New osteostracans from the Lower Devonian terrigenous deposits of Podolia, Ukraine

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New osteostracans (Agnatha, Osteostraci) *Zenaspis dzieduszyckii* sp. nov. and *Wladysagitta janvieri* gen. et sp. nov., as well as new form of *Diademaspis* are described from the Lower Devonian of Podolia (Ukraine). Among them *Zenaspis dzieduszyckii* sp. nov. differs from all other representatives of the genus by its smaller overall size and relatively larger orbits. *Wladysagitta janvieri* is remarkable by having a rostral process. This new species together with "*Cephalaspis*" *acutirostris* Stensiö, 1932 from Old Red deposits of Shropshire (Great Britain) are proposed to be united under common generic name *Wladysagitta*. Since *Diademaspis* sp. is completely unknown in outline of its shield, it could not be named as new species, although it should be a really new form. New diagnostic features, such as relative width of the orbits, relative width of the dorsal field, and the position of the posterior end of the lateral fields relatively to the margins of the headshield, are proposed to differentiate genera within the Zenaspididae. Probably, the rostral process of osteostracans should be considered as a multifunctional device having at least a sensory function for food-search, possibly hydrodynamic functions, or may play a role in scaring predators.

Key words: Agnatha, Osteostraci, Devonian, Podolia, taxonomy, morphology.

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Introduction

Podolia (Fig. 1A, B) is the only region in Ukraine where the Lower Devonian deposits with remains of ichthyofauna come to the surface. During about 150 years of collecting here the vertebrate fossils have been found in more than 90 localities situated in outcrops along banks of the Dniester River and its northern tributaries, and in sandstone quarries. At present faunal list of Early Devonian agnathans and fishes from Podolia number 72 species, including 8 Thelodonti, 39 Heterostraci, 19 Osteostraci, 4 Placodermi, 1 Acanthodii, and 1 Holocephali (Voichyshyn 2001a, modified).

In Podolia, Lower Devonian redbeds strata (the Old Red Formation or Dniester Series) are up to 1800 m thick and range from Lochkovian to Eifelian in age (Narbutas 1984; Drygant 2000, 2003). In their lower part (Ustechko and Khmeleva members of the Dniester Series) they consist of multi-coloured, mainly red, fine-grained cross-bedding massive quartz sandstones and siltstones with seams of argillites (Drygant 2000).

Zych (1927), Brotzen (1933), and Balabai (1960) tried to divide the Podolian section of Lower Devonian terrigenous deposits into biostratigraphical (faunal) zones. Among these division schemes the Brotzen's one should be regarded as the most suitable. It has three zones. The first of them, according to Narbutas (1984), including the stratigraphical interval from the Ustechko member to the lowest part of the Khmeleva member, is notable for the most diversity of agnathan species. The second zone (corresponding to the rest of the Khmeleva member) has been still characterized insufficiently because of not numerous and poorly preserved vertebrate fossils. And the third zone (apparently corresponding to the Strypa member) contains several species which never have been recorded for the first zone (Voichyshyn 2001b).

Findings of Podolian cephalaspids (Agnatha, Osteostraci) were already mentioned more than 100 years ago (Alth 1874). Despite that, they had been the subject of only a few studies until recently (Zych 1937; Pauča 1941; Balabai 1962). During the last two decades regional Early Devonian faunas including cephalaspids have been studied more intensively (Belles-Isles and Janvier 1984; Janvier 1985b, 1988; Afanassieva 1989, 1990, 1991; Afanassieva and Voichyshyn 1991; Voichyshyn 1994, 1998; Voichyshyn and Solodkyi 2004). These investigations revealed some depositional peculiarities of the Podolian representatives of this group. Specifically, Podolian cephalaspids, except for one specimen of *Parameteoraspis* (Afanassieva 1991), are linked to terrigenous sediments. Most of the 19 species known from Podolia are derived from the first faunal zone of the Podolian Old Red, according to the subdivisions proposed by Brotzen (1933). This also applies to the material described below. In contrast, only a few specimens of three species of the Benneviaspididae (Belles-Isles and Janvier 1984; Afanassieva 1989, 1990, 1991) have so far been reported from deposits referred to the third faunal zone.

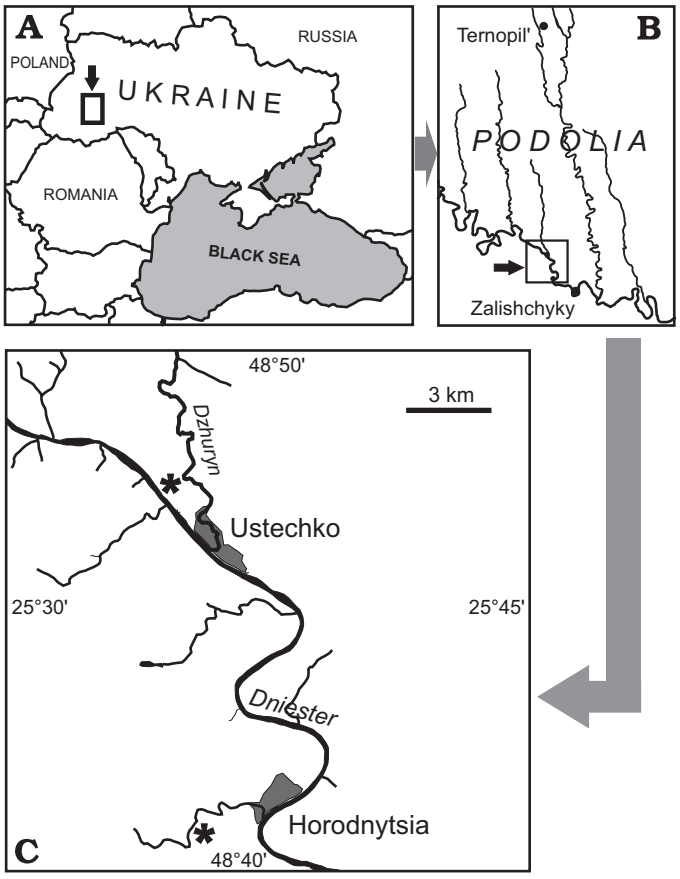

Fig. 1. Contours of Ukraine and the neighbouring countries (**A**), simplified map of Podolia with main cities and major tributaries of Dniester (**B**), locality map, showing position of the points of finds of the studied material (indicated by an asterisk) (**C**).

Here, I describe three cephalaspid taxa from Podolia, two of which belong to the Zenaspidida. However, the third taxon, which is referred here to a new genus, is represented by material that is not sufficiently well-preserved for allowing its systematic assignment within the "horseshoe-shielded" osteostracans.

Material and methods

The material examined for this study was mainly collected by the author in 1992 and 1994 at the Ustechko outcrops, and in 1992 in quarries of Horodnytsia (Fig. 1). In addition, some specimens kept in the Museum of Lviv State University, Department of Geology were also studied. No information about the collector(s) and date of collecting is available for these specimens.

All the material was mechanically prepared, if necessary, and cleaned, then measured, photographed with an Olympus C-2100 camera and studied under optical zoom.

Podolian agnathans from terrigenous deposits typically do not exhibit traces of endoskeleton. Therefore, all comparisons and conclusions are exclusively based on the external morphology of the headshield.

Measurements (Fig. 2).—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 shield and the pineal foramen; C, post-pineal length of shield: distance between the pineal foramen and the posterior margin of the shield; G, maximum length of lateral field: distance between the anterior and posterior ends of the lateral field; L, maximum length of the shield; 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; Lrc, distance between the anterior margin of the shield (without rostral process) and the tip of the cornual process; 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 nasohypophysial 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), British Museum of Natural History; The Natural History Museum (London); GMLSU, Geological Museum of Lviv State University, Department of Geology (Lviv); SMNH, State Museum of Natural History, National Academy of Sciences of Ukraine (Lviv).

Systematic palaeontology

Class Osteostraci Lankester, 1868

Subclass Cornuata Janvier, 1985a

Order Zenaspidida Stensiö, 1958

Family Zenaspididae Stensiö, 1958

Type genus: *Zenaspis* Lankester, 1870, see below.

Diagnosis.—Zenaspidida of average to large size. The headshield is dome-shaped and massive. The abdominal part of the shield has a low, more or less developed, median dorsal crest. The hypophysial division of the nasohypophysial opening is, as a rule, larger than the nasal division. The pineal plate is feebly developed or absent. The median dorsal field is broad. The lateral fields have a conspicuous dilatation (or widening) in their posterior parts reaching backwards no further than 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.

Genera included.—*Diademaspis* Janvier, 1985, and, possibly, *Tegaspis* Wängsjö, 1952.

Remarks.—The genus *Tegaspis* has several features in which it appreciably differs from other zenaspidids, such as the

shape of the headshield (its anterior margin and cornual processes), approximately same size of the two divisions of the nasohypophysial 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 *sensu* Janvier 1985b

Type species: *Cephalaspis salweyi* Egerton, 1857, Lower Devonian of Great Britain.

Diagnosis.—Zenaspididae of moderate size (L = 90–130 mm). The width of the shield is greater than its length (L/S = 0.6–0.7). The prepineal part of the shield is shorter than the postpineal one (B/C = 0.8–0.9). The cornual processes are comparatively short. The abdominal part of the shield is short with a massive median dorsal crest. The hypophysial division of the nasohypophysial opening is somewhat larger than the nasal division. The orbital openings are small (S/Os = 32–42) with a short distance between them (Omin/Os = 2.5–3.3). 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 approximately the same as to the lateral margins of the shield. The ornamentation consists of single large tubercles.

Species included.—Perhaps, *Z. metopias* (Wängsjö, 1952) from the Lower Devonian of Spitsbergen; *Z. dzieduszyckii* sp. nov. and *Z. podolica* (Balabai, 1962), both from the Lower Devonian of Podolia.

Occurence.—Lower Devonian of Great Britain, Spitsbergen (?), Podolia.

Zenaspis dzieduszyckii sp. nov.

Figs. 3, 4.

1985 *Zenaspis* cf. *salweyi* (Egerton, 1857); Janvier 1985b: 323–325, fig. 14.

Derivation of the name: In honour of the founder of SMNH, the late Count Włodzimierz Dzieduszycki (1825–1899).

Holotype: SMNH BP.103; natural mould and impression of a headshield, lacking the posterior part and cornual process of the rigth side.

Type locality: Ukraine, Podolia, right bank of Dniester, Horodnytsia (Fig. 1C).

Type horizon: Lower part of the Old Red Formation (Dniester Series, most probably its Ustechko Member).

Material.—Besides the holotype, specimens SMNH BP.1193, BP.1215.

Diagnosis.—Small *Zenaspis* species with relatively large orbits, wide lateral fields, and short and slender cornual processes.

Description.—The length of the headshield is about 100–110 mm, its maximum width (120–130 mm) is at the tips of

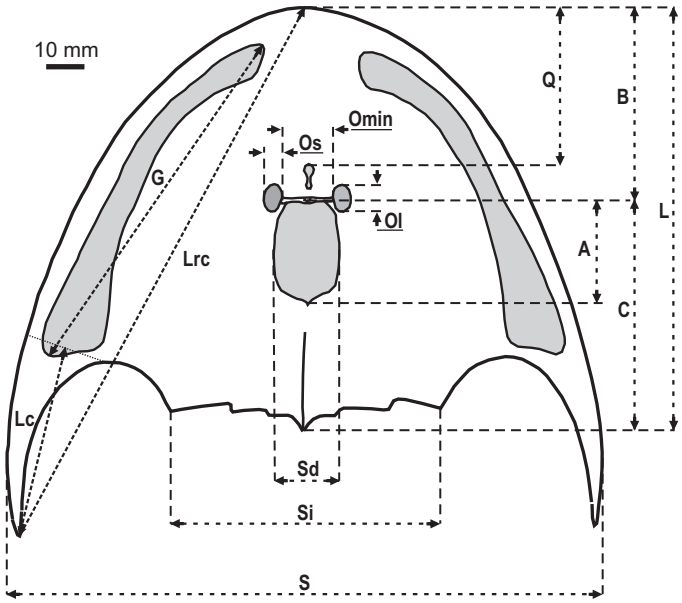

Fig. 2. *Zenaspis salweyi* (Egerton, 1857) (after Janvier 1985a: fig. 63B) with a designation of the shield measurements (after Afanassieva 1991, modified).

the cornual processes. The lateral margins of the shield are feebly convex. The cornual processes are oriented caudo-laterally (or postero-laterally), short and rapidly tapered off. The abdominal part of the headshield was most probably 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 deep, its height reaching the level of the orbits of 20 mm in the holotype. The nasohypophysial opening is relatively remote from the anterior margin of the shield (Q/A = 1.5), with a large hypophysial division (in a depression) and a smaller nasal one (opening in 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. 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 a length of 0.9 mm and a width of 1.5 mm. The median dorsal field is elongated and wide, with more or less equal width (S/Sd = 9.8). Its anterior margin is straight, its lateral ones slightly convex, and its posterior one forms an obtuse angle. 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-medial angles. The distance between the postero-lateral margin of the field and the lateral margin of the shield is 2 mm, the same as between posterior margin of the

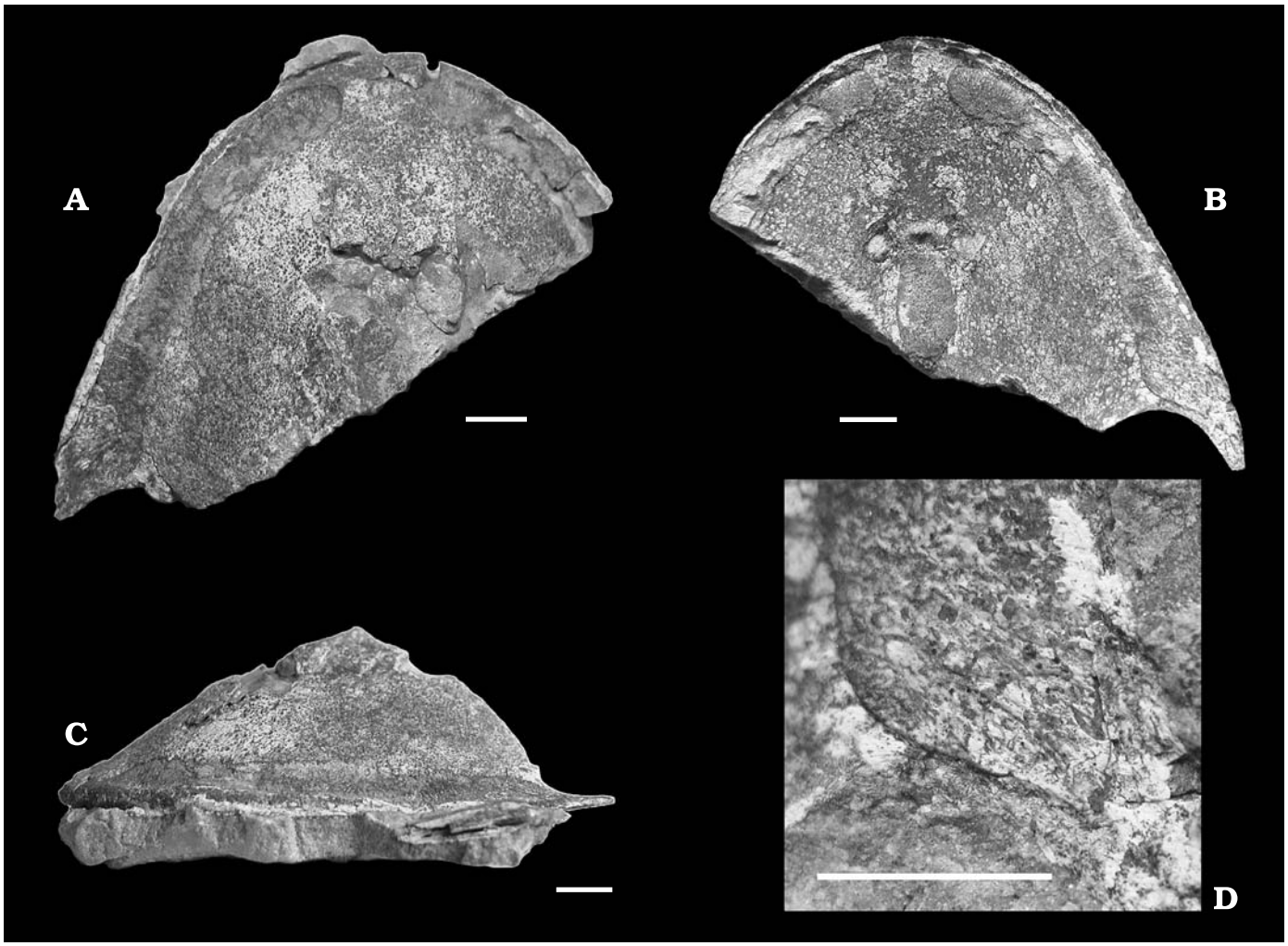

Fig. 3. *Zenaspis dzieduszyckii* sp. nov., the holotype, SMNH BP.103, Horodnytsia, Ukraine, Dniester Series, Lower Devonian, dorsal (**A**, **B**, **D**) and lateral (**C**) views. The mould (A, C) and the impression (B) of the shield; D, the impression of the proximal part of the cornual process. Scale bars 10 mm.

field and tip (anterior margin) of the pectoral sinus. 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 angles 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 exoskeleton of the shield is not preserved. Only traces of small (1–1.5 mm) polygonal fields probably corresponding to tesserae with single rounded tubercles, can be seen.

Comparison.—*Zenaspis dzieduszyckii* sp. nov. 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. In contrast to *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 exoskeleton is similar in both species. *Z. dzieduszyckii* sp. nov. 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 exoskeleton.

Remarks.—I believe that two specimens (on a large plate of sandstone, probably from Horodnytsia) kept in the GMLSU collection belong to the new species, but at present they have no numbers to be included in the type series.

Remains of *Z. dzieduszyckii* sp. nov. occur in the sandstones of Horodnytsia, alongside the Pteraspidiformes *Podolaspis* sp. and *Larnovaspis* sp.

Janvier ascribed some specimens from Horodnytsia to *Zenaspis* cf. *salweyi* (Janvier 1985b: fig. 14). Most probably, this figured specimen belongs to *Zenaspis dzieduszyckii* sp. nov., judging from the shape of the shield and morphological details. In addition, it comes from the same locality and horizon as the holotype of *Z. dzieduszyckii* sp. nov.

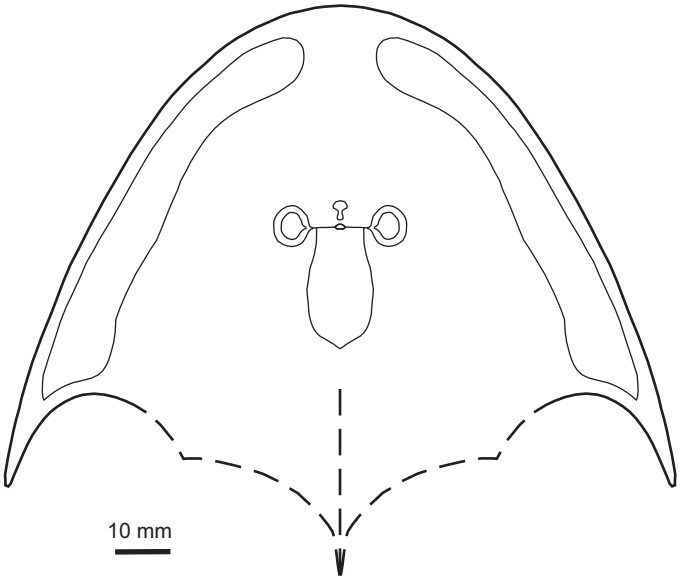

Fig. 4. *Zenaspis dzieduszyckii* sp. nov. Reconstruction of the shield, mainly based on the holotype, SMNH BP.103, in dorsal view.

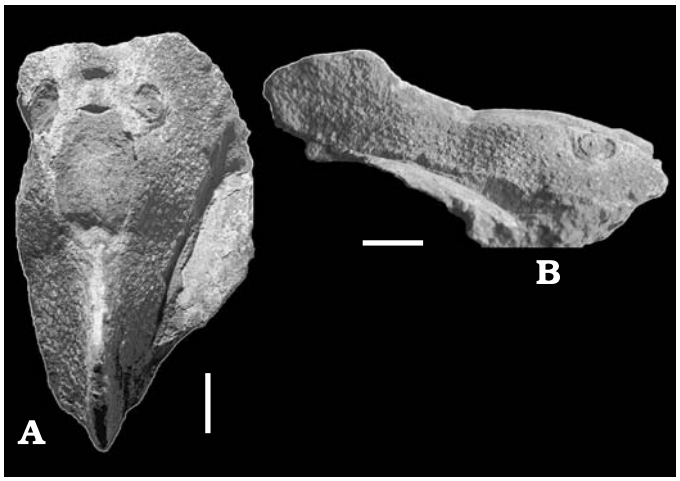

Fig. 5. *Diademaspis* sp., GMLSU 478,4. Podolia, Ukraine, Dniester Series, Lower Devonian, dorsal (**A**) and lateral (**B**) views. Scale bars 10 mm.

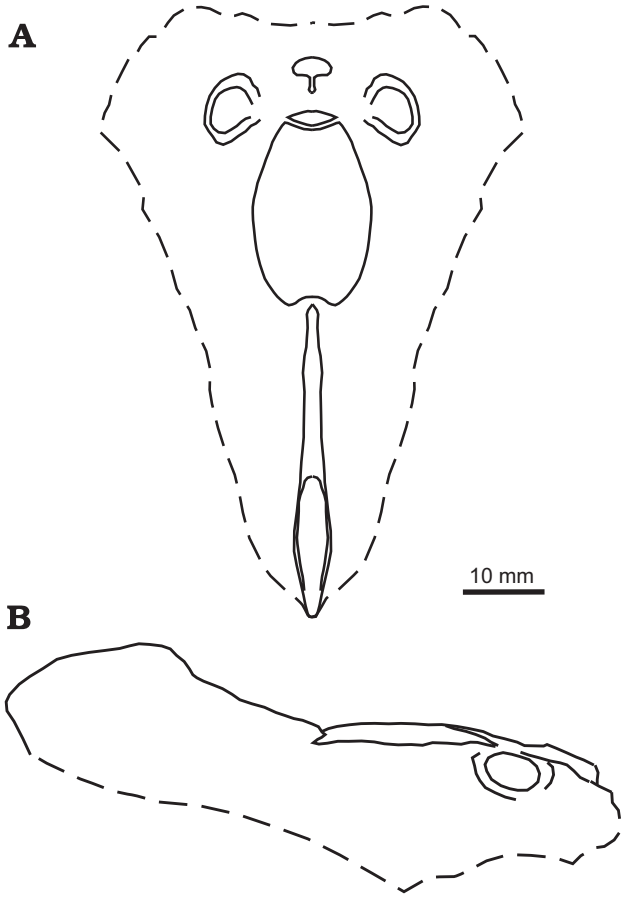

Fig. 6. *Diademaspis* sp., reconstruction of the central part of the shield, based on specimen GMLSU 478,4, dorsal (**A**) and lateral (**B**) views.

Genus *Diademaspis* Janvier, 1985a

Type species: *Diademaspis poplinae* Janvier, 1985a, Lower Devonian, upper part of Wood Bay Formation of Spitsbergen.

Emended diagnosis.—Zenaspididae of small to large size (L = 90–250 mm), 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 hypophysial division of the nasohypophysial opening is much larger than the nasal division. The pineal plate is reduced or absent. 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 index (or ratio) equals about 7). The lateral fields are enlarged posteriorly and reach to the basal (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 $\geq$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. (Modified after Janvier 1985a and Afanassieva 1989; see also Janvier 1985b; Afanassieva 1991; Adrain and Wilson 1994).

Species included.—*D. jarviki* (Wängsjö, 1952), Lower Devonian of Spitsbergen; *D. stensioei* Afanassieva, 1989, *D.* sp., both from the Lower Devonian of Podolia. *D.* sp. 1, *D.* sp. 2, *D.* sp. 3, and *D.* sp. 4 (Janvier 1985a) from the Lower Devonian of Spitsbergen.

Remarks.—As to the proportion of the divisions of the nasohypophysial opening of *Diademaspis* a possible exception is *D. jarviki*, which has nasal and hypophysial 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: 2). However, Janvier (1985a) pointed out that *D. jarviki* is similar to *D. poplinae* notably as to the shape of its nasohypophysial opening.

Some shield fragments with the ornamentation typical of *Diademaspis* have been recorded as *Diademaspis* sp. from Ustechko and Chervonograd in Podolia (Janvier 1985b).

It is doubtful that *D.*? *mackenziensis* Adrain and Wilson, 1994 from the Northwest Territories of Canada belongs to the genus *Diademaspis* because of the considerable morphological difference between this species and the European *Diademaspis* species. In contrast with the European *Diademaspis* 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 the compared taxa are different (S/Sd of the Canadian form is 12.5); the headshield is noticeably narrower and its size (L = 30 mm) is strikingly small in comparison with the size of the European *Diademaspis* headshields. Finally, the exoskeleton ornamentation, which consists of elongated tubercles in *D.*? *mackenziensis*, is not characteristic of the genus. The fact, that the hypophysial division of the nasohypophysial opening is larger than the nasal one, may indicate that the Canadian species belongs to the Zenaspidida, but there seems to be no reasons to refer it to *Diademaspis* and, thus, to make the diagnosis of this genus less precise.

Occurence.—Lower Devonian of Spitsbergen and Podolia.

Diademaspis sp.

Figs. 5, 6.

Locality and horizon: Ukraine, Podolia (Fig. 1B), precise locality unknown; Lower Devonian, probably lower part of the Old Red Formation (Dniester Series), the first Old Red faunal zone after Brotzen (1933).

Material.—Mould of the central part of a headshield (from the nasohypophysial opening to the median dorsal crest), GMLSU 478, 4 (Fig. 5A, B).

Description.—The length of the headshield is 90–100 mm (the distance between the anterior limit of the nasohypophysial opening and the posterior limit of the median dorsal crest is about 70 mm). The orbits are oval in shape 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 (broad). The distance between the orbits is relatively small for *Diademaspis*, 13 mm. The nasohypophysial opening has an enlarged hypophysial 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 chink-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 exoskeleton 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 *D. poplinae* by its chink-like shape of the pineal plate, the shape of the median dorsal field (in particular, its more convex lateral margins) (Fig. 6A), the more developed median dorsal crest (Fig. 6B), and the smaller overall size.

It differs from *D. jarviki* by its greater size of the hypophysial division of the nasohypophysial opening, the presence of a pineal plate and the shape of the median dorsal field (Fig. 6A).

This specimen differs from *D. stensioei* by its type of ornamentation (Fig. 5). Other material for comparison with this species is unavailable. The central part of the headshield, which is preserved in the specimen described above, is unknown in the material referred to *D. stensioei.* For the same reason it is not possible to compare the form described here to the shield fragment from Ustechko, assigned to *Diademaspis* sp. (Janvier 1985b: fig. 16A). Due to the state of preservation of the ornamentation in the form described here it is not clear, whether the tubercles formed groups, like in the specimen from Ustechko. In any case, they were more densely spaced than in the fragment from Ustechko.

This specimen differs from *D*. sp. 2 (Janvier 1985a) by the shape and the 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 *D*. 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.

It differs from *D*. sp. 3 by the less steep rise of the median dorsal crest (Figs. 5B, 6B).

It differs from *D*. sp. 4 by shorter orbits, the smaller distance between the anterior margin of the nasohypophysial 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 *D.* sp. 1, by its smaller overall size, and, except for *D*. sp. 4, by its more densely spaced orbits.

Remarks.—I should avoid to name the *Diademaspis* sp. described here which is completely unknown in outline of its shield, although it should be a really new form.

Subclass Cornuata incertae sedis

Genus *Wladysagitta* gen. nov.

Type species: *Wladysagitta janvieri* gen. et sp. nov.

Derivation of the name: In honour of the late Dr. Władysław Zych (1899–1981), and from the Latin *sagitta*, arrow, referring to the arrow-shaped rostral margin of the headshield.

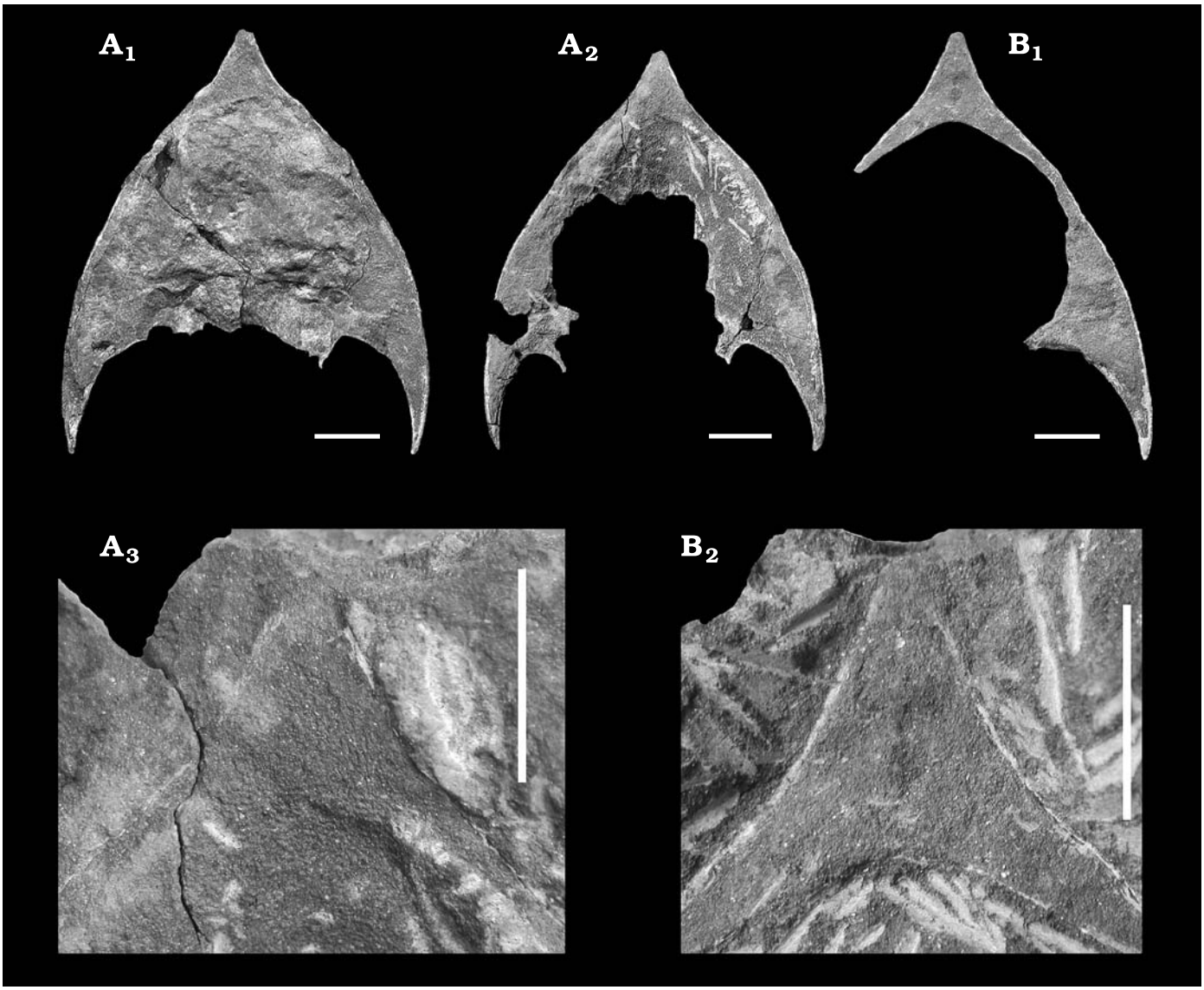

Fig. 7. *Wladysagitta janvieri* gen. et sp. nov. Ustechko, Ukraine, Dniester Series, Lower Devonian. **A**. Holotype, SMNH BP.102, the mould (A_1) and impression (A_2, A_3) of the shield, and its rostral part (A_3). **B**. SMNH BP.100, ventral view of the fragment of the shield (B_1), and its rostral part (B_2). Scale bars 10 mm.

Diagnosis.—Osteostracans of small size. 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 formes the elongated to triangle-shaped 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 exoskeleton consists of tiny elongated tubercles.

Comparison.—According to the classification of the Osteostraci proposed by Afanassieva (1991), *Wladysagitta* gen. nov. differs from the genera referred to the Benneviaspidoidei by the shape of the headshield and the presence of tubercles on the exoskeleton (and 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 Zenaspidida 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* gen. nov. appears to be similar to several representatives of *Pattenaspis* that have a rostral lobe [most developed in *P. eurhynchus* (Wängsjö, 1952)], although this lobe does not extend into a rostrum. However, this general resemblance does not answer the question of the position of the species relative to the genus *Pattenaspis*, since this genus includes a wide diversity of forms, and is possibly not a clade (Afanassieva and Voichy-

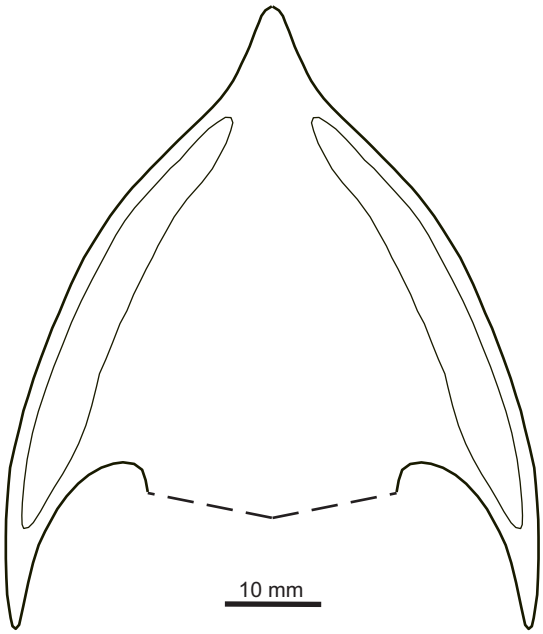

Fig. 8. *Wladysagitta janvieri* gen. et sp. nov., reconstruction of the shield, mainly based on the holotype, SMNH BP.102, dorsal view.

shyn 1991), and may not even belong to the Cephalaspididae (Janvier 1985b). One of the features that throw doubts on this assignment may be present in species of *Pattenaspis* from Spitsbergen and Great Britain. These species possess an extensive exoskeletal ornamentation, usually consisting of thorn-like tubercles, contrary to the original descriptions by Wängsjö (1952) (Philippe Janvier, personal communication 1998). Typical cephalaspidids, such as *Cephalaspis*, *Parameteoraspis*, and *Mimetaspis* have practically no ornamentation, or their ornamentation consists of very small tubercles. Except for the rostral process, *Wladysagitta* gen. nov. differs from *Pattenaspis* by the shape of lateral fields that are slightly broadened in their posterior third, possibly, by the shape and smaller size of the tubercles of the exoskeletal ornamentation, and by lacking denticles on the inner margin of cornual processes.

In contrast, *Wladysagitta* gen. nov. resembles primitive zenaspidids, in particular the genus *Zychaspis*, by its exoskeletal ornamentation. It should be noted that *Zychaspis* is also characterized by having a slight rostral lobe (Janvier 1985b; Voichyshyn and Solodkyi 2004). In sum, and considering the available data, *Wladysagitta* gen. nov. may be regarded as morphologically intermediate between *Pattenaspis* and primitive zenaspidids.

Species included.—Besides the type species, *W. acutirostris* (Stensiö, 1932), from the Lower Devonian of Great Britain.

Occurence.—Lower Devonian of Podolia and Great Britain.

Wladysagitta janvieri sp. nov.

Figs. 7, 8, 9B–D.

1985 "*Cephalaspis*" cf. *acutirostris* (Stensiö, 1932); Janvier 1985b: 331, fig. 20A.

Derivation of the name: In honour of Dr. Philippe Janvier (Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris).

Holotype: SMNH BP.102, fragmentary mould of the headshield from the dorsal side and its imprint (Fig. 7A).

Type lolcality: Ukraine, Podolia, Ustechko, left bank of Dniester (Fig. 1C).

Type horizon: Old Red Formation (Dniester Series, the lowest part of its Khmeleva Member).

Material.—Besides the holotype, a fragment of the headshield exposed in ventral view, SMNH BP.100 (Fig. 7B).

Diagnosis.—A moderately large *Wladysagitta* species 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 produced into a clearly outlined process (about 10 mm in length) with rather concave lateral sides and a rounded distal end (Fig. 7A$_3$, B$_2$). The lateral margins of the shield are moderately convex with an irregular curvature. The maxi-

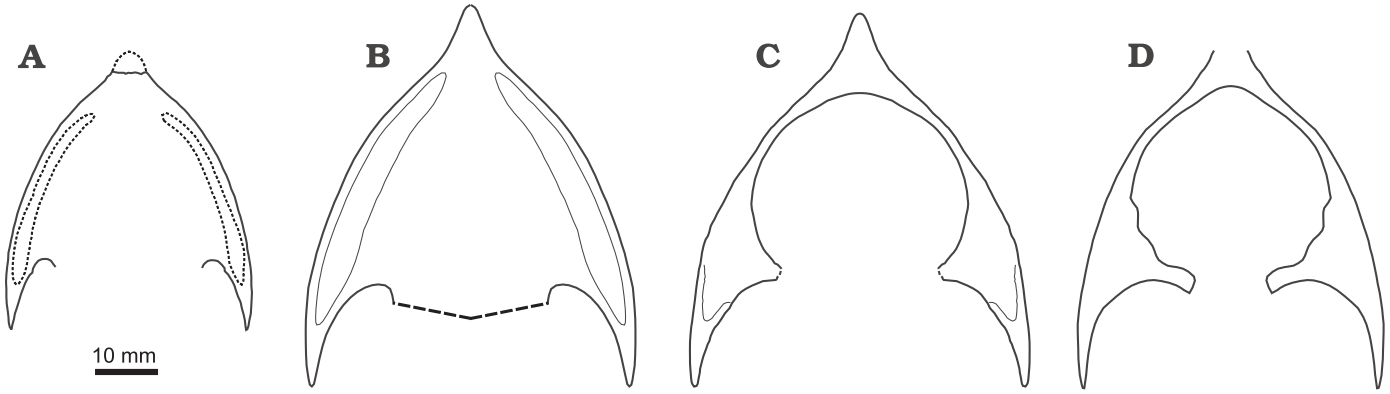

Fig. 9. Reconstruction of the *Wladysagitta* gen. nov. shields, dorsal (**B**) and ventral (**A**, **C**, **D**) views. **A**. *W. acutirostris* (Stensiö, 1932), after Stensiö (1932: text-fig. 32). **B**–**D**. *W. janvieri* sp. nov. **B**. The holotype, SMNH BP102. **C**. SMNH BP.100. **D**. BM(NH) P.20508 (the reconstruction based on Janvier 1985b: fig. 20A).

mum 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 base, and conspicuously narrow in their distal half. They start to point caudally at the level of their middle part. The lateral margin of the cornual processes is straight or feebly convex, whereas its medial margin is slightly concave. The abdominal part is narrow (Si/S = 0.47). The pectoral sinuses are asymmetrical (Fig. 7A_1, A_2), their tips (anterior margin) lying closer to the body axis. The lateral fields are slightly broader in their posterior third, with sharpened posterior ends. The surface of the headshield is relatively 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 to *Wladysagitta acutirostris* (Fig. 9A), *W. janvieri* sp. nov. (Figs. 8, 9B–D) has proximally broader and relatively longer cornual processes (Lrc/Lc of *W. janvieri* sp. nov. 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 (Stensiö 1932 considered that the specimen of *W. acutirostris* was somewhat flattened and that it must have originally been higher and narrower). 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, the poor preservation of the material examined does not allow to resolve more precisely the relationship among them.

Remarks.—The two specimens of *W. janvieri* sp. nov. housed in SMNH originate from a taphonomic assemblage containing few well-preserved carapaces mainly of osteostracans (*Benneviaspis whitei* Belles-Isles and Janvier, 1984, *Stensiopelta pustulata* Janvier, 1985b, *Pattenaspis rogalai* (Balabai, 1962), and *Zychaspis granulata* Voichyshyn, 1998). Among heterostracans *Zascinaspis heintzi* (Brotzen, 1936) and *Weigeltaspis brotzeni* Tarlo, 1964 are recorded for 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 (Fig. 9D) referred here to *W. janvieri*, 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 direction, whereas the cornual processes of the holotype are gently curved. Another specimen (Figs. 7B, 9C) 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 postmortem distortions of the shields.

General discussion

Based on the fossil material examined for the present study, many remains of Podolian Osteostraci belong to the family Zenaspididae. Also, the first of the species described here belongs to this family. This is supported by such characteristic features as the irregular outline of the lateral fields with broadenings (especially in the posterior parts of the fields), a broad median dorsal field, a deepened and (probably) enlarged hypophysial division of the nasohypophysial opening, the presence of a circumorbital ridge (thickening), the low and sharp median dorsal crest, and large tubercles in the exoskeletal ornamentation. Among the genera known today within the family Zenaspididae, the genus *Zenaspis* is the most suitable to accommodate the new species described here, although assigning it to this genus may pose some problems of paraphyly (Janvier 1985b). Comparatively small orbits and the broad median dorsal field and headshield are usually regarded as diagnostic for *Zenaspis* (Janvier 1985a, b). However, it has been pointed out that these features are not unique to this genus but also occur in other representatives of the Zenaspididae. Therefore, including in this genus several, morphologically heterogeneous species (other than the type species) may result in making it paraphyletic.

By studying the remains of *Zenaspis dzieduszyckii* sp. nov., I tried to identify the characters that are common to all *Zenaspis* species and distinguish these species from representatives of other genera of the Zenaspididae. Reflecting in some way the size of orbits, the ratio S/Os for *Zenaspis* fluctuates within 33–42, whereas in the new form it is about 30, which suggests that it is closer to *Diademaspis* that has an index of 27–29. In contrast the index Omin/Os, which reflects the characteristics of the disposition of the orbits, suggests that the new species is closer to *Zenaspis*: 3.8–4.3 in *Diademaspis*, 2.5–3.3 in *Zenaspis*, about 3 in *Z. dzieduszyckii* sp. nov. As for the relative width of the median dorsal field that can be expressed by the ratio S/Sd, a clear enough difference is observed among genera within Zenaspididae. S/Sd is about 7 in *Diademaspis*, 9–11 in *Zenaspis* (9.8 in *Z. dzieduszyckii* sp. nov.), and about 13 in *Tegaspis*. It must be noted that in case of the values of the indices for *Diademaspis*, only *D. poplinae* and *D. jarviki* are taken into account. All other forms referred to the genus, including *D. stensioei* Afanassieva, 1989, are represented by insufficiently preserved material. The S/Sd value of *Tegaspis* has been estimated on the basis of *T. kolleri* (Stensiö, 1927), *T. pedata* (Wängsjö, 1952)

and, with approximate estimation, *T. waengsjoei* Belles-Isles and Janvier, 1984.

In both genera, *Zenaspis* and *Diademaspis*, the lateral fields noticeably approach the lateral margins of the headshield in its posterior half or third. This is not observed in *Tegaspis*, where the lateral fields in the posterior half are conspicuously distant from the lateral margins of the shield. To a lesser extent this character can be seen in more primitive zenaspidids such as *Scolenaspis* or *Machairaspis*. Moreover, in "*Cephalaspis*" *verruculosa* Wängsjö, 1952, for instance, it is even inconspicuous. In addition, within the Zenaspididae a genus-specific character may be the position of the posterior end of the lateral fields relatively to the margins of the headshield (the lateral ones and the pectoral sinus). In *Zenaspis* the posterior part of the lateral fields is roughly at the same distance from both the lateral margin of the shield and the pectoral sinus. In *Diademaspis* the distance between the lateral fields and the pectoral sinus is 1.5 times and more larger than the distance to the lateral margin of the shield. Finally, in *Tegaspis* the lateral fields reach close to the top of the pectoral sinus and, in the same time, are very far from the lateral margins of the shield (in this case the latter distance is 5–8 times larger than the former one). In the new species this character completely coincides with the corresponding generic one.

The orbits of *Z. dzieduszyckii* sp. nov. are, as already mentioned, somewhat greater than in other representatives of the genus. *Z. dzieduszyckii* sp. nov. shares with *Z. metopias*, the nature of ornamentation (including small polygonal areas as on the abdominal part of the specimen from GMLSU collection). In particular *Z. dzieduszyckii* sp. nov. (Fig. 4) shares with *Z. salweyi* (Fig. 2) the same outline of the posterior margin of the median dorsal field. The shape, extent and position (relatively to the shield margins) of the lateral fields are common to all three species. Another feature shared by all species of *Zenaspis*, is the exoskeletal ornamentation consisting of large tubercles. In *Z. salweyi*, at least, the shield surface displays, at the base of the cornual processes, an ornamentation of large tubercles of more or less the same size, which form some groups corresponding to the polygonal areas of the middle layer of the exoskeleton (Stensiö 1932: pl. 32: 1).

Another specimen referred to as *Diademaspis* sp. has been assigned to this genus on the basis of the following morphological features: (1) the considerable size of the hypophysial division of the nasohypophysial opening relatively to that of the nasal one; (2) the exoskeletal ornamentation that, although poorly preserved, seems to be typical for *Diademaspis*, consisting of large tubercles surrounded by smaller ones; (3) the outline of the posterior margin of the median dorsal field, which in the described specimen is just the same as in *D.* sp. 3 (Janvier 1985a: pl. 10: 4), based on the condition that Janvier supposed to have been present in the type species as well (Janvier 1985a: 188); (4) the lateral extent of the pineal plate groove, which does not exceed the width of the anterior part of the dorsal field, and the pineal plate that has no contact with the orbits; such a condition is observed in *D.* sp. 2 (Janvier 1985a: text-fig. 101A) from Spitsbergen as well; in *D. poplinae* this groove has a somewhat greater extent (Janvier 1985a: text-fig. 99, pl. 3: 1a). The only substantial distinction from the Spitsbergen representatives of the genus, which can be noted in the described here, is the considerably smaller size of the Podolian *Diademaspis* species.

The second new form, *Wladysagitta janvieri* gen. et sp. nov., is characterized by a rostral process, which rarely occurs within the "classical" horseshoe-shaped cephalaspid shields. A similar but considerably more developed rostrum can be seen in some osteostracans from Spitsbergen, e.g., in the Boreaspididae (*Dicranaspis*, *Boreaspis*, *Belonaspis, Spatulaspis*) and the related forms *Hoelaspis angulata* Stensiö, 1927 and *Severaspis rostralis* Mark-Kurik and Janvier, 1995 (Janvier 1985a; Mark-Kurik and Janvier 1995) the latter being known from Severnaya Zemlya.

Cephalaspids with a rostrum have sometimes been mentioned in other ichthyofaunas of the Euroamerican or "Cephalaspid" province of the Lower Devonian (Young 1981). *Cephalaspis acutirostris* has been described from "old-red" deposits of Shropshire (Great Britain; Stensiö 1932). The rostral part of its headshield "is produced into a broad, but probably short, rostral process, which is, however, imperfectly preserved anteriorly" (Stensiö 1932: 98). One can see (Stensiö 1932: pl. 40: 3) that only the base of the rostral process has been preserved, and neither its shape nor its size is known. Podolian cephalaspids kept in the Natural History Museum, London, were described by Janvier, who figured remains of the shield, which he identified as "*Cephalaspis*" cf. *acutirostris* Stensiö, 1932 (Janvier 1985b: fig. 20A). Like its British "twin", this specimen from Horodnytsia has a rostrum, which was broken off at its base (Fig. 8D). The similarity between these specimens and the new material could be a reason for referring them to the same genus.

Judging from some other features that can be compared, the rostral process of the *Wladysagitta* gen. nov. and of the Boreaspididae is evidence for convergent evolution and not of close relationship between them. However, the available data are not sufficient to relate with certainty *Wladysagitta* gen. nov. to one particular higher taxon of the cornuate Osteostraci.

Among other groups of fossil jawless fishes the rostral process is worth mentioning in several Chinese galeaspids (*Lungmenshanaspis, Sanchaspis*, probably *Szechuanaspis*), Australian pituriaspids (*Pituriaspis*), some amphiaspids (*Eglonaspis*) and pteraspids (especially in *Belgicaspis* and *Rhinopteraspis*).

The function of the rostral process is not easy to interpret. The hypothesis of the protective function of the rostral process proposed by Janvier (1985a) and Belles-Isles (see Dineley 1994) evidently does not consider all its other possible functions. Dineley's point of view, that it could serve as a de-

vice for "probing or disturbing sediment and vegetation in the search for food" (Dineley 1994: p. 69) is well-founded. Possibly, in some cases, the rostral process could been used as a detector of potential food hidden in silt or muddy water, as well. The rostrum of osteostracans may have had approximately the same functions as the rostrum of other agnathans that lived under similar environmental conditions. Since the rostrum of osteostracans had certain hydrodynamic significance, its different size combined with more or less developed cornual processes may also indicate the degree of manoeuvrability of the animals. Obviously, two large processes developed from the anterolateral corners of the headshield of *Tauraspis rara* Mark-Kurik and Janvier, 1995 from Lower Devonian of Severnaya Zemlya served as a functional substitute for the rostral process, and may also reflect a certain specialization in food search.

Conclusions

The osteostracan fauna from Podolia is still unsufficiently studied. Judging from the newly collected material, and despite its poor preservation, one can expect many more forms of Podolian Osteostraci than those described at present, notably among the Zenaspidida. As the bulk of Podolian zenaspidids, *Zenaspis dzieduszyckii* sp. nov. and *Diademaspis* sp. have a smaller overall size than the related forms from Spitsbergen.

Wladysagitta gen. nov. is interesting from a paleogeographical point of view. At present only *Stensiopelta* occurs in both the British and Podolian localities and have never been found in Spitsbergen. If new material will confirms the close relationships between *W. janvieri* sp. nov. and *W. acutirostris*, *Wladysagitta* gen. nov., becomes one more evidence for paleobiogeographical relationships between Great Britain and Podolia.

Most likely, the rostral process of osteostracans should be considered as a multifunctional device having (depending on size) at least a sensory function-in the search for food, a hydrodynamic function, and a function as alert for predators. In the case of the latter function the effect could have been intensified by means of several other processes, e.g., the laterally directed cornual processes in such small osteostracans as the Boreaspididae or the horn-shaped anterolateral processes of *Tauraspis*.

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References

Adrain, J.M. and Wilson, M.V.H. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the Southern Mackenzie Mountains, N.W.T., Canada. *Journal of Vertebrate Paleontology* 14: 301–319.

Afanassieva, O.B. [Afanas'eva, O.B.] 1989. New cephalaspids (Agnatha) from the Lower Devonian of Podolia [in Russian]. *Paleontologičeskij žurnal* 3: 51–59.

Afanassieva, O.B. [Afanas'eva, O.B.] 1990. New *Benneviaspis* (Agnatha) from the Lower Devonian deposits of Podolia [in Russian]. *Paleontologičeskij žurnal* 4: 128–131.

Afanassieva, O.B. [Afanas'eva, O.B.] 1991. *Cefalaspidy Sovetskogo Soûza (Agnatha)*. 144 pp. Nauka, Moskva.

Afanassieva, O.B. [Afanas'eva, O.B.] and Voichyshyn, V.K. [Vojčyšyn, V.K.] 1991. On the revision of the Podolian osteostracans (Agnatha) [in Russian]. *Paleontologičeskij žurnal* 2: 65–72.

Alth, A. 1874. Über die paläozoischen Gebilde Podoliens und deren Versteinerungen. *Abhandlungen der Geologischen Reichsanstalt Österreich* 7 (1): 1–80.

Balabai, P.P. [Balabaj, P.P.] 1962. On the fauna of the cephalaspids of Podolian plate [in Ukrainian]. *Naukovi zapysky Naukovo-pryrodoznavčogo muzeû AN URSR* 10: 3–8.

Belles-Isles, M. and Janvier, P. 1984. Nouveaux Ostéostracés du Dévonien inférieur de Podolie (RSS D'Ukraine). *Acta Palaeontologica Polonica* 29: 195–208.

Brotzen, F. 1933. Die silurischen und devonischen Fischvorkommen in Westpodolien. I. *Palaeobiologica* 5 (3): 423–466.

Brotzen, F. 1936. Beiträge zur Vertebratenfauna des westpodolischen Silurs und Devons. I. *Protaspis arnelli* n. sp. und *Brachipteraspis* n. gen. *latissima* Zych. *Arkiv for zoology* 28A (22): 1–52.

Dineley, D.L. 1994. Cephalaspids from the Lower Devonian of Prince of Wales Island, Canada. *Palaeontology* 37: 61–70.

Drygant, D.M. 2000. Lower and Middle Paleozoic of the Volyn'-Podillya margin of the East-European Platform and Carpathian Foredeep [in Ukrainian]. *Naukovi zapysky Deržavnogo pryrodoznavčogo muzeû* 15: 24–129.

Drygant, D.M. 2003. About the problem of correlation and stratigraphic division in the Volyn'-Podillya part of the East-European Platform [in Ukrainian]. *Naukovi zapysky Deržavnogo pryrodoznavčogo muzeû* 18: 195–208.

Egerton, P.M.G. 1857. Palichthyologic notes. 9. On some fish remains from the neighbourhood of Ludlow. *The Quarterly Journal of the Geological Society of London* 13: 282–291.

Janvier, P. 1985a. *Les Céphalaspides du Spitsberg. Anatomie, phylogénie et systématique des Ostéostracés siluro-dévoniens. Révision des Ostéostracés de la Formation de Wood Bay (Dévonien inférieur du Spitsberg)*. 240 pp. CNRS, Paris.

Janvier, P. 1985b. Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.). *Bulletin British Museum (Natural History) Geology* 38 (5): 309–334.

Janvier, P. 1988. Un nouveau Cephalaspide (Osteostraci) du Devonien inferieur de Podolie (R.S.S. d'Ukraine). *Acta Palaeontologica Polonica* 33: 353–358.

Lankester, E.R. 1868–1870. The Cephalaspididae. *In*: J. Powrie and E.R. Lankester (eds.), *A Monograph of the Fishes of the Old Red Sandstone of Britain*, 1–62. The Palaeontographical Society, London.

Mark-Kurik, E. and Janvier, P. 1995. Early Devonian osteostracans from Severnaya Zemlya, Russia. *Journal of Vertebrate Paleontology* 15: 449–462.

Narbutas, W.W. [Narbutas, V.V.] 1984. *Krasnocvetnaâ formaciâ nižnego devona Pribaltiki i Podolii*. 136 pp. Mokslas, Vilnûs.

Pauča, M. 1941. Poissons paléozoïques de la rive bucovinienne du Dniester. *Comptes rendus des séances. Institut Geologique de Roumanie* 26: 14–32.

Stensiö, E. 1927. The Devonian and Downtonian vertebrates of Spitsbergen. 1. Family Cephalaspidae. *Skrifter om Svalbard og Nordishavet* 12: 1–391.

Stensiö, E. 1932. *The Cephalaspids of Great Britain*. 220 pp. British Museum Natural History, London.

Stensiö, E. 1958. Les Cyclostomes fossils ou Ostracodermes. *In*: P.P. Grassé (ed.), *Traité de Zoologie 13 (1)*, 173–425. Masson, Paris.

Tarlo, L.B. 1964. Psammosteiformes (Agnatha)—A review with descriptions of new material from the Lower Devonian of Poland. I. General part. *Palaeontologia Polonica* 13: 1–135.

Voichyshyn, V.K. [Vojčyšyn, V.K.] 1994. New species of the genus *Mimetaspis* (Agnatha) from the Lower Devonian of Podolia [in Ukrainian]. *Paleontologičnyj zbirnyk* 30: 19–24.

Voichyshyn, V.K. [Vojčyšyn, V.K.] 1997. The tapho-fishassemblages from Early Devonian of Podolia [in Ukrainian]. *Vestnik zoologii* 31 (3): 33–39.

Voichyshyn, V.K. [Vojčyšyn, V.K.] 1998. New species of the genus *Zychaspis* (Agnatha) from the Dniester Series (Early Devonian) of Podolia [in Ukrainian]. *Paleontologičnyj zbirnyk* 32: 25–29.

Voichyshyn, V. [Vojčyšyn, V.] 2001a. Early Devonian fish fauna localities of Podolia [in Ukrainian]. *Paleontologičnyj zbirnyk* 33: 134–143.

Voichyshyn, V. [Vojčyšyn, V.] 2001b. Distribution of fossil remains of Agnatha and accompanying vertebrate groups in deposits of Lower Devonian of Podolia [in Ukrainian]. *Naukovi zapysky Deržavnogo pryrodoznavčogo muzeû* 16: 47–58.

Voichyshyn, V. [Vojčyšyn, V.] and Solodkyi, S. [Solodkyj, S.] 2004. New materials concerning the genus *Zychaspis* (Agnatha, Osteostraci) from Horodnytsia (Podolia, Ukraine) [in Ukrainian]. *Naukovi zapysky Deržavnogo pryrodoznavčogo muzeâ* 19: 171–182.

Wängsjö, G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen Cephalaspids. *Skrifter Norsk Polarinstitutt* 97: 1–657.

Young, G. 1981. Biogeography of Devonian vertebrates. *Alcheringa* 15: 225–243.

Zych, W. 1927. Old-Red Podolski. *Prace Państwowego Instytutu Geologicznego* 2 (1): 1–65.

Zych, W. 1937. *Cephalaspis Kozlowskii* n. sp. from the Downtonian of Podole (Poland). *Archiwum Towarzystwa Naukowego we Lwowie* 9: 49–96.