Vestnik zoologii, **35**(1): 27–37, 2001

UDK 567.432 : 551.734(477.8)

SOME PROBLEMS OF THE TAXONOMY OF THE PTERASPIDS (AGNATHA, HETEROSTRACI) FROM PODOLIA (UKRAINE)

V. Voichyshyn

State Museum of Natural History, Lviv, 79008 Ukraine
E-mail: museum@ipm.lviv.ua

Accepted 25 September 1999

Some Problems of the Taxonomy of the Pteraspids (Agnatha, Heterostraci) from Podolia (Ukraine). Voichyshyn V. — The genus *Podolaspis* Zych, 1931 should today be considered to include three species, i. e., *Podolaspis podolica* (Alth, 1874), *P. lerichei* (Zych, 1927), and *P. zychi* (Brotzen, 1933), taking into account that distinguishing the first two of these species is difficult. The first, not quite correct description of the genera *Parapteraspis* Stensiö, 1958 and *Mylopteraspis* Stensiö, 1958 led to different nomenclative readings. Genus *Parapteraspis* is proposed to be considered sensu Novitskaya (1986) and the genus *Mylopteraspis*, sensu Blieck (1984). The analysis of published literature gives good reasons to think that the holotype of *Zascinaspis bryanti* (Brotzen, 1936) is the only known specimen of this species. One specimen of the reviewed material, which could be referred to *Z. bryanti*, shows, however, a triangular pineal plate in a non-contact type orbito-pineal belt. Its place among pteraspids remains undetermined. At this point, further progress depends upon determination of the limits of species variability of characters such as the morphology of the orbital and pineal regions. A preliminary review of this variability in *Z. heintzi* (Brotzen, 1936) is provided. Short diagnoses of Podolian pteraspid genera, suitable for practical use, are given.

Key words: Agnatha, Heterostraci, Pteraspidiformes, Podolia, taxonomy.

Некоторые проблемы систематики подольских птераспид (Agnatha, Heterostraci). Войчишин В. К. — Род *Podolaspis* Zych, 1931 сегодня целесообразно рассматривать в составе трех видов — *P. podolica* Alth, 1874, *P. lerichei* (Zych, 1927) и *P. zychi* (Brotzen, 1933), принимая во внимание при этом, что попытки различить на ископаемом материале первые два из них сопряжены со значительными трудностями. Не совсем корректное первоописание родов *Parapteraspis* Stensiö, 1958 и *Mylopteraspis* Stensiö, 1958 предопределило их номенклатурное разночтение. Род *Parapteraspis* предлагается рассматривать в понимании Л. И. Новицкой (1986), а род *Mylopteraspis* — в понимании А. Блика (Blieck, 1984). Анализ литературных данных дает основание считать, что голотип *Zascinaspis bryanti* (Brotzen, 1936) является пока что единственным известным экземпляром вида. Один образец (среди просмотренного материала), который мог бы быть отнесен к *Z. bryanti*, имеет, однако, треугольную пинеальную пластинку в неконтактном орбито-пинеальном поясе. Вопрос относительно его места в систематике птераспид остается открытым. В целом, назрела необходимость изучить пределы видовой изменчивости такого диагностического признака птераспид, как морфология орбито-пинеального пояса. Предварительный обзор такой изменчивости проведен для *Z. heintzi* (Brotzen, 1936). Даны короткие диагностические характеристики родов подольских птераспид, пригодные для практического использования.

Ключевые слова: Agnatha, Heterostraci, Pteraspidiformes, Подолье, систематика.

Introduction

The basic difficulties of the taxonomy of fossil organisms are always the incompleteness and the distortion of the material being examined by palaeontologists; therefore, knowledge of a taxon is built only by means of accumulation of new data as more complete fossil remains are found. This applies to the Podolian Early Devonian agnathans as well, a group which has received scientists' attention for a long time now. The taxonomy of Podolian armoured agnathans has been worked out well, particularly due to recent work on the question (Novitskaya, 1975, 1986; Blieck, 1984; Janvier, 1985; Afanassieva, 1991), but several questions remain.

This paper will focus on some aspects concerning the definition and number of species of the genera *Podolaspis* Zych, 1931, *Parapteraspis* Stensiö, 1958, *Mylopteraspis* Stensiö, 1958, and *Zascinaspis* Stensiö, 1958 (order Pteraspidiformes), and attempt to define a short set of diagnostic characteristics of Podolian pteraspid genera suitable for practical use.

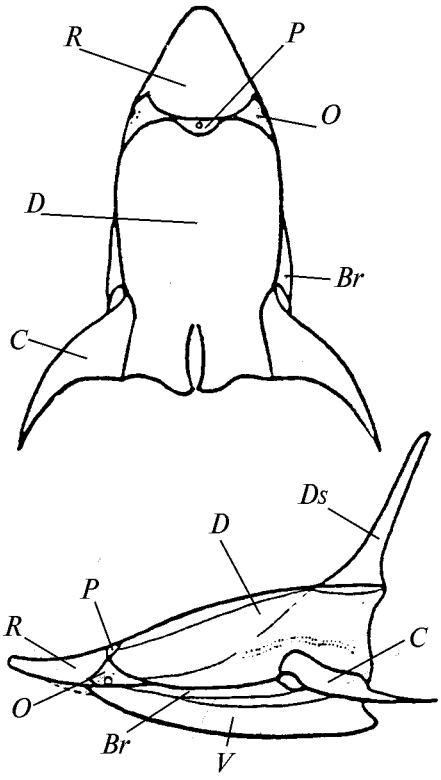

Fig. 1. The main plates of the pteraspid carapace [*Pteraspis* (=*Podolaspis*) *lerichei*, after figure by Brotzen (1933: fig. 9 a, b)]: *R* — rostral; *O* — orbital; *P* — pineal; *D* — dorsal; *Br* — branchial; *C* — cornual; *V* — ventral; *Ds* — dorsal spine.

Рис. 1. Основні пластинки панцира птераспід [*Pteraspis* (=*Podolaspis*) *lerichei*, за зображенням Бротцена (1933: fig. 9 a, b)]:: *R* — ростральна; *O* — орбітальна; *P* — пінеальна; *D* — дорсальна; *Br* — бранхіальна; *C* — корнуальна; *V* — вентральна; *Ds* — дорсальний шип.

The classification of pteraspids is based mainly on their exoskeletal morphology, because their internal anatomy is fairly uniform and, as is now known, cannot be used for definition of taxa of lower rank (Novitskaya, 1986).

The exoskeleton (armour) of pteraspids consists of paired orbital, branchial, and cornual plates; and unpaired rostral, pineal, dorsal, and ventral plates (fig. 1). Along the body axis on the posterior part of the dorsal plate one can see the groove of the dorsal spine attachment. In addition, there is a group of oral plates between the rostral and ventral plates. Remains of the oral plates are very rare, and they are used as systematic characters only when data are available for comparisons. It should be noted that the same problem occurs with the morphology of the ventral surface of the rostrum, which has been considered in some classifications (Stensiö 1958) as the main diagnostic criterion.

Classification schemes which take into account as many diagnostic characters as possible may be considered to be the most successful. The classification of pteraspids proposed by Novitskaya(1975) meets this requirement. The morphology of the orbito-pineal belt has been considered to be of prime importance in this classification. Other characters used by Novitskaya are the shape of the large plates of the carapace, the morphology of the branchial region, the position of the dorsal spine, characters of the rostral ventral surface, and the general size and proportions of the carapace. More recent reviewers (Blieck, 1984; Voichyshyn, 1999) have shown the significance in this respect of the course of the sensory line system canals as well.

Taxonomical assessment

Genus *Podolaspis* Zych, 1931

Podolaspis is possibly one of the most abundant in specimens among Podolian pteraspid genera. However, if the orbito-pineal region is poorly preserved, some samples of the morphologically similar genus *Parapteraspis* can easily be erroneously attributed to it. In addition, there is no certainty concerning species variability within the genus *Podolaspis* itself.

The generic name *Podolaspis* was introduced by Zych (1931) in the figure legends of a work dealing with the morphology of heterostracans. In particular, the species *Podolaspis rostrata* was constructed by combining previously described varieties *Pteraspis sturi* Alth mut. *rostrata* and *Pteraspis lerichei* Zych mut. *rostrata* (Zych, 1927). Later the former of these varieties was considered (Novitskaya, 1986) to be a partial synonym of *Podolaspis podolica* (Alth, 1874), and the latter as a partial (Brotzen 1933) or complete (Tarlo, 1961; Blieck, 1984; Novitskaya, 1986) synonym of *P. lerichei* (Zych, 1927).

The sample found near Zalishchyky, which, after the figure in Alth's work (1874: pl. I, fig. 5), was designated by Brotzen (1933: 441) as the type specimen, is now considered the lectotype of *P. podolica*. But the lectotype shows virtually none of the features which have been considered (Novitskaya, 1986) as characteristic of *P. podolica*, namely a deep pineal hollow and sharp narrowing of the dorsal shield in the postbranchial region. The medial projection of the posterior margin of the shield, which must be noticeably developed (Brotzen,

1933: fig. 4b; Novitskaya, 1986: text-fig. 32), barely reaches beyond the level of the posterolateral angles of the shield. This feature is clearer in the figure of the same shield in lateral view (Alth, 1874: pl. I, fig. 6a). However, in both views the shield is almost identical to its analogue in *Pteraspis lerichei* as shown by Brotzen (1933: fig. 9a, b). This similarity was noted by Blieck (1984). One can assume that, since the lectotype of *P. podolica* is the mould of a shield of an apparently juvenile individual, the features in question have not reached the adult stage of development. But it could just as well be an adult of *P. lerichei* (for instance, cf. Zych, 1927: pl. II, fig. 7). All other examples of *Pteraspis podolicus sensu* Alth, which are usually regarded as *Podolaspis podolica* (Blieck, 1984; Novitskaya, 1986), and in particular the dorsal shields (Alth, 1874: pl. I, figs. 7–8, 9–10), which are nearly rectangular in their posterior outline, bear more resemblance to *P. lerichei* than to *P. podolica* in the present (Novitskaya, 1986) sense. So, the type series of *Podolaspis podolica* as shown by Alth (1874) demonstrates characters which can apply equally to either of these species.

Novitskaya (1986) notes that the study of abundant collected material relating to the genus *Podolaspis* confirms the validity of Zych's (1927) initial differentiation of *Pteraspis sturi* and *P. lerichei* based on the shape of the dorsal plate. It will be recalled that, according to Zych, *P. lerichei* differs from *P. sturi* in having a wider carapace with a straight posterior margin and wide, fin-like cornual plates. It should be noted that the differentiation of Podolian pteraspids in this way ("mutations" in Zych's classification were of subordinate significance) was artificial and, moreover, often depended on the state of preservation of the posterior margin of the carapace (the possibility of deformation having not been taken into account). In some cases Zych was not sure to which taxonomic unit a given specimen should be referred. For instance, a specimen (Zych, 1927: pl. III, fig. 3) which was subsequently cho- sed (Tarlo, 1961) as the lectotype of *Podolaspis lerichei*, was used by Zych as illustrative of both *Pteraspis sturi* mut. *rostrata* (Zych, 1927: 16) and *P. lerichei* mut. *rostrata* (ibid.: 18); but in the plate legends, it was designated as *Pteraspis* sp. mut. *rostrata*. In any case, this is not surprising, because none of Zych's criteria can be observed in the specimen, which is an anterior part of a dorsal carapace. Zych frankly noted in his description of *Pteraspis lerichei* mut. *rostrata* that "rostrum, lateral (= branchial) plates, dorsal process, two ocular (= orbital) plates and medial (= pineal) plate are the same as in *Pt. sturi* mut. *rostrata*" (ibid.: 19). Furthermore, he made note of the "sharp end" of the dorsal shield of *Pteraspis sturi* (unlike that of *Pt. lerichei*), in particular, on the basis of *Poraspis* carapaces (order Cyathaspidiformes), and the dorsal plate (ibid.: pl. II, fig. 6) as well, which scarcely belongs to *Podolaspis*[1]. The same can be said about the "wide flat lateral horns" (cornual plates) which clearly distinguish *Pt. lerichei* (after Zych) from *Pt. sturi*, because poraspids had no cornual plates at all. So, even if one can take "the difference in general shape of dorsal plate and its posterior margin" as specific criteria within *Podolaspis* (Novitskaya, 1986: 78), this hardly applies to Zych's material concerning the genus.

According to Blieck (1984: 43), the difference between these species is slight, consisting of a somewhat wider rostral plate "with ventral preoral surface apparently without posterior medial crest", and undeveloped, claw-shaped cornual plates in *Podolaspis podolica*. Judging by the reconstruction of both species (ibid.: fig. 41C, E), which is based almost entirely on Brotzen's figures (1933: fig. 4 a-b, 9 a-b), the extent of development of the cornual plates and the outline of the posterior margin of the dorsal shield are different. The posterior margin of the shield continues back as a visible projection in *P. podolica*, but in *P. lerichei* it is comparatively smooth. At the same time, in the shape of both the shield (excepting the posterior margin, as has been mentioned above) and the pineal plate, these species are identical. On the contrary, the cornual plates, according to data presented by Novitskaya (1986: text-fig. 29, 31, pl. XVI, fig. 1, 5, p. 143, fig. 38 and 39), seem to be more developed in *P. podolica* than in *P. lerichei*. The shape of the cornual plates has also been analyzed from a

[1] Brotzen (1933: 445), for instance, did not regard it as a synonym of *Pteraspis* (= *Podolaspis*) *lerichei*. See also Blieck (1984: 34). There is more support for referring this specimen to *"Pteraspis" angustate* Alth, 1874 (Voichyshyn, 1999).

similar point of view in one of the papers of Balabai (1960). Blieck (1984: 43, 72) does not exclude the possibility that *P. podolica* is a synonym of *P. lerichei*.

According to Novitskaya (1986), *P. lerichei* differs from *P. podolica* in the shape of both the pineal plate and the dorsal shield. The posterior margin of the pineal plate is rounded in *P. lerichei*, but it forms an angle (in the description, a sharp edge) in *P. podolica*. The dorsal shield of *P. lerichei* is of uniform width, but in *P. podolica* the postbranchial portion is sharply narrowed. Besides, the branchial plates of *P. lerichei*, in contrast with those of *P. podolica*, have no lateral twist (on this point I have no material for comparison). However, in my opinion, some material illustrated by Novitskaya entirely reflects a situation in which distinction of these species is often difficult. Specifically, *P. podolica* (Novitskaya, 1986: 81, text-fig. 31, pl. XVI, fig. 5) quite resembles *P. lerichei* (ibid.: pl. XVI, fig. 2) in the shape of both the dorsal shield and the pineal plate. Both specimens show some postbranchial narrowing of the dorsal plate. The shape of the shield from the juvenile individual illustrated by Zych (1927: pl. II, fig. 7) and considered synonymous with *P. lerichei* (Blieck, 1984: 42; Novitskaya, 1986: 78) has the same character. Obviously the postbranchial narrowing of the shield in juveniles was insignificant, but increased with age (e. g., Novitskaya, 1986: text-fig. 32).

According to my own data, in certain cases a noticeable narrowing of the postbranchial part of the dorsal shield and the projection of its posterior margin are observed in fossil material. Following Novitskaya (1986), one can consider these features as characteristic of *P. podolica*, versus *P. lerichei*. However, the posterior margin of the pineal plate in the same material is a smooth curve, rather than a sharp angle; in this respect, it is practically indistinguishable from the homologous feature in *P. lerichei*.

Balabai's standpoint concerning this question is significant. He noted (Balabai, 1959a: 7) that *Pteraspis* (= *Podolaspis*) *lerichei* "was characterized by considerable variety of both size and shape of separate parts of the dorsal shield", adding moreover that "*Pt. lerichei* could be divided into as many separate species as one wishes. " In his subsequent work (Balabai, 1959b: 88–89) one reads that "*Pt. podolica* Alth from Silurian and *Pt. lerichei* from Podolian Old-Red are identical forms... Therefore, to all appearances, it is expedient to speak about one species." Later, Balabai (1961: 7) writes: "In its morphology (*Pteraspis podolica* Alth) quite resembles Lower Devonian *Pteraspis lerichei* Zych, which differs from it in its red colour only, corresponding to the colour of the surrounding sandstones and shales."

As for other *Podolaspis* species, the basis on which Novitskaya (1986) removed *Podolaspis gracilis* (Stensiö, 1958) from the genus *Parapteraspis* seem to be insufficient. Novitskaya notes a similarity between *P. gracilis* and *P. lerichei*, and takes the wider carapace and lack of preorogonial angles of the former to be distinctions. Preorogonial angles are one element of the morphology of the ventral side of the rostral plate. The characterization of the ventral side of the rostrum with regard to *P. gracilis* was made by Novitskaya (1986) after a species lectotype, in which capacity specimen C1558 of the Naturhistoriska Riksmuseet of Stockholm (NHRM) has been considered. However, this specimen, which has been studied by both Stensiö (1958) and Blieck (1984), could obviously be referred to the genus *Parapteraspis* (Blieck, 1984: fig. 10 A-C). In addition, specimen 3592/47 from the Paleontological Institute RAS of Moscow (PIN), which represents Novitskaya's own material concerning *Podolaspis gracilis* (Novitskaya, 1986: text-fig. 34, pl. XVII, fig. 1) does not exceed the variability within the *podolica-lerichei* group. One can compare it, for example, with the specimen of *P. lerichei* depicted in the same work (ibid.: text-fig. 29, pl. XVI, fig. 3).

Thus, the genus *Podolaspis* should be considered to include three species, viz. *P. podolica*, *P. lerichei*, and *P. zychi* (Brotzen, 1933), taking into account the difficulties in distinguishing between the first two species in fossil material.

Genus *Parapteraspis* Stensiö, 1958

At times, different systematic readings and nomenclatural problems appear as the result of insufficiently accurate descriptions of new taxa. This pertains to some genera and species

constructed by Stensiö (1958) on the basis of Podolian material. In particular, the question of the type species of the genus *Parapteraspis* is open to debate.

Two species, *Parapteraspis gracilis* Stensiö, 1958 and *P. plana?* (Brotzen, 1933), were referred to the genus *Parapteraspis* when it was constructed (Stensiö, 1958), but neither was indicated as the type species.

Taxon *P. plana?* cannot be related to any of the specimens shown by Brotzen (see Blieck, 1984; Novitskaya, 1986). Therefore, Novitskaya considers Stensiö to be the author of the species and the specimen NHRM C1548 as its lectotype, treating this species (*Parapteraspis plana* Stensiö) as the type species for the genus *Parapteraspis* (Novitskaya, 1986: 88). However, starting from the same point, Blieck (1984) proposed the new species name *Parapteraspis djurinensis* instead of that given by Stensiö (specimen NHRM C1548 was designated as the holotype).

Blieck designated *Parapteraspis gracilis* Stensiö as the type species of the genus, apparently because this taxon, which is based on the lectotype (NHRM C1558) shown by Stensiö (1958), is unambiguous in its interpretation. Blieck cites this figure from Stensiö's work, but Novitskaya (1986: 89) asserts that, "judging from the characteristic shape of the pineal plate," it represents *Parapteraspis plana* (*P. djurinensis sensu* Blieck) and not *P. gracilis* (i. e., not NHRM C1558). She refers specimen C1558 and, hence, the species *Pteraspis gracilis* Stensiö, to the genus *Podolaspis* because this species "has a rostrum and an orbito-pineal belt characteristic of *Podolaspis*" (ibid.: 84, 89). However, as has been noted above, Novitskaya's own material regarding *Podolaspis gracilis* should instead be considered as belonging to the *podolica-lerichei* group.

In my opinion, material pertaining to *Parapteraspis* in Blieck's work (1984: figs. 10, 11), as well as reconstructions from this material, of the species *P. gracilis* and *P. djurinensis* (*ibid.:* fig. 39 A, C), point toward their belonging to one species which is identical with *Parapteraspis plana* Stensiö, 1958 sensu Novitskaya (1986). The posterior part of the specimens NHRM C1558 and C1548 is unknown; however, the orientation of the pineal plate of the former (Blieck 1984: fig. 10 A) suggests a body shape change which would be reflected in a wide posterior part in the reconstruction of *P. gracilis* (ibid.: fig. 39 A). The narrowing of the posterior part of the carapace in the reconstruction of *P. djurinensis* (ibid.: fig. 39 C) is probably also somewhat exaggerated (cf. ibid.: fig. 11 A). The differences between these two specimens with respect to the shape and size of the pineal plate, to my mind, does not exceed the limits of variability within the species. As to the difference in size of the ventral surface of the rostral plate, fossil remains (ibid.: fig. 10 C, 11 B) scarcely offer grounds for such clear reconstructions as those cited by Blieck from Stensiö's work (ibid.: fig. 39 B, D).

Stensiö constructed the genus *Parapteraspis* without a generic diagnosis (unfortunately, this omission applies to all the other Podolian taxa he proposed). Therefore, subsequent researchers have not reached a consensus on the extent of the genus and its distinctive features. As for the shape of the orbito-pineal belt, Blieck (1984: 88) considers it to be of the non-contact type, but acording to Novitskaya (1986: 88) it is characterized by the fact that "the medial projections [of the orbital plates]... are widely separated from the pineal plate or almost in contact with it." This divergence, in particular, led Novitskaya to refer *Plesiopteraspis? lata* Stensiö, 1958 to the genus *Parapteraspis* (as *Parapteraspis lata*), and Blieck to refer the same species to the genus *Podolaspis* (as *Podolaspis? lata*). However, podolaspids might be primarily distinguished by the half-moon shape of the pineal plate, which is not found in *Plesiopteraspis? lata*. Hence, the variant proposed by Novitskaya conforms better to the actual material.

Blieck inserts *Pteraspis jackana* White, 1935 from England (Blieck, 1984: fig. 12, 39 E) in the genus *Parapteraspis* as well. But illustrative material (ibid.: fig. 12) concerning this species produces a somewhat conflicting impression. In several features it more closely resembles *Podolaspis* than *Parapteraspis*. I think the species possibly might be referred to a new genus within Podolaspididae. However, there is insufficient data to be sure of this.

Genus *Mylopteraspis* Stensiö, 1958

The genus *Mylopteraspis* was established (Stensiö, 1958) for the species *M. robusta* Stensiö, 1958 and *M. gracilis* Stensiö, 1958. The material regarding *M. gracilis* (Blieck, 1984, fig. 17 A, B) permits restoration of the anterior part of the carapace of both ventral and dorsal sides (ibid.: fig. 42 A, B), and thereby allows this species to be distinguished among new findings (ibid.: fig. 17 C–F). However, *M. robusta* is known so far only by the rostral part from the ventral side (ibid.: fig. 18). The incomplete rostral plate, also known from the ventral side, has been referred tentatively to *M. robusta* by Novitskaya (1986: pl. XVII, fig. 5), but our concept of this species remains unclear. Blieck (1984), who studied *Mylopteraspis* lectotypes, has noted that the reconstruction of *M. robusta* given by Stensiö was not quite correct. Hence, there is some doubt as to the validity of unifying the material in question under a common generic name. Since Stensiö did not designate the type species of the genus, and Tarlo (1961) designated it to be *M. robusta*, Blieck maintains that it is advisable to establish a new genus, *Mylopteraspidella*, on the basis of *M. gracilis*. Taking into account that the diagnostic basis of the genus *Mylopteraspis* in its primary sense is not grounded in a type species, and considering Blieck's (1984) other reasons, establishment of the genus *Mylopteraspidella* seems justified.

Genus *Zascinaspis* Stensiö, 1958

A series of questions arises from a more detailed review of material concerning the genus *Zascinaspis*.

Zascinaspis bryanti (Brotzen, 1936) was constructed from a single incomplete specimen (fig. 2, *b*) which, however, can be restored in dorsal view with the possible exception of the posterior part. As it appears from the original description, the species is rather small (this

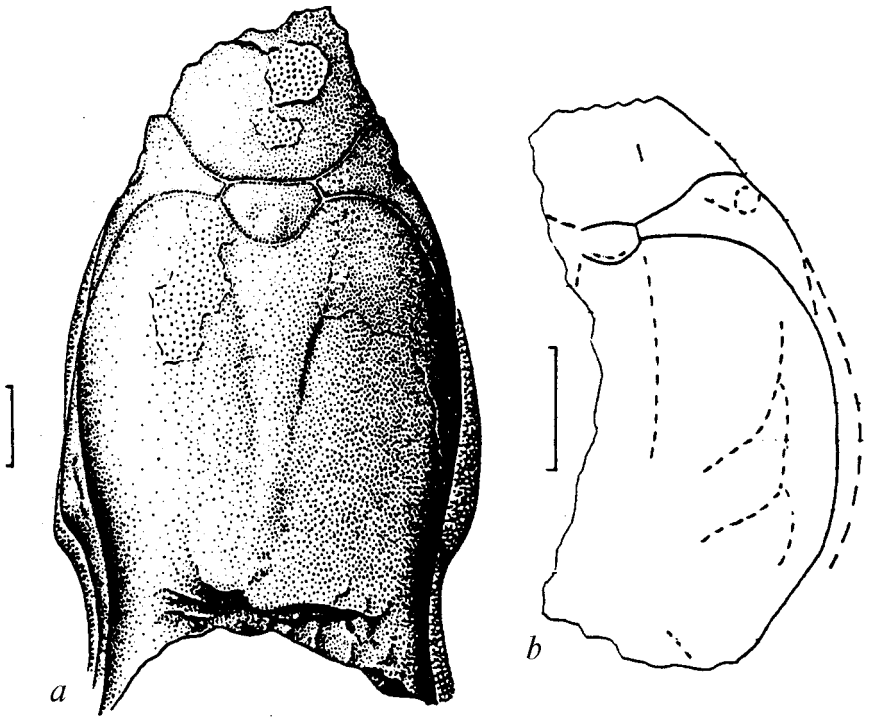

Fig. 2. *Zascinaspis bryanti*: *a* — according to Novitskaya (1986: text-fig. 52) (specimen PIN 3592/28); *b* — schematic figure of the holotype in Blieck's work (Blieck, 1984: fig. 29). The scale is equal to 1 cm in all figures.

Рис. 2. *Zascinaspis bryanti*: *a* — за Новицькою (1986: рис. 52) (екз. ПІН 3592/28); *b* — схематичне зображення голотипу у роботі Бліка (Blieck, 1984: fig. 29). Довжина мірної лінійки на всіх рисунках становить 1 см.

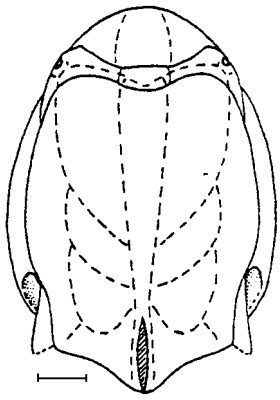

Fig. 3. *Zascinaspis heintzi*, reconstruction by Blieck (1984: fig. 46 B).

Рис. 3. *Zascinaspis heintzi*, реконструкція Бліка (Blieck, 1984: fig. 46 B).

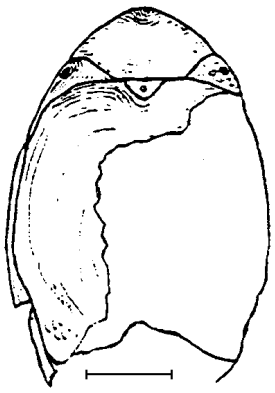

Fig. 4. *Zascinaspis*? sp. (specimen SMNH 37541; Jagilnytsja Stara).

Рис. 4. *Zascinaspis*? sp. (екз. ДПМ 37541; с. Ягільниця Стара).

was noted by Brotzen himself). It is evident that the specimen in question was no longer than 5 cm; the width of its dorsal shield was about 3.6 cm and was almost equal to the length. The holotype of the species was found east of Dobrivljany and, hence, comes from the Ivanie Horizon of the Podolian Lower Devonian.

Novitskaya (1986: 106) describes one specimen (PIN 3592/28) collected at Ivanie-Zolote as *Z. bryanti*; it is represented by an "almost complete mould of the dorsal side of the carapace" where "the edges of rostral, dorsal, pineal, and orbital plates are seen." But it is difficult from the photograph (Novitskaya, 1986: pl. XXII, fig. 2) to ascertain the preservation of the anterior margin of the rostral plate; the text-figure of the same specimen (fig. 2, *a*) indicates that the rostral plate might be longer than is characteristic of *Zascinaspis*. The anterior processes of the orbital plates seem also not to be rounded and resemble, for instance, those of *Larnovaspis*. As a whole, the mould of the dorsal carapace is more elongated and slender than is characteristic of *Zascinaspis* (fig. 3), with proportions far from those of the holotype of *Z. bryanti* (fig. 2, *b*), about which the author of the species wrote (Brotzen, 1936: 46) that "the small, very wide and flattened shape [of the shield] sufficiently differentiates [this species] from others." Furthermore, the exact size of the specimens being compared does not permit one to refer them to a common species (the holotype is about half as large as specimen PIN 3592/28).

In the caption to plate VIII, fig. 2 of Brotzen's work (1936), an enlargement of the photograph of the holotype has been erroneously designated as 1/1. If this were correct, the length of the carapace would be about 10 cm, i. e., as has been determined by Novitskaya (1986) from her own material. However, Brotzen himself wrote (1936: 44) abouth the "exceptionally small carapace" of the species ("der Panzer is auffallend klein"), and, according to the figure in the work of Blieck (1984) who studied this specimen personally, the general length of the carapace obviously did not exceed 5 cm. Consequently, taking all this into consideration, there is every reason to think that only one specimen of *Zascinaspis bryanti* is now known, namely the holotype of the species.

Balabai (1961) noted a finding of two samples of *Brachipteraspis* (=*Zascinaspis*) *bryanti* at Zalishchyky, and published a figure of one of them (ibid.: fig. 10; specimen of State Museum of Natural History 25 820). But what remains of the rostrum of this specimen is limited at the front to the moulds of the supranasal cartilage. Hence, the rostral plate has to be about one-third longer; the imprints of the sutures between the rostral and orbital plates indicate more development of the anterior orbital processes than is characteristic of *Zascinaspis*; and the dorsal shield is actually longer than what is shown in the figure, and so on. It is noted in the same work (Balabaiб 1961) that a large number of specimens of *Brachip-*

teraspis bryanti were collected by Zych at Jagilnytsja Stara. Perhaps all of them are lost with the exception of the specimen described below.

A question on the orbito-pineal belt shape characteristic of the genus *Zascinaspis* in general, and of the species *Z. bryanti* in particular, requires separate review.

According to the original description (Brotzenб 1936: 44), the orbital plates of *Z. bryanti* "reach to the pineal plate be become considerably narrow, and it is difficult to see that they touch it. The pineal plate has a half-moon shape..." This description, in light of current notions, better fits the characteristics of the orbito-pineal belt found in the genus *Podolaspis*. However, in contradiction to the description, the illustrations in Brotzen's work (ibid.: fig.15, pl. VIII, fig. 2) indicate that the specimen does belong to *Zascinaspis*. Among samples which were collected by Zych at Jagilnytsja Stara and are now kept at the State Museum of Natural History (SMNH), there is one that should manifestly be referred to *Zascinaspis* (based on the general shape and proportions of the carapace, as well as the shapes of the rostral, orbital [excepting the medial processes], dorsal, branchial, and cornual plates), were it not for the peculiarity of the morphology of the orbito-pineal belt (fig. 4).

The half-moon-shaped pineal plate and its lack of contact with the sharp medial orbital processes in this specimen are completely of "*Podolaspis* type". The very small size of the specimen (carapace 4.5 cm in length and 3.3 cm in width) suggest that it might be a juvenile. But the orbits are not disproportionately large, and the dentine ridges on the dorsal plate indicate a sufficiently deep pineal hollow, which is not observed in *Zascinaspis* (see, for example, Novitskaya, 1983: text-fig. 11a and 12). It should also be noted that the specimen in question comes from the Ivanie deposits (Jagilnytsja Stara). Thus, a number of features, including the proportions and exact sizes of the dorsal shield, suggest that the specimen gravitates to *Z. bryanti*. However, the aforementioned type of orbito-pineal belt is an obstacle to this definition. The specimen could conceivably be referred to a new genus (related to *Zascinaspis*), but doing so would necessitate an amendment of the diagnosis (and the conception) of the family Larnovaspididae which, in general, is hardly justified. Possibly this specimen indicates that the relationships within the pteraspids are too complex to be understood until sufficient data are accumulated.

Besides this manifestation of "non-standard" morphology of the orbito-pineal belt in *Zascinaspis?* sp., one can cite a number of other cases in which noticeable intraspecific variability of this morphological complex is revealed (particularly in the Larnovaspididae), or characters being discussed fall outside the ranges of the current classification. There is clearly a need to further investigate the variability of this diagnostic criterion of the pteraspids. However, a large amount of well-preserved fossil material will be necessary, by which species can be determined using other characters or their aggregates.

As a model, a preliminary review of such variability can be made for *Zascinaspis heintzi* (Brotzen, 1936) which, unlike *Z. bryanti*, is represented by dozens of specimens. An analysis of this material shows that the width of the medial processes of the orbital plates is often far from equal to the width of the lateral margins of the pineal plate at their point of contact. Sometimes the medial processes are narrower than these margins (unequicontact type of orbito-pineal belt; see Voichyshyn, 1999), and the contact could be such that the pineal plate extends beyond the orbito-pineal belt at its posterior part (fig. 5, *b*) or at both posterior and anterior parts (fig. 5, *a*). In addition, the outline of the posterior suture of the pineal plate ranges from only slightly curved (fig. 5, *a*, *b*) to salient (fig. 5, *d*, *f*) to considerably salient (fig. 5, *c*), or it extends in a rounded angle (fig. 5, *e*). The anterior margin of the pineal plate can be straight or slightly concave; its lateral margins can be straight and parallel to the body axis (fig. 5, *a*), straight and sloping (in the majority of specimens) or more or less concave, keeping at the same time a particular slope (fig. 5, *b*, *f*). Finally, the orbital plates can probably be more or less massive.

The above enumerated variations of the components of the orbito-pineal belt of *Z. heintzi* still apparently does not exhaust the variability within this species. For instance, some specimens from Ustechko (SMNH 37545, 35649, 35673, 35680) which, judging by all other observable characters, belong to *Z. heintzi*, have a somewhat different type of unequicontact orbito-pineal belt. Their medial orbital processes taper rapidly, although they do not

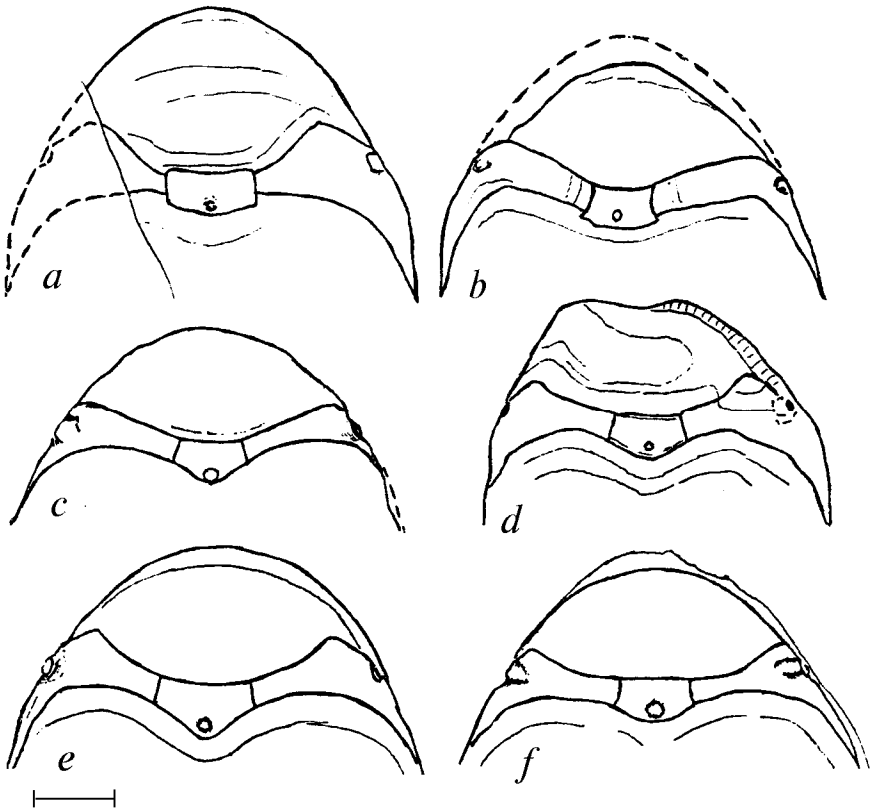

Fig. 5. The morphological variations of the orbito-pineal belt of *Zascinaspis heintzi*, collection of SMNH from Ustechko: *a* — 37536; *b* — 35565/1; *c* — 35656; *d* — 35667; *e* — 37540/1; *f* — 37540/2.

Рис. 5. Морфологічні варіації орбіто-пінеального поясу у *Zascinaspis heintzi*, колекція ДПМ з с. Устечка: *a* — 37536; *b* — 35565/1; *c* — 35656; *d* — 35667; *e* — 37540/1; *f* — 37540/2.

lose their ribbon-like shape; the anterior and posterior margins of the pineal plate are weakly and somewhat more salient, respectively. In general, the described orbito-pineal belt seems to be noticeably thinner (narrower) than is typical of *Zascinaspis*. It should be noted that in the case of the first three specimens mentioned above, their imprints (in particular parts of the orbito-pineal belt) show edges of the plates of the carapace that are always clearly distinguished. On the moulds of the carapaces lacking carapace covers, the plate edges have, as a rule, been eroded and give only a general notion about their contours.

Conclusions

The diagnostic characters of the Podolian pteraspids, which can often be observed in fossil material and are therefore suitable for practical use (disregarding the morphology of the ventral surface of the rostrum, which has been insufficiently studied as a diagnostic criterion[2]), are as follows at the generic level:

Podolaspis Zych, 1931 — pineal plate half-moon-shaped; point contact of pineal plate with orbital plates only at their sharp medial processes if at all; well-developed, more or less wide, crescent-shaped cornual plates; well-developed, vertically (or nearly so) oriented dorsal spine; dorsomedial sensory line system canals (mdl canals) of radial type (see Voichyshyn,

[2] This is due to high adaptability of the feature and, therefore, its lower taxonomic value (Novitskaya, 1975) which, moreover, is hardly studied because of the lack of actual material (the morphology of the ventral surface of the rostrum is known for few Podolian species and only by rare specimens). For this reason, Podolian genera *Mylopteraspis* Stensiö, 1958 and *Loricopteraspis* (Stensiö, 1958) are not listed here.

1999; in *Podolaspis* the type of divergence of the dorsomedial canals is not known for all species);

Dnestraspis Novitskaya, 1983 — projections of dorsal plate between pineal and orbital plates; mdl canals of radial type;

Mylopteraspidella Blieck, 1984 — wide, short, half-moon-shaped pineal plate (with tapered but blunt lateral ends); contact type orbito-pineal belt; wide cornual plates;

Parapteraspis Stensiö, 1958 — pineal plate with beveled lateral margins, non-contact type orbito-pineal belt;

Pavloaspis Voichyshyn, 1999 — large, rounded pineal plate without any contact with orbital plates; cornual plates not wide; mdl canals of radial type;

Larnovaspis Blieck, 1984 — rectangular or similarly shaped pineal plate; more or less wide, equi- or unequicontact orbito-pineal belt; elongated, more or less wide cornual plates; comparatively slender carapace; mdl canals of radial type (in some specimens which can be referred to *Larnovaspis* the mdl canals are of parallel type, but this material possibly represents a new genus);

Belgicaspis Zych, 1931 — peculiarly shaped rostral plate (with rodlike extension of anterior end) and orbital plates (with salient external lateral margins); mdl canals of radial type;

Alaeckaspis Voichyshyn, 1999 — large pineal plate (with salient posterior margin) in wide, contact type orbito-pineal belt; massive orbital plates, with considerably developed anterior processes; narrow and elongated cornual plates; mdl canals of parallel type;

Djurinaspis Novitskaya, 1983 — pineal plate wide (about one-third the extent of the orbito-pineal belt) and rounded, in a narrow orbito-pineal belt; narrow cornual plates;

Brachipteraspis Brotzen, 1936 — very wide dorsal shield in combination with triangular rostral plate and narrow, equicontact orbito-pineal belt; mdl canals of radial type;

Zascinaspis Stensiö, 1958 — short and rounded or round-beveled anterior processes of orbital plates; rostral plate rounded in front, short and wide; more or less wide, equi- or unequicontact orbito-pineal belt; wide and flattened dorsal shield; dorsal spine small, sloping up towards the back; mdl canals of parallel type;

Althaspis Zych, 1931 — long and narrowed rostral plate; narrow, equicontact orbito-pineal belt; very long dorsal spine with extreme upward slope towards the back; large, slender and elongated body; mdl canals probably of parallel type (at least, *Althaspis elongata* (Zych) and *A. leachi* (White) have this type of divergence of the mdl canals; see Zych, 1931: fig. 49; Blieck 1984: fig. 36 D);

Europrotaspis White, 1961 — combination of features including wide dorsal shield, very long and curved branchial plates (with their posterior margin reaching or extending past the posterior margin of the dorsal plate), and very small cornual plates; mdl canals of radial type.

Acknowledgements

I wish to thank Dr. Daniel Drygant and Dr. Alain Blieck for helpful comments on the draft of the manuscript. I also thank Steven Eklund, as well as Iryna Smirnova and Illya Bronshteyn for invaluable help in the translation of the text into English.

Afanassieva O. B. [*Афанасьева О. Б.* Цефаласпиды Советского Союза (Agnatha). — М. : Наука, 1991. — 144 с.] (In Russian).

Alth A. Über die palaeozoischen Gebilde Podoliens und deren Versteinerungen // Abhandlungen von der K. K. geologischen Reichsanstalt Österreich. — Wien, 1874. — **7** (1). — 80 S.

Balabai P. P. [*Балабай П. П.* До вивчення птераспід нижнього девону Поділля. Повідомлення 1 // Наукові записки Природознавчого музею АН УРСР. — 1959а. — № 7. — С. 3—21] (In Ukrainian).

Balabai P. P. [*Балабай П. П.* До фауни птераспід Подільської плити // Геологічний журнал. — 1959б. — **19**, № 4. — С. 87—90] (In Ukrainian).

Balabai P. P. [*Балабай П. П.* Про ідентичність деяких видів птераспід з нижнього палеозою Поділля // Зб. праць Зоологічного музею. — 1960. — № 29. — С. 93—95] (In Ukrainian).

Balabai P. P. [*Балабай П. П.* Гетеростраки верхнього силуру Поділля // Наукові записки Природознавчого музею АН УРСР. — 1961. — № 9. — С. 3—11] (In Ukrainian).

Blieck A. Les Hétérostracés Ptéraspidiformes. Systématique, phylogénie, biostratigraphie, biogéographie. — Paris : éd. CNRS, 1984. — 199 p. (Cahiers de Paléontologie, sect. Vertébrés).

Brotzen F. Die silurischen und devonischen Fischvorkommen in Westpodolien. I // Palaeobiologica. — 1933. — **5**, N 3. — S. 423–466.

Brotzen F. Beiträge zur Vertebratenfauna des westpodolischen Silurs und Devons. I. Protaspis arnelli n. sp. und Brachipteraspis n. gen. latissima Zych // Arkiv for zoologi. — 1936. — **28** A (22). — 52 S.

Janvier P. Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S. S. R.) // Bulletin of the British Museum (Natural History), Geology series. — London, 1985. — 38, N 5. — P. 309–334.

Novitskaya L. I. [*Новицкая Л. И.* К ревизии девонских птераспид Подолии // Палеонтологический журнал. — 1975. — № 4. — С. 72–85] (In Russian).

Novitskaya L. I. [*Новицкая Л. И.* Морфология древних бесчелюстных (гетеростраки и проблема связи бесчелюстных и челюстноротых позвоночных). — М. : Наука, 1983. — 184 с.] (In Russian).

Novitskaya L. I. [*Новицкая Л. И.* Древнейшие бесчелюстные СССР. Гетеростраки: циатаспиды, амфиаспиды, птераспиды. — М. : Наука, 1986. — 160 с.] (In Russian).

Stensiö E. Les Cyclostomes fossiles ou Ostracodermes // Traite de Zoologie. 1958. — **13**, N 1. — P. 173–426.

Tarlo L. Rhinopteraspis cornubica (McCoy) with notes on the classification and evolution of the pteraspids // Acta Palaeontologica Polonica. — 1961. — **6**, N 4. — P. 367–402.

Voichyshyn V. K. The new forms of pteraspids (Agnatha, Heterostraci) from Podolian Early Devonian // Vestn. zoologii. — 1999. — **33**, N 3. — P. 47–56.

Zych W. Old-Red Podolski // Prace Polskiego Instytutu Geologicznego. — Warszawa, 1927. — **2** (1). — 65 p.

Zych W. Fauna ryb dewonu i downtonu Podola. Pteraspidomorphi: Heterostraci. — Lwyw, 1931. — Cz. I A. — 92 s.