Phylogenetic relationships of psammosteid heterostracans (Pteraspidiformes), Devonian jawless vertebrates

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Abstract
Psammosteid heterostracans are a group (suborder Psammosteoidei) of Devonian-age jawless vertebrates, which is included in the order Pteraspidiformes. The whole group of psammosteids is represented by numerous species (more than 40); their phylogenetic relationships are still poorly known and deserve further study. Classical researchers of the psammosteids, such as D. Obruchev, E. Mark-Kurik and L. Halstead Tarlo, had different views on the phylogeny of the group (e.g. origins and evolution of Psammosteus). To check the modern hypotheses of psammosteid origins from various Pteraspidiformes and to clarify psammosteid interrelationships, the most complete phylogeny of this group (38 ingroup taxa + juvenile Drepanapsis) is presented here. Different methods of data analysis were used to explore the psammosteid data set, including equally weighted characters versus implied weighting. According to the results of the phylogenetic analysis, the monophyletic status of the group and their early development from the Pteraspidiformes are supported. The diagnoses and interrelationships of many taxa are clarified. Two new genera are proposed (Vladimirolepis gen. nov. and Elgaia gen. nov.), and two subfamilies are erected (Placosteinae subfam nov. and Psammosteinae Traquair).

Keywords: Agnatha, Heterostraci, Pteraspidiformes, psammosteids, phylogeny, classification.

Introduction
HISTORY OF GENERAL PSAMMOSTEID CLASSIFICATION IN HETEROSTRACI AND PREVIOUS PHYLOGENETIC ANALYSES

Ramsay H. Traquair (1896, p. 260) first introduced the family Psammosteidae as the name for some Middle and Upper Devonian jawless vertebrates from the Baltic Region and Scotland, grouped in the genus Psammosteus. Traquair also introduced the family Drepanaspidae for Drepanaspis and showed that both families belong to the Heterostraci (Traquair, 1899, pp. 844 , 853). He was the first to point out the similarity of the skeletal plates of Pteraspis and Drepanaspis in their general shape (Traquair, 1899, p. 851). However, he considered that the evolution to pteraspid was accompanied by consolidation of the dermal skeleton from the separate scales of thelodonts to the plates of psammosteids and further, through drepanaspids, to completely consolidated pteraspid (Traquair, 1899, pp. 856– 857). Thereafter the classification of pterasmoide sensu stricto (Drepanaspis through Psammosteus) into two families was widely used (Berg, 1940; Broten, 1936; Gross, 1933b; Obruchev, 1941; Traquair, 1900, etc.). However, some authors have used families Drepanaspidae and Psammosteidae disorderly (e.g. Gross, 1937a, b), or synonymously only as the family Drepanaspidae (Stensiö, 1927; White, 1935) or only as the family Psammosteidae (Berg, 1955; Obruchev, 1943b;
The drepanaspids and psammosteids with some new forms such as *Obruchevia* (syn. *Aspidosteus*) were united by several authors in the suborder Psammosteida (Gross, 1935; Kiaer, 1932; Tarlo, 1962), order Psammosteiformes (Berg, 1937 (*nomen nudum*); Berg, 1940). Later they were assigned to the order Psammosteida (Obruchev, 1964; Obruchev and Mark-Kurik, 1965) in the group Heterostraci. For example, the classification of psammosteids used by Leo S. Berg (1940), in which *Aspidosteus* (syn. *Obruchevia*) is included in the family Weigeltaspidae (this family would be present in the classification of psammosteids for a long time by iteration), looked like this:

**Order Psammosteiformes Berg, 1940**  
Family Psammosteidae Traquair, 1896  
Family Drepanaspidae Traquair, 1899  
Family Weigeltaspidae Brotzen, 1933  
*Aspidosteus* Obruchev, 1941 (syn. *Obruchevia*)

In his early works Dmitry V. Obruchev (1941) segregated psammosteids *sensu stricto* into the same families in the suborder of psammosteids. The genus *Aspidosteus* (syn. *Obruchevia*) was attributed to the Cardipeltidae:

**Suborder Psammosteida Kiaer, 1932**  
Family Psammosteidae Traquair, 1896  
Family Drepanaspidae Traquair, 1899  
? Family Weigeltaspidae Brotzen, 1933  
*Cardipeltis* Branson et Mehl, 1931  
*Aspidosteus* Obruchev, 1941 (syn. *Obruchevia*)

The families Cardipeltidae and Weigeltaspidae were later excluded from psammosteids (Halstead, 1993).

In his later works Berg (1955) substantially broadened the order Psammosteiformes by including the other tesselated heterostracans in it. Psammosteids *sensu stricto* were assigned to the family Psammosteidae while *Aspidosteus* (syn. *Obruchevia*) was included into a separate family Psammosteidae:

**Order Psammosteiformes Berg, 1940**  
Family Psammosteidae Traquair, 1896  
Family Aspidosteidae Berg, 1955  
*Aspidosteus* Obruchev, 1941 (syn. *Obruchevia*)  
Family Cardipeltidae Bryant, 1933  
*Cardipeltis* Branson et Mehl, 1931  
*Aspidosteus* Obruchev, 1941 (syn. *Obruchevia*)

The notion about the affinity of the tesselated heterostracan *Tesseraspis* and psammosteids *sensu stricto* was later exploited by Erik H. O. Stensio and Tor Ørvig. Psammosteids (*Drepanaspis* through *Psammosteus*) were also united with *Tesseraspis* in the order Drepanaspida (Stensiö, 1958; Ørvig, 1961). Lambert B. Halstead Tarlo united psammosteids *sensu stricto* with *Tesseraspis* and some other tesselated heterostracans in the order Psammosteiformes based on the presence of tesserae in the cephalothorax. He also introduced new families of psammosteids (Tarlo, 1962, 1967; Halstead Tarlo, 1964a, 1965):

**Order Psammosteiformes Berg, 1940**  
Suborder Tesseraspidida Tarlo, 1962  
Family Tesseraspididae Berg, 1955  
Family Weigeltaspidae Brotzen, 1933  
Family Corvaspididae Dineley, 1953  
Suborder Psammosteida Kiaer, 1932  
Family Drepanaspidae Traquair, 1899  
*Drepanaspis* Schlüter, 1887  
*Psephanaspis* Ørvig, 1961

Family Guerichosteidae Halstead Tarlo, 1964  
*Guerichosteus* Halstead Tarlo, 1964  
*Hariosteus* Halstead Tarlo, 1964  
*Schizosteus* Obruchev, 1940

Family Pycnosteidae Tarlo, 1962  
*Pycnolepis* Halstead Tarlo, 1964  
*Pycnosteus* Preobrazhensky, 1911  
*Ganosteus* Rohon, 1901  
*Tartuosteus* Obruchev, 1961  
*Yoglinia* Obruchev, 1943

Family Psammolepididae Tarlo, 1962  
*Psammolepis* Agassiz, 1845

Family Psammosteidae Traquair, 1896  
*Psammosteus* Agassiz, 1845 (*in this work, Agassiz, 1844*)  
*Crenosteus* Halstead Tarlo, 1964  
*Rohonosteus* Halstead Tarlo, 1964  
*Karelosteus* Obruchev, 1933

Suborder Obrucheviida Halstead Tarlo, 1965  
Family Obrucheviidae Halstead Tarlo, 1964  
*Obruchevia* Whitley, 1940 (syn. *Aspidosteus*)  
*Traquairosteus* Halstead Tarlo, 1964

Obruchev thought that psammosteids evolved from pteraspids and had reacquired tesserae (Obruchev, 1943b, 1945, 1972, p. 70). This parsimonious hypothesis was accepted by other scientists (Gross, 1963, 1967; Westoll, 1967, pp. 93–94). W. Gross (1963) supported Obruchev’s hypothesis with his study of a juvenile *Drepanaspis*, which had a consolidated pteraspid-like exoskeleton and lacked tesserae. Obruchev (1964) presented the following classification of psammosteids:

**Order Psammosteida Obruchev, 1964**  
Family Drepanaspidae Traquair, 1889  
*Drepanaspis* Schlüter, 1888 (*err.,* 1887)
Family Pycnosteidae Tarlo, 1962

- *Psephaspis* Ørvig, 1961
- *Schizosteus* Obruchev, 1940
- *Tartuosteus* Obruchev, 1961
- *Pycnoasteus* Preobrazhensky, 1911
- *Ganosteus* Rohon, 1901

Family Psammolepididae Tarlo, 1962

- *Psammolepis* Agassiz, 1844 (err., 1845)

Family Psammosteidae Traquair, 1896

- *Yoglinia* Obruchev, 1943
- *Psammosteus* Agassiz, 1844
- *Karelosteus* Obruchev, 1933

Family Aspidosteidae Berg, 1955 (syn. Obrucheviidae)

- *Aspidosteus* Obruchev, 1941 (syn. *Obruchevia*)

The main monographs on psammosteids (Halstead Tarlo, 1964a, 1965; Obruchev and Mark-Kurik, 1965) came out almost simultaneously. Halstead Tarlo (Halstead, 1973, 1993) noted that in fact his monographs were published in 1965 and 1966. It is important to note that the monograph by Dmitry V. Obruchev and Elga Yu. Mark-Kurik (1965) was published several months earlier (accepted for publication on 23.12.1965) and has priority over the second monograph by L. B. Halstead Tarlo (accepted for publication on 19.02.1966) for descriptions of the same taxa.

In his later works, Obruchev (Obruchev and Mark-Kurik, 1965; Obruchev, 1967, 1968) returned to his early simpler version of psammosteid classification: the number of families decreased to three (in the 1965 monograph only representatives of Psammosteidae were discussed in detail), and the genus *Yoglinia* was synonymized with *Psammosteus*:

Order Psammosteida Obruchev, 1964

Family Drepanaspididae Traquair, 1899

Family Psammosteidae Traquair, 1896

- *Schizosteus* Obruchev, 1940
- *Tartuosteus* Obruchev, 1961
- *Pycnoasteus* Preobrazhensky, 1911
- *Ganosteus* Rohon, 1901
- *Psammosteus* Agassiz, 1844
- *Karelosteus* Obruchev, 1933

Family Aspidosteidae Berg, 1955 (syn. Obrucheviidae)

- *Aspidosteus* Obruchev, 1941 (syn. *Obruchevia*)

Obruchev (1967, Fig. 1) depicted a phylogeny of heterostracans, in which pteraspids represent a sister group of psammosteids. It was suggested that the protaspids (*Glossoidaspis, Europrotaspis*) are close to the psammosteids due a reduction of the corumal plates (Obruchev and Mark-Kurik, 1965, p.38; Obruchev, 1967, 1968, 1972).

Halstead Tarlo (Halstead, 1973, p.325) considered tesseraspids as a basal group for various heterostracans. According to his new concept, tesseraspids were excluded from the order Psammosteiformes, and the family Weigeltaspidae was assigned to a new suborder, Weigeltaspida, inside Psammosteiformes. The structure of the other part of the suborder remained the same as in his 1965 work:

Order Psammosteiformes Berg, 1940

Suborder Weigeltaspida Halstead, 1973

Suborder Psammosteida Traquair, 1899

Suborder Psammosteida Keiter, 1932

Suborder Psammosteida Obruchev, 1965

Suborder Obrucheviida Halstead, 1965

Order Psammosteiformes Berg, 1940

Family Drepanaspididae Traquair, 1899

Family Guerichosteidae Halstead Tarlo, 1964

Family Pycnoasteidae Tarlo, 1962

Family Psammosteidae Traquair, 1896

Family Obrucheviidae Halstead, 1964

With the discovery of anchipteraspids (Elliott, 1984), it became clear that pteraspids evolved from cyathaspids. The hypothesis of independent evolution of cyathaspids and pteraspids from tesselated heterostracans was untenable. Psammosteids are grouped with pteraspids according to Obruchev's hypothesis. Alain Blieck in cooperation with David K. Elliott (Blieck, 1984, Fig. 61) made the first (hand-constructed) cladogram of the Pteraspiformes,
in which the psammosteid clade (coded Drepanspis gemuendenensis) is a sister group (order Psammosteiformes) of Pteraspidiformes (consistently positioned at the base of the tree). This author compared Drepanspis with Cosmaskis. He noted in detail the similar body plan of pteraspids (Protopteraspis) and psammosteids (Blieck, 1984, p. 99). In the subsequent work (Blieck, Elliott, and Gagnier, 1991), data on anchipteraspids were included, and the protopteraspids were considered as the sister group of the higher pteraspids and psammosteids on the basis of the primitive location of pinal canal. In the proposed phylogenetic scheme by P. Janvier (1996, Fig. 4.9), psammosteids were placed as the sister group to protaspids (as a development of Obruchev's traditional hypothesis) and combined with them in the new superfamily Protaspidioidea.

Vincent N. Pernègre (2002) compiled a new character-taxon matrix and produced a cladistic analysis that included Drepanspis gemuendenensis. In the most parsimonious tree, recovered by him, this psammosteid was placed as a sister taxon to Doryaspis nathorsi in the order Pteraspiformes. The close relationship between Doryaspis and psammosteids was criticized (Elliott and Mark-Kurik, 2005, p. 107) due to differences in squamation and position, pattern and number of plates in their cephalothoraxes. Pernègre and Elliott (2008) published a strict consensus tree including Drepanspis gemuendenensis, based on a substantially improved and expanded matrix. According to their cladogram, psammosteids are also included in the order Pteraspiformes and placed between the basal family Anchipteraspidae and the family ‘Protopteraspididae’ (Pernègre and Elliott, 2008, Fig. 5), Emma Randle and Robert Sansom (2016, 2017), using discrete, continuous and discretized continuous characters, encoded 47 taxa of pteraspidiforms including two well known species of psammosteids — Drepanspis gemuendenensis and Psammosteus megalopteryx. In all resulting trees using different characters / coding methods and methods of data analysis (equal character weights or implied character weighting), psammosteids fall into the clade Pteraspiformes (Randle and Sansom, 2016, Figs. 4–6). In most cases (5 of 6 presented trees), the position of psammosteids in a clade with Doryaspis and Woodjordaspis is maintained (development of Pernègè’s hypothesis). It was proposed that psammosteids should be included in the new superfamily Doryaspidae (most correct — Doryaspidioidea).

Still, the position and rank of psammosteids in the order Pteraspiformes is ambiguous. Currently psammosteids are often regarded as the family Psammosteidae (Janvier 1996; Pernègre and Elliott, 2008; Randle and Sansom, 2016). Also they are assigned to the suborder Psmmosteidae in the order Pteraspiformes (Elliott, Mark-Kurik, and Daeschler, 2004; Glinskiy and Mark-Kurik, 2016; Glinskiy and Nilov, 2017).

Presented here is a new most complete cladistic analysis, which has been carried out in order to determine the phylogenetic relationships of psammosteid heterostracans. All reasonably well known species of psammosteids have been included. These phylogenetic relationships of psammosteids were presented for the first time at the Early Lower Vertebrates Symposium in Poland (Glinskiy, 2017; abstract + poster). The results of a preliminary analysis (Anchipteraspidae were not included ) confirm the data of A. Blieck and D.K. Elliott (1984), that psammosteids are a monophyletic group (order Psammosteiiformes), and that pteraspids (Pteraspidiformes) are their sister group.

DEVELOPMENT OF VIEWS ON PHYLOGENETIC INTER-RELATIONSHIPS WITHIN PSAMMOSTEIDS

Walter Gross (1930, p. 127, 1933a, p. 7) was the first to point out the homology of the branchial plates of the Middle Devonian psammosteids with those of Drepanspis. He also made suggestions about the evolution of these exoskeletal elements, which involved their contraction and widening. Gross (1933a) divided psammosteids according to the length of their branchial plates into Psammolepis and Psammosteus. He noted similarities of the branchial plates of Schizosteus striatus (syn. Psammolepis striata sensu Gross) with those of Drepanspis. Obruchev (1940) established the genus Schizosteus, which he treated as a transitional form between Drepanspis and other psammosteids. He pointed out (Obruchev, 1940, Fig. 4, 1943b, etc.) variability in the depth of the ventral plates’ posterior notch, showing that this notch is similar in Drepanspis and Schizosteus. Obruchev (1943a) described a ‘pteraspid’ Yoglinia; later it was assigned to psammosteids (Mark, 1955), attributed to the family Psammosteidae (Obruchev, 1964) and synonymized with Psammosteus (Obruchev and Mark-Kurik, 1965). Obruchev (1943c) produced in his thesis the first phylogeny of the psammosteid genera Pycnosteus, Ganosteus and subsequently Psammolepis and Aspidosteus (syn. Obruchevia) and showed that they consistently branched out from the stem line from Drepanspis to Psammosteus (Fig. 1A). According to this scheme, psammosteids are descendants of pteraspids. This phylogeny quite accurately anticipates the phylogenetic relationships of the main psammosteid genera (with the exception of Obruchevia) obtained in the present work (Fig. 3). Mark-Kurik (Mark, 1955) described many new psammosteids from the Baltic region in her dissertation and presented a detailed discussion of their evolutionary relationships, including a phylogenetic scheme (Fig. 1C). She followed the view of Obruchev (1943c) about independent evolution of two groups (Pycnosteus + Ganosteus and Psammolepis) from Schizosteus (the data on the concentric lines of growth on branchial and ventral plates at juvenile stages of the development was taken into account). A suggestion was proposed that Schizosteus striatus is the...
ancestor of Psammolepis proia (syn. Vladimirolepis proia comb. nov.), and ‘Psammolepis’ heteraster, ‘Psammolepis’ alata and ‘Psammolepis’ undulata (syn. Placosteus) represent a separate phylogenetic line within Psammolepis.

Mark-Kurik reckoned that Tartuosteus luhai (syn. Elgaia luhai, comb. nov.) is the ancestor of the Psammosteus line, and Yoglinia (syn. Psammosteus) is close to Psammosteus (ibid., p.17), but she somehow placed Yoglinia between Tartuosteus and Psammolepis in her scheme. Halstead Tarlo (1957, 1962, etc.) described psammosteids (Guerichosteidae) from the Emsian of Poland and negated Obruchev’s view about the evolution of psammosteids from Drepanaspis (Tarlo, 1957, p.228). He further suggested that psammosteids evolved into two independent lineages — marine (represented by Drepanaspis), which didn’t produce descendants, and freshwater, represented by guerichosteids and their descendants that produced other psammosteids (Tarlo, 1957, 1962, Figs. 13, 15; Halstead Tarlo, 1964a, Figs. 30–32) (Fig. 1D). The views of Halstead Tarlo on psammosteid evolution are also based on the variation of the shape of median plates, development of their tesserae covering, and changes in proportions of branchial plates (Halstead Tarlo, 1964a, Figs. 30, 31; Halstead, 1973). The resultant phylogenetic scheme (Halstead Tarlo, 1964a, Fig. 32) differs from the previous two only slightly in details — in terms of the evolution of Yoglinia (syn. Psammosteus) and Tartuosteus luhai (syn. Elgaia, gen. nov.) (Fig. 1D). The genera Guerichosteus, Schizosteus, and Psammolepis should be considered paraphyletic, according to his scheme. The species of the genus Schizosteus (member of Guerichosteus) gave the different evolutionary lineages — pycnosteids (some Schizosteus, Pycnosteus, Ganosteus, Tartuosteus, Yoglinia) and psammodepidids-psammosteids (some Schizosteus, Psammolepis, Rohonosteus, Traquairosteus, Obruchevia, Psammosteus, Karelosteus). The genus Psammosteus, according to Halstead Tarlo, evolved from Psammolepis (Halstead Tarlo, 1964a, p.103), and Karelosteus is considered a side-branch of Psammosteus. Traquairosteus with Obruchevia, Rohonosteus and Crenosteus are considered prospective descendants of the basal and more derived psammodepidids, respectively. His views on the evolution within Psammosteus in this work are systemless. Halstead Tarlo (1964a, 1965) considered the similar characters of the branchials
of Yoglinia and Psammosteus to be a result of parallel evolution. He followed Obruchev (1961) in the erroneous attribution of the tesselated dorsal plate of 'Psammolepis' proia (Vladimiroilepis gen. nov.) to Tartuosteus giganteus.

Obruchev and Mark-Kurik (1965, p.66, 67, 1968) used quantitative data (length/width ratio) for the first time to characterize the main plates of the psammosteid exoskeleton. The authors in general shared Halstead Tarlo's viewpoint on the evolution of the group. However, they negated his (1964) hypothesis about the probable evolution of Psammosteus from late representatives of Psammolepis ('Pl'. undulata). They noted that the earliest Psammosteus bergi appeared substantially earlier than 'Pl'. undulata (though the similarity in general body shape (which is elongated) of Ps. bergi and Pl. undulata is also pointed out). The authors noted well-traced relationships between psammosteid species (Tartuosteus giganteus — Tartuosteus maximus; relationships inside the genus Pycnosteus, Ganosteus artus — Ganosteus stellatus, 'Psammolepis' alata — 'Psammolepis' undulata [syn. Placosteus], Psammolepis praecursor — Psammosteus macandrinus). Three evolutionary lineages were also distinguished (Obruchev and Mark-Kurik, 1968, p.282) based on the study of juvenile plates and concentric growth lines. They are the following: slender-bodied psammosteids (close to Drepansas, including Schizosteus striatus and almost all Psammolepis), wide-bodied psammosteids (including Schizosteus splendens [syn. Pycnolepis], Tartuosteus, Pycnosteus, Ganosteus and several species of Schizosteus and Psammolepis), and psammosteids with rhombic dorsal plate and broad branchials (Psammosteus bergi). Tartuosteus? luhai (syn. Elgaia luhai comb. nov.) and Psammosteus (Yoglinia) bergi were attributed to different phylogenetic lines (Obruchev and Mark-Kurik, 1968, p.282), despite the presence of shared characters in the structure of the branchial and dorsal plates.

Robert H. Denison (1968, pp.279, 281) attributed Psphais to pteraspsids (this genus had previously been attributed by T.Örvig to psammosteids) based on the absence of tesserae (they were mistakenly identified due to the fractured state of the remains). Denison also proposed that 'Psphais' bystrowi (Drepansas sp. according to Bystrow, 1959), described based on a tesser, should be named? Drepansas sp. Obruchev in his works (Obruchev, 1967, 1968) considered phylogenetic relationships within evolutionary lineages of psammosteids (Fig. 1B). According to him, drepansasps gave rise to psammosteids, and obruchevids evolved from psammosteids as a ‘late aberrant offset’ (Obruchev, 1967, p.42). In that work Obruchev also showed recapitulation of ancestral characters in the Middle Devonian psammosteids. In his next article Obruchev specified that obruchevids were classified as ‘aberrant descendants of psammosteids, evolved from their earliest representatives’ (Obruchev, 1968, p.26). Halstead Tarlo (Halstead, 1973, p.291) discovered pedomorphism in branchial plates of psammosteids Ganosteus and Psammosteus (Yoglinia). Scientists traced (Halstead Tarlo, 1964, p.105-107; Halstead, 1973, p.291) two evolutionary lineages in Psammosteus based on the shapes of branchial plates. Larisa I. Novitskaya (2004) used the classification by Obruchev (1964) in her revision of psammosteids. The genera Yoglinia and Crenosteus were synonymized with Psammosteus, Pycnolepis with Schizosteus and Rohonosteus with Tartuosteus. It was proposed that the most correct name for the suborder Psammooidei (Novitskaya, 2004, p.171). New data on Obruchevia and Perscheia (Elliott, Mark-Kurik, and Daeschler, 2004) showed that obruchevids are more likely to be connected to a group including Pycnolepis, Pycnosteus and Tartuosteus. Sergey V. Moloshnikov (2009) introduced the genus Oredzhosteus which was later rejected (Glinskiy and Mark-Kurik, 2016). New morpho-histological characters of the plates of some representatives of Psammosteus made it possible to compare the histology of these taxa with Traquaiosteus pustulatus and divide the genus Psammosteus on the two evolutionary lines (genera in the future) (Glinskiy and Nilov, 2017).

Phylogenetic analysis
CHARACTERS, CODING METHODS AND DATA ANALYSIS

The new matrix is composed of 49 taxa and 120 discrete characters (49 characters are new) (see Appendix 1). The list of encoded taxa, specimen information and museum numbers are organized in a table (on-line only Supplement 1 and 2). 38 species from 16 genera (constituting the ingroup taxa) are coded as belonging to the morphologically best-known psammosteid heterostracans. To understand the relationship between pteraspids and psammosteids, juvenile Drepansas gmundenensis was encoded as a separate taxon, because juvenile psammosteids show recapitulations (Gross, 1963; Obruchev, 1967). Thus, all the well known psammosteid species (except Traquaiosteus pustulatus and species of Rohonosteus) are included here. Most included psammosteid taxa are known from numerous various elements of the exoskeleton; the exception is a group of taxa from the family Psammosteidae, known primarily from the branchial plates and tesserae: Psammosteus levis, P. tenuis, Karelosteus weberi, and the group of species Psammosteus' ramosus — 'P.' falcatus. For testing various hypotheses of derivation of the psammosteids (Janvier, 1996; Pernègre, 2002; Pernègre and Elliott, 2008; Randle and Sansom 2016), eight taxa of the order Pteraspidiformes, which may form the sister group to psammosteids, were encoded: Anchipteraspis cremulata, Doryaspis nathorsti, Errivaspis waynensis, Gigantaspis laticephalus, Protaspis bucheri, Proteopteraspis vevging, Woodfjordasps felixi, and Xylaspis prima. Two cyathaspidiform taxa, Anglaspis
maccoulloughi (outgroup taxon in TNT) and Nahan-niaspis mackenzii were chosen as outgroups, because they are very useful in polarizing character states within the analysis (Pernègre and Elliott, 2008; Randle and Sansom, 2016).

Characters used in the phylogenetic analysis were obtained from direct study, published descriptions, or were taken unchanged or adapted from previous phylogenies (Ilyes and Elliott 1994; Pernègre, 2002; Per-nègre and Goujet, 2007; Pernègre and Elliott, 2008; Randle and Sansom, 2016) (Appendix 1). Figure 2 provides a visual explanation of some ratios of plates, which were used in character codings. For each psammosteid taxon, text and graphic data on the type specimens were used (Elliott, Mark-Kurik, and Daeschler, 2004; Elliott and Mark-Kurik, 2005; Halstead Tarlo, 1964a, 1965; Lyarskaya, 1971; Mark-Kurik, 1968, 1993, 1999; Novitskaya, 1965, 2004; Obruchev, 1940; Obruchev and Mark-Kurik, 1965; Růžička, 1929; Tarlo, 1961). The most recent data on the general morphology, ornamentation and histology of psammolestids were also encoded (Gлинский, 2014; Gлинский and Mark-Kurik, 2016; Gлинский and Nilov, 2017; Gлинский and Pinakhina, 2018; Keating, Marquart, and Donoghue, 2015; Moloshnikov, 2001).

All characters are discrete (binary or multistate), mostly unordered, but 21 multistate characters are ordered as specified by the relationship of character states within the transformation series (1, 8, 16, 21, 30, 31, 38, 54, 57, 64, 71, 79, 81, 83, 86, 87, 88, 89, 99, 108, 117). There are three (9, 61, 66) uninformative characters (2.5%). Characters 29, 65, 68, 81, 86, 87, 91 were used for determining the geometric ratio for some main plates of the psammosteid cephalothorax; their changes in proportions are important for understanding the evolutionary trends in the group (Halstead, 1973, p. 290; Obruchev and Mark-Kurik, 1965, pp. 41–48) (Fig. 2). Continuous or quantitative characters were not used here, due to the fact that psammolestid specimens have a high variability of measurements of the main plates, which are placed in the fields of tesserae (Randle and Sansom, 2016, p. 7). Furthermore, the lateral plates of psammolestids change in form due to life-time abrasion, and specimens discovered with associated cephalothorax also are very rare.

The character-taxon matrix was coded in NDE 0.5.0. by Roderic D.M. Page, 2001, and exported in TNT format implemented through the program Mesquite 3.2. Parsimony tree searches were conducted in TNT 1.5 (Goloboff, Farris, and Nixon, 2008) with space for holding 10000 trees. Two methods of data analysis were carried out— with equally weighted characters and with implied weighting (Goloboff, 2014). In both analyses the heuristic search mode (Traditional search) was used with the ‘branch swapping’ option (multiple Tree Bisec tion Reconnection, TBR) with 1000 replications and trees from RAM successively. In addition, the Nelsen strict consensus tree was calculated. Bremer tree support and standard Bootstrap (with traditional search, 5000 rep.) were implemented.

**PHYLOGENETIC RESULTS**

The first equal weight analysis produced 36 most-parsimonious trees (MPTs; tree length 373 steps, CI = 0.611, RI = 0.851, and RC = 0.520), giving a well-resolved strict consensus tree (Fig. 3A). Psammolestids are nested in the Pteraspidiformes and represented as a monophyletic group suborder Psammosteioidei (=Psammistes Kier, 1932 emend. Tarlo, 1962). Anchipteraspis crenulata is placed as the sister taxon of the other Pteraspid-iformes. Protopteraspis vogti fall in the one clade with the derived pteraspids and psammolestids. In Pernêgre and Elliott’s (2008) phylogeny, Doryaspis was within the ‘Protopteraspididae’, but here Doryaspis and Woodfiordiaspis fall within the same clade of Pteraspidoidei (family Doryaspidae N. Heintz in Tarlo 1962), and Xylaspis is included in the Protaspidae. Psammolestids contain six families: Drepanaspidae, Guerichos-teidae, Obrucheviidae, Pycinostidae, Psammolepididae and Psammolestidae. Psammolepis, Tartuosteus, and Schizosteus sensu Obruchev and Mark-Kurik (1965) and Halstead Tarlo (1965) are not united in a monophyletic group and need a revision. The clade with Psammolepis sensu stricto (Psammolepis abavaca, P.tarionis, P.paradoxa, P.venyukovi) is sister to a large clade that also contains the species ‘Psammolepis’ proia, P. alata, P’. undulata, and ‘Tartuosteus’? luhai (taxa requiring new generic names). This group of species forms a basal assemblage leading to a clade containing the species of Psammolestus and Karelosteus weberi. A large number of Psammolepis and Psammolestus species are in a polytomy within the consensus tree. Monophyly of Guerichosteus and Schizosteus (requires more material of S. asatkini, which is known only from a juvenile specimen) is not considered. Karelosteus weberi along with ‘Psammolestus’ livonicus — ‘Psammolestus’ asper and ‘Psammolestus’ ramosus — ‘Psammolestus’ falcatus form the most derived clade of psammolestids. ‘Psammolestus’ tenuis is the sister taxon for this clade. To increase resolution, avoiding polytomies in some clades (e.g. in Psammolestus), and to recover any phylogenetic signal, a second implied weighting analysis was conducted (Fig. 3B). Application of implied weighting resulted in 3 MPTs with a score of weighting (k=4) (MPTs length 23.55, CI = 0.610, RI = 0.850 and RC = 0.519. Relationships in the groups of taxa are somewhat better resolved in the current strict consensus tree than in the previous analysis. Protopteraspis vogti is shown here as the sister taxon to the clade, consisting of psammosteids and derived pteraspids. These results of the implied weighting data analysis support the cladistic
Fig. 2. Reconstructions of the cephalothorax of the major psammosteid genera with measurements of main plates. Reconstructions were made on the basis of the original material given in the list of taxa (On-line only Supplement 1). Numbers signify the selected characters, the following numbers in brackets represent character states. The slashes indicate variation of the character states within the given genus; character state, which is shown in the picture, is highlighted in bold. The variability of the branchial plates’ shape in dorsal and ventral view is associated with their dorsally convex shape in the transverse-longitudinal direction. For median plates of some taxa, the juvenile states of the plates are shown. The red dotted lines indicate measurements of ratio as well as proposed canals of the lateral line system; the black dotted lines indicate concentric lines of growth, reflecting the morphology of the plates in ontogenesis. Abbreviations: B, branchial plate; bs, branchial sinus; C, cornual plate; D, dorsal plate; ifc, infraorbital canal; ldc, lateral dorsal canal; lvc, lateral ventral canal; Cx, complex plate; M, marginal plate; mdc, median dorsal canal; mtc, median transverse commissure; O, orbital plate; o.br, branchial openings; Or, oral plate; P, pineal plate; Po, postorbital plate; poc, postorbital canal; polc, postoral canal; pc, pineal canal; R, rostral plate; tc, transverse commissure; soc, supraorbital canal; V, ventral plate.
hypothesis by A. Blieck, D. Elliott and P. Gagnier (1991, Fig. 6B). The varied concavity value ($k$ from 4 to 20) was implemented in the implied weighting analysis (length, topology, CI and RI indexes of MPT’s and resulted strict consensus trees did not change). Shown here (Fig. 3B) is the result with concavity value $k = 4$. The positions of the psammosteid taxa are consistent with their positions in the equally weighted analysis. The results of the implied weighting data analysis with $k$ from 1 to 3 represent some topological incongruence between trees from all previous analyses. According to these results, Doryaspis nathorsti is the most basal representative of Pteraspidiformes.
pidoidei clade (family Doryaspidae is not supported). This result appears only with three concavity values and thus requires additional testing. Tree support (standard Bootstrap with traditional search, 5000 rep.) shows high values of absolute frequencies for most clades of psammosteids (Fig. 3). Following the results of the phylogenetic analyses, previous classifications of psammosteids (Halstead, 1993; Novitskaya, 2004) are revised below.

Systematic palaeontology

Subclass Heterostraci Lankester, 1868
Order Pteraspidiformes Berg, 1940

Diagnosis (revised). Prerstral plates present (10:1; numbers represent characters and its states of the analysed matrix); anterior margin of rostral plate convex, rounded anteriorly to a point (4:1); postorbital plates present (21:3); median plates surrounded by fields of tesserae (27:1); lateral canals in fields of tesserae (49:2, 76:2); dorsal plate generally rhomboid with anterior and posterior notches (30:1), their lateral margins strongly convex or angular, may also form anterolateral and posterolateral margins (33:2); ventral plate, posterior margin with V-shaped and narrow posterior notch (67:3); branchial plate with anterolateral ledge (78:1) and unequal width of dorsal and ventral lamellae (79:2); medial margin of branchial plates with concave anterior part and slightly convex posterior part (83:1); ornamentation represented by rows of ridges and tubercles (109:2); trabecular aspidin layer (L2) in exoskeleton (120:1).


Remarks. The clad of psammosteids is well supported, however, some apomorphies change within the ingroup. The following apomorphies of the group are identified in both analyses: 10:1, 21:3, 27:1, 30:1, 49:2, 67:3, 76:2, 79:2, 83:1. Some features characterize only the basal taxa of the ingroup, e.g. family Drepanaspidae (i.e. 30:1, 83:1). Most canals of the lateral line system (soc, pc, ldc, lvc) of the basal psammosteid Drepanaspis are located in fields of tesserae (Obruchev, 1943b, p. 272; Bliček, Elliott, and Gagnier, 1991, etc.). Some presumed ‘apomorphies’ of the ingroup were established after analysis (88:1, 89:1, 90:3, 94:2, 95:2, 96:4), but are not included in the diagnosis, since these characters are known in other representatives of Pteraspidiformes (not included in current analyses). For example, reduction or full absence of the cornual plates (90:3), presence of branchial openings on the distal tip of branchial plates (88:1, 89:1) is not an unique apomorphy of psammosteids and occurs also in protaspids. All known psammosteids lack the lamellar aspidin (L3) on the scales (e.g. Elliott, Mark-Kurik, 2005, p. 107), but this character is insufficiently studied on other pteraspids and cannot be used yet.

Family Drepanaspidae Traquair, 1899

Diagnosis (revised). Prerstral plates present (10:1); anterior margin of rostral plate convex, rounded anteriorly to a point (4:1); rostro-orbital contact absent due tesseract (6:1); postorbital plates present (21:3); median plates surrounded by fields of tesserae (27:1); lateral canals in fields of tesserae (49:2, 76:0); dorsal plate generally rhomboid with anterior and posterior notches (for basal representatives) (30:1), their lateral margins angular, may also form anterolateral and posterolateral margins (33:2); ventral plate, posterior margin with V-shaped and narrow posterior notch (67:3); branchial plate with anterolateral ledge (78:1) and unequal width of dorsal and ventral lamellae (79:2); medial margin of branchial plates with concave anterior part and slightly convex posterior part (83:1).

Taxa included. Drepanaspis gemuendenensis Schlüter, 1887 (included in analysis).

Remarks. The most basal node of the ingroup (Fig. 2). The following apomorphies characterise this basal taxon of the ingroup: 6:1, 10:1, 21:3, 27:1, 30:1, 33:2, 49:2, 67:3, 76:2, 79:2, 83:1. All Drepanaspis gemuendenensis specimens (including juvenile specimens) have fields in the cephalothorax interpreted as fields of tesserae. Following the supposition of Gross (1963, p. 149), I assume that in the case of the most juvenile Drepanaspis, the smallest tesserae (more likely discrete single and complex elements) must be present in the fields of tesserae. So they probably grew more slowly than the plates, not constraining the growth of the latter (unfortunately, the juvenile exemplar of Drepanaspis was lost during WWII). The juvenile Drepanaspis differs from the adult specimens by the more consolidated cephalothorax, which has the following contacts: planar rostro-pineal (8:1), rostro-orbital (6:0), dorso-postorbital, dorso-cornual contacts; triangular pineal plate (14:0). It is possible that the juvenile specimen shows some of the characters of more distant ancestors (recapitulations) (Obruchev, 1967), which would be lost in adults of the same species. Anyway, the juvenile specimen of Drepanaspis falls well in the psammosteoid clade as the basal member.

Family Guerichosteidae Halstead Tarlo, 1964

Diagnosis (revised). Pineal opening (macula) covered by many tubercles on pineal plate (18:2); branchial plates narrow and long with fairly wide, free, laterally projecting margin (anterolateral ledge) (79:3); branchial opening situated at posterior margin (medial from)
Hariosteus are characterized by four synapomorphies (18:2, 79:3, 88:2, 109:3). ‘Harriosteus’ is known from fragmentary material, which makes revision difficult (presence of the dorsal lamella of the branchial plate is not confirmed), but the characters of the ornamentation indicate that this genus probably is a junior synonym of Guerichosteus. Guerichestus heterolepis (Preobrazhensky, 1911) is included in the genus Guerichosteus on the basis of the similar morphology of the branchial plates and ornamentation pattern (Glisnisky and Pinakhina, 2018). The genus Schizosteus, previously included in this family (Halstead Tarlo, 1964a), is excluded here given its synapomorphies with higher psammosteids. Despite their similarity, the two species of Guerichestus do not form a clade, which can be explained by the fragmentary nature of the available material.

Family Obrucheviidae Halstead Tarlo, 1964

Diagnosis (revised). Lateral margins of dorsal plate convexo-concave with branchial sinus (flexure for branchial opening) and with posterolateral process (33:5, 34:1), posterior and lateral margins with arc-shaped contact (36:2); pleromin fully covering main plates as superficial layer (117:2).

Taxa included. Obruchevia heckeri (Obruchev, 1936); Perscheia pulla Elliott, Mark-Kurik et Daeschler, 2004.

Remarks. This group is characterized by two apomorphies (33:5, 117:2). Obrucheviids have plates with a sculptured surface of pits, radial grooves or mounds, the outer layers being infilled by pleromic dentine. Obruchev (1941) believed that the plates were located in soft tissues, but later decided that the surface of the plates was not covered with epidermis (Obruchev, 1968). The presence of lateral line canals on the dorsal plate in Perscheia shows that the dorsal surface of obrucheviids was mostly covered by soft tissue in life (Elliott, Mark-Kurik, and Daeschler, 2004, p. 32). The narrow and long branchial plates of Obruchevia (Obruchev, 1968, p. 26) indicate its origin from the early psammosteids, in which the plates had not yet been shortened. I assume that the dorsal exoskeleton in the obrucheviids was strongly consolidated, and the fields of tesserae did not develop or were extremely narrow. The following characters support this conclusion: the presence of lateral canals of the lateral line on the dorsal plate in Perscheia, and the presence of the paired branchial sinus (sensu Obruchev, 1941) on the dorsal plate. Obruchevia was compared with Cardipeltis, but the similarity of dorsal plates was suggested to be caused by convergence (Obruchev, 1941, 1968).

Traquairosteus pustulatus (Traquair, 1897) is known only from an elongated dorsal (probably ventral) plate (Tarlo, 1961, Fig. 6) that is typical for Psammolestidae. Traquairosteus pustulatus isn’t included in the current analysis. Moreover, herein Traquairosteus is the proposed generic name of the group of species ‘Psammolestes’ ramosus — ‘Psammolestes’ falcatus because all these psammosteids have tubercles on aspidin mounds. The widely spaced tubercles on the main plates of Traquairosteus should be interpreted as the primordial tubercles of the rooted progressive micromeric elements (tesserae) as on the dorsal plate of ‘P. falcatus’ (Obruchev and Mark-Kurik, 1965, p. 66, pl. 88, Fig. 2).

Family Pycnosteidace Tarlo, 1962

Diagnosis (revised). Ventral plate with large U-shaped posterior notch (64:2, 67:4) with protruding edges (69:1) and anterior position of plate primordium (70:2); branchial plates wide eurybasal with length-width ratio more than 0.6 (81:2); medial margin of branchial plates short in the anterior part and convex (expressed) in posterior part (83:3).

Genera included: Ganosteus Rohon, 1901, Pycnosteus Halstead Tarlo, 1964, Pycnosteus Preobrazhensky, 1911.

Remarks. This group is characterized by two apomorphies (64:2, 67:4, 69:1). Pycnosteus is recovered as sister node to Pycnosteus. Ganosteus is sister to Pycnosteus and Pycnosteus. The genus Tartuosteus is excluded from the family Pycnosteidae, exhibiting characters (e.g. reduced shape of postorbital plates) that bring it closer to Schizosteus and Psammolepis (Fig. 3).

Family Psammolepididae Tarlo, 1962

Diagnosis (revised). Rostral plate with aligned anterior margin (4:3); tesselated dorsal plate with small non-tesselated primordium (57:2); ventral plate with lateral and posterior pattern of tesserae (71:3); branchial plates with arcuate convex anterolateral margin (82:1) and with convergently oriented distal tips (85:1).

Genera included. Psammolepis Agassiz, 1845.

Remarks. This group is characterized by apomorphies (4:3, 71:3). Psammolepis are still wide-bodied animals with the basal shape of the main plates retained, but they acquire tesserae on the dorsal and ventral plates (57:2) and oval ventral plate (67:5). Based on the results of the second analysis, Psammolepididae with Psammosteidae may be grouped in one clade of the most tesselated psammosteids on the basis of the following basic apomorphies: dorsal plate with numerous tesserae and small primordium (57:2); ventral plate with secondary convex posterior margin (67:5) and with posterior pattern of tesserae (71:2). Some species, previously grouped...
in the genus *Psammolepis* (see Halstead Tarlo, 1965; Obruchev and Mark-Kurik, 1965) have been moved into another clade (Psammosteidae).

**Psammolepis** Agassiz, 1845

**Diagnosis.** As for the family.

**Type species.** *Psammolepis paradoxa* Agassiz, 1844.

**Species included.** *Psammolepis abavica* Mark-Kurik, 1965; *P. paradoxa* Agassiz, 1844; *P. toriensis* (Mark-Kurik, 1965); *P. venyukovi* Obruchev, 1965.

**Remarks.** The unique specimen of a ventral plate of *Psammolepis venyukovi* is poorly preserved and lacks tesserae (Obruchev and Mark-Kurik, 1965, p. 200); it is the central fragment of a ventral plate with erased margins and probably detached tesserae. Phylogenetic analyses placed ‘*Psammolepis’ alata*, ‘*P*. proia’, ‘*P*. undulata’ (Halstead Tarlo, 1965; Novitskaya, 2004; Obruchev and Mark-Kurik, 1965) and true *Psammolepis* at different places on the tree (Fig. 2), indicating they do not belong within the same genus.

Family Psammosteidae Traquair, 1896 emend. Glinskiy

**Diagnosis (revised).** Dorsal plate oval/pear-shaped with narrowing front part (30:3; 31:2), its lateral margins concavo-convex (33:1) and posterior margin convex (rounded) (36:1); tessellated dorsal plate with large non-tessellated primordium (57:3); ventral plate is very elongated (65:2), rooted tesserae partly covering, large primordium, not covered by tesserae (57:3); ventral plate with anterior position of primordium (70:2) and posterior pattern of tesserae (71:2) of scale-like, rhombic, or square forms without overlapped margins (72:1); medial margin of branchial plates with anteriorly concave and posteriorly expressed convex (eurybasal) (83:2); ornamentation consist of rows of ridges and tubercles (109:2); cell imprints on the surface of tubercles expressed and numerous (116:2).

**Taxa included:** *Vladimirolepis* gen. nov., subfamilies Placosteinae subfam. nov., and Psammosteinae Traquair, 1896.

**Remarks.** The Psammosteidae form a well-supported clade, which is characterized by the following apomorphies: 30:3, 31:2, 57:3, 65:2, 71:2, 72:1, 83:2, 116:2. Some apomorphies (31:2, 57:3, 72:1, 83:2) change within this group. The psammosteids are narrow-bodied animals (shape of median plates). The growth of median plates occurs in the caudal direction (in length). More derived taxa (*Psammolestus*) have an oval dorsal plate with anterolateral lobes (for the support of the branchial plates, 30:4) with ldc canals (49:1); last one indicates the reduced (or absent) fields of tesserae (Fig. 3). Branchial plates are extended in width (the distal parts in the basal species *Vladimirolepis proia* comb. nov. still have such widening), bringing them closer to the Psammosteidae. Tubercles on the branchial plates of most all representatives can fuse into ridges. In later psammosteids (Placosteinae subfam. nov. and Psammosteinae), growth of tesserae was not constrained (progressive tesserization) (Obruchev and Mark-Kurik, 1965; Obruchev, 1972, p. 70).

Psammosteidae subfamily incertae sedis

Vladimirolepis gen. nov.


**Derivation of name.** In honor of the palaeontologist Vladimir Paul, who collected (1934–1940) many unique fish remains from the Middle Devonian deposits of Estonia, and lepis, meaning scale, gender feminine.

**Type species.** *Psammolepis proia* Mark-Kurik, 1965.

**Diagnosis.** Dorsal plate with narrowing front part (30:3), with big primordium in anterior half of plate (55:1, 57:3), first pair of transverse commissures concave anteriorly (41:1), posterior (third) pair of tc concave anteriorly (43:1); eurybasal branchial plates with convexo-linear anterolateral margin (82:0+3).

**Remarks.** The following unique apomorphies characterize only this most basal taxon of Psammosteidae: 30:3, 57:3. The shape of the primordium (juvenile stage of plate) of *Vladimirolepis proia* comb. nov. is identical to the shape of the dorsal plate of *Schizosteus striatus*. Also, the primordium of the ventral plate has a V-shaped posterior notch (64:1) as in the more primitive forms (*Schizosteus*). These characters strongly distinguish *Vladimirolepis* gen. nov. from *Placosteus*. The pattern of ornamentation with tubercles fused in ridges is similar to those in *Schizosteus striatus* and *Placosteus*.

*Vladimirolepis proia* (Mark-Kurik, 1965), comb. nov.

Mark-Kurik, 2005, pp. 101, 103, Fig. 4A; Glinsky, 2014, pp. 985, 986, 989, pl. 4, Figs. 1, 2.

**Diagnosis.** As for the genus.

**Remarks.** The specimen GIT 116–170, earlier defined as a cornual plate, is considered here as the rostral plate.

Subfamily Placosteinæ subfam. nov.

**Diagnosis.** Dorsal plate partly covered by tesserae, with the mosaic of own superficial layer (57:4), its primordium fully covered with tesserae (58:1); rooted tesserae of dorsal plate small (0.2–0.8 cm) (59:2); ventral plate with oval primordium (64:3); dorsal plate with secondarily reduced median posterior process on posterior margin (37:0).

**Type genus.** *Placosteus*, by monotypy.

**Taxa included.** Type genus only.

### Placosteus, Agassiz, 1845

*Placosteus Agassiz: Agassiz, 1833–1843, p. 33 (nomen nudum); 1845, p. 404 (pars).*

*Psammolepis Agassiz: Agassiz, 1844, p. 103 (pars); Eichwald, 1860, p. 1515 (pars); Woodward, 1891, p. 126 (pars).*

*Psammolepis Agassiz: Gross, 1933a, p. 8 (pars); 1935, p. 15 (pars); Obruchev, 1947a, p. 195 (pars); Obruchev, 1964, p. 73 (pars); Obruchev and Mark-Kurik, 1965, pp. 162–164 (pars), 296–297 (pars); Halstead Tarlo, 1965, pp. 95–96 (pars); Novitskaya, 2004, pp. 182–183 (pars).*

**Diagnosis.** Dorsal plate partly covered by tesserae, with the mosaic of own superficial layer (57:4), its primordium fully covered with tesserae (58:1); rooted tesserae of dorsal plate small (0.2–0.8 cm) (59:2); ventral plate with oval primordium (64:3); dorsal plate with secondarily reduced median posterior process on posterior margin (37:0); (59:2); ventral plate with oval primordium (64:3); dorsal plate with secondarily reduced median posterior process on posterior margin (37:0).

**Type species.** *Psammolepis undulatus* Agassiz, 1844.

**Species included.** Type species and *Placosteus alatus* (Mark-Kurik, 1965), comb. nov.

**Remarks.** The two genera *Vladimirolepis* gen. nov. and *Placosteus* gen. nov. are the two early-branching members of the family Psammosteidae; they still have the eurybasal branchial plates (83:2) but strongly differ in general morphology of the juvenile median plates (primordia).

### Placosteus undulatus (Agassiz, 1844)

*Placosteus undulatus Agassiz: Agassiz, 1833–1843, p. 33 (nomen nudum); 1845, p. 404.*

**Psammolepis undulatus Agassiz: Agassiz, 1844, p. 106, pl. 31, Fig. 11, 12; 1845, p. 417; Eichwald, 1860, pp. 1517, 1518 (pars); Woodward, 1891, p. 128.*

*Psammolepis tesselatus Traquair: Traquair, 1897, p. 377, pl. 6, Fig. 1, 2.*

*Psammolepis arenatus Agassiz: Doss, 1915, pp. 77, 78, pl. 2.*

*Psammolepis heteraster Gross: Gross, 1930, pp. 7, 14; pl. 1, Fig. 2; Gross, 1933a, p. 8; pl. 1, Fig. 2; Obruchev and Mark-Kurik, 1965, pp. 190–191, 298, pl. 50, Fig. 1, 2; Text-fig. 154; Novitskaya, 2004, pp. 185–186 (pars).*

**Psammolepis undulata (Agassiz): Gross, 1933a, pp. 8, 9, pl. 1, Figs. 3, 6; Gross, 1942, p. 410, Text-fig. 2A; Tarlo, 1961, pp. 202–204; pl. 7, Fig. 4, 5, Text-figs. 3d, 7; Halstead Tarlo, 1964a, pp. 31, 32, 37, 38, 104, 105, Text-fig. 12A; Obruchev and Mark-Kurik, 1965, pp. 201–211, 299, Text-figs. 166–175, pl. 56, Fig. 1, 2, pl. 57, Fig. 1, 2, pl. 58, Fig. 1–3; pl. 59, Fig. 1–3; pl. 60, Fig. 1–3; pl. 60, Fig. 1; pl. 74, Fig. 1 (non *Psammosteus levis*); Novitskaya, 1965, pp. 273–274, Fig. 219; Halstead Tarlo, 1965, pp. 103–106, Text-fig. 32, pl. 18, Fig. 2; Obruchev and Mark-Kurik, 1968, p. 282, Fig. 1, 3C, 4; Lyarskaya, 1971, pp. 98–101, Text-figs. 3–6; Novitskaya, 2004, p. 187, Text-figs. 122, 123; Elliott and Mark-Kurik, 2005, pp. 101, 103, (non 100), Fig. 4B, 6A–C; Plax, 2010, pp. 64, 65, pl. 1, Figs. 4–10.

? *Psammolepis undulata (Agassiz): Gross, 1935, p. 15, pl. 3, Fig. 4.*

*Psammolepis timanica* Obruchev: Obruchev, 1958, p. 48 (nomen nudum).

**Diagnosis.** As for ‘*Psammolepis* undulata’ in Obruchev and Mark-Kurik (1965, pp. 201, 299).

**Remarks.** *Psammolepis heteraster* Gross, 1930 is considered a junior synonym of *Placosteus undulatus* (Halstead Tarlo, 1964a, pp. 87, 104) on the basis of morphology of branchial plates and ornamentation characters.

### Placosteus alatus (Mark-Kurik, 1965), comb. nov.


*Psammolepis alata* Mark-Kurik: Obruchev and Mark-Kurik, 1965, pp. 184–190, 298, Text-fig. 147–153, pl. 46, Fig 3; pl. 47, Fig. 1, 2; pl. 48, Fig. 1–3; pl. 49, Fig. 1, 2; Mark-Kurik, 1966, pp. 57, 58, pl. 2, Fig. 1, 2; Obruchev and Mark-Kurik, 1968, Fig. 1; Lyarskaya, 1971, pp. 101–104, Figs. 7–9; Novitskaya, 2004, p. 185, Text-fig. 116, 117; Lebedev et al., 2009, p. 348, Fig. 21, J, 3; Johanson et al. 2013, pp. 2–5, Fig. 1b, d–r, Fig. 2.

**Diagnosis.** As for ‘*Psammolepis* alata’ Mark-Kurik, 1965 in Obruchev and Mark-Kurik (1965, pp. 184, 298).

**Remarks.** *Placosteus alatus* is very similar to *Pc. undulatus* but differs in branchial plate shape and some ornamentation characters. The dorsal plate of *Pc. alatus* was possibly fully covered by tesserae.
Subfamily Psammosteiniae Traquair, 1896

**Diagnosis.** Median plates fully covered by tesserae (57:5), which are polygonal in shape and without overlapped margins (60:2); branchial plates shortened (stenobasal) and stretched in width (length-width ratio less than 0.6) (81:3); branchial plates medial margin with short anterior part and convex, expressed posterior part (83:3); branchial plates with expanded unornamented surface on ventral side (87:1).


**Remarks.** This group is characterized by the following basal apomorphies (57:5, 60:2). Currently this group (family Psammmosteidae *sensu* Halstead Tarlo, 1965; Novitskaya, 2004) includes *Psammmosteus* and provisionally retained *Karelosteus* (Glinskiy and Mark-Kurik, 2016; Novitskaya, 2004). Herein two more genera, *Elgaia* gen. nov. and *Traquairosteus*, are included. With the availability of new data on psammosteids, the list of their unique apomorphies must be refined. Presumably all representatives of the family Psammmosteidae appear to lack cornual plates, as in the associated cephalothorax of *Psammmosteus megaloptyeryx* (Woodward, 1911, pl IX, Fig. 1). Halstead Tarlo (1965, p. 121) redescribed this specimen and identified the area with isolated tubercles as the remains of the cornual plate. However, such isolated tubercles also can be attributed to numerous discrete micromeric elements or to the ornamentation, detached from the main plates (tubercles are weakly connected with the plates of *Psammmosteus*, see Mark-Kurik, 1999). The branchial openings presumably are located behind the reduced branchial plates through the branchial sinus of the dorsal plates (Fig. 2). The characters of the Psammmosteinae appear in *Elgaia luhai* (Mark-Kurik, 1965) comb. nov. In the species of *Psammmosteus*, a full reduction of the anterior part of the median margin of the branchial plates is seen, and cyclo-morial, mostly polygonal concentric tesserae of the basic morpho-histological type are formed (Glinskiy and Nilov, 2017). *Traquairosteus* should be nested closer to *Psammmosteus*, as has been noted earlier (Glinskiy and Pinakhina, 2018; Glinskiy, 2018). In *Traquairosteus* the tesserae and other elements of progressive type may be rooted on the other elements of progressive type. *Traquairosteus* is grouped with a question with the species *Psammmosteus ramosus* Glinskiy, 2017, *P*. *pectinatus* Obruchev, 1965, *P*. *kiaceri* Halstead Tarlo, 1964, and *P*. *falcatus* Obruchev in Gross, 1942, from the Upper Devonian (Frasnian) of the Main Devonian Field, Scotland and Ellesmere Island. These psammosteids have extremely stenobasal branchial plates (l:w≤0.3) and discrete tesserae of the progressive morpho-histological type (odontodèle shape), which represent the circular stage of the tesserae development (Glinskiy and Nilov, 2017). Histology of the plates of these psammosteids is very similar to that of *Traquairosteus pustulatus* (aspidin mounds, surrounded by tubercles with massive marginal crenulations (Traquair, 1897, pl. XI, Fig. 4) and differences of tubercle shapes (Traquair, 1897, Additional notes...pl. XI, Fig 4)).

In addition, it should be noted that in the reconstruction of *Psammmosteus* by Halstead Tarlo (Tarlo, 1961, Fig. 5), the proximal parts of the branchial plates are freely located in the cephalothorax. According to this author's opinion, *Psammmosteus* has movable branchial plates (Halstead, 1973, p. 291). However, numerous specimens of *Psammmosteus* branchial plates with the strong marginal lifetime abrasion on the substrate indicate the fixed location of these plates in the cephalothorax. The medial parts of *Psammmosteus* branchial plates definitely grew under anterolateral lobes of the dorsal plate.

*Elgaia* gen. nov.

**Tartuosteus:** Obruchev: Obruchev, 1964, pp. 71–72 (pars); Halstead Tarlo, 1965, pp. 85 (pars); Obruchev and Mark-Kurik, 1968, pp. 280 (pars).


**Derivation of name.** In memory of Elga Mark-Kurik, Estonian palaeontologist and stratigrapher, gender feminine.

**Diagnosis.** Dorsal plate fully covered by dense rooted tesserae (57:5); branchial plates shortened (stenobasal) and stretched in width (81:3); their medial margin with short anterior part and convex, expressed posterior part (83:3); branchial plates with expanded unornamented surface on ventral side of plates (87:1).

**Type species.** *Tartuosteus luhai* Mark-Kurik, 1965.

**Remarks.** Tesserae are not known in the median plates of *Tartuosteus* species (Elliott and Mark-Kurik, 2005, p. 101), the dorsal and branchial plates of *Elgaia* gen. nov. are different from those of *Tartuosteus*. This new genus is the most basal representative of the subfamily Psammmosteinae and differs from *Psammmosteus* by the relative length and shape of branchial plate medial margin (83:3) and mostly scale-like, dense rooted tesserae on the dorsal plate (60:1+2, 62:0).

*Elgaia luhai* (Mark-Kurik, 1965), comb. nov.

**Fig. 4**


pl. 23, fig. 3, pl. 24, fig. 4; Obruchev and Mark-Kurik, 1968, p. 280, 282, fig. 1; Novitskaya, 2004, p. 177, fig. 102.

**Diagnosis.** As for the genus.

**Remarks.** The dorsal plate of *E. luhaei* (Mark-Kurik, 1965), comb. nov., is completely covered by scale-like, cyclomorial tesserae with eccentric position of the primordial tubercles (Fig. 4 G-I), they are consolidated with aspidin layer. A few cyclomorial tesserae are with concentric position of the primordial tubercles as in *Psammosteus* (Fig. 4 G). Branchial plates are stenobasal (Fig. 4 A, B, E, F) with length/width ratio 0.6.

*Psammosteus* Agassiz, 1844

**Diagnosis (revised).** Dorsal plate (and other main plates) with weak rooting of bases of rooted tesserae (62:1); shape of medial margin of stenobasal branchial plates expressed convex (83:4); rooted tesserae mostly polygonal (60:2).

**Type species.** *Psammosteus maeandrinus* Agassiz, 1844.

**Species included:** *P. bergi* (Obruchev, 1943); *P. maeandrinus* Agassiz, 1844; and *P. praecursor* Obruchev, 1947. Provisionally included species: *Psammosteus asper* Obruchev, 1965; *P. cuneatus* Obruchev, 1965; *P. levis* Obruchev, 1965; *P. livonicus* Obruchev, 1965; *P. megalopteryx* (Trautschold, 1880); and *P. tenuis* Obruchev, 1965.

**Remarks.** Currently, there is no way to divide the genus *Psammosteus* into several genera, as there is not enough information on the median plates of many species, their natural margins and interspecific variation. The different morphologies of the juvenile and adult branchial plates and the morpho-histological types of tesserae (Glinksky and Nilov, 2017) suggest several evolutionary lines (potentially genera). The first group (*P. bergi, P. praecursor, P. maeandrinus*; Fig. 2) has triangular branchial plates with an oblique margin of ornamentation on their dorsal side (*Psammosteus*); the second group (all other species provisionally included in *Psammosteus + Karelosteus weberi* Obruchev 1933) has extremely stenobasal branchial plates (81:4) and small zones of ornamentation (87:2). According to the results of phylogenetic analysis, *Karelosteus weberi* Obruchev 1933 is included in the *Psammosteus* clade. However, the genus *Karelosteus* is provisionally retained, because it is not known how many species of the large *Psammosteus* clade will be divided into several genera following a future analysis of all available material. *Psammosteus livonicus* was described in *Orendzechostes* (MoIoshinok, 2009), and later this genus was revised (Glinksky and Mark-Kurik, 2016). Possibly, in the future *P. livonicus* and the related species *P. asper* might be included also in *Karelosteus*. The current analysis included corrected data on the dorsal plate of *Psammosteus livonicus*, which should be expanded by the narrowed part in the caudal direction (error orientation: Mark-Kurik 1968, Fig. 11A; Elliott and Mark-Kurik 2005, Fig. 4 F).

**Traquairosteus** Halstead Tarlo, 1964


**Diagnosis (revised).** Discrete micromeric elements with aspidin mounds, surmounted by tubercles (progressive morpho-histological type) and main plates with peculiar morpho-histological structure (108:4, 119:1); tubercles with very complete marginal crenulations (branching tips and branching on the entire length of crenulations) (114:4).

**Type species.** *Traquairosteus pustulatus* (Traquair, 1897).

**Species included:** *Traquairosteus pustulatus* (Traquair, 1897) ?= *Traquairosteus ? falcatus* (Obruchev in Gross, 1942); *T. ? kiaeri* (Halstead Tarlo, 1964); *T. ? pectinatus* (Obruchev, 1965); and *T. ? ramosus* (Glinksky, 2017).

**Remarks.** This group is characterized by the following apomorphies: 108:4, 114:4. This terminal group of psammosteids has extremely stenobasal branchial plates (like other derived psammosteids) with large tubercles that are located on aspidin mounds (detailed histological and topographic comparisons are needed; this work is held jointly with D.K. Elliott). Widely spaced tubercles on the median plates of *Traquairosteus* should be interpreted as rooted progressive micromeric elements (Glinksky and Nilov, 2017) as on the dorsal plate of *Traquairosteus ? falcatus* (Obruchev and Mark-Kurik, 1965, p. 66, pl. 88, Fig. 2). The holotype of *Traquairosteus pustulatus* probably has imprints from the detached tesserae. Apparently *Traquairosteus pustulatus* and *Traquairosteus ? falcatus* Obruchev in Gross, 1942 are the same species named on different exoskeleton plates. Differences in the ornamentation of *Traquairosteus pustulatus* might be a consequence of topographic variability (branchial plates with complicated ornamentation in contrast to median plates with simple ornamentation) and different conditions of preservation between the locality of Scaat Craig (Scotland) and the Main Devonian Field. The described elongated plate (Tarlo, 1961, Fig. 6) of *T. pustulatus* is probably the ventral plate.

Psammosteidae family incertae sedis

*Schizosteus* pernerii (Růžička, 1929)

**Diagnosis.** As the species description given by Vaškaninová and Kraft (2016).
Fig. 4. *Elgaia luhai* (Mark-Kurik, 1965) comb. nov., branchial and dorsal plates from the Aruküla Regional Stage, (Givetian, Middle Devonian) of Estonia. A–C, E, F, GIT 116–112, holotype, left branchial plate, Mõra outcrop, coll. V. Paul, 1940; A, E, dorsal, B, F, ventral and C, anterolateral views; D, G, H, I, GIT 116–113, dorsal plate, Mõra outcrop, coll. V. Paul, 1934, D, G, general dorsal view, H, I, shots of tesserae are shown in Fig. 4 G (white squares). Abbreviations: arrow indicates the anterior direction, white frames on the Fig. 4 G indicates the shots Fig. 4 H, I, 1, supposed contour line of the plates; 2, supposed margin of the ornamented surface; 3, growth line; 4, primordium tubercle of tesserae (pt); 5, ornamented surface; 6, unornamented surface; 7, destroyed parts of the plate. The differences of the branchial plates’ length-width ratio in dorsal and ventral views (as seen on this figure) is associated with their dorsally convex shape in the transverse-longitudinal direction.
Remarks. 'Schizosteus' perneri (Růžička) might be attributed to guerichosteids on the basis of the presence of the typical ornamentation (fairly smooth margins of tubercles without marginal crenulations) and extremely narrow branchial plates. However, the branchial plates of this species have lost the dorsal lamella (79:4) and have more isometric eurybasal shape (81:1); the derived Middle Devonian psammosteids have such synapomorphies. Obruchev and Mark-Kurik (1965, p.15) stated that 'S. perneri should be attributed to the more basal genus (close to Drepanaspis) and did not include this species in the genus Schizosteus. Oranization of branchial plate 'S.' perneri (holotype) is fairly abraded (Vaškaninová and Kraft, 2016, pl. 1, Figs. 2d-Γ). The limits of variation in the ornamentation on the ventral side of plate are unknown. More data on 'S. perneri are needed. Furthermore it is necessary to postpone naming of a new genus for 'S. perneri until the new information on the problematic 'psammosteid-like' genus Sedowich-thys and the dorsal side of the branchial plate of 'Hariosteus' becomes known. In any case, the guerichosteids and 'Schizosteus' perneri are the early branching lineages derived from the basal psammosteids.

Schizosteus Obruchev, 1940

Diagnosis (revised). Dorsal plate with convex (rounded) posterior margin (35:2); ventral plate with middle sized posterior notch (L1/L2 = 0.3–0.5) (68:1); tubercles with small (0.3–0.7 mm) dominant sizes of bases (111:1); tubercles surfaces with poorly visible cell imprints (116:1).

Type species. Schizosteus asatkini Obruchev, 1940.

Species included. S. asatkini Obruchev, 1940, Schizosteus striatus Gross, 1933.

Remarks. Psammosteids with long and narrow branchial plates. Monophyly of the genus Schizosteus is not supported due to the lack of data on the central (median) plates of the adult specimens of S. asatkini and S. striatus. Thus, it is unknown whether the character 32:1 (straight anterior margin of the dorsal plate) describes only Schizosteus striatus, or both species of Schizosteus. To clarify the position of Schizosteus asatkini Obruchev, 1940, the specimens of Schizosteus ? sp. (Glinskiy, 2014) were included, which are probably worth attributing to this species. Pycnolepis splendens (Eichwald, 1844) was previously attributed to the genus Schizosteus (Novitskaya, 2004; Obruchev and Mark-Kurik 1965). The validity of the genus Pycnolepis Halstead Tarlo, 1964 is supported on the results of this phylogenetic analysis, and it is placed in the clade Pycnosteidae. 'Schizosteus' perneri (Růžička, 1929) is attributed here to the basal evolution line of psammosteids that is close to guerichosteids.

Tartuosteus Obruchev, 1961

Diagnosis (revised). Branchial plates are wide, eurybasal (length-width ratio more than 0.6) with a straight anterolateral margin (82:3) and wide ornamented surface (more less 1) on the dorsal side (86:2).

Type species. Tartuosteus giganteus (Gross, 1933).

Species included. Tartuosteus giganteus (Gross, 1933); Tartuosteus maximus Mark-Kurik, 1965.

Remarks. The current analysis includes only two species of this genus with a generally triangular shape of the branchial plates. Tartuosteus ? (Rohonosteus) ornatus (Rohon, 1899) and T.? zheleznogorskensis Moloshnikov, 2009 are not considered here due to the poor material. The unique specimen of the last species is possibly Psammosteus with pathology of branchial plate development and imprints of detached tesserae on ventral side. Elgaia luhaii (Mark-Kurik, 1965) comb. nov. is placed in the clade Psammosteidae as the basal taxon. Tesserae are not known in the main plates of Tartuosteus species (Elliott and Mark-Kurik, 2005, p.101). Tartuosteus and Psammolepis have a synapomorphy — their postorbital plates do not have the posterior process (24:3).

Discussion and conclusions

The results of the analyses show that psammosteids belong to the Pteraspidiformes. The derived pteraspid (Pteraspidoidae sensu Pernègre and Elliott, 2008 with Doryaspidae Heintz in Tarlo, 1962) form the sister group for the psammosteids. Results of both analyses indicate that psammosteids originate from the basal pteraspidiformes as Protopteraspis (Blieck, Elliott, and Gagnier, 1991). These results contradict a hypothesis that some pteraspid representatives of Doryaspidae Heintz in Tarlo, 1962, must be united in one clade with psammosteids (Pernègre, 2002; Randle and Sansom, 2016, 2017). The present analyses do support the classically accepted monophyly of psammosteids (suborder Psammosteoidei sensu Psammosteida Kier, 1932 emend. Tarlo, 1962) and for the most part the classical arrangement of families: Drepanaspidae; Guerichosteidae; Obrucheviidae; Pycnosteidae; Psammolepididae; and Psammosteidae. This study provides a basis for a deeper investigation into the intra-relationships of the psammosteids. The ingroup taxa have been chosen to represent only the best and most completely known genera. During the analysis the monophyly of some psammosteid genera (e.g. Schizosteus, Tartuosteus, Pycnosteus, Psammolepis) and validity of doubtful taxa (e.g. Pycnolepis splendens) were checked. From the genus Psammolepis sensu Obruchev and Mark-Kurik, 1965, Halstead Tarlo, 1965, are excluded taxa Vladimiroлепsis proia comb. nov., Placosteus undulatus and Placosteus alatus comb. nov. From Tartuosteus sensu Obruchev and Mark-Kurik, 1965, Halstead Tarlo, 1965 is
 excluded *Elgaia luhi* comb. nov. *Elgaia* gen. nov. is the most basal taxon of the subfamily Psammosteinae. Two new subfamilies (Placosteiinae subfam nov. and Psammosteiinae Traquair, 1896) are erected. Also proposed is inclusion of a number of *Psammosteus* species with progressive types of tesserae and peculiar histological structure of other plates in the genus *Traquairosteus* (Gliniskiy and Pinakhina, 2018; Gliniskiy, 2018). *Guerichosteus, Schizosteus* and *Psammosteus* are still very poorly known by median plates and represent here a paraphyletic groups (additional material is needed). New material on the median plates of these taxa and *Karelosteus* is needed for a more correct analysis. The following taxa, used in the analysis, are not assigned to the existing families (Psammosteoidei incertae sedis): ‘*Schizosteus*’ *permeri* (Rüžička, 1929); *Schizosteus* Obruchev, 1940; *Tartuusteus* Obruchev, 1961.

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Appendix 1. List of characters.

Ordered = Ordered character in the matrix.

1. Number of main plates on the dorsal side of cephalothorax: Ordered.
   - (0) one to three, (1) four-five, (2) more than five.

2. Position of the mouth: (0) ventral position, (1) dorsal position.

3. Rostral area / plate, proportions: Ordered.
   - (0) very long, (1) longer than wide, (2) equal to wide, (3) shorter than wide.

4. Rostral area / plate, anterior margin: (0) convex, (1) rounded anteriorly.
   - Modified from ch.1 of Pernègre (2002).

5. Rostral plate, lateral/posterolateral margins (rostro-orbital contact): (0) convex, (1) straight.

6. Rostral plate, posterior margin: (0) absent, (1) present.
   - Modified from ch.22 of Pernègre & Elliott (2008).

7. Rostral plate, lateral/posterolateral margins (rostro-orbital contact): (0) absent, (1) present.
   - Modified from ch.22 of Pernègre & Elliott (2008).

8. Rostral area / plate, proportions: (0) wider than long, (1) as long as wide, (2) longer than wide.
   - Modified from ch.29 of Pernègre & Elliott (2008).

9. Rostral plate, posterior margin: (0) presented, (1) absent, (2) well inserted in dorsal plate.
   - Modified from ch.10 of Pernègre & Goujet (2007). Also ch.15 of Randle & Sansom (2016).

10. Praerostral plates: (0) present, (1) absent.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

11. Oral plates, posterior contact: (0) present, (1) absent.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

12. Orogenal plates (lateral postoral plates): (0) presented, (1) absent.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

13. Pineal plate or macula, their position: (0) absent, (1) present.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

14. Pineal plate, general morphology: (0) triangular, (1) flat topped ovate / croissant, (2) general quadrangular.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

15. Pineal plate, anterior margin: (0) convex, (1) straight.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

16. Orbito-pineal contact: (0) absent, (1) present.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

17. Pineal plate position: (0) in the dorsal plate, (1) in the ventral plate.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

18. Pineal opening (macula), covering: (0) undefined, (1) defined.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).

19. Pineal canal (pc), location: (0) loops around pineal macula, (1) loops through pineal macula.
    - Modified from ch.1 of Pernègre (2002). Also ch.6 of Pernègre & Goujet (2007).
Dorsal shield/plate, width/length ratio: (0) V and U shaped pc (convex to rear), (1) Pc slightly arched, (2) radial pattern. Modified ch.52 of Pernègre & Elliott (2008). Also ch.11 of Blieck & Elliott (1984), ch.40 of Pernègre & Goujet (2007).

21. Orbital area: (0) orbit surrounded by numerous plates (sub-orbitale+dorsale), (1) orbito-cornual plate, (2) orbital plate, (3) orbital and postorbital plate. Modified ch.14, 15 of Pernègre & Elliott (2008). Ch.2 (pars) and 3 (pars) of Blieck & Elliott (1984), ch. 12 of Pernègre (2002), ch.16 of Randle & Sansom (2016). Ordered. Note: Postorbital plates are the result of decay of branchial plates of Pteraspidiformes (Obruchev, 1943).


23. Orbital plates, median process: (1) short, (2) medium, (3) long. Modified from ch. 17 of Pernègre & Goujet (2007), ch.16 of Pernègre & Elliott (2008). Note: The orbital plates of Drepanaspis have the short medial process (Gross 1963, fig. 4M).


25. Postorbital canal (poc) of lateral-line system: (0) absent, (1) present (one canal), (2) present (radial canals). Modified from ch.16 of Pernègre (2002).


27. Median plates surrounded by fields of tesserae: (0) absent, (1) present. After ch.28 from Randle & Sansom (2016). Also ch.1, ch.2 (pars) from Blieck & Elliott (1984).


29. Dorsal shield/plate, width/length ratio: (0) very elongated (width/length ratio less than 0.7), (1) elongated or broad (width/length more than 0.7), (2) isometric or very broad (width/length ≥ 1). After ch.32 of Pernègre & Elliott (2008). Also ch.16 of Pernègre & Goujet (2007).

30. Dorsal shield/plate, general shape of adult plate: (0) polygonal without reduced posterior margin (i.e. plate/shield has postero-lateral lobes which contacts with lateral plates, (1) rhomboid with anterior and posterior notches, (2) heart-shaped, (3) oval/pear-shaped with narrowing front part, (4) oval with anterolateral lobes. Ordered.

31. Dorsal plate, general shape of primordium (for psammosteids): (0) rhomboid with anterior and posterior notches, (1) heart-shaped, (2) elongated with a narrowing in front. Ordered.

32. Dorsal shield/plate, anterior margin curvature: (0) concave, (1) straight, (2) convex, (3) convex to a point. After ch.38 of Pernègre & Elliott (2008). Also ch.22 of Pernègre (2002) and ch.10, 45 of Pernègre & Goujet (2007).

33. Dorsal shield/plate, lateral margins curvature: (0) convex, (1) concavo-convex (pear shape), (2) angular, may also form anterolateral and posterolateral margins (rhomboid/heart-shaped dorsal plate), (3) straight, (4) convexo-concave, (5) convexo-concave with posterolateral process (fam. Obrucheviidae). Modified from ch.24 of Pernègre & Goujet (2007), ch.34 of Pernègre & Elliott (2008).

34. Dorsal shield/plate, branchial sinus: (0) absent, (1) present. After ch.31 of Randle & Sansom (2016). Note: Branchial sinus (Kiaer, 1932) or flexure (Voichyshyn, 2011) is located on the lateral margins of dorsal shield/plate and serves to position the branchial openings or cornual plates. D. Obruchev noted, that the some dorsal plates of Obruchevia have the branchial sinus (Obruchev, 1941, p. 18).

35. Dorsal shield/plate, posterior margin curvature: (0) concave (1) straight, (2) convex (rounded), (3) convex (angular). Modified ch.27 of Pernègre & Goujet (2007). Also ch.35 of Pernègre & Elliott (2008), ch.29 of Randle & Sansom (2016). Notes: Margin curvature without shape of median posterior process. The shape of the posterior margin of plates can be restored by growth lines. Some psammosteids with rhomboid and heart-shaped dorsal plate have very thin posterior margin, but have the median posterior process.

36. Dorsal shield/plate, contact between posterior and lateral margins: (0) obtuse angle, (1) arc-shaped contact. Modified ch.37 of Pernègre & Elliott (2008). Also ch.44 of Pernègre & Goujet (2007).

37. Dorsal shield/plate, median posterior process on the posterior margin: (0) present, (1) absent, (2) present (mid-posterior process, posterior medial peak): (0) absent, (1) present. After ch. 29, 32 of Randle & Sansom (2016).

38. Dorsal plate, posterior notch of the dorsal plate (for the independent dorsal spine or ridge-scale): (0) present, open, (1) present, enclosed, (2) absent. Ordered. Modified from ch.3 of Ilyes & Elliott (1994), ch.2 of Pernègre (2002), ch. 33, 35 of Randle & Sansom (2016). Note: Drepanaspis gemuendenensis has posterior notch with fold.

39. Dorsal spine: (0) present, fused to dorsal plate, (1) present, independent dorsal spine, (2) absent. Modified from ch.2 of Pernègre (2002). Also ch.1 (pars) from Blieck & Elliott (1984), ch.10 of Pernègre & Elliott (2008), ch. 34 of Randle & Sansom (2016). Note: Drepanaspis gemuendenensis hasn’t the dorsal spine.

40. Dorsal shield/plate, transverse commissures (to or radiating commissures): (0) 1 pair, (1) 2 pairs, (2) more than 3 pairs, (3) absent. Modified from ch.3 of Pernègre (2002). Note: The exact quantity of transverse commissures for Perschea pulsa is not known.

41. Dorsal shield/plate, transverse commissures pattern, anterior (first) pair: (0) straight or convex anteriorly, (1) concave anteriorly. After ch.40 of Pernègre & Elliott. Also ch.59 of Randle & Sansom (2016).
42. Dorsal shield/plate, transverse commissures pattern, middle (second) pair: (0) straight or convex anteriorly, (1) concave anteriorly. After ch.41 of Pernègre & Elliott (2008). Also ch.30 of Pernègre & Goujet (2007), ch.60 of Randle & Sansom (2016).

43. Dorsal shield/plate, transverse commissures pattern, posterior (third) pair: (0) straight, (1) concave anteriorly. (2) convex anteriorly. After ch.42 of Pernègre & Elliott (2008). Also ch.31 of Pernègre & Goujet (2007) and ch.61 of Randle & Sansom (2016). Note: In the analysis, we have used data on juvenile Placosteus undulatus (GIT 116-231) in which the represented lateral system line.

44. Dorsal shield/plate, median transverse commissures (mtc): (0) absent, (1) presence on the anterior part of the plate (near with pair tc1-tc2), (2) presence on the posterior part of the plate (near with pair tc2-tc3). After ch.43 of Pernègre & Elliott (2008). Also ch.62 of Randle & Sansom (2016).

45. Dorsal plate, median transverse commissures (mtc), quantity: (0) two, (1) one. Note: The exact quantity of median transverse commissures for Perscheia pulla is not known.


47. Dorsal shield/plate, anterior mdc begins on the dorsal shield/disc without connection to any other canals: (0) absent, (1) present. After ch.54 of Randle & Sansom (2016). Also ch.45 of Pernègre & Elliott (2008).


49. Dorsal shield/plate, lateral dorsal canal (ldc): (0) absent, (1) present on the shield/plate, (2) present in the fields of tesserae. Note: The lateral dorsal canal of Perscheia pulla and of some Psammosteus is located along the lateral margins of the plate. Perhaps Perscheia pulla had narrow fields of tesserae, or they were not at all.

50. Dorsal shield/plate, contact between the anterior transverse commissures (tc) and the lateral dorsal canal (ldc): (0) the anterior tc contacts the ldc on its anterior third, (1) the anterior tc contacts the ldc on its medial third. (2) the anterior tc contacts the ldc somewhere in the fields of tesserae. Modified ch.46 of Pernègre & Elliott (2008), Ch.22 of Pernègre & Goujet (2007), ch.65 of Randle & Sansom (2016). Note: Psammosteus megalepotheryx and Psammosteus bergi perhaps have the contact in the bases of the rooted tesserae.

51. Dorsal shield/plate, position of the lateral dorsal canal (ldc): (0) ldc very far from the lateral margins of the dorsal plate, (1) ldc moderately far from the lateral margins of the dorsal plate, (2) ldc close to the lateral margins of the dorsal plate. After ch.47 of Pernègre & Elliott (2008), Ch.21 of Blieck & Elliott (1984), ch.25 of Pernègre & Goujet (2007).

52. Posterior prolongation of the supraorbital canals (soc): (0) soc between the orbital and pineal areas or in the pineal plate, (1) soc on the orbital plate. After ch.48 of Pernègre & Elliott (2008). Ch.20 of Pernègre & Goujet (2007) and ch.50 of Randle & Sansom (2016).

53. Position of posterior part of soc: (0) medial, (1) lateral (also in the fields of tesserae). Modified ch.51 of Randle & Sansom (2016).

54. Dorsal shield/plate, type of ornamentation & growth: (0) lateral addition of dentine ridges (longitudinal ridges), (1) concentric ridges from a primordium, (2) concentric rows of tubercles from a primordium, (3) absent (tesserae). Modified from ch.6 of Pernègre & Elliott (2008). Also ch.17 (pars) of Blieck & Elliott (1984), ch.10 of Pernègre (2002), ch.6 of Pernègre & Elliott (2008), ch.43 of Randle & Sansom (2016). Ordered.

55. Dorsal shield/plate, growth center (ornamentation’s primordium), their position: (0) lack of primordium, (1) anterior half of the plate, (2) near half of the plate, (3) posterior half of the plate. Modified from ch.11 of Pernègre (2002) and ch.44 of Randle & Sansom (2016).

56. Dorsal shield/plate, density of ornamentation on the dorsal disc: (0) ridge (or tubercle) density equal or superior to 10 per millimetre, (1) density inferior to 10 per millimetre. After ch.7 of Pernègre & Elliott (2008). Also ch.29 of Pernègre (2002), ch.6 of Pernègre & Goujet (2007).

57. Dorsal shield/plate, degree of coverage of the rooted tesserae: (0) absent, (1) rare single tesserae, (2) numerous tesserae (small primordium not covered by tesserae), (3) numerous tesserae (large primordium independent plate not covered by tesserae), (4) numerous tesserae (partial coverage with the mosaic of own superficial layer (see Obruchev & Mark-Kurik, 1965, text-fig. 170)), (5) dorsal plate full covered by tesserae. Ordered.

58. Dorsal plate, tesserae on the primordium: (0) absent, (1) present.

59. Dorsal plate, maximal sizes of the rooted tesserae: (0) large (more than 1.6 cm), (1) medium (0.8-1.6 cm), (2) small (0.2 — 0.8 cm).

60. Dorsal plate, dominated shape of the rooted tesserae and overlapping: (0) scale-like, rhombic, square, with overlapped margins, (1) scale-like, rhombic, square, not overlapped margins, (2) polygonal, not overlapped margins.

61. Dorsal plate, groove type of the rooted tesserae: (0) cyclomorial, concentrical position of primordial tubercle, (1) cyclomorial, eccentric position of primordial tubercle, (2) synchronomorial.

62. Dorsal plate (and other main plates), degree of rooting of the bases of the rooted tesserae: (0) dense rooting, (1) weak rooting with development canals in the aspidin.

63. Dorsal shield/plate, internal organ impressions on the visceral surface: (0) absent, (1) present. After ch.38 of Pernègre & Goujet (2007), ch.36 of Pernègre & Elliott (2008), ch.41 of Randle & Sansom (2016).

64. Ventral plate, form of the primordium (shape of the juvenile plate): (0) posterior notch is present (small V-shaped), (1) posterior notch is present (large V-shaped), (2) posterior notch is present (large U-shaped), (3) oval shape, posterior notch is absent, (4) primordium isn’t distinguishable due the tesserae pattern. Ordered.

65. Ventral plate, width/length ratio: (0) elongated (width/length ratio 0.5 — 0.7), (1) broad (width/length ratio more than 0.7), (2) very elongated (width/length ratio less than 0.5).

66. Ventral shield/plate, anterior margin shape: (0) concave or straight in the middle, (0) convex. Notes: Data on Drepanaspis from Gross (1963), Obruchev & Mark-Kurik (1965), pp. 38, 39. Lateral margins of ventral plates of all representatives have the same shape.
67. Ventral shield/plate, posterior margin shape and shape of posterior notch: (0) convex angular, (1) convex, (2) straight or slightly concave, (3) V-shaped / thin posterior notch, (4) U-shaped / broad posterior notch, (5) secondary convex (overgrown of V-shaped posterior notch/ O-shaped growth center), (6) secondary convex, with posterior middle process (Psammolestes). Note: Character state provisionally indicated for the juvenile Drepanaspis.

68. Ventral plate, ratio of length of posterior notch (L1) and ventral plate (L2): (0) short posterior notch (L1/L2 = 0.1-0.25), (1) middle sized (L1/L2 = 0.3-0.5), (2) long (L1/L2 more than 0.5), (3) extreme long (L1/L2 = 0.8).

69. Ventral plate, protruding edges of the posterior notch: (0) absent, (1) present (visceral side bears a thin line of ornamented surface, protruding edges usually covering by pleuronin (Pycnosteus, Ganosteus).

70. Ventral shield/plate, position of primordium (growth center): (0) posteriorly, (1) middle/near the middle, (2) anteriorly.

71. Ventral shield/plate, covering by rooted tesserae (Schizostegus, Tortuostegus, Ganosteus): (0) absent, (1) few tesserae in posterior notch and on the posterior parts of plate, (2) posterior pattern of tesserae, (3) lateral and posterior pattern of tesserae, (4) full covering by tesserae. Ordered.

72. Ventral plate, shape of rooted tesserae and overlapping margins (Psammolepis’-shape): (0) scale-like, rhombic, square, not overlapped margins, (2) mostly polygonal (Psammolestes’-shape).

73. Ventral plate, groove type of the rooted tesserae: (0) cyclomoral, concentrical position of primordial tubercle, (1) cyclomoral, eccentrical position of primordial tubercle, (2) synchronomoral.

74. Ventral plate, sizes of the rooted tesserae: (0) big (more than 1.6 cm) (1) medium (0.8-1.6 cm) (2) small (0.2 — 0.8 cm).


76. Ventral shield/plate, presence of the paired lateral ventral canal (lvfc): (0) lvc (only) present, (1) lvc with transverse commissures, (2) absent, only transverse commissures. Note: The most psammosteids have lvc in the ventrolateral fields of tesserae.

77. Branchial plates reaches the proximal margins of the cephalothorax: (0) absent, (1) present.

78. Branchial plates, lateral/anterolateral ledge: (0) absent, (1) present. Note: Anglaspis and psammosteids have the lateral/anterolateral ledge on the branchial plates.

79. Branchial plates, dorsal lamella: (0) lack of dorsal lamella, (1) width of ventral and dorsal lamellae equal, (2) unequal width of lamellae, (3) lamellae are partly fused, free anterolateral ledge and distal tip, (4) lamellae are fully fused. Modified ch.4 of Pernègre & Elliott (2008), ch.20 of Blicke & Elliott (1984). Ordered. Note. The anterolateral ledge also call as the free laterally projecting margin (Halstead Tarlo, 1965, p. 40).

80. Branchial plates, branchio-dorsal contact: (0) long, more than half disc length, (1) short, less than the half disc length, (2) lack of contact. After ch.33 of Pernègre & Elliott (2008). Also ch.23 of Blicke & Elliott (1984), ch.23 of Pernègre & Goujet (2007). Note: Psammosteids probably have the contact of medial part of branchial plates with visceral side of the dorsal plate, but we do not see this contact under the tesserae. For either psammosteid the character state established on the basis of eurybasal/ stenobasal form of branchial plates.

81. Branchial plates, length-width ratio (l:w): (0) narrow eurybasal (more than 1.5 — 2), (1) isometric eurybasal (more than 0.9 to 1.5), (2) wide eurybasal (more than 0.6), (3) stenobasal (less than 0.6), (4) extremely short stenobasal (less than 0.3). Note: Narrow eurybasal branchial plates perform mainly the function of the bearing surface (underwater gliding), more wide plates also adapted for the supports on the ground. Modified ch.4 (pars), ch.17 (pars), ch.23 (pars) of Blicke & Elliott (1984). Ordered.

82. Branchial plates, shape of lateral/anterolateral margin: (0) slightly convex, (1) arcuate convex (arc-shape for Protaspis, Psammolepis), (2) generally concave, (3) linear. Modified ch.23 of Blicke & Elliott (1984).

83. Branchial plates, shape of medial margin: (0) straight or concave (also arc-shape for Protaspis), (1) anterior part is concave and posterior part is slight convex (eurybasal), (2) with anterior concave and posterior expressed convex (eurybasal), (3) anterior part is short (straight/concave) and posterior part is expressed convex (eurybasal/stenobasal), (4) expressed convex (stenobasal). Ordered.

84. Branchial plates, shape of posterior margin: (0) convex posteriory, (1) straight or concave posteriorly. Note: The juvenile branchial plate of Pycnosteus palaiformis, described by Glinskiy (2014) not included in the analysis.

85. Branchial plates, distal tip: (0) back oriented (divergent), (1) back oriented (convergent), (2) forward oriented, (3) truncated (for Obruchevio).

86. Branchial plates, ratio of the ornamented/unornamented surface (w1:w2) on the dorsal side of plates: (0) ornamented surface is narrow (from 0.2 up to 0.5), (1) equally (from 0.5 up to 1), (2) ornamented surface is wide (more less 1). Ordered.

87. Branchial plates, ratio of the ornamented/unornamented surface (w1:w2) on the ventral side of plates: (0) unornamented surface is narrow, (1) expanded unornamented surface, (2) extremely expanded unornamented surface (for representatives of Psammolestes). Ordered.

88. Branchial openings, position: (0) at the second half of branchial plate, (1) at the distal tip of branchial plate, (2) at the posterior margin of branchial plate. Modified ch.1 of Pernègre & Elliott (2008). Ch.1 of Ilyes & Elliott (1994), ch. 20 of Pernègre (2002), ch.5 of Pernègre & Goujet (2007), and ch.20 of Randle & Sansom (2016). Ordered.


91. Cornual plates, length-width ratio: (0) narrow (l=w), (1) broad (l=w), (2) very broad (l<w). Modified ch.13 of Pernègre & Elliott (2008). Also ch. 24 of Blicke & Elliott (1984), ch.23 of Randle & Sansom (2016).
92. Cornual plates, general shape: (0) triangular, (1) rectangular, trapezium-shape. Note: Shape of cornual plates of *Drepanaspis gemuendenensis* is variable (Obruchev & Mark-Kurik, 1965, p. 35), juvenile form has triangular cornual plates.

93. Cornual plates, margins: (0) lateral (external) and posterior margins straight/convex, (1) lateral (external) margin concave and posterior margin convex, (2) lateral (external) margin convex and posterior side concave. Modified ch.22 of Randle & Sansom (2016).

94. Cornual plates, posterior extension: (0) less than posterior margin of dorsal plate, (1) equal to posterior margin of dorsal plate, (2) greater than posterior margin of dorsal plate. After ch.24 of Randle & Sansom (2016).

95. Cornual plates, ornamentation: (0) scale-like ornamentation, (1) long ridges parallel to the lateral (external) edge, (2) like on the median plates. After ch.25 of Randle & Sansom (2016).

96. Cornual plates, lateral projection: (0) lateral projection less than brachial plate, (1) lateral projection the same as brachial plates, (2) lateral projection just up to greater than double that of the branchial plates, (3) lateral projection vastly greater than brachial plate, (4) cornual plates placed on dorsal shield. After ch.23 of Randle & Sansom (2016).

97. Cornual — ventral contact: absent (0), present (1). After ch.21 of Pernègre. (2002). Note: Ornamentation doesn't present on the visceral side of cornual plate, which not contacting with ventral plate.

98. Flank scales, morphology: (0) short and broad, (1) rombic shape with short unornamented surface, (2) rombic/round shape with extended unornamented surface.

99. Flank and ridge scales, groove lines and ornamentation: (0) longitudinal / transversal ridges, (1) V-arc-ordered ridgelets/tubercles, (2) areal groove zones of ridgelets/tubercles (like in cyclomorial tesserae, primordial tubercle located close to the center of scale). Ordered.

100. Flank scales, rows of lateral squamation: (0) reduced number of rows, about two, (1) more than 2 rows. After ch.17 of Pernègre (2002). Ch.58 of Pernègre & Elliott (2008). Note: The squamation is unknown in many taxa, but the size of isolated scales allows an approximation of the number of lateral rows of scales.

101. Flank scales, relative width in different rows: (0) different width, (1) same width. After ch.26 of Pernègre, 2002.

102. Flank scales, relative length: (0) > than ridge scales, (1) equal to ridge scales, (2) < than ridge scales. After ch.18 of Pernègre (2002). Ch.59 of Pernègre & Elliott (2008).

103. Flank scales, sizes: (0) large (up to 1.6 mm), (1) medium (0.8-1.6 mm), small (less than 0.8 mm) (*Psammosteus*).

104. Flank scales, row of subperpendicular denticle ridges on the free margins (like in *Drepanaspis*, *Schizosteus*): (0) present, (1) absent. Note: *Psammosteus toriensis*, *Traquairosteus ramosus* have circular pattern of dentine ridgelets not on the free margins.

105. Caudal fin, type: (0) heterocerical, (1) hypocerical, (2) homocerical.

106. Fields of tesserae, average sizes of discrete tesserae: (0) large (1.8-3 cm) (1) medium (1 mm up to 1.8 cm) (2) small (less than 1 mm). Note: In case if the material on the isolated tesserae is not known, were also used data on rooted tesserae.

107. Fields of tesserae, presence of the single elements and complex elements (not in juvenile forms): (0) absent, (1) present.

108. Tesserae, morphology, morpho-histological type of the discrete elements: (0) scale lake with overlapping zones, (1) scale-like without overlapping zones, (2) mostly polygonal, basic type, discrete tesserae with high neck, (3) mostly polygonal, basic type, discrete tesserae with low neck, (4) progressive type. Note: In cases where material of the isolated tesserae is not known, data on rooted tesserae were used. For the additional information see Glinskiy & Nilov (2017). Ordered.

109. Ornamentation, general pattern on the main plates: (0) uniform (continuous ridges / continuous tubercle bands pattern), (1) undulating ridges (tuberculated ridges only), (2) rows of ridges and tubercles, (3) rows of discrete tubercules (up to 3 tubercles may fuse together in the «ridgelets»), (4) pleromin. Modified ch.42, 47 of Randle & Sansom (2016). Ch.2 of Ilyes & Elliott (1994), partly ch.9 of Pernègre & Elliott (2008). Note: *Drepanaspis gemuendenensis* has rows of ridges and tubercles, see Gross, 1963, p. 139.

110. Ornamentation, relative position of ridges/tubercles: (0) very dense position (so called ‘parquet’), (1) between the tubercles are visible the solitary pores of aspidin, (2) far position of relative tubercles.

111. Ornamentation, the dominant sizes of tubercle bases: (0) very small (less than 0.3 mm), (1) small (0.3 — 0.7 mm), (2) middle (0.7 — 1 mm), (3) large (1 — 1.5 mm), (4) very large (more than 1.5).

112. Ornamentation, primordial tubercles surrounds by satellite tubercles (on the main plates excluding tesserae): (0) absent, (1) present.

113. Ornamentation, tops of dentine ridges/tubercles: (0) smooth, (1) crested/sharpened. Adapted from ch.46 of Randle & Sansom (2016).

114. Ornamentation, margins of dentine ridges/tubercles: (0) smooth (radial ribs do not pass into the marginal serrations/crenulations), (1) radial ribs form the serrations, (2) simple crenulations (tips branch rare), (3) complete crenulations (tips branch often), (4) very complete crenulations (branching tips and branching on the entire length of crenulations). Modified ch.45 of Randle & Sansom (2016). Also ch.6 of Bleek & Elliott (1984), ch.21 of Pernègre & Goujet (2007), partly ch.9 of Pernègre & Elliott (2008).

115. Ornamentation, orientation of dentine ridges on the branchial plates: (0) subparallel to the anterolateral margin (1) worm-like shapes, (2) subperpendicular to the anterolateral margin, convex distally, (3) subperpendicular to the anterolateral margin, convex proximally.

116. Cell imprints on the surface of tubercles: (0) absent, (1) present, poorly visible or maybe rare, (2) present, expressed and numerous.

117. Pleromin: (0) absent, (1) present, (2) present (full covering). Ordered.

118. Aspidin reticular layer (L1) of the median plates of cephalothorax: (0) absent, (1) present. Histological information from Novitskaya (1965), Novitskaya (2004), Keating et al. (2015).

119. Aspidin mounds (ridges of L1 on the main plates): (0) absent, (1) present.

120. Aspidin layer (L2) of the median plates of cephalothorax: (0) cancellar, (1) compact. Note: Histological information from Novitskaya (1965), Novitskaya (2004), Keating et al. (2015) etc.