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A NEW MIDDLE DEVONIAN (GIVETIAN) PSAMMOSTEID (VERTEBRATA: HETEROSTRACI) FROM POLAND

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Abstract: A new genus and species of psammosteid heterostracan, *Psarkosteus mediocris* gen. et sp. nov., is described from the Middle Devonian (Givetian) of the Skały Formation, the Holy Cross Mountains, Poland. The dorsal plate of *Psarkosteus* is constricted in its anterior part and the postorbital plate is long and narrow. Both features, along with the morphology and variety of tubercles, distinguish it from other representatives of the group. Most distinctive are big, teardrop-shaped tubercles, each with a flat or slightly concave surface and with its tip directed posteriorly, and a crenulated base, located along the branchial plates. The lateral line system in *Psarkosteus* is similar to that of *Drepanaspis gemuendenensis* and confirms earlier reconstructions.

Key words: Pteraspidomorphi, Heterostraci, Psammosteidae, Middle Devonian, Holy Cross Mountains.

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INTRODUCTION

The fossil record of the Heterostraci is poor in Poland, although fossils are known from Upper Silurian, Lower and Middle Devonian deposits. From a core sample of the Upper Silurian (Přidoli) succession in Mielnik a representative of the Tolypelepididae was described (Dec, 2015). Some basal heterostracan groups (Traquairaspididae and Cyathaspididae) have been described from Lower Devonian drill cores in Poland. A rich vertebrate assemblage from Emsian sandstones in the Holy Cross Mountains (Podłazie Hill and Bukowa Hill) includes fish remains belonging to the sarcopterygians, osteichthyans, acanthodians, placoderms and ostracoderms (*sensu* Janvier, 1996a). The latter comprise two pteraspidiform groups, the Pteraspididae with *Rhinopteraspis sanctacrucensis* (Tarlo) and Psammosteidae with *Guerichosteus kozlowskii* Tarlo and *Hariosteus kielanae* Tarlo (for details, see Dec, 2019). The specimens are curated in the Institute of Palaeobiology of Polish Academy of Sciences with specimen numbers cited in the text.

PHYLOGENETIC BACKGROUND

In the present account, psammosteids are considered to represent the family Psammosteidae (*sensu* Janvier, 1996b; Pernègre and Elliott, 2008; Randle and Sansom, 2017a, b) which generally is regarded as monophyletic and allied to the Pteraspidiformes (Blieck, 1984; Blieck and Elliott, 2017; Glinskiy, 2018). The main problem is concerned with their relationships within the Pteraspidiformes. The Psammosteidae were supposed to be (1) a sister group to the pteraspids *s.l.*, that is Protopteraspididae + Pteraspididae *s.l.* (in Blieck, 1984), or (2) a sister group to solely the Protaspididae (*sensu* Blieck, 1984; Janvier, 1996a), or (3) a derived clade within the Pteraspidiformes, with Pteraspididae (‘pteraspidids’) as a sister group (Blieck *et al.*, 1991; Janvier, 1996b).

The phylogenetic relationships within psammosteids were studied by several authors (Tarlo, 1964; Obruchev and Mark-Kurik, 1965, 1968). Tarlo (1965) considered that the ‘main lineage’ of psammosteids diverged from *Guerichosteus kozlowskii*. Glinskiy (2018) compiled the findings of earlier authors about in-group relationships and proposed the phylogenetic analysis of the group, in which *Drepanaspis* and *Guerichosteus* are basal to all other psammosteids. The most recent study (Dec, 2019) of *Guerichosteus* shows its close affinity to *Drepanaspis,* while features of *Hariosteus* indicate its affinity to younger genera, such as *Pycnosteus.*

MATERIAL AND GEOLOGICAL SETTING

The material described here was obtained from an outcrop located to the east of Śniadka village, on the left bank of Psarka River and south of the entrance of the ravine called Sitka (Fig. 1). It comprises limestone and marly and clayey shales, representing the upper part of the Skały Formation (Sobolev, 1909; Kłossowski, 1985; Woroncowa-Marcinowska, 2012). The sedimentary structures on the layer surfaces show that the strata in the exposed section are overturned (Kłossowski, 1985). This lithostratigraphic unit is a part of the Świętomarz-Śniadka section, located in the NE of the Holy Cross Mountains, in the Łysogóry Mountains (Fig. 1A, B). The interpretation of the geological cross-section of the central part of the Bodzentyn Syncline, located between Świętomarz and Śniadka and exposed along the Psarka River, has been investigated by many authors: Sobolev (1909), Mizerski (1981), Kłossowski (1985), Turnau and Racki (1999), Malec (1993), Halamski (2005), Halamski and Segit (2006), and Woroncowa-Marcinowska (2012). Most of the discussion concerned the tectonic and stratigraphic interpretation of this site (Turnau and Racki, 1999; Woroncowa-Marcinowska, 2012). The clastic influx represented by these sediments shows a terrigenous influence from the north (Kłossowski, 1985; Racki, 1997).

The layer with psammosteids is located (Fig. 2) just below the goniatite horizon and corresponds with the *rhenanus/varcus* Conodont Zone (Woroncowa-Marcinowska, 2012) that in standard conodonts zonation is correlated with the Lower *varcus* Zone (Narkiewicz and Bultynck, 2007). A sedimentological analysis made by Kłossowski (1985) shows relatively shallow-water conditions, which have been confirmed by the assemblage analysis of the fauna including conodonts, bivalves, gastropods and brachiopods (Dzik, 2002).

The ichnofossil *Alpetria sanctacrucensis* Orłowski and Radwański, 1986, interpreted as a sea-anemone burrow, also indicates a shallow, sublittoral environment. Furthermore, they indicate hydrodynamic agents, such as currents or waves, as being responsible for the rapid burial of the organisms (Orłowski and Radwański, 1986).

Most of the collection was obtained by Magdalena Borsuk-Białynicka in 1978–1979, but during fieldwork in 2012–2013 new material was collected by the present author. The psammosteid remains at Śniadka occur in marly and clayey shales. All specimens are flattened; moreover, some are deformed (stretched, foliated). Most of the fossiliferous material was found in one horizon, below the part with the cephalopod fauna, and preserved as isolated plates. In some cases, plates were associated with accumulations of scales (Fig. 2).

The rock matrix with specimens was impregnated with dilute cyanoacrylic in order to prevent fracture due to the drying of the slab. The specimens were cleaned mechanically and brushed with detergent. The procedure was repeated until the desired result was obtained.

For photographic purposes, the specimens were coated with ammonium chloride.

SYSTEMATIC PALAEONTOLOGY

Class Pteraspidomorphi Goodrich, 1909
Subclass Heterostraci Lankester, 1868
Order Pteraspidiformes Berg, 1937
Family Psammosteidae Traquair, 1896
Genus *Psarkosteus* gen. nov.

Type and only species: *Psarkosteus mediocris* gen. et sp. nov.
Etymology: In reference to the type locality near the Psarka River.
Diagnosis: As for the type species. The genus is monotypic.

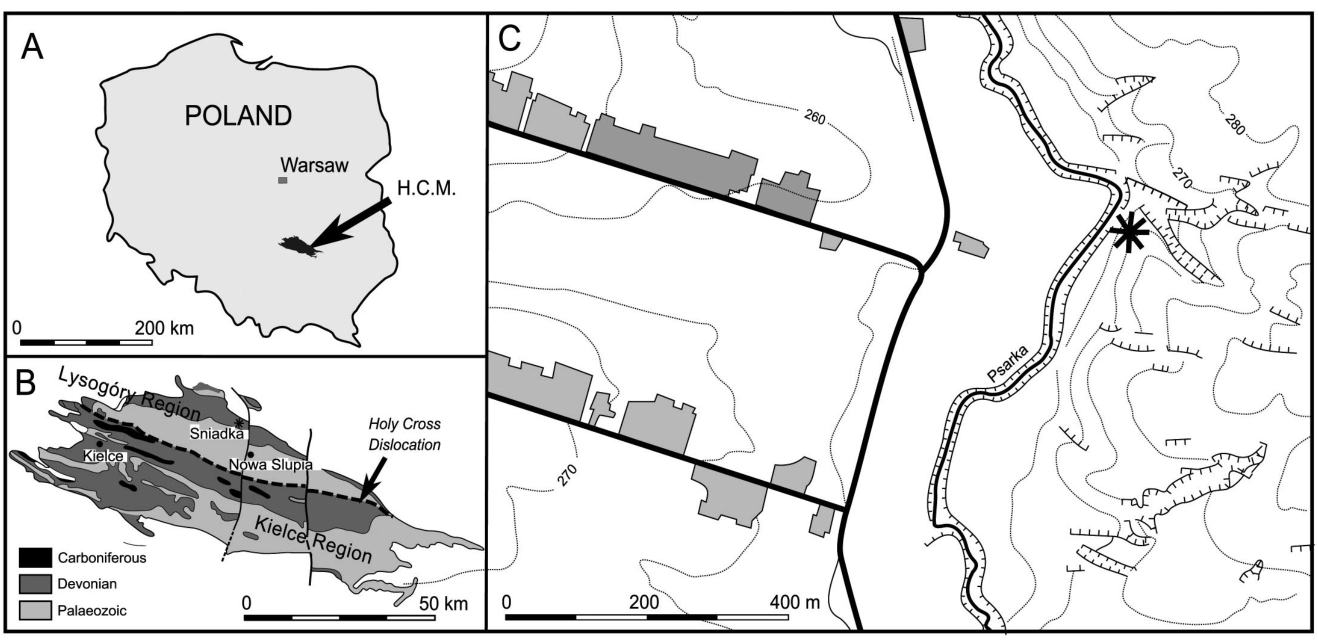

Fig. 1. Map showing the location of: **A.** Holy Cross Mountains (HCM). **B.** Śniadka in HCM. **C.** Collection site on the left bank of the Psarka River.

Psarkosteus mediocris gen. et sp. nov.

Etymology: From Latin *mediocris*, in reference to its moderate size.
Holotype: Dorsal plate ZPAL Ag–I/32 (Figs 3A, 9A)
Reference material: ZPAL Ag. I/1.1 (Figs 5A, 11), ZPAL Ag. I/1.2 (Fig. 3E), ZPAL Ag. I/2 (Fig. 4E), ZPAL Ag. I/3 (Fig. 4A), ZPAL Ag. I/4 (Figs 4B, 10B), ZPAL Ag. I/5 (Fig. 5B), ZPAL Ag. I/6 (Figs 6E, 7E), ZPAL Ag. I/7 (Figs 6B, 7B, 12B), ZPAL Ag. I/8 (Figs 4C, 10A), ZPAL Ag. I/9 (Fig. 5C), ZPAL Ag. I/10 (Fig. 3D), ZPAL Ag. I/11 (Fig. 6A), ZPAL Ag. I/12 (Figs 6C, 7C), ZPAL Ag. I/15.1 (Fig. 8E), ZPAL Ag. I/15.2 (Fig. 8F), ZPAL Ag. I/15.3 (Fig. 8D), ZPAL Ag. I/16 (Fig. 8G), ZPAL Ag. I/17.1 (Figs 6G, 7G), ZPAL Ag.

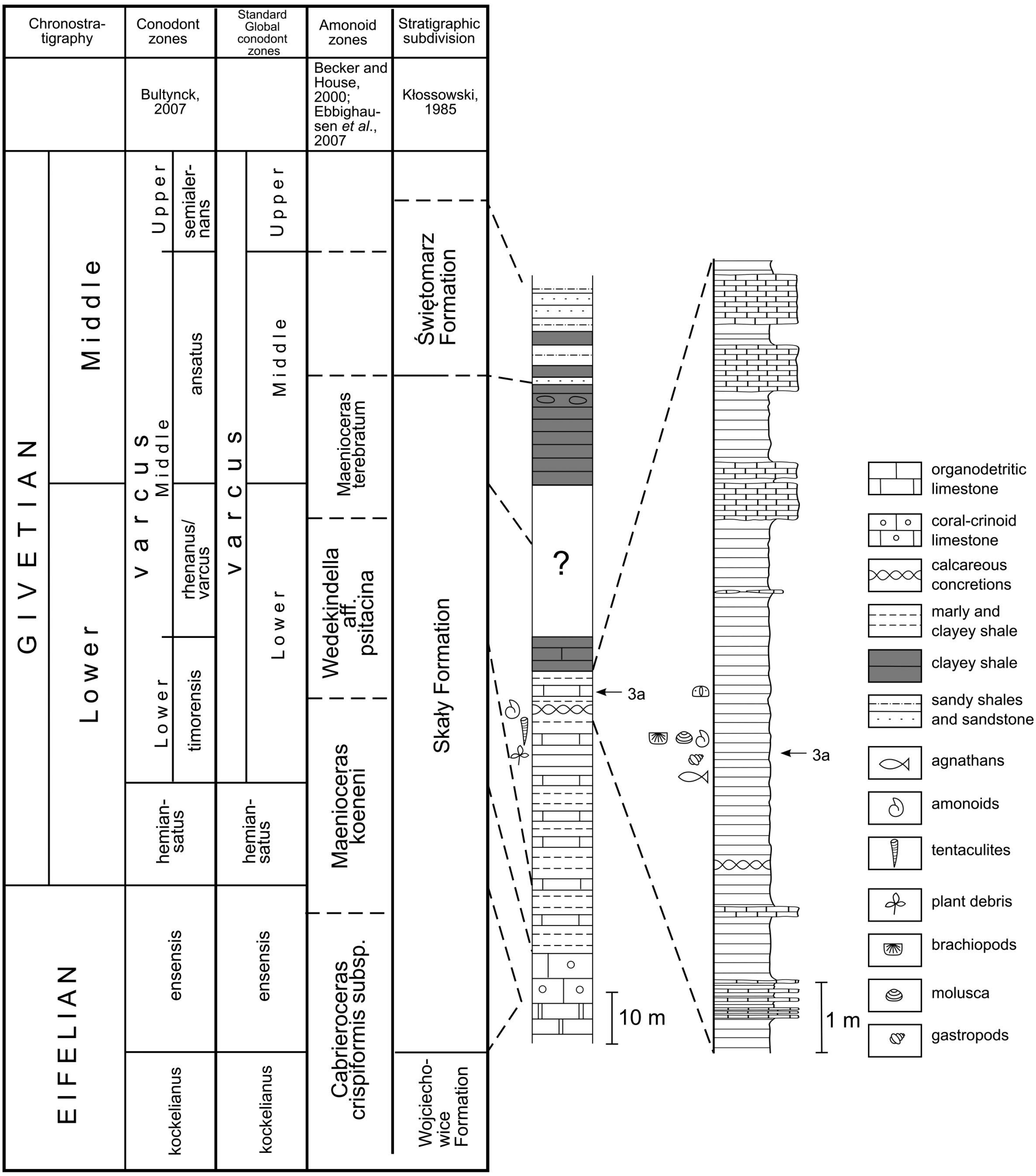

Fig. 2. Stratigraphical location of the psammosteids-bearing level with the geological column in part of the Skały Formation at the locality shown in Figure 1C.

I/17.2 (Figs 6F, 7F, 12A), ZPAL Ag. I/18 (Figs 6H–J, 7H–J), ZPAL Ag. I/19 (Fig. 3C), ZPAL Ag. I/20 (Fig. 4D), ZPAL Ag. I/22 (Fig. 8A), ZPAL Ag. I/23 (Fig. 8B), ZPAL Ag. I/26 (Fig. 8C), ZPAL Ag. I/31 (Figs 3B, 9B, 14D), ZPAL Ag. I/32 (Figs 3A, 9A, 14C),

Type locality: Śniadka, outcrop located on the left bank of the Psarka River, south of the entrance of the Sitka Ravine (GPS coordinates 50°57'32.4"N 21°00'51.6"E). The village is in the administrative district of Gmina Bodzentyn, within Kielce County, Świętokrzyskie Voivodeship, in south-central Poland (Fig. 1).

Stratigraphical occurrence: Middle Devonian (Givetian) Skały Formation, Lower *varcus* conodont Zone.

Occurrence: Middle Devonian (Givetian) Skały Formation, the conodot Lower *varcus* Zone. Locality: Śniadka, the outcrop located on the left bank of the Psarka River, south of the entrance of the Sitka Ravine (Fig. 1).

Diagnosis: Relatively medium-sized species (up to 16 cm in dorsal plate length). Dorsal plate is elongated, with an elliptical shape (width ratio 1.5–1.8). It differs from that in other psammosteids in constriction of its anterior part. Ventral plate oval in shape with a deep posterior notch that almost reaches the growth centre, located posterior to mid-length of the plate. Postorbital plates triangular and slender. Branchial plates narrow, triangular in shape with convex lateral edge; ornamented part of the dorsal surface relatively narrow. The distinctive big teardrop-shaped tubercles with flat or slightly concave surface and well-developed basal crenulation extend along the lateral margin of the branchial plates.

Description: Dorsal plate. Two complete specimens ZPAL Ag. I/31–32 and three partially preserved specimens ZPAL Ag. I/1.2, 10, 19, were recognized (Fig. 3). The large plate (ZPAL Ag. I/32) is elongated, with an elliptical shape (l:w = 1.48). Its length is 15.8 cm, measured along the central axis of the plate, the maximum width 10.7 cm, at the level of growth centre. The specimen has its anterior margin broadly rounded with front part of the plate (2.3 cm in length) narrowed to 7.8 cm in width. The lateral margin turns posteriorly over right angle, diverge strongly to maximum width, and extend parallel by a certain length (about 5 cm). From about ⅔ of its length the plate tapers, its lateral margins turning posteriorly at an angle of 75°. The distal end is pointed. The plate bears well marked growth lines that surround the growth centre situated a little in front, 7 cm from the anterior margin.

Two dorsal plates of small individuals ZPAL Ag. I/31 (Fig. 3B) and ZPAL Ag. I/10 (Fig. 3D) are considered as juvenile. The former is complete, 6.4 cm in length and 3.6 cm in width (l:w = 1.8), with the same overall shape as in the largest specimen, but much more slender. The second one is incomplete and looks wider than the former, but the margins of the plate are damaged. The length of the preserved part is just 5.3 cm and its width is 5.3 cm, but the shape of the plate can be restored (Fig. 3D) on the basis of the growth lines visible around the centre of growth. The estimated length-to-width ratio of the plate is 1.2.

Ventral plate. Five incomplete specimens ZPAL Ag. I/2–4, 8, 20 are known (Fig. 4). The largest specimen ZPAL Ag. I/3 represents a central and right part of a plate and measures 13.3 cm in length (on more complete natural mould 16.3 cm in length) and 11.6 cm in width (Fig. 4A). Most edges are broken-off; only the margin of the posterior notch is preserved, but the growth lines are clearly visible around the centrally located growth centre. Anterior part of the plate is trapezoidal (Fig. 4A); the plate widens to the middle of the plate and smoothly turns to the posterior notch. Right fragment of ventral plate of small specimen ZPAL Ag. I/8, 4.7 cm in length and 2.1 cm in width (Fig. 4C). It allows estimation of its total width as 4.2 cm. Lateral, posterior margin as well as posterior notch margins are well preserved. Posterior notch extends well into the central area, but it does not reach the growth centre.

Branchial plate. Eight specimens of plates are preserved (Figs 5–7), including two large and near-complete ones (Fig. 7). The first one (ZPAL Ag. I/5) has its postero-lateral corner broken off (Fig. 7B1), while the second one (ZPAL Ag. I/9) is almost complete (Fig. 7C1). As far as the natural mould of the first specimen is preserved, the shape of the plate can be restored. The plate is triangular, its length varies from 58 mm to 150 mm (the largest was probably 190 mm). The lateral margin is convex, the posterior almost straight margin smoothly turns (about 110°) to the straight medial margin. Anterior tip of the plate is best preserved on the specimen ZPAL Ag. I/9 and ZPAL Ag. I/17 (Figs 5E1, 7C1), where the angle between lateral and medial margin is 50° (measured in the most anterior part which is undisturbed). The ZPAL Ag. I/17 specimen has very narrow dorsal surface covered with tubercles, while it is wider and extends posteriorly in the larger specimen ZPAL Ag. I/15 (Figs 5F, 6F). The posterior part of the free surface is visible only on imprints of ZPAL Ag. I/12 (Figs 5C2, 6C2) and ZPAL Ag. I/6–7 (in parts where bone is broken-off), it turns along the lateral margin and tapers to the postero-median corner, so the branchial opening was probably located more medially.

Postorbital plate. Only one, near-complete specimen ZPAL Ag. I/1.1 of a left postorbital plate has been collected (Fig. 7A1). The plate is slender, the maximum length is 13.3 cm. Anterior half of the plate is the widest part, and its width is 3.1 cm. Then, from the mid-length the plate tapers posteriorly. The rounded front edge of the plate smoothly turns into the medial margin. The most anterior lateral part of the plate gradually increases in thickness (from 3 mm to 6 mm) anteriorly but does not bend to internal side. The lateral margin is arched only near the growth centre, about 5.5 cm from the front part of the plate. Anterior and posterior to the growth centre, the lateral margin extends almost straight and the angle between them is 163°. The growth lines run parallel to the medial and front margins of the plate (Fig. 7A).

Scales. Different scales are preserved, varying from small body scales to larger ridge scales (Fig. 8). The small scales are diamond-shaped, with anteriorly placed narrow area (specimen ZPAL Ag. I/22–23; Fig. 8A, B) overlapped by the more anterior scales. The specimen ZPAL Ag. I/26 is triangular (8 mm long and 6 mm high), with an undulate anterior margin of tuberculated area and a narrow anterior area overlapped (Fig. 8C). Four incomplete ridge scales (Fig. 8D–G) are preserved, and only two are near-complete and vary in length from 38 cm (ZPAL Ag. I/16, Fig. 8G) to 70 mm (estimated on the basis of ZPAL Ag. I/15.1, Fig. 8E). The maximum width is up to 26 mm (ZPAL Ag. I/15.1, Fig. 8E).

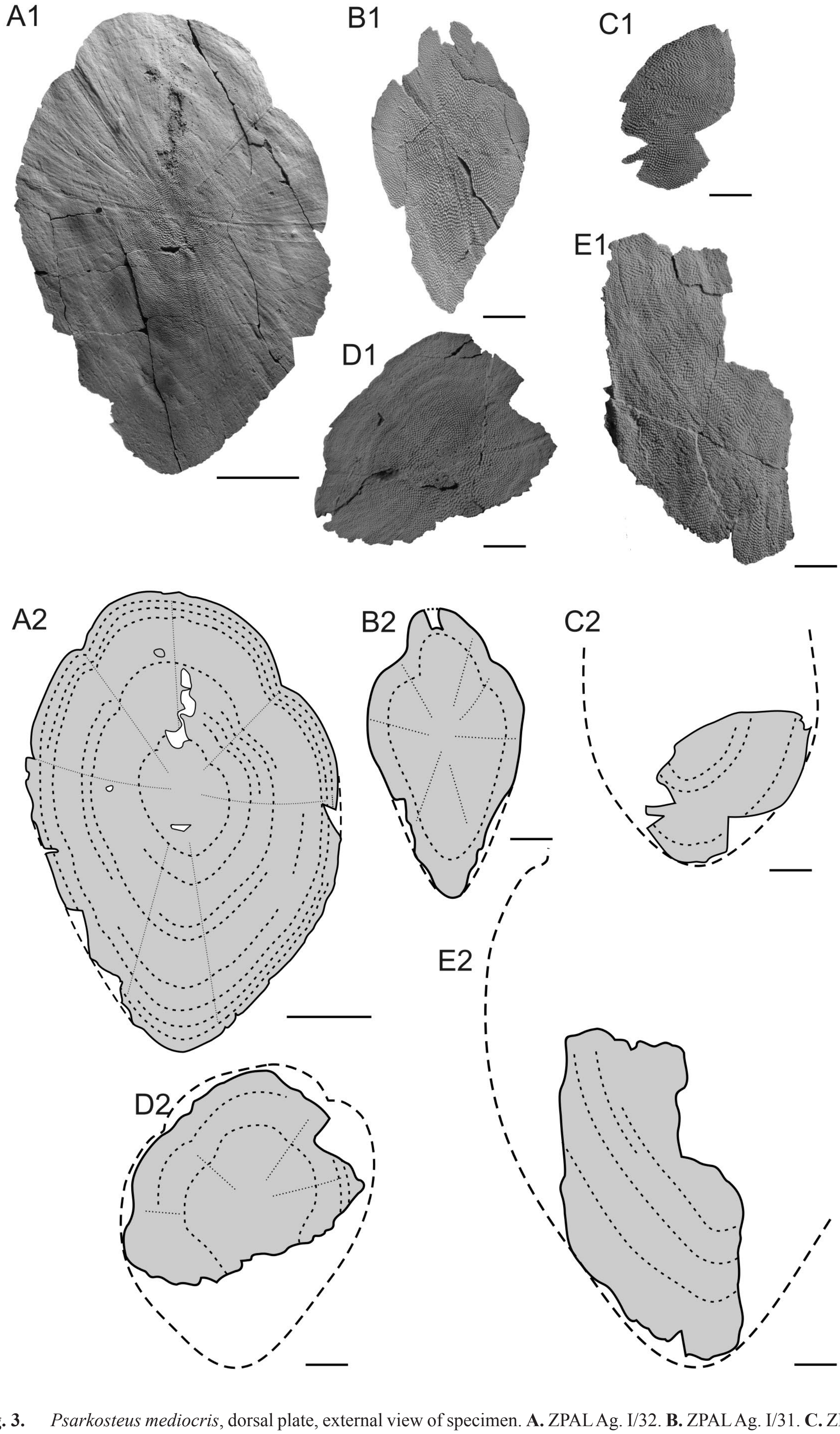

Fig. 3. *Psarkosteus mediocris*, dorsal plate, external view of specimen. **A.** ZPAL Ag. I/32. **B.** ZPAL Ag. I/31. **C.** ZPAL Ag. I/19. **D.** ZPAL Ag. I/10, **E.** ZPAL Ag. I/1.2. **A2–E2.** Specimens drawing with growth line marked (densely dashed line) and lateral line (dotted line). Plate shape restoration marked with loosely dashed line. Scale bar equals 1 cm.

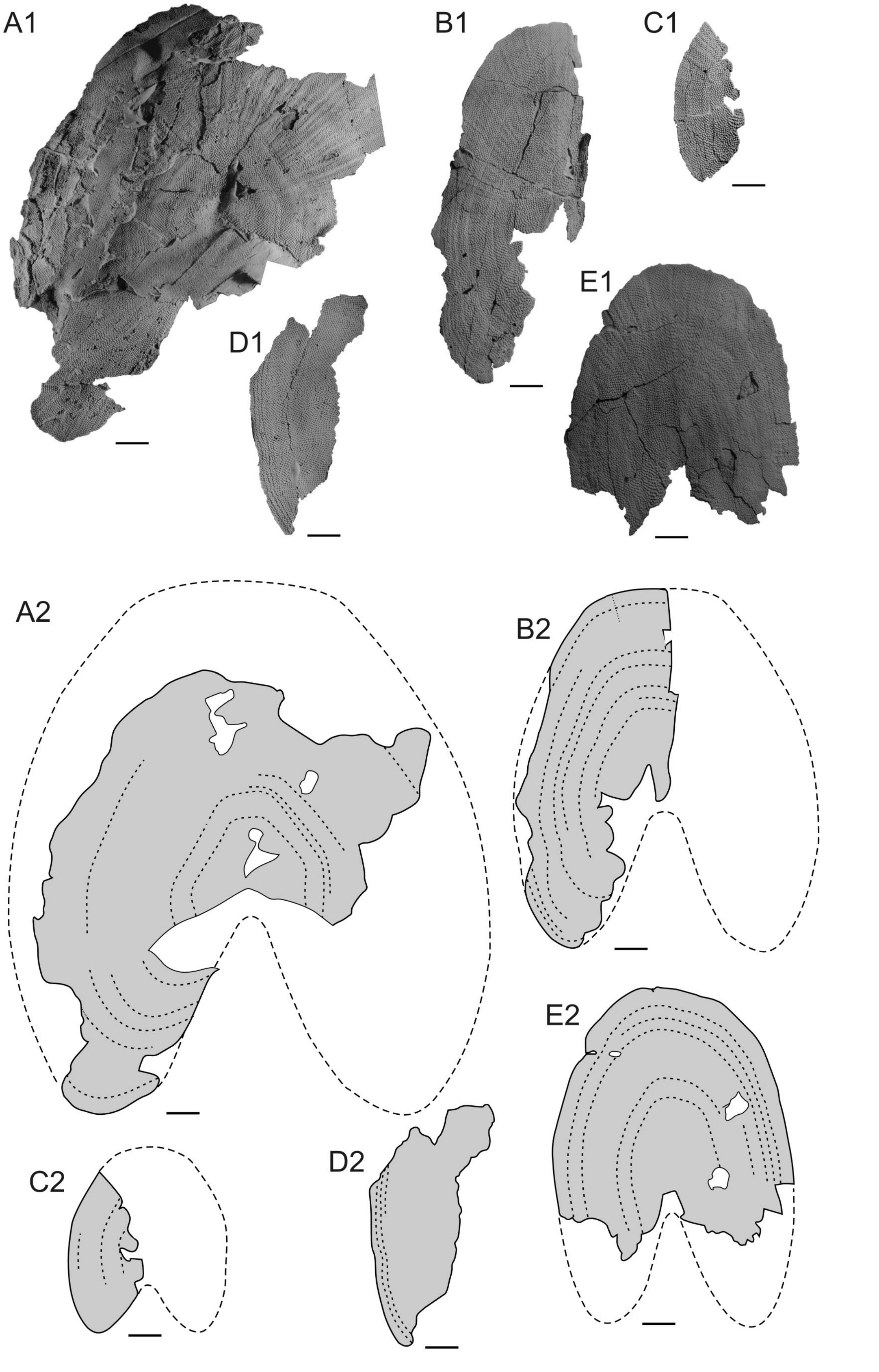

Fig. 4. *Psarkosteus mediocris,* ventral plate, external view of specimen. **A.** ZPAL Ag. I/3. **B.** ZPAL Ag. I/4. **C.** ZPAL Ag. I/8. **D.** ZPAL Ag. I/20. **E.** ZPAL Ag. I/2. **A2–E2**. Specimens drawing with growth line marked (densely dashed line) and lateral line (dotted line). Plate shape restoration marked with loosely dashed line. Scale bar equals 1 cm.

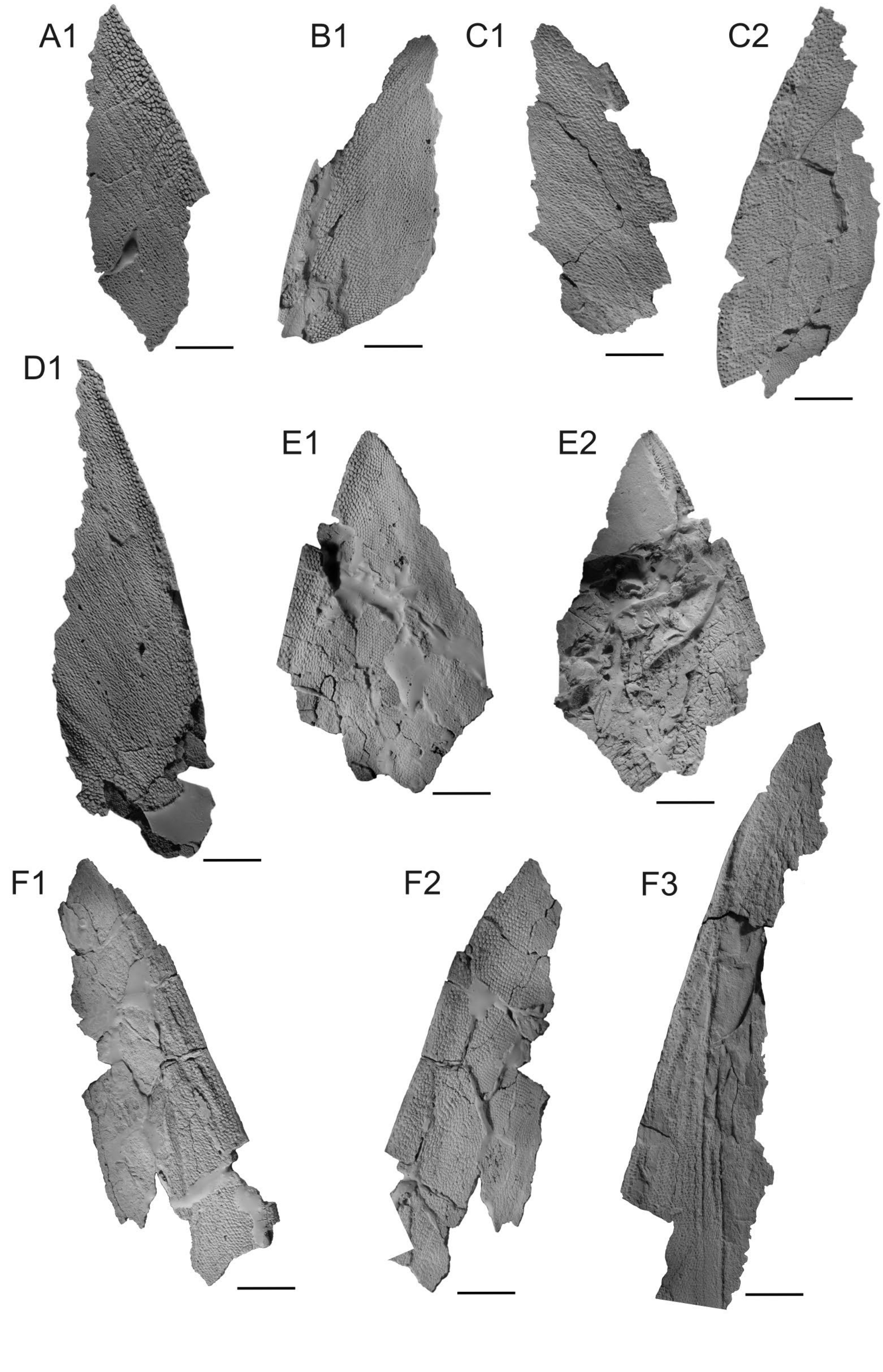

Fig. 5. *Psarkosteus mediocris,* branchial plate, specimen. **A.** ZPAL Ag. I/ 11, ventral view of left branchial plate. **B.** ZPAL Ag. I/7, ventral view of right branchial plate. **C1.** ZPAL Ag. I/12, ventral view of right branchial plate. **C2.** ZPAL Ag. I/12, imprint with small broken fragment of plate where dorsal side with ornamentation is preserved. **D.** ZPAL Ag. I/6, ventral view of left branchial plate. **E.** ZPAL Ag.I/17, right branchial plate: ventral (**E1**) and dorsal (**E2**) views. **F.** ZPAL Ag. I/18, left branchial plate: dorsal (**F1**), ventral (**F2**) and imprint of dorsal (**F3**) views. Scale bar equals 1 cm.

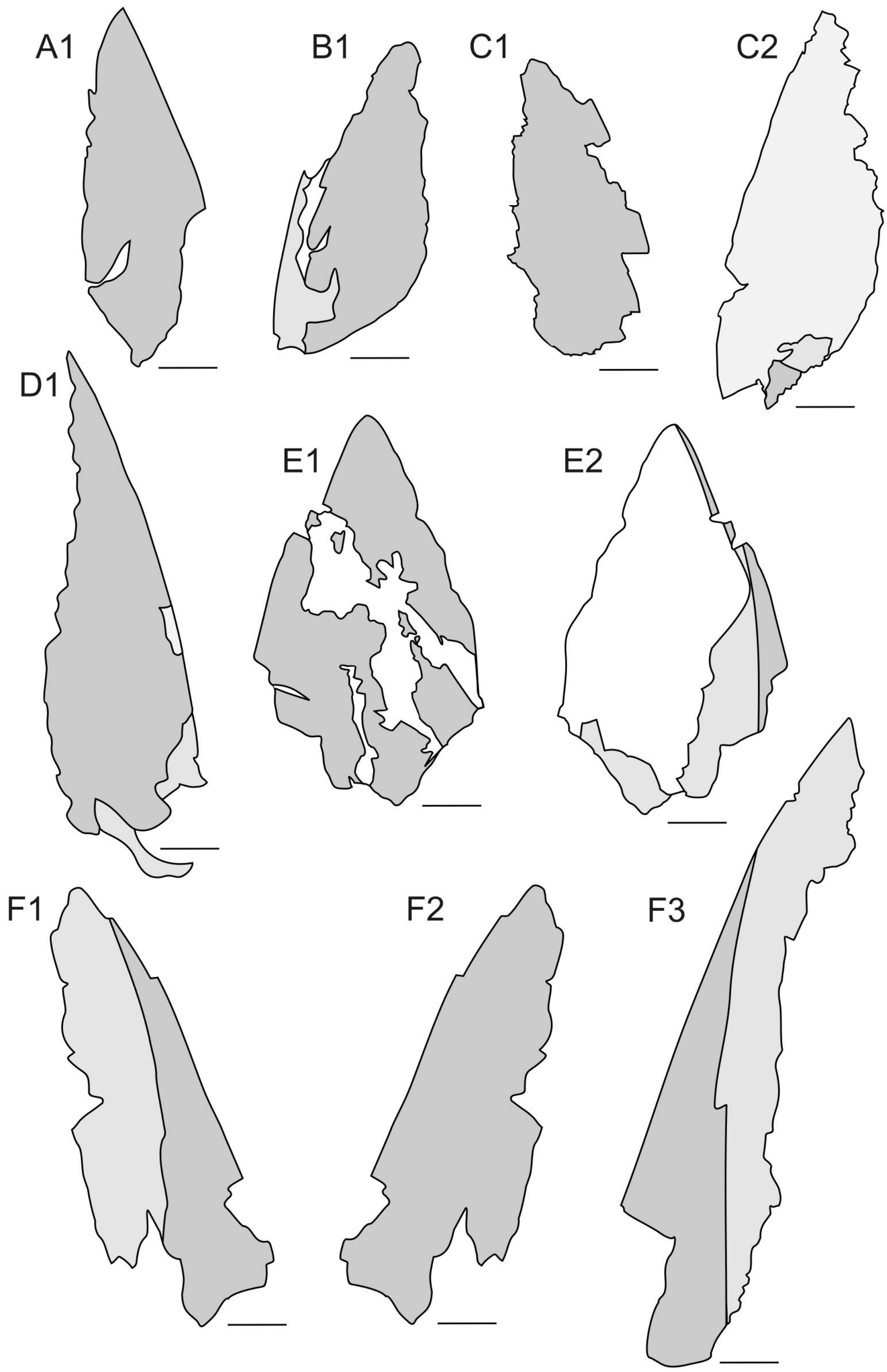

Fig. 6. *Psarkosteus mediocris,* branchial plate, drawings of specimens showed on Figure 5. Scale bar equals 1 cm.

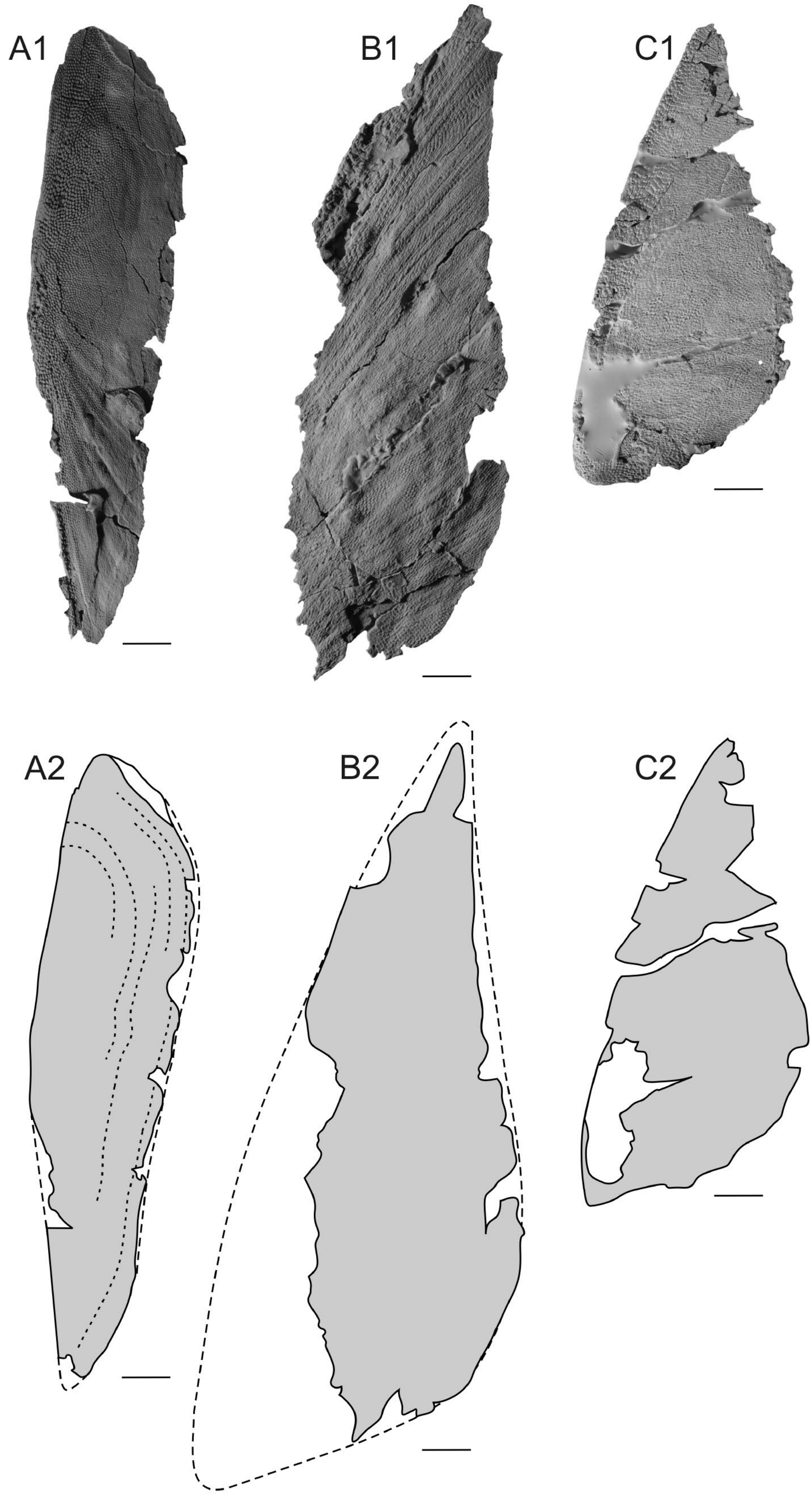

Fig. 7. *Psarkosteus mediocris* gen. et sp. nov. **A.** ZPAL Ag. I/1.1, left postorbital plate, external view. **B.** ZPAL Ag. I/5, ventral view of right branchial plate. **C.** ZPAL Ag. I/9, ventral view of right branchial plate. **A2–C2**. Specimens drawing with growth line marked (densely dashed line) and plate shape restoration marked with loosely dashed line. Scale bar equals 1 cm.

Most specimens are long and slender and the anterior margin, preserved only on the specimen ZPAL Ag. I/15.3, is sinusoidal is also marked by a visible growth line (Fig. 8D2).

Ornamentation. It consists of tubercles that vary in size according to the region of the body and even within individual plates. The ornamentation also depends on the growth stage of the plate. At the growth centres of dorsal and ventral plates, the tubercles are variable in size, generally small (0.60 mm; 17 per cm) and conical, with their tips pointed upwards (Figs 9B2, 10B3). A little away from centre, they are still conical, although the tip is directed posteriorly and they are crenulated at the base (Figs 9B3–4, 10A2, 10B3). Distant from the middle, the tubercles decrease in height (Figs 9A, 10B2) and vary in shape; anteriorly the tubercles are symmetrical and teardrop-shaped with a flat or slightly concave surface, with the tip directed posteriorly. Sides of the plate are covered with asymmetrical tubercles where the tip is directed to the mid-line (Fig. 9A2, A3). Therefore, the

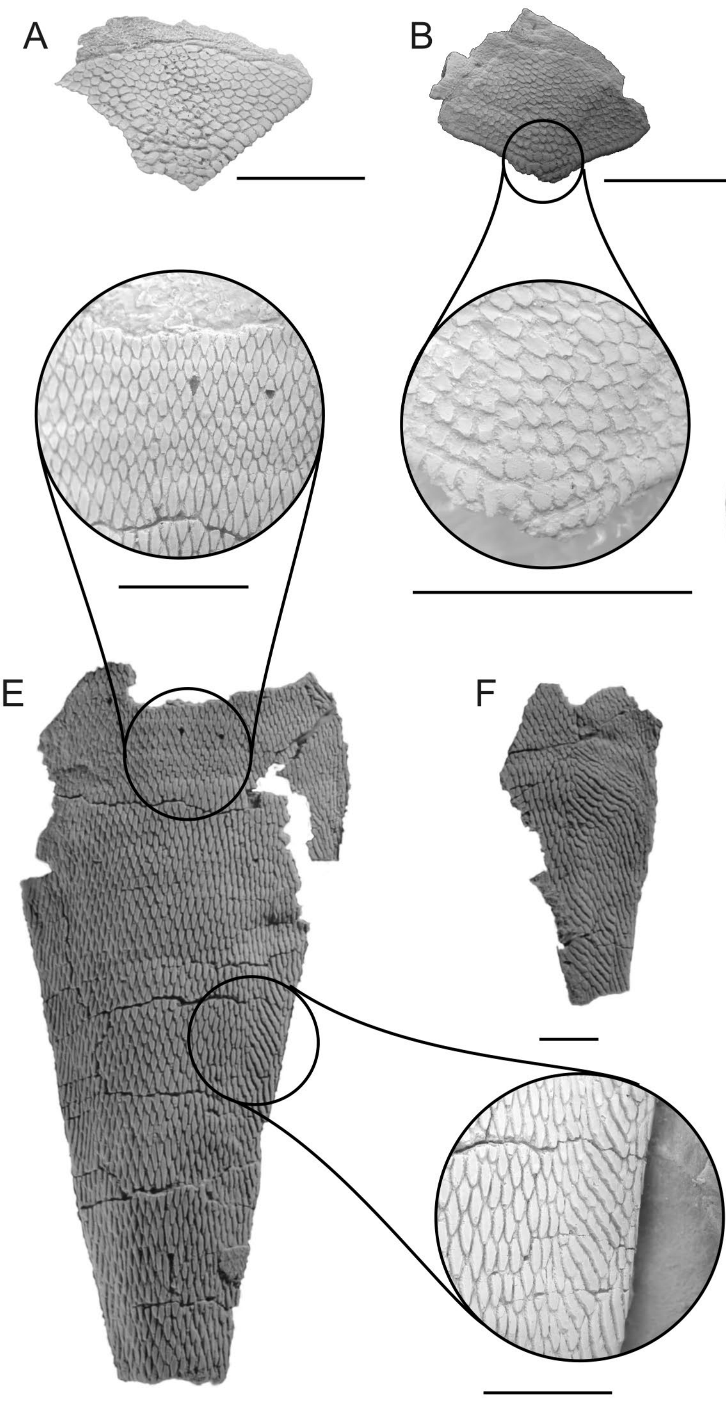

Fig. 8. *Psarkosteus mediocris.* **A.** ZPAL Ag. I/22, body scale. **B.** ZPAL Ag. I/23, body scale with close-up on tubercles. **C.** ZPAL Ag. I/26, body scale. **D.** ZPAL Ag. I/15.3, ridge scale, external view of anterior tip fragment (**D1**) and drawing with growth line marked (**D2** – dashed line). **E**. ZPAL Ag. I/15.1, ridge scale, external view with close-up on tubercles. **F.** ZPAL Ag. I/15.2, ridge scale, external view. **G.** ZPAL Ag. I/16, ridge scale, external view. Scale bar equals 5 mm.

tubercles situated posteriorly to the growth centre, at midline axis, converge inward (Fig. 9B4). The smallest (0.40–0.45 mm; 22–25 per cm) and lowest tubercles are located near the edge of the dorsal and ventral plates, as well as near the medial border of branchial (Fig. 12A4) and postorbital plates (Fig. 11D). In contrast at the lateral (outer) margins of the branchial and postorbital plates, that create the margins of the animal body, the tubercles are the biggest (Figs 11B, 12B2–3). Also anterior to the growth centre, on the postorbital plate, the tubercles are almost fused and show the signs of abrasion of the ornamentation (Fig. 11C). Toward the anterior part of the plate, the tubercles are separated and the tips become slightly less flattened (Fig. 11B). On branchial plates along the lateral edge, the tubercles range from 0.70 to 0.90 mm (11–14 per cm), while decreasing in size toward the anterior tip.

Remarks: *Psarkosteus mediocris* is a medium-sized psammosteid, its size estimation being based on the length of the dorsal plate. It is 15 cm in the largest, whereas it usually reaches 20 cm in other psammosteids. In the Śniadka material, the smallest dorsal plate is 6 cm long and is considered to be a young individual. The elongated dorsal plate of *Psarkosteus* with an elliptical shape has a distinctive anterior constriction (Figs 3, 13A). This shape stands out among psammosteids. With the value 1.5–1.8, the length-to-width ratio of *Psarkosteus* is quite high. In most psammosteids, the value covers a range from 0.7 to 1.3 and only *Psammosteus undulata* (1.4–1.6 length-to-width ratio) falls outside of the range. The overall shape of the dorsal plate of *Psarkosteus* resembles those of *Schizosteus striatus* (Obruchev and Mark-Kurik, 1965, fig. 37), except that growth lines undulate in the latter.

The variability of plates may be related to ontogenetic growth or to individual variation, but other factors, such as diagenetic and tectonic stretching, may also be involved, and probably had a greater impact for the biometric differences. A reconstruction of *Psarkosteus mediocris* that takes into account the above factors is shown on Figure 13. To receive the deep ventral plate, the flat plate reconstruction was printed in natural size and bent, so that the inner margins of the posterior notch were parallel to each other, as they are in psammosteids like *Schizosteus* and *Tartuosteus.*

The very long and narrow postorbital plate is distinctive among Psammosteidae even more than in derived *Psammolepis*.

The general morphology and variety of tubercles presented in *Psarkosteus mediocris* distinguish it from *Schizosteus striatus* and other psammosteids. Most characteristic are tubercles, located along the branchial plate margin. The big, teardrop-shaped tubercles each have a flat or slightly concave surface with clearly visible crenulation of the base. The tips of tubercles are pointed posteriorly.

LATERAL LINE SYSTEM

The heterostracan lateral line system consists of a network of canals, closed in a cancellous layer of dermal bone and connected to the surface by pores. The psammosteid sensory line system was identified by Gross (1963, fig. 3; Fig. 14A) in *Drepanaspis gemuendenensis* dorsal and ventral plates. According to latter author, the ridges radiating from the centre of plate represent sensory line canals. Tarlo (1964) disagreed with this interpretation and considered those ridges as associated with the pattern of the plate growth. Also, Obruchev and Mark-Kurik (1965) did not support the identification by Gross at the time. However, the *Drepanaspis gemuendenensis* material from Rhineland, Germany stored in Tallinn, allowed confirmation of the identification by Gross (Elliott and Mark-Kurik, 2005). *Psarkosteus* gen. nov. (Figs 3, 14C, D) has radial ridges on the dorsal plates, similar to those observed in *Drepanaspis gemuendenensis*, which look like traces of more pronounced distortion. Occasionally, they bear collapsed superficial tubercles that trace the radial lines. Apparently, as a result of the plate compaction, the largest deformation occurred in the weaker parts of plates previously occupied by canals of the sensory line system. The distortion is probably due to tectonic flattening, which is only visible on flattened specimens of *Drepanaspis* or *Psarkosteus* gen. nov. Less deformed plates, such as those seen in *Guerichosteus kozlowskii*, *Tartuosteus maximus* or *Psammolepis venyukovi*, have natural curves and a lack of compaction-related deformation. The deformation is also observed on a specimen in the geological collection at Tallinn University of Technology (GIT 116–51) that contains a dorsal plate of *Schizosteus striatus* (personal observation). Three genera *Drepanaspis*, *Schizosteus* and *Psarkosteus* show the same pattern of four pairs of canals radiating from the growth centre (Fig. 14). The original description by Gross (1963) presented four pair of the sensory canals. The first (dc1) and second (dc2) pair placed in the anterior region, dc1 near the front recces and dc2 placed laterally of the front corner. The two others (dc3 and dc4) are placed in the posterior region, dc3 near the side edges of the plate and the fourth pair dc4 on the side of the rear corners. In *Psarkosteus*, the divergence of the canals is similar to that in *Drepanaspis* (Fig. 14A) and *Schizosteus* (Fig. 14E). However, the dc3 canal is placed more anteriorly than in *Drepanaspis* or *Schizosteus*. On the basis of Elliott and Mark-Kurik's (2005) review of the lateral line sensory system in psammosteids, it can be concluded that dc2 and dc3 canals shown by Gross (1963) correspond to the transverse commissure of *Psammolepis proia* (Fig. 14F). The dc1 and dc4 canals of *Drepanaspis* apparently represent the median dorsal canal of *Psammolepis proia* (Fig. 14F). However, Glinskiy (2018) in figure 2 showed the dc4 canal of *Drepanaspis* as a third transverse commissure (Fig. 14B). He added a medial canal, despite the fact that there is no evidence of one more pair of canals in known *Drepanaspis* remains. Therefore, more probable is the occurrence of one pair of median canals and two oblique commissures that radiate from the growth centre in *Drepanaspis*, *Schizosteus* and *Psarkosteus* dorsal plate. In that state, the dc1, dc4 in the latter genera correspond to the *Psammolepis proia* median canal (mc), and dc2, dc3 to the transverse commissure (tc) shown in Elliott and Mark-Kurik (2005).

DISPERSAL OF PSAMMOSTEIDS

Psammosteids have an exclusively Devonian distribution and are restricted to the coastlines of Laurussia (Fig. 15),

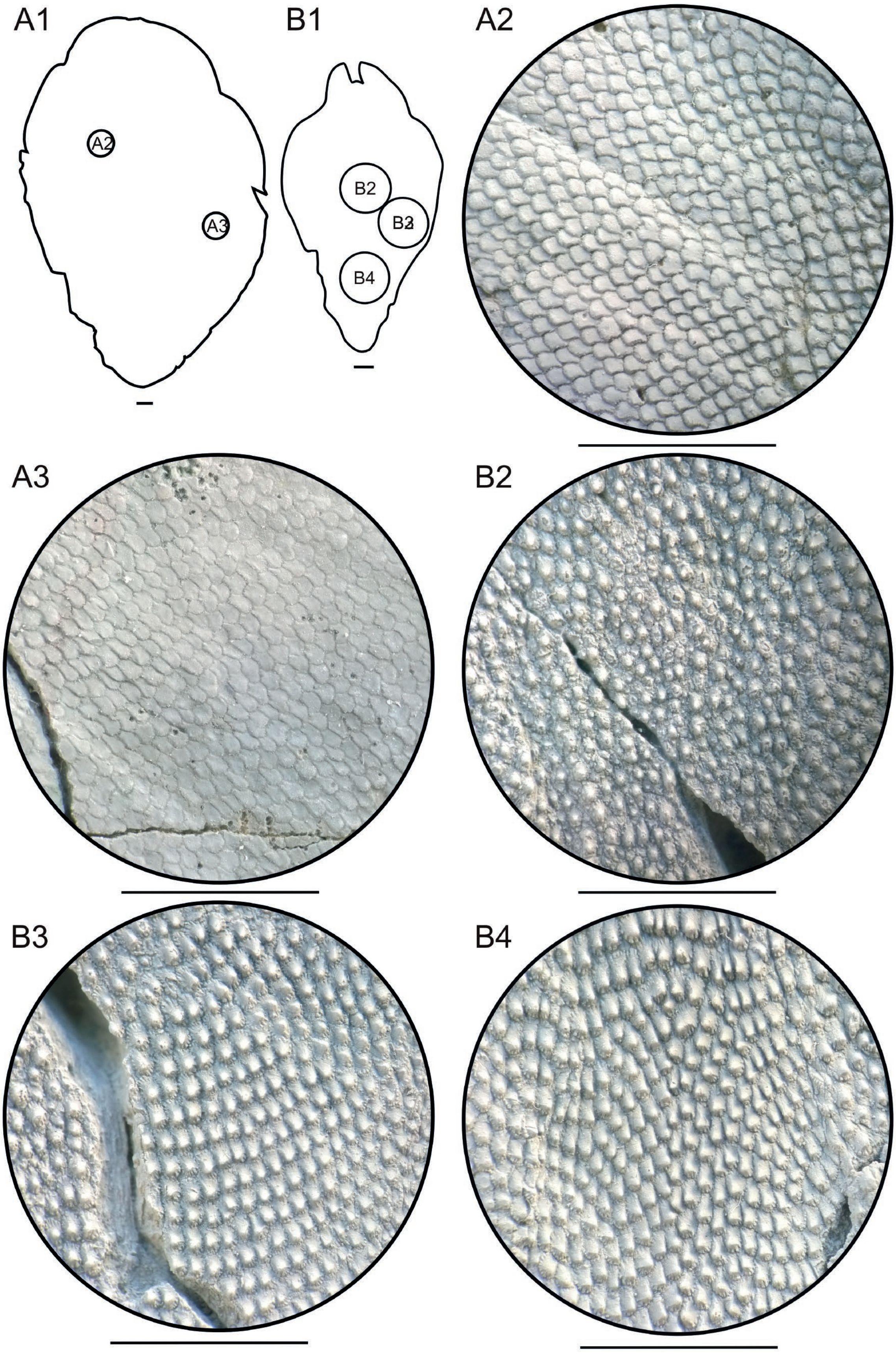

Fig. 9. *Psarkosteus mediocris*. **A1.** ZPAL Ag. I/32, dorsal plate with fragment showing the detail of ornamentation (**A2, A3**). **B1.** ZPAL Ag. I/31, dorsal plate with fragment showing the detail of ornamentation (**B2, B3, B4**). Scale bar equals 5 mm.

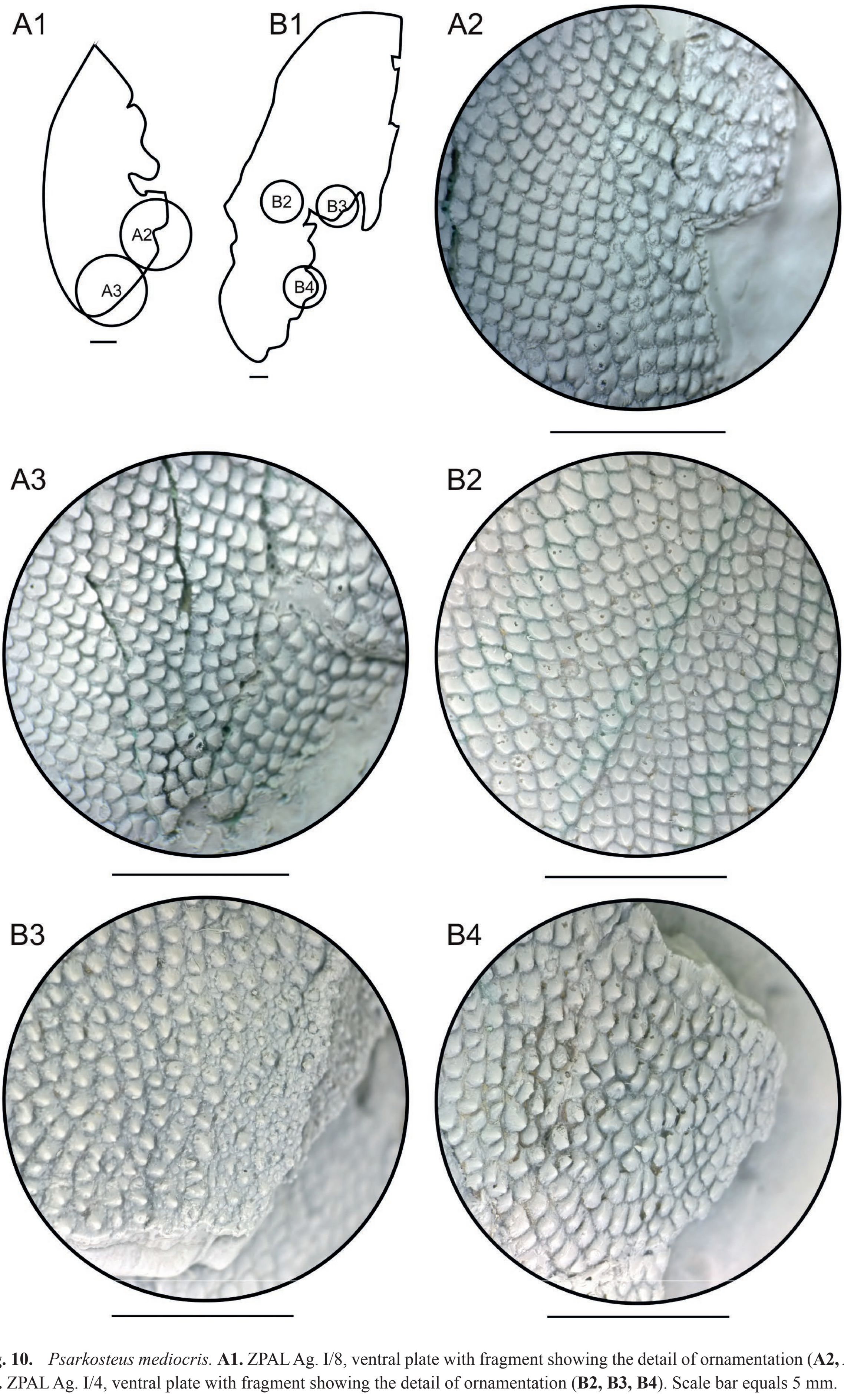

Fig. 10. *Psarkosteus mediocris.* **A1.** ZPAL Ag. I/8, ventral plate with fragment showing the detail of ornamentation (**A2, A3**). **B1.** ZPAL Ag. I/4, ventral plate with fragment showing the detail of ornamentation (**B2, B3, B4**). Scale bar equals 5 mm.

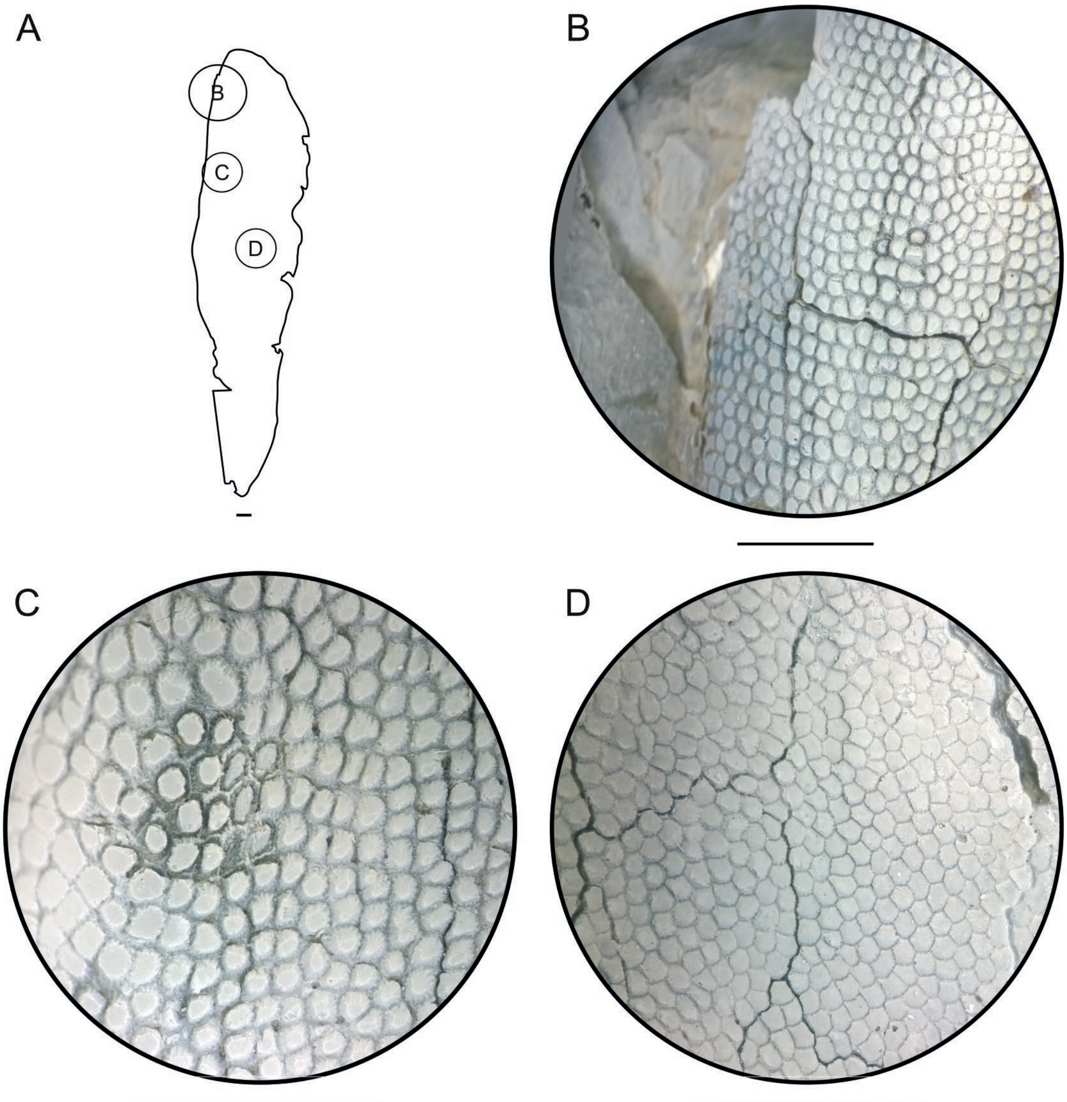

Fig. 11 *Psarkosteus mediocre.* **A.** ZPAL Ag. I/1.1, postorbital plate with fragment showing the detail of ornamentation (**B**–**D**). Scale bar equals 5 mm.

with the one exception of Lower/Middle Devonian *Schizosteus perneri* Růžička, known from the Prague Basin on the peri-Gondwanan shelf (Vaškaninová and Kraft, 2016). The earliest species of psammosteids is the Early Devonian *Drepanaspis*, known from the Pragian–Emsian of England (Cornwall), western Germany (Rhenish Slate Massif), Belgium and Luxembourg (Ardennes). Apparently, from this region psammosteids may have spread northward along the continent, where *Guerichosteus* and *Hariosteus* are known in the Emsian sandstone deposits of the Holy Cross Mountains (Tarlo, 1964, 1965; Szrek *et al*., 2014; Dec, 2019). During the Emsian/Eifelian, *Schizosteus perneri* is noted from the peri-Gondwanan (Prague Basin) shelf, while the main radiation took place to the north in the Middle Devonian. The Eifelian dispersal of psammosteids (*Schizosteus* and *Pycnolepis*) to the north (Estonia and Latvia) was the beginning of the Givetian diversification. Six genera (21 species): *Psammosteus*, *Psammolepis*, *Ganosteus*, *Tartuosteus*, *Schizosteus* and *Pycnosteus* are known from Estonia, Latvia and Russia at that time. Although the geographical distribution is not restricted to only this part of Laurussia, *Psarkosteus mediocris* gen. et sp. nov., described here from the Holy Cross Mountains, shows a more southern dispersal at that time. The youngest known psammosteids are Frasnian species of *Psammosteus meandrinus* from Estonia and *Obruchevia heckeri* and *Persheia pulla* from the Canadian Arctic. Both of the latter genera are the most northerly and westerly recognized representatives of the group.

CONCLUSIONS

Psarkosteus mediocris gen. et sp. nov. from the Middle Devonian of the Holy Cross Mountains is described. The study of the morphology and ornamentation of plates present in the material shows differences in size (9 to 15 cm), proportion (width ratio 1.5–1.8), shape of the dorsal plate (oblong with an anterior constriction) and ornamentation

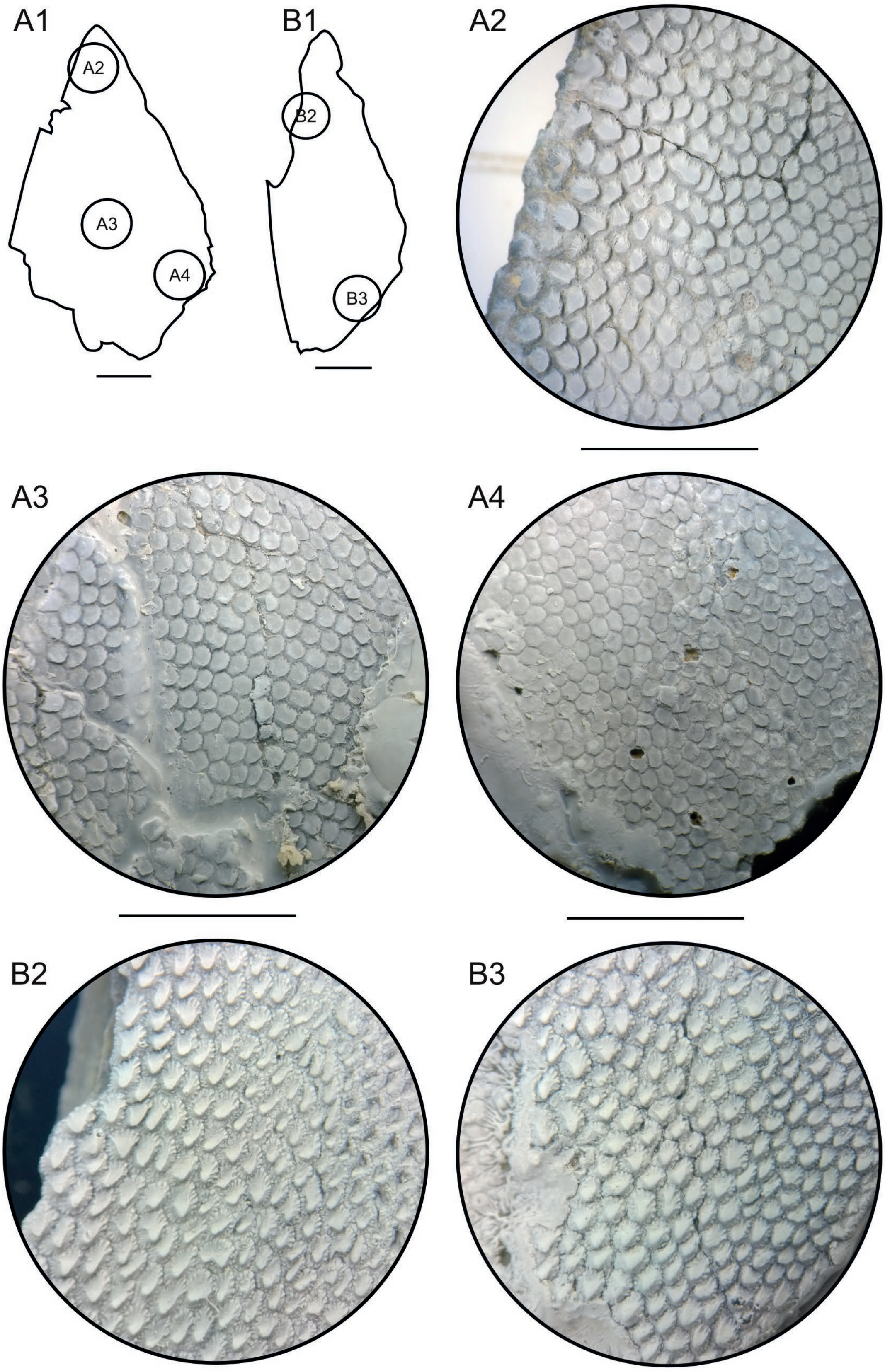

Fig. 12. *Psarkosteus mediocris*. **A1.** ZPAL Ag. I/17.2, branchial plate with fragment showing the detail of ornamentation (**A2, A3**). **B1.** ZPAL Ag. I/7, branchial plate with fragment showing the detail of ornamentation (**B2, B3, B4**). Scale bar equals 5 mm.

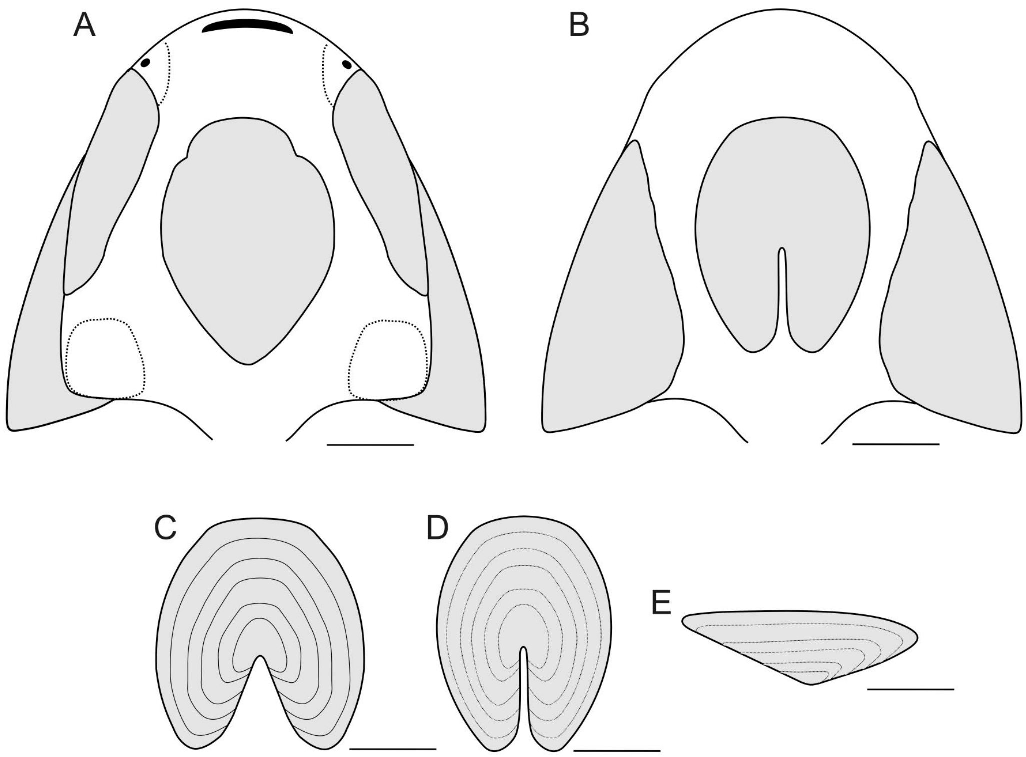

Fig. 13. *Psarkosteus mediocris* reconstruction. **A.** Dorsal view. **B.** Ventral view, restoration of flattened ventral plate (**C**) to deep ventral plate in ventral view (**D**) and lateral view (**E**). Scale bar equals 5 cm.

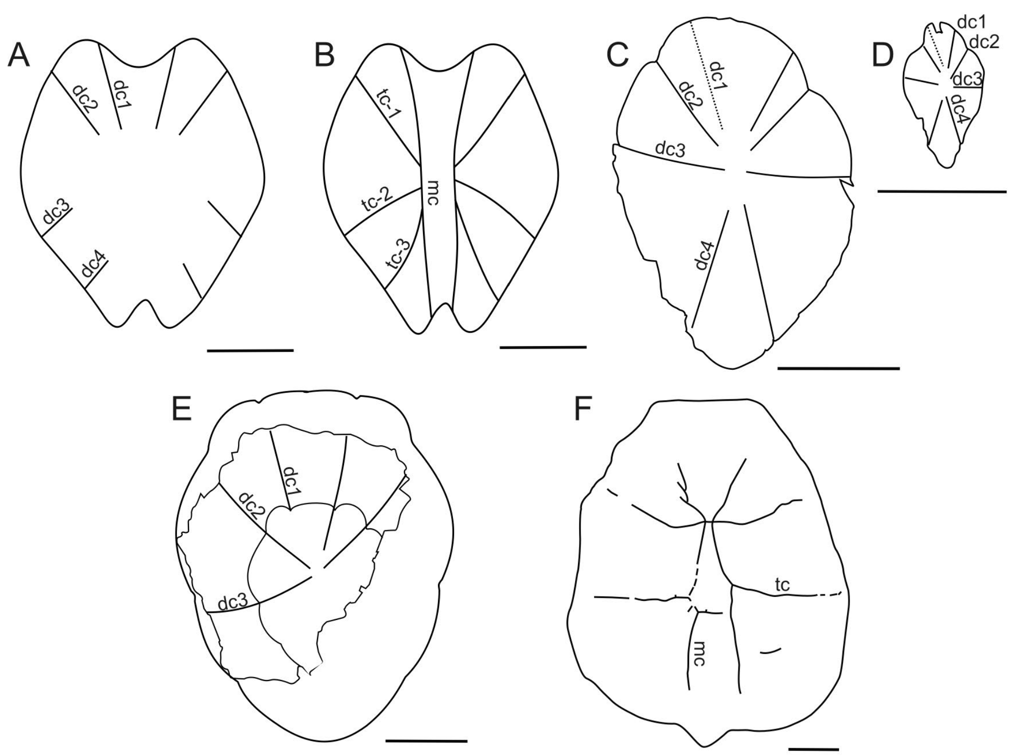

Fig. 14. Sensory lateral line system in the dorsal plates of psammosteid *Drepanaspis gemuendenensis*. **A.** Sensory lateral line system of dorsal plate in *Drepanaspis gemuendenensis* (model after Gross, 1963). **B.** *Psarkosteus mediocris* (after Glinskiy, 2018). **C.** Adult. **D.** Juvenile. **E.** *Schizosteus striatus* (modified from Obruchev and Mark-Kurik, 1965). **F.** *Psammolepis proia* (after Elliot and Mark-Kurik, 2005). Median commissure (mc), transverse commissure (tc). Scale bar equals 5 cm

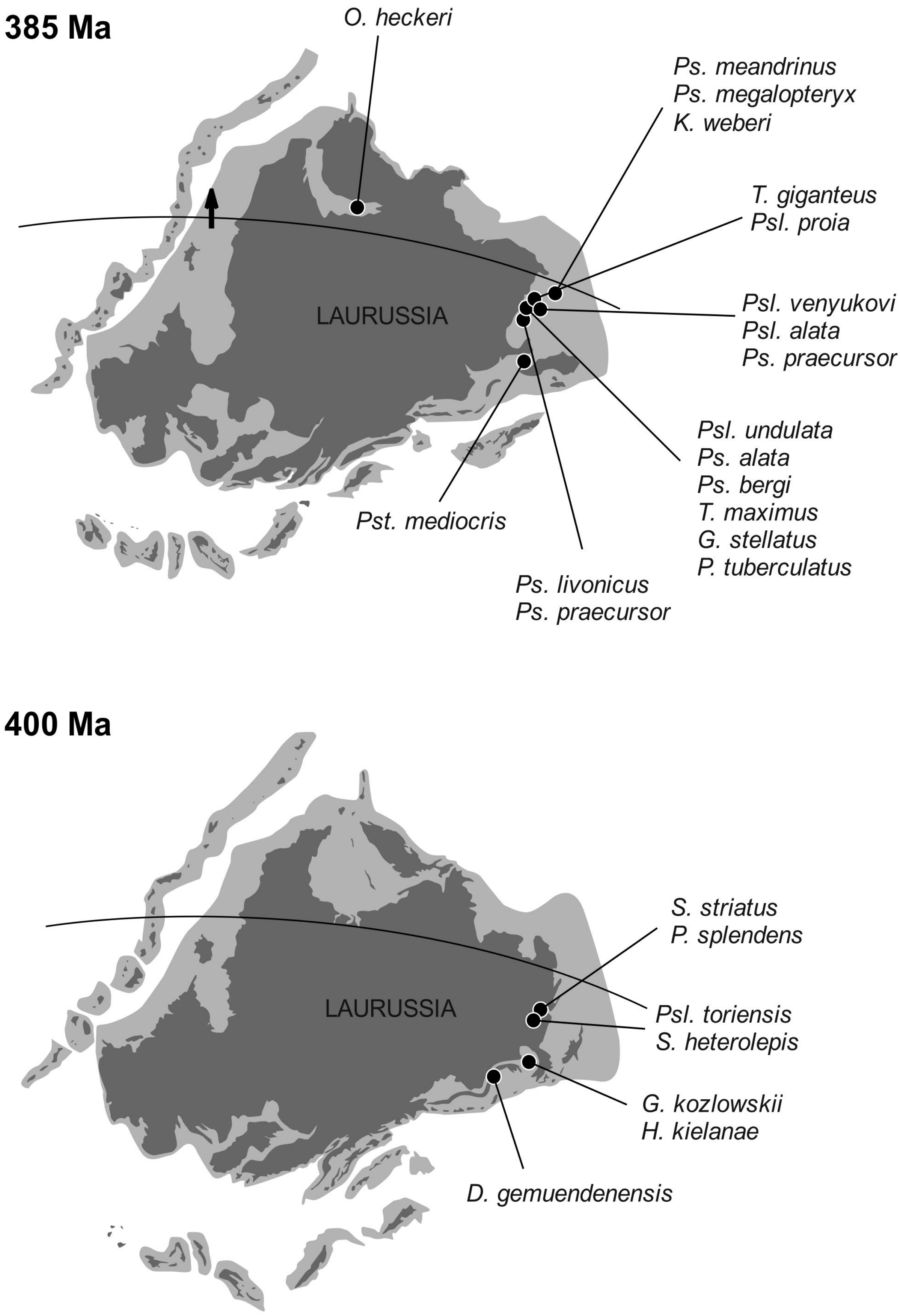

Fig. 15. Palaeogeographical distribution (modified from Scotese, 2001) of psammosteids in the Lower (400 Ma) and Middle Devonian (385 Ma).

(big, teardrop-shaped tubercles, each with a flat or slightly concave surface, and a crenulated base, extending along the lateral margin of the branchial plates) by comparison with other psammosteids, which are considered sufficient for the erection of a new genus and species. *Psarkosteus mediocris* is the first Middle Devonian psammosteid genus and species to be described from Poland. The new genus marks the southernmost occurrence of the Psammosteidae in the Middle Devonian. The new genus is considered most similar to and probably most closely related to *Schizosteus striatus* on the basis of their lateral line system and the shape of growth lines of the dorsal plate. This relationship with *Schizosteus striatus* indicates the possibility of migration of Laurussia from north to south.

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REFERENCE

Berg, L. S., 1937. A classification of fish-like vertebrates. *Bulletin of the Academy of Sciences of USSR*, 4: 1277–1280.

Blieck, A., 1984. *Les Hétérostracés Pteraspidiformes, Agnathes du Silurien-Dévonien du Continent Nord-Atlantique et des blocs avoisinants - Révision systématique, phylogénie, biostratigraphie, biogéographie.* Cahiers de paléontologie (Section Vertébrés), C.N.R.S. *édit*., Paris, 199 pp.

Blieck, A. & Elliott, D. K., 2017. Pteraspidomorphs (Vertebrata), the Old Red Sandstone, and the special case of the Brecon Beacons National Park, Wales, UK. *Proceedings of the Geologists' Association*, 128: 438–446.

Blieck, A., Elliott, D. K. & Gagnier, P. Y., 1991. Some questions concerning the phylogenetic relationships of heterostracans, Ordovician to Devonian jawless vertebrates. In: Chang, M.-M., Liu, Y.-H. & Zhang, G.-R. (eds), *Early Vertebrates and Related Problems of Evolutionary Biology.* Science Press, Beijing, pp. 1–17.

Dec, M., 2015. A new tolypelepidid (Agnatha, Heterostraci) from the Late Silurian of Poland. *Journal of Paleontology*, 89: 637–44.

Dec, M., 2019. Revision of the Early Devonian psammosteids from the "Placoderm Sandstone": Implications for their body shape reconstruction. *Palaeontologia Electronica,* 22.2.36A: 1–26.

Dzik, J., 2002. Emergence and collapse of the Frasnian conodont and ammonoid communities in the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, 47: 565–650.

Elliott, D. & Mark-Kurik, E., 2005. A review of the lateral line sensory system in psammosteid heterostracans. *Revista Brasileira de Paleontologia*, 8, 99–108.

Goodrich, E. S., 1909. Vertebrata Craniata. First Fascicle: cyclostomes and fisches. In: Lankester, R. (ed.), *A Treatese on Zoology*. London, Adam and Charles Black, pp. 1–518.

Glinskiy, V., 2018. Phylogenetic relationships of psammosteid heterostracans (Pteraspidiformes), Devonian jawless vertebrates. *Biological Communications*, 62, 219–243.

Gross, W., 1963. *Drepanaspis gemuendenensis* Schlüter, Neuuntersuchung. *Palaeonogreaphica*, *Abteilung A,* 121A: 133–155.

Halamski, A. T., 2005. Annotations to the Devonian Correlation Table, R220dm05: Poland; Holy Cross Mts; Łysogóry Region. *Senckenbergiana lethaea*, 85: 185–187.

Halamski, A. T. & Segit, T., 2006. A transitional stringocephalid from the Holy Cross Mountains, Poland, and its evolutionary and stratigraphic significance. *Acta Geologica Polonica*, 56: 171–176.

Janvier, P., 1996a. The dawn of the vertebrates: characters vs. common ascent in the rise of current vertebrate phylogenies. *Palaeontology*, 39: 259–287.

Janvier, P., 1996b. *Early Vertebrates*. Oxford Science Publications, Clarendon Press, Oxford, 393 pp.

Kłossowski, J., 1985. Sedimentation of the Middle Devonian in the Łysogóry Region (Świętomarz-Śniadka profile). *Przegląd Geologiczny*, 33: 264–267. [In Polish, with English summary.]

Lankester, E. R., 1868. *A monograph of the fishes of the Old Red Sandsone of Britain*. Part I. The Cephalaspidiae. Monograph of the Palaeontographical Society, London, pp. 1–62.

Malec, J., 1993. Upper Silurian and Lower Devonian in the western Holy Cross Mts. *Geological Quarterly*, 37: 501–536.

Mizerski, W., 1981. Structural analysis of Devonian exposures within the middle part of the Bodzentyn Syncline in the Holy Cross Mts. *Acta Geologica Polonica*, 31: 251–263.

Narkiewicz, K. & Bultynck, P., 2007. Conodont biostratigraphy of shallow marine Givetian deposits from the Radom-Lublin area, SE Poland. *Geological Quarterly*, 51: 419–442.

Obruchev, D. & Mark-Kurik, E., 1965. *Psammosteids of the Devonian of the USSR*. Akademiya Nauk Estonskoy SSR, Institut Geologii, Trudy, Tallinn, 304 pp. [In Russian, with English abstract.]

Obruchev, D. & Mark-Kurik, E., 1968. On the evolution of the psammosteids (Heterostraci). *Eesti NSV Teaduste Akadeemia Toimetised, Keemia, Geoloogia,* 17: 279–284. [In Russian, with English abstract.]

Orłowski, S. & Radwański, A., 1986. Middle Devonian sea-anemone burrows, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., from the Holy Cross Mountains. *Acta Geologica Polonica*, 36: 233–250.

Pernègre, V. N. & Elliott, D. K., 2008. Phylogeny of the Pteraspidiformes (Heterostraci), Silurian–Devonian jawless vertebrates. *Zoologica Scripta*, 37: 391–403.

Racki, G., 1997. Devonian eustatic fluctuations in Poland. *Courier Forschungsinstitut Senckenberg*, 199: 1–12.

Randle, E. & Sansom, R. S., 2017a. Exploring phylogenetic relationships of Pteraspidiformes heterostracans (stem-gnathostomes) using continuous and discrete characters. *Journal of Systematic Palaeontology*, 15: 583–599.

Randle, E. & Sansom, R. S., 2017b. Phylogenetic relationships of the 'higher heterostracans' (Heterostraci: Pteraspidiformes and Cyathaspididae), extinct jawless vertebrates. *Zoological Journal of the Linnean Society*, 181: 910–926.

Scotese, C. R., 2001. *Atlas of Earth History*. *Volume 1, Paleogeography.* Paleomap Project, Arlington, Texas, 52 pp.

Sobolev, D., 1909. Srednij devon Kelecko-Sandomirskogo Krjazha. *Materialy dla Geologii Rossii*, 24: 41–536. [In Russian.]

Szrek, P., Niedźwiedzki, G. & Dec, M., 2014. Storm origin of bone-bearing beds in the Lower Devonian placoderm sandstone from Podłazie Hill (Holy Cross Mountains, central Poland). *Geological Quarterly*, 58: 795–806.

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.

Tarlo, L. B., 1965. Psammosteiformes (Agnatha) - a review with descriptions of new material from the Lower Devonian of Poland. II – systematic part. *Palaeontologia Polonica*, 15: 1–168.

Turnau, E. & Racki, G., 1999. Givetian palynostratigraphy and palynofacies: new data from the Bodzentyn Syncline (Holy Cross Mountains, central Poland*). Review of Palaeobotany and Palynology*, 106: 237–271.

Traquair, R. H., 1896. The extinct Vertebrata of the Moray Firth Area. In: Harvie-Brown, J. H. & Buckley, T. E. (eds), *Vertebrate Fauna of the Moray Basin*. Brown and Buckley, Edinburgh, pp. 235–285.

Vaškaninová, V. & Kraft, P., 2016. A unique occurrence of a psammosteid heterostracan on the peri-Gondwanan shelf in the Lower/Middle Devonian boundary marine deposits. *Fossil Imprint*, 72: 155–160.

Woroncowa-Marcinowska, T., 2012. Middle Devonian conodonts and structural implications for Świętomarz-Śniadka section (Holy Cross Mountains). *Annales Societatis Geologorum Poloniae*, 82: 349–360.