

NOTES ON THE SQUAMATION IN PSAMMOSTEIDS

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Of the numerous psammosteids (Agnatha, Heterostraci) only one species, *Drepanaspis gemuendenensis* Schlüter (Lower Devonian, Rhineland), shows an articulated squamation and a well-preserved caudal fin. *Drepanaspis* exhibits the three main kinds of scales characteristic of all psammosteids: flank scales, ridge scales and tail fin scales. Narrow overlapping margins of scales are also a noteworthy feature in psammosteids. In this paper, partly preserved squamation of the Middle Devonian *Schizosteus striatus* (Gross) and *Psammosteus* sp. is demonstrated. The *Psammosteus* species differ from other psammosteids in possessing small and rather uniform scales. This type of squamation could hardly have been derived from that of *Psammolepis* and, consequently, *Psammosteus* was not a descendant of *Psammolepis*.

KEY WORDS: Psammosteids, Agnatha (Heterostraci), Devonian, squamation, caudal fin, relationships

INTRODUCTION

Among the Devonian heterostracans (Agnatha), psammosteids present a later group that flourished in the Euramerican area after the extinction of the majority of the diverse groups of early heterostracans (cyathaspids, pteraspids, etc.). The suborder Psammosteida Kiaer, 1932 includes five families: the Lower Devonian Drepanaspidae and Guerichosteidae and the Middle-Upper Devonian Pycnosteidae, Psammolepididae and Psammosteidae (Halstead Tarlo, 1964). Despite the rather large number of psammosteid taxa (more than 10 genera and 50 species), the group is comparatively poorly known. Except for a single species, *Drepanaspis gemuendenensis* Schlüter, all the psammosteids have been described on the basis of disarticulated material; in particular, on the branchial plates which are the most commonly preserved massive skeletal elements. The actual squamation and tail fin are seen in *D. gemuendenensis* only, even though the available specimens are deformed (Gross, 1963). In the other psammosteids, i.e. *Psammolepis*, *Psammosteus*, *Schizosteus* and *Pycnosteus*, the scale pattern and the shape of the tail fin have been restored using *Errivaspis* (*Pteraspis* of White, 1935) and/or *Drepanaspis* (figured by different authors) as models.

Several authors (Denison 1971; Janvier 1981; Blicek *et al.* 1991) have reviewed the structure of heterostracan tails. The caudal fin is better known in pteraspids and, particularly, in cyathaspids and does not vary much, resembling in most cases a simple pad (Janvier 1981). However, in *Ctenaspis* (Dineley 1976) it is fan-like and *Athenaegis* (Soehn and Wilson 1990), it is forked and nearly symmetrical. In *Cardipeltis*, a peculiar three-lobed tail has been described (Denison 1971). It should be mentioned that some (or most?) of these caudal fins were certainly compressed in sediment and rock, so that they became more slender and their delicate parts

remained unnoticed or were lost. The pteraspids *Cosmaspis?* (Denison 1971, figure 9) and *Stegobranchiaspis* (Elliott 1983, figure 6) show almost undeformed articulated tail fins which broaden rapidly in their posterior portion, this being twice as high as the anterior portion. Some heterostracan caudal fins (in *Drepanaspis*, *Ctenaspis*, *Errivaspis* and *Athenaegis*) display finger-like rows of larger scales serving for reinforcement of the fin. The position of the notochord relative to the fin lobes (if present) is unclear, as was pointed out by Denison (1971). The dorsal and ventral ridge scales or scutes, occurring in the vast majority of heterostracans, restricted the flexibility of the caudal region and the tail fin. A comparatively large surface area and some degree of rigidity are the normal conditions needed for a single propulsion instrument such as the heterostracan tail. According to Belle-Isles (1987), the pteraspids were powerful swimmers. One can fully agree with this conclusion. In the psammosteid *Drepanaspis*, the tail fin was more than a quarter of the length of the animal, again evidencing good swimming ability.

The present paper gives a review of, and some new information on, the squamation and the caudal fin of the psammosteids of different families. The figured specimens are housed in the fish collection (with the index Pi) of the Institute of Geology, Estonian Academy of Sciences in Tallinn.

PSAMMOSTEID SQUAMATION

Drepanaspididae

The squamation and the caudal fin in *Drepanaspis gemuendenensis* have repeatedly been restored and figured (see Gross 1963, p. 134; Obruchev and Mark-Kurik 1965, figures 1–8, 10). Gross's restoration (1963), based on carefully documented specimens, can be considered as the most authentic (Figure 1). The richness of the material has compensated for the effects of the deformation characteristic of specimens from the Hunsrückschiefer. It is worth mentioning that, as a rule, the rather wide and dorsoventrally flattened body took a position parallel to the bedding plane, so that the posterior of the trunk became twisted, the flank scales piled (Gross 1963, pl. 7, fig. 4, plus figures 8B, D, E; Halstead Tarlo 1965, pl. 6, fig. 1) and the length of the caudal region diminished. Consequently it is not quite clear just how widely the scales overlap one another. At least one *D. gemuendenensis* specimen (Obruchev and Mark-Kurik 1965, pl. 2) shows that the anterior edge of the scales is convex or

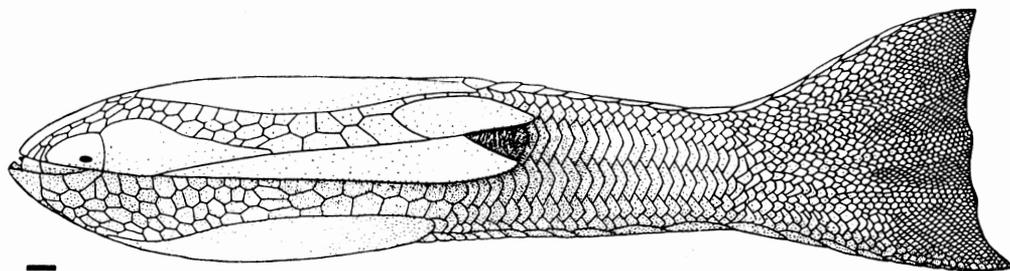


Figure 1 *Drepanaspis gemuendenensis* Schlüter in lateral view. Restoration from Gross, 1963. Bar = 10 mm.

slightly sinuous and the overlapping margin is rather narrow, resembling the condition in another *Drepanaspis* species, *D. jaegeri* Tarlo (Halstead Tarlo 1965, pl. 7, fig. 5). A character that could, to some extent, also be the result of compression of the *Drepanaspis* specimens is the position of the ridge scales, lying flat on the body surface. In the other psammosteids they were evidently situated in the soft tissues at some angle, their posterior ends being raised to form a tile-like row.

Nevertheless, *Drepanaspis* serves as a model for the main kinds of scales in psammosteid squamation. Three kinds can be recognized: (1) the trunk scales, which are comparatively large and, on the body sides, rather high and short; (2) scales covering the tail fin; these are small or very small, oval or angular; and (3) ridge scales arranged along the midline on the dorsal and ventral sides; the more anteriorly placed of these scales are shorter and wider, the posterior ones becoming longer and narrower. According to Gross (1963, figure 10), there are fourteen larger scales on the dorsal side and ten on the ventral side. The six ventral ridge scales in the middle of the row are the largest. Both ridge scale rows end with very narrow and small scales on the caudal fin.

Guerichosteidae

Two Early Devonian representatives of this family, *Guerichosteus* and *Hariosteus*, have yielded only fragmentary scales and ridge scales (Halstead Tarlo 1965, pls. 11–13). This state of preservation is characteristic of the material from the Daleszyce locality (Holy Cross Mountains, Poland). The flank scales are rather high, with a moderately convex anterior edge and a narrow overlapping margin. Different kinds of ridge scales, flatter and wider or more strongly arched and longer, have been discovered, some of them showing an unornamented proximal area that was in contact with soft tissues. The scales overlapped one another, their distal parts overhanging the proximal parts of those succeeding (Halstead Tarlo 1965). This position of ridge scales in the rows permitted upward and downward movement of the posterior part of the body and the tail, a capacity emphasized by Denison, 1971. The overlap of ridge scales observed in guerichosteids is universal for psammosteids, except perhaps the drepanaspid.

The characteristics of the third representative of the family, *Schizosteus*, are particularly well seen in *S. striatus* (Gross), where not only isolated scales (Obruchev and Mark-Kurik 1965, pls. 15, 17, plus figures 42, 43) but also a portion of the articulated squamation (Pi 416) have been found (*op. cit.*, pl. 18, fig. 3, plus figure 44; Figure 2 herein). The locality of the specimen is Gorodenka, NE Estonia (Middle Devonian, Eifelian, Narva Formation). In contrast to the earlier interpretation (*op. cit.*, p. 106), the fragment of the squamation is thought to come from the distal part of the trunk (not from the tail), as the ventral ridge scales (vrs) of this specimen are comparatively flat; the ridge scales of the tail should have sharp crests and be strongly arched. The flank scales, predominantly square and belonging mainly to the right side, are exposed from their visceral surfaces. A number of dorsoventrally elongated scales occur in the anterior portion of the specimen, whereas the posteriorly placed scales are longer than high. All these kinds of scales have been found separately, some being up to 30 mm high and almost as long.

The specimen Pi 416 is unique in showing the structure and position of the lateral line on the body of the psammosteids (Figure 2, sc). Judging by the shallow grooves on the spongy visceral surface of the scales, the sensory canal was situated in soft

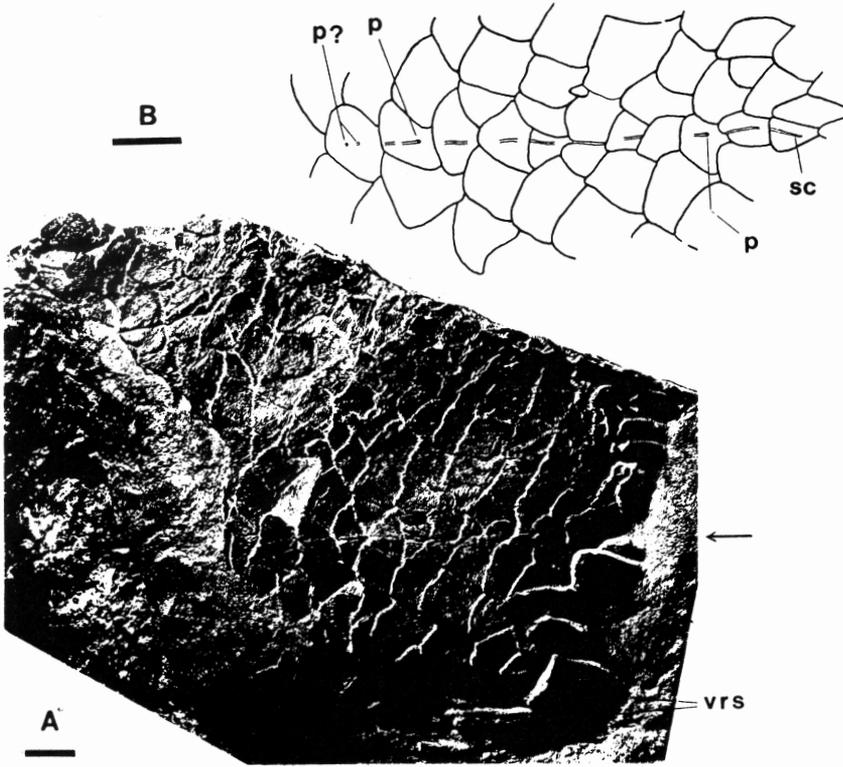


Figure 2 *Schizosteus striatus* (Gross), a large fragment of squamation, Pi 416, in left lateral view showing lateral line. In 2A the arrow points the direction of the sensory canal. Abbreviations: p—pore; sc—groove left by lateral line canal; vrs—ventral ridge scales. Bars = 10 mm.

tissue immediately under these scales. The canal ran mostly along the central part of the scales, but its direction might also coincide with the contact line of some adjacent scales. In two scales, short sections of grooves become deeper and end with a minute pore (p). Evidently the branches of the sensory canal pierced the scales here. The other branches might reach the external surface by running through the space between scales. This structure of the lateral line is usual for a fish-like animal (cf. figure 8–40 in Jollie 1973).

Pycnosteidae

In the representatives of this family, particularly in *Pycnosteus* and *Tartuosteus*, numerous scales are known. These two forms are the largest among psammosteids, having huge (up to 100 mm long) and massive ridge scales (Obruchev and Mark-Kurik 1965, pl. 23, plus figures 50, 54, 70–72, 92, 93). The posterior portion (if not even more) of the ventral ridge scales can be heavily abraded and the distal ends broken. Overlap of the scales does not exceed that in the guerichosteids. In *Ganosteus* it may be somewhat more developed (*op. cit.*, pl. 31, plus figures 104,

118). One of the *Tartuosteus* scales (*op. cit.*, figure 67g) is close in character to the high flank scales in *Drepanaspis* that were overlapped by three anteriorly placed scales. Nevertheless, in *Tartuosteus* and other psammosteids of different families, usually two scales overlapped the succeeding one. A narrow band of ornament on the visceral surface at the posterior margin of scales shows that they slightly overhung the following ones, thus probably increasing the flexibility of the body and its lateral movements. These bands occur, e.g., on the scales of *T. maximus* Mark-Kurik and *Psammolepis paradoxa* Agassiz of the family Psammolepididae (*op. cit.*, pl. 44, fig. 5, plus figures 67, 145; Gross 1933, pl. 2, fig. 8).

Considering the tails of the representatives of the family Pycnosteidae, it should be pointed out that a caudal fin similar to that in *Drepanaspis* cannot automatically be assumed for such psammosteids as *Tartuosteus* or *Pycnosteus*, as has been done in several cases by the author of the present paper (Obruchev and Mark-Kurik 1965, figure 96; Mark-Kurik 1968, figure 6; Mark-Kurik 1984, figure 3). In these forms the branchial plates were widely spaced and the ventral shield was markedly convex; consequently, the body form was rather different.

In connection with the family Pycnosteidae a taxonomic remark is needed. In his monograph, Halstead Tarlo (1964, 1965) retained the genus *Yoglinia* Obruchev; however, its author considered this to be an invalid taxon (see Obruchev and Mark-Kurik 1965). The species *bergi* should be properly attributed to the genus *Psammosteus*. *P. bergi* is the earliest and also the largest known species of the genus.

Psammolepididae

The family includes one genus, *Psammolepis*, with numerous species, some of them being rather different from the type species *P. paradoxa*. *Psammolepis* scales do not differ markedly from those in guerichosteids or pycnosteids (Gross 1933, pl. 2; Obruchev and Mark-Kurik 1965, pls. 42, 44–45, 53, plus figures 134, 144–145, 153, 161–163; Lyarskaya 1971, figure 9). They are shown in the well-known restoration of *P. venyukovi* Obr. drawn by Bystrow (Obruchev and Mark-Kurik 1965, figure 164 plus frontis.; Blicek *et al.* 1991, figure 1D; for another version of the drawing see Heintz 1957). However, in this restoration the squamation is too regular and the caudal fin, influenced by White's restoration of *Pteraspis* (as also noted by Denison in 1971), is shown as having a strongly developed fleshy ventral lobe, even though there is no evidence for such a lobe. One further misinterpretation should be indicated: in *Psammolepis* and other psammosteids, the ossification centre of the cornual plates is situated at their posterior margin and not in the geometrical centre (see e.g. Figure 126 in Obruchev and Mark-Kurik 1965; Mark-Kurik 1968, figure 4).

Psammosteidae

Scales, including more commonly occurring ridge scales, are known in several *Psammosteus* species, including *P. levis* Obr. ascribed by Halstead Tarlo (1965) to a different genus, *Crenosteus*. Most of the *Psammosteus* ridge scales are narrow (Obruchev and Mark-Kurik 1965, pls. 54, 67, 74, 80; Halstead Tarlo 1965, pl. 17). The scales in *P. cf. meandrinus* Agassiz are small, their length and height being rather constant at 5 and 7 mm, respectively (Obruchev and Mark-Kurik 1965, pl. 70). In *P. megalopteryx* Trautschold they may be larger, up to 12 mm (rarely 20 mm) high

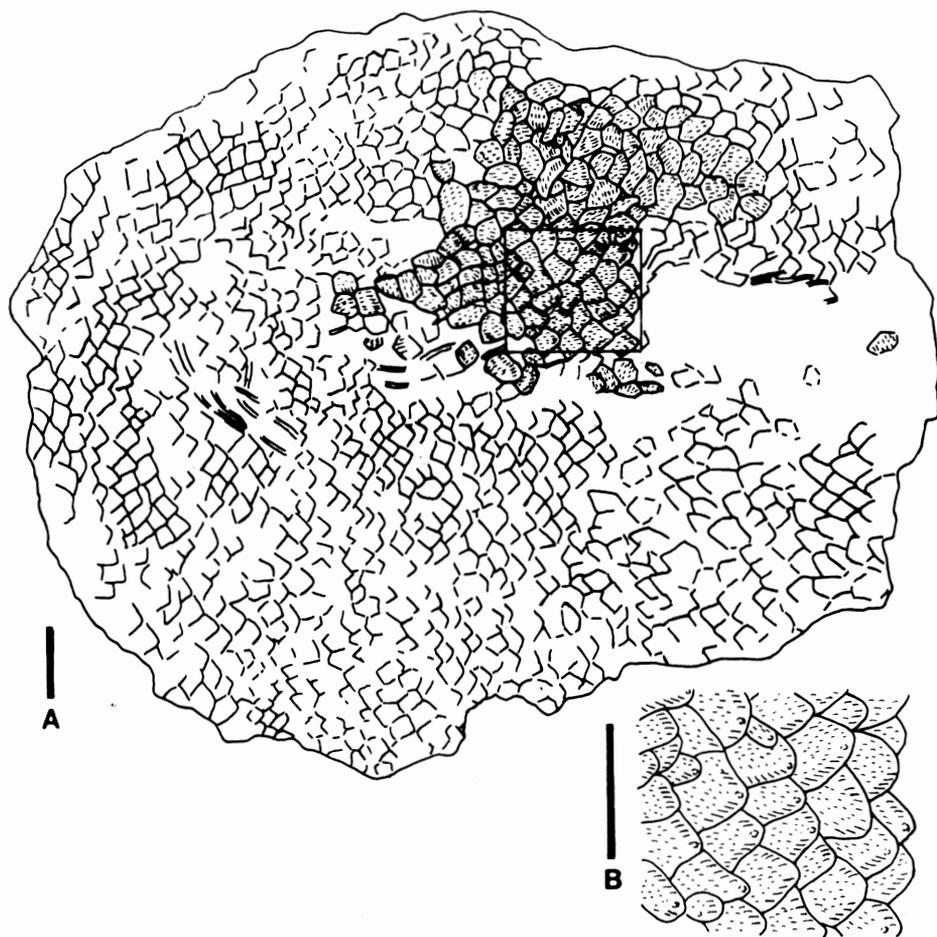


Figure 3 *Psammosteus* sp., partly preserved squamation; most of the scales occur as imprints or are visible from the visceral surface (lower right part in 3A). Both in 3A and 3B the ornament is shown schematically. Bars = 10 mm.

(*op. cit.*, pls. 80, 85). The anterior overlapping margin of scales is narrow in both forms.

The specimen Pi 705 (Figure 3 herein; Joosu locality, Estonia), showing a considerable portion of the squamation, belongs to a undescribed early species of *Psammosteus*. Like *P. bergi*, it comes from the Burtneki Formation (Middle Devonian, Givetian). The specimen is somewhat laterally compressed (in the figure, flattened). Quite a number of scales have been preserved as imprints; the others are exposed from the visceral surface. The scales are square and small, their dimensions (length 3–5 mm) coinciding with those in tesserae of *P. bergi*. Several scales reveal an ornament consisting of minute elongated tubercles possessing crenulations; the marginal tubercles are more prominent. A round tubercle occurs at the posterior end

of some scales (Figure 3B herein). Tesserae of *P. maeandrinus* and *P. megalopteryx* are also furnished with a round tubercle surrounded by other tubercles of variable shape.

The isolated scales of *Psammosteus* species indicated above, and the articulated squamation of *Psammosteus* sp. just described, show that a scale pattern consisting predominantly of small square elements could not derive from that in *Psammolepis*. As indicated earlier (Obruchev and Mark-Kurik, 1968), a direct relationship between these genera is hardly possible.

With reference to the narrow overlapping margins of scales in psammosteids, it would be useful to present some data on the squamation of recent osteichthyids. Representatives of this group, e.g. cyprinids, thoroughly studied by Burdak (1979), show a squamation in which the scales cover one another to a very great extent; the free ornamented surface is therefore much smaller than the covered portion. In some forms this process has reached its extreme stage (seven scales overlapping one another). Burdak (*op. cit.*) has made several interesting correlations between the degree of scale overlap and the habitat of the fishes. The more significant of these are: (1) in the benthonektic forms developing a closer contact with the bottom and hard substrate, the degree of scale overlapping increases (cf. the weakly expressed overlapping in supposed benthic psammosteids); and (2) in several benthic forms (gobitids) which bury themselves into sediment or use other hiding places, degeneration of squamation and diminishing of the degree of the scale overlap are observed (cf. e.g. the bottom-dwelling, well-armoured osteostracans with burrowing habits). These differences should be taken into account in future studies of fossil forms.

CONCLUSIONS

The squamation is the worst-preserved part of the psammosteid exoskeleton; indeed, this seems to apply to the majority of heterostracans. Of numerous representatives of the suborder Psammosteida, only a single species, *Drepanaspis gemuendenensis* Schlüter, shows the articulated squamation. Some parts of the squamation have been discovered in two other forms, *Schizosteus striatus* (Gross) and *Psammosteus* sp., whereas in most psammosteids only isolated scales are known.

The scale pattern of *Drepanaspis* is characteristic of the psammosteids in general, except *Psammosteus*. The structure of the squamation of this form, consisting of small square scales, contradicts any derivation of *Psammosteus* from *Psammolepis*. The same conclusion has been drawn previously on the basis of the other morphological characteristics of these psammosteids (Obruchev and Mark-Kurik 1968).

The structure of the psammosteid caudal fin is of much importance, since it was the only means for propulsion of the animals. In *Drepanaspis* the fin was large, almost symmetrical and reinforced by special rows of larger scales. The psammosteids resembling *Drepanaspis* in their structure, e.g. the representatives of the family Guerichosteidae, might have had a similar caudal fin. Such a caudal fin as that of *Drepanaspis* can hardly be automatically assumed to occur in the psammosteids with different body forms, e.g. *Pycnosteus* which possessed large, widely spaced branchial plates and a markedly convex ventral shield.

The degree of the overlap of scales is significant from the functional aspect. In the supposedly benthic psammosteids, the scales covered one another only slightly. On the contrary, in osteichthyids developing a close contact with the bottom and hard

substrate, the overlap of scales increases. This dissimilarity in morphology should be explained by further studies.

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