent dorsomedial crest (*Ukrainaspis*) or extremely developed dorsomedial spine (*Machairaspis*). This contrasts to scolenaspidians with low (*Stensiopelta*), sometimes almost flattened headshields with dorsomedial crest that is hardly visible (*Zychaspis*). But at present I follow the understanding of the family by Afanassieva (1991, 2004).

Genus *Ukrainaspis* Sansom, 2009

1937. *Cephalaspis*; Zych 1937: pp. 62–94.
1985. "*Cephalaspis*"; Janvier 1985b: p. 331.
1991. *Heraspis*; Afanassieva 1991: pp. 92–93.
2004. *Heraspis*; Afanassieva 2004: pp. 254–255.
2009. *Ukrainaspis*; Sansom 2009a: p. 111.

Type species: *Cephalaspis kozlowskii* Zych, 1937; Early Devonian (upper part of the Tyver formation to lower part of the Dniester Formation) of Podolia.

Diagnosis. — Rather large-sized scolenaspidians (L ~100 mm). Shield is convex, rounded anteriorly, with insignificant curvature of lateral margins. Width of the shield exceeds its length. The prepineal part of the shield is a little shorter than the postpineal one. The cornual processes are not long, narrow. The abdominal division of the shield is comparatively wide, and has appreciable dorsomedial crest. The nasohypophyseal opening is key-hole in shape. The pineal plate is developed. The orbits are small. The dorsal field is elongated. Lateral fields are narrow enough, long, pulled together anteriorly, slightly expanded at the anterior ends and more appreciably at posterior ones. Surface of the shield is covered with small, convex tubercles.

Species included. — Only the type species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Ukrainaspis kozlowskii (Zych, 1937)
(Figs 37E, 36G, 86B, C)

1937. *Cephalaspis kozlowskii*; Zych 1937: pp. 62–94, pls. 1–4.
1985. *Cephalaspis kozlowskii*; Janvier 1985a: p. 133.
1985. "*Cephalaspis*" *kozlowskii*; Janvier 1985b: p. 331.
1991. *Heraspis kozlowskii*; Afanassieva 1991: pp. 93–96, text-fig. 15, pls 18, 19.
2004. *Heraspis kozlowskii*; Afanassieva 2004: p. 255, text-fig. 34, pl. 13.

Type specimen: Holotype NHRM C.131, headshield; Zalishchyky, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.17, 62, 85, 95, 1222, and GMLSU 585.

Diagnosis. — Large-sized scolenaspidid species with rounded anterior margin of the shield and dermal skeleton ornamentation consisting of densely set almost equal in size tubercles of 1–1.5 mm in diameter.

Description. — The shield is widest approximately at the ends of cornual processes, convex (height up to a level of orbits equals 12–23 mm), with a wide rostral margin. The abdominal division of the shield is wide (Si/S 0.5). Length of the dorsomedial crest is not less than 23 mm, height equals 11 mm. The hypophyseal division of the nasohypophyseal opening is situated in a deep depression of triangular shape, and nasal one on an elevation. Both divisions are drop shaped, and of same size. The pineal plate is wide. The orbits are relatively small, oval, widely disposed with distance between them 2–3 times more than their width, and surrounded by a distinct circumorbital thickening. The dorsal field is elongated, moderately wide, and rounded posteriorly. The lateral fields are long (~80 mm) and narrow, with insignificant enlargement on the anteriorly approaching ends (distance between them almost equals or slightly exceeds average width of the field) and significant at the posterior ends, which approach bases of the cornual processes. Surface of the shield is covered with convex tubercles, almost equal in size, low. Their diameter is from ~1 mm on the preorbital part of the shield to 1.5 mm on the postorbital one (Figs 37E, 86C).

Localities and age. — Horodnytsia, Ustechko, Zalishchyky, Verbivtsi and Vorvulyntsi; Lochkovian to early Pragian (from Ivanie Stage of the Tyver formation to the boundary between the Ustechko and Khmeleva Stages of the Dniester Formation) of Podolia (Ukraine).

Genus *Zychaspis* Janvier, 1985

1985. *Zychaspis*; Janvier 1985b: pp. 315–316.
1991. *Zychaspis*; Afanassieva 1991: pp. 96–97.
2004. *Zychaspis*; Afanassieva 2004: p. 254.
2004. *Zychaspis*; Voichyshyn and Solodkyi 2004: pp. 172–173.
2006. *Zychaspis*; Voichyshyn 2006b: p. 16.

Type species: *Zychaspis siemiradzkii* Janvier, 1985; Early Devonian (lower part of the Dniester Formation) of Podolia.

Diagnosis. — Scolenaspidids of average to large size (L 60–80 mm). The width of the shield exceeds its length (L/S 0.6–0.8). The prepineal part of the shield is of equal length to the postpineal one, or somewhat longer (B/C 1.0–1.3). Anterior margin of the shield somewhat narrows and has a prominence (rostral lobe) variously developed. The cornual processes are rather long and narrow. The abdominal part of the shield is short and narrow, having very small and low dorsomedial crest. The hypophyseal division of the nasohypophyseal opening is almost equal, or somewhat larger than the nasal one. Orbits are relatively small (S/Os 21–22) and oval. Pineal plate is well developed. The dorsal field is narrow and elongated. It slightly narrows frontally. Lateral fields are rather narrow, narrowing in the first third and widening in their posterior part, reaching back not farther than to the middle of the cornual processes. The dermal skeleton is covered with tiny, almost equal in size, densely set tubercles.

Species included. — Besides the type species, *Z. granulata* Voichyshyn, 1998, *Z. concinna* Voichyshyn *et* Solodkyi, 2004, *Z. elegans* (Balabai, 1962), possibly *Zychaspis* sp. (Voichyshyn and Solodkyi 2004: fig. 4); all from the Early Devonian of Podolia.

Remarks. — Janvier (1985b, 1988) referred also *Cephalaspis bucovinensis* Văscăuţanu, 1931 to *Zychaspis*, indicating its similarity to the type species. Unfortunately, it was based on fragmentary specimen, illustrated only with photograph of the anterior part of the shield (Pauča 1941: pl. 1, fig. 5), with features resembling those of *Z. siemiradzkii*.

Occurence. — Early Devonian of Podolia (Ukraine).

Zychaspis siemiradzkii Janvier, 1985
(Figs 87C, 88A, 89A)

1985. *Zychaspis siemiradzkii*; Janvier 1985b: pp. 316–317, figs 5, 6.
1988. *Zychaspis bucovinensis*; Janvier 1988: p. 358.
1991. *Zychaspis siemiradzkii*; Afanassieva 1991: pp. 97–98, text-fig. 16a, pl. 20.
2004. *Zychaspis siemiradzkii*; Afanassieva 2004: p. 254, text-fig. 33, pl. 12, figs 2–4.
2008. *Zychaspis siemiradzkii*; Carlsson and Blom 2008: fig. 3Bh.

Type specimen: Holotype BM(NH) P.17714, mould of headshield; Khomiakivka E, Chortkiv rayon, Ternopil' oblast' (Podolia).

Referred material. — Specimens SMNH BP.38, 40, 105, 1221, 1452, and 1473.

Diagnosis. — Moderately large sized *Zychaspis* species with medially curved cornual processes.

Description. — The shield is relatively short (L ~80 mm, S 100 mm), widest at the middle of the cornual processes. On the anterior margin, it has more or less wide rostral lobe. The cornual processes are not wide, comparatively long, caudally directed, at the ends they are directed a little medially. Their outer margins are rather convex, the inner ones are concave and bear no denticles. The nasohypophyseal opening is elongated, the nasal division is of equal length to the hypophyseal one, or shorter. The orbits are relatively small and oval in shape. The interorbital distance is approximately 1.5 times more than the orbit width. The pineal plate is narrow. The dorsal field is long and narrow, in a forward third more narrowed. Its posterior end is pointed. The lateral fields are long and of equal width and, only in a posterior part, they are a little bit narrowed. Their anterior rounded ends reach the basis of the rostral lobe, and the posterior pointed ones reach up to part of length of the cornual processes.

Comparison. — The species differs from *Z. granulata* by contour of the rostral margin of the shield, shape of the pectoral sinuses, relatively longer and considerably narrower shield, and by shape of the lateral fields. *Zychaspis concinna* differs from *Z. siemiradzkii* by general shape of the shield (less bulging on lateral sides, considerably wider disposed cornual processes), by morphology of the central part of the shield (larger orbits, lengthened hypophyseal division of the nasohypophyseal opening, shape of the dorsal field), farther penetration of posterior ends of the lateral fields into cornual processes and probably greater mature size, possibly also by ratio between the pre- and postpineal portions of the shield. These species are similar in general size of the shield, shape and size of its abdominal part, pectoral sinuses, dorsomedial crest and cornual processes, and the type of the dermal skeleton ornamentation.

Zychaspis sp. 1 differs from *Z. siemiradzkii* by general shape of the shield, in particular, by presence of a large rostral lobe at its anterior margin, lower curvature of lateral sides of the shield, shorter and widely situated cornual processes, and deeper pectoral sinuses. It also differs probably by wider settled orbits and different ornamentation of the dermal skeleton.

Remarks. — Possibly, the type specimen of *Cephalaspis bucovinensis* Pauča, 1941 belongs to this species. If true, the Pauča (1941: pp. 30–31, pl. 1, fig. 5) species name has priority. However, since the holotype of *Zychaspis siemiradzkii* is more complete, I prefer to preserve the *Zychaspis siemiradzkii* name and consider *C. bucovinensis nomem obliteratum*.

Localities and age. — Ustechko, Horodnytsia, Buriakivka and Khomiakivka; Lochkovian (from Ivanie Stage of the Tyver formation to Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Zychaspis granulata Voichyshyn, 1998
(Figs 36C, 87A, 88C, D, 89D)

1998. *Zychaspis granulata*; Voichyshyn 1998: pp. 27–29, text-fig. 2, pl. 1.
2004. *Zychaspis granulata*; Voichyshyn and Solodkyi 2004: fig. 5D.
2006. *Zychaspis granulata*; Voichyshyn 2006c: p. 33, pl. 3, fig. 1A, B.
2008. *Zychaspis granulata*; Carlsson and Blom 2008: fig. 3Bf.

Type specimen: Holotype SMNH BP.49, imprints of the dorsal side and of a fragment of the ventral side of headshield, also a fragment of headshield; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

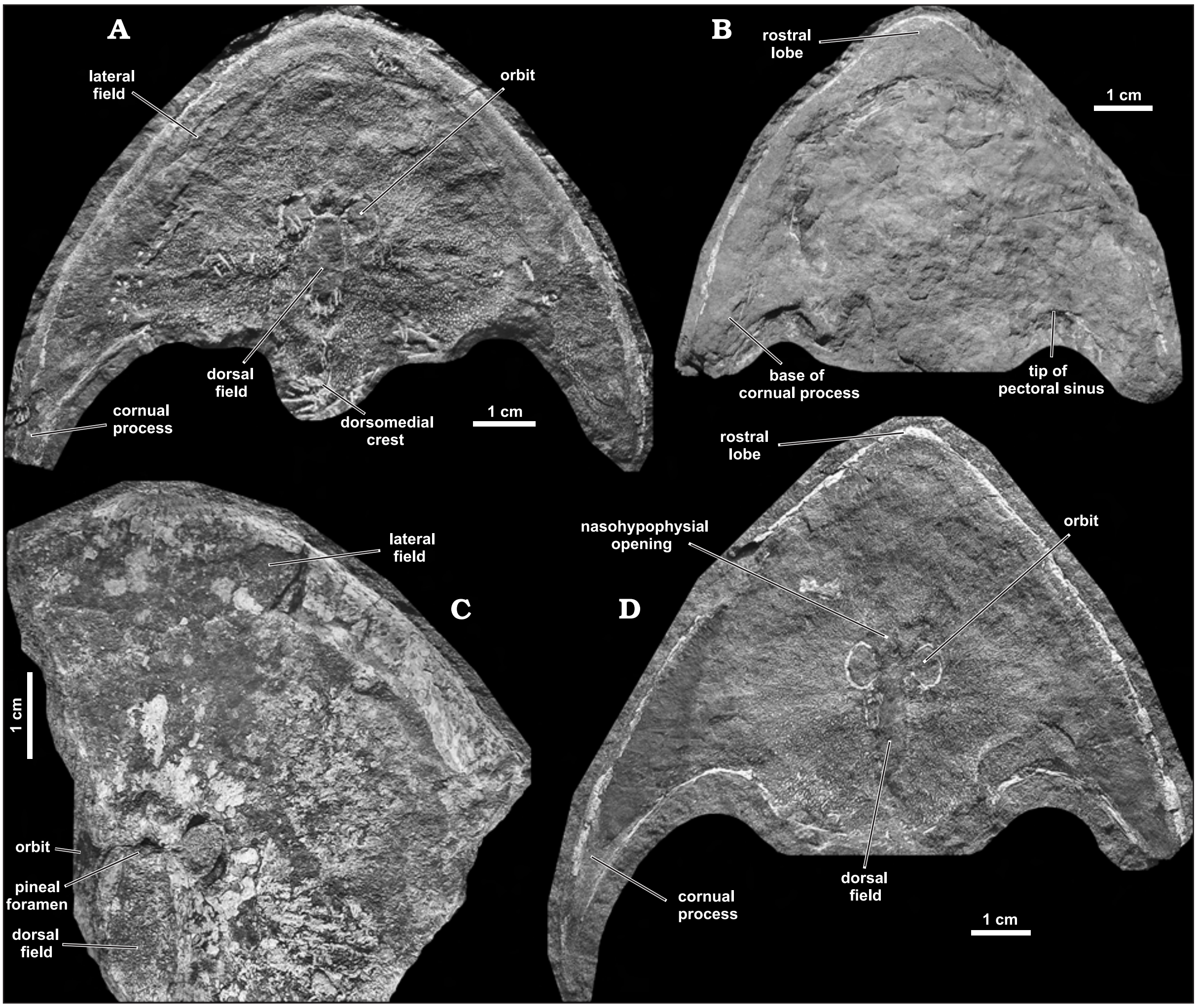


Fig. 87. Scolenaspidid *Zychaspis* from various localities of the Dniester Formation in Podolia. **A**. *Zychaspis granulata* Voichyshyn, 1998, imprint of the holotype headshield SMNH BP.49 (see also Figs 36C, 88C) without partial mould of abdominal division from Ustechko, lower part of Khmeleva Member, dorsal view. **B**. *Zychaspis elegans* (Balabai, 1962), the holotype partial margin of headshield SMNH BP.41 from Khmeleva, Khmeleva Member, ventral view. **C**. *Zychaspis siemiradzkii* Janvier, 1985, partial imprint of headshield SMNH BP.1221 from Buriakivka NE, probably Ustechko Member, dorsal view. **D**. *Zychaspis concinna* Voichyshyn *et* Solodkyi, 2004, the holotype almost complete imprint of headshield SMNH BP.966/1 (see also Fig. 36F) lacking distal part of left cornual process from the Horodnytsia quarry, Ustechko Member or lower part of Khmeleva Member, dorsal view.

Diagnosis. — Medium sized *Zychaspis* species with wide shield and wide rostral part of the anterior margin.

Referred material. — Besides the holotype, also impressions of partial crushed headshields SMNH BP.901/5 and 901/6 from Nagiriany.

Description. — The shield of the holotype is slightly convex, relatively short and wide (L/S 0.6; S/A 6). Its length is 60 mm and maximum width, which falls probably at the middle of cornual processes, is 100 mm. The prepineal part of the shield is somewhat larger than the postpineal one (B/A 2; C/A 1.8). Lateral margins of the shield are rather convex and the anterior one has a wide rostral zone. The cornual processes are wider in the proximal part, probably rather long, flattened, widely disposed, narrow gradually, from the middle of its length are directed caudally. Their inner margin has no denticles. The abdominal part of the shield is relatively narrow (Si/A 2.3) and short. The dorsomedial crest is low (~3 mm). The pectoral sinuses are shallow, with their tips displaced admedially. The nasohypophyseal opening is bean-shaped and located on significant distance from rostral margin of the shield (Q/A 1.7). The hypophyseal division is of approximately the same size as the nasal one. The orbits are oval, relatively small (length is 5.8 mm, width 4.7 mm, Ol/A 0.35, Os/A 0.28), and located one from another on distance equal to the length of orbits. They are surrounded by a thin

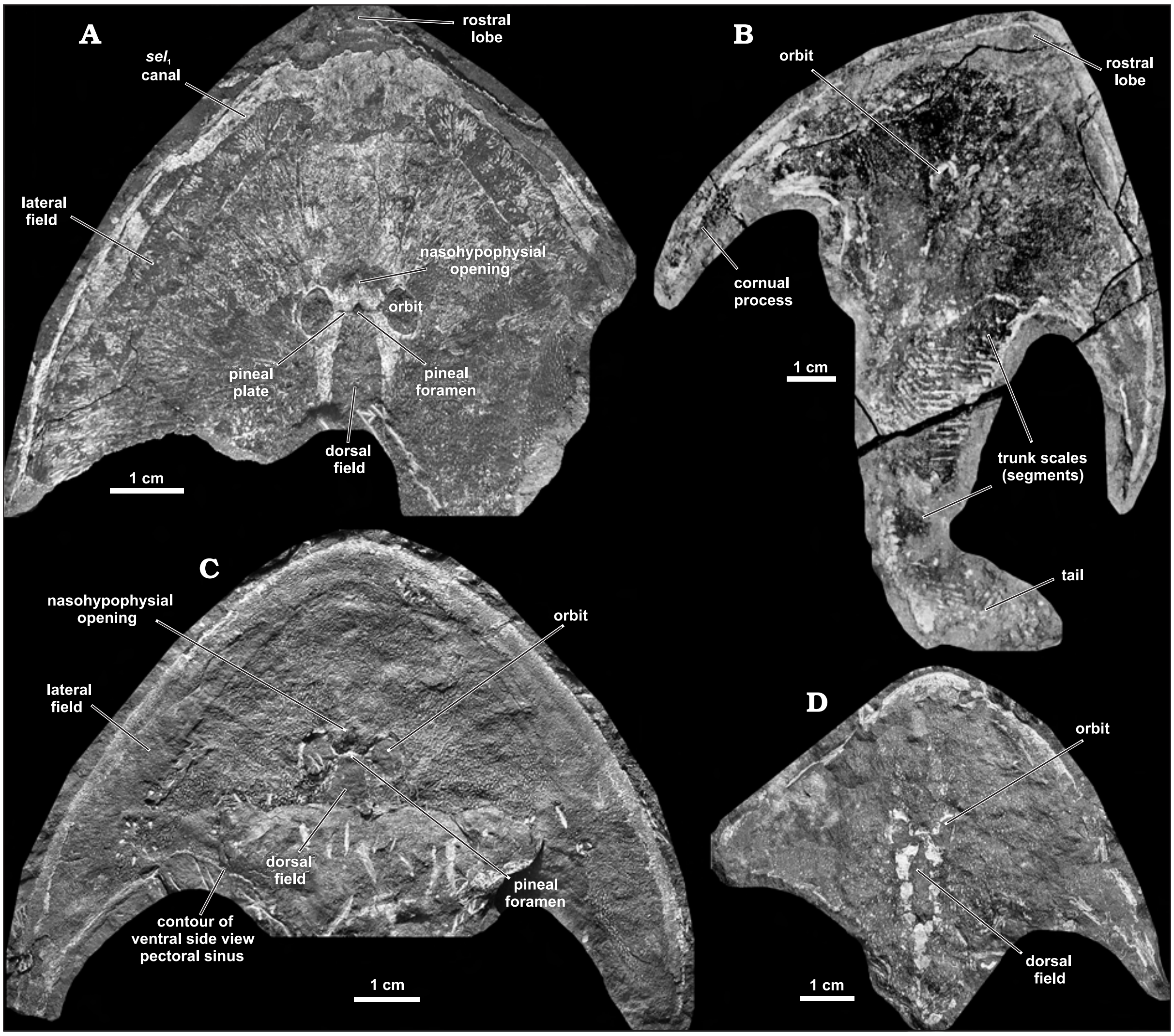


Fig. 88. Scolenaspidid *Zychaspis* from various localities of the Dniester Formation in Podolia. **A**. *Zychaspis siemiradzkii* Janvier, 1985, inside of partial headshield SMNH BP.105 from the Horodnytsia old quarry, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. *Zychaspis* sp. 1, articulated carapace (field photo) from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorsal view. **C**. *Zychaspis granulata* Voichyshyn, 1998, the holotype imprint of headshield SMNH BP.49 (see also Figs 36C, 87A) with partial mould of abdominal division from Ustechko, lower part of Khmeleva Member. **D**. *Zychaspis granulata* Voichyshyn, 1998, imprint of partial crushed headshield SMNH BP.901/5 (see also Fig. 101B, E) from Nagiriany, slab from talus at SE slope of Dzhuryn River, Ustechko Member or lower part of Khmeleva Member, dorsal view.

circumorbital thickening (Fig. 36C). The pineal plate is narrow, and merges the dorsal field. The pineal opening is crack-shaped at 1.7 mm in length that takes a little bit more than 1/3 of anterior margin of the dorsal field. The dorsal field is long and rather narrow (L/Ld 3.9, Sd/A 1.8), narrows a little anteriorly, and is rounded posteriorly. The lateral fields are long (~64 mm in length, G/A 3.9), rounded at their ends, reach proximal parts of the cornual processes. Their width gradually increases from the anterior end to the posterior one, from 5 mm to 8 mm. The dorsal surface of the shield is covered with tiny tubercles. The shape of the base of each tubercle changes from round (in particular on the abdominal division of the shield) to elongate-oval and simple elongate (on the cornual processes, at least on their medial margin). The diameter of the tubercles ranges from 0.3 mm to 0.6 mm. Their height equals their diameter. The largest of them are located on the abdominal division, especially in area adjoining the pectoral sinuses. The finest tubercles cover the prepineal part of the shield and the cornual processes. The distance between tubercles is less than their diameter. They are densly arranged.

Comparison. — *Zychaspis concinna* differs from *Z. granulata*, except for already mentioned features, by a greater length of the nasohypophyseal opening, wider pineal plate that is not continuous with the dorsal field, shape of the orbits and dorsal field. Both the species share general proportions of the shield, shape of the pectoral sinuses and ornamentation of the dermal skeleton, however, tubercles of *Z. concinna* are a little smaller in average. Possibly, ratio of the pre- and postpineal lengthes of the shield is also similar. *Zychaspis* sp. 1 differs in having large rostral lobe, perhaps narrower posterior part of the lateral fields, wide situated cornual processes and ornamentation of the dermal skeleton. Both these forms are similar by general proportions of the shield. Comparison with *Z. siemiradzkii* is given in its description.

Remarks. — This species differs from typical *Zychaspis* species by a number of significant features: contour of the anterior margin of the shield, wider cornual processes, considerably wider and shorter shield. Similar distinction could be considered sufficient for creation of a separate genus. However, common features are not less essential. They are low dorsal side of the shield, very small size of the dorsomedial crest, character of the ornamentation, extent of the lateral fields and dilation of their posterior ends, shape and relative sizes of the dorsal field, proportions in orbital and nasohypophyseal regions. This list testifies to relationship of compared forms. Although both the complete cornual processes and shape of the abdominal division of the shield of *Z. granulata* remain unknown, it seems reasonable to classify it in *Zychaspis*.

Localities and age. — Nagiriany, Ustechko; early Pragian (from upper part of Ustechko Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Zychaspis concinna Voichyshyn *et* Solodkyi, 2004

(Figs 36F, 87D, 89B)

2004. *Zychaspis concinna*; Voichyshyn and Solodkyi 2004: pp. 173–176, figs 1, 2, 5B.

2006. *Zychaspis concinna*; Voichyshyn 2006c: p. 33, pl. 2, fig. 2.

2008. *Zychaspis concinna*; Carlsson and Blom 2008: fig. 3Bg.

Type specimen: Holotype SMNH BP.966/1, almost complete imprint of headshield, lacking a distal part of left cornual process; a quarry in the vicinity of Horodnytsia, Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia).

Referred material. — Besides the holotype, there is also an impression of the cornual processes, a fragment of abdominal part of the shield BP.966/2, and imprint of an orbital region BP.966/3. They all share the characteristic ornamentation, and occur in the same piece of rock (light-grey aleurolite).

Diagnosis. — Medium sized *Zychaspis* species with widely angular rostral margin of the shield rounded at its tip.

Description. — Length of the shield equals 70–80 mm. Its maximum width (100–115 mm) falls in the posterior third of the cornual processes. The rostral margin of the shield forms a lobe. Its sides virtually without any bend smoothly pass into slightly convex lateral margins of the shield. The cornual processes are of medium length and of latero-caudal orientation. Their posterior third turns towards the body axis. The abdominal division of the shield is narrow (Si 36 mm, Si/S 0.35) and short. The dorsomedial crest is small. In specimen BP.966/2, its height is probably no more than 2 mm, length about 15 mm. The shield is very low. Its prepineal part is somewhat longer than the postpineal one (B/C is probably 1.25). The nasohypophyseal opening (Fig. 36F) is distant from the rostral margin of the shield (Q/A 1.9), elongated (up to 4 mm), key-hole in shape. Its hypophyseal division (in depression) is about three times longer than the nasal one, situated on a slight elevation. Orbits are of medium size (Ol/A 0.3, Os/A 0.2), oval in shape, and situated in moderate distance one from another (Omin/A 0.36), with narrow (up to 1 mm) framing of the contour, but without circumorbital thickening. The pineal plate (Fig. 36F) is clearly outlined, not wide, and in contact with the orbits. Round pineal opening is within the pineal plate. The dorsal field (Fig. 36F) is narrow (S/Sd 21.4) and elongated, somewhat narrowed in its anterior third. Its posterior margin is sharpened. The lateral fields are long. Right field in the holotype has 76 mm. The field anterior ends are narrower than the posterior ones. Contours of the fields in their medium part are unknown. Posterior ends of the fields are sharp and reach middle part of the cornual processes, extending behind the level of posterior margin of the shield. The ornamentation of the shield consists of tiny rounded or fairly elongated tubercles, the smallest of which (from 0.2×0.2 to 0.3×0.4 mm) are characteristic mainly for epibranchial part of the shield, whereas the largest ones (up to 0.7 mm in length) occur especially on the abdominal interzonal part. The distance between the tubercles slightly exceeds their own size. Elongate tubercles in the interzonal part of the shield are consistently oriented more or less along the axis of body.

Comparison. — *Zychaspis concinna* differs from other species of the genus by the shape of rostral margin of the shield. Besides, from *Z. elegans*, it differs by larger general size of the shield and shape of the pectoral sinuses. Other aspects cannot be compared because of bad preservation of *Z. elegans* specimens. *Zychaspis* sp. 1 differs in having smaller total size, shorter rostral lobe, different shape and larger size of the pectoral sinuses, relatively shorter cornual processes, probably different ornamentation of the dermal skeleton. Comparisons with *Z. siemiradzkii* and *Z. granulata* are given in their descriptions.

Localities and age. — Horodnytsia; late Lochkovian (probably Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Zychaspis elegans (Balabai, 1962)
(Figs 87B, 89C)

1962. *Cephalaspis elegans*; Balabai 1962: p. 8, fig. 10.
1985. *Zychaspis elegans*; Janvier 1985b: p. 318, fig. 7A.
2004. *Zychaspis elegans*; Voichyshyn and Solodkyi 2004: p. 180, fig. 5E.
2006. *Zychaspis elegans*; Voichyshyn 2006b: pp. 16–17, text-fig. 3, pl. 3, fig. 2.
2006. *Zychaspis elegans*; Voichyshyn 2006c: pp. 32–33.

Type specimen: Holotype SMNH BP.41 (old number 17329), partial headshield in ventral view; Khmeleva, left bank of the Dniester River, Zalishchyky rayon, Ternopil' oblast' (Podolia). The species name was originally given by Zych in collection. The name "*C. elegans* Z." is present also on Zych's label of specimen SMNH BP.199 (old number 17308) from Chervonograd, representing a mould of a shield lacking cornual processes. However, this specimen may belong to another species and this is probably why Balabai (1962) attributed only one specimen to *C. elegans*.

Diagnosis. — Relatively small *Zychaspis* species with large rostral lobe.

Description. — The cephalic shield of the only known specimen is of rather small size (L 57 mm, S 84 mm, J > L, Lrc > 72 mm, Ls 55.5 mm). The anterior margin of the shield forms large (width 22 mm and length 7.5 mm), well expressed rostral lobe, resulting in a roughly triangular shield. Lateral margins of the shield are rather convex. The right margin being depicted with simple straight line by Balabai (1962) in fact is broken off. The cornual processes are preserved only at their bases (not indicated by Balabai 1962: fig. 3).

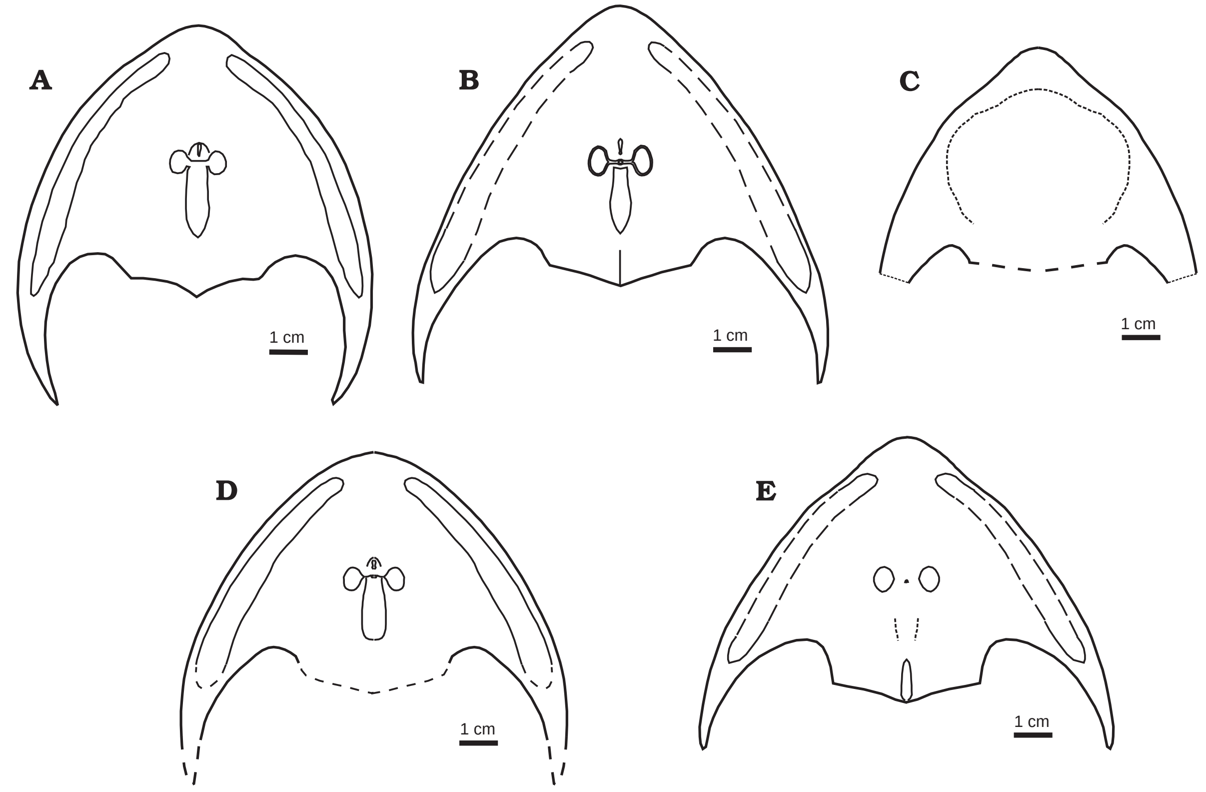


Fig. 89. Reconstructions of *Zychaspis* headshields. **A**. *Zychaspis siemiradzkii* Janvier, 1985 (after Janvier 1985b: fig. 5). **B**. *Zychaspis concinna* Voichyshyn *et* Solodkyi, 2004 (after Voichyshyn and Solodkyi 2004: fig. 5B). **C**. *Zychaspis elegans* (Balabai, 1962) (after Voichyshyn and Solodkyi 2004: fig. 5E). **D**. *Zychaspis granulata* Voichyshyn, 1998 (after Voichyshyn and Solodkyi 2004: fig. 5D). **E**. *Zychaspis* sp. 1 (after Voichyshyn and Solodkyi 2004: fig. 5C).

Probably the cornual processes were of average length for the genus and of lateral-caudal orientation. The abdominal part of the shield is rather narrow (Si ≤ 37 mm).

Comparison. — *Zychaspis elegans* differs from all other species of the genus in the shape of the shield, especially in outline of its anterior and lateral margins. The species has the best-expressed rostral lobe within the genus. It seems to be the smallest in size in the genus. *Zychaspis* sp. 1 differs from *Z. elegans* in its larger size, more widely disposed cornual processes, and different shape of the pectoral sinuses. They are similar in presence of large rostral lobe.

Remarks. — Attribution of this species to *Zychaspis* by Janvier (1985b) is followed on the basis of shape of the anterior margin of the shield. Because of scarcity of data, a different relationship remains a possibility.

Localities and age. — Khmeleva; Pragian (Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Zychaspis sp. 1

(Figs 88B, 89E)

2004. *Zychaspis* sp.; Voichyshyn and Solodkyi 2004: pp. 176–178, figs 3, 4, 5C.

Referred material. — Impression of headshield and abdominal-caudal part of the body known only from a photograph of the specimen *in situ*. The specimen has not been preserved.

Description. — Length of the shield is almost 70 mm. Its maximum width (107 mm) falls almost at the ends of the cornual processes. Rostral margin of the shield forms a wide lobe. The cornual processes have moderate length, and directed latero-caudally. Their ends, probably, do not bent to the body axis. The abdominal part of the shield is narrow (Si 38 mm, Si/S 0.36) and short. The dorsomedial crest is probably small, about 10 mm in length. The prepineal part of the shield is slightly longer than the postpineal one (B/C about 1.15). Shape and size of the nasohypophyseal opening are unknown. The orbits are of moderate size and oval in shape. The pineal plate was not preserved. The dorsal field was, probably, narrow and elongate, but it is not possible to reconstruct its precise shape. Only anterior and posterior ends of the narrow lateral fields are visible on the photograph. The anterior ends situated within rostral lobe, the posterior ones reach second third of the cornual processes, but did not cross the level of posterior margin of the shield. It is difficult to tell anything certain about ornamentation of the dermal skeleton. Perhaps it consisted of densely set fairly convex tesseriforms areas or tubercles (1–1.5 mm in diameter). If true, this character would make this form different from all other species of the genus, except of *Z. elegans* with unknown ornamentation.

The abdominal part is covered by rows of scales, which are elongated across the body axis. There are series of dorso-lateral and lateral scales. The length of the abdominal-caudal part seems to take about 54% of total body length which equals approximately 150 mm.

Localities and age. — Horodnytsia; late Lochkovian (Ustechko Stage or lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Genus *Victoraspis* Carlsson *et* Blom, 2008

2008. *Victoraspis*; Carlsson and Blom 2008: p. 315.

Type species: *Victoraspis longicornualis* Carlsson *et* Blom, 2008; Early Devonian of Podolia.

Diagnosis (based on data of Carlsson and Blom 2008). — Medium sized scolenaspidians (L is about 65 mm). The width of the shield considerably exceeds its length (L/S about 0.5). The prepineal part of the shield is somewhat shorter than the postpineal one (B/C 0.8). Anterior margin of the shield somewhat narrows and has poorly expressed obtuse rostral corner. The cornual processes are very long, narrow, and bent caudally. The abdominal division of the shield is narrow and probably narrows backwards. The hypophyseal division of the nasohypophyseal opening is larger than the nasal one. Orbits are small (S/Os about 32) and oval. The pineal plate is well developed. The dorsal field is moderately narrow and, probably, relatively short (Ld/Sd is about 2.25). Lateral fields are rather narrow, reaching back not farther than to the proximal part of the cornual processes. The ornamentation of the dermal skeleton consists of tesserae covered by minute tubercles.

Remarks. — The shield of this form is especially wide due to long cornual processes with latero-caudal orientation. Long and slender cornual processes are slightly bent towards the medial body axis in their 1/4 length to the caudal end. Index Lrc/Ls 2.375. No information is available about dorsomedial crest, but, if present, it probably was rudimentary, as in *Zychaspis concinna*. The hypophyseal division of the nasohypophyseal opening is somewhat larger than the nasal one, similar to the conditions in *Stensiopelta* and *Zychaspis*. The lateral fields are not well preserved, probably of irregular contour. Position of their caudal ends is intermediate between that in *Stensiopelta* and *Zychaspis*. Tubercles of the dermal skeleton are, probably, more or less of the same size.

Species included. — Only type species.

Occurrence. — Early Devonian of Podolia (Ukraine).

Victoraspis longicornualis Carlsson *et* Blom, 2008

2008. *Victoraspis longicornualis*; Carlsson and Blom 2008: pp. 315–317, figs 1, 3Be, 4.

Type specimen: Holotype PMU 25052, headshield with partial trunk segments and their counterpart; Rakovets', Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia) (Carlsson and Blom 2008).

Remarks. — The origin of type specimens is an open question. The original description of the species was based on two specimens. The holotype was labelled "Racowiec (Rakovets') in Podolia" (Carlsson and Blom 2008) but this place is not among the 97 Early Devonian Podolian fish localities in the SMNH collection and literature sources (Voichyshyn 2001a). There are at least three villages with such name in Podolia. One of them is in the Zbarazh rayon, but no Devonian strata crop out there. Another is in Terebovlia rayon, on the Strypa River but the Devonian strata exposed along Strypa, reach northward only to Zolotnyky (from where a few specimens of *Althaspis* were found by Józef Siemiradzki early in the 20th century), 8 km from Rakovets'. The third village with such name is in Horodenka rayon on the right bank of Dniester River. Finds of Devonian fish are known from outskirts of villages Unizh and Pidverbtsi located down-stream and up-stream of Rakovets', respectively (Fig. 4; Voichyshyn 2001a). The most probable origin of the holotype of *V. longicornualis* is thus Rakovets' on Dniester. If true, this species belongs to the assemblahe of the Strypa Stage (Pragian).

"Iwanje Horodnica" is indicated on the label of the other specimen (PMU 25053), which is a fragment of cornual process and, probably, also belonged to *V. longicornualis* (Carlsson and Blom 2008). It has to be understood that the specimen was found on the slopes of Dniester River between villages Ivanie-Zolote and Horodnytsia. This implies Ustechko Stage as its stratigraphic origin (late Lochkovian).

Thus, *V. longicornualis* may be the only Podolian armoured agnathans species, distribution of which covers first to third faunistic zones of the Podolian Old Red (from Ustechko Stage to Strypa Stage of the Dniester Formation). This does not seem supported well enough with the available evidence.

Localities and age. — Rakovets'; exact age is unknown, possibly either Late Lochkovian or Pragian of Podolia (Ukraine). No similar material is represented in the SMNH collection.

Genus *Stensiopelta* Denison, 1951

1951. *Stensiopelta*; Denison 1951: pp. 159, 191.
1952. *Cephalaspis*; Wängsjö 1952: pp. 243–252 (pars).
1964. *Stensiopelta*; Obruchev 1964: p. 103.
1985. *Stensiopelta*; Janvier 1985b: p. 318.
1991. *Stensiopelta*; Afanassieva 1991: pp. 98–99.
2004. *Stensiopelta*; Afanassieva 2004: pp. 255–256.

Type species: *Cephalaspis woodwardi* Stensiö, 1932; Early Devonian of Wales.

Diagnosis. — Medium sized osteostracans (L is 50–65 mm). The shield is very wide and short. Its anterior margin is rounded and has small lobe or corner. The cornual processes are long, rather narrow, with laterocaudal orientation or slightly bent towards the medial body axis. The abdominal division of the shield is narrow and elongated. The dorsomedial crest is low and short. The nasohypophyseal opening has divisions of similar size. The pineal plate is well developed. The dorsal field is narrow. The lateral fields are not long, of uniform width. Their pointed posterior ends may reach the middle of the cornual processes.

Species included. — Besides the type species: *S. pustulata* Janvier, 1985, Early Devonian of Podolia.

Occurrence. — Early Devonian of Wales (Great Britain) and Podolia (Ukraine).

Stensiopelta pustulata Janvier, 1985
(Figs 6D, E, 35E, 37A, 90A–C, 91A, B, D, 92D, E)

1985. *Stensiopelta pustulata*; Janvier 1985b: pp. 318–322, figs 8–11.

1991. *Stensiopelta pustulata*; Afanassieva 1991: pp. 99–101, text-fig. 16b, pl. 21.

2004. *Stensiopelta pustulata*; Afanassieva 2004: p. 256, text-fig. 35, pl. 14, figs 1–4.

2008. *Stensiopelta pustulata*; Carlsson and Blom 2008: fig. 3Ba.

Type specimen: Holotype BM(NH) P.17703-4, headshield; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Moulds and imprint of the shield or its parts SMNH BP.6, 8, 23, 31/2, 50, 92, 292/2, 901/3, 902/2, 971, 1266, 1267, 1268, 1270, 1271, 1272 and 1336.

Diagnosis. — *Stensiopelta* species with elongate abdominal division, and an obtuse, slightly lobate rostral margin of the shield.

Description. — The shield (L is 55–65 mm, S is ~120 mm) has an arch-shaped anterior margin; sometimes a small lope is present. The cornual processes rapidly narrow and are latero-caudally directed. They are straight or slightly bent backwards in their distal part, or near the ends. Their outer margin is straight or somewhat convex and bent under angle of ~45°. Their inner margin is straight or slightly concave, without denticles. The abdominal division of the shield is narrow and long, with medial ledge at its posterior margin.

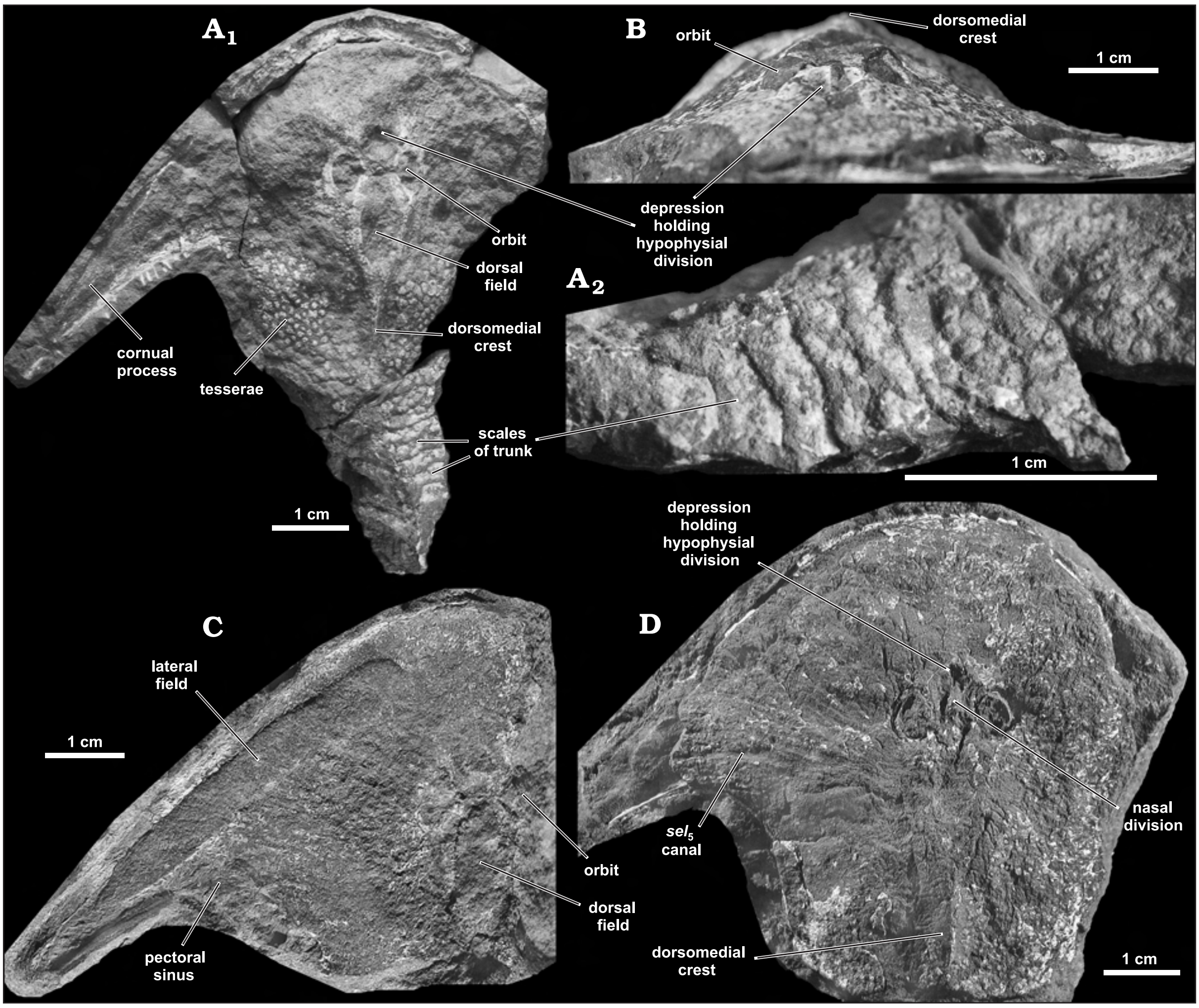


Fig. 90. Scolenaspidid *Stensiopelta* from various localities of the Dniester Formation in Podolia. **A**. *Stensiopelta pustulata* Janvier, 1985, partial headshield SMNH BP.50 with articulated trunk part from Nagiriany, talus at the bottom of slope of Dzhuryn River, Ustechko Member or lower part of Khmeleva Member, dorsal view and trunk in lateral (right side) view. **B**. Same species, partial headshield SMNH BP.8 (see also Figs 37A, 91A) lacking cornual processes from the Horodnytsia old quarry, Ustechko Member or lower part of Khmeleva Member, frontal view. **C**. Same species, imprint of right part of headshield SMNH BP.1270, same locality, dorsal view. **D**. *Stensiopelta* sp., partial mould of headshield SMNH BP.7, same locality, dorsal view.

The dorsomedial crest is displaced forward in relation to posterior margin of the shield (Figs 37A, 90A$_1$, 91A, B). The nasohypophyseal opening is narrow, of elongated key-hole-like shape. The orbits are oval and relatively small. The dorsal field is elongated, most widely in the middle or in its back third, in front a little bit narrowed, and rounded in the posterior part. The lateral fields have uniform width. Their anterior ends are rounded and divergent, the posterior ones are pointed and reach the first part of the cornual processes. The ornamentation of the dermal skeleton consists of small tesserae. Each of them has a group of tubercles of different size.

Comparison. — *Stensiopelta woodwardi* has a different contour of the anterior margin of the shield, as well as location of the dorsomedial crest, bent cornual processes with denticles in their inner margins, shorter abdominal division, and a smaller shield.

Remarks. — The genus *Stensiopelta* is represented in Podolia by several forms. Except for the typical *S. pustulata*, specimens with significantly different morphology of the shield occur there. Janvier (1985b) identified two forms of *Stensiopelta* sp., one with the cornual processes somewhat bent caudally (Janvier 1985b: fig. 12A; in fact, Janvier has described *Stensiopelta pustulata* as having straight cornual processes), the other has large denticles in the inner margin of the cornual processes (Janvier 1985b: fig. 12A). Thus, the latter is similar to *S. woodwardi*. SMNH collection keeps specimens with a wide anterior margin of the shield or with apparent angular lobe (Fig. 90D). At the same time, both these forms share features characteristic for *Stensiopelta*, *S. pustulata* in particular, such as elongated abdominal division with small dorsomedial crest, that is displaced forward from posterior margin of the shield, long cornual processes, etc.

Localities and age. — Ustechko, Nagiriany, Khmeleva and Horodnytsia; Lochkovian to Pragian (from Ustechko Stage to Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Scolenaspidoids incertae sedis

"*Cephalaspis*" *microlepidota* Balabai, 1962

(Fig. 91C)

1962. *Cephalaspis mikrolepidota*; Balabai 1962: p. 6.
1962. *Cephalaspis microlepidota*; Balabai 1962: pp. 6, 8, text-fig. 8.
1985. "*Scolenaspis*" *mikrolepidota*; Janvier 1985b: p. 327.
1991. "*Cephalaspis*" *microlepidota*; Afanassieva and Voichyshyn 1991: pp. 69–71, text-fig. 3, pl. 9, figs 3, 4.
2004. "*Cephalaspis*" *microlepidota*; Afanassieva 2004: p. 257, text-fig. 36, pl. 14, fig. 5.
2006. "*Cephalaspis*" *microlepidota*; Voichyshyn 2006b: pp. 9–10.
2006. "*Cephalaspis*" *microlepidota*; Voichyshyn 2006c: pp. 33–34.

Type specimen: Lectotype SMNH BP.989, mould of headshield in dorsal view, lacking the right cornual process and dorsomedial crest, with remains of trunk segments; vicinity of Horodnytsia, right bank of the Dniester River, Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia).

Referred material. — Only the lectotype.

Diagnosis. — Medium sized and narrow-shielded scolenaspidioid species with prominent dorsomedial crest and tiny irregular polygonal fields in the middle layer of the dermal skeleton.

Description. — The shield of the only known specimen is elongated (L ~80 mm, S ~100 mm), with maximum width at the level of distal part of the cornual processes, having in front a wide rostral lobe. The cornual processes are flattened, not wide in the proximal part, and rapidly tapering. The abdominal division of the shield is short (~40 mm), with well developed dorsomedial crest (or broken spine?). Nasohypophyseal depression is small (Q 30 mm). Nasal division of the nasohypophyseal opening is narrow. The hypophyseal one are not preserved. The orbits are small and oval (Ol 6 mm, Os 4 mm), placed at distance 6 mm one from another. The pineal plate is developed, narrow. The dorsal field is of moderate length (Ld ~15 mm; L/Ld 5.5), rather wide (Sd 6 mm), narrowed in its anterior part, and in the posterior one probably has two symmetrical lobes. Lateral fields are long (not less than 57 mm), narrow, and somewhat broadened in the posterior part. The posterior margin is not preserved. Rounded anterior ends of lateral fields reach the rostral lobe. Polygonal fields in the middle layer of the skeleton are of 0.5–2.5 mm in diameter (Fig. 91C$_1$).

Comparison. — The species is similar to those of *Machairaspis* Janvier, 1985 by size of the shield, shape of the cornual processes and the lateral fields, size of the orbits, and development of the dorsomedial crest. The shape and proportions of the shield are especially similar in the Podolian *Machairaspis* sp. (Janvier

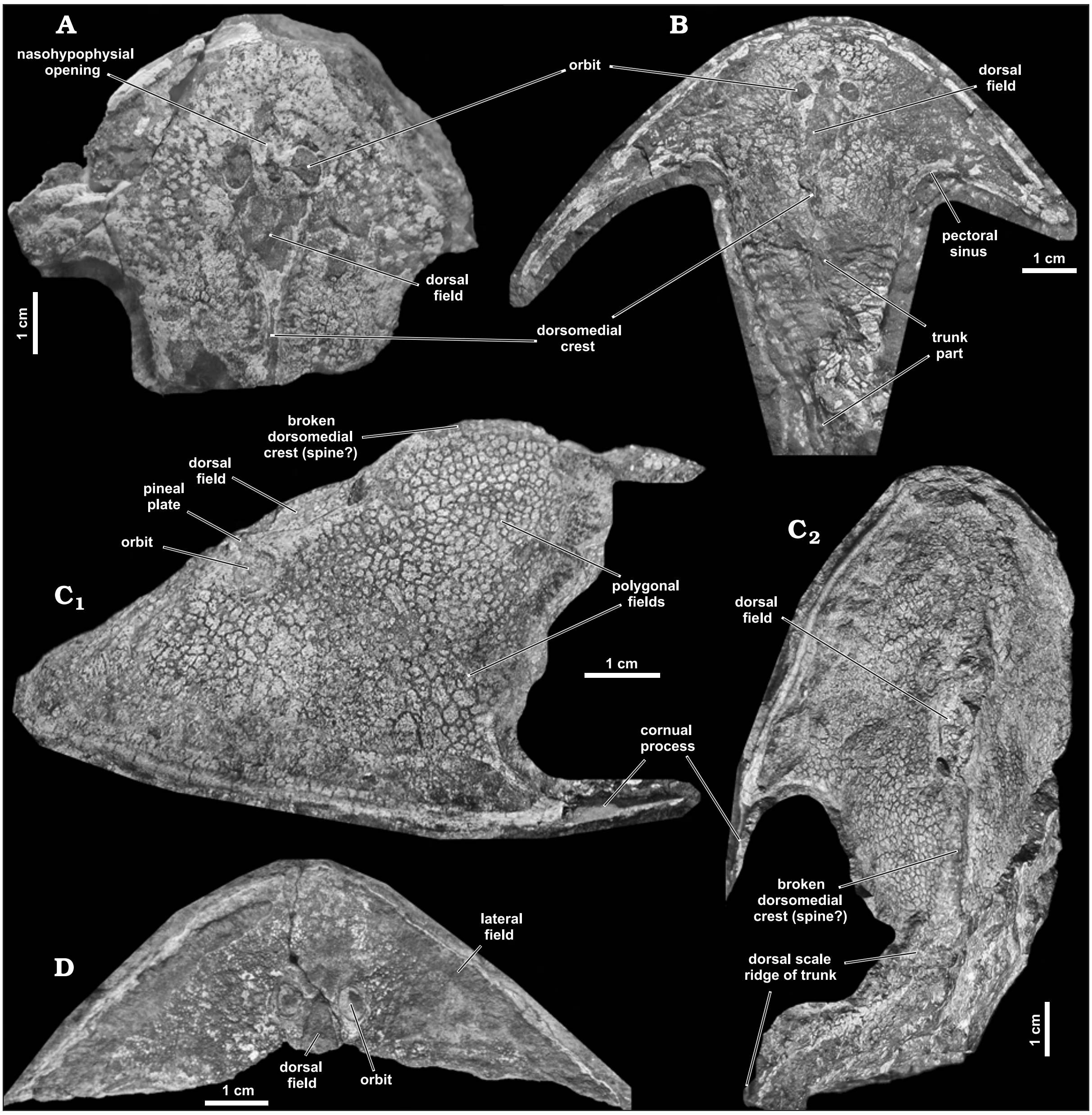


Fig. 91. Scolenaspidid *Stensiopelta* and related form from various localities of the Dniester Formation in Podolia. **A**. *Stensiopelta pustulata* Janvier, 1985, partial headshield SMNH BP.8 (see also Figs 37A, 90B) lacking cornual processes from the Horodnytsia old quarry, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. Same species, headshield SMNH BP.902/2 with articulated trunk part from Nagiriany, slab from talus at SE slope of Dzhuryn River, Ustechko Member or lower part of Khmeleva Member, dorsal view. C. “*Cephalaspis*” *microlepidota* Balabai, 1962, partial headshield SMNH BP.989 lacking right cornual process with some trunk scales from Horodnytsia, lateral (left side) and dorsal views. **D**. *Stensiopelta pustulata* Janvier, 1985, imprint of partial headshield SMNH BP.292/2, same locality, dorsal view.

1985b: fig. 15) from Horodnytsia. Nevertheless, machairaspids have a wide shield and its abdominal part, and widely disposed orbits.

Localities and age. — Horodnytsia; probably Late Lochkovian (probably Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

“*Cephalaspis*” *djurinensis* Balabai, 1962

(Fig. 92A)

1962. *Cephalaspis djurinensis*; Balabai 1962: p. 6, fig. 7.

1985. ?*Zychaspis djurinensis*; Janvier 1985b: p. 318, fig. 7B.

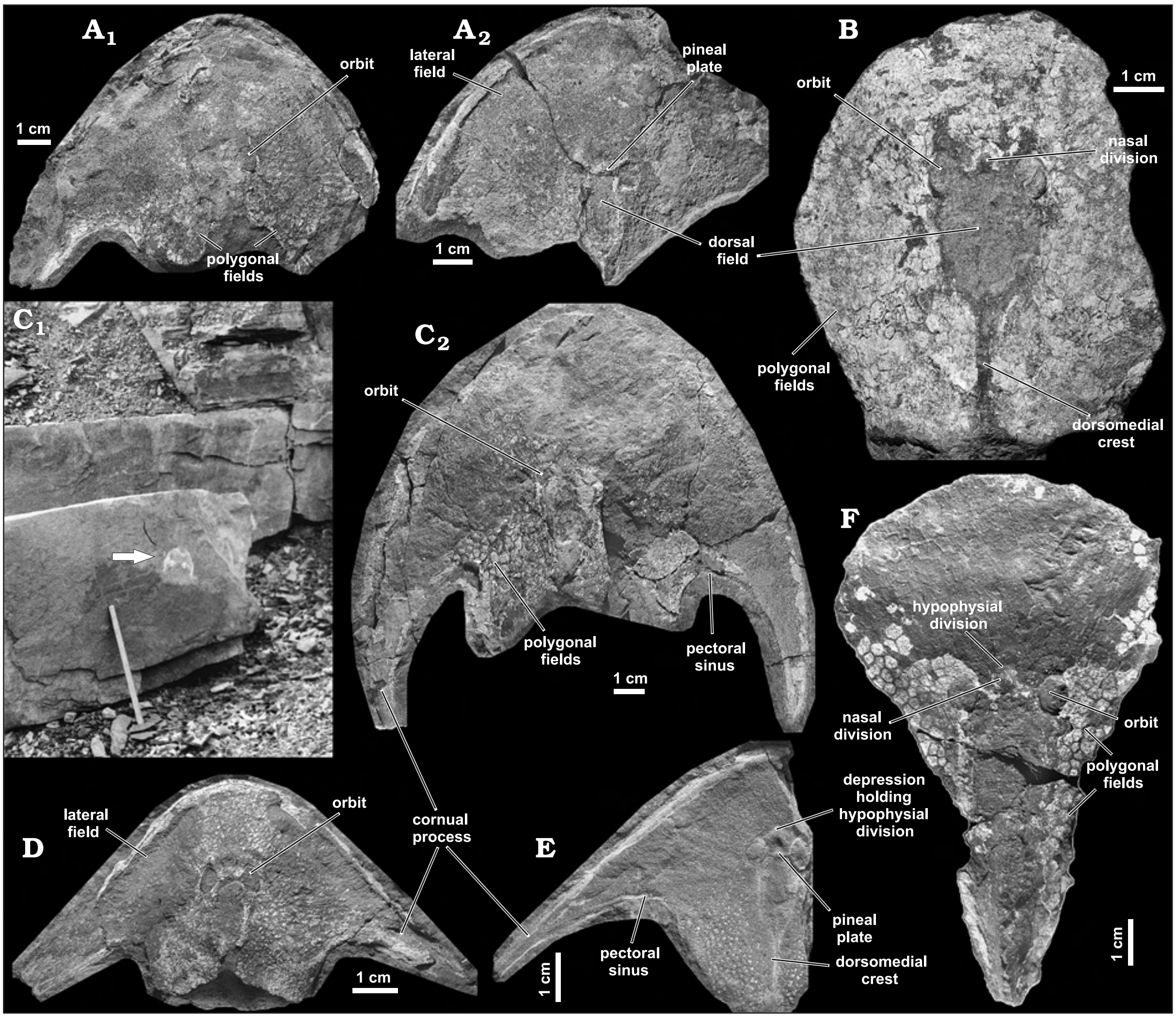


Fig. 92. Scolenaspidids and zenaspidids from various localities of the Dniester Formation in Podolia. **A**. “*Cephalaspis*” *djurinensis* Balabai, 1962, the holotype partial mould of headshield SMNH BP.42 from Buriakivka, left bank of Dzhuryn River, most probably Ustechko Member of the Dniester Formation, part and counterpart. **B**. Zenaspididae gen. indet., partial mould of headshield SMNH BP.86 (see also Fig. 36A) lacking cornual processes and margins, except for abdominal division from Ustechko, Ustechko Member to lower part of Khmeleva Member, dorsal view. **C**. *Zenaspis podolica* (Balabai, 1962), crushed headshield SMNH BP.39 from the Horodnytsia quarry, Ustechko Member or lower part of Khmeleva Member, field photo (marked by white arrow) and dorsal view. **D**. *Stensiopelta pustulata* Janvier, 1985, partial mould of headshield SMNH BP.1271, same locality, dorsal view. **E**. Same species, imprint of right headshield part SMNH BP.971 from unknown locality, lower part of the Dniester Formation, dorsal view. **F**. *Zenaspis podolica* (Balabai, 1962), partial mould (central part) of headshield LDU (unnambered) from unknown locality, lower part of the Dniester Formation, dorsal view.

2006. “*Cephalaspis*” *djurinensis*; Voichyshyn 2006b: pp. 17–19, text-fig. 4, pl. 3, fig. 1A, B.
2006. “*Cephalaspis*” *djurinensis*; Voichyshyn 2006c: pp. 34–35.

Type specimen: Holotype SMNH BP.42 (old numbers 25563 and 25565), incomplete mould and imprint of headshield of the same individual; Buriakivka, the left bank of the Dzhuryn River, Zalishchyky rayon, Ternopil’ oblast’ (Podolia).

Referred material. — Only the holotype.

Diagnosis. — Medium sized scolenaspidoid species with appreciable convexity and *Zychaspis*-like shape of the shield, as well as polygonal fields in the middle layer of the dermal skeleton.

Description. — Shield size of the only known specimen is average as for the scolenaspidoids (L ~70 mm; Lrc > 100 mm). The maximum width of the shield falls probably on the posterior part of the cornual processes and is much greater than its lengths (S > 114 mm). The shield is dorsally convex (hso ~12 mm). The specimen lacks in anterior margin of the shield and the cornual processes are incomplete, contrary to Balabai (1962: fig. 7). Its anterior margin seems to forms a hardly visible wide rostral lobe. The lateral margins of the shield are rather convex. The cornual processes are probably of moderate length and wide at the basis. Its outer contour and the posterior part are unknown. The abdominal part of the shield is narrow (Si ≤ 46 mm) and likely to be short. The prepineal part of the shield is probably longer than the postpineal one (B ~38 mm, C ~32 mm). Rather large pineal plate is present. Orbits are of moderate size (Ol 5.9 mm, Os 5.7 mm, Omin 5.3 mm), rounded and surrounded by narrow (~1 mm) circumorbital thickening. The dorsal field is elongated, not wide, with narrowed anterior and pointed posterior ends. Width of the lateral fields in their middle part equals 7 mm. Probably, they are equally wide along the whole length. Shape of their posterior ends and their extent are unknown. The ornamentation of the dermal skeleton consists of tesserae from 1.6 to 2.1 mm in size. Each tessera has a group of tiny tubercles probably of the same size.

Comparison. — "*Cephalaspis*" *djurinensis* probably belongs to a separate genus, which may occupy an intermediate position between primitive scolenaspidoids, such as *Zychaspis*, and more specialised *Stensiopelta*. Similar features of all these taxa are: relative arrangement, size and proportions of central part of the shield (orbits, nasohypophyseal opening and dorsal field). This species shares the contour of anterior margin of the shield with species of *Zychaspis* and the general shape of the shield with *Z. granulata* (Voichyshyn 1998). Differences are in significant camber of the shield and in another sculpture of the dermal skeleton of "*C.*" *djurinensis*. It has also common features with *Stensiopelta*, namely the general proportions of the shield and probably structure of the dermal skeleton (polygonal fields of *djurinensis* similar in their shape and size to tesserae of *Stensiopelta*), but differs from it by details of the shield contour.

Localities and age. — Buriakivka; Late Lochkovian or early Pragian (probably Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

Family **Zenaspididae** Stensiö, 1958

Emended diagnosis. — Medium to large-sized osteostracans. The headshield is dome-shaped and massive. The abdominal part of the shield has a low, more or less developed, median dorsal crest. The cornual processes are of various lengths. The hypophyseal division of the nasohypophyseal opening is, as a rule, larger than the nasal division. The pineal plate is poorly developed or lacking. The median dorsal field is broad. The lateral fields have a conspicuous dilatation (or widening) in their posterior parts, reaching backwards not further than to the proximal part of the dorsal surface of the cornual processes. The ornamentation includes either single large tubercles or groups of tubercles of different size on tesserae.

Included genera. — Besides the type genus: *Diademaspis* Janvier, 1985a, and, possibly, *Tegaspis* Wängsjö, 1952.

Remarks. — The genus *Tegaspis* differs in several aspects from other zenaspidids, such as the shape of the headshield, its anterior margin and cornual processes, approximately the same size of the two divisions of the nasohypophyseal opening, a comparatively narrow median dorsal field, and the position of the posterior parts of the lateral fields, which does not extend on the dorsal surface of cornual processes at all.

Genus *Zenaspis* Lankester, 1870

1870. *Zenaspis*; Lankester 1870: p. 43.
1952. *Cephalaspis*; Wängsjö 1952: pp. 243–252 (pars).
1985. *Zenaspis*; Janvier 1985b: p. 322.
2006. *Zenaspis*; Voichyshyn 2006a: p. 133.
2006. *Zenaspis*; Voichyshyn 2006b: pp. 10–11.

Type species: *Cephalaspis salweyi* Egerton, 1857; Early Devonian of Great Britain.

Emended diagnosis. — Moderate to large sized zenaspidids (L 90–140 mm). The width of the shield is greater than its length (L/S 0.65–0.8). The prepineal part of the shield is shorter than the postpineal one (B/C 0.7–0.9). The cornual processes are, as a rule, relatively long. The abdominal part of the shield is short, with a massive median dorsal crest. The hypophyseal division of the nasohypophyseal opening is somewhat larger than the nasal division. The orbital openings are small (S/Os 25–42) with a short distance between them (Omin/Os 2.1–3.3). The median dorsal field is comparatively broad (index S/Sd is 9–11). The lateral fields are considerably dilatated (widened) in their posterior parts and extend into the base of the cornual processes. The distance between the posterior part of the lateral fields and the anterior margin of the pectoral sinus is ap-

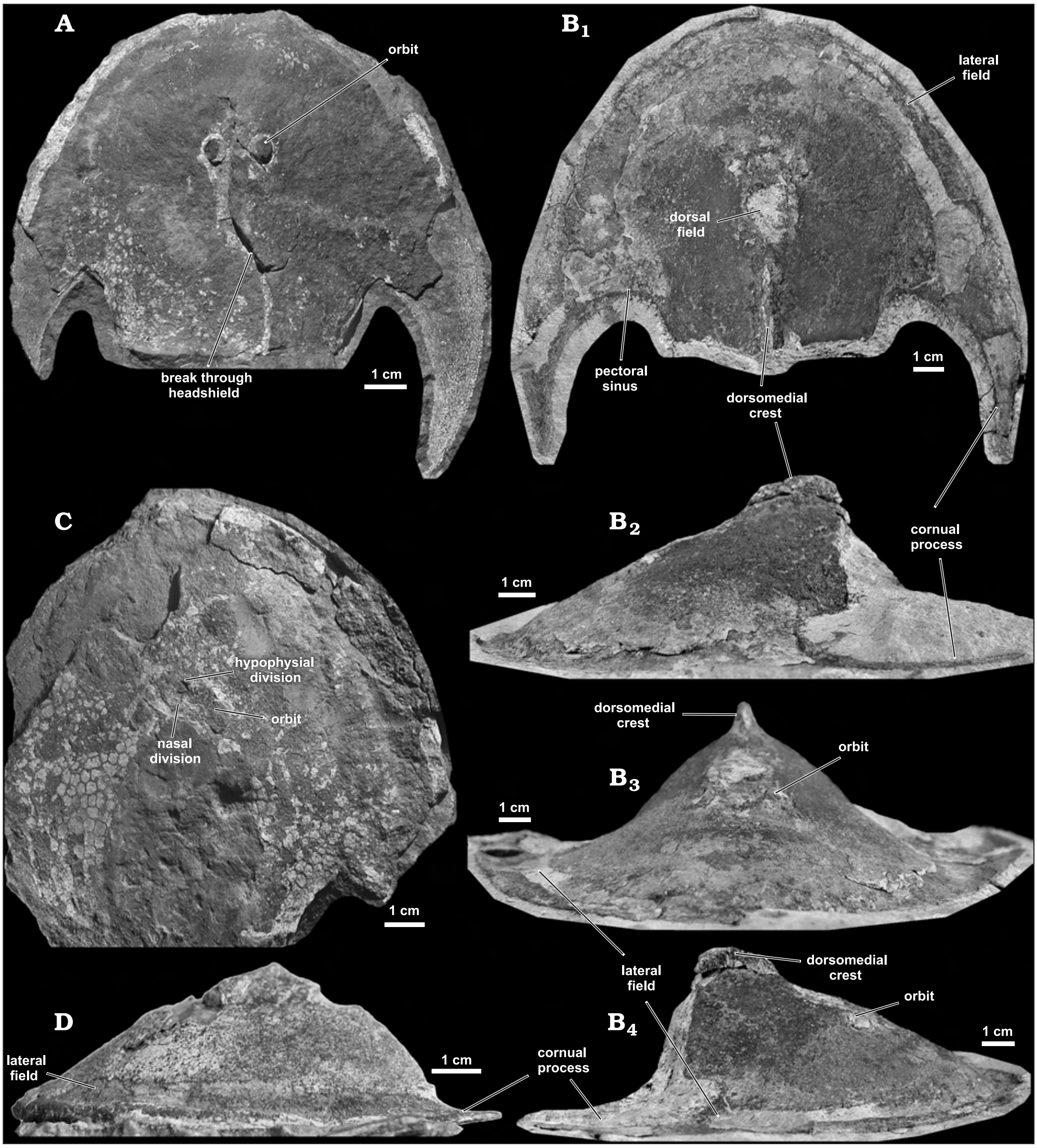


Fig. 93. Zenaspidid *Zenaspis* from various localities of the Dniester Formation in Podolia. **A**. *Zenaspis podolica* (Balabai, 1962), lectotype partial crushed mould of headshield SMNH BP.37 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. Same species, complete mould of headshield SMNH BP.14, same locality, dorsal, lateral (left side), frontal, and lateral (right side) views, respectively. **C**. Same species, partial mould of headshield SMNH BP.36 (see also Fig. 36B) from Ustechko, dorsal view. **D**. *Zenaspis dzieduszyckii* Voichyshyn, 2006, the holotype mould of headshield SMNH BP.103 (see also Figs 36D, 95A) from the Horodnytsia old quarry talus, Ustechko Member or lower part of Khmeleva Member, lateral (left side) view.

proximately the same as to the lateral margins of the shield. The ornamentation consists of single large tubercles or of those grouping within tesserae.

Species included. — Besides the type species, *Z. podolica* (Balabai, 1962), *Z. dzieduszyckii* Voichyshyn, 2006, *Z. kasymyri* sp. n., and possibly *Z. major* (Balabai, 1962), all from the Early Devonian of Podolia; perhaps *Z. metopias* (Wängsjö, 1952), the Early Devonian of Spitsbergen.

Occurence. — Early Devonian of Great Britain, Podolia (Ukraine), and perhaps Spitsbergen.

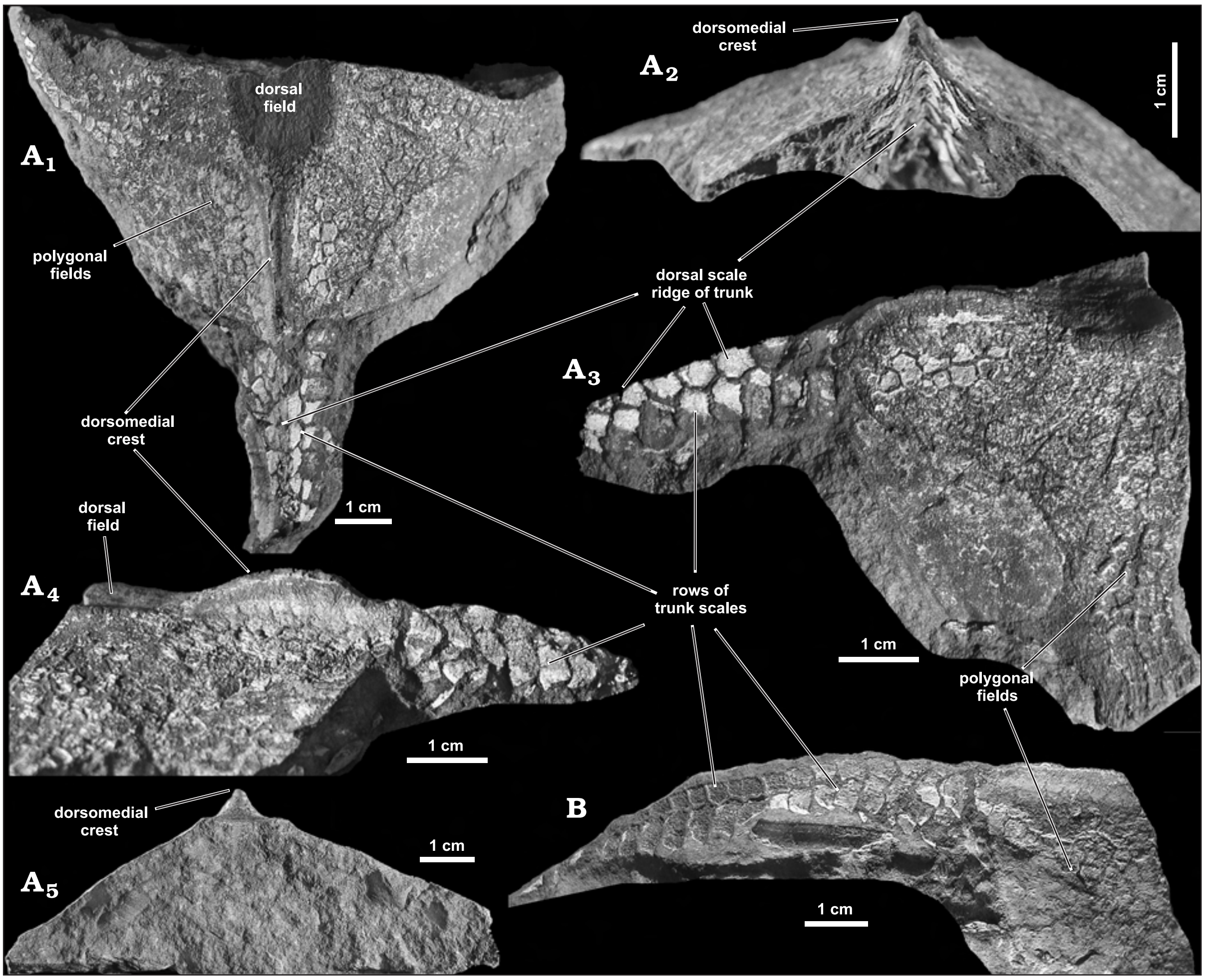


Fig. 94. Zenaspidid *Zenaspis podolica* (Balabai, 1962) from various localities of the Dniester Formation in Podolia. **A**. Abdominal part of headshield SMNH BP.9 with articulated trunk from unknown locality, probably Ustechko or Khmeleva Member, dorsal, posterior, dorso-lateral (right side), lateral (left side), and frontal views. **B**. Right part of abdominal division of headshield SMNH BP.30 (see also Fig. 37B) and articulated trunk body part from Ivanie-Zolote, lower part of Ustechko Member of the Dniester Formation, lateral (right side) view.

Zenaspis podolica (Balabai, 1962)
(Figs 6B, C, 36B, 37B, F, 92C, F, 93A, B, C, 94A, B, 98E)

1874. Cephalaspiden; Alth 1874: pl. 4, fig. 8.

1962. *Cephalaspis podolica*; Balabai 1962: pp. 4–5, fig. 4.

1985. "*Zenaspis*" *podolica*; Janvier 1985b: p. 323, fig. 13.

2006. *Zenaspis podolica*; Voichyshyn 2006b: pp. 9, 11–14, text-figs 1, 2D, pl. 1, pl. 2, figs 2, 3.

2006. *Zenaspis podolica*; Voichyshyn 2006c: p. 31.

Type specimen: Lectotype (selected by Janvier 1985b) SMNH BP.37 (old number 17538), almost complete, but crushed mould of headshield; vicinity of Horodnytsia, Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia). Wrong number SMNH 25562, now BP.36 was mistakenly attributed to this specimen in figure caption in Balabai (1962).

Referred material. — More or less complete moulds of shields or their fragments SMNH BP.9, 11, 14, 26, 29, 30, 36, 39, 1166 and also a specimen without number from the GMLSU collection (Fig. 92F); probably specimens SMNH BP.27, BP.28 and BP.31/1. Only three of ten specimens studied by Balabai (1962), that is BP.37 (lectotype), BP.30, and BP.36, are still represented in the collection. For specimens BP.34 and BP.35 originally labelled "*Cephalaspis podolica* sp. n.", a new label "*C. microlepidota* sp. n." has been given by that author, but apparently they belong to an unknown genus of scolenaspidoids.

Diagnosis. — Medium sized *Zenaspis* species with massive dorsomedial crest and cornual processes, and large (regular in size) polygonal fields in the middle layer of the dermal skeleton.

Description. — The shield is dome-shaped dorsally (Figs 93B_2–B_4; L 90–110 mm, S 130–160 mm; Lrc 160–165 mm; hso in SMNH BP.14 ~25 mm), with the maximum width usually in the middle of the cornual processes. Its anterior margin is more or less widely rounded, lateral margins are little convex. The cornual processes are thick, rather long, and wide at their basis, caudally directed, sometimes at their ends slightly bent to the axis of the shield. Their internal margin bears no denticles. The abdominal part of the shield is relatively narrow, rather short, has a strong but rather low dorsomedial crest with the powerful basis (Figs 93B, 94A_4). Height of the crest equals 5 mm, width at their bases is 6 mm, length 27 mm in SMNH BP.14. The pectoral sinus is asymmetric, wide, deep enough. Its top is displaced to the medial axis of the body from 1/4 to 1/5 width of the sinus. The hypophyseal division of the nasohypophyseal opening is elongated and probably somewhat larger than the nasal division (Fig. 36B), or approximately the same in size (Fig. 92F). Orbits of round to oval shape are rather small, widely disposed, apparently surrounded by the circumorbital thickenings.

The pineal plate is obscure. Perhaps, as stated by Janvier (1985b), it was “fused laterally with the orbital margin”. This opinion was probably based on the illustration in Balabai (1962) of the lectotype that is too damaged to judge with confidence. Also in the present material the interorbital area is insufficiently preserved. Nevertheless, among four specimens with slightly better preservation of this region, only one shows the seams which can be interpreted as traces of a narrow pineal plate.

The dorsal field is wide, rather short. Its exact shape remains unknown. It was probably rectangular, with convex lateral sides and rounded corners. Lateral fields are rather narrow in their anterior third, then they widen posteriorly, having the medial blade in their posterior part. Lateral fields range to the bases of cornual processes. The distance between anterior ends of the lateral fields is more than the width of both orbits and distance between them taken together. The middle layer of the dermal skeleton contains rather large, up to 2–3 mm in a diameter, polygonal, irregular honeycomb-shaped, fields. There are numerous groups of fine tubercles almost equal in size on the polygonal fields (Fig. 92F). According to Janvier (1985b), the dermal skeleton of the species is ornamented with large tubercles.

Some specimens in SMNH collection show articulated parts of headshield and trunk (Fig. 94A, B). Scales of the trunk part seem to be covered with tiny ribs of variable size (Fig. 37B).

Comparison. — The species is similar to *Z. salweyi* by general shape of the shield and the dorsomedial crest. It differs from it by details of shape of the lateral fields, more massive and thick cornual processes, rather larger orbits, approximately the same size of both divisions of the nasohypophyseal opening, and probably reduced pineal plate. In comparison with *Z. metopias*, *Z. podolica* has other proportions of its narrower shield (L/S 0.60 in *Z. metopias* against 0.70–0.75 in *Z. podolica*), relatively larger orbits and cornual processes, and larger polygonal fields in the middle layer of the dermal skeleton. Comparisons with *Z. dzieduszyckii*, *Z. major*, and *Z. kasymyri* sp. n. are given in their descriptions.

Localities and occurence. — Horodnytsia, Ivanie-Zolote, Ustechko, and Khmeleva; Lochkovian to early Pragian (from Ustechko Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Zenaspis dzieduszyckii Voichyshyn, 2006
(Figs 35D, 36D, 93D, 95A–C, 98D)

1985. *Zenaspis* cf. *salweyi*; Janvier 1985a: pp. 323–324, fig. 14.

2006. *Zenaspis dziedushyckii*; Voichyshyn 2006a: pp. 133–134, figs 3, 4.

2006. *Zenaspis dziedushyckii*; Voichyshyn 2006b: text-fig. 2C.

2006. *Zenaspis dziedushyckii*; Voichyshyn 2006c: p. 32.

Type specimen: Holotype SMNH BP.103, natural mould and imprint of headshield lacking the posterior part and cornual process of the right side; Horodnytsia, Horodenka rayon, Ivano-Frankivs’k oblast’ (Podolia).

Referred material. — Specimens SMNH BP.1193 and 1215. Two unnambered specimens (on a large plate of sandstone, probably from Horodnytsia) kept in the GMLSU collection (Fig. 95B) also belong to this species.

Diagnosis. — Small sized *Zenaspis* species with relatively large orbits, wide lateral fields, and short and slender cornual processes.

Description. — The length of the headshield is 100–110 mm. Its maximum width (120–130 mm) is at the tips of the cornual processes. The lateral margins of the shield are slightly convex. The cornual processes are oriented postero-laterally, short and rapidly tapered off. The abdominal part of the headshield was most prob-

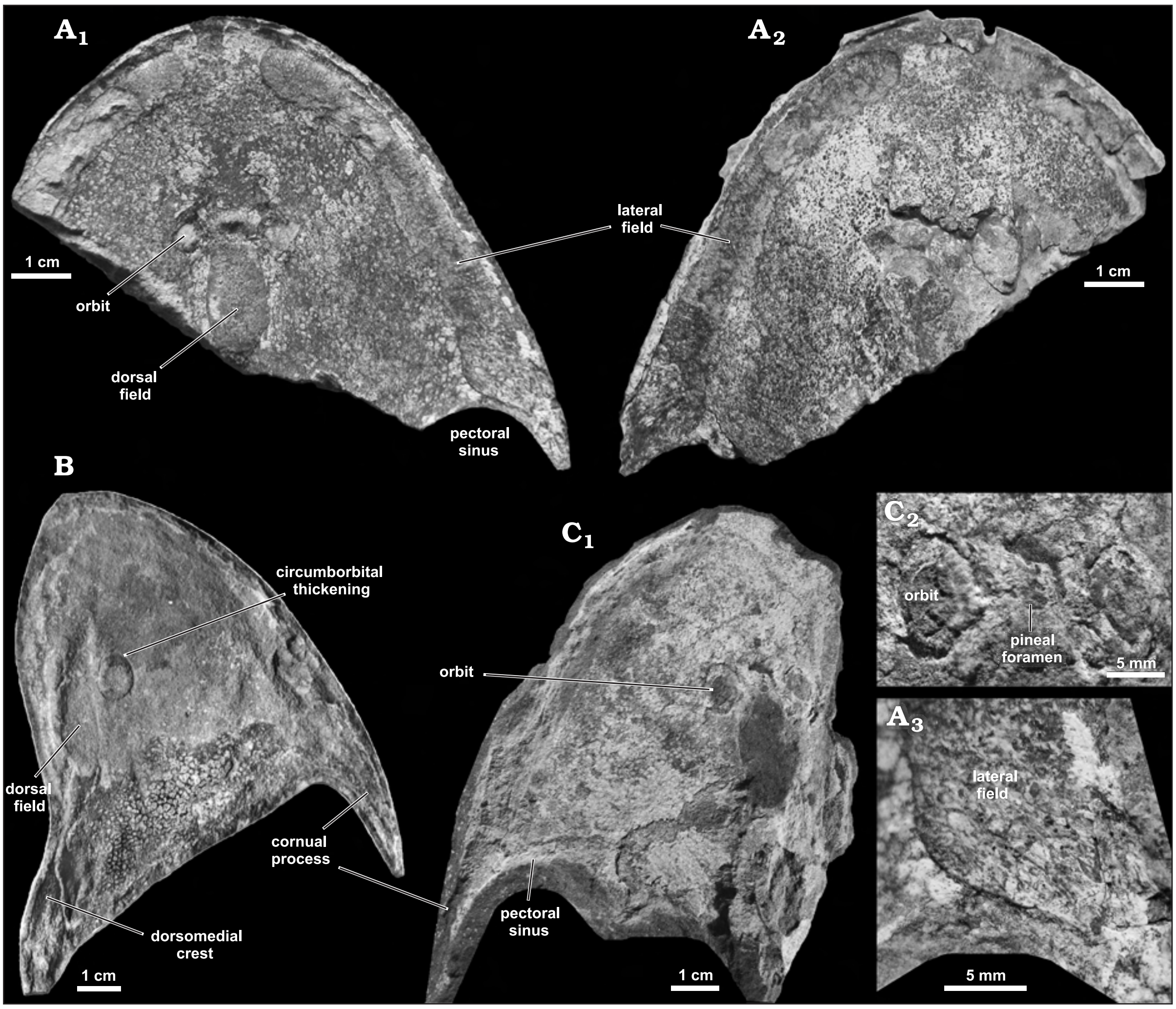


Fig. 95. Zenaspidid *Zenaspis dzieduszyckii* Voichyshyn, 2006, from various localities of the Dniester Formation in Podolia. **A**. The holotype imprint of headshield SMNH BP.103 (see also Figs 36D, 93D) lacking posterior part and cornual process of the right side from the Horodnytsia old quarry talus, Ustechko Member or lower part of Khmeleva Member, part and counterpart and enlarged posterior end of lateral field. **B**. Right part of headshield LDU (unnumbered) probably from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorso-lateral (right side) view. **C**. Mould of left part of headshield SMNH BP.1193 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view and enlarged nasohypophyseal and orbito-pineal zone.

ably broad (Si 50–60 mm). The median dorsal crest is elongated along the body axis, extending beyond the posterior margin of the shield. Its total length is up to 35 mm, the length at the base of the median dorsal crest is 28–30 mm, and its height is about 10 mm. The headshield is high, its height at the level of orbits is 20 mm in the holotype. The nasohypophyseal opening is relatively remote from the anterior margin of the shield (Q/A 1.5), with a large hypophyseal division (in a depression) and a smaller nasal one (opening on the anterior slope of a slight elevation). The orbits are small (Ol/A 0.26, Os/A 0.2), oval to rounded, widely spaced (Omin/A 0.6), with broad (up to 2 mm) circumorbital thickenings (Figs 36D, 95B, C_2). The pineal plate is very narrow, possibly narrower than the pineal foramen, which exceeds the limits of the pineal plate posteriorly. The pineal foramen is oval in shape, laterally elongated, with length of 0.9 mm and width of 1.5 mm (Fig. 36D). The median dorsal field is elongated and wide, with more or less equal width (S/Sd 9.8). Its anterior margin is straight, the lateral ones slightly convex, and the posterior one forms an obtusely angular corner. The lateral fields are long (G 78–81 mm in the holotype) and wide, with their anterior ends somewhat broadened and thus relatively closer to each other, whereas the posterior ones reach the base of the cornual processes and have postero-lateral corners (Fig. 95A_3). The distance between the posterolateral margin of the field and the lateral margin of the shield is 2 mm, the same as between posterior margin of the field and tip (anterior margin) of the pectoral sinus (Fig. 95A). In the preorbital part of the shield, the lateral fields are rather narrow, so that their width (in the left lateral field of the holotype) at the anterior end, at the point of narrowing, and at the level of the posteromedial corners is 9.3, 7.5, and 10.8 mm, respectively. The distance between the lateral fields and the margin of the shield does not exceed 3 mm. The ornamentation of the dermal skeleton of the shield is not preserved. Only traces of small (1.0–1.5 mm) polygonal fields probably corresponding to tesserae with single round tubercle can be seen.

Comparison. — *Zenaspis dzieduszyckii* differs from all other representatives of the genus by its smaller overall size and relatively larger orbits. Besides, it differs from *Z. salweyi* by the details of the outline of lateral fields, shorter cornual processes, and shape of abdominal part of the shield. Both species share the shape of the median dorsal field, especially the contour of its posterior margin. Compared with *Z. metopias*, the new species has a narrower shield, and relatively wider lateral fields, whereas the size of polygonal fields in the middle layer of the dermal skeleton is similar in both species. *Zenaspis dzieduszyckii* differs from *Z. podolica* by its smaller and posterolaterally directed cornual processes, the shape of both the abdominal part and median dorsal crest, and its considerably smaller polygonal fields in the middle layer of the dermal skeleton. Comparison with *Z. kasymyri* sp. n. is given in its description.

Remarks. — Janvier (1985b: fig. 14) ascribed a specimen from Horodnytsia to *Zenaspis* cf. *salweyi* but it may belong to *Zenaspis dzieduszyckii*, judging from the shape of the shield and morphological details, as well as its derivation from the type locality and horizon of this species. *Zenaspis dzieduszyckii* co-occurs with *Podolaspis* sp. and *Larnovaspis* sp.in the sandstones of Horodnytsia.

Localities and age. — Horodnytsia; probably Late Lochkovian (Ustechko Stage or lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Zenaspis major (Balabai, 1962)
(Figs 96A, 98F)

1962. *Cephalaspis major*; Balabai 1962: p. 4, fig. 3.
1985. *“Cephalaspis” major*; Janvier 1985b: p. 330, fig. 19C.
2006. *Zenaspis major*; Voichyshyn 2006b: pp. 15–16, text-fig. 2E, pl. 2, fig. 1.
2006. *Zenaspis major*; Voichyshyn 2006c: pp. 31–32.

Type specimen: Lectotype SMNH BP.995 (former number 25579), headshield contour without abdominal part; Horodnytsia, Horodenka rayon, Ivano-Frankivs’k oblast’ (Podolia).

Referred material. — Balabai (1962: p. 4) listed four specimens represented “mainly by shield contours”. Besides the lectotype I found one more specimen labelled by him “*Cephalaspis major*”, SMNH BP.31/1. It shows only imprints of cornual processes and is appreciably smaller in the shield size (Voichyshyn 2006b: pl. 2, fig. 2), belonging rather to *Z. podolica*.

Diagnosis. — Large sized *Zenaspis* species with relatively wide and massive cornual processes directed caudally.

Description and comparison. — The shield is sizable (L >118 mm, S 181 mm, Lrc 192 mm, H 160 mm, J 170 mm). Its shape is similar to that of *Z. podolica*, from which it differs (of a few features accessible to comparison) only by larger size. The cornual processes of average length are caudally directed and sharply narrowing to the ends. Their external sides are rather convex. The abdominal part of the shield is rather narrow (Si ≤ 89 mm). Lateral fields are somewhat dilated in their posterior part, in the same way as in *Z. podolica*, approaching bases of the cornual processes. Margins of the fields in this part are situated approximately in equal distances from the margins of the shield, 6 mm from the pectoral sinus and 7 mm from lateral margin of the shield. This is one of diagnostic features of the genus (Voichyshyn 2006).

Shields in other species of the genus are of smaller size than *Z. major*, and differ in their outline.

Remarks. — By its large size, an arrangement of the posterior part of lateral fields and general outlines of the shield this form is close to representatives of *Zenaspis* and *Diademaspis*. Considering the shape and position of posterior end of the lateral fields, this form should be attributed to the genus *Zenaspis*. However, lack of any other data on morphology of the shield does not permit one to be sure of this affiliation. It is possible that *Z. major* is conspecific with *Z. podolica*.

Localities and occurence. According to Balabai (1962), specimens of the type series of the species come from Horodnytsia and Ivanie, where strata of the lowest part of the Old Red are exposed; Lochkovian (likely Ustechko Stage of the Dniester Formation) of Podolia (Ukraine).

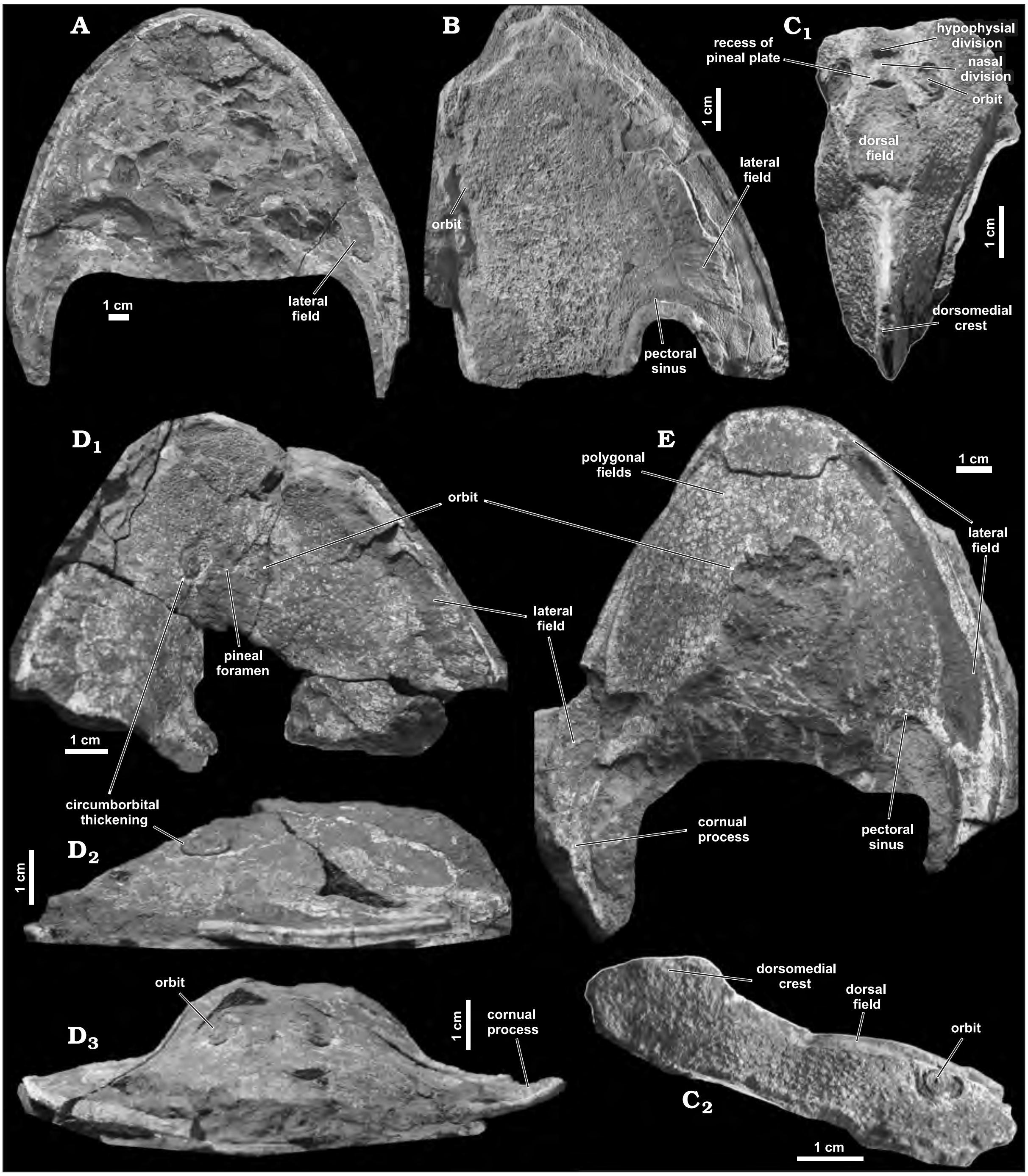


Fig. 96. Zenaspidids *Zenaspis* and *Diademaspis* from various localities of the Dniester Formation in Podolia. **A**. *Zenaspis major* (Balabai, 1962), margin of lectotype headshield SMNH BP.995 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. *Diademaspis stensioei* Afanassieva, 1989, imprint of left part of headshield SMNH BP.10, same locality, dorsal view. **C**. *Diademaspis* sp. 1, partial mould (central part) of headshield LDU (unnumbered) from unknown locality, lower part of the Dniester Formation, dorsal and lateral (right side) views. **D**. *Diademaspis stensioei* Afanassieva, 1989, partial mould of headshield SMNH BP.945 (see also Figs 36E, 99A) from the Horodnytsia new quarry talus, Ustechko Member or lower part of Khmeleva Member, dorsal, lateral (left side) and frontal views. **E**. *Zenaspis kasymyri* sp. n., the holotype fragmentary mould of headshield SMNH BP.1489 lacking its central and abdominal parts from Horodnytsia, Ustechko Member or lower part of Khmeleva Member, dorsal view.

Zenaspis kasymyri sp. n.
(Figs 96E, 97, 98C)

Derivation of the name: In honour of my father Dr. Kasymyr Voichyshyn.

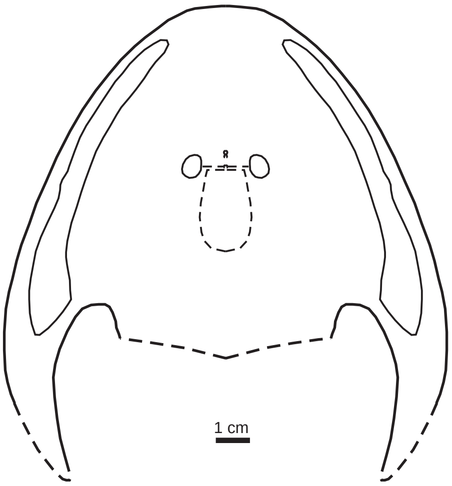


Fig. 97. *Zenaspis kasymyri* sp. n., reconstruction of the headshield in dorsal view.

Type specimen: Holotype SMNH BP.1489, fragmentary mould of the headshield lacking its central and abdominal parts, and the caudal ends of cornual processes; system of quarries SW of Horodnytsia (lower part of the "Old Red", probably Ustechko Stage of the the Dniester Formation), Horodenka rayon, Ivano-Frankivs'k oblast' (Podolia).

Referred material. — The holotype only.

Diagnosis. —*Zenaspis* species with medium sized narrow shield and massive cornual processes that bent admedially.

Description. — The shield is dorsally dome-shaped (hso 27 mm), about 100 mm in length, and narrowed anteriorly. Its maximum width (130 mm) is approximately at the level of the posterior end of lateral fields (L/S 0.77). Abdominal part of the headshield, probably, wide (Si ~60 mm, Si/S 0.47), but its outline remains unknown. The anterior margin of the shield is very widely rounded. The lateral margins are slightly convex. The cornual processes are thick and massive, long, and relatively wide, especially at their basis, and oriented postero-medially. Their internal margin bears no denticles. Pectoral sinus is asymmetric, and deep but not wide (F < 10 mm, Xsin <13 mm). Its tips are displaced to the medial axis of the body at 2/3 width of the sinus. The nasohypophyseal opening is not preserved. Orbits are of round to oval shape and rather small, widely disposed (Ol 6 mm, Os about 5 mm, Omin approximately equals 13 mm, S/Os 26, Omin/Os is about 2.6). Evidently, they were surrounded by a thin, somewhat more than 1 mm, circumorbital thickening. Neither pineal plate nor the dorsal field are preserved. The lateral fields are long (G 95 mm), and narrow in their anterior third. Then, they widen posteriorly, developing a medial blade in their posterior part. Their width ranges from about 5 mm at the anterior ends and in the "isthmus" between 2/3 and 3/3 of their length, to about 6 mm along the anterior third, and up to 11 mm in the posterior widening. Lateral fields reach the base of cornual processes. The distance between anterior ends of the lateral fields is considerably larger than the width of both orbits and distance between them taken together (I ~33 mm). The middle layer of the dermal skeleton contains polygonal, irregularly honeycomb-shaped medium sized units, about 2 mm in a diameter. The dermal skeleton of the shield, at least anteriorly, was rather thick. Distance between middle layer and outer surface is not less than 1 mm. The armour surface is visible in a small area of on the anterior part of the shield. It is not well preserved, but seems to be composed of much larger units than the middle layer, about 5 mm in diameter. The tubercles of surface ornamentation seem to be not preserved.

The shield of the holotype bears traces of being damaged *post mortem* on its left side. Left shield margin has an indentation, from which it is crushed medially to the inner margin of the lateral field. Also the left cornual process with adjacent part of the headshield was broken away and is displaced backward (Fig. 96E).

Comparison. — The species in question differs from all other species of *Zenaspis* by its narrow shield, relatively narrower anterior parts of the lateral fields and a large distance between them (value I), narrower pectoral sinuses, and postero-medially directed cornual processes. These features, together with unknown morphology of central and abdominal parts of the shield, make generic affiliation of the species to the genus somewhat problematic. However, other aspects of the morphology of *Z. kasymyri* sp. n., that is the shape and extent of the lateral fields, position of their caudal ends, size of the orbits and of the distance between them, and, possibly, character of the shield ornamentation, seem consistent with such placement. The new species is similar to *Z. podolica* and, to a less degree, to *Z. salweyi*, especially in the shape of the lateral fields and general shape, except for narrowing and bending of cornual processes, as well as size of the shield. *Zenaspis metopias* and *Z. major* are larger, while of *Z. dzieduszyckii* is of smaller shield size.

Among other genera of the family Zenaspididae, *Tegaspis* shows too peculiar shape of the headshield and lateral fields to be closely related with the species in question. The values of indexes L/S, B/C (approximately), S/Os, Omin/Os in the new species are out of range observed in *Diademaspis*, but agree with those of *Zenaspis*. Besides, the distance from the margin of the posterior part of the lateral field to the tip of the pectoral sinus is slightly smaller than that to the lateral margin of the shield, the condition shared by *Zenaspis* and *Tegaspis*, but not *Diademaspis* (Voichyshyn 2006a).

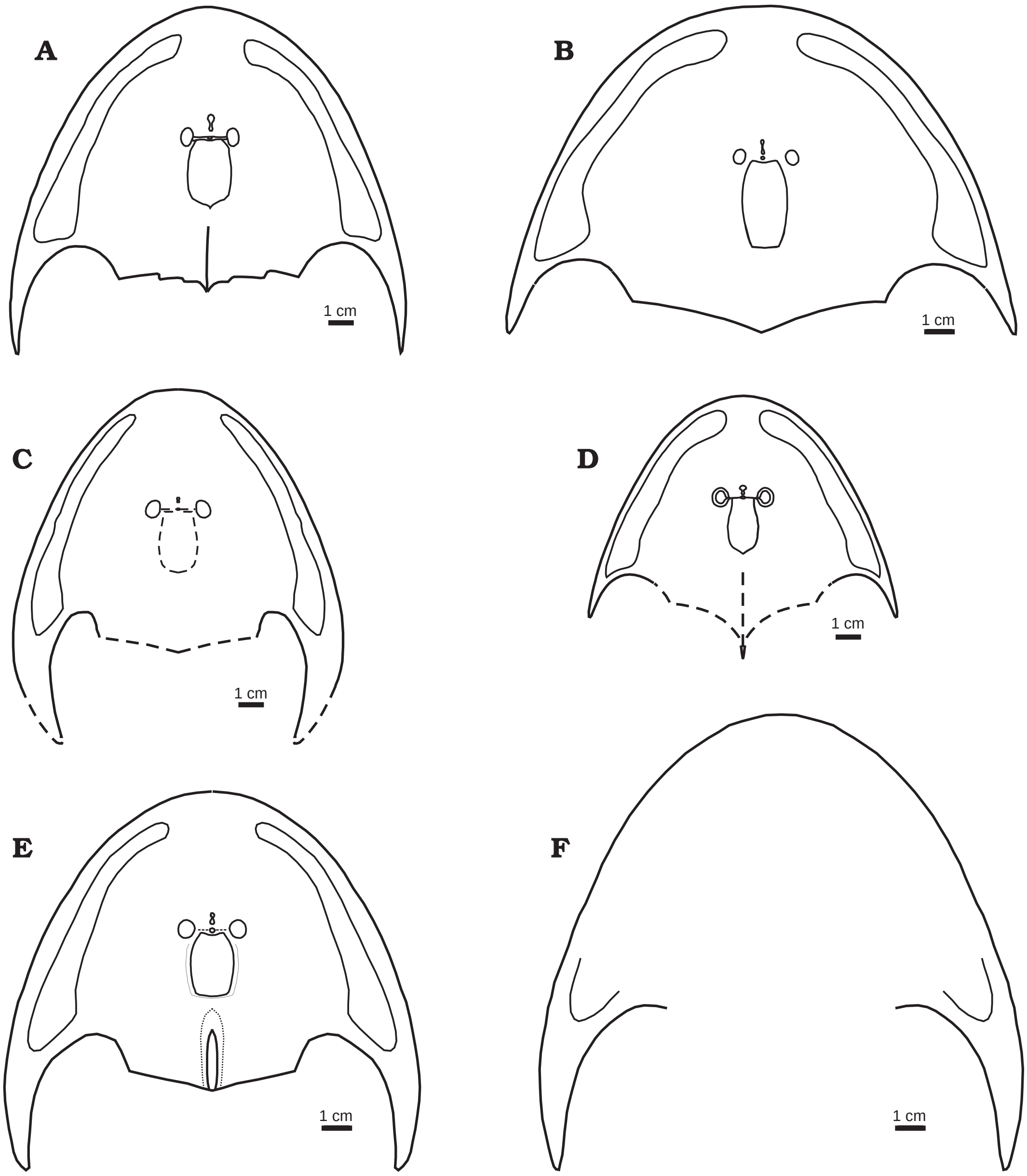


Fig. 98. Reconstructions of *Zenaspis* headshields. **A**. *Zenaspis salweyi* (Egerton, 1857) (after Janvier 1985a: fig. 63B). **B**. *Zenaspis metopias* (Wängsjö, 1952) (after Wängsjö 1952: fig. 56). **C**. *Zenaspis kasymyri* sp. n. **D**. *Zenaspis dzieduszyckii* Voichyshyn, 2006 (after Voichyshyn 2006a) **E**. *Zenaspis podolica* (Balabai, 1962) (after Voichyshyn 2006b: fig. 1A). **F**. *Zenaspis major* (Balabai, 1962) (after Voichyshyn 2006b: fig. 2E).

Localities and occurence. — Horodnytsia; Lochkovian, possibly to early Pragian (from Ustechko Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Genus *Diademaspis* Janvier, 1985a

1985. *Diademaspis*; Janvier 1985a: p. 183.
1985. *Diademaspis*; Janvier 1985b: p. 325.
1989. *Diademaspis*; Afanassieva 1989: pp. 55–56.
1991. *Diademaspis*; Afanassieva 1991: pp. 101–102.
1994. *Diademaspis*; Adrain and Wilson 1994: p. 315 (pars).
2004. *Diademaspis*; Afanassieva 2004: p. 258.
2006. *Diademaspis*; Voichyshyn 2006a: pp. 135–136.

Type species: *Diademaspis poplinae* Janvier, 1985a; Early Devonian (upper part of Wood Bay Formation) of Spitsbergen.

Diagnosis [modified after Janvier (1985a) and Afanassieva (1989)]. — Small to large sized zenaspidids (L 9–25 cm), with a headshield that is almost as long as wide (L/S 0.9–1.0). The prepineal part of the shield is considerably shorter than the postpineal one (B/C 0.6). The abdominal part of the shield narrows backwards and has a median dorsal crest. The hypophyseal division of the nasohypophyseal opening is much larger than the nasal division. The pineal plate is reduced or lacking. The orbital openings are relatively small (S/Os 27–29) and loosely spaced (Omin/Os is about 4), with a broad circumorbital thickening. The dorsal field is wide (S/Sd ratio equals about 7). The lateral fields are enlarged posteriorly and reach to the proximal part of the cornual processes. The distance from the margin of the posterior part of the lateral field to the tip of the pectoral sinus is ≥ 1.5 times larger than that to the lateral margin of the shield. The ornamentation consists of tesserae-like areas displaying groups of tubercles of different sizes.

Species included. — Besides the type species: *D. jarviki* (Wängsjö, 1952) from the Early Devonian of Spitsbergen; *D. stensioei* Afanassieva, 1989 and *Diademaspis* sp. 1, both from the Early Devonian of Podolia; *Diademaspis* sp. 1, *Diademaspis* sp. 2, *Diademaspis* sp. 3, and *Diademaspis* sp. 4 (Janvier 1985a) from the Early Devonian of Spitsbergen.

Remarks. — As to the proportion of the divisions of the nasohypophyseal opening of *Diademaspis*, a possible exception is *D. jarviki*, which has nasal and hypophyseal divisions that are almost equal in size (Wängsjö 1952: text-fig. 59). On the photograph of the holotype, this region is unclear, probably unsufficiently preserved (Wängsjö 1952: pl. 46, fig. 2). However, Janvier (1985a) pointed out that *D. jarviki* is similar to *D. poplinae* as to the shape of its nasohypophyseal opening.

Some shield fragments with the ornamentation typical of this genus were already reported as *Diademaspis* sp. from Ustechko and Chervonograd in Podolia (Janvier 1985b).

It is doubtful that *Diademaspis*? *mackenziensis* Adrain et Wilson, 1994 from the Northwest Territories of Canada belongs to the genus, because of considerable morphological difference between this species and the European species of *Diademaspis*. In contrast with the European species, the pineal plate of the Canadian species contacts the orbits which are considerably larger (S/Os 15) and more closely-set (Omin/Os 1.5). Also, the shape and size of the median dorsal field in these taxa are different (S/Sd of the Canadian form is 12.5). The headshield is noticeably narrower and its size (L 3 cm) is strikingly small in comparison with the size of the European headshields of *Diademaspis*. Finally, the dermal skeleton ornamentation which consists of elongated tubercles in *D.*? *mackenziensis* is not characteristic of the genus. The fact that the hypophyseal division of the nasohypophyseal opening is larger than the nasal one, may indicate that the Canadian species belongs to the Zenaspididae, but there seem to be no reasons to refer it to *Diademaspis* and, thus, to make the diagnosis of this genus less precise.

Occurrence. — Early Devonian of Spitsbergen and Podolia (Ukraine).

Diademaspis stensioei Afanassieva, 1989
(Figs 36E, 96B, D, 99A)

1989. *Diademaspis stensioei*; Afanassieva 1989: pp. 56–58, text-figs 2, 3.
1991. *Diademaspis stensioei*; Afanassieva 1991: pp. 102–104, text-fig. 17, pl. 22.
2004. *Diademaspis stensioei*; Afanassieva 2004: p. 258, text-fig. 37, pl. 15, figs 1, 2.

Type specimen: Holotype, PIN 3592/95, partial imprint of right part of headshield in dorsal view; Ustechko, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Fragments of the shield imprints SMNH BP.10, 945 and possibly BP.1225.

Diagnosis. — Relatively small sized *Diademaspis* species with large pineal opening and wide circumorbital thickening.

Description. — The length of the shield is ~90 mm, the maximum width, in the middle of the cornual processes, is a little bit more. The cornual processes are narrow, thick enough, of moderate length and laterocaudal direction. The abdominal division of the shield is narrow and rather short. The orbits are relatively small (Ol/A 0.3, Os/A ~0.2). Circumorbital thickening is wide enough. The nasohypophyseal opening is poorly preserved, though there are grounds to consider that its shape was typical for the genus. The hypophyseal division is in a deepening. The pineal plate is lacking. The pineal opening is large (~2×2.3 mm). The lateral fields are long enough, somewhat broadened in the posterior part, and reach the base of the cornual processes. Traces of the ornamentation were preserved in general only. It consisted of tubercles of ~0.7 mm in diameter, which were grouped in 3–5.

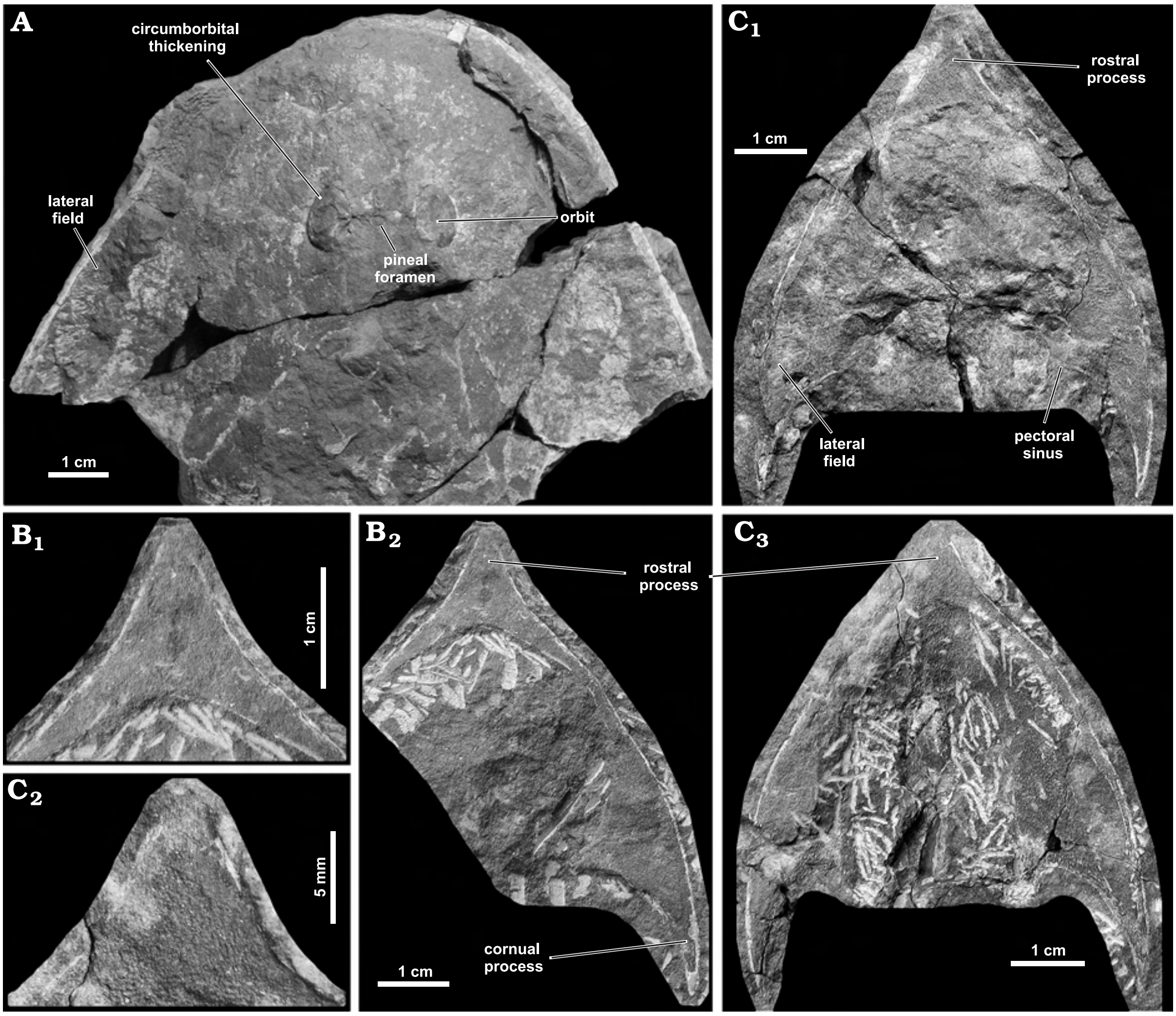


Fig. 99. Zenaspidids and problematic osteostracans from various localities of the Dniester Formation in Podolia. **A**. *Diademaspis stensioei* Afanassieva, 1989, partial mould of headshield SMNH BP.945 (see also Figs 36E, 96D) from the Horodnytsia new quarry talus, Ustechko Member or lower part of Khmeleva Member, dorsal view. **B**. *Wladysagitta janvieri* Voichyshyn, 2006, fragmentary headshield SMNH BP.100 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member, rostral part and complete ventral view. **C**. Same species, the holotype fragmentary mould of headshield SMNH BP.102, same locality, dorsal view, enlarged rostral part and imprint.

Comparison. — The considered species differs from all Spitsbergen species of the genus by larger pineal opening, wider circumorbital thickening, and lesser size. Besides, *D. poplinae* has pineal plate, shorter and thickener cornual processes, while *D. jarviki* has wider shield, and lesser distance between the lateral margin of the shield and posterior part of the lateral fields.

Diademaspis sp. 1 differs from *D. stensioei* by its type of ornamentation. Other material for comparison with this species is unavailable.

Localities and age. — Ustechko; probably from Late Lochkovian to early Pragian (probably from Ustechko Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

Diademaspis sp. 1
(Fig. 96C)

2006. *Diademaspis* sp.; Voichyshyn 2006a: p. 136, figs 5, 6.

Referred material. — Mould of the central part of a headshield, from the nasohypophyseal opening to the median dorsal crest, GMLSU 478, 4; locality unknown.

Description. — The distance between the anterior limit of the nasohypophysial opening and the posterior limit of the median dorsal crest is 70 mm. Thus, the length of the headshield is, probably, 90–100 mm. The orbits are oval and relatively small. Their length is 7 mm and the width is about 5 mm. The circumorbital thickening is 1.2–1.3 mm wide. The distance between orbits is relatively small as for *Diademaspis*, 13 mm. The nasohypophyseal opening has an enlarged hypophyseal division, that is sunken into a depression and a small nasal division. The pineal plate seems to be reduced, without any contact with the orbits. Its width does not exceed the extent of the anterior margin of the median dorsal field. The recess of the pineal plate has a cleft-like shape with a maximum length along the body axis of 1.5 mm and width of 6.5 mm. The median dorsal field is 22 mm long and has concave and narrowed anterior and posterior margins, and convex lateral ones. The posterior margin of the dorsal field displays two lateral processes separated by a 2 mm deep cavity between them. The maximum width of the median dorsal field (13 mm) is at the level of its second third. The median dorsal crest is well developed. Its length is about 25 mm, the height up from the level of the median dorsal field is 10 mm, with a slope that begins immediately behind the posterior margin of the median dorsal field. The ornamentation of the dermal skeleton is poorly preserved. It seems to consist mainly of tesserae-like areas (about 1 mm in size), which include relatively large rounded tubercles surrounded by considerably smaller ones.

Comparison. — This form differs from *Diademaspis poplinae* by its chink-like shape of the pineal plate, the shape of the median dorsal field (in particular, its more convex lateral margins), the more developed median dorsal crest, and the smaller overall size. It differs from *D. jarviki* by its greater size of the hypophyseal division of the nasohypophyseal opening, the presence of a pineal plate and the shape of the median dorsal field.

It is not possible to compare the form described here to the shield fragment from Ustechko, assigned to as *Diademaspis* sp. (Janvier 1985b: fig. 16A), because they represent different parts of a shield. It is not clear, whether the tubercles formed groups in the form described here, as it is in the specimen from Ustechko. In any case, they were more densely spaced than in the fragment from Ustechko.

This specimen differs from *Diademaspis* sp. 2 (Janvier 1985a) by the shape and greater size of the orbits, the longer (along the body axis) pineal plate, and the concave anterior margin of the median dorsal field, which becomes conspicuously broader in its middle part. This form is, however, similar to *Diademaspis* sp. 2 by the lateral extent of its pineal plate. Like in the following cases, other features cannot be compared because of the poor preservation of the specimens. From *Diademaspis* sp. 3, it differs by the less steep rise of the median dorsal crest. From *Diademaspis* sp. 4, it differs by shorter orbits, smaller distance between the anterior margin of the nasohypophyseal opening and the line connecting the anterior margins of the orbits, and probably by its different type of ornamentation. Besides, this form differs from all *Diademaspis* species from Spitsbergen, including *Diademaspis* sp. 1, by its smaller overall size, and, except for *Diademaspis* sp. 4, by its more closely spaced orbits. Comparison with *D. stensioei* is given in its description.

Localities and age. — Precise locality is unknown; probably from Late Lochkovian to early Pragian (probably lower part of the Dniester Formation) of Podolia (Ukraine).

Genus *Tegaspis* Wängsjö, 1952

1927. *Cephalaspis*; Stensiö 1927: pp. 278–279 (pars).
1952. *Tegaspis*; Wängsjö 1952: pp. 437–438.
1984. *Tegaspis*; Belles-Isles and Janvier 1984: p. 202.
1985. *Tegaspis*; Janvier 1985a: p. 130.
1991. *Tegaspis*; Afanassieva 1991: pp. 104–105.
2004. *Tegaspis*; Afanassieva 2004: pp. 258–259.

Type species: *Cephalaspis kolleri* Stensiö, 1927; Early Devonian of Spitsbergen.

Diagnosis. — Osteostracans of medium to large size (L 90–150 mm, S > L). Anterior margin of the shield usually has a wide rostral corner. The cornual processes are long and flattened. The abdominal division of the shield is narrowed backwards. Dorsomedial crest is low. Size of the divisions of the nasohypophyseal opening is about equal. The pineal plate is lacking. The dorsal field is not wide. The lateral fields are long, have posteromedial ledge, and do not transgress on the surface of the cornual processes.

Species included. — Besides the type species, *Tegaspis waengsjoei* Belles-Isles *et* Janvier, 1984, possibly *T.*? sp. 1, both from the Early Devonian of Podolia, and possibly *T. pedata* (Wängsjö, 1952) from Spitsbergen.

Occurrence. — Early Devonian of Spitsbergen and Podolia (Ukraine).

Tegaspis waengsjoei Belles-Isles *et* Janvier, 1984

1984. *Tegaspis waengsjoei*; Belles-Isles and Janvier 1984: pp. 202–205, figs 3, 4, pl. 27, fig. 3a, b.
1991. *Tegaspis waengsjoei*; Afanassieva 1991: p. 105.
2004. *Tegaspis waengsjoei*; Afanassieva 2004: p. 259, text-fig. 38.

Type specimen: Holotype NHRM C1a, b, incomplete headshield in dorsal view and its partial imprint around posterior part of left lateral field; Zastinoche, Terebovlia rayon, Ternopil' oblast' (Podolia).

Remarks. — The headshield length (95 mm) and width (145 mm) are approximate due to incomplete preservation. The shield exhibits such characteristic features of the genus as the presence of a posteromedial ledge of lateral fields and narrowing of the shield's abdominal part. Belles-Isles and Janvier (1984) consider *T. waengsjoei* more primitive than the species from Spitsbergen.

Localities and age. — Zastinoche; probably Lochkovian (possibly Ivanie Stage of the Tyver formation) of Podolia (Ukraine). No similar material is known in the SMNH collection.

Tegaspis? sp. 1

(Fig. 35F)

Referred material. — Rim of headshield including cornual processes SMNH BP.53; from Nagiriany W.

Description. — Medium sized *Tegaspis* form, L about 120 mm, S 156 mm. Anterior margin of the shield is widely rounded. Lateral margin seems being divided on two segments by hardly visible corner. Both the segments are almost straightened. The abdominal division of the shield is narrowed backwards (Si 58 mm). Pectoral sinuses are large and deep (F 20 mm), their tips are rounded. The cornual processes are well developed (M 60 mm, Lrc 160 mm, Ls 100 mm, Lrc/Ls 1.6) and considerably bent to the body axis, so that the maximum width of the shield falls on their middle.

Comparison. — The described form differs from *Tegaspis kolleri* (see Wängsjö 1952: text-fig. 75, pl. 65, fig. 1, pl. 66) by the outline of rostral margin of the shield, widely rounded in *T.*? sp. 1 and having an angle in *T. kolleri*, wider and more bent inwards cornual processes, considerably narrower pectoral sinuses, and narrower shield of smaller size.

Comparison with *T. pedata* is difficult because of poor preservation of specimens in both forms. The shape of abdominal division of the headshield in the Podolian specimen is similar to that of *T. pedata*, but the proximal part of the cornual processes seems to be wider.

The described form differs from *T. waengsjoei* by its somewhat larger size, and, probably, by less wide shield, and shares with this species shape of the abdominal division of the shield. Too few features have preserved in both the taxa for comparison.

Remarks. — The main problem in determination the relationship of this form with genus *Tegaspis* is lack of data about shape of posterior ends of lateral fields.

Localities and age. — Nagiriany; from Late Lochkovian to early Pragian (Ustechko Stage or lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

“Cornuata” incertae sedis

Genus *Wladysagitta* Voichyshyn, 2006

1985. “*Cephalaspis*”; Janvier 1985b: p. 331 (pars).
2006. *Wladysagitta*; Voichyshyn 2006a: pp. 136–138.

Type species: *Wladysagitta janvieri* Voichyshyn, 2006; Early Devonian (Ustechko Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia.

Diagnosis. — Small sized cornuate osteostracans. The length of the headshield (40–60 mm) is more or less the same or somewhat smaller than its width (L/S 0.8–1.0). The anterior margin of the headshield forms an elongated to triangular rostral process. The lateral fields are long, somewhat broadened in their posterior third. Their rounded anterior ends are closely approaching the base of the rostral process, and their sharp posterior ends reach to the middle parts of the cornual processes. The cornual processes are relatively short and narrow. The ornamentation of the dermal skeleton consists of tiny elongated tubercles.

Comparison. — According to the classification of the Osteostraci, proposed by Afanassieva (1991), *Wladysagitta* differs from the genera referred to the Benneviaspidoidei by the shape of the headshield and the presence of tubercles on the dermal skeleton. It differs from some superficially similar representatives of the

Boreaspididae, in particular *Dicranaspis*, by having one, instead of two pairs of lateral fields, and by its considerably greater general size. It differs from the known genera of the Zenaspididae by the presence of a rostral process.

Taking into account the proportions of the shield, the relative size, shape and orientation of the cornual processes, and the extent of the lateral fields, *Wladysagitta* appears to be similar to several representatives of *Pattenaspis* having a rostral lobe, best developed in *P. eurhynchus* (Wängsjö, 1952), although this lobe does not extend into the rostrum. *Pattenaspis* includes a wide diversity of forms, and may be heterogenous (Afanassieva and Voichyshyn 1991). It may even not belong to the Cephalaspididae (Janvier 1985b). Typical cephalaspidids, such as *Cephalaspis*, *Parameteoraspis*, and *Mimetaspis* have virtually no ornamentation, or it consists of very small tubercles. Instead, headshields of the species of *Pattenaspis* from Spitsbergen and Great Britain have a prominent ornamentation, usually consisting of thorn-like tubercles, contrary to the original descriptions by Wängsjö (1952; Janvier, personal communication 1998). Along with the presence of rostral process, *Wladysagitta* differs from *Pattenaspis* by the shape of lateral fields that are slightly broadened in their posterior third, probably by the shape and smaller size of the tubercles of the headshield ornamentation, and by lacking denticles on the inner margin of cornual processes.

In contrast, *Wladysagitta* resembles primitive zenaspidids, in particular *Zychaspis*, by its exoskeletal ornamentation. It should be noted that *Zychaspis* is also characterised by having an incipient rostral lobe (Janvier 1985b; Voichyshyn and Solodkyi 2004). Thus, considering the available data, *Wladysagitta* may be regarded as morphologically intermediate between *Pattenaspis* and primitive zenaspidids.

A similar development of the rostral process characterises *Yvonaspis campbelltonensis* (Otto *et* Laurin, 1999) from the Early Devonian Campbellton Formation of New Brunswick, Canada (Sansom 2009a: fig. 3), but there are other differences between these forms.

Species included. — Besides the type species, *Wladysagitta acutirostris* (Stensiö, 1932), Early Devonian of Great Britain.

Occurrence. — Early Devonian of Podolia (Ukraine) and Great Britain.

Wladysagitta janvieri Voichyshyn, 2006
(Fig. 99B, C)

1985. "*Cephalaspis*" cf. *acutirostris*; Janvier 1985a: p. 331, fig. 20A.
2006. *Wladysagitta janvieri*; Voichyshyn 2006a: pp. 138–139, figs 7, 8, 9B–D.
2006. *Wladysagitta janvieri*; Voichyshyn 2006c: p. 34.

Type specimen: Holotype SMNH BP.102, fragmentary mould of headshield and its imprint; Ustechko, left bank of the Dniester River, Zalishchyky rayon, Ternopil' oblast' (Podolia).

Referred material. — Besides the holotype, fragment of the headshield exposed in ventral view SMNH BP.100.

Diagnosis. — A moderately large species of *Wladysagitta* with asymmetrical pectoral sinuses and with narrowed anterior and posterior ends of lateral fields.

Description. — The headshield is narrow (L about 50 mm; S 55–58 mm; Lrc about 60 mm). The rostral part of the shield is extended into a clearly outlined process, about 10 mm in length, with concave lateral sides and a rounded distal end (Fig. 99B, C). Lateral margins of the shield are moderately convex with an irregular curvature. The maximum width of the shield is either in the middle part of the cornual processes or at their tips. The cornual processes are relatively short, not very broad at their bases, and conspicuously narrow in their distal part. They start to point caudally at the level of their middle part. The lateral margin of the cornual processes is straight or slightly convex, whereas its medial margin is slightly concave. The abdominal part is narrow (Si/S 0.47). The pectoral sinuses are asymmetrical (Fig. 99C). Their tips (anterior margin) lie closer to the body axis. The lateral fields are slightly broader in their posterior third, with pointed posterior ends. The surface of the headshield is rather evenly covered with oval to elongated, closely set tubercles, the length of which ranges from 0.3 mm in the preorbital region (0.3–0.5 mm on the interzonal part) to 0.6 mm along the medial margin of the proximal part of the cornual processes.

Comparison. — In contrast with *W. acutirostris*, this species has proximally broader and relatively longer cornual processes (Lrc/Ls of *W. janvieri* is 3.2–3.6 whereas it is 4.0 in *W. acutirostris*), a narrower abdominal part of the shield, different shape, and greater width of pectoral sinuses, larger overall size, and a possibly wider headshield, originally higher and narrower.. Stensiö (1932) considered the specimen of

W. acutirostris somewhat flattened. The two species are similar in their general contours of the headshield, in particular by the curvature of their lateral headshield margins. Nevertheless, the imperfectly preserved rostral part of *W. acutirostris* and, as a whole, poor preservation of the material examined does not allow resolving the relationship between them.

Remarks. — The two specimens of *W. janvieri* housed in SMNH belong to an assemblage containing few well-preserved carapaces mainly of osteostracans: *Benneviaspis whitei*, *Stensiopelta pustulata*, *Pattenaspis rogalai*, and *Zychaspis granulata*. Among heterostracans, *Zascinaspis heintzi* and *Weigeltaspis brotzeni* are represented in this assemblage. Since the sediment is fine-grained, with an admixture of argillaceous fractions, the assemblage may have formed under quiet hydrodynamic conditions. The relatively good preservation of the carapaces seems to indicate that this assemblage is autochtonous (Voichyshyn 1997).

One of the specimens, referred here to *W. janvieri*, i.e. BM(NH) P.20508 (Janvier 1985b: fig. 20A) from Horodnytsia, differs from the holotype by somewhat longer and thinner cornual processes of more or less caudal orientation, whereas the cornual processes of the holotype are gently curved. Another specimen (Fig. 99B) from the same locality and layer as the holotype is represented by a fragment of the shield exposed in ventral view, with preserved rostral and cornual processes. The contours and proportions of the cornual processes, lateral margins of the shield and rostral process in this specimen are practically the same as in the holotype, but its cornual processes seem to be somewhat more diverging, i.e., the maximum width of the shield is found at the tips of the cornual processes. Possibly, all these differences are either due to individual variation, or post-mortem distortions of the shields.

Localities and age. — Ustechko and Horodnytsia; late Lochkovian to early Pragian (from Ustechko Stage to lower part of Khmeleva Stage of the Dniester Formation) of Podolia (Ukraine).

STRATIGRAPHIC DISTRIBUTION OF THE PODOLIAN AGNATHANS AND GNATHOSTOMES

The Early Devonian agnathan fossil assemblages of Podolia are among the richest, best preserved and oldest known in the world. They actually serve as the reference standard to the international correlation of continental strata of this part of the geological time scale. It is thus of special importance to describe properly and understand their succession.

A network of faults splits the Palaeozoic strata of Podolia into numerous blocks, which makes a long distance tracing of particular beds exposed in the banks of the Dniester tributaries virtually impossible. The uneven distribution of fossils within the succession further complicates the picture. Because of this, biostratigraphic zonations of the Early Devonian based on vertebrate fossils is still rather crude. Presumably, the stratigraphic distribution of armoured agnathans in Podolia is controlled both by their evolution and dependence on environmental changes.

The rarity of fish fauna remains in the Silurian of Podolia is probably a result of relatively deep-water conditions of sedimentation. The remains of near-shore early vertebrates had little chance to be transported to such environments (Fig. 7) and, instead, the dominant chordates were conodonts. Only near the end of the Silurian, considerable shallowing of the sea took place as a result of uplifting of the craton (Fig. 1B). The oldest known Podolian agnathan, represented by the fragmentary rostro-orbital part of the shield of *Irregulareaspis skalskiensis*, described by Novitskaya (1986) from the vicinity of Dnistrove village (see also Abushik *et al.* 1985), from the upper part of the latest Silurian Skala Stage (Dzvenygorod Beds; Fig. 1). Scales of *Turinia polita* and “*Nostolepis*” have been also mentioned from this locality (Blieck and Janvier 1991). Together with unnumerous acanthodian scales (*Nostolepis* sp. and “*Gomphodus*” sp.) found in the same rock unit at Myshkivtsi, these are the oldest vertebrate founds on the territory of Ukraine (Voichyshyn 2001a). In the Late Silurian of Estonia (Märss and Einasto 1978), acanthodians dominated in shoal, open-shelf, and slope deposits. Only in lagoonal deposits, the contribution of thelodonts was similar to that of acanthodians. The situation in Podolia was probably similar. The abundance of vertebrates in Estonia decreased with deepening of the basin. Blieck and Janvier (1991) suggested that general scarcity of Silurian vertebrates reflects their low preservational potential because many species had only unfused microscopic size skeletal elements.

MARINE DEVONIAN STRATA

The Podolian basin was gradually shallowing in the earliest Devonian and the amount of vertebrate remains in its deposits increased. However, from the Borshchiv Stage, the oldest unit of the Devonian of Podolian, no representative of the vertebrate groups contributed to fish faunas of that time elsewhere. No cyathaspidids, pteraspidids, or cephalaspidids has been reported, except for unumerous scales of thelodonts and acanthodes, and fin spines of the latter (Karatajūtė-Talimaa 1978; Voichyshyn 2001b). Valiukevičius (2000) listed seven acanthodian species from the Borshchiv Stage based on isolated scales.

Open-sea facies. — The subsequent in age, Chortkiv Stage is characterised by yet shallower marine deposits. There is a mass occurrence of scales of thelodonts *Turinia pagei* (Powrie, 1870), *T. polita* Karatajūtė-Talimaa, 1978, *Nikolivia balabayi* Karatajūtė-Talimaa, 1978, *N. elongata* Karatajūtė-Talimaa, 1978, *Apalolepis obruchevi* Karatajūtė-Talimaa, 1968, rare scales of *Gampsolepis insueta* Karatajūtė-Talimaa, 1978 (Karatajūtė-Talimaa 1978), scales and fin spines of the acanthodians (*Nostolepis* sp. ind., "*Gomphodus*" sp. ind., *Onchus* sp. ind.) (Obruchev and Karatajūtė-Talimaa 1968), small plates of arthrodires (*Tyriolepis radiata* Karatajūtė-Talimaa, 1968), and scales of the probable chondrichthyan *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 (Karatajūtė-Talimaa 1968), in these strata. Also, scales of the chondrichthyan elasmobranch? *Seretolepis elegans* Karatajūtė-Talimaa, 1968 (Karatajūtė-Talimaa 1968; Obruchev and Karatajūtė-Talimaa 1968), *Knerialepis mashkovae* (Karatajūtė-Talimaa, 1997), *Altholepis composite* Karatajūtė-Talimaa, 1997 and *Ivanelepis costulata* Karatajūtė-Talimaa, 1997 (Karatajūtė-Talimaa 1997; Hanke and Karatajūtė-Talimaa 2002; Märss *et al*. 2008) were found in limestone beds of the Chortkiv Stage. The number of recognised acanthodian forms reached 17, including all species from the preceding Stage (Valiukevičius 2000) as well. The cyathaspidids are represented by the single known specimen of *Seretaspis zychi* (Novitskaya 1986), a few *Poraspis sturi* from Zozulyntsi and Doroshivtsi (Novitskaya 1986), as well as mainly microscopic fragments of *Poraspis* sp. and *Irregulareaspis* sp. from the upper part of the unit (Figs 14B–D, F, G, 15D, E, 16C). Microscopic fragments of *Corvaspis kingi* (Fig. 17D, E, H, M, N) and *Corvaspis* sp. (Fig. 17B, I, J–L), fragments (Fig. 29A, C, E–G) and scales (Fig. 28A, J, M, P–R) of pteraspidids, tesserae of *Lepidaspis*-like heterostracans (Fig. 79A, F, I), and other not identifiable vertebrate microremains (ichthyoliths) occur here.

Novitskaya (1986) suggested that *Ctenaspis kiaeri* also comes from the Chortkiv Stage, but all known specimens of this species, belonging to the SMNH collection of Zych, are from Jagilnytsia Stara, where the Ivanie Stage is exposed. The Ivanie Stage was earlier understood by some authors as a "transitional beds" from the Chortkiv Stage to the Dniester Formation (Obruchev and Karatajūtė-Talimaa 1968; Nikiforova and Predtechenski 1972; Talimaa 1981).

The oldest Podolian pteraspidids come from the Chortkiv Stage (Fig. 26A, B) too. Blieck (1984: fig. 23) figured a cast of perfectly preserved specimen of *Larnovaspis kneri* from Gorodok (see also Lebedev *et al.* 2009: fig. 1), probably also referred to by Obruchev (1973). *Podolaspis lerichei* and *Larnovaspis major* of Talimaa (1981) may correspond to this and similar unpublished specimens. Possibly *Semipodolaspis slobodensis* gen. et sp. n. (Fig. 54A) comes from the Chortkiv deposits too. Otherwise, remains of pteraspidids, preserved well enough to be determined at species level, are extremely rare in the Podolian marine deposits. Among remains of other heterostracans, isolated tesserae of *Traquairaspis* (probably *Lepidaspis*) are recorded from there (Obruchev and Karatajūtė-Talimaa 1968). Some remains of *Cephalaspis* sp. were reported from the same stage (Nikiforova and Predtechenski 1972; Obruchev and Karatajūtė-Talimaa 1968: fig. 51).

Near-shore facies. — The Ivanie Stage strata were deposited in a coastal area of a very shallow sea. They yielded numerous and diverse fish fossils. Among cyathaspidids, *Poraspis sturi* (Dobrivliany) and all the remaining (except for *Irregulareaspis skalskiensis*) endemic Podolian species of the order Cyathaspidiformes (*Poraspis simplex*, *P. siemiradzkii*, *P. pompeckji*, *Ctenaspis kiaeri*, *Irregulareaspis seretensis*, and *I. stensioei*) are present (Novitskaya 1986, 2004). The only Podolian corvaspidid species, *Corvaspis kingi*, reaches beyound the Chortkiv-Ivanie boundary (Fig. 17A, F, O).

Among the pteraspidids, *Podolaspis* is the most abundant in the Ivanie Stage, represented by *P. lerichei* and rare *P. zychi* (Figs 51A, C, D, 52A). *Larnovaspis kneri* ranges probably throughout the entire Stage (Fig. 62A, B, E), while *L. major* is restricted to its upper part, and *L. iwaniensis* is sporadic (Novitskaya 1986, 2004). Blieck (1984) reported also the single specimen of *Alaeckaspis*? *depressa* from Kasperivtsi.

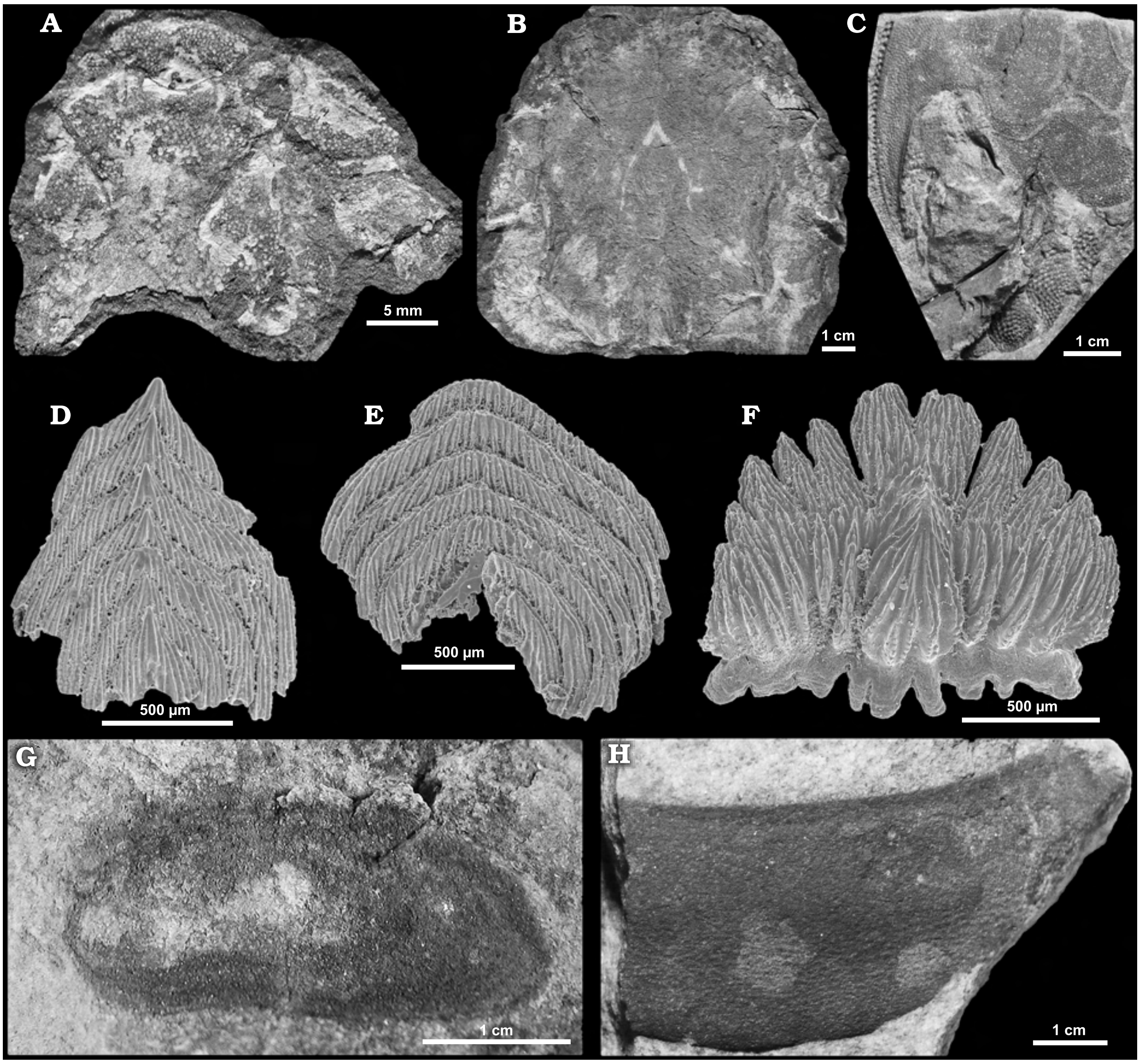


Fig. 100. Fossils of correlative value and palaeocological indicators associated with the Podolian armoured agnathans. **A**. Placoderm *Kujdanowiaspis podolica* (Brotzen, 1934), mould of skull roof and right cheek SMNH BP.901/1 from Nagiriany, slab from talus at SE slope of Dzhuryn River meander, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view. **B**. Same species, mould of skull roof SMNH BP.145 from Khmeleva, left bank of Dniester River at (river) water level, Khmeleva Member, dorsal view. **C**. Same species, partial imprint of plastron and dermal elements of the tail SMNH BP.137 from Ustechko, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation, dorsal view. **D**. Chondrichthyan *Seretolepis elegans* Karatajūtė-Talimaa, 1968, posterior part of scale SMNH BP.1545/8 from outcrop 2 (Fig. 3B), right bank of Dniester River, middle to upper part of Ivanie Member of the Tyver Formation. **E**. Same species, fragmentary scale SMNH BP.1539/2 from Zalishchyky, right bank of Dniester River, upper part of Ivanie Member of the Tyver Formation. **F**. Chondrichthyan *Polymerolepis whitei* Karatajūtė-Talimaa, 1968, scale (lost specimen) from outcrop 8 (Fig. 3B), right bank of Dniester River, lower to middle part of Ivanie Member of the Tyver Formation. **G**. Bivalve shell mould SMNH BP.595/2 from Zaryvyntsi, quarry, Strypa Member of the Dniester Formation. **H**. *Eurypterus* sp., fragmentary mould of body segment SMNH 37702 from Zaryvyntsi quarry, Strypa Member of the Dniester Formation.

Parapteraspis lata and *Zascinaspis bryanti* seem to be restricted to the Ivanie Stage (Dobrivliany, Zalishchyky, Jagilnytsia Stara, and Ivanie Zolote), whereas *Zascinaspis heintzi* ranges up to the lower part of the Dniester Formation. It is commonly asumed (Novitskaya 1986, 2004; Obruchev and Karatajūtė-Talimaa 1968) that *Belgicaspis crouchi*, which is one of index fossils in the zonation of the Early Devonian in Western Europe, has a similar stratigraphic distribution also in Podolia. However, until now, this species is known in Podolia only as a deformed rostral plate from Pechirna, described by Novitskaya (1986), and a few other incomplete rostral plates, possibly belonging to the species from the SMNH collection (Fig. 19B, C). Articulated specimens, enabling species determination with a reasonable confidence, are still lacking. Blieck (1984) identified some of dorsal shields, figured by Zych (1927) and Brotzen (1933a) from the upper part of the Ivanie Stage and the lower part of the Ustechko Stage (first zone of the Old Red according to Brotzen 1933a), as *B. crouchi*. Similar shields were found by myself at Ustechko in the lowest part of the Khmeleva Stage and referred to as "*Pteraspis*" *angustata* (Fig. 21B, C; Voichyshyn 1999). Without questioning the presence of *B. crouchi* in Podolia, in the present study, the existing evidence seems to be insufficient to prove this fact.

Parameteoraspis dobrovlensis, from the Ivanie Stage deposits at Dobrivliany, is the oldest known Podolian osteostracan (Afanassieva 1991). It is believed that *Ukrainaspis kozlowskii* (Zych 1937: Zalishchyky and Vorvulyntsi) and possibly *Zychaspis siemiradzkii* (Janvier 1985b: Khomiakivka) come from these strata (Afanassieva 1991). However, according to Dikenshtein (1957), the Ustechko Stage is exposed at Khomiakivka, and in the upper part of the section at Zalishchyky. The claim of Janvier (1985b) and Afanassieva (1991) that *Mimetaspis glazewskii* at Ustechko occurs in the Ivanie Stage is unlikely, because only a few metres of that unit are exposed at this locality in the lowermost part of the section on the right bank of Dzhuryn River. According to present observations, this species (Fig. 83A–D) is widespread from the middle part of the Ustechko Stage to lower part of Khmeleva Stage.

Among microscopic-size fish remains, the thelodonts and acanthodians are the most diverse in the Ivanie Stage. All thelodont species, known from the Chortkiv Stage except for *Nikolivia balabayi*, range to it. In addition, *Nikolivia oervigi* (Karatajūtė-Talimaa, 1968) and *Apalolepis brotzeni* Karatajūtė-Talimaa, 1978 appear there for the first time (Karatajūtė-Talimaa 1978). All the chondrichthyan species of the Chortkiv time were present also in the Ivanie basin (Fig. 100D–F). Ørvig (1961) reported a fragment of dermal plate, that is now referred to as *Tesseraspis orvigi*, at Jagilnytsia Stara in strata referred to the "upper part of Czortków Group". The scale-based number of acanthodian species decreased to 10 (Valiukevičius 2000). Many pteraspid scales (Fig. 28B, D, G–I, K, L), scales and shield fragments of *Poraspis* sp. (Figs 11H–J, 15A, C), *Irregulareaspis* sp. (Fig. 14A, E), and *Lepidaspis*-like heterostracans (Fig. 79B, G, H, J, L, M) are represented in the Ivanie Stage deposits as microremains.

Macroremains of the climatiid acanthodian *Ptomacanthus* sp. are represented by a shoulder girdle from Zalishchyky (Miles 1973; Denison 1979).

Age of the strata bearing fish remains at the middle of the Seret River, which is one of the main tributaries of the Dniester River in Podolia (Fig. 4), is considered as corresponding to Ivanie time, but the depositional conditions are similar to those of Dniester time elsewhere, i.e., lowered salinity lagoons or lakes. If true, the fresh-water fish fauna of the Ivanie time consisted of the pteraspidids *Alaeckaspis verbivciensis*, *Djurinaspis secunda* sp. n., *Larnovaspis mogielnensis*, *Podolaspis lerichei*, *Zascinaspis heintzi*, the osteostracan *Pattenaspis rogalai*, *Tegaspis waengsjoei* from Zastinoche (Belles-Isles and Janvier 1984), and the placoderm *Ericaspis zychi* (Stensiö, 1945).

TERRIGENOUS DEVONIAN STRATA

Unike the Ivanie Stage deposits, represented to a large degree by marine carbonates, organodetrital limestone in particular, the Dniester Formation is exclusively terrigenous (sandy-argillaceous, often reddish). The Ustechko section recorded an upward transition from offshore to inshore lagoon or bay, and finally to a fluvial-estuarine plain (Uchman *et al.* 2004). The rather rich fossil fish assemblage characterises the lowest unit of the Dniester Formation, the Ustechko Stage, the deposits of which accumulated in a low-salinity lagoon (Narbutas 1984). However, *Poraspis sturi*, the only cyathaspidid, was found here (Ustechko, Dzhuryn River). Except for already mentioned *Zascinaspis heintzi*, *Larnovaspis major* (Horodnytsia) and *Podolaspis lerichei* range to there from the Ivanie Stage as well. The pteraspidids *Djurinaspis prima* and *Mylopteraspis gracilis* seem to belong to species restricting in distribution to the Ustechko Stage. According to Novitskaya (1986), the oldest occurrence of *Brachipteraspis latissima* is from this rock unit. *Brachipteraspis* sp. cf. *B. latissima* was reported by Dumbrava and Blieck (2005) at Babyn from, presumably, also Ustechko Stage deposits, however, it is poorly supported (see the Taxonomy Chapter).

Although osteostracan remains are considerably less common than those of the pteraspidids, in the Ustechko Stage they are numerous enough, and diverse. *Stensiopelta pustulata* (Horodnytsia, Buriakivka, Bily Potik, Nagiriany), *Zychaspis siemiradzkii* (Horodnytsia, Chervonograd), *Zenaspis podolica*, *Z. kasymyri* sp. n., *Mimetaspis concordis*, and *Ukrainaspis kozlowskii* (Horodnytsia), *Mimetaspis glazewskii*, and, possibly, *Diademaspis stensioei* (Ustechko), together with *Benneviaspis whitei* (Ustechko) and *Machairaspis* sp. (Horodnytsia) are represented (Belles-Isles and Janvier 1984; Janvier 1985b; Afanassieva 1991, 2004).

Scales of the thelodonts *Turinia pagei*, *T. polita*, and possibly *Nikolivia elongata* (Karatajūtė-Talimaa 1978), as well as seven acanthodians (Valiukevičius 2000) are reported from the Ustechko Stage, although the siliciclastic rocks of the Dniester Formation cannot be disintegrated with acetic acid, which prevents extraction of well-preserved vertebrate microremains.

In the Ustechko Stage, placoderms are represented by *Ericaspis zychi* (Ivanie Zolote, Ustechko, Buriakivka) and *Kujdanowiaspis podolica* (Brotzen, 1934) (Horodnytsia, Ustechko; Fig. 100C). Remains of both species occur also in the Khmeleva Stage deposits.

The placing of the boundary between the Ustechko and Khmeleva Stages at Ustechko, one of the best studied Podolian agnathan localities, is still disputed. According to Dikenshtein (1957) and Drygant (1988), almost all the Lower Devonian section exposed on the left bank of the Dniester River upstream of Ustechko, near the old destroyed bridge, is the lowest part of the Khmeleva Stage. But, according to the stratigraphic scheme proposed by Narbutas (1984), only the Ustechko Stage is exposed at Ustechko. I adhere to the former opinion, suggesting 52–54 m thickness of the Ustechko Stage (Levets' and Ustechko Stages of Dikenshtein 1957). Due to a fault along the Dzhurin River, the section of Lower Devonian, starting from the upper part of the Ivanie Stage, is exposed on the left river bank, being older than exposed on the left bank of Dniester near the destroyed bridge (Narbutas 1984). The upper 10 m of the Ivanie Stage, the whole Ustechko Stage section (54.5 m) and, possibly, the a few lowest metres of the Khmeleva Stage are exposed in the former of these sections, reaching more than 64 m in thickness. Strata of the Khmeleva Stage, according to Dikenshtein (1957) 120–170 m in thickness, are characterised by thick layers of siltstones with subordinate intercalations of sandstone (Dikenshtein 1957), visible also in exposed on the left bank of Dniester 40 m thick section.

There is a small but important difference between the fossil assemblage in the lowest part of the Ustechko section on the left bank of Dniester, approximately at the boundary between the Ustechko and Khmeleva Stages, and in its middle part, i.e. the lowest part of the Khmeleva Stage. Poraspid remains are lacking in the latter, while in the former they are abundant and dominate the assemblage. Still, two specimens (probably of *Poraspis sturi*) have been found recently in Ustechko, in beds of the lowest part of Khmeleva Stage of the Dniester Formation.

Possibly, this is an expression of a change from lagoon to river or delta environment. There is a similarity between the fossil vertebrate assemblage from Ustechko and that from Horodnytsia, according to Dikenshtein (1957) (see also Uchman *et al.* 2004) representing the Khmeleva Stage, but poraspid remains are missing in Horodnytsia. Rare shields of *Poraspis* sp. were found on slopes of the old river-bed of the Dzhuryn River between Nyrkiv and Nagiriany villages.

It appears that the lower part of the Khmeleva Stage (Ustechko, the left bank of the Dniester River) is characterised by abundant fish fossils. Near the base of the stage, *Poraspis sturi*, *Pavloaspis pasternaki*, and *Ukrainaspis kozlowskii* occur. *Alaeckaspis ustetchkiensis*, *Weigeltaspis alta*, *W. brotzeni*, *Zychaspis granulata*, *Mimetaspis concordis*, *Benneviaspis whitei*, and *Wladysagitta janvieri* were found a few metres above this horizon. *Zascinaspis heintzi*, *Podolaspis podolica*, *Parapteraspis plana*, *Zychaspis siemiradzkii*, *Stensiopelta pustulata*, *Pattenaspis rogalai*, *Zenaspis podolica*, and others range there from the Ustechko Stage.

The vertebrate fauna of the second faunal Old Red zone of Brotzen, as understood and discussed in the next section, is much less known than the first and to some extent the third faunal zones, because of its usually poor preservation. Nevertheless, it includes at least four osteostracan species, "*Cephalaspis*" *dniestrensis* (*Pattenaspis rogalai*) (Janvier 1988), *Zychaspis elegans* (Fig. 87B), *Stensiopelta*? *pustulata* (Fig. 6D), and *Zenaspis podolica*, from the vicinity of Khmeleva. Among them, *Z. elegans* is represented by its only known specimen (Voichyshyn 2006b, c). Pteraspidids are probably represented by *Zascinaspis heintzi*, placoderms by *Erikaspis zychi* and *Kujdanowiaspis podolica* (Dupret and Blieck 2009; Dupret 2010; Fig. 100A, B). The fish fossil assemblage of the middle to upper parts of the Khmeleva Stage is poorly known, because uncertain extend of this unit. Dikenshtein (1957) traced Khmeleva Stage deposits along Strypa River from its mouth up to Buchach, whereas Novitskaya (1986) referred to this unit the lower and middle parts of the section between Kydaniv and Sapova, which, probably, are part of the younger Strypa Stage.

Deposits of the Strypa Stage, represented mainly by quartz sandstone (Dikenshtein 1957), were formed in deltaic conditions (Narbutas 1984). This is reflected in rare vertebrate remains. Agnathans occur as moulds of ventral, less commonly of dorsal plates or shields. Pteraspid finds are restricted to the lower and middle parts of the section exposed in the quarry between Kydaniv and Sapova. *Althaspis elongata*, *A. sapovensis*, *Brachipteraspis latissima*, and *Europrotaspis arnelli* occur there (Novitskaya 1986), accompanied by *Benneviaspis zychi* and *Citharaspis junia* (Afanassieva 1991). A few specimens of *Althaspis longirostra* were described from Kopachyntsi on the Dniester by Zych (1927), and *A. sapovensis* (Novitskaya 1986) has been found in upper part of the section. The single specimen of *Althaspis*? *spatulirostris* is known from an outcrop in vicinity of Soroky (Blieck 1984). An imprint of the rostral plate of a large widesnouted pteraspidid *Palanasaspis chekhivensis* gen. et sp. n. from vicinities of Chekhiv (Fig. 19A) does not resemble any known species of established stratigraphic position (Voichyshyn 1999). Pteraspidid remains, that are too poorly preserved to be classified, occur also in other fossil fish localities of the lower part of the Strypa River and Koropets' River basins (Voichyshyn 2001a). Osteostracans of the Strypa Stage deposits possibly include also *Citharaspis polonica* from Buchach (Belles-Isles and Janvier 1984; Afanassieva 1991) and *Victoraspis longicornualis* (Carlsson and Blom 2008). The shoulder girdle of relatively large climatiid acanthodian *Erriwacanthus falcatus* Ørvig, 1967 was described from Zvenygorod (Ørvig 1967; Denison 1979).

Outcrops of the Strypa Stage are not precisely enough correlated with the regional stratigraphy to enable reliable presentation of the distribution of vertebrates within the unit.

The Smerkliv Stage of the Dniester Formation, which concludes the exposed section of the Dniester Formation in Podolia, can be traced along the Dniester River from Smerkliv to Nyzhniv, partially along the Koropets' River (Dikenshtein 1957) and possibly also in the small outcrop at Zavadivka. However, there are no reliable finds of fish remains in these deposits. Only Balabai (1960) reported the pteraspid *Brachipteraspis latissima* from Zavadivka (Voichyshyn 2001a).

VERTEBRATE BIOSTRATIGRAPHIC UNITS IN THE DEVONIAN OF PODOLIA

Zych (1927), Brotzen (1933a) and Balabai (1960) tried to divide the Podolian succession of the Early Devonian into biostratigraphic assemblage ("faunal") zones. Zych's (1927) subdivision into eight zones was based on classification of the agnathans, which is now considered artificial. Brotzen (1933a) offered a more reliable scheme, dividing the Podolian Old Red into three zones. The lowest corresponds, in present understanding, to lithostratigraphic interval from the Ustechko Stage to the lower part of Khmeleva Stage of the Dniester Formation. The middle corresponds to the remaining part of the Khmeleva Stage. The highest zone corresponds probably to the Strypa Stage. Narbutas (1984) inclined to a similar identification of these zones with lithostratigraphic divisions. Balabai (1960) criticised validation of the second Brotzen's zone, but he himself divided the Podolian red-colored deposits into three zones, admitting that his scheme coincided with that of Brotzen (1933a). Novitskaya (1986) used in her work a zonal division of the Old Red after Obruchev (1973), who applied his scheme after Brotzen (1933a), as indicated before (Obruchev 1958). Other researchers (Blieck 1984; Janvier 1985b) also used the same scheme, focusing mainly on the first and third zones that are represented by completely different assemblages (Table 1, Figs 104, 105; but see the probable distribution of *Victoraspis longicornualis* in the Taxonomy Chapter). The middle zone, in comparison with the two others, is almost barren, with rare fossils that mainly cannot be identified at the species level. Neither Brotzen (1933a) nor Balabai (1960) was successful in characterizing that zone precisely. It is necessary to note that Novitskaya (1986) divided the third Brotzen's zone into her own second (with *Althaspis elongata* and *Europrotaspis arnelli*) and third (with *Althaspis longirostra*) faunal zones within the Dniester Formation, which seem unclearly defined.

Parallel to the agnathan zonation, three assemblage zones are distinguished in the Podolian Old Red, based on succession of placoderms (Dupret and Blieck 2009). The lower unit is characterised by the occurrence of *Kujdanowiaspis podolica* (Brotzen, 1934) and *Ericaspis zychi* (Stensiö, 1945). The middle zone contains *Kujdanowiaspis podolica*, *K. buczacziensis*, and *Ericaspis zychi*. The upper one is characterised by the presence of *Kujdanowiaspis buczacziensis* only. Dupret and Blieck (2009) considered this species as the index fossil for the beginning of the Pragian in the Podolian section, but its remains are restricted to the Strypa Stage of the Dniester Formation. Probably, the Lochkovian–Pragian boundary in the Podolian section is located rather within the lower part of the Ustechko Stage of the Dniester Formation (Drygant, personal communication 2010). The lower and upper zones of the placoderm-based scheme correspond to the first and third zones of Brotzen's scheme; however, the boundaries of the middle zone remain unclear.

BIOSTRATIGRAPHIC CORRELATION OF THE PODOLIAN SECTION

Correlation of the Podolian section, based on unique agnathans, with those in other regions of the world, based on the principle of homotaxy, can hardly refer to occurrences of common species but, at the best, on generic composition of fossil fish assemblages (Table 2). This makes precision of interregional correlation rather low.

The scheme of correlation of the Podolian section, in particular that of Old Red deposits, with Early Devonian deposits of Spitsbergen and England is based on agnathans (Blieck 1984) and is generally accepted (Afanassieva 1991; Novitskaya 1983; Janvier 1985b). Such application of homotaxy at the generic level, to the Early Devonian agnathan fossil assemblages, allows their rough correlation between geographically distant regions.

Thus, the fossil assemblage of the "*Vogti*" horizon (middle part of the Ben Nevis Formation) of the Early Devonian of Spitsbergen, including *Larnovaspis goujeti*, *Irregulareaspis* sp., *Poraspis rostrata*, *Ctenaspis cancellata*, *Ctenaspis* sp., *Corvaspis* sp., and *Lepidaspis* sp. (Blieck 1982), is similar in its composition to the fossil assemblage from the Ivanie Stage of Podolia, including *Larnovaspis kneri*, *Irregulareaspis stensioei*,

Table 2. Geographic distribution of armoured agnathan genera from Podolia (number of Podolian species/ number of all species of the genus given in parentheses).

	Great Britain	Spitsbergen	France and Belgium	Canadian Arctic	Other regions
Ctenaspis (1/6)	?	■	–	■	Severnaya Zemlya
Irregulareaspis (3/5)	–	■	–	–	Severnaya Zemlya
Poraspis (4/9)	■	■	■	■	Severnaya Zemlya
Seretaspis (1/1)	–	–	–	–	–
Corvaspis (1/4)	■	■	–	■	Lithuania
Alaeckaspis (4/4)	–	–	–	–	–
Althaspis (5/8)	■	–	■	–	–
Belgicaspis (1/1)	■	–	■	–	–
Brachipteraspis (1/1)	–	–	–	–	–
Djurinaspis (2/2)	–	–	–	–	–
Dnestraspis (1/1)	–	–	–	–	–
Europrotaspis (1/3)	■	–	?	–	–
Larnovaspis (4/6)	■	■	–		
Loricopteraspis (1/1)	–	–	–	–	–
Mylopteraspis (1/1)	–	–	–	–	–
Mylopteraspidella (1/1)	–	–	–	–	–
Palanasaspis gen. n. (1/1)	–	–	–	–	–
Parapteraspis (2/2)	–	–	–	–	–
Pavloaspis (1/1)	–	–	–	–	–
Podolaspis (4/4)	–	–	–	–	–
Semipodolaspis gen. n. (1/1)	–	–	–	–	–
Zascinaspis (2/4)	–	?■	–	–	USA (Ohio)
Tesseraspis (1/6)	■			■	Germany, Lithuania
Weigeltaspis (2/4)	■	■	–	–	–
Benneviaspis (3/8)	–	■	–	–	Severnaya Zemlya
Citharaspis (2/2)	–	–	–	–	–
Diademaspis (1/3)	–	■	–	–	–
Mimetaspis (2/5)	–	■	–	–	–
Parameteoraspis (1/11)	–	■	–	–	–
Pattenaspis (1/12)	■	■	–	–	Germany
Stensiopelta (1/2)	■	–	–	–	–
Tegaspis (1/2)	–	■	–	–	–
Ukrainaspis (1/1)	–	–	–	–	–
Victoraspis (1/1)	–	–	–	–	–
Wladysagitta (1/2)	■	–	–	–	–
Zenaspis (4/6)	■	■	–	–	–
Zychaspis (4/4)	–	–	–	–	–

Poraspis sturi, *P. siemiradzkii*, *Ctenaspis kiaeri*, *Corvaspis kingi*, and *Lepidaspis* sp. Blieck (1982) correlated the "*Vogti*" horizon with the lower part of the Middle Dittonian of England.

The upper part of the Ben Nevis Formation ("*Benneviaspis*" horizon; late Lochkovian according to Blieck 1984) resembles the first zone of the Podolian Old Red in containing remains of *Zenaspis metopias* and small shields of *Benneviaspis holtedahli* in Spitsbergen on one side, and *Zenaspis* species and small-size *Benneviaspis talimaae* in Podolia on the other.

The lower part of the Wood Bay Formation (Sigurdfjellet Division) contains remains of large *Benneviaspis* (*B. maxima*, *B. loevgreeni*, and *B. grandis*), which are similar to *B. zychi* from the third zone of the Podolian Old Red (Afanassieva 1991). However, only in the Fraenkelryggen Formation, which was compared by Blieck 1984 to the Borshchiv and Chortkiv Stages of the Tyver formation, and in the "*Vogti*" horizon, *Pattenaspis* and *Machairaspis* occur. They are related to the Podolian *Pattenaspis rogalai* and "*Cephalaspis*" *microlepidota* from the first Old Red zone. A possible cause of such disparity, in correlation of sections based on agnathan assemblages, is their ecological sensitivity. In fact, the main problem with applying the principle of homotaxy for reliable correlation is that it can be applied only for correlation between ecologically similar successions.

A correlation of the Early Devonian deposits of Russia, Belarus, Ukraine, and Baltic States was based on acanthodian scales by Valiukevičius (2000). According to him, deposits of the Borshchiv Stage and lower part of the Chortkiv Stage are of early Lochkovian time, while the interval from the upper part of Chortkiv Stage to the lowermost part of the Dniester Formation corresponds to the late Lochkovian.

FOSSIL FISH ASSEMBLAGES IN THE EARLY DEVONIAN OF PODOLIA

The concept of fossil assemblage denotes series of fossil remains of organisms preserved in a rock unit (layer, lens etc.). Recognition of fossil communities is the first step in the inference leading to restoration of living community of ancient organisms. It also provides insight into the conditions of sedimentation and fossilization. The main obstacle preventing interpretation of fossil communities, as directly representing structure (standing crop) of their living counterparts, is that they usually are products of prolonged supply of skeletal remains to the sediment, resulting in time averaging of the record. The contribution of particular species to the fossil community reflects, in such a situation, their participation in the biological productivity rather than contribution to the biomass (standing crop). The picture is further disturbed by preservational bias during sedimentation (e.g., Gekker 1954; Korth 1979; Behrensmeyer 1988; Wilson 2008; Zohar *et al.* 2008) and selective diagenesis. Skeletal remains can be transported for a long distance and while exposed to the seawater environment easily disintegrate as a result of bioerosion. The correspondence between fossil and living communities may be almost direct if the former originated as a result of a catastrophic sedimentation event. Yet another problem, related to recognition and interpretation of fossil communities, is sampling bias. To limit it, the fossil specimens ought to be collected from a rock unit of possibly restricted time and space dimension. In the case of relatively rare fossil vertebrate remains, they have to be assembled from a rock of considerable thickness and extent. In practice, one has to refer to a fossil locality rather than a stratum as the source of the Early Palaeozoic armoured fish.

Two sources of evidence on fossil assemblages of armoured fossil fish have to be considered separately: microremains (ichthyoliths) below a few millimetres in size and macroremains, mostly centimetre, but frequently decimetre, in size. Most fish microremains from Podolia, except for tiny armour fragments difficult to classify taxonomically, represent acanthodian gnathostomes and thelodont agnathans. Their easily disintegrating skeletal armour consisted of discrete dermal denticles, tesserae, or teeth. Macroremains belong mainly to heterostracan (cyathaspidids and pteraspidids) and osteostracan agnathans. Their skeleton formed a consolidated carapace covering the head region, which consisted of a single skeletal unit (osteostracans) or a number of plates (heterostracans). Armoured agnathans of this kind make the bulk of species in the Early Devonian fish fauna of Podolia.

Marine clay and carbonate deposits (Tyver Formation). — Phosphatic skeletons of fish contribute to rich fossil assemblages of the Early Devonian grey-coloured marine deposits of Podolia, composed of

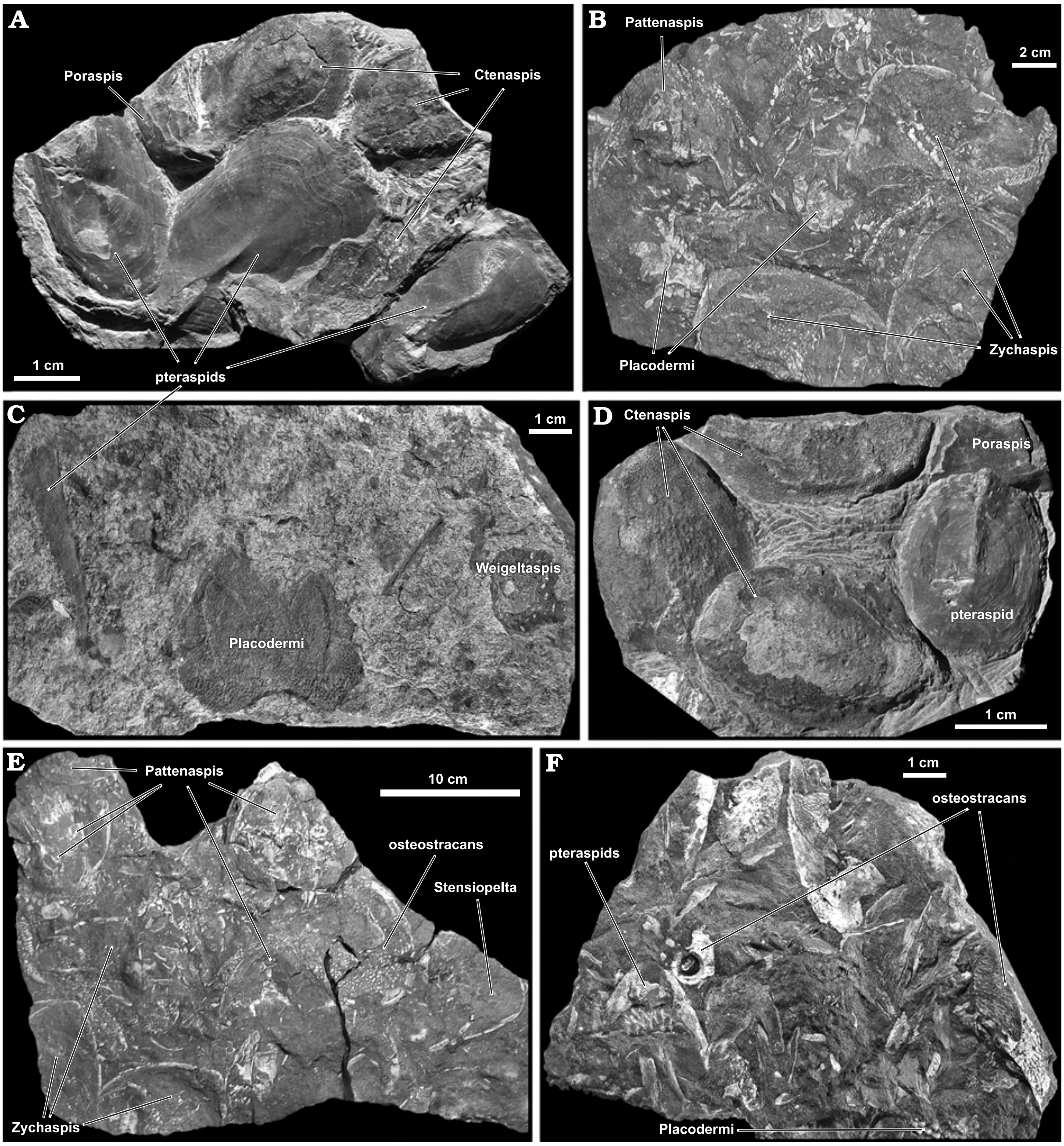


Fig. 101. Mass occurrence of vertebrate remains from the Devonian of Podolia showing co-occurrence of various fish species. **A**. Fossil assemblage with accumulation of agnathans (*Ctenaspis*, *Poraspis* and pteraspidid remains) on slab SMNH BP.916 from Jagilnytsia Stara, Ivanie Member of the Tyver Formation. **B**. Fossil assemblage with association of agnathan and placoderm fishes (*Pattenaspis*, *Zychaspis* and Placodermi remains) on slab SMNH BP.902 (counterpart of SMNH BP.901; see Fig. 101E) from Nagiriany, from talus at SE slope of Dzhuryn River, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **C**. Agnathan-placoderm accumulation (*Weigeltaspis*, pteraspidid and Placodermi remains) on slab SMNH BP.1126 from Horodnytsia, Ustechko Member or lower part of Khmeleva Member of the Dniester Formation. **D**. Agnathan accumulation (*Ctenaspis*, *Poraspis*, and pteraspidid remains) on slab SMNH BP.915 from Jagilnytsia Stara. **E**. Agnathan accumulation (*Pattenaspis*, *Zychaspis, Stensiopelta* and other osteostracan remains) on slab SMNH BP.901 (counterpart of SMNH BP.902; see Fig. 101B) from Nagiriany, talus at SE slope of Dzhuryn River meander, Ustechko Member or lower part of Khmeleva Member. **F**. Agnathan-placoderm accumulation (osteostracan, pteraspidid and placoderm remains) on slab SMNH BP.201 from Ustechko, left bank of Dniester River, lower part of Khmeleva Member.

calcitic shells of brachiopods and ostracods, moulds of originally aragonitic shells of gastropods, bivalves, and nautiloids, phosphatic conodonts, organic scolecodonts, and others. Vertebrates from the latest Silurian and earliest Devonian Borschiv and Chortkiv Stages, as well as a considerable part of the Ivanie Stage, are almost exclusively represented by microremains of thelodonts and acanthodians. From the Chortkiv Stage and higher, minute fragments of heterostracan carapaces and scales are also encountered (Figs 28A, J, M, P–R, 29A, E; Obruchev and Karatajute-Talimaa 1968). They express a general tendency of increasing density and diversity of vertebrate remains upwards through the section.

Macroscopic agnathan fossils occur in assemblages of marine origin at Jagilnytsia Stara, corresponding in age to Ivanie time (Lochkovian). Material from this locality was collected by Władysław Zych in 1934 and is kept in the SMNH collection, but also in the GMLSU and the NHRM collection (Balabai 1957, 1962; Blieck 1984). The collections consist of numerous fragments of shields and plates of heterostracan carapaces as well as their imprints and moulds in claystone, mudstone or limestone (Fig. 101A, D). Both lithology and associated fossils prove their marine origin. Taphonomic conditions at the beginning of sedimentation of these deposits, as well as the generally small size of the agnathans, promoted preservation of undamaged external moulds of the carapaces or intact carapaces. The assemblage consists mostly of cyathaspidids: *Ctenaspis kiaeri*, *Irregulareaspis stensioei*, and *Poraspis siemiradzkii*. Along with the cyathaspidids, pteraspidids were found as well. Small-sized (about 20–40 mm in length) dorsal and ventral shields are the most numerous. The armour abraded or dissolved molds of ventral and rare dorsal shields of medium size (60–100 mm in length) specimens of undetermined genera are less common. Blieck (1984) suggested that they may belong to *Parapteraspis lata*. Among the pteraspidids, seven specimens were identified as *Zascinaspis bryanti* (Figs 24G, H, 70A–D, G). Fragments of a carapace of *Corvaspis* sp. are the only other heterostracans (Fig. 17C).

The fossil fish assemblage from Jagilnytsia Stara is unique for Podolia in two respects. First, most pteraspidid and cyathaspidid specimens are very small, with few exceptions. However, the small-sized cyathaspidids apparently represent mature individuals, whereas the pteraspidids are probably juveniles. Most of their dorsal shields still have no dorsolateral sensory canals (Fig. 34A, C, D, G, H, J). Except for the dorsal and ventral, other plates of the pteraspidid carapace are rare (Figs 19G, 24D). This suggests transportation of the pteraspidids from a distant source, disintegration, and size sorting. Also, the relatively large specimens of the pteraspidids (ventral and dorsal plates) were redeposited. Because of their weight, they were apparently not transported in suspension but rolled over the bottom, losing the armour surface cover.

The second unusual aspect of this fossil fish assemblage is its high taxonomic diversity. Jagilnytsia Stara is the only locality in Podolia with more than one cyathaspidid species. This is also the only place in Podolia where cyathaspidids prevail over pteraspidids in number of species and volume of fossil remains. Remains of *Poraspis sturi* dominate also in a bed near the Ustechko and Khmeleva Stages boundary at Ustechko. The rarity of macroscopic remains, in the marine deposits of Podolia outside Jagilnytsia Stara, may have resulted from unfavorable living conditions for the agnathans in relatively deep-water, or taphonomic factors preventing accumulation of their remains. The taphonomic factor seems to be supported by the distribution of the irregulareaspidids, with the unique specimen of *Irregulareaspis skalskiensis* encountered in the latest Silurian deposits (Novitskaya 1986) and the subsequent occurrence of taxonomically identifiable irregulareaspidids (and cyathaspidids in general) in the Ivanie Stage. They are absent in the Borshchiv and Chortkiv Stages, except for carapace fragments of the Poraspididae reported from the Chortkiv Stage by Obruchev and Karatajūtė-Talimaa (1968) and those in the SMNH collection. Still, the fossil assemblage from Jagilnytsia Stara testifies that cyathaspidids flourished in Podolia during the Ivanie time.

Blieck and Heintz (1983) noticed a similar domination of cyathaspidids both in biological productivity (number of fossilised specimens) and species diversity in the heterostracan assemblages from deposits of the Upper Red Bay Group in northwest Spitsbergen. Together with *Poraspis*, *Irregulareaspis*, and *Ctenaspis* known from Jagilnytsia Stara, species of *Dinaspidella*, *Homalaspidella*, and several species of *Anglaspis* are also present in Spitsbergen. Novitskaya (2007) indicated that the worldwide peak of diversity for cyathaspidids was in the Lochkovian.

Unlike the cyathaspidids, there is no convincing indication of water salinity preferences for the pteraspidids from Jagilnytsia Stara. Later pteraspidids inhabited probably flowing fresh water. Probably, they were able to live in water of unstable salinity, and could accompany marine cyathaspidids in the original community. This is consistent with the relatively good, not different from that of the cyathaspidids, preservation of the armour cover of pteraspidids, suggesting short post-mortem transportation. Remarkably, remains of the osteostracans, usually indicating fresh-water, are completely lacking at Jagilnytsia Stara.

The geologically oldest of the Podolian osteostracans known till now have been found among agnathan macroremains on the left bank of the Dniester River eastward of Dobrivliany (Fig. 5A), where the lower part of the Ivanie Stage crops out. They are *Parameteoraspis dobrovlensis* (Afanassieva 1991), shields of *Poraspis* sp., plate and separate tesserae of *Corvaspis kingi* (Fig. 17A, F, O), fragmentary imprint of the median plate of *Weigeltaspis brotzeni* (Fig. 82C) along with ventral and dorsal shields, and other carapace plates (Figs 22J, 23A, 25F, 33E, G) of pteraspidids (including ?*Larnovaspis kneri*; Fig. 19H). Unfortunately, lack of precise information on their collecting sites does not allow identification of fossil assemblages.

At least two fossil assemblages can be distinguished in deposits of the upper part of the Ivanie Stage at Zalishchyky (Fig. 5B). The first comes from limestone beds, extraordinarily rich in fish microremains. Most of the thelodont species known from Podolia, numerous remains of acanthodians and arthrodires, tiny fragments of heterostracan carapaces (in particular of *Poraspis* and pteraspidids), and also fragments of large shells of ostracods (genus *Leperditia*) were found there. Of agnathan macroremains, rare pteraspidid ventral plates occur.

Rather complete moulds of agnathan carapaces are parts of the second fossil assemblage at this locality. They co-occur with intact ostracod shells in marly limestone, deposited in rather quiet conditions that enabled better fossil preservation. These are poraspidid remains (Figs 9B, 11A–C), shields of numerous rather small-sized pteraspidids (with carapace length of 60–80 mm), mainly *Podolaspis lerichei*, *Parapteraspis lata*, also fragments of the carapace of *Larnovaspis* sp. and *L. kneri* (Figs 19D, 24B, 32B, 51A, D, 58A, 62A, B, E). In the Ivanie Stage, the agnathans rarely reached sizes such as in the lower part of the Dniester Formation, even if they represented the same species. This may be a result of different mortality patterns or *post mortem* sorting.

Grey-coloured terrigenous deposits. — The fish fossil assemblage from the sandstone at Verbivtsi originated during Ivanie time but under continental influence atypical for other localities of that age. Agnathan remains are represented by moulds of dorsal carapaces of the pteraspidids. Skeletons are preserved rather well, mostly in peripheral not-elevated parts of the carapace, but they are generally abraded, probably while transported (Figs 51B, 66B, D, F). Specimens of *Alaeckaspis verbivciensis* are numerous. Single specimens of *Podolaspis lerichei* and *Zascinaspis heintzi* were also found. Probably, they all come from a freshwater environment.

At the transition from Ivanie to Dniester time, taphonomic conditions significantly changed. Sedimentation took place in a shallowing sea, to which rivers, floods, and winds transported terrigenous material (dust, sand, washed off soil) from the land. This deeply influenced the nature of the fossil assemblages of the Old Red:

(1) Fine carbonate silt, clay and detritus of marine invertebrates skeletons were replaced with quartz sand and mud. Transportation by high-energy waters together with sand grains resulted in abrasion of skeletal remains of marine agnathans. The outer layer is frequently missing. The porous rock enabled late diagenetic dissolution of the calcium phosphate composing the vertebrate skeleton. As a result, moulds or natural casts only preserve information about the original morphology of the agnathan skeleton.

(2) The same abrading and corrosive factors of the environment of sedimentation and diagenesis affected phosphatic microremains of vertebrates, considerably softer and chemically less resistant than quartz. They are poorly preserved in the sandstone. Their preparation is difficult, and even the fossil material extracted from clay it is of low quality.

(3) Long-range transportation together with the terrigenous sediment by fresh waters resulted in extensive mixing of remnants of organisms originally living in different environments. The fish fossil assemblages of Dniester time may have include species of inhabitants of fresh, brackish, hypersaline, and normal salinity waters.

Red-coloured continental deposits (Dniester Formation). — The lower part of the Dniester Formation, from the Ustechko Stage to the lower part of the Khmeleva Stage, is the richest in macroremains of armoured vertebrates within the whole Devonian section, not only in number of specimens but also species diversity (Table 1; Figs 104, 105). Within the Ustechko to early Khmeleva time, almost all morphological types of Podolian osteostracans are represented, from the smallest *Mimetaspis concordis* (20 mm in length) to the largest *Zenaspis major* (up to 120 mm in length), from high-vaulted *Pattenaspis rogalai* and "*Cephalaspis*" *microlepidota* (Afanassieva and Voichyshyn 1991) with developed dorsal crest (spine) to species of *Benneviaspis* with wide flat shields lacking spines, from horseshoe-shaped *Ukrainaspis kozlowskii* to *Wladysagitta janvieri* with the anterior margin of the shield stretched out in a rostrum. The pteraspidids are no less diverse. Some pteraspidid species (e.g., *Dnestraspis firma*, *Alaeckaspis ustetchkiensis*) were found only in the lower part of the Khmeleva Stage. The cyathaspidids (*Poraspis sturi*) occur only at the transition from the Ustechko to Khmeleva Stage. The amount and size of macroremains increases at the transition from the underlying alternation of mudstone with organodetrital limestone to reddish sand-clay rocks (Old Red facies). It gives an impression that it is a result of change in freshwater influences.

At Ustechko (Fig. 5E), two fish-bearing horizons have been sampled in detail. The lower horizon yielded remains of *Poraspis sturi* and corresponds roughly to the boundary between the Ustechko and Khmeleva Stages of the Dniester Formation (Figs 10D, 41A, D, 42B). The second layer, with remains of *Mimetaspis concordis*, is located about 16 m higher and belongs to the lower part of the Khmeleva Stage.

In the older layer with the *Poraspis* assemblage, fossils are common but their orientation within the rock is chaotic. The dominant rock type is a red mudstone, mainly stratified. Beds are of changing thickness, that may not exceed a few millimetres, and then contain small and fragmentary fossils, or may achieve thicknesses of 5–10 cm, with relatively complete carapaces or their large fragments. The pteraspidids are represented by single, but relatively well-preserved mature individuals of *Zascinaspis heintzi*, *Parapteraspis plana*, *Podolaspis podolica*, and *Pavloaspis pasternaki* (Figs 49A, B, 57B, 67A, 78A). Separate shields of the osteostracans *Pattenaspis rogalai* (Fig. 85E), *Ukrainaspis kozlowskii*, and *Zenaspis podolica*, possibly also *Stensiopelta pustulata* were found. Their preservation is worse than that of the pteraspidids, probably because of their relatively large size, except for *Pattenaspis*. Imprints or moulds (rarely with fragments of the armour) of dorsal and ventral shields of poraspidids (*Poraspis sturi*) are characteristic for this level. They outnumber all other vertebrate fossils taken together, although they occur as isolated specimens.

In the second fish-bearing (*Mimetaspis concordis*) horizon, in the lower part of the Khmeleva Stage, four accumulations of fish remains of different taxonomic composition were found. In the exposure, they are at roughly the same level. These four fossil assemblages are apparently of the same geological age, and their species composition is similar, but they represent different episodes in the evolution of the local environment.

The *Mimetaspis* fossil assemblage occurs in a clearly defined lens that extends laterally at 1.5–2.0 m with maximum thickness in its central part of up to 4 cm. Fossils are represented by small and middle-size fragments of carapaces, ventral and dorsal shields, separate rostral, sometimes orbital, plates of pteraspidids, small shields (*Mimetaspis*) or fragmentary armour remains of the osteostracans, sometimes with traces of exoskeletal ornamentation (*Stensiopelta*, *Pattenaspis*; Figs 85B, F, 101F). Their orientation is irregular, so they were probably deposited in high-energy fluviatile environment. The assemblage is characterised by the presence of *Mimetaspis concordis* (Voichyshyn 1994; Figs 83E, 84A, C). Heterostracans include *Podolaspis* sp., *Mylopteraspidella gracilis*, *Dnestraspis firma*, *Larnovaspis major*, *Parapteraspis plana*, *Zascinaspis heintzi*, *Zascinaspis* sp., "*Pteraspis*" *angustata*, *Weigeltaspis altha*, *W. brotzeni, W.* sp. 1, and *W.* sp. 2 (Figs 21B, 54B, 57C, 59C, 69C, D, 70F, 82A, D–F). Osteostracans, along with *Mimetaspis*, belong to *Stensiopelta pustulata*, *Pattenaspis rogalai*, and *Zenaspis podolica*. Placoderms are represented by remains of *Kujdanowiaspis* sp.

The *Benneviaspis* fossil assemblage was collected from the same lens 1 cm above the assemblage with *Mimetaspis*. Unlike the latter, it contains relatively well-preserved carapaces mainly of the osteostracans (*Benneviaspis whitei*, *Stensiopelta pustulata*, *Pattenaspis rogalai*, *Zychaspis granulata*, and *Wladysagitta janvieri*) (Figs 87A, 99B, C). *Zascinaspis heintzi* and *Weigeltaspis brotzeni* are identified among heterostracan remains. The rock is fine-grained, with considerable admixture of clay. It was probably deposited in a quieter environment than the stratum below, perhaps in somewhat greater water depth. Possibly, for some specimens, it was the primary burial place, suggested by life orientation of carapaces and good preservation of the armour.

Two other assemblages of fish fossils from the same horizon at Ustechko are not as rich. One of them is represented by only two specimens of osteostracans in a grey-green claystone, *Zychaspis siemiradzkii* and *Zenaspis podolica*, very abraded, practically deprived not only of external but also of the middle layer of the armour. Another assemblage contains numerous moulds and imprints of dorsal plates or almost complete carapaces of *Zascinaspis heintzi* (Figs 67B, D, 68F, 69A, F). Single specimens of *Podolaspis podolica* and *Alaeckaspis ustetchkiensis*, together with fragments of placoderms (*Kujdanowiaspis* sp.), were also found there (Figs 50G, 65A). Armour cover is not preserved in all specimens, but details of the external sculpture (dentine ridges) of the shields imprinted in the rock show that it was a result of late diagenetic dissolution. Agnathan specimens were disposed alongside or stacked each on the other, with dorsal shields downward or upwards, and at different orientations. Recently, several specimens of *Poraspis sturi*, *Weigeltaspis alta*, and *Kujdanowiaspis* sp. have been collected in the same outcrop from the level between *Poraspis* and *Mimetaspis* fish-bearing horizons.

The fish-bearing rocks in the quarries at Horodnytsia (Fig. 5D) consist of a red argillite and sandstone (as in Ustechko), and also a light-grey sandstone. Species composition of fish at this locality is nearly the same as from fish-bearing horizons at Ustechko, but less diverse. Unlike at Ustechko, neither *Poraspis* nor any other cyathaspidid has been found at Horodnytsia. *Mimetaspis glazewskii*, found in the upper part of the Ustechko Stage at Ustechko, *Zenaspis podolica* among osteostracans, *Larnovaspis mogielnensis* and other representatives of genus *Larnovaspis* among heterostracans are more numerous at Horodnytsia. Although remains of armoured agnathans from Horodnytsia were collected from the talus, some specimens co-occur in a single rock fragment, or originated from the same horizon. This enables recognition of some fossil assemblages.

Moulds and imprints of osteostracan shields or contours of their shields are preserved on a large slab from the quarry in the vicinity of Horodnytsia. These are at least three species: *Zenaspis dzieduszyckii*, *Stensiopelta pustulata*, and *Mimetaspis concordis* (Fig. 83F). The first is represented by a few specimens, others by single specimens. Unidentifiable pteraspidid remains have been also found. Many carapaces of *Larnovaspis major* together with rare *Zascinaspis heintzi* and placoderm plate fragments, but none of the osteostracans, are present within a layer in one of the new branches of quarries SW of Horodnytsia. There are remains of *Weigeltaspis alta*, a probable larnovaspidid pteraspidid, and a placoderm in a single rock fragment from Horodnytsia (Fig. 101C). Sometimes, only single specimens occur within a great volume of rock, for example, shield remains of *Zenaspis podolica* (Figs 6A, 92C).

Two slabs with numerous remains of fish (Fig. 101B, E), of Ustechko or early Khmeleva age, were found in a talus at the foot of the slope on the western outskirts of the village Nagiriany (Fig. 5C). Osteostracans are most abundant there, especially *Pattenaspis* shields (Fig. 85A, D). A few specimens of *Stensiopelta* (Figs 35J, 91B), and a destroyed shield imprint of *Zychaspis*, probably *Z. granulata* (Fig. 88D), were identified. Partially preserved osteostracan trunks (Figs 35J, 91B) are rare in this assemblage, and they are disarticulated from the shield. Apparently this indicates a sudden burial event. Placoderms are represented by a single, almost complete carapace of *Kujdanowiaspis podolica* (Fig. 100A). No heterostracan remains have been recorded.

The fossil assemblage from light-grey sandstone exposed in the lower part of the quarry at Zaryvyntsi probably belongs to the Strypa Stage of the Dniester Formation. Fish remains at this locality are rare and preserved almost exclusively as moulds and imprints of carapaces (as a rule, by ventral and dorsal shields) of *Althaspis*, in particular *A. sapovensis* (Figs 72D, 73C, E, 74A, 75D, E, 77D). Along with them, fragments of arthrodire plates were found. The carapace sculpture was probably abraded by sand during reburials. Probably, species of *Althaspis* inhabited fresh water. A single mould of a bivalve shell (Fig. 100G) and fragmentary mould of a large eurypterid body segment (Fig. 100H) were identified from this locality. Fish remains are rarely associated with such fossils in the Dniester Formation.

Cyathaspidids are absent in the Strypa Stage. It is possible that they inhabited an off-shore marine environment or lagoons with salty or brackish waters. From the Ustechko and the lower part of the Khmeleva stages, which were deposited in a low-salinity lagoon, only one poraspidid species (*Poraspis sturi*) is known, probably adapted to fluctuations in water salinity.

It should be noted that all species known from Strypa time show a high level of anatomical specialization. Large specimens of *Althaspis*, with the carapace length of 140–180 mm, exhibited an elongated torpedo-like shape. Also, the elongated rostral plate and considerably increased length of the posteriorly declined dorsal spine are characteristic for them. These species, possibly, were adjusted to a more active way of life than the earlier pteraspidids. The Strypa Stage fish fauna includes also large, wide-shielded, dorso-ventrally compressed *Brachipteraspis* and *Europrotaspis*, which probably lived resting at the bottom. These morphological specializations terminate the evolutionary history of the order Pteraspidiformes (Novitskaya 1986, 2007).

The osteostracans acquired similar adaptations. In the the Strypa Stage, they are represented almost exclusively by dorso-ventrally flattened benneviaspidids (Afanassieva 1991), that, as compared with *Benneviaspis whitei* from the lower part of the Khmeleva Stage, were considerably larger (up to 120 mm in widths of *Benneviaspis zychi*). However, they did not reach sizes comparable to related forms from Spitsbergen. At the same time, neither pteraspidids nor osteostracans with vertical dorsal ridges or spines are known from these strata. Probably, such ridges or spines became unadapted in high energy water conditions, while passive defence was no longer important.

In the youngest deposits of the Dniester Formation (the Smerkliv Stage and higher up in the section), which are known practically only from boreholes, fish remains have not not been found to date.

SUCCESSION OF THE AGNATHAN FAUNAS OF PODOLIA

As usual for near-shore and continental fossil-bearing deposists, and also in Podolia, it is difficult to separate taphonomic bias from ecologically influenced changes resulting from migrations and local extinctions, from that of evolutionary changes. Although it seems premature to offer a biologically sound picture of faunal successions of the agnathans in the Early Devonian of Podolia, some preliminary attempts to settle basic problems of biostratigraphy and chronology of events seem necessary.

PATTERN OF SUCCESSION

Differences between fossil fish assemblages in Podolia, as in other Devonian regions, seem to have been controlled mainly by two factors. The major one is taphonomic conditions. As it was shown above, this factor may significantly distort information on the extinct faunas, represented in the fossil assemblage. The second factor is the true faunal evolution, which reflects long-term environmental change by forcing animal adaptation.

A probable case of taphonomic bias is the low taxonomic diversity of the latest Silurian heterostracans as compared with those of the Early Devonian (Novitskaya 2007). The late Lochkovian rise of the heterostracan diversity is recorded at many sites within the Old Red Sandstone Continent (Blieck *et al.* 2002). It is suggested that the Silurian fish fauna, in the Podolian part of the basin, was actually not less rich than in the Baltic basin (Estonia, Saaremaa Island), where thelodonts, numerous primitive osteostracans, anaspids, acanthodians, and actinopterygians are recorded, numbering more than 40 species altogether (Mark-Kurik and Noppel 1970; Obruchev 1972; Märss and Einasto 1978; Märss 1986; Blieck and Janvier 1991). The evidence of a diverse fauna is offered by the deposits of the Skala Stage of the Silurian, where a partial shield of *Irregulareaspis*, obviously brought there from the shoal, was found. The evidence is so scarce only because of unfavorable conditions during burial of the shallow-water animals in deep-water sediments.

Shallowing of the sea at the end of the Silurian and its fluctuations during the Borshchiv time did not substantially influence the amount of fossil fish remains and their state of preservation. The water depth remained too large for armoured agnathans. However, for the first time the thelodonts, which inhabited shallow seas in their littoral and deeper-slope parts (Karatajūtė-Talimaa and Märss 2004), appeared in the fossil assemblage.

Perhaps the gradual shallowing of the sea during Chortkiv time enabled enrichment of the fossil assemblage by fishes inhabiting marine (acanthodians), lower salinity [thelodonts; according to Karatajūtė-Talimaa and Märss (2004) the Early Devonian *Turinia* possibly could enter estuaries], and freshwater (pteraspidids?) environments.

The trend towards increase of ecological and taxonomic diversity was further strengthened during Ivanie time. Ecologically disparate skeletal remains were buried in the shallowest parts of the sea. The distance from the place of animal death to the place of its burial was thus short. In addition, unlike during Dniester time, marine species (majority of Podolian cyathaspidids and corvaspidids) still contributed to the assemblage, while the freshwater component (probably pteraspidids and osteostracans) expanded.

If dating of the fossil assemblages from the sandstone of the catchment basin in the middle of the Seret River is correct, those strata provide the richest freshwater vertebrate fauna from Ivanie time. The fauna was dominated by the relatively large pteraspidids *Larnovaspis* and *Alaeckaspis*, the cosmopolitan osteostracan *Pattenaspis*, and the first Podolian placoderm *Ericaspis zychi*.

At the boundary between Tyver and Dniester times, when conditions changed to seasonally low-saline or fresh-water, the marine fish species gradually disappeared. The only cyathaspidid species of the Ustechko age was *Poraspis sturi*. Meanwhile, the diversity of the osteostracans increased dramatically up to 14 species. To some degree, this trend was observed also in the pteraspidids, and yet less in the placoderms. On the contrary, thelodonts reduced their contribution to the fauna, although the picture may be biased by difficult extraction of fish microremains from terrigenous rocks.

The fish fauna at the beginning of Khmeleva time was diverse (Voichyshyn 1997), both within the osteostracans and pteraspidids. The placoderms were represented by two species out of four known until now from Podolia. Agnathans reached their maximum morphological diversity. Probably, all or almost all species were inhabitants of fresh, or at least brackish, mainly quiet waters. However, in finely grained deposits of the Khmeleva Stage, fossils are rare and their preservation is often insufficient to allow taxonomic identification.

Because stratigraphic afiliation of particular rock units remains uncertain in many cases, the second Old Red faunal zone is still inadequately characterised.

Sediments of Strypa time originated in deltaic and, possibly, in-shore conditions with intense water flow, as indicated by coarse-grained sand. The high water dynamics probably prevented local fossil accumulation, such as those from the lowest part of the Dniester Series. Moreover, fossil remains tend to be abraded. Judging from the available material, the fish fauna of this time lost much of its previous taxonomical richness, but became highly specialised, adapted to inhabiting high-energy running waters.

In the latest Early Devonian, deposition of terrigenous material in Podolia was very intense, resulting in formation of rock units of large thickness. Neither invertebrate nor fish fossils have been reported from those strata.

THE PROBLEM OF AGNATHAN ENDEMISM IN PODOLIA

As has been noted by Janvier and Blieck (1993), "endemism in palaeontology is in principle untestable, since one can never expect to have a complete record of the biotas for a given time". This applies also to the agnathans of Podolia, although most of the Podolian agnathan species have not been reported from elsewhere.

Thelodonts are among few exceptions. None of their species is endemic for Podolia, as interpreted by Karatajūtė-Talimaa and Märss (2004). *Turinia pagei* was identified also in Volhynia (Ukraine), the Brest Depression (Belarus), Baltic region (Lithuania, Latvia), Great Britain, Spitsbergen, and Russia (Kaliningrad oblast', the Middle Urals, Timan-Pechora region, Novaya Zemlya, and Severnaya Zemlya); *T. polita* Karatajūtė-Talimaa, 1978 from Volhynia, Baltic, Great Britain, Canadian Arctic, and Russia; *Nikolivia oervigi* (Karatajūtė-Talimaa, 1967) from Lithuania, Great Britain, and Spitsbergen; *N. elongata* from the Brest Depression, the Baltic, Russia, Spitsbergen, and Canadian Arctic; *N. balabayi* from Lithuania and Russia; *Gampsolepis insueta* from Timan-Pechora region of Russia; *Apalolepis obruchevi* from Lithuania and Spitsbergen; and *A. brotzeni* Karatajūtė-Talimaa, 1978 from Lithuania (Karatajūtė-Talimaa and Märss 2004). Among heterostracans, *Corvaspis kingi* occurs also in Great Britain and Spitsbergen, *Belgicaspis crouchi* in Great Britain, Belgium, and France, and *Europrotaspis arnelli* in Great Britain. Although originally of the eight species of Podolian thelodonts, only three were known from elsewhere (Karatajūtė-Talimaa 1978; Voichyshyn 2001b), it has to be noted that thelodonts and *Corvaspis* are known in Podolia only from isolated fragments of dermal skeleton (scales, tesserae, small plates; Fig. 17A, C, D, O, etc.), which do not guarantee reliable specific identification (Novitskaya 1971, 2006).

Presence of *Belgicaspis* in Podolia still needs confirmation, as discussed above. Thus, all eight species of thelodonts and three species of heterostracans (among 42) are known also from other regions. At the same time, all representatives of cyathaspidids (nine species), others heterostracans (two species), and cephalaspidids (24 species) are restricted to Podolia. Several species from the region have close relatives elsewhere classified in the same genera, which shows that Podolia was not isolated (Table 2). Among thelodonts, these are *Turinia*, *Nikolivia*, *Gampsolepis*, and *Apalolepis* (all four genera known from Podolia). Among cyathaspidids, these are *Poraspis*, *Irregulareaspis*, and *Ctenaspis* (three of four). Corvaspidids are represented by the only genus *Corvaspis*. Among pteraspidids, these are *Larnovaspis*, *Belgicaspis*, *Brachipteraspis*, *Zascinaspis*, *Althaspis*, and *Europrotaspis* (six of seventeen). Other heterostracans are represented by *Weigeltaspis*, *Lepidaspis*, and *Tesseraspis* (three of three), and among osteostracans these are *Mimetaspis*, *Parameteoraspis*, *Pattenaspis*, *Benneviaspis*, *Stensiopelta*, *Zenaspis*, *Diademaspis*, *Tegaspis*, and *Wladysagitta* (nine of thirteen).

If the Podolian agnathans were truly endemic, the region would have to have been isolated from the rest of the world for most of the time during deposition of the Early Devonian strata, preventing faunal interaction. This was definitely not the case, as the same genera, grouping closely related species, are identified in Podolia and other regions. At least three solutions to the question can thus be proposed: (1) species of the Early Devonian brackish- or fresh-water agnathans had limited geographic distribution and other regions are too distant to share them with Podolia, (2) fossil assemblages elsewhere are of ages different enough to be represented by other stages in the evolutionary development of agnathan lineages, or (3) although not completely isolated, Podolia accepted only rare immigrants from time to time, and they started local lineages evolving independently of their relatives from other regions of the world. To test these hypotheses it would be necessary to see whether the Podolian agnathans can be arranged into chronological lineages and, if so, whether it is possible to identify immigrants that gave beginning to those lineages. The basic prerequisite for such studies is recognition of the exact succession of species in the Podolian sections of the Early Devonian.

IMMIGRATION AND EVOLUTION OF THE PODOLIAN AGNATHANS

The Palaeozoic fish fauna of Podolia was dominated by armoured agnathans, with ten species of the Cyathaspidiformes, 33 of the Pteraspidiformes, seven of other Heterostraci, and 27 species of the Osteostraci (Table 1). Only eight species of the Thelodonti, four species of the Placodermi, five of the Acanthodii and five of the Chondrichthyes contributed. The Old Red-type ecosystem of Podolia gradually emerged with retreat of the sea and simultaneous immigration of the agnathans from other regions. Presumably, some persisted in the region adapting anatomy in a course of their evolution. Others became extinct or were replaced by new immigrants. Below, it is attempted to reconstruct this succession of events based on the fossil evidence available.

Morphologically advanced, with still unrecognised ancestry, species of the Pteraspidiformes and Osteostraci coexisted in the Podolian fauna from the mid Lochkovian to the early Pragian. In fact, almost all the Cyathaspidiformes and other Heterostraci were restricted in their occurrence to this time interval. Therefore, it is difficult to trace their evolution in Podolia and elsewhere. But, as will be shown, some trends, expressed mostly in increase of body size in different lineages, are traceable.

The tesseraspidids have possibly the least recognised ancestry among Silurian–Devonian ostracoderms known to date, with uncertain affinities among the heterostracans (Tarlo 1962; Elliott and Loeffler 1989; Janvier and Blieck 1993; see also Märss and Karatajūtė-Talimaa 2009). They include 6 species of *Tesseraspis* (Fig. 102), which are known after isolated carapace fragments, except for *T. tesselata*, and range from the Late Silurian to Early Devonian (Lochkovian) in the Canadian Arctic, Great Britain, Germany, Lithuania, and Podolia (Novitskaya 2004). One fragment of *Tesseraspis* armor indicates affinity between vertebrate faunas of Podolia and those regions.

The genera *Weigeltaspis* and *Lepidaspis* represent "tessellate heterostracans" of uncertain affinities (Janvier 1996) known mostly after microremains from Spitsbergen, *Weigeltaspis* alone from Great Britain, and *Lepidaspis* from the Canadian Arctic. In Podolia (Fig. 102), *Lepidaspis*-like heterostracans were common from rocks of Chortkiv-Ivanie ages (Fig. 79) and two or more species of *Weigeltaspis* from Ivanie to early Khmeleva ages (Figs 81A, 82A, D, E). Their fossils provide too limited information to allow any evolutionary interpretation.

The same applies to the corvaspidids. It remains unknown whether they did truly possess common branchial openings, regarded as the heterostracans diagnostic feature (Janvier 1996: p. 98). Corvaspidids occurred in the same regions as the tessellate heterostracans, but also in Lithuania and Severnaya Zemlya (*Corveolepis*). In Podolia, the geographically widespread *Corvaspis kingi* is known from the Chortkiv and Ivanie ages (Fig. 102).

Many more species of the Cyathaspidiformes are widely known, from the Late Silurian and Lochkovian coastal zone along Baltica and Laurentia. Among 23 cyathaspidid genera, 16 are known from the Arctic Canada and Spitsbergen (Novitskaya 2007). That region of Laurentia may be the centre of cyathaspidid origin and phyletic radiation. The Podolian cyathaspidids are represented by 9 or 10 species (Fig. 102). Among them, a single species of *Seretaspis* is restricted to Podolia, although it may have been related to *Archegonaspis* from central Europe, Russia, and Canada (see Taxonomy Chapter). *Irregulareaspis skalskiensis* from the Late Přidoli of Podolia is the oldest member of the genus, with specimens smallest in size. Two species more from Podolia, two from Spitsbergen (Ben Nevis Formation; Blieck and Heintz 1983), and indetermined remains from Severnaya Zemlya (Pod'emnaya Formation; Blieck *et al.* 2002) are all from the late Lochkovian. Therefore, unlike among the cyathaspidids, the expansion seems to had originated from Podolia to Spitsbergen and Severnaya Zemlya (Fig. 1A).

Poraspis was probably the most taxonomically diverse cyathaspidid genus with about 14 species, including several very small Late Silurian (and Early Devonian) species from the Canadian Arctic, and rather large Early Devonian (Lochkovian) ones from Spitsbergen, Severnaya Zemlya (*Poraspis* cf. *P. polaris*; Blieck *et al.* 2002), Great Britain, northern France, and Podolia. An evolutionary trend towards increased size took place. The relatively large representatives of the four or more Podolian species are probably successors of an immigrant from the Canadian Arctic.

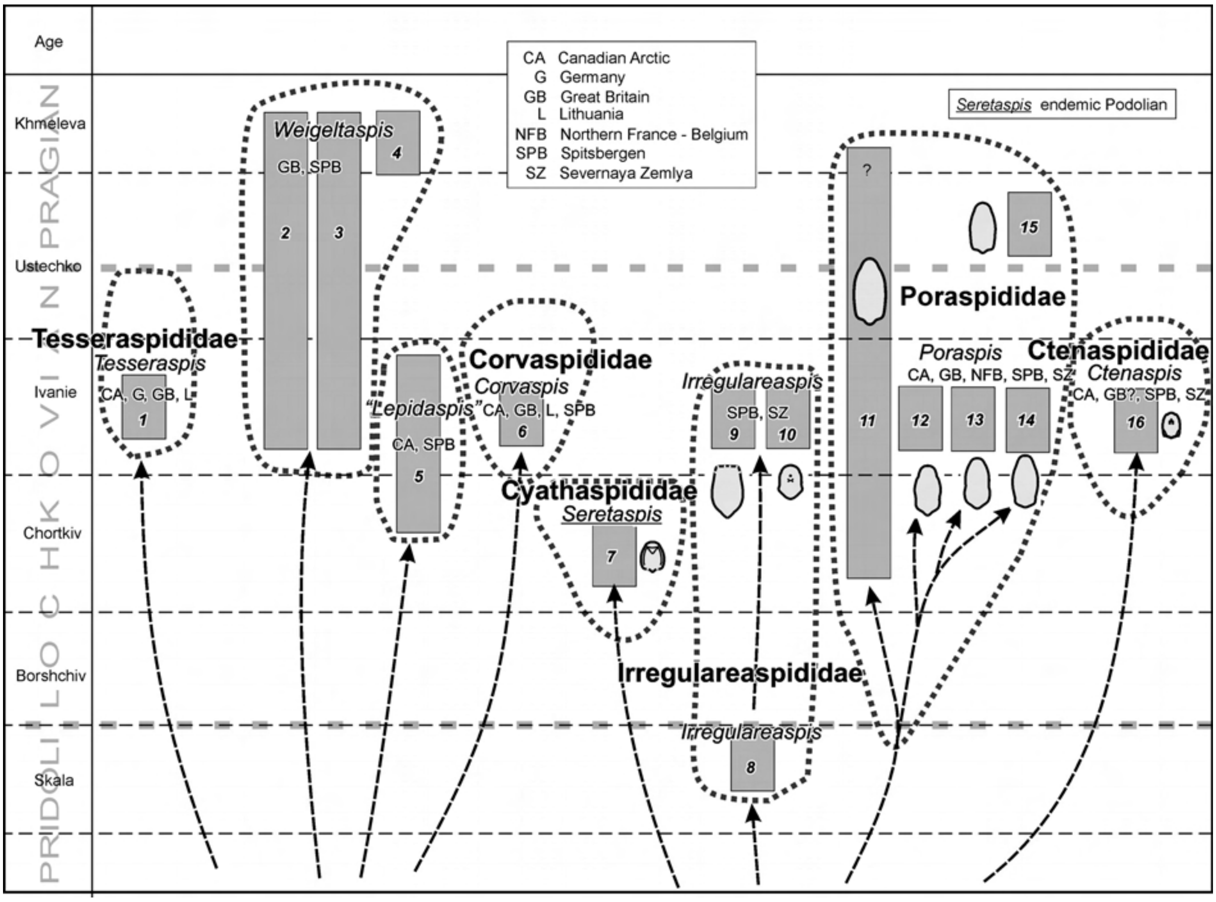


Fig. 102. Taxonomy of the Podolian Cyathaspidiformes and heterostracans of undetermined phylogentic status in stratigraphic context. 1, *Tesseraspis orvigi*; 2, *Weigeltaspis alta*; 3, *Weigeltaspis brotzeni*; 4, *Weigeltaspis* sp. 1 and 2; 5, "*Lepidaspis*" sp.; 6, *Corvaspis kingi*; 7, *Seretaspis zychi*; 8, *Irregulareaspis skalskiensis*; 9, *Irregulareaspis seretensis*; 10, *Irregulareaspis stensioei*; 11, *Poraspis sturi*; 12, *Poraspis pompeckji*; 13, *Poraspis siemiradzkii*; 14, *Poraspis simplex*; 15, *Poraspis* sp. 1; 16, *Ctenaspis kiaeri*.

The origin and affinity of Lochkovian *Ctenaspis*, with six known species from the Canadian Arctic, Spitsbergen, Severnaya Zemlya, Podolia, and, possibly, Great Britain (Novitskaya 2007), remain unclear. Janvier (1996) considered this genus to be related to the amphiaspidids from NW Siberia. In fact, Severnaya Zemlya is believed to be a palaeozoogeographical link between the Old Red Sandstone Continent and Siberia (Blieck *et al*. 2002). Both ctenaspidids and amphiaspidids occur in the late Lochkovian of Severnaya Zemlya (Blieck *et al*. 2002: fig. 4). However, the opposite direction of the evolution is likely, that is, ancestry of the amphiaspidids from the cyathaspidids (Novitskaya 2004: p. 97).

The Pteraspidiformes include about 30 genera and 67 species (Novitskaya 2007) from Belgium, northern France, Great Britain, Podolia, Spitsbergen, Canadian Arctic, Idaho, Montana, Nevada, Ohio, Utah, and Wyoming (Blieck 1984; Ilyes and Elliott 1994). Their occurrence in Lithuania, Germany, and Poland is less certain (Blieck 1984; Novitskaya 2004, 2007), and even more problematic in Chukotka and Novaya Zemlya (Blieck *et al*. 2002; Novitskaya 1986, 2004). The oldest pteraspidids, namely several *Protopteraspis* and anchipteraspidids species, occurred in the Přidolian of the Canadian Arctic (Elliott 1983b; Janvier 1996; Novitskaya 2007). *Anchipteraspis*, *Ulutitaspis*, and *Rhachiaspis* are of intermediate carapace morphology between the cyathaspidids and other pteraspidids (Elliott 1983b). Because of its geological age and primitive features, *Protopteraspis* may be also related to the ancestral stock of the pteraspidids. All other known pteraspidid species are Devonian (Novitskaya 2007), becoming frequent during the mid Lochkovian. By the end of the Lochkovian, pteraspidids reached their highest diversity and were common also in the Pragian. The last representatives of the group are noted in Europe in the Emsian. But, the very large and wide-shielded specimens of *Helaspis* are from the Late Givetian of Alberta, Canada (Elliott *et al*. 2000).

The oldest Podolian pteraspidids (Fig. 104) from the Chortkiv age are *Larnovaspis kneri* (Blieck 1984: fig. 23) and *Errivaspis* (*Alaeckaspis*?) *depressa* (Blieck 1984: fig. 21). Although showing some archaic aspects of their morphology (especially *L. kneri*), they are hardly ancestral to other Podolian pteraspidids. Presumably, there could be more than one immigration wave of the pteraspidids to Podolia from, probably, the Canadian Arctic (e.g., see Blieck and Tarrant 2001).

A preliminary scheme of potential relationships among early pteraspidids can be proposed based on arrangement of sensory canals ("pineal" canal and mdl canals) (Fig. 103). Both *Anchipteraspis* and *Protopteraspis* had the same arrangement of the sensory line system ("pineal" canal on the dorsal shield + radial type of mdl canals, VR), which may be traced back to their probable cyathaspidid ancestor. The Lochkovian *Protopteraspis* descended from a Canadian ancestor, expanding eastward to Spitsbergen with several species, then southward to Great Britain and northern France (Fig. 1A), where *P. gosseleti* is known from the early Lochkovian (Blieck and Tarrant 2001). The Canadian Lochkovian *Canadapteraspis*, with developed cornual plates but less derived orbito-pineal belt in respect to the protopteraspidids but the same sensory canal arrangement, apparently continues the local lineage. It is proposed that a lineage developed, from Silurian protopteraspidids or similar forms, with the supraorbital sensory canals ("pineal" canal) closed behind the pineal plate on the dorsal shield. Having this structure displaced forward within the limits of the pineal plate, and associated with mdl canals of radial type, they gave ancestry to pteraspidids with "pineal" canal on the pineal plate associated with mdl canals of radial type (Fig. 103, R). Presumably, already during the Silurian, pteraspidids, with the "pineal" canal on the dorsal shield associated with mdl canals of parallel type, originated (Fig. 103, VP) from a cyathaspidid ancestor, common with *Anchipteraspis* and *Protopteraspis*. Those dispersed eastward gave ancestry to the Lochkovian *Miltaspis* of Spitsbergen. Some Canadian relative of *Miltaspis* could be ancestor of highly advanced late Lochkovian *Stegobranchiaspis* and *Unarkaspis*. Another relative of *Miltaspis* may have developed convergently the "pineal" canal within limits of pineal plate, and gave ancestry to the late Lochkovian *Pteraspis* (zone *crouchi* of Great Britain) and all other pteraspidids with parallel type of mdl canals (Fig. 103, P). As far as it is known, the "pineal" canal on dorsal shield (Fig. 103, V) does not occur among other Lochkovian genera, except for the anchipteraspidids or Pragian and later pteraspidids.

Expanding from Canada, the pteraspidids developed predominantly endemic fauna in southwestern North America and Spitsbergen (Blieck 1982; Pernègre 2003, 2004, 2006). This suggests that faunal exchange between different regions was limited during the Lochkovian by some environmental factors. Also, the Early Devonian Podolian pteraspidids developed during partial isolation that resulted in developing a degree of fauna endemism. Elements similar to those of Podolia can be found only in the coeval British and Franco-Belgian fauna. The lineages of Podolaspididae, *Pavloaspis*, and *Palanasaspis* gen. n. seem to have no close relatives in other regions (Fig. 104).

The podolaspidids include at least five lineages that could have radiated in Podolia. *Semipodolaspis* gen. n. is the earliest one. Of the remaining four, *Mylopteraspis* is poorly known but others seem to form two probably monophyletic clades. The first one, consisting of *Podolaspis* and *Dnestraspis*, is characterised by the radial type of mdl canals, and a moon-like shape of the pineal plate in, mainly, a discontinuous orbito-pineal belt. *Semipodolaspis* gen. n., with its one species, may be related to the first podolaspidids in having the same morphology of the orbito-pineal belt, although its mdl canals type remains unknown. But, other features of this genus set it apart from all the Podolaspididae (see Taxonomy Chapter). The second group possibly unites *Mylopteraspidella* and *Parapteraspis*, having parallel mdl canals and the pineal plate of varied shape in, mainly, a continuous orbito-pineal belt.

The Podolian endemic *Pavloaspis pasternaki* may be a late representative of an archaic lineage. Its orbito-pineal belt suggests derivation from a protopteraspidid-like form with mdl canals of radial type, but advanced "pineal" canal arrangement (Fig. 103, R).

Palanasaspis gen. n. was a large and advanced pteraspid similar to other pteraspidiforms of the Strypa fauna. Its relationship and origin remain unknown, but it evidently belongs to one of the Podolian terminal pteraspidids.

The Rhinopteraspididae and Protaspididae are represented also in the fauna of Great Britain and the Franco-Belgian region. The rhinopterapidid *Althaspis* includes four or five Podolian species. Most of them come from late (?) Pragian Strypa time, coeval with their western European relatives. But one, *Althaspis tarloi* sp. n., is known from the late Lochkovian or early Pragian Ustechko time. Its morhology and age make

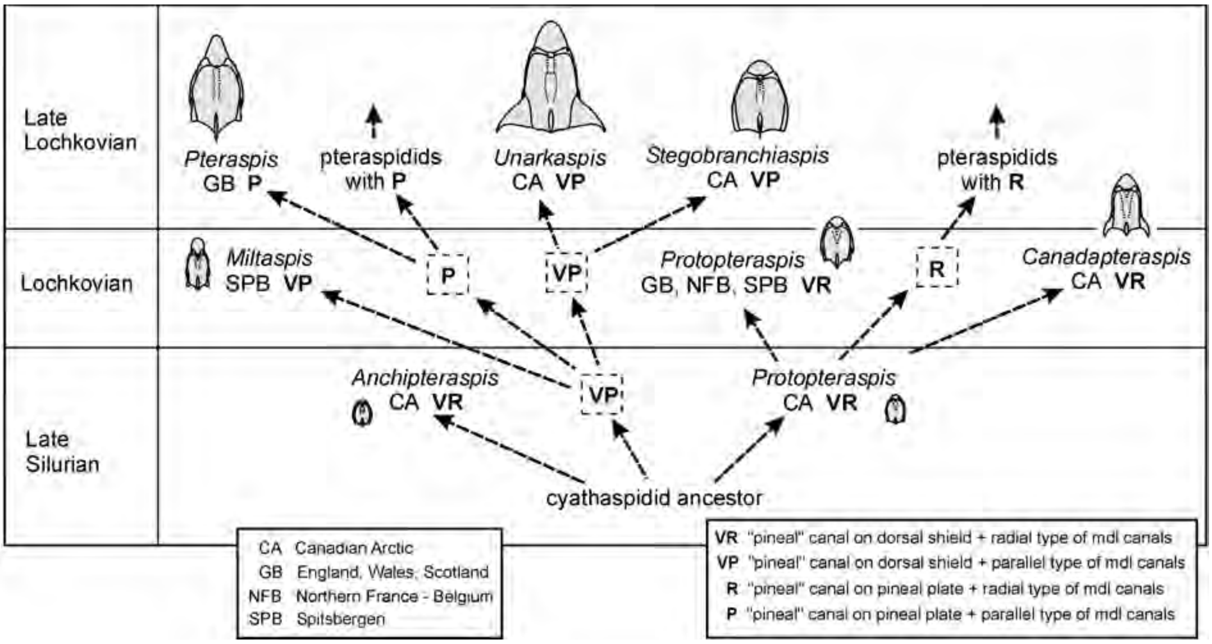


Fig. 103. Possible phylogenetic relationship within early pteraspidids in the light of sensory line system development.

it the most primitive althaspidid known, suggesting Podolian origin of the clade, which dispersed westward to Belgium and British areas. At least in *A. leachi* and *A. elongata*, the mdl canal arrangement seems to be parallel (see Taxonomy Chapter).

Europrotaspis, with two or three species from Europe (Great Britain, Belgium, and Podolia), seems related to western North American protaspidids, judging from their overall morphology and especially the morphology of branchio-cornual region (Denison 1970; Novitskaya 1986, 2004). If this is true, it is an unique case of relation between these distant faunas. Nevertheless, *Europrotaspis arnelli* has mdl canals of radial type (Blieck 1984: fig. 47C), whereas the protaspidids possess rather the parallel type (Blieck 1984: fig. 49A, C). Moreover, the European and American species differ also in other sensory canal arrangements (cf. Blieck 1984: figs 47A, C, 49A).

The Larnovaspididae includes almost half of Podolian pteraspidid species known until now. There are some affinities to British, Spitsbergen, and USA faunas (*Larnovaspis, Zascinaspis*), but presence of *Belgicaspis* in Podolia is still questionable. At least three lineages (*Alaeckaspis, Djurinaspis,* and *Brachipteraspis*) seem to be restricted to Podolia. *Larnovaspis* may be polyphyletic because both types of dorsomedial (mdl) sensory canals occur among its species. *Larnovaspis stensioei* (Great Britain) and *L. goujeti* (Spitsbergen) show mdl canals of parallel type. The same morphology is probably characteristic for *L. kneri* from Podolia. Three other species from Podolia, including *L. major* and *L. mogielnensis*, have the radial type of mdl canals. In *L. iwaniensis*, that condition is unknown.

Among four species of *Zascinaspis,* three exhibit the parallel type of mdl canals (*Z. heintzi* and *Z. bryanti* from Podolia, and *Z. laticephala* from Spitsbergen). The condition is unknown in *Z. carmani* from Ohio, which in other respects is quite similar to the Podolian species (Novitskaya 1986: p. 103), but is of considerably larger size (cf. Blieck 1984: fig. 46B, C, E). Small *Z. bryanti*, from the Lochkovian Ivanie Stage, may be close to the ancestral stock and, if true, the lineage may be of Podolian origin.

Possible Podolian *Belgicaspis* ranges across the Lochkovian–Pragian boundary from the Ivanie to the early Khmeleva age, which makes it a long-lasting form that may be compared in this respect only with *Zascinaspis heintzi*. Its relatives from western Europe (Great Britain, northern France and Belgium) are known from the late Lochkovian (Novitskaya 2004, 2007). *Belgicaspis* shows an elongated rostral plate and morphology of the orbito-pineal belt that makes it superficially similar to the Rhinopteraspididae. Probably, this is a result of convergent adaptation to similar living conditions. *Belgicaspis* has the radial type of mdl canals, while the rhinopteraspidids probably have the parallel one.

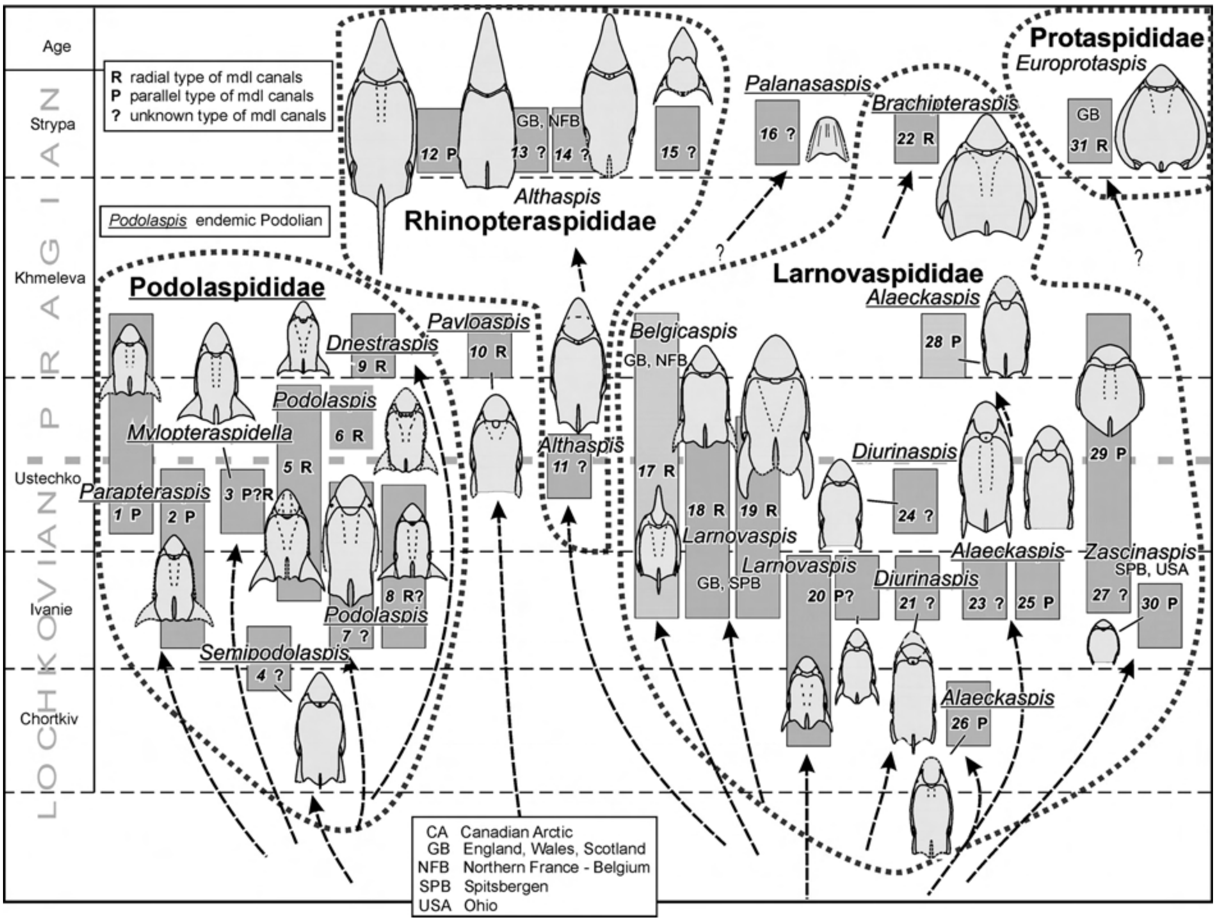


Fig. 104. Taxonomy of the Podolian Pteraspidiformes in stratigraphic context. 1, *Parapteraspis plana*; 2, *Parapteraspis lata*; 3, *Mylopteraspidella gracilis*; 4, *Semipodolaspis slobodensis* gen. et sp. n.; 5, *Podolaspis podolica*; 6, *Podolaspis danieli* sp. n.; 7, *Podolaspis zychi*; 8, *Podolaspis lerichei*; 9, *Dnestraspis firma*; 10, *Pavloaspis pasternaki*; 11, *Althaspis tarloi* sp. n.; 12, *Althaspis elongata*; 13, *Althaspis longirostra*; 14, *Althaspis sapovensis*; 15, *Althaspis*? *spathulirostris*; 16, *Palanasaspis chekhivensis* gen. et sp. n.; 17, *Belgicaspis crouchi*; 18, *Larnovaspis major*; 19, *Larnovaspis mogielnensis*; 20, *Larnovaspis kneri*; 21, *Larnovaspis iwaniensis*; 22, *Brachipteraspis latissima*; 23, *Djurinaspis secunda* sp. n.; 24, *Djurinaspis prima*; 25, *Alaeckaspis verbivciensis*; 26, *Alaeckaspis*? *depressa*; 27, *Alaeckaspis magnipinealis*; 28, *Alaeckaspis ustetchkiensis*; 29, *Zascinaspis heintzi*; 30, *Zascinaspis bryanti*; 31, *Europrotaspis arnelli*.

The four species of *Alaeckaspis* range from the mid Lochkovian to the early Pragian, and are restricted to Podolia. Except for the carapace morphology, most of the species are united by the parallel type of mdl canal arrangement. Rare finds of two species of *Djurinaspis* are also restricted to Podolia. They form a succession from Ivanie to Ustechko time. Most of *Alaeckaspis* and *Djurinaspis* species have a rather rounded and enlarged pineal plate and considerably narrow cornual plates as compared with other larnovaspidids. Possibly both genera had a common ancestor.

The Podolian *Brachipteraspis* species shows some similarity with *Pteraspis rostrata* var. *monmouthensis* from Great Britain. It is possible that this resulted from faunal exchange.

There are only three faunas from other regions, namely Great Britain, Spitsbergen, and Severnaya Zemlya (Fig. 105), with osteostracans showing relationships to the Podolian Cephalaspidiformes. The osteostracans occurred in Podolia since the late Chortkiv age (Fig. 35I), but their oldest identified species, the wide-shielded *Parameteoraspis dobrovlensis*, lived during the early Ivanie age. At least two more osteostracan species are known from Lochkovian Ivanie time, *Ukrainaspis kozlowskii* and *Tegaspis waengsjoei*. These forms differ strongly in the headshield morphology, indicating their long but unknown evolutionary history.

The suborder Cephalaspidoidei is represented in Podolia by three genera *Parameteoraspis*, *Mimetaspis*, and *Pattenaspis*, all including numerous non-Podolian species. The overwhelming majority, namely eight of

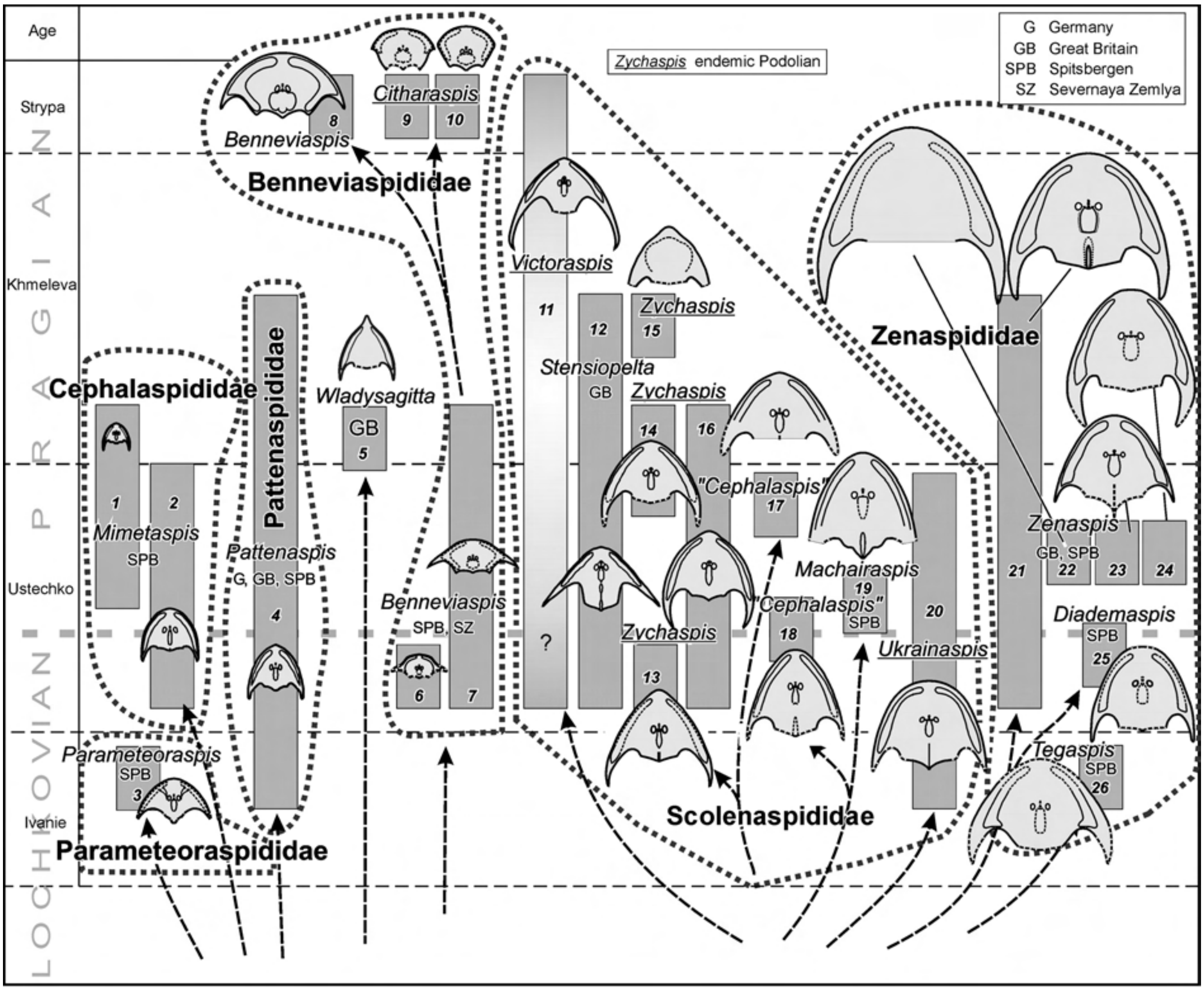


Fig. 105. Taxonomy of the Podolian Osteostraci in stratigraphic context. 1, *Mimetaspis concordis*; 2, *Mimetaspis glazewskii*; 3, *Parameteoraspis dobrovlensis*; 4, *Pattenaspis rogalai*; 5, *Wladysagitta janvieri*; 6, *Benneviaspis talimaae*; 7, *Benneviaspis whitei*; 8, *Benneviaspis zychi*; 9, *Citharaspis polonica*; 10, *Citharaspis junia*; 11, *Victoraspis longicornualis*; 12, *Stensiopelta pustulata*; 13, *Zychaspis concinna*; 14, *Zychaspis granulata*; 15, *Zychaspis elegans*; 16, *Zychaspis siemiradzkii*; 17, "*Cephalaspis*" *djurinensis*; 18, "*Cephalaspis*" *microlepidota*; 19, *Machairaspis* sp.; 20, *Ukrainaspis kozlowskii*; 21, *Zenaspis podolica*; 22, *Zenaspis major*; 23, *Zenaspis dzieduszyckii*; 24, *Zenaspis kasymyri* sp. n.; 25, *Diademaspis stensioei*; 26, *Tegaspis waengsjoei*.

eleven species of *Pattenaspis*, and all species of *Parameteoraspis* and *Mimetaspis*, belong to the Spitsbergen fauna. *Mimetaspis* includes five species of Lochkovian–Pragian time (Afanassieva 2004), three small-sized from Spitsbergen. The size of *M. concordis* from Podolia is comparable with that of the Spitsbergen species, but *M. glazewskii* is much larger. In contrast with *Mimetaspis*, individuals of the single Podolian species of *Parameteoraspis* are of smaller size in comparison with their Spitsbergen relatives. *Pattenaspis* includes species of different headshield morphology and may be heterogenous (Afanassieva and Voichyshyn 1991). Besides Spitsbergen (eight species) and Podolia (one species), pattenaspidids also are known from Great Britain and Germany, that is, along the possible migration route from Spitsbergen to Podolia (Fig. 1A). The majority of pattenaspidids occur in the Lochkovian (Afanassieva 2004) and the largest among them, the Podolian *P. rogalai*, ranges to the Pragian. Probably all these osteostracans migrated to Podolia from Spitsbergen, increasing size of their bodies in the course of evolution.

Wladysagitta, with one Podolian and one British species, is regarded as intermediate between *Pattenaspis* and the Scolenaspididae (Voichyshyn 2006a).

The Benneviaspididae, with flat, very wide headshield and peculiar arrangement of the lateral fields, is represented in Podolia by two genera, *Benneviaspis* and *Citharaspis*. The former is represented (except for Podolian ones) by several species from Spitsbergen and one species from Severnaya Zemlya. A number of probably primitive *Benneviaspis* species, which differ from the typical ones, particularly, in having a narrow dorsal field, occur in Great Britain (Janvier 1985a; Afanassieva 2004). Species of *Benneviaspis* from the Lochkovian are relatively small forms such as *B. holtedahli* from Spitsbergen, *B. talimaae* and *B. whitei* from Podolia. In the Pragian, they are replaced by large-shielded forms: *B. maxima*, *B. loevgreeni*, and *B. grandis* in Spitsbergen, *B. zychi* in Podolia, and *B. urvantsevi* in Severnaya Zemlya. Most probably, Spitsbergen was the homeland of the genus, but Podolia might have been a second such area. *Benneviaspis talimaae* seems to be the smallest and the most primitive species among the Podolian forms. *Citharaspis* is a close relative of *Benneviaspis*, differing in lacking the cornual processes. It is restricted to Podolia, where it appeared during the Pragian, most probably derived from a species of *Benneviaspis*.

The Scolenaspididae are the family richest in species among the Podolian osteostracans, including probably ten species. They seem to be represented by four groups, *Ukrainaspis*-like, *Zychaspis*-like, *Stensiopelta*-like, and *Machairaspis*-like. The first lineage represented by *Ukrainaspis kozlowskii* is restricted to Podolia and strongly differs from most other scolenaspididids by the headshield being prominent and rounded anteriorly, with short cornual processes, appreciable dorsomedial crest, and the skeleton ornamentation. These features make it closer to the zenaspidids, but morphology of the cephalic fields and central part of the headshield suggest that it was rather close to the ancestral stock of the Scolenaspididae. It occurred in the Ivanie and not later than the Ustechko age, that is from the mid Lochkovian to early Pragian, being thus the oldest scolenaspidid in Podolia.

The second, *Zychaspis*-like group is much more numerous and includes five *Zychaspis* species (Fig. 89) and, possibly, "*Cephalaspis*" *djurinensis*, all restricted to Podolia. They are characterised by a more or less developed rostral lobe, rather flat headshield and shallow pectoral sinuses, medium sized cornual processes, and by tiny, densely set tubercles on the skeleton. The range of the group is from the late Lochkovian to Pragian.

The third, *Stensiopelta*-like group unites *Stensiopelta* and the exclusively Podolian *Victoraspis*. Its characteristic features are a wide and short headshield, due to very long cornual processes, elongated abdominal division of the headshield, and low and short dorsomedial crest. *Stensiopelta* has two species, one in Podolia and another in Great Britain, along with *Wladysagitta* indicating faunal connections between Podolia and Great Britain, but not Spitsbergen or other regions. *Victoraspis* has probably a long stratigraphic range and, as the only Podolian scolenaspidid, enters the late (?) Pragian third Old Red faunal zone.

The fourth, *Machairaspis*-like group includes two forms, *Machairaspis* sp. and "*Cephalaspis*" *microlepidota* both from the same locality (Horodnytsia) probably of early Pragian age (Janvier 1985b; Afanassieva and Voichyshyn 1991). *Machairaspis* elsewhere is known from the Lochkovian of Spitsbergen, which is somewhat earlier than the Podolian form. This may suggest migration from Spitsbergen to Podolia.

The last major osteostracan group from Podolia is the Zenaspididae. All its genera, *Zenaspis*, *Diademaspis*, and, possibly, *Tegaspis*, are represented both in Podolia and Spitsbergen, but only one species of *Zenaspis* occurs in Great Britain. They are characterised by a prominent and massive headshield, broad dorsal field, enlargement of posterior lateral fields end, and mostly a greater hypophyseal than nasal division of the nasohypophyseal opening.

Zenaspis includes probably six species, the majority of which are Podolian, ranging from relatively small *Zenaspis dzieduszyckii* to twice as large *Z. major* (Fig. 98). They occurred near the boundary between the Lochkovian and Pragian (Ustechko age). Only *Z. podolica* has a longer range from early Ustechko to mid Khmeleva ages, that is, being mainly Pragian in age. Their non-Podolian relatives are known only from the Lochkovian (Janvier, unpublished manuscript). There is some narrowing of the headshield in a series ranging from *Z. metopias* of Spitsbergen, through the British *Z. salweyi*, to the Podolian *Z. dzieduszyckii*, *Z. podolica*, and *Z. kasymyri* sp. n. The clade radiated in Podolia but its origin remains unknown.

Diademaspis flourished in Spitsbergen with at least two known species and a lot of forms described in open nomenclature because of their poor preservation (Janvier 1985a), but it is not reported from Great Britain, and in Podolia it is represented by one species. The Podolian species differs from its Spitsbergen relatives in considerably smaller headshield size (see Janvier 1985a; Afanassieva 2004; Voichyshyn 2006a), and it is of older age. Diademaspids in Spitsbergen come from the mid to late Pragian, whereas in Podolia they occurred around the boundary between the Lochkovian and Pragian, or in the early Pragian. *Tegaspis* shows the same geographical distribution as *Diademaspis*, but it is even older. Its two Spitsbergen species are of mid to late Lochkovian age, like the Podolian species (Ivanie age, possibly also Ustechko age), but *Tegaspis waengsjoei* is probably more primitive (Belles-Isles and Janvier 1984).

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INDEX OF GENERIC AND SPECIES NAMES

Explanation to index: * — text-fig., bold — description.