

A REVIEW OF THE LATERAL LINE SENSORY SYSTEM IN PSAMMOSTEID HETEROSTRACANS

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ABSTRACT – The heterostracan lateral line system consists of a network of closed canals within the dermal plates that open to the surface by pores. This system is well known in some heterostracans, where it consists of a symmetrical arrangement of canals, but is known in only a few psammosteids, where the pattern is more irregular. A new obruchevid from the Late Devonian of arctic Canada shows a typical heterostracan pattern, but the canals were held in open surface grooves, generally considered a derived feature in heterostracans. A second new arctic species similar to *Psammosteus* features a reticulate dorsal canal system with the canals delineating polygonal areas and the normal pattern of longitudinal and transverse canals lost. This pattern is unique within heterostracans and may be a derived feature related to a need for increased sensory function. The canals were situated below the surface tesserae and are thus only exposed by abrasion. Species with small tesserae have canals enclosed in tubes and their position may be indicated on the surface as ridges formed by the presence of small, elongated tesserae. Those with large tesserae have canals enclosed within the spongy layer of the dermal plate. Some species of *Psammosteus* may have had a double sensory canal system in the dorsal plate, with one system deeper in the spongy layer, the other close to the surface of the plate but still under the ornament. Behind the carapace the sensory canal system is situated directly below the scales and connects to the surface with short branches. These penetrate the scales, which are thin and have no basal layer.

Key words: Heterostracans, psammosteids, lateral line canals, Devonian.

RESUMO – O sistema da linha lateral em heterostráceos consiste de uma rede de canais fechados dentro das placas dérmicas que abrem-se na superfície através de poros. O sistema é bem conhecido em heterostráceos, onde ele consiste de um arranjo simétrico de canais, mas é conhecido em apenas alguns poucos psammosteídeos, onde o padrão é irregular. Um novo obruchevídeo do Devoniano Superior do Ártico canadense, apresenta um típico sistema de canais heterostráceo, mas os canais conservavam-se em valetas abertas à superfície., um caráter geralmente considerado derivado em heterostráceos. Uma segunda nova espécie ártica similar a *Psammosteus*, apresenta um sistema de canais dorsais reticulados, no qual delinham áreas poligonais e o padrão normal de canais longitudinais e transversais está perdido. Esse padrão é único dentre os heterostráceos e pode ser uma característica derivada relacionada a necessidade de um aumento da função sensorial. Os canais situavam-se abaixo das tesseras e conseqüentemente estão expostos somente por abrasão. Espécies com tesseras pequenas tem canais envolvidos por tubos e sua posição pode ser indicada na superfície pela presença de pequenas tesseras alongadas. Espécies com tesseras grandes têm canais encapsulados dentro da camada de osso esponjoso da placa dérmica. Algumas espécies de *Psammosteus* podem ter tido um sistema duplo de canais sensoriais na placa dorsal, com um sistema situado mais profundamente na camada esponjosa e o outro próximo à superfície, mas ainda abaixo da ornamentação. Atrás da carapaça, o sistema do canal sensorial está situado diretamente abaixo das escamas e conecta-se à superfície através de ramificações curtas. Essas penetram nas escamas, que são finas e não têm camada basal.

Palavras-chave: Heterostráceos, psammosteídeos, canais da linha lateral, Devoniano.

INTRODUCTION

The lateral line system in fishes consists of a series of surface or near surface canals and tubes containing the neuromasts. These sensory organs are sensitive to disturbances in the water and provide the fish with information

that contributes to obstacle avoidance and orientation of the body relative to currents. Hagfish and lampreys do not have neuromasts in canals although they do tend to be linearly arranged. In heterostracans the sensory canal system consists of a series of closed canals in the cancellous layer of the dermal bone opening to the surface by pores and is

usually only visible if the surface of the plate has been eroded. In cyathaspidids and pteraspids the system is well known and usually consists of an almost diagrammatically simple pattern of longitudinal canals and transverse commissures (Figure 1A, D), although in some species it can be greatly elaborated (Figure 1B, C). Trends can be recognized in the arrangement of the system, with short sections of canal in earlier cyathaspidids evolving into a more connected system in later forms and then culminating in the completely connected system of the pteraspids (Figure 1A, D). Details of the arrangement of these canals has been used in the identification of both cyathaspidid and pteraspidid species (Denison, 1964; Blicek, 1984), but has not proved useful within the psammosteids because until recently the sensory canal system was known mainly from the dorsal plates of just a few Middle and Late Devonian forms such as *Psammolepis*, *Psammosteus* and *Tartuosteus* (Halstead Tarlo, 1964, 1965; Obruchev & Mark-Kurik, 1965, 1968). In these forms two medial dorsal canals and 1-3 cross-commissures, and rarely lateral dorsal canals are present. Gross (1963:fig. 10) identified radial ridges of dorsal and ventral plates of the Early Devonian *Drepanaspis gemuendenensis* as sensory line canals, however, Obruchev and Halstead Tarlo did not agree with the interpretation of these structures, as they were too symmetrical and situated on the visceral surface of the plates (Obruchev & Mark-Kurik, 1965:43). Although canals are not generally known from the other plates the orbital plates of *Psammolepis paradoxa* and *Psl. undulata* and the pineal plate of *Psammolepis* (?) sp. reveal several narrow and short radial grooves. The discovery of sensory lines in a new Late Devonian obrucheviid psammosteid (Elliott *et al.*, 2004) and another new species, both from the Canadian Arctic, is significant in adding to the limited current information on this group.

Abbreviations. CMN-NUFV, National Museum of Canada, Ottawa; **Pi**, Institute of Geology, Tallinn University of

Technology; **PIN**, the Palaeontological Institute, Russian Academy of Sciences, Moscow.

NEW INFORMATION ON THE SENSORY CANAL PATTERN

Drepanaspis

Gross (1963: figs. 1, 10) identified radial ridges in the dorsal and ventral plates in the Early Devonian psammosteid *Drepanaspis gemuendenensis* Schlüter as sensory line canals. Obruchev and Halstead Tarlo did not agree with the interpretation of these structures, as they were too symmetrical and situated on the visceral surface of the plates (Obruchev & Mark-Kurik, 1965:43). However, a specimen in the collections of the Institute of Geology, Tallinn (Pi 297), from the Odenspiel quarry, Rhineland, Germany that contains two incomplete dorsal plates, two branchial plates and several fragments of *Drepanaspis gemuendenensis* shows features suggesting that Gross could be correct. One of the dorsal plates, which is rather convex (more than 1 cm high) and approximately 12.5 cm wide, has on its visceral side two subparallel longitudinal ridges 3 and 4 cm long, respectively. The ridges are somewhat asymmetrical, shallow and are in some places divided into two parts by a fine groove. The structure of the ridges coincides with that given by Gross (1963:137). Two more poorly preserved ridges are also visible in the right lateral portion of the plate. The longitudinal canals correspond to the sensory canals dc_1 , and the laterally situated ones to dc_3 and dc_4 , as illustrated by Gross (1963:fig. 1P). It is notable that the *Drepanaspis* remains from Odenspiel, preserved in hard gray argillaceous siltstone are less deformed than those from the Hunsrück Shale. The dorsal plates are very thin (less than 1 mm) but it can be seen that the

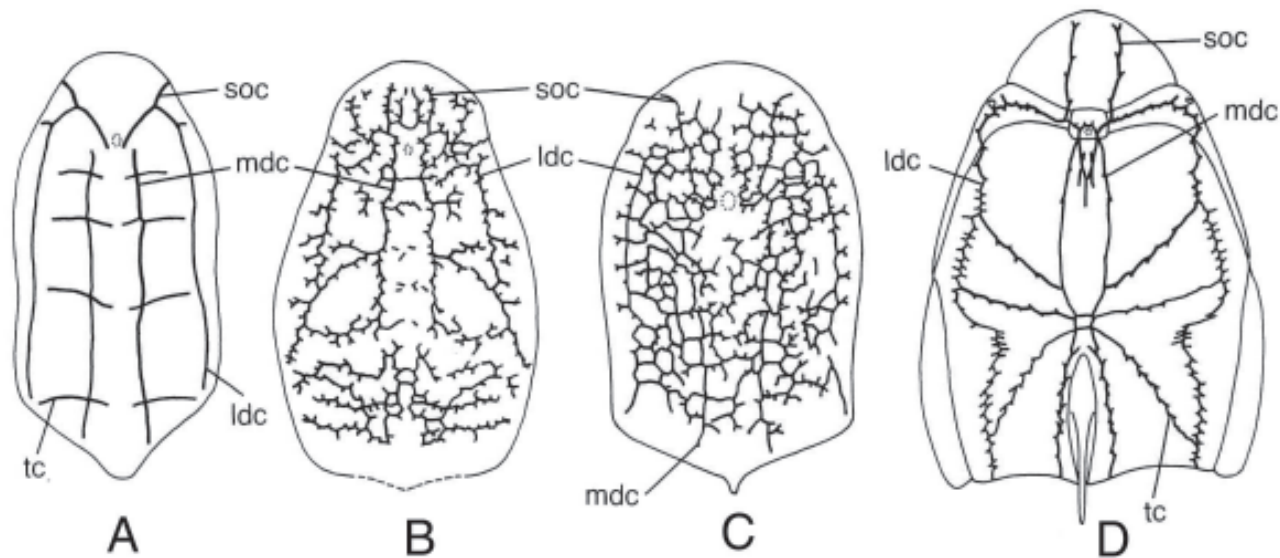


Figure 1. Dorsal lateral line sensory canal systems of heterostracans. **A**, *Poraspis polaris*; **B**, *Dikenaspis yukonensis*; **C**, *Irregulareaspis complicata*; **D**, *Stegobrachiaspis baringensis*; (A-C from Denison 1964, D from Elliott 1983). **Abbreviations:** **ldc**, lateral dorsal canal; **mdc**, median dorsal canal; **soc**, supraorbital canal; **tc**, transverse commissure. Not to scale.

sensory line canals were situated in the plate above the smooth and extremely thin basal layer.

New Canadian obruchevid

Obruchevia is a derived psammosteid from the Frasnian of the Novgorod Region, NW Russia. The plates are thick and lack any surface tesseræ but the external surface of the bone is strengthened by the addition of pleromic dentine. No sensory canals have been reported for this genus (Obruchev, 1941), however, material of a new obruchevid *Perscheia* from the Frasnian of southern Ellesmere Island, Canadian Arctic, does show sensory canals as shallow grooves in the surface of the dorsal plate (Elliott *et al.*, 2004). Although the specimens are fragmentary (Figure 2B, C) the system can be reconstructed for the posterior part of the plate and shows the presence of paired medial and lateral longitudinal canals joined by at least one commissure (Figure 3B). Lateral dorsal canals are rarely seen in psammosteids (Figure 4) and their presence here may be a function of the large size of the dorsal plate in this species. The presence of the system as open grooves is also unusual although not unexpected in a species in which the surface covering of dentine tubercles is missing. An intermediate stage can be seen in *Traquairosteus pustulatus*, a Frasnian species from Scotland in which the outer surface of aspidin is thrown up into conical mounds, each surmounted by a small crenulated dentine tubercle, which are thus very sparsely distributed (Tarlo, 1961). In the holotype (BM P.8297; Halstead Tarlo, 1965:fig.17:1) two canals can be seen as open grooves on the surface indicating that as the dentine tubercles were reduced the canals became exposed and were only covered by the dermis.

New Canadian *Psammosteus*?

A partial dorsal plate of a new psammosteid similar to *Psammosteus* from the Frasnian of southern Ellesmere Island (Figures 2A, 3A) shows a pattern of sensory canal grooves exposed by the loss of the dentine tubercles to erosion. The left anterior part of the plate is preserved and shows a reticular pattern of grooves in which what appear to be paired medial canals anteriorly are connected laterally and posteriorly to canals that delineate large polygonal areas that extend laterally to the edges of the plate. Fragments of dorsal plates of *Psammosteus megalopteryx* illustrated by Halstead Tarlo (Tarlo, 1961:fig. 4; Halstead Tarlo, 1964:fig. 13) also show a pattern of branching and connecting grooves that seems to indicate a more complex pattern than is usual in psammosteids, however, he reconstructed these as parts of a more typical branching system.

This system is quite unlike that reported for other psammosteids (Figure 4), or for typical cyathaspidids or pteraspids (Figure 1). However, in the cyathaspidid *Dikenaspis* (Figure 1B) the canal system has become greatly branched and in some cases these branches have joined to form polygonal areas. A further stage is reached in *Irregularaspis* (Figure 1C) in which the branching has become so complex that the main canals are difficult to recognize and the system has become a network of polygonal

areas. The pattern shown in the anterior part of the dorsal shield of *Irregularaspis* does show a number of points of similarity with that in the psammosteid particularly in the shape and orientation of the polygonal areas. No reasons have been suggested for such a complex system in *Irregularaspis* and the presence of a similar network in the new psammosteid is even more difficult to explain, as psammosteids in general appear to have a poorly developed sensory canal system (Figure 4). Given that the lateral line system provides information about local water turbulence, enabling the animal to sense its surroundings, a more complex system such as that developed by the new *Psammosteus*? might indicate a movement into a more turbulent environment or the development of a new method of feeding that required a greater sensitivity to movement in its surroundings.

Juvenile psammosteids

Two dorsal plates exemplify the sensory canal system of juvenile psammosteids. One of them, belonging to *Tartuosteus maximus* (Obruchev & Mark-Kurik, 1968:fig. 3A) shows very poorly preserved and short medial dorsal canals and three commissures, the posterior ones forming a pair. In the dorsal plate of a juvenile *Psammosteus bergi* (Figure 4D) that is slender and about half the size of a large individual (Figure 4E), the canals form an irregular cross-like configuration. No lateral dorsal canals are present.

The dorsal plates of adult *Psammolepis proia* (Figure 4A) and *Psl. undulata* (Lyarskaya, 1971:fig. 4; Obruchev & Mark-Kurik, 1965:fig. 170) are narrower anteriorly. The anterior portion of the same plate of a comparatively younger individual of *Psl. undulata* (Figure 4B) is still narrower. In these plates the commissures almost reach the lateral margins of the plate and no space is left for the lateral dorsal canals. The case could be similar in *Psammosteus* species with a comparatively narrow anterior portion, such as *Ps. praecursor* and *Ps. livonicus* (Figure 4C, F). In contrast to this arrangement the dorsal plate of *Ps. bergi* (Figure 4E) is wide anteriorly and includes the lateral dorsal canals. In the other cases just indicated the lateral canals might have run in the tesserated bands lateral to the dorsal plate.

The plate of *Psl. undulata* in the Tallinn collection (Pi 247) that was erroneously identified by Halstead Tarlo (1964:fig. 12A; 1965:fig. 32A) as a ventral plate is actually a juvenile dorsal plate (Figures 4B, 6A-C). Another error in Halstead Tarlo's monograph concerns the identification of a dorsal plate of *Psl. proia* with an exposed sensory line system as that of *Tartuosteus giganteus* (Gross) (Halstead Tarlo, 1964:fig. 12B; 1965:fig. 24A). The plate and the other one with ornament (Halstead Tarlo, 1965:fig. 24B) have tesseræ, not known in the large armour plates of *Tartuosteus* species.

Parallel canals

One more recently discovered character in the sensory line system of psammosteids is the occurrence of parallel paired canals, e.g. in *Psl. undulata* in which short parallel sections of sensory lines occur at the distal ends of commissures (Figures 4B; 6B, C). A section of a parallel line

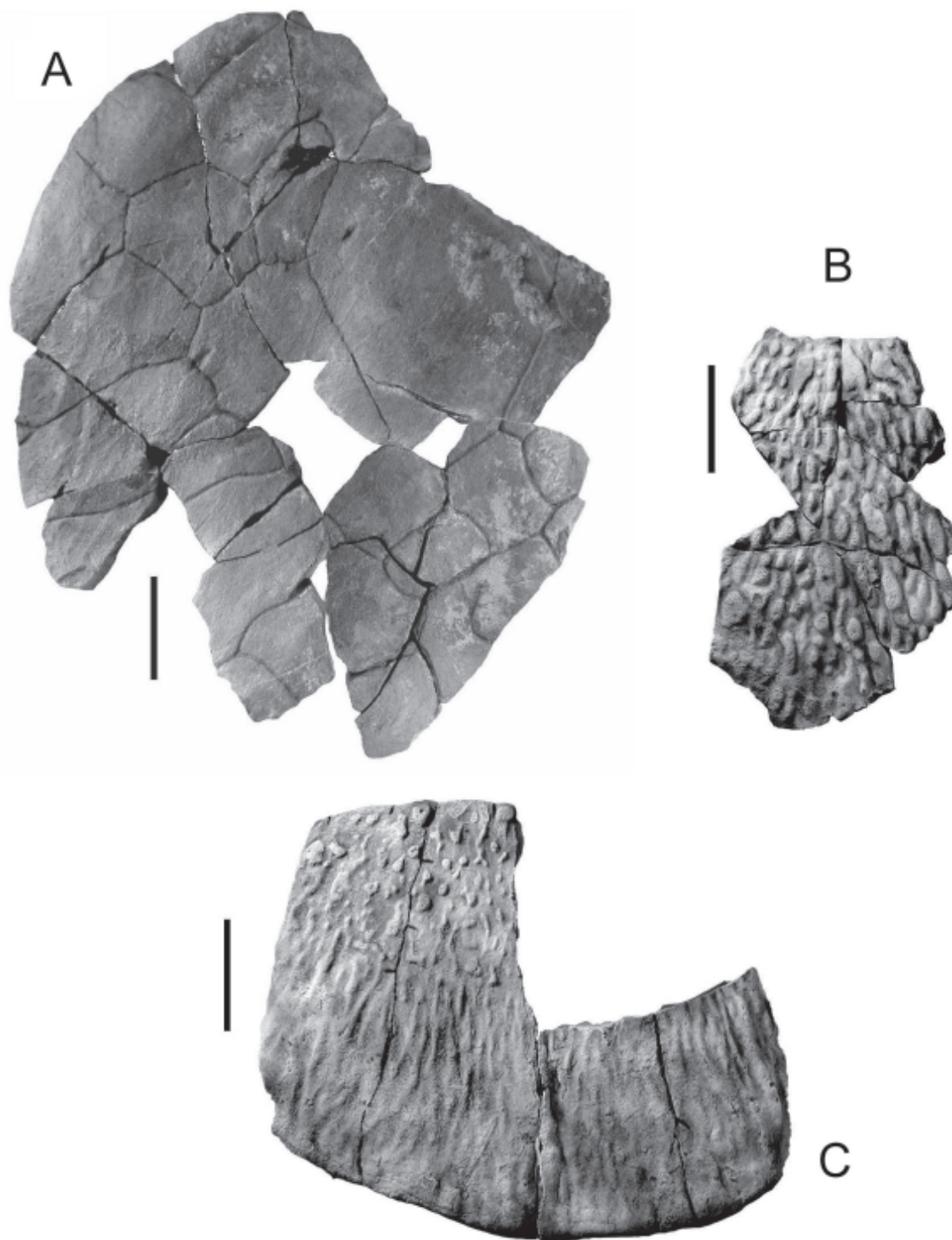


Figure 2. Lateral line system of new psammosteids from the Late Devonian of the Canadian Arctic. **A**, left anterior part of the dorsal plate of a psammosteid similar to *Psammosteus* (CMN-NUFV108) showing a reticulated canal system exposed by the removal of the surface tesserae (see Figure 3A for an explanatory drawing of this specimen); **B-C**, obruchevid *Perscheia* showing sensory system of open grooves on the surface of the dorsal plate; **B**, CMN-NUFV103, fragment of dorsal plate with a transverse canal running horizontally across the central part; **C**, CMN-NUFV101, posterior part of a dorsal plate with a cross commissure forming the upper left boundary and a part of the median dorsal canal running from the central part of that edge towards the posterior edge of the plate (see Figure 3B for a reconstruction). Scale bars = 50 mm (**A**), 100 mm (**B**, **C**).

occurs also in *Psammosteus bergi* (Figure 5E). In *Psl. undulata*, a juvenile dorsal plate was described by Lyarskaya (1971:fig. 5), the arrangement of the medial dorsal canals and a pair of long cross commissures coinciding with those in the specimen figured in the present paper (Figure 4B). Lyarskaya (1971:fig. 4) figured two medial canals in the dorsal plate of an adult *Psl. undulata*.

POSITION OF CANALS WITHIN PLATES

Generally psammosteid sensory canals, situated just under the tubercles, become visible only in rare cases when the ornament is abraded and the upper surface of the spongy layer is exposed, e.g. in the dorsal plates of *Tartuosteus maximus* Mark-Kurik, *Psammolepis proia* Mark-Kurik (Figure 4A), and *Psl. undulata* (Figure 4B). The latter two *Psammolepis* species had comparatively large tesserae, but in *Psammosteus* with generally smaller tesserae, tubes, enclosing canals and situated below the tesserae were exposed by wear as e.g. in *Psammosteus bergi* (Obruchev). The dorsal plate of *Ps. bergi* (Figure 5A, B) and several of its fragments (Figure 5C-E) particularly reveal the structure of the sensory lines. One of them (Figure 5C), was earlier figured by Obruchev & Mark-Kurik (1965:fig.187; pl.64, fig.2). Halstead Tarlo (1965:fig.28A) also figured the specimen but used the generic name *Yoglinia* (Obruchev, 1943), which was considered to be a junior synonym of *Psammosteus*

(Obruchev & Mark-Kurik, 1965: 215). The specimens of *Ps. bergi* that have lost practically all their ornament have both open grooves and partly broken aspidin tubes raised somewhat above the bare surface of the plate or its fragments. One of the fragments shows a short section of a parallel groove (Figure 5E, indicated by a white arrow). The dorsal plate of a large individual of *Ps. bergi* (Figures 5A, B) has one more remarkable feature. In its posterior left portion the middle commissure crosses a short (8 mm long) section of the lateral dorsal canal. This canal section is situated deeper in the aspidin layer of the plate (the crossing point is indicated in Figure 5B by a white arrow). The crossing grooves, actually canals, point to the presence of a double canal system, supposed to exist also in another representative of the genus *Psammosteus* (*Ps. megalopteryx*), and otherwise only known in a quite different group of heterostracans, the amphiaspids (see the discussion below).

In unworn shields of *Psammosteus* small elongated tesserae mark the position of sensory canals in the plates, e.g. in *Ps. praecursor* Obruchev. In this species the sensory canal pattern appears to be more developed than figured earlier (Obruchev & Mark-Kurik, 1968:fig.3H; Figure 4C). In the dorsal plate of *Psammosteus livonicus* Obruchev (Figure 4F) in which almost all the tesserae have been lost, the canals exposed from above by abrasion are visible as narrow ridges of spongy aspidin with a groove in the middle and slightly raised above the surface of the plate. The canal pattern

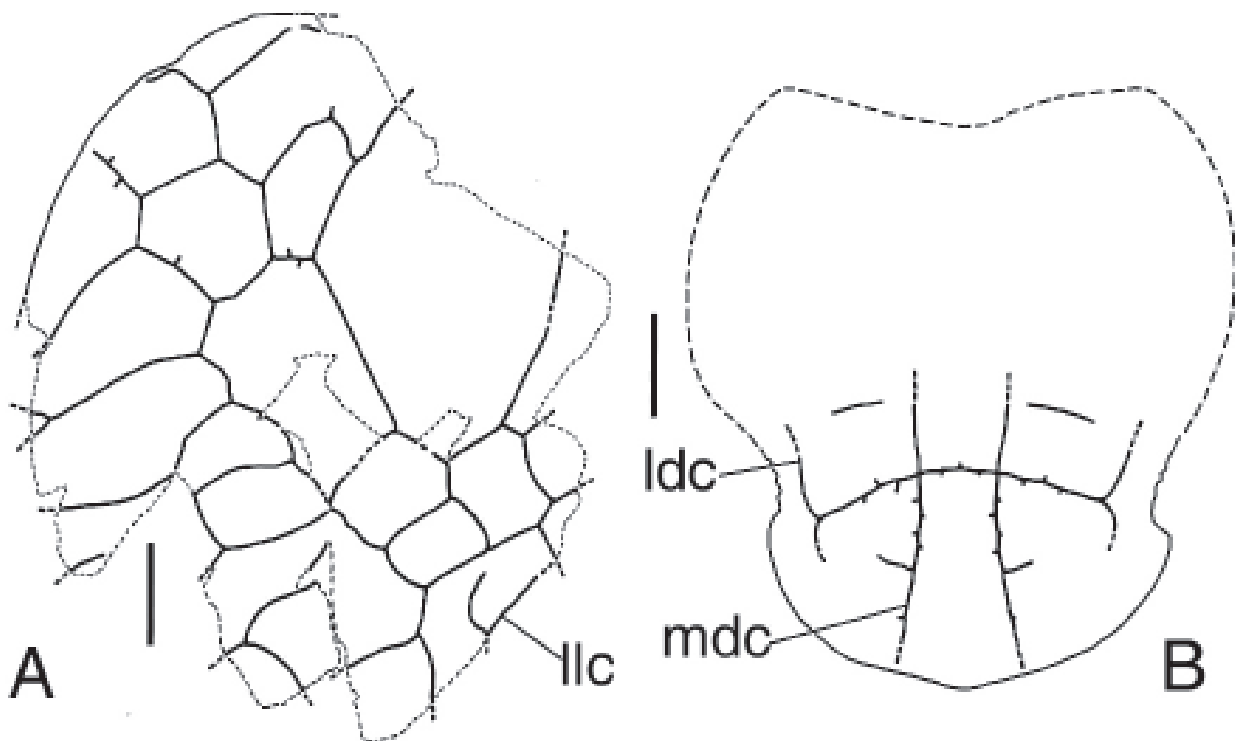


Figure 3. Lateral line system of new psammosteids from the Late Devonian of the Canadian Arctic. **A**, left anterior part of the dorsal plate of a psammosteid similar to *Psammosteus* (CMN-NUFV108) showing the reticulated canal system (same specimen as Figure 2A), scale bar = 50 mm; **B**, reconstruction of the canal system in the posterior part of the dorsal plate of the new obruchevioid *Perscheia* (Elliott *et al.*, 2004), scale bar = 100 mm. **Abbreviations:** **ldc**, lateral dorsal canal; **llc**, lateral commissure; **mdc**, median dorsal canal.

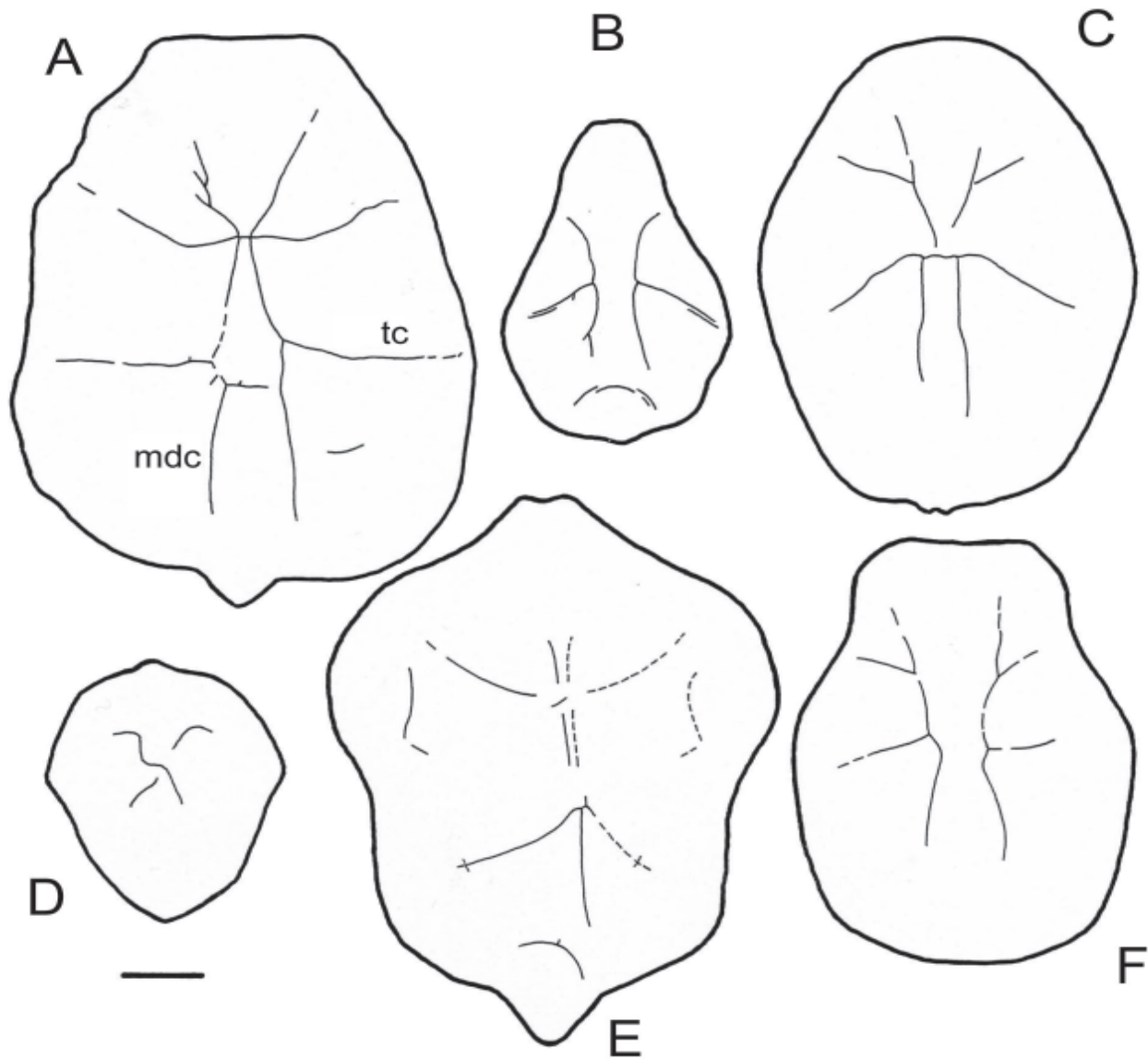


Figure 4. Lateral line pattern in the dorsal plates of psammosteids. **A**, *Psammolepis proia* Mark-Kurik, adult plate, Pi 123; **B**, *Psil. undulata* (Ag.), juvenile plate, Pi 247; **C**, *Psammosteus praecursor* Obr., adult, Pi 164; **D**, **E**, *Psammosteus bergi* (Obr.); **D**, juvenile, Pi 912; **E**, adult, Pi 739; **F**, *Ps. livonicus* Obr., adult, Pi 722. **Abbreviations:** **mdc**, median dorsal canal; **tc**, transverse commissure. Scale bar = 50 mm (modified after Obruchev & Mark-Kurik, 1968).

appeared to be more complete than figured earlier (Obruchev & Mark-Kurik, 1968:fig.3D) and, in general, resembles that in *Ps. praecursor* (Figure 4C).

Two medial canals situated under rows of smaller tesseræ can be observed in the dorsal plate of a large individual of *Psammosteus megalopteryx* (Trautschold) (Obruchev & Mark-Kurik, 1965:pl.80, fig.2), a phenomenon visible in the dorsal plate of *Ps. praecursor* (Figure 6D-F). That the sensory canal pattern in *Ps. megalopteryx* was actually more complicated was demonstrated by Halstead Tarlo (1964:fig.13) who figured worn dorsal plate fragments with medial and lateral dorsal canals and several transverse commissures and/or canal branches. In *Ps. megalopteryx* another variant

of the canal structure has been described. According to Obruchev in a plate fragment of this psammosteid the sensory canals formed shallow and very narrow branching ridges on tesseræ (Obruchev & Mark-Kurik, 1965:pl.78, fig.2; Figure 5F). Thus, it is not excluded that *Ps. megalopteryx* could also possess a double sensory canal system: an upper one in the tesseræ and the lower one under the tesseræ in the upper part of the spongy layer of the dorsal plates. As shown by the Canadian Arctic *Psammosteus?* specimen the lower system may be more complex and form a reticulated pattern. If the double sensory line system really existed in *Ps. megalopteryx*, and also in *Ps. bergi*, then it could be compared with that in the amphiaspid *Siberiaspis plana*

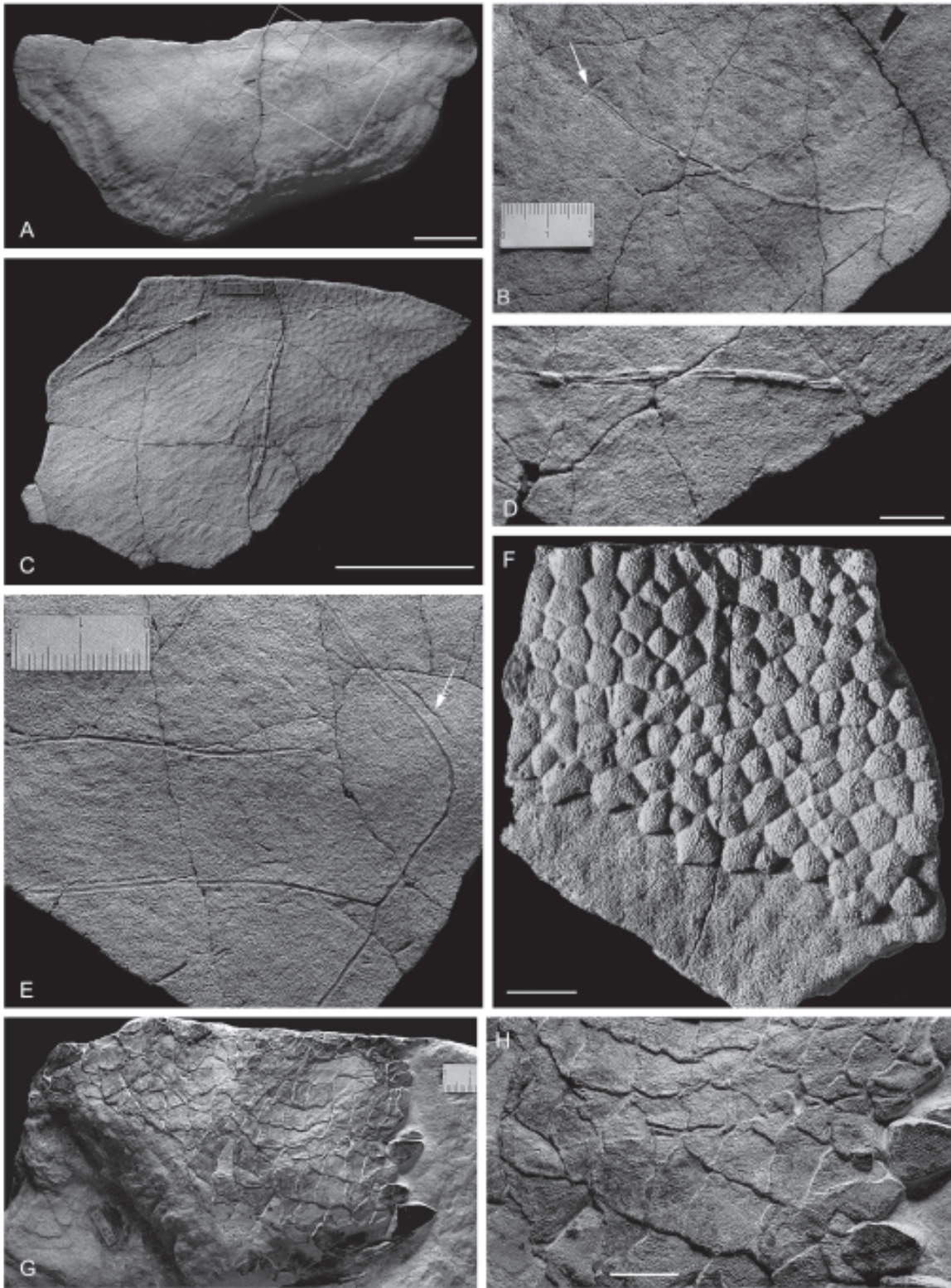


Figure 5. Sensory canals in various psammosteids. **A-E**, *Psammosteus bergi* (Obr.), dorsal plate (A, B, Pi 739) and dorsal plate fragments (C, Pi 161; D, Pi 188; E, Pi 727); **A-D**, showing sensory canals enclosed in tubes (note that the area delineated in A indicates that shown in B, and that the arrow in B shows the point at which a more surface canal crosses one deeper in the plate); **E**, showing parallel development of canals (indicated by the arrow). Karksi, Estonia; Middle Devonian, Burtneki Formation; **F**, *Psammosteus megalopteryx* (Trautschold), fragment of dorsal plate PIN 220/541, showing surface pattern of branching ridges. Stolbovo, Russia; Upper Devonian, Porkhov Beds; **G-H**, *Schizosteus striatus* (Gross), fragment of squamation, Pi 416, showing lateral line canal. Gorodenka, Estonia; Middle Devonian, Narva Formation. Scale bars = 50 mm (A, C), 10 mm (D, F, H).

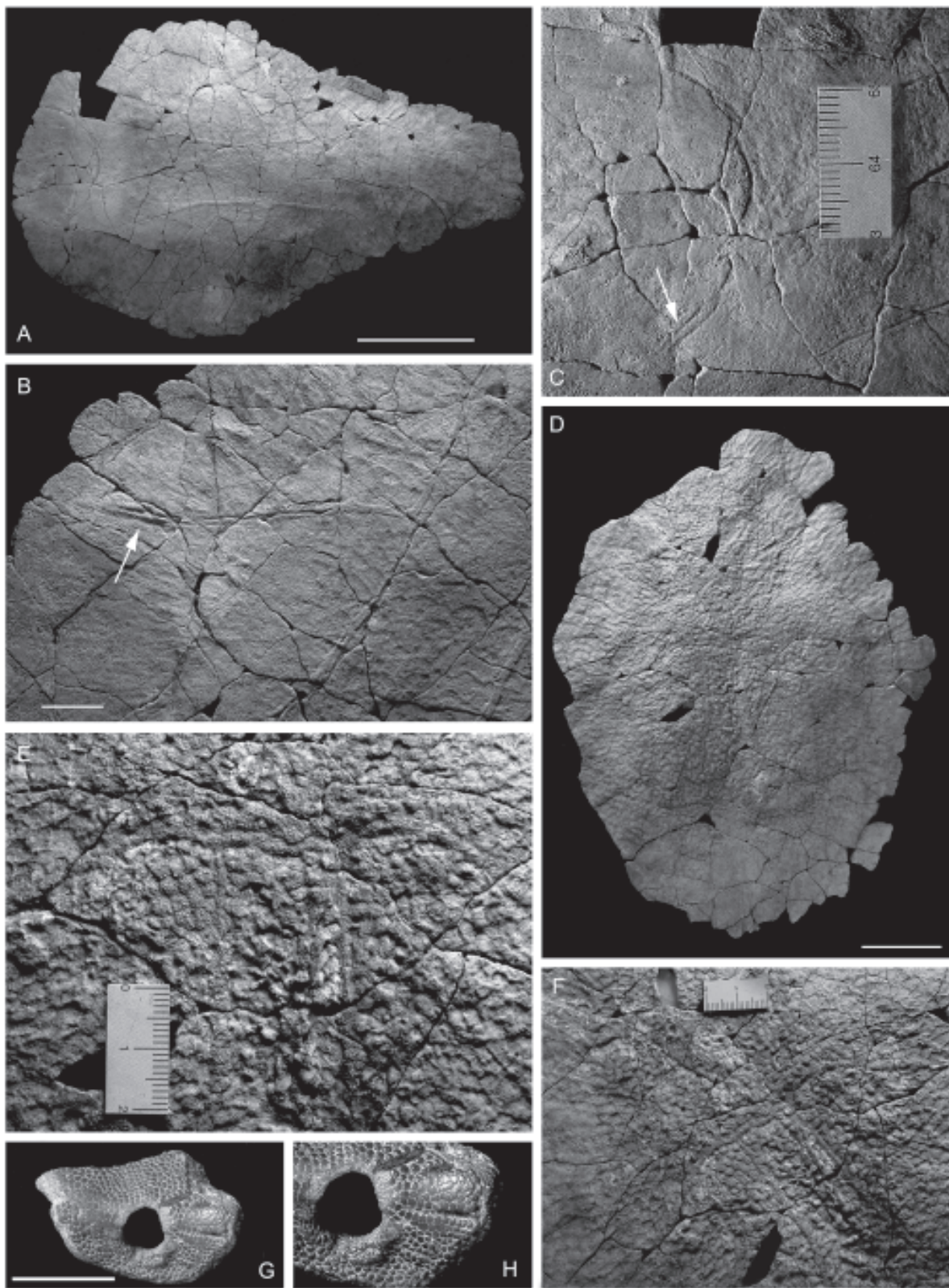


Figure 6. Sensory canals in various psammosteids. **A-C**, *Psammolepis undulata* (Ag.), juvenile dorsal plate, Pi 247, showing the canal system (A) and details of the development of parallel paired canals (indicated by arrows in B and C). Kuke, Latvia; Middle(?) Devonian, Amata Formation; **D-F**, *Psammosteus praecursor* Obruchev, dorsal plate, Pi 164, showing the two medial canals under rows of smaller tesserae. Vastseliina, Estonia.; Middle(?) Devonian, Amata Formation; **G, H**, *Psammolepis paradoxa* Agassiz, left orbital plate, Pi 246, showing radial grooves considered to be part of the sensory canal system. Straupe, Latvia; Middle Devonian, Gauja Formation. Scale bars = 50 mm (A, D), 10 mm (B, G).

Obruchev, described in detail by Novitskaya (1971:fig.7; 1983:fig. 37). In *Siberiaspis* the upper system was developed as open grooves on the surface, and the lower one as canals within the carapace, however, it is worth noting that the lower system was complex and branching as appears to be the case in *Psammosteus*. Novitskaya (1983:279) remarked that she discovered the double sensory line system in many forms, not only in *Siberiaspis* but also in *Argyriaspis*, *Olbiaspis*, *Angaraspis*, and *Gabreyaspis*.

Although open grooves were earlier supposed to occur in smaller plates of *Psammolepis*, a recent study of the orbital plate of *Psl. paradoxa* shows these could be due to the fossilization process. One of these narrow but deep grooves is partly covered with a row of small tubercles and it is suggested that these tubercles could form a “roof” over the canals in the orbital plate (Figure 6G, H) so that they occur in fact occur below the surface of the plate.

The structure of the sensory line system of the body behind the carapace is somewhat different (Mark-Kurik, 1993) from that of the carapace. A large fragment of squamation in *Schizosteus striatus* shows that the sensory canal was situated in soft tissue immediately under the scales leaving a shallow groove on their visceral surface (Mark-Kurik, 1993:fig. 2; Figure 5G, H). Short branches connected canals with the external surface of the body. Scales in psammosteids were much thinner than the armor plates and had no compact basal layer.

CONTRIBUTION TO AN UNDERSTANDING OF RELATIONSHIPS

There has been some discussion of the position of psammosteids within the heterostracans with the traditional view being that they are the most derived member of the Pteraspidoformes (see e.g. Janvier, 1996). Recent work by Pernègre (2002) suggests that they may be more correctly sited within the Pteraspidoformes as a derived member of the Pteraspidina and sister group to *Doryaspis*, however, it should be noted that a number of psammosteid features indicate that the traditional view may be the correct one. In particular the squamation of psammosteids consists of a large number of rows of flank scales as is the case in pteraspids but not in *Doryaspis*, and the position, pattern, and number of lateral plates in the carapace of psammosteids differs significantly from those in *Doryaspis*. Although this study of the sensory canal system in psammosteids provides new morphological information it does not at present shed any additional light on the relationships of the psammosteids which must come as part of a complete review of the Pteraspidoformes, a study that is currently overdue.

CONCLUSIONS

Until recently the sensory canal system was known in psammosteid heterostracans mainly from the dorsal plates of a few Middle and Late Devonian forms such as *Psammolepis*,

Psammosteus and *Tartuosteus* in which two medial dorsal canals and 1-3 cross commissures, and rarely lateral dorsal canals are present. This review of current information provides the following new information:

Gross (1963:fig. 10) identified radial ridges of dorsal and ventral plates of *Drepanaspis gemuendenensis* as sensory line canals. Although this identification was not supported at the time (Obruchev & Mark-Kurik, 1965:43) new specimens confirm the original interpretation.

The discovery of sensory lines in the new Late Devonian obruchevioid *Perscheia* psammosteid from the Canadian Arctic (Elliott *et al.*, 2004) shows that canals were present in open surface grooves and that lateral dorsal canals were present. No canals are reported for *Obruchevia* although open surface grooves are also known in the related *Traquairosteus* (*Psammosteus*) *pustulatus* (Halstead Tarlo, 1965).

A dorsal shield of *Psammosteus*? from the Canadian Arctic shows a system of canals that ramifies and branches to form a reticulate pattern. A similar pattern had been reported for *Psammosteus megalopteryx* (Halstead Tarlo, 1964:fig. 13) although from plate fragments only.

Where exposed by abrasion the canals can be seen enclosed by tubes and situated below the tesserae as in *Psammosteus bergi*. In unworn shields small elongated tesserae mark the position of sensory canals on the plates, e.g. in *Psammosteus praecursor*.

Another variant is known in *Psammosteus megalopteryx* in which sensory canals form shallow branching ridges on tesserae (Obruchev & Mark-Kurik, 1965:pl. 78:2). As canals are often also present in deeper parts of the carapace this suggests that psammosteids may have possessed a double sensory canal system as has previously been reported in the amphispids.

The sensory line system of the body behind the carapace was situated immediately under the scales (Mark-Kurik, 1993:fig. 2). Short branches connected canals with the external surface of the body. Scales in psammosteids were much thinner than the armour plates and had no compact basal layer.

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