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New Data on *Pycnosteus palaeformis* Preobrazhensky (Heterostraci, Psammosteiformes) from the Aruküla Deposits of the Leningrad Region

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Abstract—New materials on the psammosteid heterostracan *Pycnosteus palaeformis* Preobr. characteristic of the Aruküla deposits (Middle Devonian, Eifelian) of the Main Devonian Field are presented. A pentagonal rounded, slightly convex dorsal plate previously unknown is described. This plate bears a shallow notch at its anterior margin. A low crest that served for the attachment of the axial musculature extends medially on the visceral surface. The shape of the cornual plate is reconstructed based on its overlap surface over the branchial plate. This species is characterized by the unusually strongly convex keel-shaped ventral and weakly convex dorsal sides, as well as a wide spread of the supporting planes of the branchial plates. This allowed the animal to stay away from the bottom longer than other psammosteids. Morphological armor features and trunk reconstruction suggest a planktonophagous type of feeding for this animal.

INTRODUCTION

Detailed study of psammosteids from the Main Devonian Field started in the 1930s by Gross (1930, 1933), Obruchev (1933, 1940, 1941, 1947, 1961; Obruchev and Mark-Kurik, 1965) and was continued by Mark-Kurik (Mark, 1956, 1961; Mark-Kurik, 1968, 1984, 1991, 1992, 1995). However, to date, only for some species are the complete description of exoskeleton and body reconstructions available.

Pycnosteus palaeformis was described by Preobrazhensky (1911) based on the ventral plate from the collection of Yuriev University (Tartu, collected by Kh. Asmuss and K. Grewingk), which was considered as a dorsal plate by Preobrazhensky. The description was based on the microscopic structure of exoskeleton.

Gross (1930) described the microscopic structure of *Pycnosteus palaeformis* exoskeleton in detail, but included the spatulate shield of *P. palaeformis* in the *Psammosteus* reconstruction as a dorsal plate. Later, he indicated (Gross, 1933) that in the Psammosteiformes, as in many other Heterostraci, the ventral plate should be more convex than the dorsal, and, hence, the spatulate shield of *Pycnosteus* is a ventral plate.

Mark (1956) included the following species in the genus *Pycnosteus: P. imperfectus, P. palaeformis, P. tuberculatus*, and *P. pauli*. In this paper, she reconstructed the ventral side and the cross section through the trunk of *P. palaeformis*.

Obruchev and Mark-Kurik (1965) included three species in the genus *Pycnosteus: P. palaeformis, P. pauli*, and *P. tuberculatus*. *P. imperfectus* was synonymized with *P. palaeformis*. The ventral and branchial plates, as well as ridge scales were described in *P. palaeformis*, the ventral side and cross section of the body were reconstructed. Novitskaya (1965) studied the microscopic structure of the psammosteid exoskeleton, including that of *P. palaeformis*. Material on this species came from the same locality as the specimens described in the present paper.

The present paper focuses on the reconstruction of the external appearance and interpretation of the armor morphology (clearly distinguishing the Pycnosteidae from the other Heterostraci) to supplement the description of *P. palaeformis* Preobr.

MATERIAL

In 1997, O.A. Lebedev, a research fellow of the Laboratory of Fishes and Agnathans of the PIN RAS and, in 1998, the author of the present paper collected the remains of agnathans and fish from the deposits of the Aruküla Regional Stage (Middle Devonian, Eifelian) of the Leningrad Region. Most material was found in the Kobyl'skaya Sluda locality. An outcrop of red, thinly obliquely bedded sandstones interbedded with white sands and clays 12-meters thick is exposed on the right bank of the Luga River near the village of Staritsa. Vertebrate remains are distributed over the entire section and do not form accumulations, but are more abundant in the lower part. Complete and fragmentary plates of psammosteids (*Pycnosteus palaeformis, Tartuosteus giganteus*, and *Psammolepis proia*); placoderms (*Homostius latus, Coccosteus* sp., *Byssacanthus dilatatus*, and *Asterolepis* sp.); and scales, teeth, and bones of crossopterygians (*Glyptolepis* sp. and Osteolepidae) were found. *P. palaeformis* prevail. A previously unknown dorsal plate belonging to this species was found here.

Collection no. 220 is housed in the Paleontological Institute of the Russian Academy of Sciences. The branchial plate (specimen no. 220/843) from Obruchev's collection was used for species description.

SYSTEMATIC PALEONTOLOGY

Family Pycnosteidae Tarlo, 1962

Genus *Pycnosteus* Preobrazhensky, 1911

Pycnosteus palaeformis Preobrazhensky, 1911

Pycnosteus palaeformis: Preobrazhensky, 1911, pp. 21–27, pl. 1, figs. 1–5; Gross, 1930, pp. 5, 11, and 13 (pars); Obruchev, 1940, p. 768, text-fig. 3; Mark, 1956, pp. 76, 77, pl. 1, fig. 1, pl. 2, fig. 1, text-figs. 1b, 2b, and 3a; Obruchev and Mark-Kurik, 1965, pp. 135–137, pl. 25, figs. 1–3, pl. 26, figs. 1 and 2, text-figs. 79–81; Novitskaya, 1965, pp. 260 and 261, text-fig. 202.

Psammosteus imperfectus: Preobrazhensky, 1911, pp. 27–28, pl. 1, fig. 6.

Schizosteus (?) *imperfectus*: Obruchev, 1940, p. 767.

Pycnosteus imperfectus: Mark, 1956, pp. 74–76, text-figs. 1a and 2a.

Holotype. GM ASE (Geological Museum of the Academy of Sciences of Estonia), no. Pi 102, ventral plate, Estonia, Aruküla, near Tartu; Middle Devonian, Aruküla Horizon, *Pycnosteus palaeformis* Zone (Preobrazhensky, 1911, pl. 1, figs. 1–5).

Description (Figs. 1–4). Large form. Exoskeleton plates are covered with large (7 to 17 per 1 cm of plate length), simple, and high dentin tubercles. Tubercle apices are blunt. Denticles (usually five) do not ramify. In some dentin tubercles, small crests extending from the apex become denticles basally. Dentin tubercles are widely spaced, in the ridge scales they occasionally merge and form short crests.

The ventral plate (Fig. 1) is oval, strongly convex, and spatulate. The lateral surfaces of the plate are inclined in relation to the ventral side at 60°. A fragmentary right half of the plate (specimen PIN, no. 220/846) is 29 cm long, 17 cm wide, 12 cm deep, and 0.1–0.8 cm thick. The external surface bears dentin tubercles, which are absent on the external rim 1–4 cm wide. The internal (visceral) surface of the plate is smooth, covered with scarce pores. A deep notch occupying about two-thirds of the plate length ends at the anterior part of the plate near its growth center. Externally, the notch is bordered by a strip of fused and, in some areas, very strongly eroded dentin tubercles, 1–1.5 cm wide.

The dorsal plate (Fig. 2) is pentagonal, rounded, and weakly convex. A shallow notch occupies the anterior margin. The external surface bears dentin tubercles, which are absent on the external rim, which is 0.5–5 cm wide. The internal surface is smooth and bears scarce pores. A low crest, probably serving for the attachment of the axial muscles, extends along the longitudinal axis of the plate. It is strongly expressed in the posterior part and disappears anteriorly (Fig. 2b). An almost complete dorsal plate (specimen PIN, no. 220/844) is 31 cm long, 32 cm wide, and 0.2–0.5 cm thick. The second dorsal plate (specimen PIN, no. 220/845) is about 33 cm long and 32 cm wide.

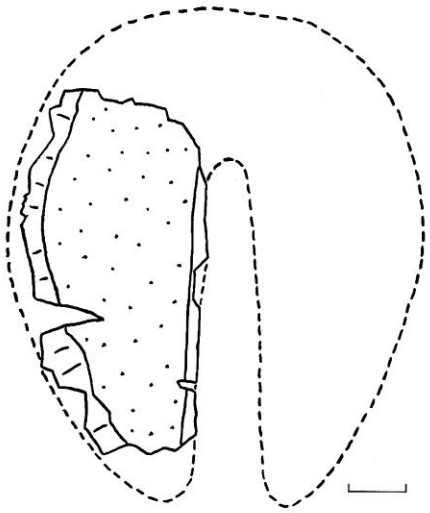

Fig. 1. *Pycnosteus palaeformis* Preobrazhensky, ventral plate, specimen PIN, no. 220/846; Leningrad Region, Luga River, village of Staritsa; Aruküla Horizon. Scale bar, 5 cm.

The branchial plate (Fig. 3) is rounded triangular. Dentin tubercles occur over both dorsal and ventral surfaces. On the dorsal side of the right branchial plate (specimen PIN, no. 220/843), the width of the surface covered by tubercles is approximately equal to the surface lacking tubercles. The boundary between the surfaces forms a notable, slightly curving ledge; the posterior part has an imprint of the cornual plate. The ventral side is covered by dentin tubercles, except for the narrow 1-cm wide rim bordering the internal margin. Dentin tubercles on the dorsal side are larger (7–8 per cm) than those on the ventral side (12–13 per cm).

The cornual plate of this species is unknown. However, it is possible to reconstruct its shape and size by an imprint on the branchial plate. This plate was oval and its lateral margin overlapped the branchial plate.

Ridge scales (Fig. 4) are elongated and triangular. The external side of partially preserved scales (specimens PIN, nos. 220/847 and 220/848) has elongated and high dentin tubercles, with short denticles; occasionally, two neighboring tubercles fuse to form short crests.

Comparison. *Pycnosteus palaeformis* is distinguished from other species of the genus by a simpler plate sculpturing, its dentin tubercles bear short nonbranching denticles, in contrast to *P. pauli* and *P. tuberculatus*, in which the dentin tubercles bear long, and bifurcating or trifurcating denticles. The lateral margin of the branchial plate is weakly convex, while in

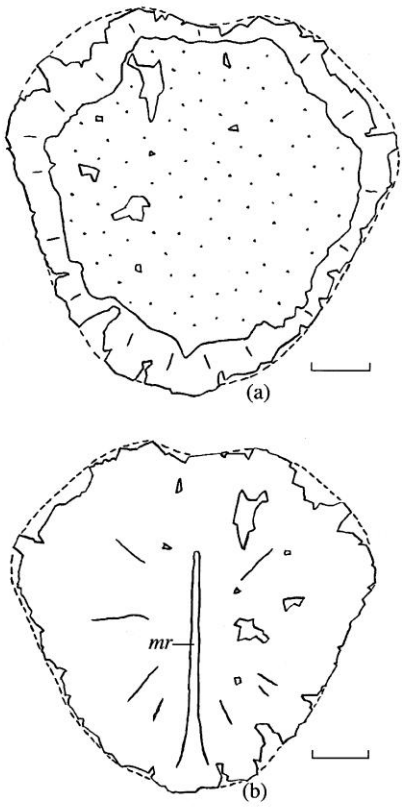

Fig. 2. *Pycnosteus palaeformis*, dorsal plate, specimen PIN, no. 220/844, Leningrad Region, Luga River, village of Staritsa; Aruküla Horizon: (a) dorsally and (b) ventrally. Designations: (*mr*) median ridge. Scale bar, 5 cm.

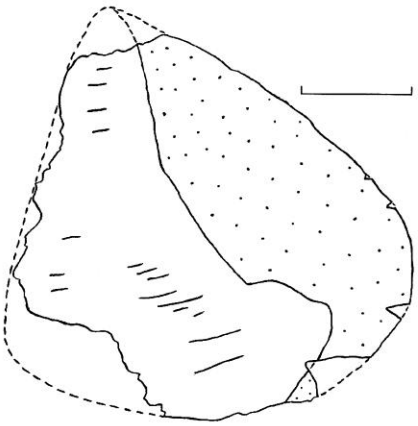

Fig. 3. *Pycnosteus palaeformis*, branchial plate, specimen PIN, no. 220/843; Leningrad Region, Luga River, village of Staritsa; Aruküla Horizon. Scale bar, 5 cm.

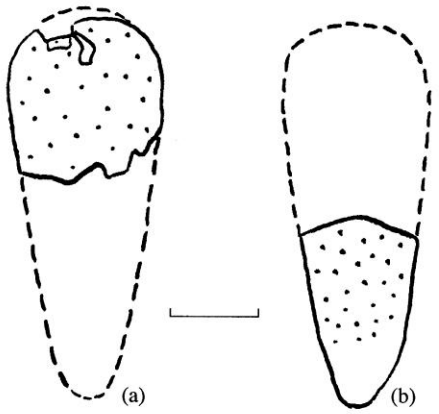

Fig. 4. *Pycnosteus palaeformis*, ridge scales, Leningrad Region, Luga River, village of Staritsa; Aruküla Horizon: (a) specimen PIN, no. 220/848 and (b) specimen PIN, no. 220/847. Scale bar, 1 cm.

P. pauli and, especially, in *P. tuberculatus*, it is concave. The sculptured area on the dorsal side of the branchial plate is wider than or equal to unsculptured area, and in *P. pauli*, it is narrower. On the ventral side, the rim lacking dentin tubercles is significantly narrower than those of the other species. In contrast to other species, the cornual plate overlapped the branchial plate.

Occurrence. Middle Devonian, Eifelian, Aruküla Horison *Pycnosteus palaeformis* Zone; Estonia: Kallaste, Tartu, and Muuga at the Emajõgi River; Peetrijõue at the Reiu River; and Soluveski at the Kõlu River; Russia: Leningrad Region, Novo-Petrovskoe and Siverskaya at the Oredezh River; villages of Kleskushi, Staritsa, and Tverdyat' at the Luga River; and village of Khotnezha at the Lemovzha River.

Material. Complete (specimen PIN, no. 220/844) and fragmentary (specimen PIN, no. 220/845) dorsal plates, the posterior part of the right half of the ventral plate (specimen PIN, no. 220/846), complete branchial plate (specimen PIN, no. 220/843), and two fragmentary ridge scales (specimens PIN, nos. 220/847 and 848).

DISCUSSION

Reconstruction and Functional Interpretation of the Pycnosteus palaeformis armor

Mark (1956, 1961) reconstructed the ventral side and the cross section of the *Pycnosteus palaeformis* trunk. Ridge scales were not shown on the ventral side of the body. However, the ridge scales available in the collection showing wear traces were obviously placed on the ventral side (Fig. 5a). The presence of the dorsal plate makes possible reconstruction of the dorsal side of the animal body (Fig. 5b).

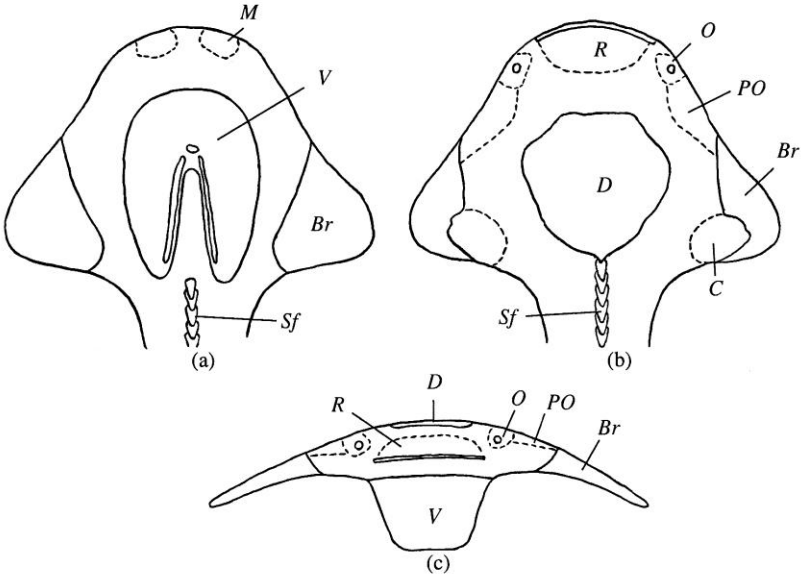

Fig. 5. *Pycnosteus palaeformis*, reconstruction: (a) ventrally (after Mark, 1961, complemented); (b) dorsally; and (c) frontally. Designations: (*D*) dorsal, (*V*) ventral, (*R*) rostral, (*M*) median marginal, (*O*) orbital, (*PO*) postorbital, (*Br*) branchial, and (*C*) cornual plates, and (*Sf*) ridge scale.

The unusual shape of the armor and, especially, the ventral side of the *Pycnosteus palaeformis* trunk provokes discussion on the functional interpretation of the armor features. The ventral plate of this species is strongly convex; consequently, the mouth opening was lifted high above the ground surface (Fig. 5c). Such shape of the ventral plate and position of the mouth indicate a special position of *Pycnosteus* among other psammosteids, traditionally considered to be bottom dwelling animals (Obruchev and Mark-Kurik, 1965).

Studies of hydrodynamic properties of heterostracans determined by external morphology of their armor were performed by Aleev and Novitskaya (1983). These researchers demonstrated the swimming mode of these animals by the examples of amphiaspids (genera *Eglonaspis* and *Olbiaspis*) and cyathyaspids (genus *Poraspis*) models. On raising from the sea bottom along an arched ascending trajectory, using the tail as a propelling source, the animal moved down, with its armored anterior part of the body sinking faster than the tail. As a result, the rostral part soon became directed downwards. Subsequently, the propelling tail either started functioning again and the arched ascending movement repeated or the animal landed on the bottom. Living anuran larvae were used as ecological and ethological analogues.

Dineley (1994) regarded the osteostracan cornua as lifting surfaces used by these animals for gliding swimming. Probably, the same function was also performed by the psammosteid branchial plates, the latter being wider than the osteostracan cornua. The same character distinguishes psammosteids (especially pycnosteids) from cyathaspids and amphiaspids (Fig. 6). The presence of such plates suggests long gliding in water, in contrast to fast movement to the bottom of the animal after the tail fin stopped moving, as was shown by Aleev and Novitskaya (1983) for cyathaspids and amphiaspids.

Belles-Isles (1987) demonstrated by the example of the Recent Scombridae that the swimming type of fish is, in many respects, determined by the relative positions of the gravity center and the hydrostatic center.

The cross section of the *Pycnosteus palaeformis* body suggests that, in this animal, the hydrostatic center was placed above the gravity center (Fig. 6a). The gravity center of *P. palaeformis* was placed lower than those of other psammosteids at the expense of the strongly convex ventral side of the trunk. The distance between these centers in *P. palaeformis* is also larger than in other psammosteids (Fig. 6); this indicates a better stability in water.

The armor of *Pycnosteus palaeformis* is comparable in shape to the deltaplane (Figs. 5c and 6a) designed for gliding flight. Thus, the relative positions of the hydrostatic and gravity centers, deltaplane-like shape of armor, wide branchial plates serving as lifting surfaces, and strongly convex ventral plate functioning as a keel suggest the ability of *P. palaeformis* for longer swimming in water than in other heterostracans. Such long gliding might be realized in searching for food, possi-

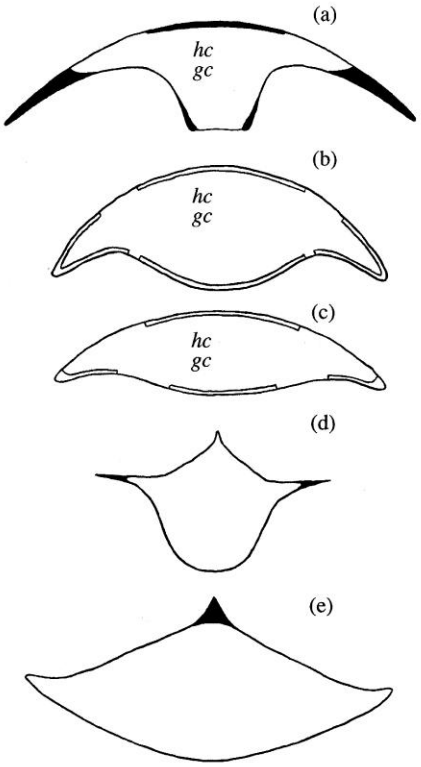

Fig. 6. Cross section of trunks in various Heterostraci: (a) *Pycnosteus palaeformis*; (b) *Drepanaspis gemuendenensis*; (c) *Psammosteus megalopteryx*; (d) *Siberiaspis plana*; and (e) *Pelaspis teres*; (a) from Mark, 1961, complemented; (c) after Tarlo, 1961; and (d, e) after Novitskaya, 1971. Designations: (*gc*) gravity center and (*hc*) hydrostatic center. The position of centers are hypothetical.

bly plankton. The presence of a band of eroded dentin tubercles on the ventral plate may be a result of staying on the bottom, for example, during rest.

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REFERENCES

Aleev, Yu.G. and Novitskaya, L.I., Experimental Research of Hydrodynamic Characters of Devonian Heterostracans, *Paleontol. Zh.*, 1983, no. 1, pp. 3–12.

Belles-Isles, M., La nage et l'hydrodynamique de deux Agnathes du Paléozoïque: *Alaspis macrotuberculata* et *Pteraspis* rostrata, *Neues Jahrb. Geol. Paläontol. Abh.*, 1987, vol. 175, no. 3, pp. 347–376.

Dineley, D.L., Cephalaspids from the Lower Devonian of Prince of Wales Island, Canada, *Palaeontology*, 1994, vol. 37, part 1, pp. 61–70.

Gross, W., Die Fische des mittleren Old Red Sudlivlands, *Geol. Paläontol. Abh.*, 1930, vol. 22 (n. f. 18), no. 2, pp. 123–156.

Gross, W., Die Fische des Baltischen Devons, *Palaeontographica*, A, 1933, vol. 79, pp. 1–98.

Mark, E.Yu., On the Genus *Pycnosteus* (Psammosteidae, Agnatha), *Tr. Inst. Geol. Akad. Nauk Eston. SSR*, 1956, no. 1, pp. 74–88.

Mark, E., Mõningatest kohastumisnähtustest psammosteiididel (Certain Adaptation Phenomena in the Psammosteids), *Geol. Märkmed*, 1961, no. 1, pp. 30–34.

Mark-Kurik, E., New Finds of Psammosteids (Heterostraci) in the Devonian of Estonia and Latvia, *Izv. Akad. Nauk Eston. SSR, Ser. Khim. i Geol.*, 1968, vol. 17, no. 4, pp. 409–424.

Mark-Kurik, E., Multifunctionality of Pleromin in Psammosteid Heterostracans, *Izv. Akad. Nauk Eston. SSR, Ser. Geol.*, 1984, vol. 33, pp. 169–171.

Mark-Kurik, E., On the Environment of Devonian Fishes, *Proc. Estonian Acad. Sci., Geol.*, 1991, vol. 40, no. 3, pp. 122–125.

Mark-Kurik, E., Functional Aspects of the Armor in the Early Vertebrates, in *Fossil Fishes as Living Animals*, Mark-Kurik, E., Ed., Tallinn: Academia, 1992, pp. 107–115.

Mark-Kurik, E., Trophic Relations of Devonian Fishes, *Geobios*, 1995, Mém. spec., no. 19, pp. 121–123.

Novitskaya, L.I., Microstructure of Some Psammosteida, Obruchev, D.V. and Mark-Kurik, E.Yu., *Psammosteidy (Agnatha, Psammosteidae) devona SSSR* (Psammosteids (Agnatha, Psammosteidae) in the Devonian of the USSR), Tallinn: Inst. Geol. Akad. Nauk Eston. SSR, 1965, pp. 257–282.

Novitskaya, L.I., Les Amphiaspides (Heterostraci) du Dévonien de la Sibérie, *Cahieres Paléontol.*, Paris: CNRS, 1971.

Obruchev, D.V., Description of Four New Fish Species from the Leningrad Devonian, *Materialy TsNIGRI, Paleontol. i Stratigr.*, 1933, vol. 1, pp. 12–15.

Obruchev, D.V., On Some Psammosteids of the Leningrad and Baltic Devonian, *Dokl. Akad. Nauk SSSR*, 1940, vol. 28, no. 8, pp. 766–768.

Obruchev, D.V., Materials on Devonian Fishes of the USSR, *Tr. Paleontol. Inst., Akad. Nauk SSSR* (Moscow), 1941, vol. 8, vol. 4, pp. 3–52.

Obruchev, D.V., On the Genus *Psammosteus* (Heterostraci), *Dokl. Akad. Nauk SSSR*, 1947, vol. 56, no. 5, pp. 517–520.

Obruchev, D.V., The Genus *Tartuosteus* (Psammosteidae) from the Middle Devonian of the Baltic Region, *Paleontol. Zh.*, 1961, no. 2, pp. 107–111.

Obruchev, D.V. and Mark-Kurik, E.Yu., *Psammosteidy (Agnatha, Psammosteidae) devona SSSR* (Psammosteids (Agnatha, Psammosteidae) in the Devonian of the USSR), Tallinn: Inst. Geol. Akad. Nauk Eston. SSR, 1965.

Preobrazhensky, I.A., On Some Members of the Family Psammosteidae, *Ad. Protokoly O–va Estestvoispyt. Yurievskogo Un-ta*, 1911, vol. 19, nos. 3–4, pp. 21–36.

Tarlo, L.B., Psammosteids from the Middle and Upper Devonian of Scotland, *Quart. J. Geol. Soc. London*, 1961, vol. 117, no. 2, pp. 193–213.