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Silurian synziphosurine horseshoe crab *Pasternakevia* revisited

WIESŁAW KRZEMIŃSKI, EWA KRZEMIŃSKA, and DARIUSZ WOJCIECHOWSKI



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The synziphosurine horseshoe crab *Pasternakevia* was until now known only from a single specimen. Herein we describe three new specimens from the outcrop close to the type locality of monotypic *P. podolica* that show several features that were unknown or only assumed in this genus. These characters include: a smooth surface of the carapace; an opisthosoma composed of ten segments, the first one being a microtergite (strongly reduced first opisthosomal segment usually hidden under the carapace), two or three last segments fused into a metasoma, and the telson. *Pasternakevia* is included in Bunodidae due to a hypertrophied tergite 2, but it is linked to the Pseudoniscidae by the shape of the opisthosoma.

Key words: Arthropoda, Xiphosura, Bunodidae, *Pasternakevia*, microtergite, phylogeny, Silurian, Ukraine.

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Introduction

Horseshoe crabs (Xiphosura) are an archaic lineage of Chelicerata, whose origins date back to the Ordovician (Rudkin et al. 2008). Within this group, the synziphosurines constitute a paraphyletic stem group (Anderson and Selden 1997), whose members show distinct segmentation of the opisthosoma, whilst in the extant lineage Xiphosurida, fusion of proximal opisthosomal segments is evident (the basic terminology is explained in Fig. 1). Synziphosurines existed at least until the Carboniferous (Mississippian) (Moore et al. 2007), whilst Xiphosurida are still represented by the extant genera *Limulus*, *Tachypleus*, and *Carcinoscorpius*.

The synziphosurine monotypic genus *Pasternakevia* was described from the Silurian of the Ukraine by Selden and Drygant (1987) based on *P. podolica*, a species represented in that time by a holotype only. Recently, three new specimens from an adjacent quarry in strata of roughly equivalent age have become available for study. This provides us with the opportunity to complete the descriptions of some generic characters (i.e., the definite number of opisthosomal segments, the presence of a microtergite, and the morphology of the telson) which were poorly defined in the holotype of *Pasternakevia* and therefore were included with some question marks in the phylogenetic analysis of the Synziphosurina by Anderson and Selden (1997). Furthermore, on comparing the shapes and proportions of the carapace and opisthosoma, it became obvious to us that these specimens, although similar to the holotype, differ in size and shape of

carapace and pleurae. Therefore, the diagnosis of the genus and species is emended to accommodate the variation now recognized within this species.

The systematic position of the genus was discussed by Anderson and Selden (1997). *Pasternakevia* belongs in the synziphosurines, a group previously of the rank of order but since it emerged as paraphyletic in the cladistic analysis of Anderson and Selden (1997), the name should only be used in an informal sense enclosed in quotation marks. *Pasternakevia* is ascribed to the Bunodidae on the basis of a hypertrophied second opisthosomal segment (Anderson and Moore 2004). The family was represented in the Silurian by four distinct genera: two from the Wenlock (Eldredge 1974): *Bunodes* Eichwald, 1854 (Oesel Island) and *Limuloides* Woodward, 1865 (England), *Pasternakevia* from the Ludlow of the Ukraine, and the oldest *Bembicosoma* Laurie, 1899 from the Llandovery of Scotland (Anderson and Moore 2004).

Institutional abbreviations.—ISEA, Museum of the Institute of Systematics and Evolution of Animals, Kraków, Poland; WNoZ, Museum of the Department of Earth Sciences of the Silesian University, Sosnowiec, Poland.

Stratigraphy and geological setting

The holotype of *Pasternakevia podolica* was collected from a talus in a quarry of Velyka Slobidka village (Ukraine); the rock matrix belongs the Ustye Suite series of the Bagovytsa horizon and its stratigraphic level was placed at lowermost

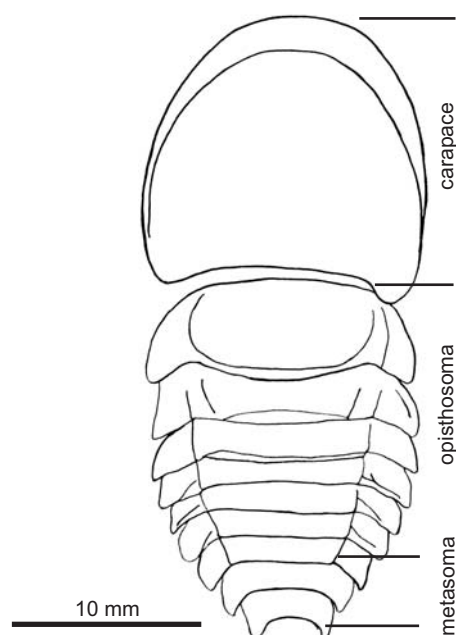


Fig. 1. Synziphosurine *Pasternakevia podolica* Selden and Drygant, 1987; reconstruction of holotype (redrawn after Selden and Drygant 1987: fig. 3d; changed).

Leintwardinian (Ludlow) by Tsegelnjuk et al. (1983). Details of the stratigraphy were also presented by Selden and Drygant (1987).

The three specimens described herein were found in a quarry at Zalissia village (Fig. 2), 12 km NW of Kamenets Podilsky and 27 km NW of Velyka Slobidka. The exact stratigraphic level in which the specimens occurred cannot be estimated directly because they were found in the talus at

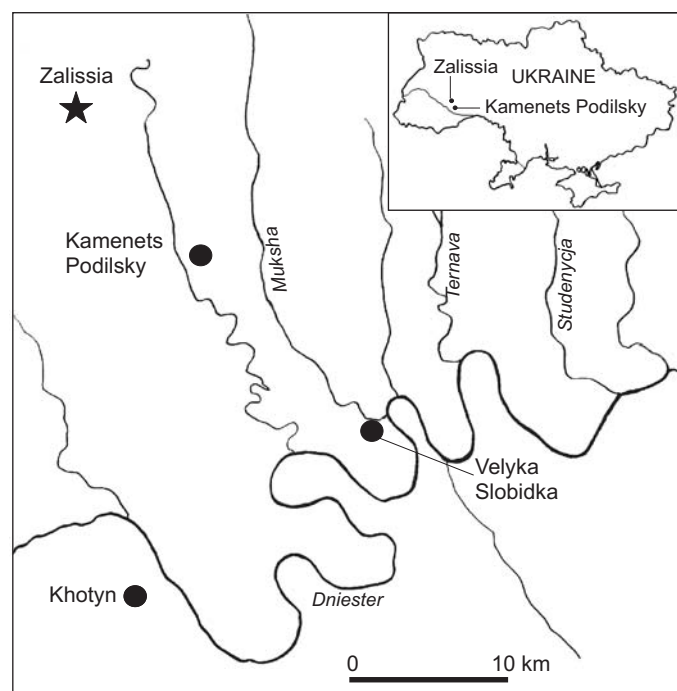


Fig. 2. Region of the Silurian (Ludlow) localities with synziphosurine shoe crabs in Ukraine, star indicates locality described herein).

the foot of the quarry face. However, we present the following arguments for considering all known specimens of *Pasternakevia* to be of equivalent stratigraphic age. The three specimens described herein all occur enclosed in a light grey, lamellar, pelitomorph dolomite (domerite) of lagoonal origin. This rock, common in the vicinity of Kamenets Podilsky, is typical of the upper layer of the stratigraphic series of the Ustye Suite of the Bagovytsa horizon. A further supporting argument is the discovery of *Baltoeurypterus tetragonophthalmus*, a eurypterid which, although rare worldwide, is quite frequently found in the Ustye Suite domerites; this eurypterid species was also found co-existing with the holotype of *Pasternakevia podolica*.

Systematic paleontology

Phylum Chelicerata Heymons, 1901

Class Xiphosura Latreille, 1802

Order "Synziphosurina"

Family Bunodidae Packard, 1886

Genus *Pasternakevia* Selden and Drygant, 1987

Type species: Pasternakevia podolica Selden and Drygant, 1987; middle Ludlow, Podolia, Ukraine.

Emended diagnosis.—Body length c. 30 mm. Carapace large, as broad as or wider than opisthosoma, spatulate, smooth, devoid of other superficial structures and grooves; genal cornua rounded. Opisthosoma 1.2–1.4 times longer than carapace, composed of ten free tergites, of which first, microtergite, is narrow, crescentic, hidden under carapace. Second tergite hypertrophied, arched; two last tergites 9–10 probably ankylosed (fused with respective sternites), forming an indistinct metasoma. Pleurae are well developed on tergites 2–10, shortest on second tergite; remaining are 0.3–0.5 times width of axial region of respective tergite. Telson with broad base; shape and size unknown.

Pasternakevia podolica Selden and Drygant, 1987

Figs. 1, 3–5.

Diagnosis.—The same as for the genus, by monotypy.

Material.—Specimen 1: part ISEA I-F/MP/2a/1499/08 (positive, convex cast; Fig. 3A) and counterpart ISEA I-F/MP/2b/1499/08 (negative, concave cast; Fig. 3B); both parts housed in ISEA. Measurements (mm). Specimen 2: negative cast ISEA I-F/MP/3/1499/08 (Fig. 4A₁), eight tergites of opisthosoma preserved. Specimen 3: part WNoZ/S/3/40 (Fig. 4B₂) (positive), and counterpart (negative) ISEA I-F/MP/1/1499/08 (Fig. 4B₃). In both part and counterpart a complete specimen of *Baltoeurypterus tetragonophthalmus* Fischer, 1839 is preserved (Fig. 4B₁).

All specimens from Zalissia village, 12 km north of Kamenets Podilsky, Ukraine, Podolia; Ustye Suite series of the Bagovytsa horizon, lowermost Leintwardinian, Ludlow, Silurian.

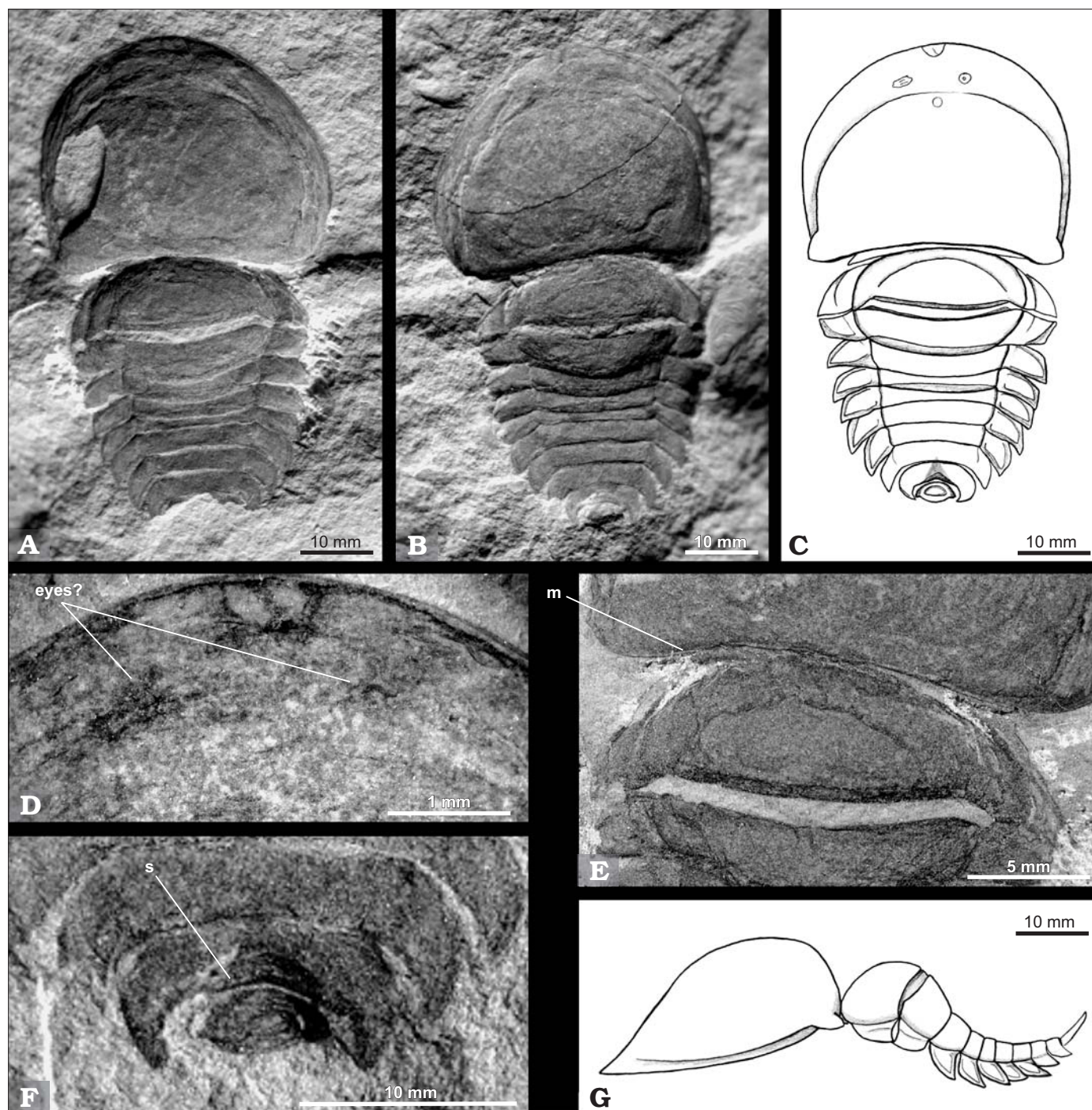


Fig. 3. Synziphosurine horseshoe crab *Pasternakevia podolica* Selden and Drygant, 1987. Specimen ISEA I-F/MP/2a/1499/08: part (A) and counterpart ISEA I-F/MP/2b/1499/08 (B), reconstruction (C), front of carapace (D), region of microtergite, m indicates microtergite (E), base of telson, s indicates structure within tergite 10 (F), plausible original position of the animal preserved, only carapace and tergites shown (G).

Measurements (mm).—Specimen 1: Entire length of complete specimen 29.0; carapace 12.8 long and 16.1 wide; opisthosoma (part) 16.6 long. Specimen 2: length 15.2, greatest width 14.1. Specimen 3: entire length 34.1; carapace 15.2 long and 22.0 wide; opisthosoma 18.4 mm long.

Description.—The first specimen comprises a carapace and the first nine tergites of an opisthosoma in positive (convex) part ISEA I-F/MP/2a/1499/08; in the negative ISEA I-F/MP/

2b/1499/08, all 10 tergites and the base of the telson are preserved. This is the most complete specimen of the species and genus yet described. The body is preserved in a flexed attitude, the opisthosoma being arched in the region of tergites 2–3 and depressed around tergite 5. Length ratio of carapace to opisthosoma is 1.22, but this value is probably underestimated, as the opisthosoma is flexed, and thus shortened sagittally. Carapace is 1.3 times wider than long, and dis-

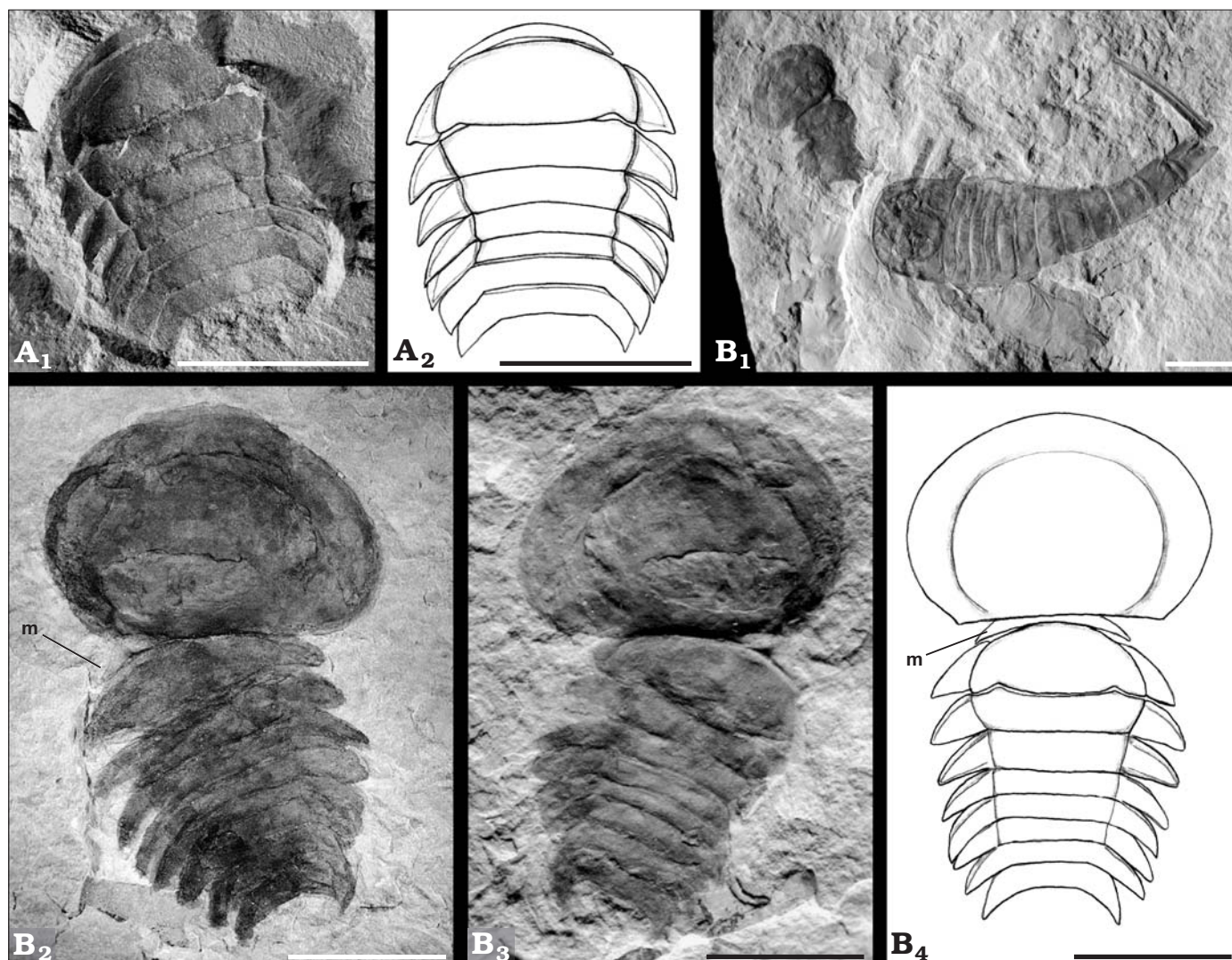


Fig. 4. **A.** Synziphosurine horseshoe crab *Pasternakevia podolica*, specimen ISEA I-F/MP/3/1499/08 (A_1) and reconstruction (A_2). **B.** Slab comprising a counterpart ISEA I-F/MP/1/1499/08 and a carcinoid, *Baltoeurypterus tetragonophthalmus* (B_1); part of specimen WNoZ/S/3/40 (B_2) and counterpart ISEA I-F/MP/1/1499/08 (B_3); reconstruction (B_4). Scale bars 10 mm.

tinctly wider than the opisthosoma. Anterior and lateral portions are rounded; major central part strongly convex, separated from narrow crescent flat margin by inconspicuous ridge, which is less pronounced in front, central section (Fig. 3C). Surface of carapace seemingly smooth, without other ridges or grooves visible. Two small darkened spots are traceable on a ridge in the positive part, and their symmetrical position may suggest a pair of anterior eyes (Fig. 3D). However, no trace of lensar structures was detected within these spots or elsewhere on carapace (for further comment see the discussion chapter). Centrally situated on the anterior margin a round structure is detectable on both parts. The posterior border of the carapace (in contact with the opisthosoma) is slightly deflected anteroproximally from genal cornua, which are rounded, prominent, delimited by small incisions in lateroposterior margin of carapace.

The opisthosoma comprises 10 tergites, entirely preserved in negative cast (Fig. 3B; reconstruction Fig. 3C). The

first tergite (microtergite) is hidden under the carapace and only lateral portions are partially detectable (m on Fig. 3E). The second tergite hypertrophied (almost twice length of the third, sagittally), strongly convex, ellipsoidal with lateral portions bent about 50° posteriorly; tergite 3 equally wide, but almost half as long. A posterior margin of tergite 2 has two small incisions in distal margin, matching the proximal margin of an adjacent tergite 3. Tergites 2 and 3 are flexed up exposing area of articulation preserved as two darker margins; the mid portion of this area is filled with sediment (Fig. 3E). Both outlines of these tergites combined form a complete regular ellipse; also their adjacent pleurae are directed to each other, suggesting close functional fit. The tergite 4 not much shorter than the preceding one, and twice the length of subsequent tergites. The axial region beyond tergites 2 and 3 gradually narrowing, except for tergites 5 and 6, which are of the same width (transversely). In the region of tergite 6 the body is flexed down, so that this tergite is seemingly narrow-

est and constricted medially, being partially hidden by the preceding one; the area of superimposition is detectable as darker strip. Distinct axial furrows reach tergite 8, but are less developed than in preceding segments; in the tergite 9 the furrows are still more shallow, and in tergite 10 not detectable. This last tergite is semicircular, forming an entity with its pleurae, and partially encloses the base of telson. The base is preserved in cross-section, exposing a raised core inside the base (Fig. 3F). The outline of the base is oval shaped, with an upper margin more arched, and laterally flanked by two small teeth directed posterolaterally, which are possibly remnants of lateral ridges flanking the telson, preserved in cross section. This appearance suggests that the telson was originally preserved in upturned position (plausible reconstruction of this position in Fig. 3G). Opposite the base of telson, and in its direct prolongation, a widely triangular structure is detectable within the tergite 10 (s on Fig. 3F). It might be identified as a portion of the posterior margin of tergite 10 compressed by the upturned telson. From this structure a brown triangle extends from over the entire tergite 10; the apex of the triangle almost reaches the middle of tergite 9 and is also detectable in the positive cast. This colored area may indicate a part of the system of muscles underneath connected with the telson. The initial width of the telson must have been about half that of last tergite. In spite of our efforts, no further portion of the telson was found.

Pleurae are well developed in all tergites 2–10, shortest in a second tergite (proportionally and also absolutely—only 0.2 times its width). Subsequent pleurae are longer (0.3–0.5 times width of axial region of respective tergite) and, beginning from tergite 4, directed posteriorly, with the angle of inclination growing gradually in the more posterior segments. Pleurae have sculpture: central portions are raised and delimited from thinner margins by sharp ridges. Basal portions adjacent to axial furrows appear more robust.

Specimen ISEA I-F/MP/3/1499/08 has only first eight opisthosomal tergites preserved in excellent condition (Fig. 4A₁); the absence of the carapace suggests a molt. If so, it is noteworthy that the microtergite was left with opisthosoma after molting. Earlier views on the function of this small tergite held that it functionally belongs to a carapace (Eldredge 1974). The microtergite is completely exposed and has a shape of a narrow, crescentic strip devoid of pleurae and as wide (transversely) as axial region of tergite 2. The anterior margin of tergite 3 is hidden under tergite 2. The general shape of the opisthosoma is congruent with that in specimen ISEA I-F/MP/2a/1499/08. Also in this specimen the tergites 5 and 6 are narrowest (sagittally). Axial furrows are deep only in first four full tergites (2–5), gradually becoming more shallow in tergite 6, and almost flat in tergites 7 and 8. Furrows are convergent in tergites 3 and 4, parallel in tergite 5 and 6, and slightly convergent in two subsequent ones. Pleurae of tergites 4–9 pointed, more elongated than in specimen ISEA I-F/MP/2a/1499/08, reaching half of axial region width in tergites 5–8 (comparison of shapes in next section). Central regions of pleurae are more robust and delimited

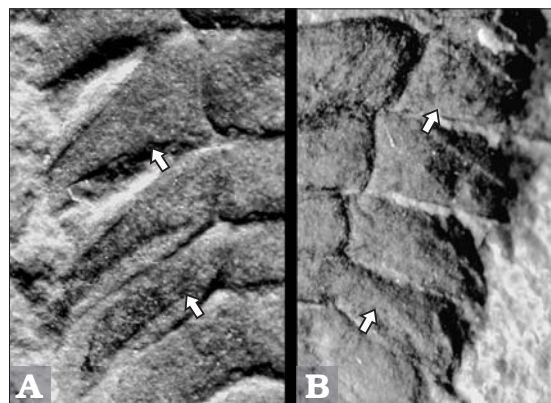


Fig. 5. Comparison of pleurae in synziphosurine horseshoe crab specimen ISEA I-F/MP/3/1499/08 (A) and specimen ISEA I-F/MP/2a/1499/08 (B). Arrows indicate borders between basal and distal portion of pleura and the position where “pseudofurrows” may arise (further explanation in text). Out of scale.

from thinner margins not only by ridges, but also by darker colour, especially so in tergites 5 and 6 (Fig. 5A).

The third specimen comprises a carapace and nine opisthosomal tergites in part WNoZ/S/3/40 and counterpart ISEA I-F/MP/1/1499/08. Both parts are in poor condition, showing initial stages of decomposition (Fig. 4B₂, B₃). The carapace is only weakly connected with the opisthosoma; tergites are greatly flattened, so that axial furrows are barely detectable; also, the borders between tergites are partially obscured due to their superimposition. The counterpart (negative) has right pleurae of tergites 2–6 torn off. The carapace is large, ca. 1.4 times wider than long, ellipsoid, spatulate, without any superficial structures preserved. The details of the posterior margin are not preserved. The traces of the edge of the microtergite are poorly visible in both parts of opisthosoma (m on Fig. 4B₂, B₄). General appearance of the opisthosoma similar to that in both previous descriptions: tergite 2 hypertrophied, with two small incisions in the distal margin, and matching the proximal margin of an adjacent tergite 3; the tergite 3 equally wide, but almost half as long. Tergite 4 only little shorter than preceding, but conspicuously narrower; tergites 5 and 6 are narrowest (sagittally), the former seems biconcave (constricted medially); subsequent tergites are slightly longer. Axial furrows in part WNoZ/S/3/40 greatly flattened; better detectable in a counterpart ISEA I-F/MP/1/1499/08. A reconstruction (Fig. 4B₄) is based on both parts.

Comparison of four specimens described.—The differences between the four known specimens of *Pasternakevia podolica* relate to the shape of the carapace and the pleurae. Carapaces of two specimens described here are conspicuously wider than the corresponding opisthosoma. Their length/width ratio equals 1.3 and 1.4, respectively, when compared to 1.1 in the holotype (Fig. 1). A poor state of preservation of the specimen WNoZ/S/3/40 (positive part) and ISEA I-F/MP/1/1499/08 (negative) suggests that some of the extra width of this carapace might be gained in a result of partial decomposition and

compression. On the other hand, the differences between the holotype and specimen ISEA I-F/MP/2a/1499/08 are most probably genuine, considering a very good state of their preservation, especially of the posterior margin of carapaces.

Regarding the shape of pleurae, some discrepancy is observed in the original illustrations of the holotype. The reconstruction (Selden and Drygant 1987: fig. 3d; redrawn herein as Fig. 1) is based on one photograph and shows very short pleurae, and axial region oval and relatively wide. On the other hand, the second photograph of the same specimen (Selden and Drygant 1987: fig. 3b), made under low angle light, shows the axial region more narrow and the furrows parallel-sided in tergites 6 and 7; accordingly, the pleurae are longer. This latter view is also conveyed in the schematic drawing of *Pasternakevia* (Anderson and Selden 1997: fig. 2F). In our opinion this discrepancy may be explained by the structure of the pleurae, in which, under compression, a “pseudofurrow” may appear between the robust basal portion, and the more delicate remainder. The “pseudofurrows” aligned form a row parallel and distal to axial furrows. It is conceivable that in the first photograph of the holotype the rows of pseudofurrows appeared more distinct than real axial furrows, and were pictured in the reconstruction. In our two first described specimens the pseudofurrows did not appear, probably because of relatively low compression applied to the specimens during fossilization. However, the borders between both portions of pleurae are to be detected (arrow in Fig. 5). The pseudofurrows were illustrated in nearly all “Synxiphosura” (and also are present in the schematic drawings in Anderson and Selden 1997: fig. 2). The most complex system of furrows is documented in the photograph of *Cyamocephalus* cf. *C. loganensis*, which shows even three rows of furrows (Eldredge and Plotnick 1974: fig. 2). These authors regard the axial furrows as real structures, and the other furrows “may be (but in our opinion, probably are not) compressional features” (Eldredge and Plotnick 1974: 8).

On comparing the pleurae of all specimens of *Pasternakevia*, we state that the pleurae of the holotype are comparable with those of specimen ISEA I-F/MP/2a/1499/08 (the specimen WNoZ/S/3/40 is greatly flattened and hence not taken in consideration), while the pleurae of specimen ISEA I-F/MP/3/1499/08 are distinctly more elongated (Fig. 5A, B). The axial regions of these specimens are in very good condition and retain much of their natural convexity; the pleurae are perfectly symmetric. Thus we assume that these differences are plausibly genuine. What is the primeval cause of this variation, remains to be explored.

Summarizing, on assumption that the characters of the carapace and pleurae were present in living specimens, three morphotypes may be discerned among the four specimens described: Morphotype 1: Holotype with smaller carapace and short pleurae; Morphotype 2: Specimen ISEA I-F/MP/2a/1499/08 (and possibly WNoZ/S/3/40) with larger carapace and same short pleurae; Morphotype 3: Specimen ISEA I-F/MP/3/1499/08 with longer pleurae, and the carapace unknown.

The variation described may be due either to sexual dimorphism, or intra-specific variation, or might indicate the different species.

Discussion

Vision in *Pasternakevia*

Intriguing features found on the part of specimen ISEA I-F/MP/2a/1499/08 are symmetrical, dark spots, the right one with a small regular circle inside (Fig. 3D), which may suggest the presence of simple anterior eyes.

In Xiphosura (and many other Arachnomorpha) the sight apparatus consists of a pair of large, lateral compound eyes and 1–2 simple, median eyes (“ocelli”), which merely tell light form dark (and hence the possible approach of a predator). Within the “Synxiphosura”, the eyes are best known in both genera of the family Weinberginidae: *Legrandella* and *Weinbergina*. Especially in the former the eyes are known in great detail. The visual surface occupies most of the lateral portions of the carapace and is composed of tightly packed lensar structures, which are organized in dorsolateral files of 2–3 lenses per file (Eldredge 1974: fig. 4A). The median eyes are positioned at anterior margin of the cardiac lobe near the midline.

In other synxiphosurans the eyes are less well known. The lensar structures are identified with globular structures containing pyrite or carbonate crystals, especially when organized in vertical files, occupying lateral portions of the ophthalmic ridge. According to Eldredge (1974), in the Bunodiidae the undoubted lensar structures were found in *Bunodes* and *Limuloides*; in both the lateral eyes are much smaller than in *Legrandella* (reconstruction of eyes in *Limuloides* is presented in Stürmer and Bergström 1981: fig. 1). Within the Pseudoniscidae, the presence of lensar structures is doubtful in *Pseudoniscus*; there are globular protuberances formed of microcrystals, which were identified with “eye” remnants; however, according to Eldredge (1974), such structures are distributed also in other areas of the carapace and more likely represent some microornamental features. Also, no definite trace of lensar structures were found in *Cyamocephalus* Currie, 1927 (Eldredge and Plotnick 1974).

No lensar structures could be found within the spots (or elsewhere on the carapace) in the specimens of *Pasternakevia* described herein. Also their position is rather unusual, as in known Xiphosura endowed with sight the small simple eyes are set much more closely together or even are interpreted as a single, central eye, as in another bunodiid, *Limuloides* (Stürmer and Bergström 1981: fig. 1). Therefore in our opinion these front spots are either artifacts, or traces of other symmetric structures beneath the carapace.

Characters of phylogenetic importance

Shape of microtergite.—The present study revealed that the microtergite of *Pasternakevia* is strongly reduced and devoid

of pleurae. These conditions are apomorphic and as such were treated in the phylogenetic analysis by Anderson and Selden (1997: character 3). Especially the absence of the pleurae on the microtergite seems to be a rare feature among the synziphosurines. Within the Bunodidae, the bluntly terminated, very short pleurae were found in *Bunodes* (Eldredge 1974), while in *Bembicosoma*, the oldest member of the family, the microtergite is not crescentic and has distinct, broad pleurae (Anderson and Moore 2004: figs. 2–4). In *Limuloides* the shape of microtergite is unknown. Among other synziphosurines, the crescentic microtergite without pleurae is met in weinberginiid *Willwerathia* (Anderson et al. 1998), although in the same family short pleurae produced into spines were found in *Legrandella* (Eldredge 1974). Both genera of the Pseudoniscidae have pleurae on microtergite, described as short (*Pseudoniscus*: Eldredge 1974) or very short (*Cyamocephalus*: Eldredge and Plotnick 1974).

Tagmosis and the phylogenetic relationships of *Pasternakevia*.—Within the “Synxiphosura”, two modes of opisthosomal differentiation are observed. In Weinberginidae and Bunodidae (but with exception of *Pasternakevia*) the opisthosoma is divided into meso- and metasoma. The metasoma is formed of three last tergites (7–10), which are strongly narrowed and ankylosed; pleurae on these tergites are absent, or reduced to spines. Also this configuration of three posterior tergites is present in the youngest synziphosurine, the Carboniferous *Anderella* (Moore et al. 2007). In this genus the total number of tergites is reduced to nine, and the metasoma consists of tergites 7–9.

A different mode is observed in Pseudoniscidae and *Pasternakevia*: the differentiation into meso- and metasoma is very indistinct, as the posterior tergites became narrower only gradually, and have fully developed pleurae. This group was regarded by Anderson and Selden (1997) as the more advanced one, because of the documented trend to the reduction in number of tergites. The initial stage of this reduction is observed in pseudonisciid *Cyamocephalus* where two tergites of mid opisthosoma (6 and 7) are fused, leaving only nine free tergites. Nine tergites are present in a most advanced synziphosurine, *Kasibelinurus*, and the Xiphosura. However, the finding of *Anderella* indicates that the ways of evolution might have been more complicated, and the reduction could happen independently in two lineages of synziphosurines.

Pasternakevia maintains an important, intermediate position between these two groups of “Synxiphosura”. The genus is included in Bunodidae due to a hypertrophied tergite 2, but it is linked to the Pseudoniscidae by the shape of the opisthosoma, which is very similar to that of *Pseudoniscus* (as estimated from the photographs in Eldredge 1974). In *Pasternakevia* only the 10th tergite is undoubtedly ankylosed and devoid of axial furrows. The preceding two tergites do not differ in shape from the more anterior ones; their width and the axial furrows get reduced only gradually, and the pleurae are fully developed. Thus we cannot be absolutely sure whether the tergite 9 is also ankylosed.

The phylogeny of the entire group “Synxiphosura” requires extensive revision based in part on the new information supplied here. Since the analysis by Anderson and Selden (1997) a number of new taxa have been described. Furthermore, the stem lineages proposed by Anderson and Selden (1997) are now questioned. *Lemoneites*, a basalmost taxon for Synxiphosura and Aglaspidida, seems to show non-arthropod affinity (Moore and Braddy 2005). The Weinberginidae were considered the most plesiomorphic lineage of Synxiphosura because of their opisthosoma composed of 11 tergites. However, in a weinberginiid *Willwerathia* only 10 tergites were found (Anderson et al. 1998), and doubts are expressed as to the actual count of tergites in remaining genera of this family.

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