

Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.)

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Synopsis

The osteostracans in the Zych collection of lower vertebrates from Podolia, belonging to the British Museum (Natural History), are described. There are 16 species which may be referred to either scolenaspicians or cephalaspicians, and a few undetermined osteostracans. One new genus and species, *Zychaspis siemiradzki*, and two new species, *Stensiopelta pustulata* and *Mimetaspis glazewskii*, are described. Comments are added on Podolian species which have been very poorly diagnosed. The osteostracan fauna of Podolia is compared with that of the upper part of the Red Bay Group, Spitsbergen and Dittonian II of the Welsh Borderlands.

Introduction

Prior to World War II and particularly between 1934 and 1936, the Polish palaeontologist Wladislaw Zych collected excellent material of Lower Devonian osteostracans from the Podolian 'Old Red', with the help of Swedish and English sponsors. Consequently, part of this material was donated to the Naturhistoriska Riksmuseet, Stockholm, and part to the British Museum (Natural History). Zych began to publish this osteostracan material with the description of *Cephalaspis kozlowski* (Zych 1937), in which he announced forthcoming monographs on the Osteostraci of Podolia. Unfortunately, this remarkable detailed anatomical description was the only paper he published on this subject, for his researches were interrupted by the war and a succession of tragic events which forced him to give up palaeontological activities.

Wladislaw Zych was born on 5 June 1899, in Bučač, a small village of Podolia (see map, Fig. 2, p. 313). After the liberation of Poland in 1920, he became Professor of Palaeontology at the Jana Kazimierza University of L'vov. During this period, he worked actively on the geology of the Devonian along the Dniestr valley and in adjacent areas (Zych 1927, 1931). When war broke out, Zych became a member of the resistance movements, fighting in Silesia and in the southeastern provinces of the Polish Republic. He was a commanding officer in the Z.W.Z., under the pseudonym 'Szary' ('the Grey'). In the middle of the war, he was arrested by the Germans and sent to two concentration camps, firstly Oswięcim (Auchwitz) and then Dachau. The severe maltreatment he underwent there injured his mind and he lost his memory, so was unable to restart his scientific activities after the war.

Zych then went to Italy, where he was given a position at the Osrodka Szkoleniowego, an organization providing scholarships for students whose studies had been interrupted by the war. With this organization, he came to England and decided to stay, devoting the rest of his life to catholic religious activities. He founded a chapel in St Briavel's, Glos., and worked actively for the 'Stettin' scout centre. He died on 22 May 1981, in Chepstow Hospital, and lies buried in the Hereford cemetery. For his activities during the war, Zych received both the Polonia Restituta Order and the golden cross of the Swedish Order of Wasa. His first steps in the field of lower vertebrate palaeontology were guided by the late Professor Erik Stensiö of Stockholm, who remembered him as a hard-working and humble person. His scientific work reflects his honesty by the care of the anatomical descriptions.

This paper is to report on the Podolian cephalaspid material represented in the collections of the British Museum (Natural History), and to compare it with the better-known

osteostracan faunas of the Lower Devonian of Spitsbergen and Great Britain. It remains to be completed by future description of the specimens deposited in the Naturhistoriska Riksmuseet and in the Institute of Palaeontology of the Academy of Science, of the U.S.S.R. (Moscow) and of the Ukrainian S.S.R. (L'vov). Zych (1937) mentioned some specimens deposited in German institutions, but these are still elusive. Specimens belonging to the British Museum (Natural History) are referred to by register number with or without the prefix P; those belonging to other institutions are referred to with register number and with the full title of the institution.

Phylogeny and classification of the cornuate Osteostraci

The majority of the Osteostraci are represented by species which possess a pair of laterally pointed processes, the cornual processes, in front of the paired fins. These processes of the cephalic shield consist of endoskeletal and exoskeletal components and are likely to have appeared only once in the history of the group, yet they have been secondarily reduced or have even disappeared several times independently. The osteostracans with cornual processes have been referred to as 'cornuate' Osteostraci and are regarded as a monophyletic group (Janvier 1980, 1981a, b). This group probably arose from an ensemble of osteostracans which were primitively devoid of cornual processes, and are often referred to as 'non-cornuate' osteostracans (Ritchie 1967). Among the known non-cornuate osteostracans, some are more closely related to the cornuate ones than the others are, and thus this ensemble of primitive forms is paraphyletic (Janvier 1980, 1981a, b).

The interrelationships of the cornuate osteostracans are still obscure and consequently their systematics is mainly based on their degree of overall resemblance or divergence. This explains why, beside a small number of monophyletic groups with conspicuous autapomorphies, the majority of the cornuate osteostracans are represented by forms mainly with features ('horseshoe-shaped' shield) primitive for this group; these have in the past been referred to the genus *Cephalaspis*, because the type species of this genus, *C. lyelli* Agassiz, while one of the least known is apparently one of the least derived representatives of the cornuate Osteostraci. But it appears that the genus *Cephalaspis* has now to be restricted to its type species and perhaps a few others which share with it some synapomorphies, such as the shape of the median dorsal field or the elongate preorbital division of the shield. All the other known '*Cephalaspis*' species have to be referred to new genera, according to their respective phylogenetic relationships. In most cases, a careful revision of the specimens is needed before this can be achieved. Lankester (1870), Stensiö (1932, 1958), Denison (1951a), Wängsjö (1952) and Janvier (1980, 1981a) referred some of the species previously referred to as '*Cephalaspis*' to new genera, and this policy will be continued in the present paper, except when no particular phylogenetic position can be given to a '*Cephalaspis*'-like species.

I recognize five major monophyletic groups of still undetermined taxonomic rank among the cornuate Osteostraci: the cephalaspidians, kiaeraspidians, benneviastpidians, thyestidians and scolenaspidians (Janvier 1980, 1981a, b). All these groups are characterized by conspicuous autapomorphies, except perhaps for the cephalaspidians, the monophyly of which deserves to be more thoroughly tested. These five groups will be briefly commented on below. This classification of the Osteostraci will probably be modified in the future, following new investigations on the internal anatomy of the best-preserved non-cornuate forms (*Aceraspis*, *Hemicyclaspis*). At present, the lack of detailed information on the internal anatomy of the non-cornuate forms makes it difficult to use internal characters in determining the phylogeny of the cornuate forms, since out-group comparisons are impossible for these characters. For example, it is difficult to establish the significance of the presence or absence of the medial recess of the posteroventral myodome of the cornuate forms (Janvier 1980, 1981a).

The thyestidians are characterized by the medial course of the infraorbital sensory-line canal, which does not pass onto the lateral field, and by a relatively narrow pineal plate.

Most thyestidians, except the most primitive known species *Procephalaspis oeselensis* (Robertson), show two longitudinal rows of large tubercles on the dorsal face of the abdominal division of the shield. The thyestidians contain an important monophyletic subgroup, the Tremataspidae, characterized by the considerable elongation of the abdominal division and the loss of the paired fins (excluding *Tyriaspis*, *Didymaspis* and *Sclerodus*, which deserve a revision, but including *Timanaspis*). The sister-species of this highly derived subgroup is *Thyestes verrucosus* Eichwald, with which it shares the very narrow pineal plate, the enameloid cap on the tubercles (similar to the superficial layer of cosmine in tremataspids; Denison 1951b), the rows of large tubercles on the abdominal division, and the dermal denticles on the supra-oral field.

The kiaeraspadians are characterized by an elongate and narrow abdominal division which tends to become shorter in the most derived taxa, a considerable reduction of the cornual processes and of the prebranchial fossae, and an enlargement of the supra-oral fossae (Janvier 1981a).

The benneviaspadians have a dorsoventrally flattened shield. Their exoskeleton is generally devoid of ornamentation and lacks radiating canals in the middle layer.

The scolenaspidians have a massive and generally elevated shield characterized by a nasohypophysial opening in which the hypophysial division is larger (sometimes much larger) than the nasal division, and which opens in the floor of a relatively deep depression. The ornamentation of the scolenaspidian exoskeleton generally consists of large, rounded tubercles, and the scolenaspidians often possess a well-developed median crest or spinal process on the abdominal division. The cornual processes are generally thick, strongly curved medially, and ornamented with spiny tubercles.

Finally, the cephalaspadians may be defined by the condition of the first 'sinus expansion of the labyrinth' canal leading from the otic region to the lateral fields ('s.e.l.' canal), which branches at a point close to the orbit, bending there sharply. They also have lateral fields extending far backwards onto the dorsal face of the cornual processes. The latter are generally broad, flattened, but not very long. It must be stressed that the monophyly of this group is still uncertain.

I include in the cephalaspadians the genus *Cephalaspis*, restricted to *C. lyelli* and a few other immediately related species, and the genus *Meteoraspis* (Janvier 1981a), characterized by lateral fields occupying only the lateral part of the cornual processes, and extending almost to the tip of the latter. The genera *Pattenaspis* (Stensiö 1958), *Mimetaspis* (Stensiö 1958) and *Hildenaspis* (Janvier 1976) are also provisionally placed in the cephalaspadians on the basis of the condition of the first 's.e.l.' canal.

The relationships between these five groups are still uncertain, mainly because of the difficulty of out-group comparisons with the non-cornuate forms. The cladogram proposed here (Fig. 1; Janvier 1981a) is admittedly supported by rather tenuous arguments and depends largely on a number of arbitrary generalizations, but it has not yet been refuted. There remains, for instance, an uncertainty as to the relationships of the kiaeraspadians, although I would be inclined to consider the structure of the posteroventral myodome (with no medial recess) shared by them and the thyestidians as a more reliable derived character than the 'orthobranchiate' condition, shared with the benneviaspadians.

The benneviaspadians, kiaeraspadians and thyestidians share at least one synapomorphy: the first 's.e.l.' canal branching at a point very close to the lateral field. I could find no satisfactory synapomorphy of the genus *Securiaspis* (Stensiö 1932), and I suspect that it may be paraphyletic, forming a possible stem-group for the three groups mentioned above.

The position given to the scolenaspidians in this cladogram is based only on the absence of a large median dorsal scute which replaces the anterior dorsal fin in *Hemicyclaspis* and the cephalaspadians. This lack of any trace of median dorsal scute is also known to occur in *Thyestes verrucosus* (and hence, perhaps, in all the thyestidians). The squamation of the trunk is unknown in the benneviaspadians and kiaeraspadians. By contrast, this large median scute, similar to that of *Hemicyclaspis purchisoni* (Stensiö 1932) is known in *C. lyelli* (White 1958) and in *Meteoraspis pinnifera* (Wängsjö 1952). Although the lack of a character must be

used with caution, it is, for the moment, the only available criterion for assigning the scolenaspidians to a particular position within the cornuate osteostracans. The ornamentation of the dermal skeleton of the scolenaspidians is more similar to that of the thyestidians and kiaeraspidians than to that of cephalaspidians and *H. murchisoni*, in which it is covered with a smooth cosmine-like hard tissue.

It would be premature to propose a Linnean classification of these major osteostracan groups, and I retain the admittedly imperfect classification outlined in this section, which does not suggest any particular taxonomic rank.

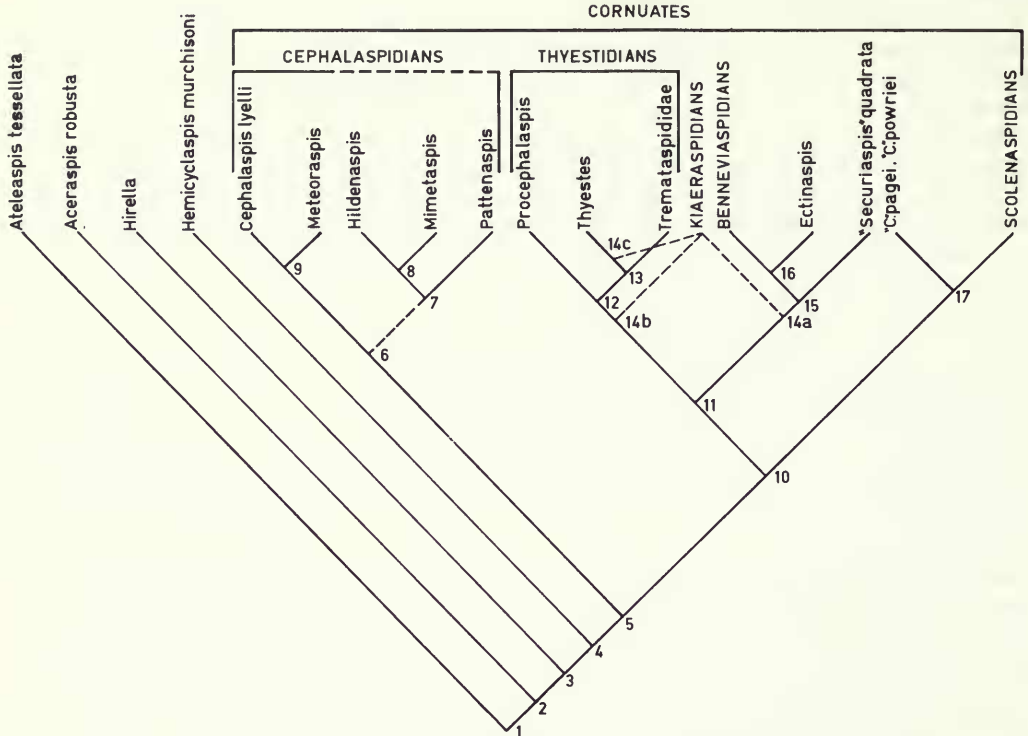


Fig. 1 Theory of phylogenetic interrelationships of the Osteostraci (from Janvier 1980, 1981a).

Key to the synapomorphies: 1, cephalothoracic shield with median and lateral 'sensory' fields, horizontal lobe of the tail; 2, solid marginal and rostral parts of the shield, slightly more stenobasal paired fins; 3, stenobasal paired fins, large dermal plates on the ventral side of the shield; 4, anterior median dorsal fin transformed into a large dermal scute, large trunk scales, cosmine-like dermal covering; 5, cornual processes; 6, first 's.e.l.' canal abruptly curved midway between the orbit and the lateral field, and branching at this point; 7, slender cornual processes with medial denticles, ornamentation consisting of minute elongate tubercles; 8, no independent pineal plate, large orbits; 9, flattened cornual processes with lateral fields extending posteriorly onto them; 10, no trace of anterior median dorsal fin, broad pectoral sinus (?), ornamentation consisting primitively of costulate tubercles (?); 11, first 's.e.l.' canal branching near the lateral fields; 12, infraorbital sensory-line canal running near the mid-line, narrow pineal plate; 13, enameloid cap on the tip of the tubercles, elongate abdominal division bearing longitudinal rows of large tubercles, external opening of endolymphatic duct outside median dorsal field, small pineal plate, denticles on supra-oral field; 14a, 'orthobranchiate' condition; 14b, no medial recess of the posterior ventral myodome; 14c, elongate abdominal division, short cornual processes; 15, flattened shield, large pectoral sinus; 16, strongly divergent cornual processes, very flat shield, broad posterior part of the lateral fields; 17, hypophysial division of nasohypophysial opening slightly larger than the nasal division, and situated in a depression.

Geological setting

The geology of the Lower Devonian 'Old Red' of Podolia was first described by Zych (1927), who published the most reliable geographical data on the area where the osteostracan-bearing localities are located (Fig. 2). Later, Balabai (1962) published a simplified geological map of the area, showing the areal extent of the three major units defined by Zych. However, this map is largely erroneous. The Lower Devonian of Podolia has a monoclinical structure, dipping to the northwest, and crossed by the Dniestr valley which runs at right angles to the strike. Consequently, the oldest layers occur in the east (Borshchov) and the youngest in the west (Dniestr Series).

Three major horizons, or stages (cf. Nikiforova 1977, addendum), have been recognized in the Lower Devonian of Podolia: the Borshchov (Borszczow), Čortkov (Czortkow) and

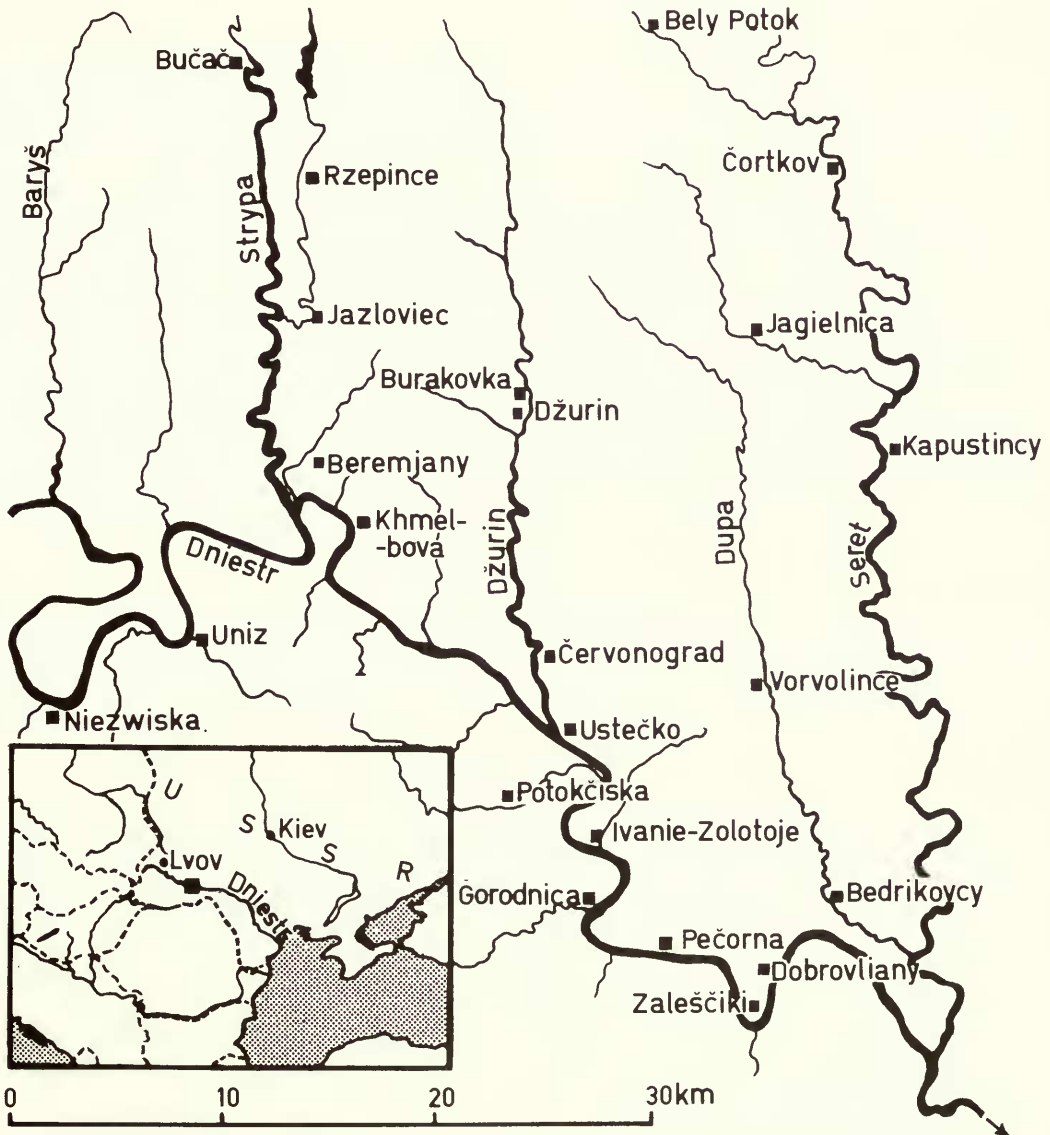


Fig. 2 Locality map. The locality names are transliterated from Ukrainian into the Latin alphabet. The Polish transliteration is indicated in the text.

LOWER DEVONIAN	Emsian	II Plant group	Dniestr series
	Siegenian	I	
		III II 'Old Red' = Babin sandstone I	
	Gedinnian (Dittonian)	Ivanie (Iwanie) hor.	
		Čortkov (Czortkow) hor.	
		Borshchov (Borszczow) hor.	
UPPER SILURIAN	Pfidoli	Skala hor.	
	Ludlow		

Fig. 3 Stratigraphy of the Lower Devonian and Upper Silurian of Podolia (from Zych 1927, Boucot & Pankiowskyj 1962, Balabai 1962 and Karatayute-Talimaa 1981).

Ivanie (Iwanie) horizons. The latter is overlain by the 'Old Red', or Babin Sandstone, which in its turn overlain by the Plant Group, referred to the Siegenian and Emsian. The 'Old Red' and Plant Group together form the Dniestr Series (Fig. 3).

The material described herein has been collected mainly in the 'Old Red' and Ivanie horizons, but the precise stratigraphical position of some finds is difficult to determine, because the labels written by Zych himself lack indication of the altitude at which they were found. Most of the exposures occur in the cliffs of the banks of the Dniestr and adjacent creeks. Some of these cliffs cut through several horizons and fossils coming from the same locality may belong to different faunal assemblages. Consequently, any precise stratigraphical conclusions arising from the present study can only be drawn by geologists who have access to the localities, and can compare the facies of the matrix of the specimens with those of the sections themselves.

Systematic descriptions

Most of the available Podolian osteostracans belong to the scolenaspidians, and only a few specimens can be referred to the cephalaspidians and, questionably, benneviaspidians. No kiaeraspidian or thyestidian has yet been recorded from the Lower Devonian of Podolia.

SCOLENASPIDIANS

The genus *Scolenaspis* was erected by Jarvik (1954) for *Cephalaspis signata* Wängsjö (1952), which shares with *C. lyelli* only primitive cornuate osteostracan characters. As early as 1870, Lankester had noticed that some of the '*Cephalaspis*' species of Great Britain were quite different from *C. lyelli* in the shape and ornamentation of the shield, and he proposed the subgeneric name *Zenaspis* for *C. salweyi* Egerton. The name 'zenaspidians' would thus have been more suitable for the monophyletic group called here scolenaspidians, but I prefer to keep the generic name *Zenaspis* for a restricted subgroup of the scolenaspidians, which is relatively derived by comparison with *S. signata*. The latter corresponds to a more generalized pattern of the group and the name scolenaspidian is thus more appropriate to designate the whole group.

The scolenaspidians comprise several groups of much derived forms, such as *Diademaspis*, *Zenaspis*, *Machairaspis*, and probably also *Tegaspis* (Fig. 4), and an ensemble of less derived forms which have a shield of '*Cephalaspis*' type (generalized cornuate osteostracan pattern),

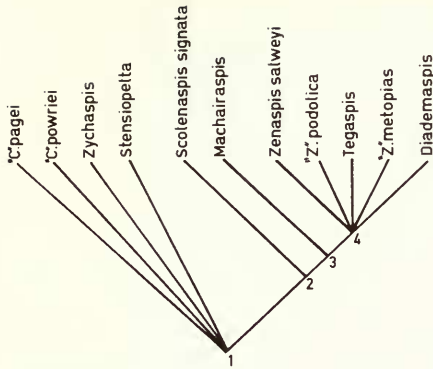


Fig. 4 Theory of phylogenetic relationships of the scolenaspidians and some closely related cornuate osteostracans. Key to the synapomorphies: 1, hypophysial division of the nasohypophysial opening slightly larger than the nasal division, narrow and thick cornual processes, lateral fields with irregular limits; 2, spinal process or prominent median dorsal ridge; 3, hypophysial division of the nasohypophysial opening much larger than the nasal division, and situated in a deep depression; 4, broad and massive shield, short cornual processes, coarse ornamentation, broad median dorsal field, posterior part of the lateral fields produced medially into a distinct lobe.

although showing the typical scolenaspidian characters. *S. signata* belongs to these 'stem' scolenaspidians and, for the moment, is the only species included in *Scolenaspis*. The species '*Cephalaspis* pagei', '*C.* powriei' and '*C.* spinifer' (Lankester 1870, Stensiö 1932), from the Devonian of Great Britain, can also be regarded either as primitive scolenaspidians or as the closest relatives of that group. They show incipient scolenaspidian characters (shape of the nasohypophysial opening, ornamentation, outline of the lateral fields) and any one of these three species may be regarded as the sister-species of all scolenaspidians. A theory of interrelationships of the scolenaspidians is presented in Fig. 4.

In the material from Podolia, as well as in that from Spitsbergen, highly derived and primitive scolenaspidians may coexist in the same locality. In Spitsbergen, however, the topmost part of the Wood Bay Formation (Stjørdalen Division) contains only remains of very large *Diademaspis* species. Some of the Podolian forms are quite similar to species known from Spitsbergen and Great Britain, but there are a few taxa which are unique to Podolia. The species which show only general scolenaspidian characters will be referred to here as '*Scolenaspis*'.

Genus *ZYCHASPIS* nov.

DIAGNOSIS. Primitive scolenaspidians with a slight rostral lobe and slender cornual processes. The ornamentation of the exoskeleton consists of small, closely-set tubercles, and scattered large ones. The lateral fields are relatively narrow.

NAME. After the late Dr W. Zych.

TYPE SPECIES. *Zychaspis siemiradzkii* sp. nov.

REMARKS. The shield referred here to *Zychaspis* recalls in many respects that of some other primitive scolenaspidians or taxa closely related to them ('*C.* powriei' '*C.* pagei', '*C.* watsoni'), in particular in the shape of the median dorsal field, the type of ornamentation, and the shape of the cornual processes. The scolenaspidian characters are feebly expressed in *Zychaspis*, but the hypophysial division of the nasohypophysial opening is slightly larger than the nasal division. The shape of the lateral fields is also very much of scolenaspidian type, with irregular medial margin and slightly enlarged anterior ends.

The phylogenetic position of *Zychaspis* within the scolenaspidians cannot be determined. It is probably a primitive taxon in this group, but it is uncertain whether it shares unique characters with any of the known monophyletic subgroups of the scolenaspidians. *Zychaspis* resembles '*C.* campbelltonensis' (Whiteaves 1881, Robertson 1936, Pageau 1969), from the Devonian of Canada, in the shape of the rostral region of the shield and the cornual processes. However, I doubt that this resemblance can be regarded as an indication of close relationships. In point of fact, neither the ornamentation nor the shape of the nasohypophy-

sial opening of this Canadian species is suggestive of scolenaspidian affinities (personal observations on various specimens from Campbellton, especially BM(NH) P.56167). I would thus be inclined to consider this resemblance a convergence.

Zychaspis siemiradzki sp. nov.

Figs 5, 6

DIAGNOSIS. A moderately large species of *Zychaspis* with medially curved cornual processes.

HOLOTYPE. BM(NH) P.17714, labelled by Zych as '*Cephalaspis siemiradzki* var. *elegans*'; 'Old Red' (probably Ivanie horizon), Chomiakówka East, north of Bely Potok, Podolia (now Ukrainian S.S.R.). Fig. 6.

NAME. After Professor J. Siemiradzki, of the Geological and Palaeontological Museum, L'vov.

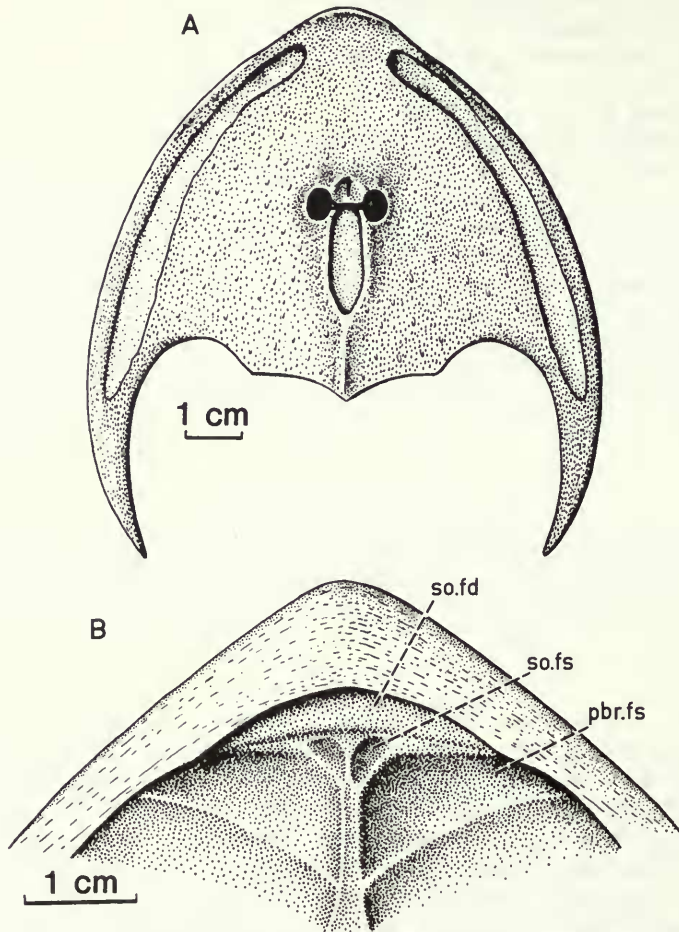


Fig. 5 *Zychaspis siemiradzki* gen. et sp. nov., 'Old Red' and Ivanie horizons, Lower Devonian of Podolia, Ukrainian S.S.R. A, reconstruction of the shield, based on the holotype (P.17714) and numerous other specimens from the type locality, dorsal view. B, anterior part of the oralbranchial chamber, based on C.1324a in the Naturhistoriska Riksmuseet (Stockholm), ventral view. Abbreviations: pbr.fs, prebranchial fossa; so.fd, supraoral field; so.fs, supraoral fossa.



Fig. 6 *Zychaspis siemiradzkii* gen. et sp. nov., 'Old Red' (probably Ivanie horizon), Chominkówka East, north of Bely Potok, Podolia, Ukrainian S.S.R. **Holotype** (P.17714), dorsal view. $\times 0.75$.

MATERIAL. Holotype; Červonograd (Czerwonograd): P.17717; Gorodnica (Horodnica): P.20457, P.20459, P.20461, P.20465, P.20470, P.20475–9, P.20480–2, P.20486–7, P.20492, P.20496, P.20504, P.20516–7, P.20548, P.53358–60, P.53363–8. All BM(NH).

REMARKS. This species is extremely abundant in the red-green sandstone of Gorodnica (or Horodnica on Zych's labels), which represents either the base of the 'Old Red' or the top of the Ivanie horizon.

Most of the specimens from Gorodnica are poorly preserved and much flattened. Many shields are only represented by the marginal and rostral rims and the cornual processes. The reconstruction in Fig. 5 is based on several specimens, including the holotype, Fig. 6. The rostral region is generally well defined and separated from the marginal region by a slight embayment, but in many specimens the rostromarginal transition is straight (Fig. 5B). The anterior part of the oralobranchial cavity can be observed in one specimen (C.1324a) in the Naturhistoriska Riksmuseet, Stockholm (Fig. 5B), and shows well-defined supraoral fossae (*so.fs*) and relatively large prebranchial fossae (*pbr.fs*). The pattern of fossae and ridges of this part of the oralobranchial cavity is like that in typical scolenaspidians, such as *S. signata* (Wängsjö 1952, Jarvik 1954). The median dorsal field is narrow and limited anteriorly by a thin, but separate, pineal plate. The ornamentation consists of very small closely-set tubercles. These are somewhat elongate in shape on the abdominal division, where one can also observe some scattered larger tubercles. This type of ornamentation resembles that of '*C. powriei*' from the Lower Devonian of Great Britain, but is probably a primitive type for scolenaspidians. The cornual processes are relatively slender, falciform and flattened. The lateral fields extend onto their proximal part only.

The two following species are referred with some doubt to the genus *Zychaspis*, since they have been erected by Balabai (1962) without adequate figures, and without reference to type specimens. I refer these species to *Zychaspis* on account of Balabai's sketches, which are reproduced as Fig. 7.

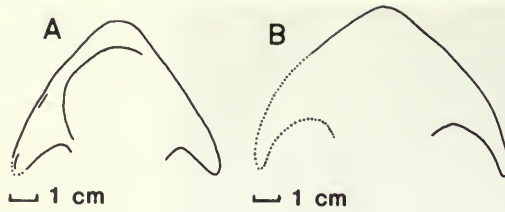


Fig. 7 *Zychaspis elegans* (Balabai), 'Old Red', Chmelbova, Podolia, Ukrainian S.S.R. B, *Zychaspis djurinensis* (Balabai), 'Old Red', Džurin, Podolia, Ukrainian S.S.R. (both after Balabai, 1962).

Zychaspis elegans (Balabai)

Fig. 7A

1962 *Cephalaspis elegans* Zych in coll.; Balabai: 7; fig. 10.

Balabai gave no diagnosis of this species, but the figure he published shows an elongate rostral region, as in *Z. siemiradzskii*, which is regarded as characteristic for the genus. In *Z. elegans* the cornual processes are more divergent than in *Z. siemiradzskii*. Type locality: Khmelbova, Podolia.

? *Zychaspis djurinensis* (Balabai)

Fig. 7B

1962 *Cephalaspis djurinensis* Balabai: 6; fig. 7.

This species did not receive any diagnosis in Balabai's paper. From the figure, it seems that the rostral region is produced anteriorly into a lobe as in *Z. siemiradzskii*, but the shape of the cornual processes is different, being stouter and more divergent. Type locality: Djurin, Podolia.

Genus *STENSIOPELTA* Denison 1951a

DIAGNOSIS. Primitive scolenaspidians with very elongate, straight and strongly divergent cornual processes. Abdominal division elongate and narrow, with a slight median elevation just behind the median dorsal field. Short prehypophysial division of the shield.

TYPE SPECIES. *Cephalaspis woodwardi* Stensiö (1932); Abergavenny, Monmouthshire.

REMARKS. The genus *Stensiopelta* was erected by Denison (1951a: 191) for *Cephalaspis woodwardi* Stensiö, which he regarded as very different from the other *Cephalaspis* species. Contrary to Wängsjö's footnote (1952: 250), this generic name is valid. Wängsjö (1952) considered *S. woodwardi* to be close to *Pattenaspis* [*'Cephalaspis'*] *deltoides* (Wängsjö) from Spitsbergen, but the resemblance in the shape of the cornual processes is superficial. *P. deltoides* belongs to the monophyletic genus *Pattenaspis*, characterized by the enlargement of the orbits, reduction of the prebranchial fossae (but in a way different from kiaeraspidians) and the elongation of the cornual processes. *Pattenaspis* does not share any synapomorphy with the scolenaspidians, whereas the two known species of *Stensiopelta* share with the scolenaspidians the shape of the nasohypophysial opening and the type of ornamentation, which consists of clusters of small rounded tubercles.

Stensiopelta pustulata sp. nov.

Figs. 8, 9, 10, 11

DIAGNOSIS. *Stensiopelta* species with elongate abdominal division, and with an obtuse, slightly lobate rostral margin.

HOLOTYPE. BM(NH) P.17703-4, labelled by Zych as '*Cephalaspis woodwardi* var. *junior*'. 'Old Red' I, Ustečko (Uscieszko) West, Podolia, Ukrainian S.S.R.



Fig. 8 *Stensiopelta pustulata* sp. nov., 'Old Red' I, Ustečko, Podolia, Ukrainian S.S.R. Holotype (P.17703), dorsal view. Silicone rubber cast from natural mould, whitened with magnesium oxide.

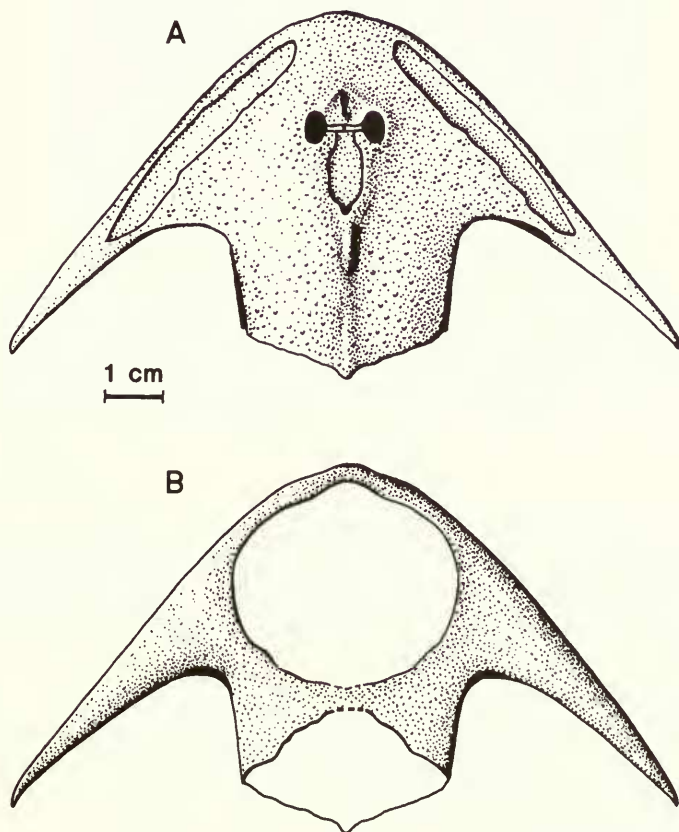


Fig. 9 *Stensiopelta pustulata* sp. nov., reconstruction of the shield, mainly based on the holotype (P.17703). A, dorsal view; B, ventral view.

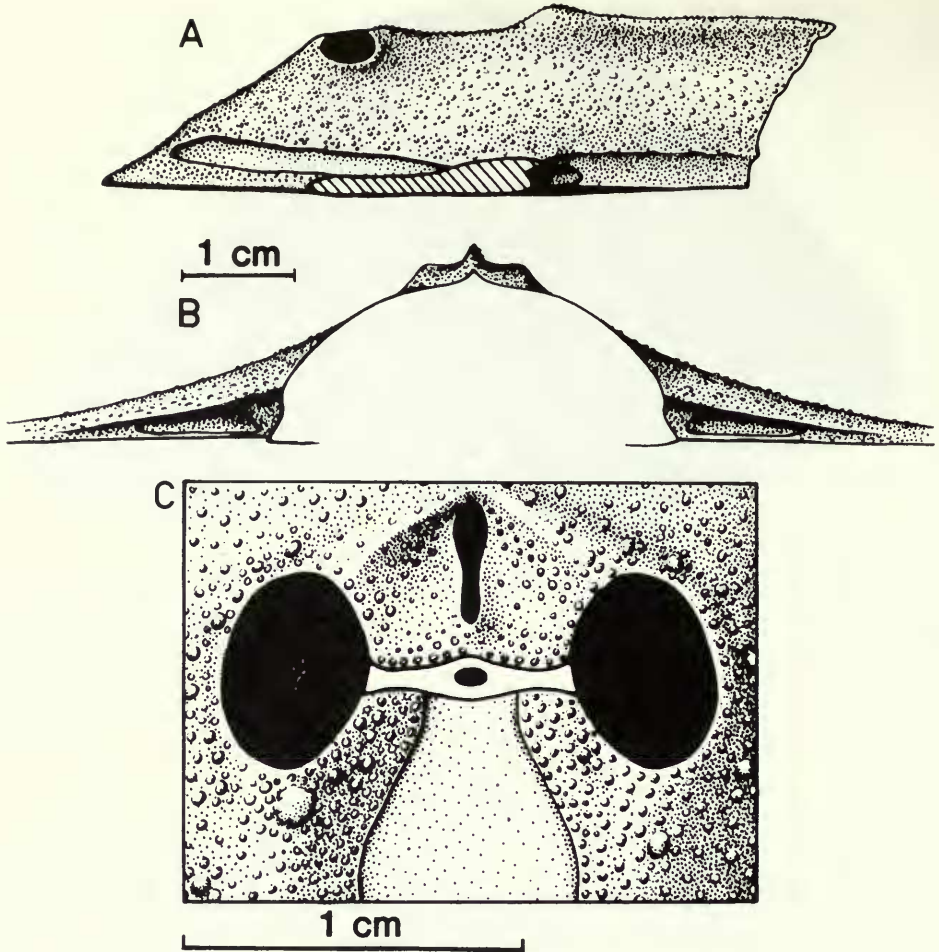


Fig. 10 *Stensiopelta pustulata* sp. nov., reconstruction of the shield, mainly based on the holotype (P.17703–4). A, lateral view; B, posterior view; the abdominal division has been cut just behind the area of attachment of the paired fins. C, orbital and nasohypophysial regions of the shield; the pineal plate is not known, and it is reconstructed here according to the shape of the groove which housed it.

NAME. From the pustulated type of ornamentation.

MATERIAL. (Well preserved specimens only). Holotype; Ustečko (Uscieszko): P.20534, P.20540–1; Burakówka (Burakowka): P.17702; Bely Potok (Potok Biały): P.17707; Černovograd (Czerwonograd): P.20933; Gorodnica (Horodnica): P.20530–1, P.20553–4, P.20564–5. All BM(NH).

REMARKS. This species is slightly larger than *S. woodwardi* from the Lower Devonian of Wales (Stensiö 1932: fig. 51; pl. 20, figs 1, 2), and has a somewhat longer abdominal division. It differs also in having a more obtusely rounded rostral margin, which shows a faint rostral lobe, and in that the cornual processes of *S. woodwardi* are slightly less divergent than those of *S. pustulata*. Nevertheless, the two species can be regarded as extremely closely related.

The most noteworthy features of *S. pustulata* are the slight rostral lobe and the position of the median dorsal elevation of the abdominal division, which seems to be slightly closer to

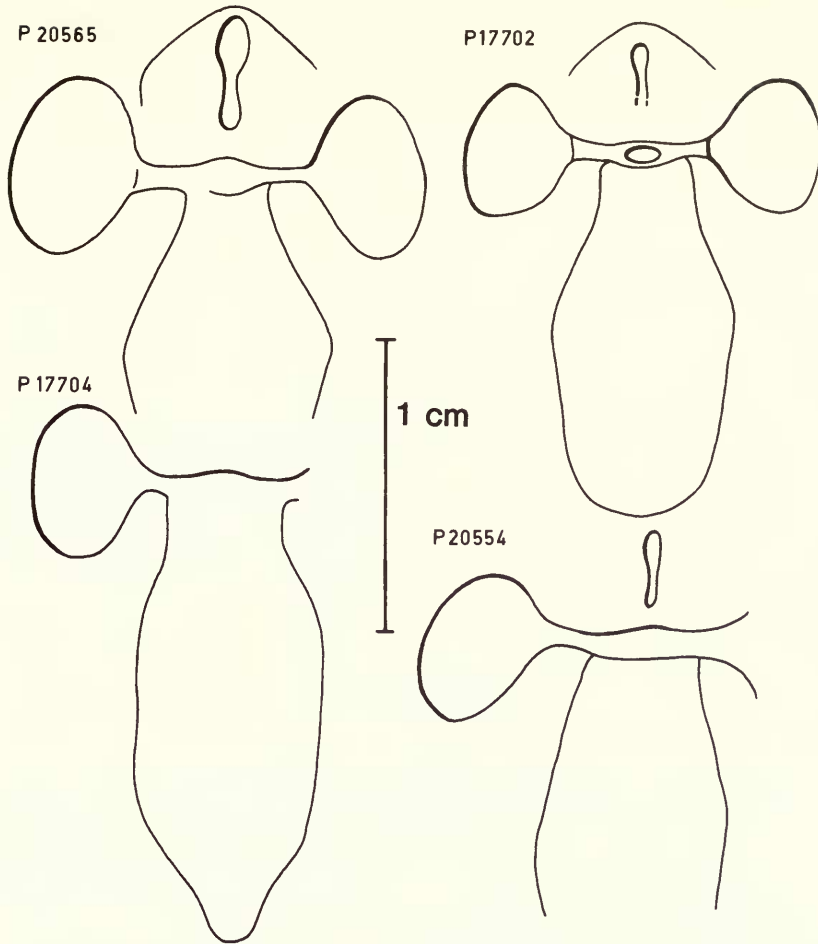


Fig. 11 *Stensiopelta pustulata* sp. nov.; variations in the shape of the median dorsal field.

the median dorsal field than in *S. woodwardi* (Figs 9A, 10A). As in *S. woodwardi*, the lateral flanges of the abdominal division are slightly concave behind the areas of attachment of the paired fins (Figs 9A, 10A, 10B). This longitudinal depression probably accommodated the medial edge of the fin.

The hypophysial division of the nasohypophysial opening is slightly enlarged (Fig. 10C), but this scolenspidian character is not as well marked as in *Zenaspis* or *Diademaspis*. It is comparable to the condition in *Zychaspis* or '*C.*' *powriei*.

The ornamentation of the dermal skeleton consists of large tubercles, each surrounded by a ring of smaller ones. The large tubercles are generally in the centres of the tesserae. Between these patches of tubercles, the whole surface of the shield is covered with minute, scattered tubercles. The large tubercles are lacking on the cornual processes, the marginal region, the rostral region and the ventral side. This type of ornamentation is quite typical for scolenspidians, and more closely resembles that of *Zenaspis* and *Diademaspis* than that of *Machairaspis* and the primitive forms of the group.

In all the other features of the shield (shape of the lateral and median fields, the orbits and the pineal plate), *S. pustulata* is very similar to *S. woodwardi*. There is, however, an important variation in the shape of the median dorsal field (Fig. 11), which may be more constricted anteriorly in some specimens than in others.

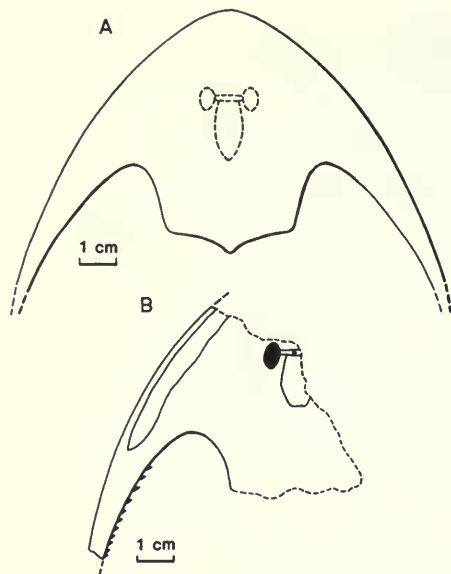


Fig. 12 *Stensiopelta* sp., labelled by Zych as '*Cephalaspis woodwardi* var. *subrotunda*'. A, P.17701, 'Old Red', Zascinovče (near Trembovla, on the Seret river), Podolia, Ukrainian S.S.R. B, P.17708, 'Old Red', Rcepiniče, Podolia, Ukrainian S.S.R.

Stensiopelta sp.

Fig. 12

Some specimens have been labelled by Zych as '*Cephalaspis woodwardi* var. *subrotunda*', in particular P.17700–1 from Zascinovče ('Old Red') and P.17708 from Rzepiriče. This form differs from *S. pustulata* in its gently curved cornual processes. In P.17708 (Fig. 12B), the cornual processes bear medial denticles. These specimens may fall within the range of variation of *S. pustulata* or may belong to a different species. The material available, however, is not sufficient to determine this.

Genus *ZENASPIS* Lankester 1870

DIAGNOSIS. Medium-sized to large scolenaspidians with a broad median dorsal field and a very broad posterior part of the lateral field. Hypophysial division of nasohypophysial opening much larger than the nasal division. Low but sharp median dorsal crest (or spinal process) on abdominal division. Orbits comparatively small.

TYPE SPECIES. *Cephalaspis salweyi* Egerton (1857); Ludlow, Shropshire.

REMARKS. The name *Zenaspis* was erected by Lankester (1870: 43) as a subgenus of *Cephalaspis* for *C. salweyi*, which differs in many respects from *C. lyelli* (more massive shield, thicker cornual process, spinal process, tuberculate ornamentation). *Zenaspis* may be retained as a generic name for all the scolenaspidian species sharing the overall morphology of *Z. salweyi*, but there is no clear derived character for this genus, and the diagnosis given above contains characters which are possibly plesiomorphous for more derived scolenaspidian genera, e.g. *Tegaspis* and *Diademaspis* (Wängsjö 1952, Janvier 1980). We cannot therefore rule out the possibility that the genus *Zenaspis* would become paraphyletic if species other than the type species were included in it. For this reason, the reference to '*Zenaspis*' of the species *Cephalaspis metopias* Wängsjö (1952) from Spitsbergen, and one of the two species from Podolia described below, is only provisional until the interrelationships of these advanced scolenaspidians are revised in detail. This uncertainty of the monophyly of *Zenaspis* is expressed by a polychotomy in Fig. 4, p. 315.

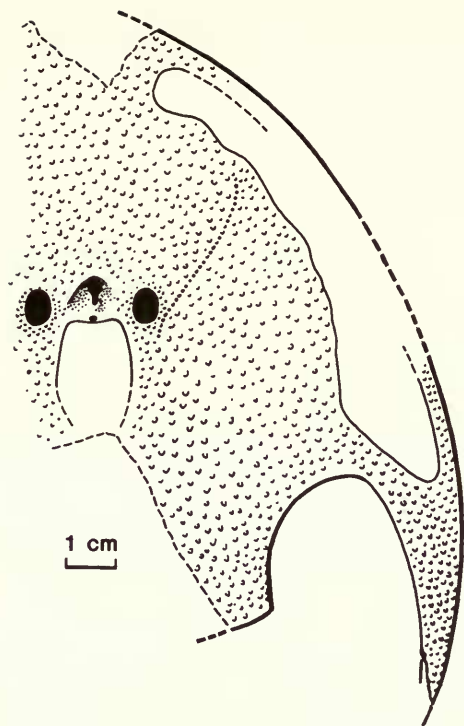


Fig. 13 *Zenaspis podolica* (Balabai), 'Old Red' I, Lower Devonian, Ustečko, Podolia, Ukrainian S.S.R. Based on P.17713.

'*Zenaspis*' *podolica* (Balabai)

Fig. 13

1962 *Cephalaspis podolica* Balabai: 4; fig. 4.

DIAGNOSIS (emended). Relatively large *Zenaspis*-like species, with medially curved cornual processes. Pineal plate fused laterally with the orbital margin. Exoskeleton ornamented with large, single tubercles.

HOLOTYPE. Specimen no. 23562 of the Museum of the Academy of Sciences of the Ukrainian S.S.R.; probably 'Old Red' I, Ustečko, Podolia, Ukrainian S.S.R.

MATERIAL. Ustečko (Uscieszko): BM(NH) P.17713, labelled by Zych as '*Cephalaspis salweyiformis*'.

REMARKS. This species is the only one which has been adequately figured by Balabai (1962: fig. 4), and can be compared with the material in the British Museum (Natural History). I refer to it an imperfect shield (P.17713), which resembles the holotype and came from the same locality. However, a number of large scolenaspidian shield fragments with large tubercles probably also belong to this species.

'*Z.* *podolica* resembles '*Z.* *metopias* from Spitsbergen in the reduction of the pineal plate, and the fusion of its lateral parts with the orbital margin, a character also met with in some *Machairaspis* species, as well as in *Tegaspis* and *Diademaspis*. The lateral fields are also similar in shape in the two species, but the cornual processes are much longer in '*Z.* *podolica*.

Zenaspis cf. *salweyi* (Egerton)

Fig. 14

A number of shields in the collection of the British Museum (Natural History) have been labelled by Zych as '*Cephalaspis salweyi* var. *podolica*'. They differ from '*Z.* *podolica* in

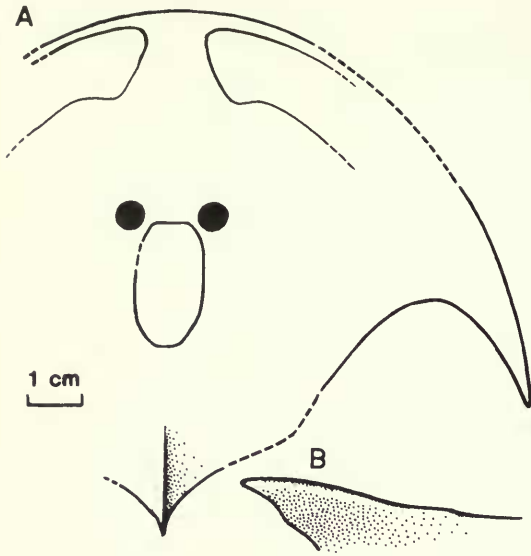


Fig. 14 *Zenaspis* cf. *salweyi* (Egerton), 'Old Red' II, Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.20490. A, dorsal view; B, lateral view of the spinal process.

being smaller but have very much the same type of ornamentation. This Podolian material cannot be specifically identified with the type material of *Z. salweyi* from Great Britain, because the latter species is defined mainly by its overall shape and size, and no specimen from Podolia is well enough preserved to allow for detailed comparisons. It is thus preferable to refer to the Podolian material as *Z. cf. salweyi*. Among the best-preserved specimens, BM(NH) P.20526-7 is almost identical to the specimens of *Z. salweyi* from Great Britain.

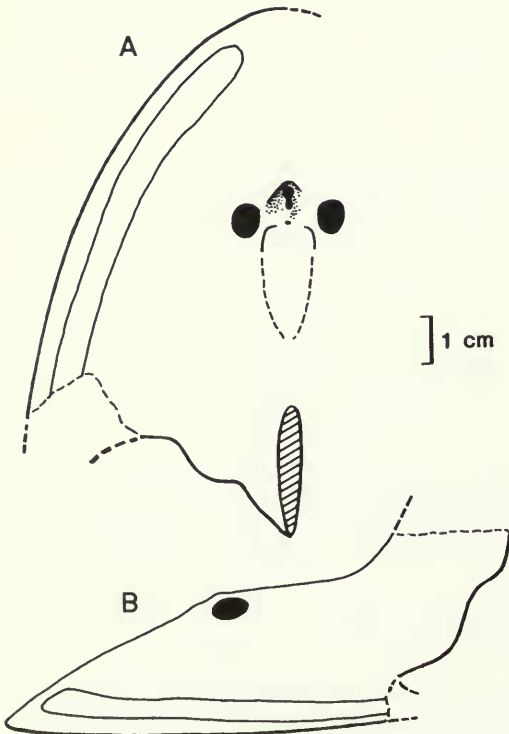


Fig. 15 *Machairaspis* sp., 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.17720, labelled by Zych as '*Cephalaspis salweyi* var. *podolica*'.

Specimen BM(NH) P.20490-1 (Fig. 14) is also referred here to *Z. cf. salweyi*, but differs from the others in its slightly more expanded shield and in its broad lateral fields. However, this difference may be due to a distortion of the fossil.

MATERIAL. Gorodnica (Horodnica) N II: BM(NH) P.20426-7, P.20463, P.20490-1, P.20494, P.20515; Ustečko (Uscieszko): P.20532-3, P.20536-7, P.20538.

Genus *MACHAIRASPIS* Janvier 1980

TYPE SPECIES. *Cephalaspis corystis* Wängsjö (1952); east side of Red Bay, north-west Spitsbergen.

Machairaspis sp.

Fig. 15

The specimen BM(NH) P.17720, labelled by Zych as '*Cephalaspis salweyi* var. *podolica*' differs from *Z. cf. salweyi* in its elongate shield and its much larger dorsal spinal process on the abdominal division. It is very similar to some of the species I referred to the genus *Machairaspis* (*M. corystis*, *M. ibex*, *M. battaili*, *M. hastata*; Janvier 1980). The dorsal spinal process is not preserved but its base is elongate, as in *M. corystis* or *M. battaili* (Wängsjö 1952: fig. 52; Janvier 1980: fig. 163). The lateral fields are relatively narrow, as is usual in the species of this genus. This specimen is from Gorodnica N II, and probably comes from the 'Old Red' I or II.

Genus *DIADEMASPIS* Janvier 1980

DIAGNOSIS. Medium-sized to very large scolenaspidians with very large hypophysial division of the nasohypophysial opening, and with an ornamentation of clusters of large tubercles in the centre of each tessera. Pectoral sinuses situated far back. Cornual process short.

TYPE SPECIES. *D. poplinae* Janvier (1980); James I Land, Spitsbergen.

REMARKS. The generic name was erected for huge scolenaspidians from the upper part of the Wood Bay Formation of Spitsbergen (namely *D. poplinae* Janvier 1980: 263, '*C.*' *jarviki* Wängsjö 1952: 378, and '*C.*' *fracticornis* Wängsjö 1952: 385). Some of the species of this genus have an extremely enlarged hypophysial division; in *D. poplinae*, for instance, it is almost as large as the orbits (Janvier 1980: fig. 156). The ornamentation of most *Diademaspis* species is quite characteristic, and can easily be recognized on small exoskeleton fragments. A character *Diademaspis* shares with *Zenaspis* and *Tegaspis* is the broad posterior part of the lateral fields, produced medially into a small lobe. It shares also with some '*Zenaspis*' species the fusion of the lateral part of the pineal plate with the orbital margin. Whether this latter character can be regarded as a synapomorphy is uncertain because it is known to occur also in some species of *Machairaspis*, as well as, probably, in *Tegaspis*, and it is likely that this modification of the pineal plate took place independently in several subgroups of the scolenaspidians and perhaps also in other osteostracan groups.

Diademaspis sp.

Fig. 16

Some fragmentary shields of large scolenaspidians from Podolia show the typical ornamentation of *Diademaspis*; that is, clusters of large tubercles in the centres of the tesserae. In some of them, the lateral fields are partly visible, and they have exactly the same shape as in *D. poplinae* Janvier, from the Kapp Kjeldsen, Lykta and Stjørdalen Divisions of the Wood Bay Formation of Spitsbergen. None of these specimens is complete enough to allow detailed comparisons with the species known from Spitsbergen.

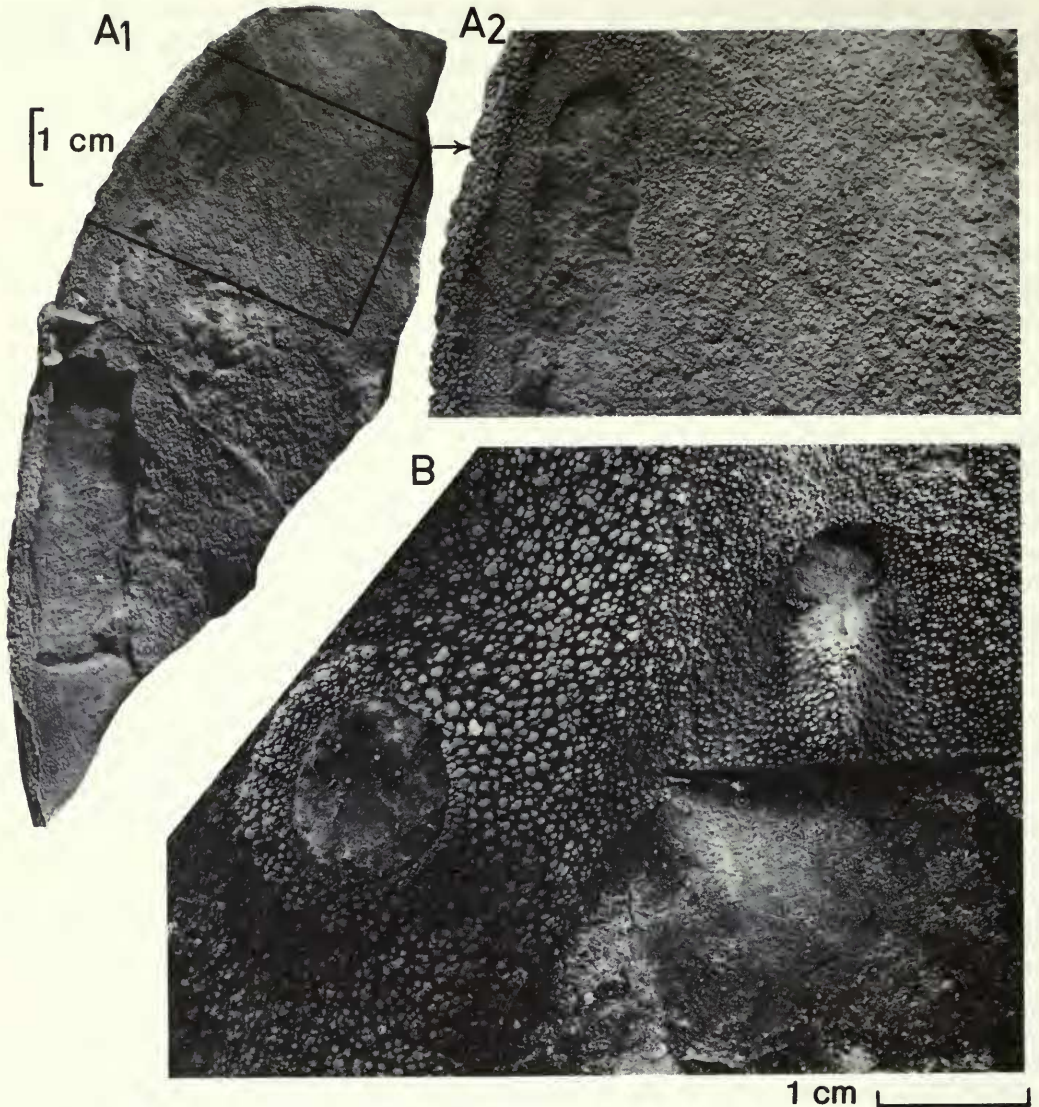


Fig. 16 A, *Diademaspis* sp., 'Old Red'?, Ustečko, Podolia, Ukrainian S.S.R. Specimen P.17729, labelled by Zych as '*Cephalaspis tesseyrei*'. Latex cast of the anterodorsal part of the shield (A1) and enlarged view of the ornamentation (A2). B, *Diademaspis* sp., Wood Bay Formation, Lykta Division, Wagnerfjellet, Spitsbergen; specimen in Muséum National d'Histoire Naturelle, Paris (SVD 1108), showing the orbitotemporal and nasohypophysial regions of the shield.

MATERIAL. Červonograd (Czerwonograd) N: BM(NH) P.17729 (labelled by Zych as '*Cephalaspis teisseyreii*'), probably from the 'Old Red'; Ustečko (Uscieczko): BM(NH) P.17727 (labelled by Zych as '*Cephalaspis morniewiczzi*', probably from the 'Old Red' or Ivanie horizon). The specimen C.85 of the Naturhistoriska Riksmuseet, Stockholm, had been labelled by Zych as the holotype of '*C. teisseyreii* var. *major*', but it is uncertain whether specimen BM(NH) P.17729 can be assigned to Zych's *C. teisseyreii* var. *major*.

INCERTAE SEDIS

The Podolian material in the British Museum (Natural History) includes a large number of shield fragments which can be referred to scolenaspidians on account of the ornamentation and the shape of the cornual processes and lateral fields, but which cannot be assigned to any particular genus, either because they show too generalized features of the group or because they are too fragmentary.

'Scolenaspis' mikrolepidota (Balabai)

1962 *Cephalaspis mikrolepidota* Balabai: 6; fig. 8.

Balabai gave a relatively good figure of the type specimen of this species, which seems to be a scolenaspidian, recognizable by the shape of its lateral fields and spinal process. The shield is elongate in shape, as in *Machairaspis*, but the spinal process does not seem to be as large as in the latter genus. For the moment, it is preferable to refer to this species as '*Scolenaspis*' *mikrolepidota* to suggest its scolenaspidian affinities and also its primitive condition within the group. The type specimen, no. 17323 of the Museum of the Academy of Sciences of the Ukrainian S.S.R., is from Ustečko and comes probably from the 'Old Red'.

There are a number of specimens in the collection which can be identified as scolenaspidians, but for which no more precise information can be given: P.20485 – cornual process, Gorodnica N II; P.20427 – imperfect low cephalic shield, Gorodnica W II; P.20528 – imperfect shield, Gorodnica W II; P.20569 – cornual process, Gorodnica W Ia; P.20572 – cephalic shield resembling that of *Z. salweyi*, Gorodnica S.

CEPHALASPIDIANS

The cephalaspidians comprise at least the genera *Cephalaspis* s.str. and *Meteoraspis*, but the genera *Pattenaspis*, *Mimetaspis* and *Hildenaspis* are provisionally regarded as cephalaspidians on the basis of the shape of the first 's.e.l.' canal, which is also geniculated. However, this group deserves a careful revision and may turn out to be paraphyletic. The cephalaspidians are relatively rare in the Podolian material, and the few species of that group which can be recognized show mainly generalized characters; that is, medium-sized shield with no conspicuous ornamentation, short abdominal division, and short and flattened cornual processes with lateral fields extending posteriorly onto their dorsal surface. Apart from one species which is referable to the genus *Mimetaspis*, the other cephalaspidians from Podolia are referred to here as '*Cephalaspis*' but must be regarded as *incertae sedis* within the group.

Genus MIMETASPIS Stensiö 1958

DIAGNOSIS. Small to medium-sized cephalaspidians with no independent pineal plate, short cornual processes and almost smooth surface of the exoskeleton. Median dorsal field anteriorly pointed. Orbits relatively large.

TYPE SPECIES. *Cephalaspis hoeli* Stensiö (1927); Ben Nevis, north-west Spitsbergen.

REMARKS. The generic name *Mimetaspis* was erected by Stensiö (1958) for *Cephalaspis hoeli* Stensiö (1927) which was considered to differ from the 'typical' *Cephalaspis* species in the orthobranchiate condition of the oralobranchial chamber. Although this latter character cannot be upheld (Janvier 1980: 163), the generic name *Mimetaspis* can be used for *C. hoeli*, *C. exilis* Wängsjö, and some other species from Spitsbergen and Podolia, which form a monophyletic group in which the pineal plate is no longer independent and the ornamentation of the exoskeleton consists of very small elongate tubercles which are only visible under the microscope.

Mimetaspis glazewskii sp. nov.

Figs 17, 18

DIAGNOSIS. Large *Mimetaspis* species with relatively broad anterior end of the median dorsal field.

HOLOTYPE. BM(NH) P.20958-9, labelled by Zych as '*Cephalaspis glazewskii*'; Ivanie horizon or 'Old Red' I, Ustečko (Uscieczko) W, Podolia, Ukrainian S.S.R. Fig. 18.

NAME. After Mr K. Glazewski, of the University of L'vov.

MATERIAL. Holotype; Ustečko (Uscieczko): P.20961-4.

REMARKS. The general shape of the shield resembles that of *M. hoeli* (Stensiö 1927, Wängsjö 1952), but differs from it in its larger size and the broader anterior end of the median dorsal field.

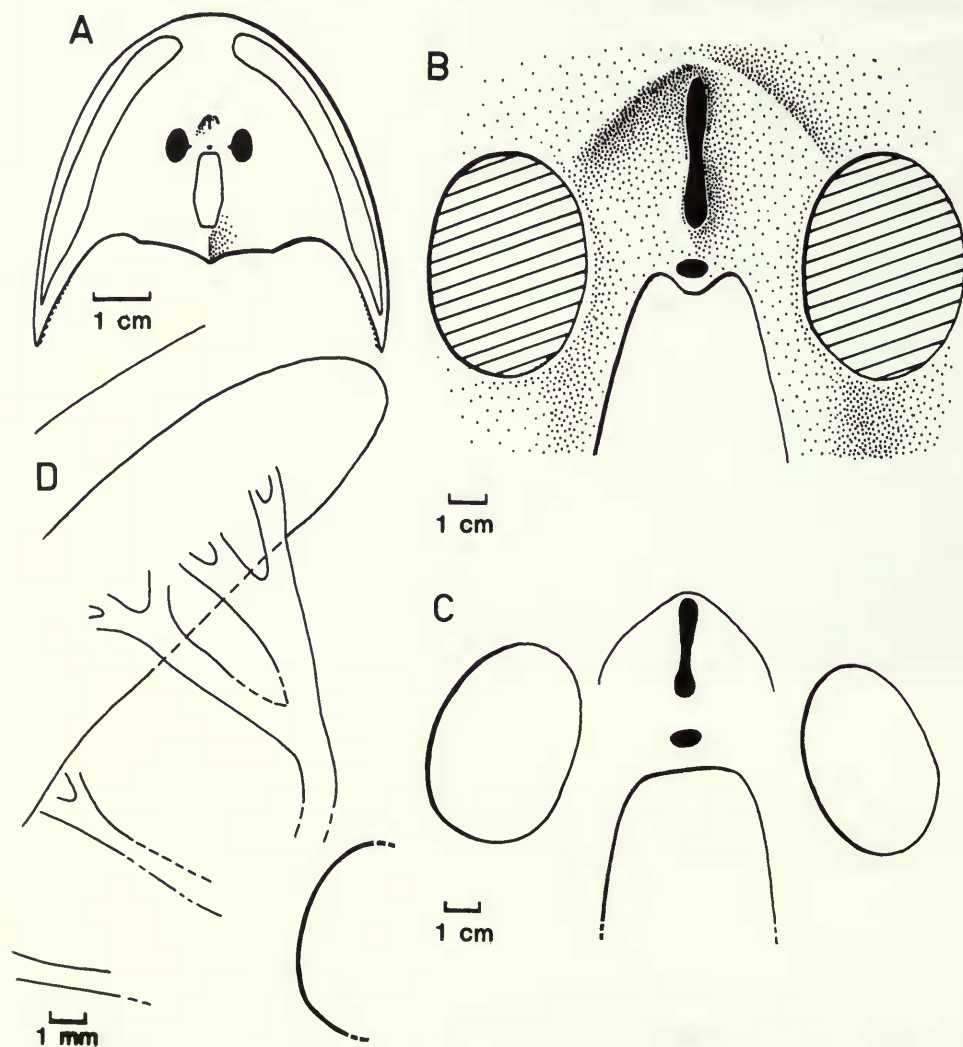


Fig. 17 *Mimetaspis glazewskii* sp. nov., 'Old Red' I or Ivanie horizons, Ustečko, Podolia, Ukrainian S.S.R. A, reconstruction of the shield based on the holotype (P.20958-9), dorsal view. B, C, orbitopineal and nasohypophysial regions of the shield, based on the holotype (B) and P.20961-4 (C). D, first 's.e.l' canal of the left side in P.20961.



Fig. 18 *Mimetaspis glazewskii* sp. nov., Ivanie horizon, 'Old Red' I, Ustečko (Uscieszko) W, Podolia, Ukrainian S.S.R. **Holotype** (part, P.20958), dorsal view. $\times 0.85$.

field. The surface of the exoskeleton is covered with extremely small (about 0.05 mm) and elongate tubercles of the same type as in *M. hoeli* and *Hildenaspis digitalis* Janvier (1976). The lateral fields have regular limits and extend far backwards onto the dorsal face of the cornual processes, as is usual in cephalaspicians. The cornual processes are broad and flattened and bear minute denticles on the medial edge. The abdominal division is very short, with a faint median elevation. The median dorsal field is narrow anteriorly but slightly broader than in other species of the same genus, and sends off two 'horns' on each side of the pineal foramen (Fig. 17B). In some specimens (Fig. 17C) the anterior end of the median dorsal field is blunt and situated far behind the pineal foramen. There is no trace of an independent pineal plate and there is no indication as to how it had become fused or reduced. The two divisions of the nasohypophysial opening are equal in size, as in most cephalaspicians and non-cornuate osteostracans (Fig. 17B, C).

In BM(NH) P.20961 (Fig. 17D), the first 's.e.l.' canal can be traced and it branches at a point half way between the orbit and the lateral field, bending strongly at this point. This is regarded as a common feature of cephalaspicians.

M. glazewskii is larger than any of the other *Mimetaspis* species, but its size fits that of some shield fragments referred to *Mimetaspis* sp. from the base of the Wood Bay Formation of Spitsbergen.

INCERTAE SEDIS

'*Cephalaspis*' *rogalai* Balabai

Fig. 19A

1962 *Cephalaspis rogalai* Zych in coll.; Balabai: 3, fig. 1a, b.

This species is known from Ostrovčik (Ostrowczyk, north of Džurin, on the Džurin river), Ustečko (Uscieszko), Gorodnica (Horodnica) and Džurin (Djurin). It is somewhat smaller than *M. glazewskii* and its shield is more elongate in shape. It may also belong to the genus *Mimetaspis*, but the figure given by Balabai is too imprecise to be certain. If the presence of

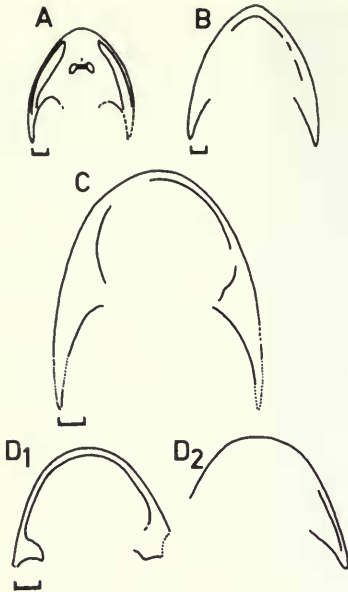


Fig. 19 A, '*Cephalaspis* rogalai Balabai, 'Old Red', Ustečko, Gorodnica, Podolia, Ukrainian S.S.R. B, '*Cephalaspis* feliciae Balabai, 'Old Red', Bilomu bridge, Podolia, Ukrainian S.S.R. C, '*Cephalaspis* major Balabai, 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen 25579, Museum of the Ukrainian Academy of Sciences, L'vov. D, '*Cephalaspis* sjoestremi Balabai, 'Old Red', Ustečko, Ruzdviani and Kijdanov (the two latter localities are on the Strypa river, north of Bučač), Podolia, Ukrainian S.S.R. (all after Balabai 1962). Scale bars all 1 cm.

a pineal plate and the ogive-like rostral margin described by Balabai are correct, then it may also be suggested that this species belongs to the genus *Pattenaspis*.

In the British Museum (Natural History) collections, some specimens (e.g. P.17712) from Ustečko W. have been labelled by Zych as '*Cephalaspis rogalii*' (*sic*), but they are only undeterminable cephalaspidian fragments.

'*Cephalaspis* feliciae Balabai

Fig. 19B

1962 *Cephalaspis feliciae* Balabai: 4; fig. 2.

This species, from Bilomu bridge (north of Bely Potok, on the Seret river) is poorly known and I regard it as a *nomen dubium*.

'*Cephalaspis* major Balabai

Fig. 19C

1962 *Cephalaspis major* Balabai: 4; fig. 3.

This remarkably large species, from Gorodnica and Ivanie, has slender cornual processes. It is uncertain whether it is a cephalaspidian or a scolenspidian.

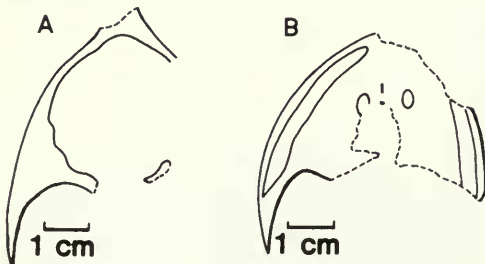


Fig. 20 A, '*Cephalaspis* cf. acutirostris Stensiö, 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.20508, ventral view. B, undetermined cephalaspidian, 'Old Red', Gorodnica, Podolia. Specimen P.20498, dorsal view.

'Cephalaspis' sjoestremi Balabai

Fig. 19D

1962 *Cephalaspis sjoestremi* Balabai: 5; fig. 5.

This species is from Ustečko, Rizdvano (Ruzdwiány) and Kijdanov (Kujdanow), the two latter localities being on the Strypa river, north of Bučač. It resembles *'C.' kozlowskii* in the outline of the shield (Fig. 19D). *A nomen dubium.*

'Cephalaspis' kozlowskii Zych1937 *Cephalaspis kozlowskii* Zych: 63; pls 1–4.

This species is known from Zaleščiki (Zaleszczyki) and Vorvolinče (Worwolincze) where it occurs in the Ivania horizon and the 'Old Red' I (Karatayute-Talimaa 1981: table 7). The internal anatomy has been described in detail by Zych (1937) but the central part of the shield and the shape of the nasohypophysial opening are unknown. However, the shape of the lateral fields, the cornual processes, and the mode of branching of the first *'s.e.l.'* canal (Zych 1937: pl. 2) incline me to consider it a cephalaspidian, although features of the oralbranchial chamber (branchial impressions, well-marked interbranchial ridges and nerve and blood vessel impressions) suggest scolenaspidian affinities. If it is a scolenaspidian, it must be a primitive form, like *'C.' pagei* or *'C.' powriei*. *'C.' kozlowskii* well illustrates the problem of the limits of the scolenaspidians and the cephalaspidians, a re-examination of which may show that some of the so-called cephalaspidian or scolenaspidian characters are only those of primitive cornuate osteostracans. I suspect that the flattened cornual processes and the narrow lateral fields are such characters, and this would explain why they occur also in the most primitive scolenaspidians.

'Cephalaspis' cf. acutirostris Stensiö

Fig. 20A

Specimen BM(NH) P.20508–9, from Gorodnica N ('Old Red' II), is very similar to the holotype of *'C.' acutirostris* (Stensiö 1932: fig. 32; pl. 40, fig. 13) from the Lower Old Red Sandstone of Shropshire. However, since the dorsal face of the shield is not known in either specimen it is uncertain whether this resemblance is superficial or not. In both specimens the rostral process is broken off and only its proximal part is known. The only difference between the Podolian specimen and the holotype is that the cornual processes are broader in the former than in the latter.

Undetermined Cephalaspidians

BM(NH) P.17726 – This specimen from Bely Potok (Potok Bialy) has been labelled by Zych as *'Cephalaspis potokiensis'*, but I regard it as an undetermined cephalaspidian.

BM(NH) P.20498–9 – This specimen (Fig. 20B) from Gorodnica may belong to the genus *Mimetaspis*, but is too distorted to allow closer determination.

UNDETERMINED OSTEOSTRACANS

Besides a number of undeterminable osteostracan fragments which are too badly preserved to assign to any of the species mentioned above, there are two specimens which certainly do not belong to any of the species hitherto described from Podolia but which are too poorly preserved to be described as new taxa.

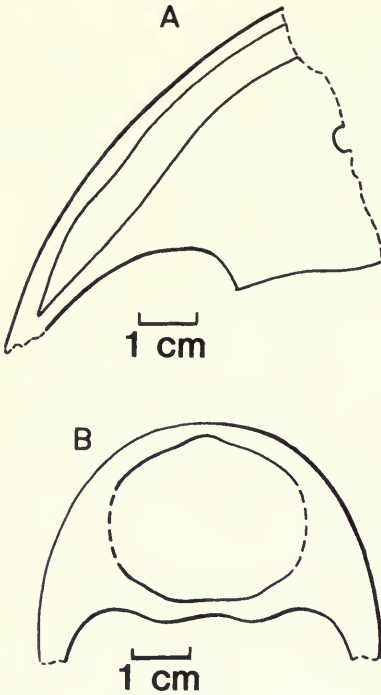


Fig. 21 A, specimen P.17722, labelled by Zych as '*Cephalaspis arnelli*', 'Old Red'?, Potok-čiska, Podolia, Ukrainian S.S.R. B, ? benneviaspidian, 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.20518.

BM(NH) P.17722 – This shield fragment (Fig. 21A) from Potoczyska N has been labelled by Zych as '*Cephalaspis arnelli*', a species name found also on the label of specimen C.129 in the Naturhistoriska Riksmuseet, Stockholm. The latter specimen closely resembles *Z. salweyi*, but is somewhat smaller and has posteriorly narrower lateral fields extending onto the cornual processes.

BM(NH) P.20518 – This is the ventral rim of a small shield (Fig. 21B) from Gorodnica N ('Old Red' I); it is suggestive of a primitive benneviaspidian because of its regularly rounded marginal region. It is the only possible benneviaspidian specimen from Podolia in the British Museum (Natural History) collection.

Faunal comparisons and Stratigraphical remarks

The osteostracan fauna described here on the basis of the British Museum (Natural History) material can be considered as coming from the Ivanie horizon and, mainly, from the 'Old Red' I and II. The nature of the sediment in which the specimens are preserved suggests that none of them comes from the Čortkov and Borshchov horizons. Comparisons can be carried out with the faunas from the Devonian of the Anglo-Welsh area and Spitsbergen.

Two aspects of the Podolian fauna are particularly striking: the lack of *Meteoraspis* (and the rarity of the cephalaspadians in general) and the abundance of the scolenaspidians. This is true for all the localities cited in this paper. The benneviaspadians are also rare, although the more recently collected material in the Palaeontological Institute of the Academy of Sciences of the U.S.S.R. contains several well-preserved large benneviaspadians (Karatayute-Talimaa, personal communication). The kiaeraspadians and thyestidians are totally absent. The large scolenaspidians (*Zenaspis* cf. *salweyi*, '*Z.* *podolica*') compare satisfactorily with species from the top part of the Red Bay Group of Spitsbergen (Ben Nevis Formation) such as '*Z.* *metopias*'. The association of *Z.* cf. *salweyi* and *Stensiopelta pustulata* is also very suggestive of that of *Z. salweyi* and *S. woodwardi* in the 'Dittonian II' of Wales (Stensiö

1932: 199–202). The few fragments referable to *Diademaspis* do not reach the size of the huge specimens which occur in the upper part of the Wood Bay Formation of Spitsbergen.

As far as the osteostracan fauna is concerned, the lowest formations of the Red Bay Group of Spitsbergen are characterized by the abundance of small cephalaspicians such as *Pattenaspis* and *Mimetaspis*. These small forms become rare in the Ben Nevis Formation (with *M. hoeli* only) and in the Wood Bay Formation. In Podolia, there seems to be only one or two species of *Mimetaspis* resembling *M. hoeli*.

The osteostracan fauna of the Podolian 'Old Red' and Ivanie horizon does not contain the classical taxa of the Wood Bay Formation, but contains taxa which are suggestive of those of the upper part of the Red Bay Group of Spitsbergen, and those of the 'Dittonian II' of Great Britain.

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