Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere

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Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere

H. Blom, T. Märss and C. G. Miller

ABSTRACT: The sculpture of scales and plates of articulated anaspids from the order Birkeniida is described and used to clarify the position of scale taxa previously left in open nomenclature. The dermal skeleton of a well-preserved squamation of *Birkenia elegans* Traquair, 1898 from the Silurian of Scotland shows a characteristic finely tuberculated sculpture over the whole body. *Rhyncholepis parvula* Kiær, 1911, *Pterygolepis nitida* (Kiær, 1911) and *Pharyngolepis oblonga* Kiær, 1911, from the Silurian of Norway show three other sculpture types. Northern Hemisphere disarticulated scales and plates are described here, supporting a new anaspid taxonomy that includes both articulated and disarticulated material. The diversity, distribution, evolutionary trends and biostratigraphy of anaspids are described in the context of this new taxonomy, which includes six families (two are new) subdivided into 16 genera (10 are new) and 22 species (15 are new).

New taxa among Birkeniidae Traquair, 1898 are *Birkenia robusta* sp. nov. and *Hoburgilepis papillata* gen. et sp. nov.. Rhyncholepididae Kiær, 1924 includes *Rhyncholepis butriangula* sp. nov., *Silmalepis erinacea* gen. et sp. nov., *Vesikulepis funiforma* gen. et sp. nov., *Maurylepis lacrimans* gen. et sp. nov., and the previously described *Schidiosteus mustelensis* Pander, 1856 and *Rytidolepis quenstedtii* Pander, 1856. Tahulalepididae fam. nov. is represented by *Tahulalepis elongituberculata* gen. et sp. nov. and the revised *T. kingi* (Woodward, 1947). Septentrioniidae fam. nov. contains *Septentrionia lancifera* gen. et sp. nov., *S. mucronata* gen. et sp. nov., *S. dissimilis* gen. et sp. nov., *S. seducta* gen. et sp. nov., *Liivilepis curvata* gen. et sp. nov., *Spokoinolepis alternans* gen. et sp. nov. and *Manbrookia asperella* gen. et sp. nov. The family level position of *Ruhnulepis longicostata* gen. et sp. nov. is uncertain. Pterygolepididae Obruchev, 1964 and Pharyngolepididae Kiær, 1924 remain monogeneric.

KEY WORDS: Agnatha, Anaspida, Arctic and northwestern Canada, Birkeniida, British Isles, Central Urals, correlation, dermal skeleton, Estonia, Norway, Palaeozoic, Severnaya Zemlya, Sweden, taxonomy.

The study of exceptionally preserved anaspids from the Silurian of Scotland and Norway has had a profound impact on the way in which the early evolution of vertebrates has been interpreted, despite the fact that their detailed morphology and distribution are still poorly known (Janvier 1996a). The recovery of early vertebrates by acetic acid preparation has highlighted the study of microscopic phosphatic remains (Blieck & Turner 2000). Detailed stratigraphical and geographical distribution data often provided by such material are a necessary supplement to morphological data, for evolutionary and phylogenetic interpretations of early vertebrates. However, both the stratigraphical and geographical distribution of anaspids have been poorly documented because earlier studies were based mainly on the few well-preserved articulated taxa from Scotland and Norway (Traquair 1898, 1899; Kiær 1924; Ritchie 1964). Disarticulated scales and plates are fairly abundant in Silurian marine sediments in many regions of the Northern Hemisphere, with many of these scales recovered by acetic acid treatment in the search for vertebrates and conodonts. These collections show great potential for providing a much higher resolution anaspid biostratigraphy (Gross 1958, 1968; Märss 1986; Blom *et al.* 1999).

Anaspids have been defined, mainly on body gross morphology, as jawless vertebrates with a fusiform head, laterally flattened elongate body with one slanting row of branchial openings on both lateral sides, and a strongly hypocercal tail. All anaspids have their hard tissue composed of aspidine which forms dorsal ridge plates or spines, tri-radiate post branchial spines and in most forms body scales and plates.

Anaspid taxonomy has previously been based on the shape and size of the body, number of gill openings, features of the head plates, dorsal ridge scales, paired lateral ('pectoral') and anal fins (*sensu* Kiær 1924; Stensiö 1964; Ritchie 1964, 1980). Whole specimens were needed to identify taxa on this basis and disarticulated scales and plates were described in open nomenclature (Märss 1986, 2002). Anaspids of the order Birkeniida help to bridge the gap between 'scale' and 'whole body' taxonomy because they have a well-developed external skeleton of scales and plates covering the whole body. The only exception is the naked form *Lasanius* Traquair, 1898 where hard parts were developed only as dorsal median ridge spines and a row of post branchial spines (Traquair 1898, 1899; Simpson 1926).

The present study illustrates almost all known birkeniid anaspids from the Silurian–Devonian of the Northern Hemisphere (Fig. 1), describing the sculpture of individual scales and plates of articulated specimens such as the very well-preserved *Birkenia elegans* Traquair, 1898, *Rhyncholepis parvula* Kiær, 1911, *Pterygolepis nitida* (Kiær, 1911) and *Pharyngolepis oblonga* Kiær, 1911. Histological preparations have also been made with the initial aim of finding taxonomic criteria for the scales, but also for future evaluation of the microstructural changes during ontogeny and phylogeny. The taxonomy of disarticulated specimens previously left in open nomenclature is revised with reference to the articulated material. This revision clarifies our knowledge of the diversity and distribution of anaspids, and enhances their stratigraphic utility.
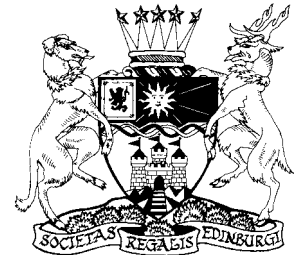
Figure 1 Geographical distribution of Silurian and earliest Devonian birkeniid anaspids of the Northern Hemisphere; main areas described in the present study are represented by dots and those mentioned in literature by squares: (1) Baillie-Hamilton and Cornwallis islands, Arctic Canada. (2) Hall Land, N Greenland. (3) Welsh Borderland, U.K. (4) Scotland, U.K. (5) Ringerike, Norway. (6) Skåne, Sweden. (7) Gotland, Sweden. (8) Estonia and Latvia, E Baltic. (9) Pioneer Island, Severnaya Zemlya Archipelago, Russia. (10) October Revolution Island, Severnaya Zemlya Archipelago, Russia. (11) Komsomolets Island, Severnaya Zemlya Archipelago, Russia. (12) Central Urals, Russia. (13) Ireland. (14) Washington Land, N Greenland. (15) Mackenzie Mountains, Canada.

1. Historical review

Research on anaspids was started in the mid 19th century by the Baltic German palaeontologist Christian Heinrich Pander (1794–1865) (Fig. 2A). He introduced, in a series of remarkably illustrated monographs, the study of early vertebrates of the Baltic. He based his work on well-preserved isolated fragments of bone from the present Baltic countries, most notably from Estonia, and was among the first to describe histological structures. Pander (1856) illustrated and described from the Silurian of Saaremaa Island, Estonia, three elongated scale fragments that are now known as birkeniid anaspids (Fig. 3). He based the taxonomy on morphology and histology and named them *Coccopeltus asmusi* (Fig. 3A) (Pander 1856, pl. 5, fig. 1), *Rytidolepis quenstedtii* (Fig. 3B) (Pander 1856, pl. 5, fig. 2) and *Schidiosteus mustelensis* (Fig. 3C) (Pander 1856, pl. 5, fig. 13).

Rohon (1893) expanded the study of Silurian vertebrates from the Baltic region, but did not consider the above taxa as vertebrates. He based this conclusion on the homogeneous laminar microstructure that he and Pander had observed independently, and could not see any similarity to other known bone histology.

The discovery of the famous fossil fish fauna of Lanarkshire and the Pentland Hills in Scotland was the true springboard of anaspid research. Ramsay Heatley Traquair (1840–1912) (Fig. 2B), known mainly for his research on jawless fishes from Scotland, described two new genera with a ventral (later realised to be dorsal) median row of thorn-like scutes (Traquair 1898, 1899). He found *Birkenia* Traquair, 1898 and *Lasanius* Traquair, 1898 so unlike any other fishes known that he established the new family Birkeniidae within the new order Anaspida (Traquair 1899). He also noted that the body of *Birkenia* was covered with several rows of longitudinal narrow and finely tuberculated scutes. Although Traquair in the same work noted the homogeneous mass of microstructure, he did not compare them with Pander's specimens.

Traquair (1898) based the genus *Lasanius* on two species, *L. problematicus* and *L. armatus*, which lack the typical rows of elongated dermal scutes found in *Birkenia*. Another naked form, *Euphanerops longaevus* from the Upper Devonian of Canada, was described by Woodward (1900, 1902) and further

intensified the interest in these laterally compressed jawless fishes with strongly hypocercal tails. Jaekel (1911) suggested, based on the morphology of the tail, that Traquair had confused the ventral and dorsal side of *Lasanius* and *Birkenia*. Woodward (1900) followed Traquair in his upside-down illustration of *Euphanerops*. Jaekel's (1911) correct view was not adopted by most palaeontologists until the discovery of closely related forms from Ringerike, Norway.

A very large collection of anaspids was made at Rudstangen, Ringerike (Fig. 4A), during excavations (1909–13) lead by the Norwegian Professor Johan Kiær (1869–1931) (Fig. 2C). Kiær (1911) made a short preliminary report on the anaspids and associated fauna from Rudstangen. In his monograph, Kiær (1924) described in detail *Rhyncholepis parvula*, *Pharyngolepis oblonga* and *Pterygolepis nitida* (originally *Pterolepis*) which cleared up many of the taxonomic questions left unanswered by Traquair (1898, 1899, 1905), including the correct dorsal and ventral orientation of anaspids. Kiær (1924) noted that the dermal scale and plate pattern resembled that of *Birkenia*. Despite a large and well-preserved collection, he did not evaluate the finer morphological structures nor the problematic homogeneous histology. However, Kiær (1924) presented the first attempt at anaspid classification, establishing within the class Anaspida separate families for each of the known anaspid genera: Birkeniidae Traquair, 1899, Lasaniidae Abel, 1919, Pharyngolepidae Kiær, 1924, Pterolepidae Kiær, 1924, Rhyncholepidae Kiær, 1924 and Euphaneropidae Woodward, 1900. One imperfect specimen from the Silurian of New Brunswick, Canada, was previously described by Matthew (1907) as *Ctenopleuron nerepisense*, and Kiær (1924) suggested a possible connection to Pharyngolepidae.

Following Kiær's work on classification several scientists contributed to discussions on the group (Raymond 1925; Stromer 1926, 1930; Stetson 1928; Sewertzoff 1928). Stetson (1927) and Bulman (1930) both mentioned *Lasanius* and its relevance to vertebrate origins, following a new reconstruction of *Lasanius* by Simpson (1926). Stetson (1928) further explored this issue with a new restoration of *Birkenia elegans*.

George M. Robertson (1937) (Fig. 2D) reported several incomplete specimens of birkeniids from the Ludlow of Saaremaa Island (Oesel), Estonia, saying, without referring to
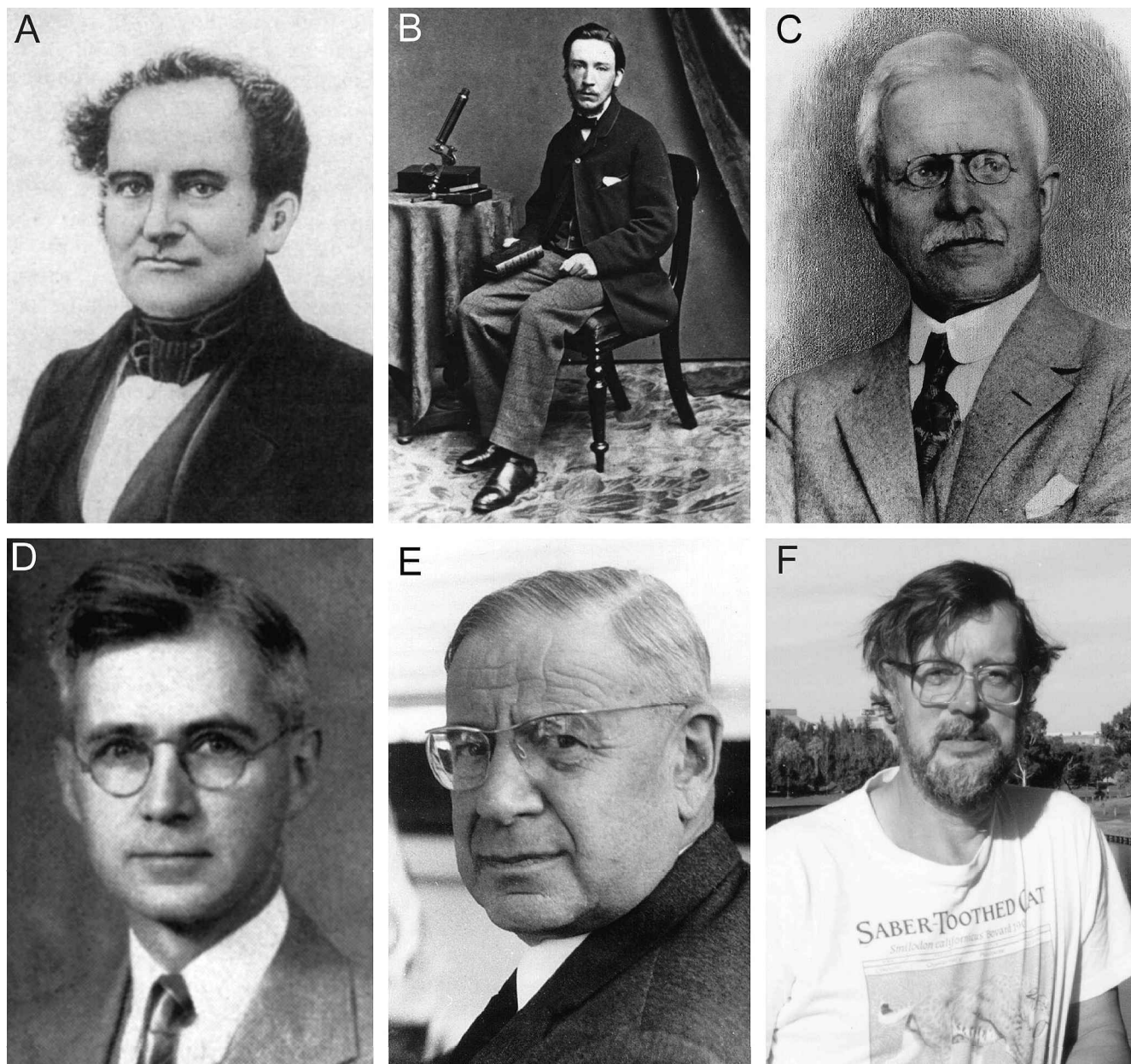
Figure 2 Portraits of six scientists who have contributed substantially to research on anaspids: (A) Christian Heinrich Pander (1794–1865), Baltic German anatomist and palaeontologist, and the first to describe vertebrate fragments that today are considered anaspids. (B) Ramsay Heatley Traquair (1840–1912), researcher of Scottish early vertebrates and the first to describe articulated anaspids from Scotland; photograph from the archives of the Natural History Museum, London with permission. (C) Johan Kiær (1869–1931), who described articulated anaspids from Ringerike; photograph courtesy of the Paleontological Museum, University of Oslo, Norway. (D) George M. Robertson, who described Estonian articulated anaspids; photograph reproduced with permission from Reveille, yearbook 1941 of Fort Hays State University, U.S.A. (E) Walter Gross (1903–74); photograph obtained from A. Rõõmusoks, Tartu University, Estonia. (F) Alexander Ritchie, Australian Museum; photograph taken during the Conference on Australian Vertebrate Evolution, Palaeontology and Systematics (CAVEPS) in Adelaide, April 1993 and published with permission from A. Ritchie.

Pander's (1856) work, that these were the first anaspids found on Saaremaa Island. The material that Robertson (1937, 1941, 1945) described came from the famous and productive Himmiste–Kuigu Quarry which has yielded numerous articulated specimens of osteostracans, the thelodont *Phlebolepis elegans* Pander, 1856, and less frequent fragments of anaspids. This fish locality was found in 1928 by A. Luha, professor of Tartu University, and later collected by him and a large team led by William Patten in 1929–32 (Fig. 4B). A huge collection of material was brought back to the United States by Patten and kept at the Dartmouth College, New Hampshire. A few anaspid articulated specimens from that collection, now at the American Museum of Natural History, New York, were subsequently described and named *Anaspis oeselensis* (Robertson 1941). The name was changed for reasons of priority, from *Saarolepis oeselensis* (Robertson, 1945), to *Rhyncholepis oeselensis* (Ritchie 1980). This issue is discussed further in the present study.

During the same period, Walter Gross (1903–74) (Fig. 2E), well known for his detailed studies of microscopic Silurian and Devonian vertebrate remains, described the histology of some anaspid scales from Wales, U.K. (Gross 1938). He concluded that the descriptions of Traquair and Kiær fitted well with his histological observations.
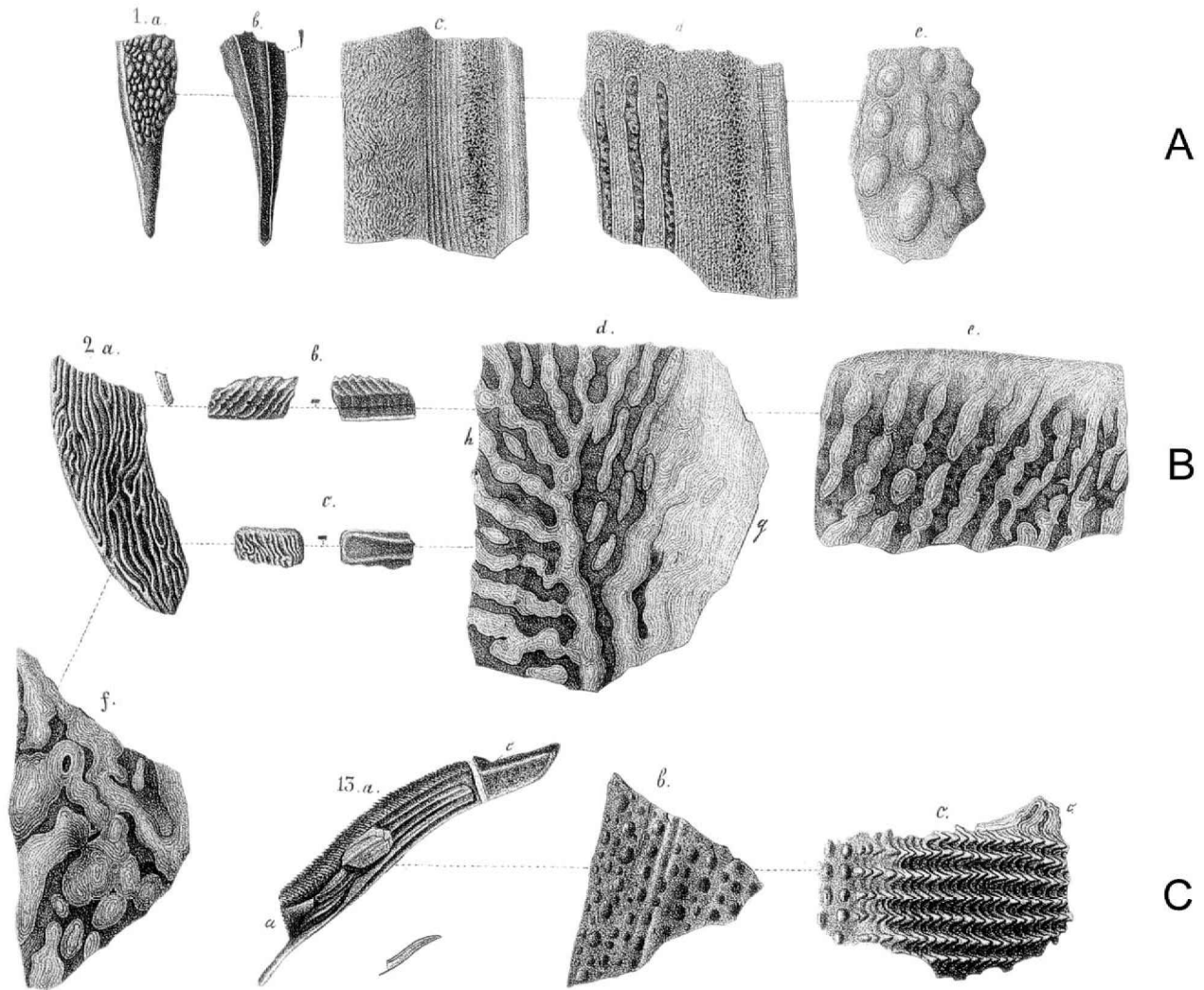
Figure 3 Reproduction of Pander's first illustrations of birkeniid anaspid fragments: (A) *Coccopeltus asmusi* Pander, 1856 (pl. 5, fig. 1a–e); (B) *Rytidolepis quenstedtii* Pander, 1856 (pl. 5, fig. 2a–h); (C) *Schidiosteus mustelensis* Pander, 1856 (pl. 5, fig. 13a–c). Specimens are lost.

In 1939 the Swedish palaeontologist Erik Stensiö described a new anaspid from Scaumenac Bay (in fact Escuminac Bay), Québec, Canada, and also made remarks on other anaspids. He grouped Birkeniidae, Pterolepidae, Rhyncholepidae and Pharyngolepidae without formally naming a group, left *Lasanius* in a group of its own, and did the same with Euphaneropsidae and the new Endeiolepidae. The larger 'Group A' was characterised by the presence of hard dermal scaled skeleton. Without exploring the taxonomy further, Stensiö (1958, 1964) also made detailed reconstructions of the anaspid head and body, including internal anatomy, with special reference to form and function. The nature of anaspids in general was also considered by Parrington (1958) based on a new reconstruction of *Lasanius*, given by new data on the skin, orbit and the postbranchial spines.

A new primitive fish-like chordate from the Silurian of Lanarkshire, Scotland, *Jamoytius kerwoodi* was described and placed in a new order by White (1946). He suggested that it was an early ancestor of cephalochordates. Stensiö (1958, 1964) included *J. kerwoodi* in the anaspids, although its assignment has remained controversial for many years (for details, see Ritchie 1960, 1968, 1984; Janvier 1996a, b; Donoghue *et al*. 2000).

Studies of the group of anaspids with high dermal scales and plates, referred to as birkeniids, continued with Smith (1956, 1957). He noted (Smith 1956) the presence of an axial skeleton in a new species, *Pharyngolepis kiaeri*. In the following year Smith further described this taxon and made the first attempt to compare the differences in scale sculpture between *Birkenia*, *Pharyngolepis*, *Pterygolepis* and *Rhyncholepis*. During this revival in interest about anaspids, Heintz (1958) made a new head reconstruction of *Birkenia*.

Gross (1958) described the histology and morphology of anaspid scales from Saaremaa and the Beyrichienkalk, referring some of them to the stratigraphically contemporary *Saarolepis oeselensis* (Robertson, 1941). The histology was described in detail and showed wide variation in anaspid scales (Gross 1958), but no classification was established. In his paper on the agnathan fauna of Gotland, Sweden, Gross (1968) illustrated a new variety of anaspid scale ornamentation, since it was new, indirectly showing potential for future biostratigraphical use of anaspids.

Along with the renewed interest in morphology and histology of disarticulated anaspid scales and plates came a new extensive study of the Scottish and Norwegian articulated anaspids by Alexander Ritchie (Fig. 2F). This resulted in
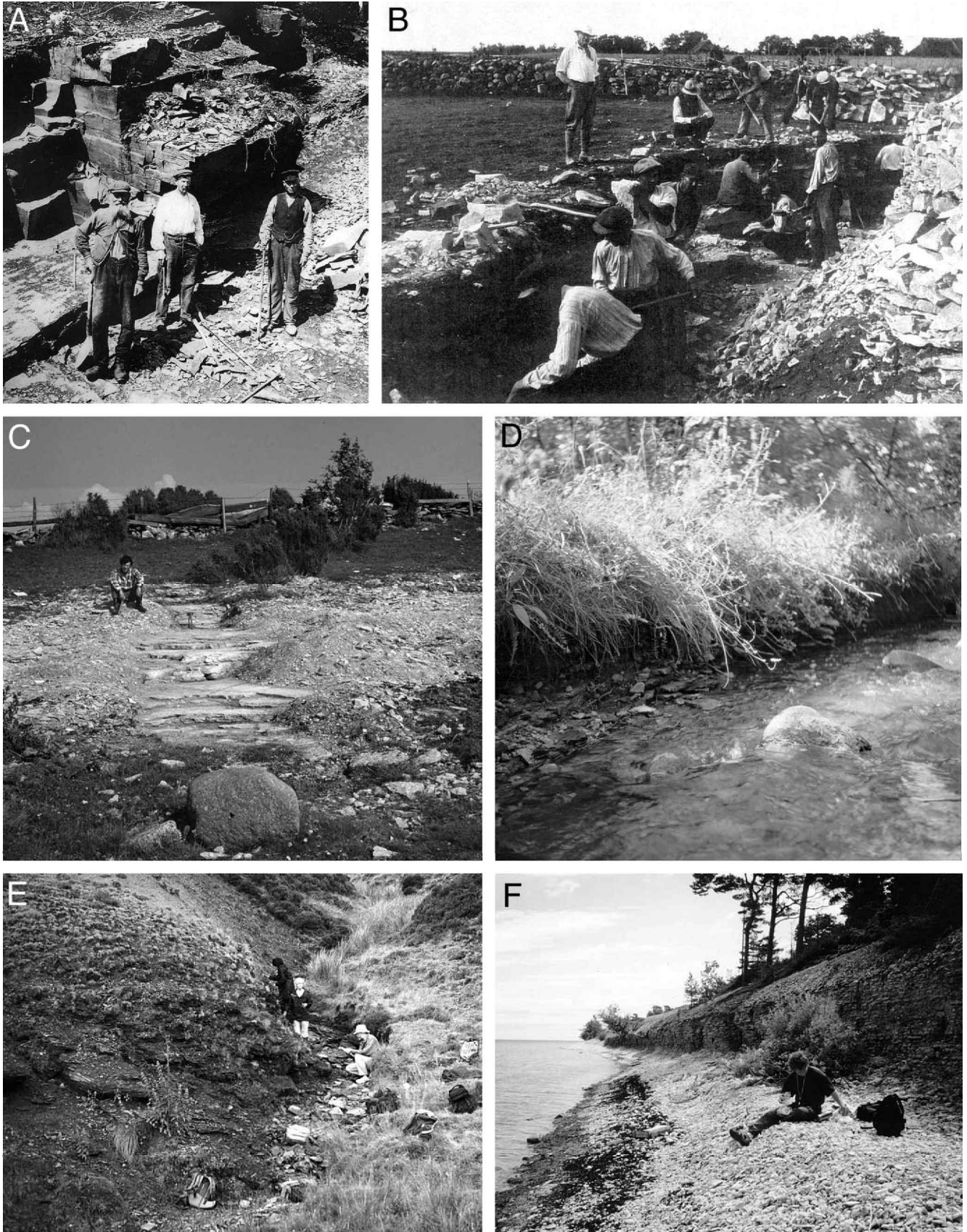
Figure 4 Important anaspid localities: (A) Excavation at Rudstangen, Ringerike, Norway, field season 1909–13; photograph courtesy of Paleontological Museum, University of Oslo, Norway. (B) Excavation in 1932 of Himmiste Quarry, Saaremaa, Estonia; William Patten is supervising the excavation. (C) Silma Cliff locality, Saaremaa, Estonia, summer 1998. (D) Vesiku Brook, Saaremaa, Estonia, summer 1998; the bank of the brook is about 0·5 m high. (E) Slot Burn, Scotland, U.K., summer 1997. (F) Gothemshammar, Gotland, Sweden, summer 1998.

several papers that so far are the largest contributions to the study of both naked and scaled 'anaspids' (Ritchie 1960, 1964, 1968, 1980, 1984). Among the Norwegian birkeniids, Ritchie (1964) looked deeper into the morphology of *Pharyngolepis* and revised Smith's (1956, 1957) work on head squamation and presence of an axial skeleton. He established a new species, *Pharyngolepis heintzi,* based on fewer branchial openings and differently shaped lateral fins. Ritchie (1980) also reinterpreted the Estonian anaspid material described by Robertson (1937, 1941, 1945). One species, previously described as *Saarolepis oeselensis,* he compared with the Norwegian *Rhyncholepis*, renaming it *Rhyncholepis oeselensis.* In this study we argue that the Estonian collection contains at least two species based on head plate arrangement, morphology and sculpture of the dermal scales and plates.

A specimen referred to as Birkeniida indet. has been reported from the Upper Silurian of Sichuan, China (Liu Shi Fan 1983). This is the only anaspid recorded from China, but since the specimen is associated with galeaspid headshields (*Eugaleaspis*), there is a strong probability that it is in fact a scale from the galeaspid squamation (Janvier pers. comm. 2000).

Märss (1986) described some anaspids from Estonia and Latvia, applying an open nomenclature to anaspid scales of different sculpture and structure; this material forms the basis of the present study. Otherwise, during the last 20 years the main interest in anaspids has concerned their importance in phylogeny, and their role in the evolution of agnathans and gnathostomes (Janvier 1981, 1996a, b; Forey 1984; Maisey 1986; Donoghue *et al.* 2000). It has subsequently been proposed that true anaspids only include forms with a tri-radiate post-branchial spine (Forey 1984; Arsenault & Janvier 1991; Janvier 1996a, b). This monophyletic view of the anaspids is in accordance with the new taxonomy presented in this paper, excluding taxa such as *Euphanerops* and *Jamoytius*. These two taxa lack the tri-radiate postbranchial spine, but are similar to the 'true' anaspids by their hypocercal tail and branchial openings arranged in slanting row (Arsenault & Janvier 1991; Janvier 1996a, b).

2. Material and methods

2.1. Material examined

The material studied herein comes from the Early Silurian (late Llandovery) to Early Devonian (early Lochkovian) of the Baltic Sea region (Gotland Island, Sweden, and Saaremaa and Ruhnu islands in Estonia), southern Scandinavia (Ringerike, Norway and Skåne, Sweden), British Isles (Scotland and Welsh Borderland), N Greenland, Arctic Canada (Baillie-Hamilton and Cornwallis islands), northwestern Canada (Mackenzie Mountains), Central Urals and the Severnaya Zemlya Archipelago (October Revolution, Komsomolets and Pioneer islands), Russia.

The number and quality of scales studied from each region varies greatly. The largest scale collections are from the late Wenlock and early Ludlow of Gotland and Saaremaa islands; the best-preserved scales are from Gotland. On Gotland the most important and richest locality is Gothemshammar (Fig. 4F) and on Saaremaa, Vesiku Brook (Fig. 4D) and Silma Cliff (Fig. 4C).

Abbreviations used in the text refer to the following institutions and museums:

AMNH: American Museum of Natural History, New York, USA.
D: University Museum, Oxford, United Kingdom.

GGU: Geological Survey of Denmark and Greenland, Copenhagen, Denmark.
GI Pi: Geological Institute of Tallinn Technical University, Estonia.
KIMMG: Dick Institute, Kilmarnock, United Kingdom.
LIG: Institute of Geology, Vilnius, Lithuania.
LO: Department of Historical Geology and Palaeontology, Lund University, Sweden.
MGUH VP: Geological Museum, Copenhagen, Denmark.
NHM P: Natural History Museum, London, United Kingdom.
NRM P: Swedish Museum of Natural History, Stockholm, Sweden.
PMO E: Palaeontological Museum, Oslo University, Oslo, Norway.
PMU G: Museum of Evolution, Uppsala University (former Palaeontological Museum, Uppsala University), Uppsala, Sweden.
UALVP: Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada.

2.2. Localities

Canada. Arctic: *Baillie-Hamilton Island section 1*, levels 85·5, 90·0, 106·5, 130·5 m, early Wenlock; *Baillie-Hamilton Island section 2*, levels 28·5, 73·5, 96·5 m, late Wenlock, and levels 204·5, 249·0, 270·5, 294·0 371·0 m, Ludlow; *Cornwallis Island Cape Phillips section*, level 59·0 m, early Wenlock?; *Cornwallis Island Red Bay southern section*, level 61·5 m (talus), early Lochkovian?. All are from the Cape Phillips Formation. For details see Märss *et al.* (1998). Mackenzie Mountains: *Avalanche Lake section AV-1G,* Whittaker Formation, late Llandovery.

North Greenland. *Observatory Bluff* (Halls Grav), Hall Land, Chester Bjerg Formation, late Ludlow; *Monument*, Hall Land, Chester Bjerg Formation, early Lochkovian. For details see Blom (1999b).

Norway. *Rudstangen* (Fig. 4A), Ringerike, Sundvollen Formation, late Wenlock; *Ranberget Member sample*, Ringerike, Steinsfjorden Formation, late Wenlock. For details see Kiær (1924) and Worsley *et al.* (1983).

Sweden. Gotland: *Gothemshammar* (Fig. 4F), Halla Beds, unit c, late Wenlock; *Slitebrottet 1*, Slite marlstone of Slite Bed, early Wenlock; *Möllbos 1*, Halla Beds, unit b; *Uddvide*, Burgsvik Beds, late Ludlow; *Hoburgen 2*, Hamra Beds, late Ludlow; *Hoburgen 3*, Hamra Beds, unit b, c, late Ludlow. For details see Laufeld (1974). Skåne: *Ramsåsa*, Öved-Ramsåsa Formation, early Přídolí (late Ludlow?). For details see Jeppsson & Laufeld (1986), Larsson (1979) and Jeppsson (1974).

East Baltic. Saaremaa: *Ohesaare Borehole*, core at depth 163·3 m, Maasi Beds, Jaagarahu Stage, early Wenlock; *Vesiku Brook* (Fig. 4D), Vesiku Beds, Rootsiküla Stage, late Wenlock; *Vesiku Borehole*, core at depth 3·2–3·4 m, Vesiku Beds, Rootsiküla Stage, late Wenlock; *Elda Cliff*, Kuusnõmme Beds, Rootsiküla Stage, late Wenlock; *Viita Trench*, Viita Beds, Rootsiküla Stage, late Wenlock; *Paadla Borehole*, core at depth 11·55–11·75 m, Sauvere Beds, Paadla Stage, early Ludlow; *Silma Cliff* (Fig. 4C), Himmiste Beds, Paadla Stage, middle Ludlow; *Himmiste Quarry* (Fig. 4B), Himmiste Beds, Paadla Stage, middle Ludlow; *Paadla Quarry*, Himmiste Beds, Paadla Stage, middle Ludlow; *Paadla Borehole*, depth 1·3–1·4 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Sakla Borehole*, core at depth 20·45–25·70 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Suurlahe Borehole 738*, core at depth 21·82–21·95 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Uduvere-968 Borehole*; core at depth 3·6–4·5 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Kaarmise Borehole*,

Saaremaa, core at depth 2·7–3·6 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Varbla-502 Borehole*, core at depth 31·8–32·3 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Vätta-817 Borehole*, core at depth 62·5 m, Himmiste Beds, Paadla Stage, middle Ludlow; *Laadjala outcrop*, Tahula Beds, Kuressaare Stage, late Ludlow; *Kihnu-526 Borehole*, core at depth 90·1 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Varbla-502 Borehole*, core at depth 19·1–22·0 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Lahetaguse-573 Borehole*, core at depth 14·0–14·5 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Sakla Borehole*, core at depth 7·88–13·4 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Kuressaare Borehole*, core at depth 14·50–18·38 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Sutu-605 Borehole*, core at depth 21·4–23·7 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Tahula-709 Borehole*, core at depth 7·6–10·0 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Kaugatuma Borehole*, core at depth 52·05 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Sõrve-514 Borehole*, core at depth 143·4–144·4 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Ohesaare Borehole*, core at depth 93·15–95·17 m, Tahula Beds, Kuressaare Stage, late Ludlow; *Ohesaare Cliff* section, Ohesaare Stage, Přídolí; *Ruhnu-500 Borehole*, core at depth 163·2 m and 172·6 m, Ohesaare Stage, Přídolí. Latvia: *Kolka-54 Borehole*, depth 284·2–284·5 m, Tahula Beds, Kuressaare Stage, late Ludlow. For details see Märss (1986).

British Isles. Scotland: *Slot Burn* (Fig. 4E), Seggholm, Ayr, Lesmahagow Inlier, Slot Burn Formation, Waterhead Group, early Wenlock (Fig. 4E); *Smithy Burn*, Fish Bed Formation, Glenbuck Group, Hagshaw Hills Inlier, early Wenlock. For details see Märss & Ritchie (1998). England: *Man Brook*, near Trimpley, Worcestershire, late Přídolí. Grey Grit, *Ledbury*, Herefordshire; Grey Grit, Ledbury Passage Beds, Přídolí. For details see Piper (1898) and Dineley (1999b).

Severnaya Zemlya. October Revolution Island: *Matusevich River*, Ust' Spokoinaya Formation, Ludlow; *Spokoinaya River*, Ust' Spokoinaya Formation, Ludlow, and Krasnaya Bukhta Formation, Přídolí; *Ushakov River*, Samoilovich Formation, Wenlock, and Ust' Spokoinaya Formation, Ludlow; *Pod'emnaya River*, Severnaya Zemlya Formation, early Lochkovian. *Pioneer Island*, Wenlock to Ludlow. *Komsomolets Island*, Ludlow. For details see Märss (2000).

Central Urals. *Excavations on the right bank of Ufa River*, downstream from the mouth of Tabuska River, Tabuska Beds, late Ludlow. For details see Chekhovich *et al*. (2000).

2.3. General methodology

A large collection of articulated anaspids from Ringerike was studied at the Palaeontological Museum, University of Oslo, to find specimens with well-preserved dermal skeleton that would give characteristic features of sculpture on the external surface. Often only the visceral surface or a cast of it was visible and the sculpture on the external surface was hidden in the matrix, and initially only a reconstruction of the visceral side was made. Small areas of specimens with well-preserved bone were removed with hydrochloric acid, to make latex-casts from the exposed external moulds. Pieces of the latex were mounted on stubs, coated with gold and digital images taken using a Philips Scanning Electron Microscope at Uppsala University.

External moulds of parts and counterparts of articulated specimens of *Birkenia elegans* at the Natural History Museum, London were treated with a consolidant (Butvar) and cast using silicone rubber. The rubber was then mounted on stubs, coated in gold and negatives produced using a Hitachi S-2500 Scanning Electron Microscope. Articulated material of

B. elegans from the Dick Institute, Kilmarnock, was photographed uncoated from a complete latex cast, using an ISI-ABT-55 environmental chamber Scanning Electron Microscope. They were all taken at the Natural History Museum, London.

The disarticulated scales and plates have been obtained from limestones, marls, calcareous siltstones and sandstones by dissolution in 10–15% acetic acid, mostly using the buffering method developed by Jeppsson *et al*. (1985). Some of the residues were separated by heavy liquid density separation using bromoform or the non-toxic sodium polytungstate. Scale fragments were picked from the residues, and occasionally two to five smaller fragments were glued together. Images of disarticulated material were also taken using the above-mentioned scanning electron microscopes at Uppsala University and the Natural History Museum, London, as well as a JEOL ISM 840A scanning electron microscope at Tallinn Technical University. SEM negatives from the images taken at the Natural History Museum, London and Tallinn Technical University were then scanned and reproduced digitally in Uppsala in connection to all other additional material.

Scale histology was studied for most taxa. Standard thin section or objects immersed in aniseed oil to make the bone transparent were studied by transmitted light microscopy.

2.4. Systematic methodology

This study develops an anaspid taxonomy to include both articulated and disarticulated material. Its starting point is the well-preserved articulated specimens that have an already established taxonomy based on size and full-body morphology of *B. elegans* from Scotland, and *Pterygolepis nitida*, *R. parvula* and *Pharyngolepis oblonga* from Norway (Fig. 5). Each has a unique scale and plate morphology which complemented the already established set of morphological body characters. The taxonomic criteria were then applied to disarticulated material.

In the taxonomic description of scale and plate, morphology diagnostic features are defined for fragments or scales of the same type, i.e. species. For this reason, as much as possible, body scales have been used, although the study of *B. elegans* shows that the sculpture is more or less the same over the whole body.

The diagnostic characters for scales and plates can vary between different groups, but in general, the shape, orientation and size of the sculpture have been used. The presence and form of external and visceral ribs have been shown to be useful for classification. Histological characters, such as the development of a vascular canal system, are used mostly for taxonomy at genus and higher levels. Family level classification is mainly based on body gross morphology such as number of branchial openings when present, and histology, and to some degree also on general gross sculpture. Genus level taxonomy is usually based on general variations in the sculpture. Species level taxonomy is based on size, orientation and detailed variations in sculpture.

2.5. Terminology

The terminology for description of articulated specimens is well established. The present study follows Kiær (1924) and Ritchie (1964, 1980) and a summary of terms is given in Figure 6. For discrete scales the terminology is less well established. However, Gross's (1958) terminology has been used as a base, with the addition of a number of new terms for morphology (Fig. 7) and histology (Fig. 8). All scales that are long and narrow are treated as trunk scales. Fragments that are short, slightly convex and irregular in shape are regarded as plates. There
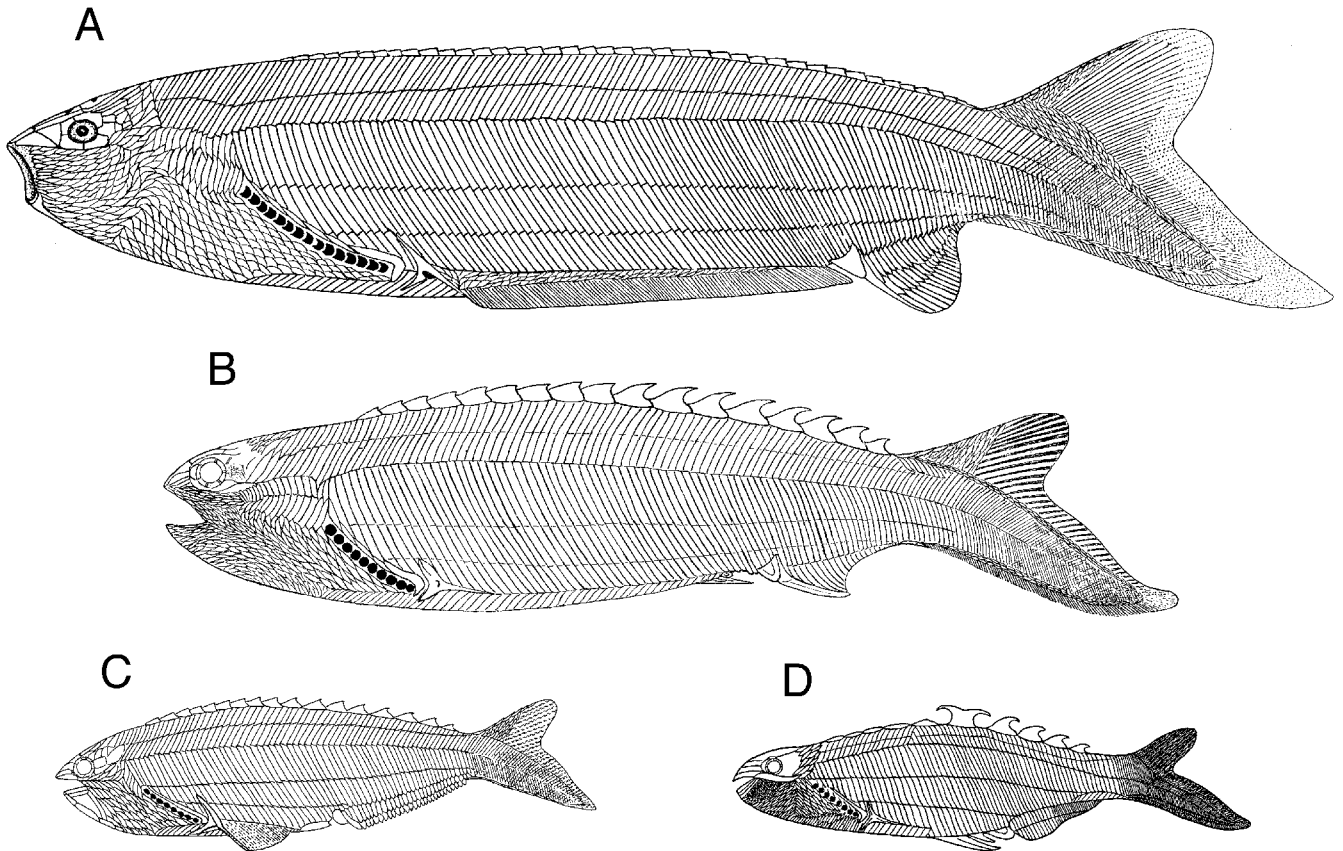
Figure 5 Reconstructions of known articulated birkeniid anaspids at normal size: (A) *Pharyngolepis oblonga* Kiær, 1911, modified from Kiær (1924); (B) *Pterygolepis nitida* (Kiær, 1911), modified from Ritchie (1964); (C) *Rhyncholepis parvula* Kiær, 1911, modified from Ritchie (1980); (D) *Birkenia elegans* Traquair, 1898, modified from Stetson (1928).

are also a number of specialised fragments such as anal spines, preanal plates, postbranchial spines and dorsal ridge scales.

2.6. Abbreviations used in illustrations
Abbrevations used in histological illustrations are:

aer, anterior external rib; **avr**, anterior visceral rib; **gl**, growth lines; **mvr**, medial visceral rib; **ovsc**, openings for vascular canals; **per**, posterior external rib; **r**, ridge; **rf**, radial fibres; **s**, spine; **sf**, Sharpey's fibres (*sensu* Gross); **t**, tubercle; **vsc**, vascular canal.

3. Distribution

3.1. Baltic
Anaspid localities from the Baltic Sea region include Silurian exposures of Gotland and Skåne, Sweden, borehole cores from the Baltic countries (Estonia and Latvia) and the main Silurian exposures on Saaremaa and Ruhnu islands, Estonia. They provide an anaspid distribution from early Wenlock–Přídolí (Fig. 9).

The earliest birkeniid anaspid in the E Baltic, *Rhyncholepis parvula*, has been found in the Maasi Beds of the Jaagarahu Stage, Sheinwoodian, early Wenlock. It is at 163·3 m in
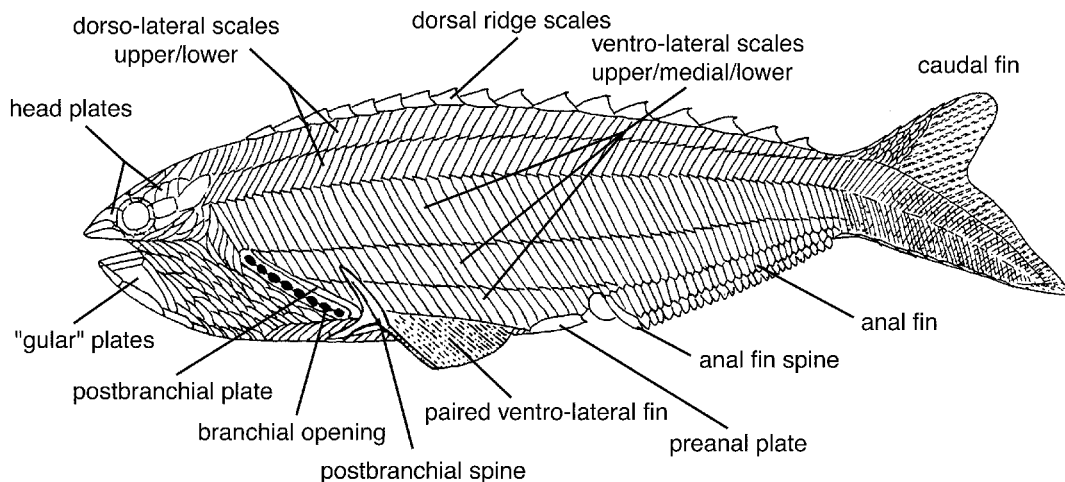
Figure 6 Terminology of birkeniid body morphology after Kiær (1924) and Ritchie (1980).
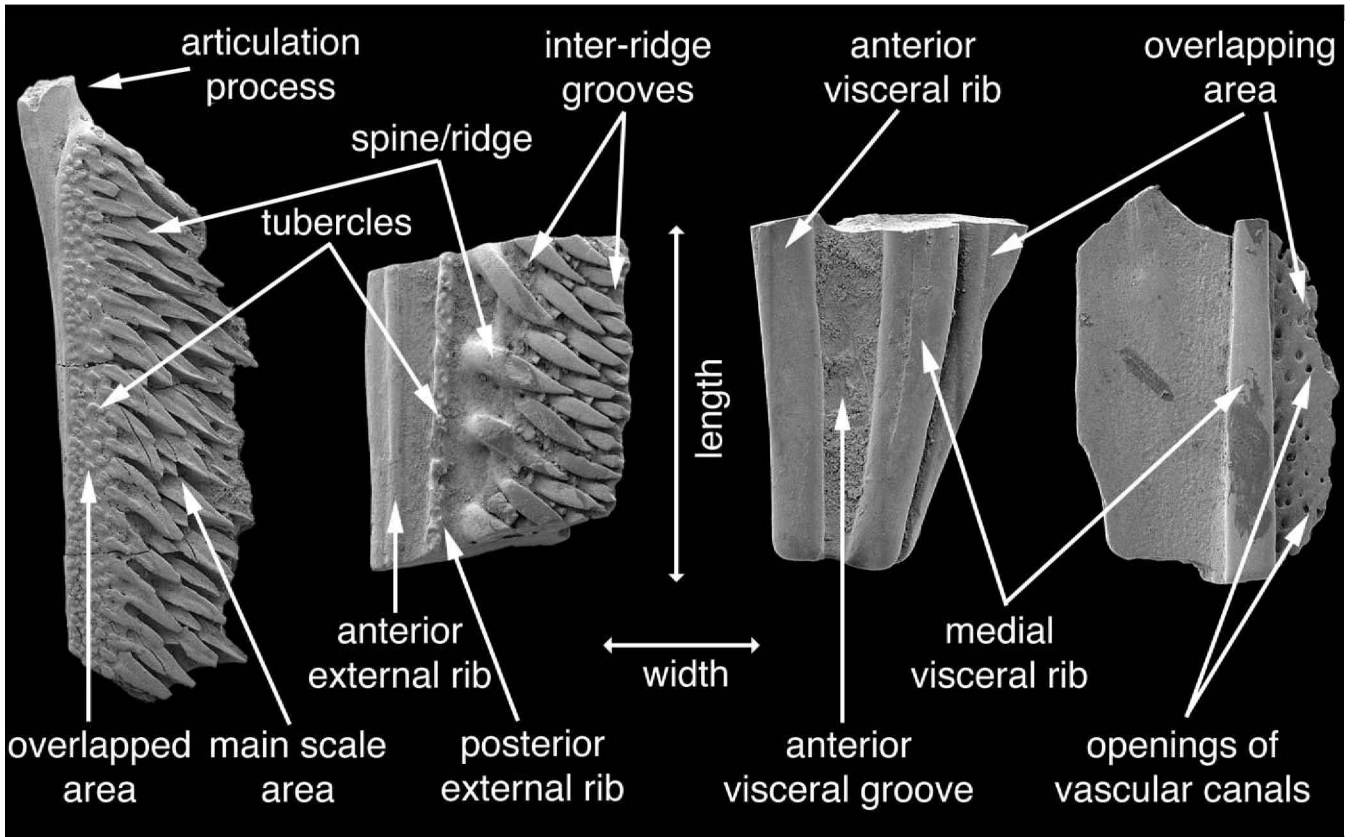
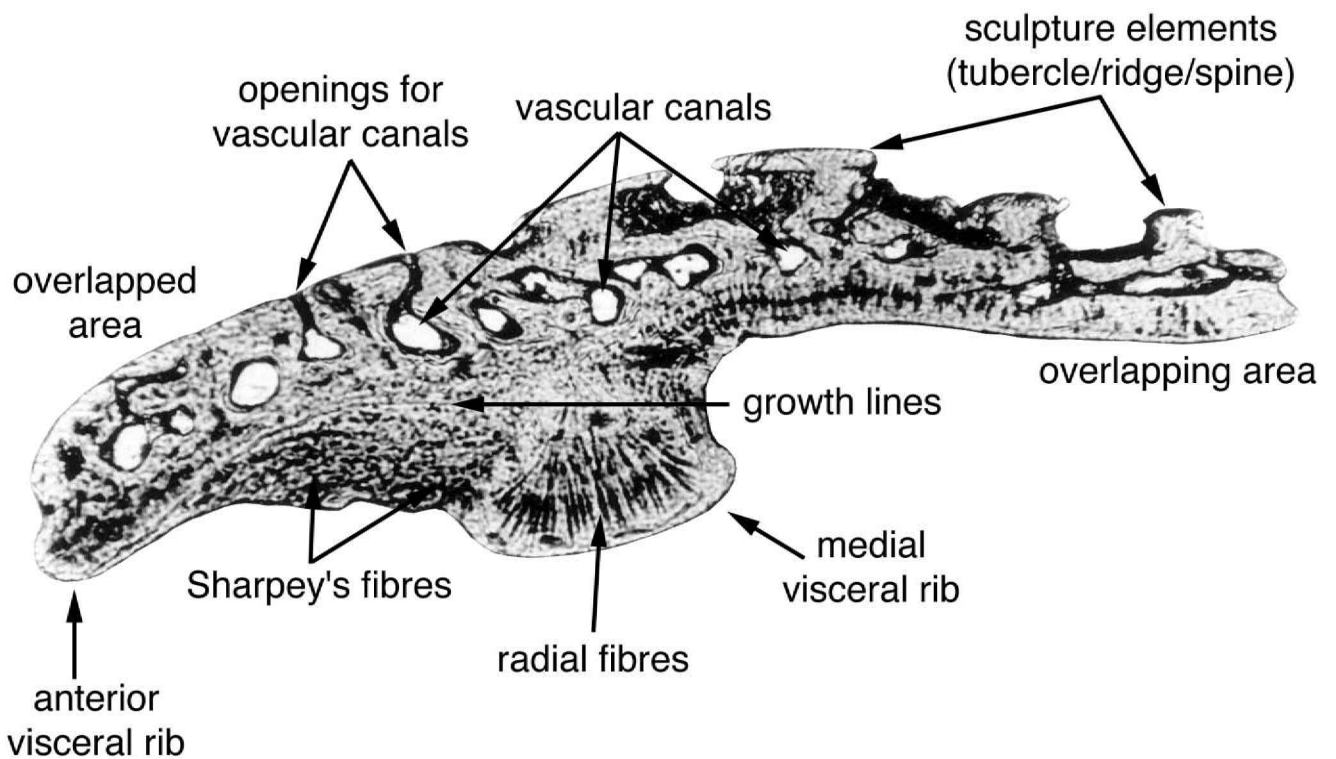**Figure 7** Terminology of birkeniid scales.

Figure 8 Terminology of birkeniid histology (modified from Gross, 1958); for illustration, *Vesikulepis funiforma* scale is used from Märss (1986, pl. 27, fig. 5).

		SILURIAN																		
			WENLOCK						LUDLOW							PRIDOLI				
		Sheinwoodian	Homerian					Gorstian	Ludfordian											
EAST BALTIC		Jaagarahu Fm	Rootsiküla Fm					Paadla Fm			Kuressaare Fm					Kaugatuma Fm			Ohesaare Fm	
		Maasi Beds / Tagavere Beds	Viita Beds	Kuusnõmme Beds	Vesiku Beds	Soeginina Beds		Sauvere Beds	Himmiste Beds	Uduvere Beds	Eke Beds	Burgsvik Beds	Hamra Beds	Tahula Beds	Kudjape Beds	Äigu Beds	Lõo Beds			
GOTLAND		Slite Beds	Halla/Mulde Beds			Klinteberg Beds			Hemse Beds							Sundre Beds					
																SKÅNE				
																Öved Sandstone Formation				
Rhyncholepis parvula Kiær, 1924	E?	G	G E			E			E											
Pterygolepis nitida (Kiær, 1924)	G		G E																	
Rhyncholepis butriangula sp. nov.		G G E	G E			E		E												
Birkeniida sp. Fredholm, 1990		G																		
Schidiosteus mustelensis Pander, 1856		G	G			E			G											
Rytidolepis quenstedtii Pander, 1856		G	G			E			E?											
Birkenia robusta sp. nov.		E	E			E		E												
Vesikulepis funiforma gen. et sp. nov.		E	E			E		E												
Silmalepis erinacea gen. et sp. nov.								E												
Vesikulepis funiforma ? gen. et sp. nov.								E												
Pharyngolepis ? sp.								E G												
Septentrionia mucronata gen. et sp. nov.											G G									
Hoburgilepis papillata gen. et sp. nov.											G									
Liivilepis curvata gen. et sp. nov.											G						S			
Tahulalepis elongituberculata gen. et sp. nov.											E						E S			
Ruhnulepis longicostata gen. et sp. nov.																				E	

Figure 9 Stratigraphical distribution of birkeniid anaspids from the Baltic Sea region: G = Gotland, Sweden; S = Skåne, Sweden; E = East Baltic. Stratigraphical hiatuses in Estonia after Nestor & Nestor (1991), Märss (1992) and Jeppsson *et al.* (1994).

Ohesaare Borehole core. Scales of this taxon occur higher in the Viita and Vesiku beds of Rootsiküla Stage, in the Viita Trench and Vesiku Brook localities, respectively. The Viita Trench also reveals the new taxa, *Rhyncholepis butriangula* sp. nov., *Birkenia robusta* sp. nov. and *Vesikulepis funiforma* gen. et sp. nov., as well as scale fragments that have been identified as *Pterygolepis nitida*.

The Vesiku Beds of the Rootsiküla Stage are rich in birkeniid anaspid scale and plate fragments. Several samples taken from the Vesiku Brook locality, Elda Cliff, and Vesiku Borehole, core at depth 3·2–3·4 m, yield *B. robusta, Rytidolepis quenstedtii, Rhyncholepis parvula* and *Rhyncholepis butriangula*. The last-mentioned species occurs higher, in the Sauvere Beds of Paadla Stage, early Ludlow in the Paadla Borehole, core at depth 11·55–11·75 m. *V. funiforma* gen. et sp. nov. is found in the Vesiku Beds and also higher.

Rich fragments of scales, head plates and spines of anaspids occur in the Himmiste Beds of the Paadla Stage, middle Ludlow. Material comes from the Himmiste (Fig. 4B) and Paadla quarries and Silma Cliff (Fig. 4C), and boreholes such as Paadla (depth 1·3–1·4 m), Sakla (depth 20·45–25·70 m), Suurlahe-738 (depth 21·82–21·95 m), Uduvere-968 (depth 3·6–4·5 m), Kaarmise (depth 2·7–3·6 m), Varbla-502 (depth 31·8–32·3 m) and Vätta-817 (depth 62·5 m). Common to the Himmiste Beds are *Schidiosteus mustelensis, V. funiforma, Silmalepis erinacea* gen. et sp. nov., *Pharyngolepis*? sp.; in addition, *R. quenstedtii* might be present. The Himmiste Beds mark the last occurrence for the Wenlock and middle Ludlow taxa described.

In the late Ludlow Tahula Beds of the Kuressaare Stage, *Tahulalepis elongituberculata* gen. et sp. nov., appears and continues into the Kudjape Beds of the same stage. Scales of this taxon have been found at the Laadjala outcrop, and several borehole cores: Kihnu-526 (depth 90·1 m); Varbla-502 (depth 19·1–22·0 m); Lahetaguse-573 (depth 14·0–14·5 m); Sakla (depth 7·88–13·4 m); Kuressaare (depth 14·50–18·38 m); Sutu-605 (depth 21.4–23.7 m); Tahula-709 (depth 7·6–10·0 m); Kaugatuma (depth 52·05 m); Sõrve-514 (depth 143·4–144·4 m); Ohesaare (depth 93·15–95·17 m); all in Estonia, and Kolka-54 (depth 284·2–284·5 m) in Latvia.

In the Ohesaare Stage, Přídolí, a few birkeniid anaspid scales have been discovered. *Liivilepis curvata* gen. et sp. nov. is found at the Ohesaare Cliff section and Ruhnu-500 Borehole, core at depth 172·6 m, and *Ruhnulepis longicostata* gen. et sp. nov. in Ruhnu-500 Borehole, core at depth 163·2 m.

In the W Baltic on Gotland, anaspids have been found in beds of early Wenlock to late Ludlow age. The earliest known occurrence is rare scales from the late early Wenlock (late Sheinwoodian), uppermost Slite Marl, Slite Beds, at Slitebrottet 1. They are described and illustrated by Fredholm (1990, fig. 7K, L), and are very similar to the scales found in the younger lower part of the late Wenlock (early Homerian) Halla Beds, unit c at Gothemshammar. This scale type is illustrated and described in this study as *P. nitida*. From the slightly older Halla Beds, unit b at Möllbos 1, several types of anaspid scales described by Fredholm (1990) include *R. butriangula* and an undescribed form, referred to as Birkeniida sp. It is excluded from this study because only very few specimens are known.

The most important and well-known anaspids from Gotland were described by Gross (1968) and Fredholm (1990) from localities at Gothemshammar, in the Halla Beds, unit c, where abundant thelodonts and osteostracans are found with the anaspids *P. nitida, R. butriangula, S. mustelensis* and *R. parvula*. Fragments from the early Ludlow Hemse Beds, unit c at Sigvalde 1, illustrated by Fredholm (1988, fig. 12D) are here referred to *S. mustelensis*. Fredholm (1988, fig. 12C) also

illustrated a fragment with similar but much coarser sculpture that may represent a different taxon of *Pharyngolepis* type. The youngest known anaspids from Gotland are found in the Burgsvik and Hamra beds, at Uddvide and Hoburgen and are of late Ludlow age; that is *Hoburgilepis papillata* gen. et sp. nov., *Septentrionia mucronata* gen. et sp. nov. and *L. curvata*.

In Skåne, anaspids have been found in samples from Ramsåsa, preserved in the Swedish Museum of Natural History, Stockholm, probably referring to one of several localities close to Ramsåsa Church. The vertebrates are most likely from limestone bands within the upper part of the Öved Sandstone Formation. In these samples of late Ludlow or Přídolí age (Jeppson & Laufeld 1986: Larsson 1979: Jeppsson 1974), *T. elongituberculata* and *L. curvata* occur together with fragments of other vertebrates, such as thelodonts (Lehman 1937), osteostracans and acanthodians.

Three specimens of *Septentrionia lancifera* gen. et sp. nov. have also been recorded from an East Baltic-derived erratic from Oosterhaule, Netherlands (Vergoossen 1999).

3.2. Ringerike, Norway
Four species of articulated anaspids from Ringerike come from the Sundvollen Formation at the famous Rudstangen locality: *Pterygolepis nitida, R. parvula, Pharyngolepis oblonga* and *Pharyngolepis*? *heintzi*. Disarticulated scales and plates of *P. nitida* and *R. parvula* have been found in the Ranberget Member (9g of Kiær 1908) of the Steinsfjorden Formation. Thelodonts from the same Ranberget Member of the Steinsfjorden Formation and other limestone horizons of the Sundvollen Formation suggest a late Wenlock age for the whole fauna (Turner & Turner 1974; Märss 1982, 1996).

3.3. British Isles
The birkeniid anaspid material studied here is from Scotland and the Welsh Borderland but there is also one record from the Republic of Ireland. Scottish material consists of moulds of articulated *B. elegans* from the Slot Burn Formation, Waterhead Group of the Lesmahagow Inlier and the Fish Bed Formation, Glenbuck Group of the Hagshaw Hills Inlier. Dating of these stratigraphical units is problematic since certain of the fish and arthropod species that they contain are endemic (Rolfe 1993). The Ree Burn Formation is older than the Fish Bed Formation, and has been dated as early Wenlock by acritarchs (Dorning 1982). Beds higher in the Glenbuck Group, including the Fish Bed Formation may be Wenlock/Ludlow in age, partly by comparison with similar Ludlow faunas in Norway and also because they are overlain by Old Red Sandstone containing the Early Devonian fish *Cephalaspis* Agassiz, 1835 (Rolfe 1993). Spores (Wellman 1993; Wellman & Richardson 1993) suggest an early Wenlock age for the *Birkenia* faunas (see also Märss & Ritchie 1998, fig. 5). *Birkenia* specimens, probably of another species, are also present in the late Llandovery Kip Burn Formation (Ritchie 1985; Märss & Ritchie 1998).

The one record of an anaspid from the Republic of Ireland is a specimen identified as *B.* cf. *elegans* which was noted from Wenlock–Ludlow mud-silt laminates of the Bunnamohaun Siltstone Formation of southern Clew Bay and Clare Island, Co. Mayo (Gilmore 1992; Palmer *et al*. 1989). From the same beds, thelodont scales have been found that suggest a similar age to the early Wenlock fish beds of the Southern Uplands of Scotland (Gilmore 1992; Turner 2000).

A sample with disarticulated material from Man Brook, near Trimpley, Worcestershire, includes *Manbrookia asperella* gen. et sp. nov. and *S. lancifera*. The exact stratigraphical position of this material is problematic because it was collected from a

single sample in a stream section in a region without continuous sections. The Man Brook section has been extensively collected for vertebrates, with collections and field notes relating to that locality housed at the Natural History Museum, London. Whitehead & Pocock (1947) recognised several separate horizons in the 'Trimpley Fish Zone' of King (1921, 1934). A map drawn by W. W. King on the back of a letter to E. I. White (Vergoossen 2000, fig. 1) indicates that the present sample was collected from locality Man Brook 7 with associated collections at the Natural History Museum including *Tesseraspis tessellata* Wills, 1935, *Didymaspis* Lankester, 1867 cephalaspid fragments and assorted acanthodian spines/scales. *Kallostrakon* Lankester 1870 sp. is also present in the NHM collections from Man Brook. Allen (1977) reported similar faunas from isolated exposures of the Ledbury Formation of this area. The Man Brook fauna suggests that the sample came from below the base of the *Traquairaspis symondsi* Biozone of White & Toombs (1948). White & Lawson (1989) used the base of this biozone as an approximation of the base of the Devonian in the United Kingdom also taking into account thelodonts (Turner 1973) and miospores (Richardson *et al*. 1981). This classical heterostracan biozonation was later revised to *Phialaspis* Zone (Blieck & Janvier 1989) and the biostratigraphical correlations of Early Devonian vertebrate assemblages was further explored (for review see Blieck & Cloutier 2000; Blieck *et al*. 2000). Thelodonts identified from our sample include *Goniporus alatus* (Gross, 1947) and *Paralogania kummerowi* (Gross, 1967), but not *Turinia pagei* (Powrie, 1870), suggesting a late Siluran age. Vergoossen (2000) studied acanthodians from a residue at Man Brook 7 and, on the basis of co-occuring thelodonts, considered the sample highest Přídolí in age.

A single articulated specimen assigned here to *Tahulalepis kingi* (Woodward, 1947), was recovered from the Grey Grit, Ledbury Passage Beds, Silurian of Ledbury, Herefordshire, England. The Passage Beds are now referred to as the Ledbury Formation (Allen 1977) of Přídolí age (Brandon 1989). From the lithological and faunal descriptions of Piper (1898), it is likely that the specimen was collected from the middle of the formation where abundant fish remains have been identified as *Hemicyclaspis murchisoni* (Egerton, 1857) and *Thyestes egertoni* (Lankester, 1870) by Woodward (1947). Dineley (1999b) gives a detailed account of the lithostratigraphy and fish faunas across the Ledbury section but does not mention the anaspid material described by Woodward (1947).

A few specimens have been found in the Stonehaven Beds at Cowie Harbour, Stonehaven, Scotland (Ritchie 1964: Waterston 1965; R. G. Davidson pers. comm. 1999). The anaspids and some eurypterids show a striking similarity with Ringerike and the Welsh Borderlands (Waterston 1965). The Cowie Harbour Fish Bed has been dated from sporomorph evidence as late Wenlock, possibly earliest Ludlow (Wellman 1993). This dating can, however, be challenged by the unique cephalaspid and heterostracan fauna that shows similarities with Welsh Borderland faunas Přídolí in age (Dineley 1999a). An undescribed anaspid from the south shore of Kererra, western Scotland, is of similar age (Waterston 1965).

3.4. N Greenland

Four localities in N Greenland have yielded fragments of anaspids. Three of them, Observatory Bluff (Halls Grav), Monument and Kap Tyson East Outcrop are located on Halls Land and the fourth at Kap Independence, Washington Land (Fig. 1) (Blom 1999a, b, 2000).

The rich material from Halls Grav and Monument contains the endemic anaspid species *Septentrionia seducta* gen. et sp.

nov., and remains of thelodonts, heterostracans, osteostracans, acanthodians and chondrichthyans (Blom 1999b). Blom (1999b) suggested that Halls Grav locality is Přídolí in age and that the Monument is Lochkovian. *S. seducta* thus crosses the Silurian–Devonian boundary.

Two larger fragments of articulated scales (identified by R. Thorsteinsson) were also reported by Norford (1972) from the Kap Tyson E Outcrop. They are of *Birkenia* type with large round tubercles covering the external scale sculpture (H. Blom's personal observation). The outcrop was referred by Norford (1972) to the Cape Phillips Formation but in a redefinition of the Silurian stratigraphy, Hurst (1980) referred the outcrops to the Hauge Bjerg Formation, Washington Land Group. Graptolites collected by Norford (1972) support a late Llandovery age, indicating the *Monograptus spiralis* Biozone of Arctic Canada.

An unidentified tuberculated postbranchial plate described by Bendix-Almgreen (1986) from Kap Independence, Washington Land, comes from the top of the Lafayette Bugt Formation, and seems to be of Wenlock or even early Ludlow age (Bendix-Almgreen 1986; Bjerreskov 1981, 1992). Dermal fragments of indeterminable species of two cyathaspids and one pteraspid have also been found at this locality (Bendix-Almgreen 1986; Blom 2000).

3.5. Canada

In Arctic Canada the disarticulated scales described herein come from four sections: Baillie-Hamilton Island sections 1 and 2, and the Cape Phillips section and Read Bay sections on Cornwallis Island (Märss *et al*. 1998). The stratigraphical distribution of vertebrates and conodonts was studied and compared with carbon isotope curves by Märss *et al*. (1997, 1998). The Baillie-Hamilton Island sections are the richest in anaspids and the first specimens appear just above the boundary between the Llandovery and Wenlock. These poorly preserved scales are very similar to *B. elegans* and are present at several levels in the Sheinwoodian of Baillie-Hamilton section 1. The same scales have also been found in the lower parts of Baillie-Hamilton section 2 at 28·5 m, which has been dated to late Sheinwoodian or possibly earliest Homerian by conodonts. This is the highest occurrence of *B. elegans* in these sections. In the Cape Phillips section, poorly preserved fragments of *B. elegans* type scales have been found at 61·5 m. This level is perhaps of Wenlock age, although conodonts from slightly lower levels (29·0–35·5 m) indicate a Telychian age.

In Baillie-Hamilton section 2, *Maurylepis lacrimans* gen. et sp. nov. appears at levels 73·5 m and 96·5 m. It occurs together with other vertebrates in a high diversity fauna typical of the Homerian of this region. *Septentrionia dissimilis* gen. et sp. nov. is found at 37·0 m in Baillie-Hamilton section 2, a level dated by conodonts and carbon isotope data as Ludfordian. At several levels between 204·5–294·5 m in this section, anaspid fragments of Gorstian to Ludfordian age have been referred to *Septentrionia dissimilis*? gen. et sp. nov. because of slight differences in sculpture. The youngest record of anaspid scales from Arctic Canada is *S. lancifera* from the upper part of the Read Bay southern section of Cornwallis Island. It is from a talus sample at 61·5 m and has been referred to the early Lochkovian (Märss *et al*. 1998).

There is also a record of articulated anaspids from the Cape Phillips Formation, Sheinwoodian, 90·0–92·5 m interval at Baillie-Hamilton section 1 and Cornwallis Island (Thorsteinsson 1967; Märss *et al*. 1998), showing a coarse *Birkenia*-like sculpture (collections of R. Thorsteinsson and M.V.H. Wilson, pers. obs. of Blom and Märss).

In the Mackenzie Mountains, northwestern Canada, *Birkenia* sp. has been identified in the Avalanche Lake section AV-1G. The age has been determined by P. Männik, Tallinn, as Telychian, late Llandovery based on conodonts.

3.6. Severnaya Zemlya, Russia

About 20 samples from the late Wenlock to Přídolí interval of Severnaya Zemlya contain fragments of anaspid scales, and a limestone nodule from the early Lochkovian, Early Devonian, yielded a trunk squamation (Märss 2002). Three main anaspid assemblages can be recognised in the Silurian sequence.

The first assemblage characterises the Samoilovich Formation, Wenlock, on October Revolution Island (samples 31–208 and MF 46–23) and its equivalents on Pioneer Island (samples 5d and 8g). The assemblage comprises *P. nitida*, *Rhyncholepis parvula*, *Rytidolepis quenstedtii*, *S. mustelensis* and some unidentifiable fragments of which some are similar to *B. elegans*.

The second assemblage is from the lower part of the Ust-Spokoinaya Formation (samples 30, 30–1, 47–14, 2–21 and MF 157–4), Ludlow, and coeval strata on Pioneer Island (sample number 5m). Scales with variable sculpture are most frequent. In addition to the Wenlock forms, *V. funiforma* appears. In the middle part of the Ust-Spokoinaya Formation, middle Ludlow, the diversity of forms decreases markedly (samples 2–12, 2–14). A third assemblage from the upper part of the Ust-Spokoinaya Formation, late Ludlow (samples 2–1 and MF 157–3 on October Revolution Island, 2055 zh and 2803 on Pioneer Island, and 20568 on Komsomolets Island) has no common forms with the lower assemblages. *Spokoinolepis alternans* gen. et sp. nov. appears and ranges into the early Přídolí (sample MF 157–2). In the Severnaya Zemlya Formation, early Lochkovian, Early Devonian, a new articulated anaspid, *Vilkitskilepis valentinae* Märss 2002 occurs (sample 67–12).

3.7. Central Urals, Russia

Reported occurrences of anaspid scales from the Central Urals are few and contain only two species, *Schidiosteus mustelensis* and *Septentrionia mucronata*. These have been found together with *Thelodus parvidens* Agassiz, 1839, *Thelodus sculptilis* Gross, 1967, *Andreolepis hedei* Gross, 1968, *Poracanthodes porosus* Brotzen, 1934, *Nostolepis striata* Pander, 1856 and some new species of *Archegonaspis* Jaekel, 1927 in the Tabuska Beds, late Ludlow. Samples containing anaspid scales were taken from the excavations on the right bank of the Ufa River, downstream from the mouth of the Tabuska River. Märss (1992) proposed that in the E Baltic the co-occurrence of *T. sculptilis* and *A. hedei* falls within a stratigraphical hiatus in the uppermost part of the Paadla Stage.

4. Correlation and evolution of faunas

Evolutionary trends in anaspids are expressed clearly in the species sculpture and microstructure. The change in sculpture which is used as a basis for taxonomy is also of utility for correlation during most of the Silurian (Fig. 10).

4.1. Llandovery–early Wenlock

Birkeniid anaspids are rare in the Llandovery and it was only in the Telychian and early Wenlock that they become established. The best known, *B. elegans*, comes from the early Wenlock of Scotland, but there are other closely related *Birkenia* species from the same area which are late Llandovery in age (Ritchie 1985; Märss & Ritchie 1998). This distribution can be correlated with the occurence of undescribed material of

Birkenia-type found in N Greenland, northwestern Canada and Arctic Canada (collections of R. Thorsteinsson and M. V. H. Wilson, pers. obs. of H. Blom and T. Märss). The few specimens from the Hauge Bjerg Formation, N Greenland are of late Llandovery age (*Monograptus spiralis* Biozone). The large collection of similar specimens from Arctic Canada is from the early Wenlock, Cape Phillips Formation (Thorsteinsson 1958; Märss *et al*. 1998).

The earliest faunal assemblage of birkeniid anaspids is restricted to *Birkenia* itself. This early *Birkenia* fauna shows a dermal skeleton with scales and plates composed of a very compact internal microstructure. The external sculpture is characterised by simple round tubercles covering almost the whole surface. These characters represent an early type of scale sculpture and histology, which form the basis for the evolutionary trends visible through the distribution of anaspids. In Arctic Canada and N Greenland articulated specimens of *Birkenia* type show a larger and coarser sculpture than the Scottish, more or less similar to the younger *B. robusta* sp. nov.

4.2. Late Wenlock–middle Ludlow

In general late Wenlock–early Ludlow birkeniid anaspids correlate well between Ringerike, Gotland, Saaremaa and Severnaya Zemlya. The typical late Wenlock–early Ludlow assemblages extended slightly higher in Severnaya Zemlya and the Central Urals.

Late Wenlock faunas around the Baltic are characterised by *Rhyncholepis parvula*, *Rhyncholepis butriangula* and *Rytidolepis quenstedtii*. *R. parvula* and *R. quenstedtii* are also present in the Samoilovich Formation and age equivalent beds of the Severnaya Zemlya Archipelago. Another typical late Wenlock taxon, *P. nitida* is found in the Halla Beds of Gotland and in the late Wenlock assemblages of Severnaya Zemlya and Ringerike. It is present in the Viita Beds, Saaremaa, but is absent from the very rich fauna of the late Wenlock Vesiku Beds. It is suggested that the Vesiku Beds may be slightly younger than Halla Beds unit c, at Gothemshammar (Jeppsson *et al*. 1994), which is supported by the absence of *P. nitida*. This correlation is complicated, however, by the occurrence of *P. nitida*, *Rhyncholepis parvula* and *Rytidolepis quenstedtii* in the early Ludlow of Severnaya Zemlya. Other taxa typical for the late Wenlock–early Ludlow with local variations in distribution are *V. funiforma* and *S. mustelensis*. *V. funiforma* is absent from Gotland, but *S. mustelensis* has been recorded from both the late Wenlock, Halla Beds and the early Ludlow Hemse Beds, unit c.

The early Ludlow of the E Baltic characteristically lacks *Rhyncholepis* species. The Himmiste fauna is also characterised by occurrences of *Schidiosteus*, *Silmalepis* and rare occurrence of *Vesikulepis*. The suggested correlation between Hemse Beds, unit c on Gotland and the Himmiste Beds on Saaremaa (Jeppsson *et al*. 1994) is well supported. Both contain *S. mustelensis* and some fragments bearing larger sculpture of the *Pharyngolepis* type. *S. mustelensis* and *V. funiforma* from the Samoilovich and Ust-Spokoinaya formations, Wenlock and Ludlow, are conspecific with Baltic forms so the formations can be correlated with the Rootsiküla and Paadla stages of the E Baltic, and Halla and Hemse beds of Gotland, Sweden (Märss 1986; Fredholm 1988, 1990).

The birkeniid fauna during the late Wenlock–middle Ludlow is dominated by the family Rhyncholepididae Kiær, 1924. The sculpture in this group is characterised by tuberculated overlapped areas and a posterior sculpture with a pattern of differently arranged rows of triangles or modified triangles. This evolutionary change from the simple tuberculated sculpture of the older *Birkenia* fauna is also illustrated by the development of a well-expressed vascular canal system. It is also

	SILURIAN						Dev.
	LLAND.	WENLOCK		LUDLOW		PRIDOLI	
	Telych.	Sheinw.	Homer.	Gorstian	Ludford		Lochk.
Birkenia sp.	■						
Birkenia elegans? Traquair, 1898	■	■	?				
Birkenia elegans Traquair, 1898		■					
Rhyncholepis parvula Kiær, 1911		?					
Rhyncholepis butriangula sp. nov.			■	■			
Birkeniida sp. Fredholm 1988			■				
Schidiosteus mustelensis Pander, 1856				■	■		
Rytidolepis quenstedtii Pander, 1856				?			
Birkenia robusta sp. nov.					■		
Vesikulepis funiforma gen. et sp. nov.					■		
Pterygolepis nitida (Kiær, 1911)			■				
Pharyngolepis heintzi Ritchie, 1964			■				
Pharyngolepis oblonga Kiær, 1911			■				
Maurylepis lacrimans gen. et sp. nov			■				
Vesikulepis funiforma? gen. et sp. nov.					■		
Silmalepis erinacea gen. et sp. nov.					■		
Pharyngolepis? sp.					■		
Septentrionia dissimilis? gen. et sp. nov.					■		
Septentrionia dissimilis gen. et sp. nov.					■	■	
Septentrionia mucronata gen. et sp. nov.					■	■	
Septentrionia mucronata? gen. et sp. nov.						■	
Liivilepis curvata gen. et sp. nov.					■	■	
Liivilepis curvata? gen. et sp. nov.						■	
Hoburgilepis papillata gen. et sp. nov.						■	
Tahulalepis elongituberculata gen. et sp. nov.						■	
Tahulalepis kingi (Woodward, 1947)						■	
Spokoinolepis alternans gen. et sp. nov.						■	
Septentrionia lancifera gen. et sp. nov.						■	■
Septentrionia seducta gen. et sp. nov.						■	■
Manbrookia asperella gen. et sp. nov						■	
Ruhnulepis longicostata gen. et sp. nov.						■	
Vilkitskilepis valentinae Märss, 2002							■

Figure 10   Stratigraphical distribution of birkeniid anaspids from the Northern Hemisphere.

possible to see an evolutionary trend within this period of time, from the simple sculpture in *Rhyncholepis* with regular row of triangles, to the more complex specialised triangles and spines seen in *Schidiosteus*, *Vesikulepis* and *Silmalepis*.

4.3. Late Ludlow–early Lochkovian
The late Ludlow–early Lochkovian faunas of the Northern Hemisphere are characterised by anaspids of the family Septentrioniidae fam. nov. There is one questionable occurrence of *S. dissimilis* from the early Ludlow beds of Baillie-Hamilton Island, Arctic Canada, but the earliest confirmed occurrence is of scales in the early Ludfordian of the same sections. *S. mucronata* from the late Ludlow of Gotland and the Central Urals is the first well-correlated taxon of this group. *L. curvata*, which has been found in the late Ludlow, Hamra Beds in Gotland, upper Ludlow/lower Přídolí bone beds in Skåne, Přídolí Ohesaare Stage on Saaremaa and Ruhnu islands and the late Ludlow of the Central Urals, is also stratigraphically useful. Although *Spokoinolepis alternans* from the Přídolí of Severnaya

Zemlya seems to be endemic, it shows similar stratigraphic distribution to the other taxa of family Septentrioniidae. In the late Ludlow–Přídolí interval, *Tahulalepis* has been found in Estonia, Sweden and the U.K. *T. elongituberculata* gen. et sp. nov. is typical for the late Ludlow Tahula and Kudjape Beds of the Kuressaare Stage in the E Baltic and can be correlated with the same occurrence in Ramsåsa, Skåne, which might be of latest Ludlow or earliest Přídolí age. *T. kingi* from the Přídolí Grey Grit, Ledbury, Herefordshire, England, supports the contention that this genus is confined to the Ludlow–Přídolí.

The late Přídolí *S. lancifera* has been found in the U.K., Arctic Canada and erratic boulders in the Netherlands. The typical late Ludlow–early Lochkovian Septentrioniidae fauna has restricted occurrences of *S. seducta* from the late Přídolí–early Lochkovian of N Greenland, *R. longicostata* from Ohesaare Stage, Přídolí of Saaremaa, the articulated early Lochkovian *V. valentinae* from Severnaya Zemlya and *M. asperella* from the late Přídolí Man Brook fauna of Worcestershire, England.

The late Ludlow–early Lochkovian Septentrioniidæ fauna is represented by two dominant families, Septentrioniidæ and Tahulalepididae, and shows another evolutionary trend in the sculpture and histology of the scales. The sculpture of these scales is modified in the overlapped area by being smooth or ribbed instead of tuberculated as in older forms. These seemingly more specialised scales indicate a new and more complicated style of overlapping, which possibly offered greater flexibility. The sculpture of the main area is also changed slightly from previous styles with more dominant larger ridge-like or spiny sculptural elements of variable size and shape. The vascular canal system is also modified in this group, showing a less developed system of canals which are only present in the middle or more posterior parts of the scale interior.

5. Systematic palaeontology

Class Anaspida Traquair, 1899

Diagnosis. Jawless vertebrates with elongate and fusiform body; dorsal ridge scales or spines; one slanting row of branchial openings on both lateral sides; strongly hypocercal tail; triradiate postbranchial spine; trunk covered with scales or naked; scales, plates and spines of aspidine.

Remarks. Anaspida includes all anaspids of order Birkeniida and the naked *Lasanius*, which is excluded from the birkeniids due to the lack of a well-developed dermal skeleton on the trunk.

Order Birkeniida Berg, 1937

Diagnosis. Dermal skeleton very well developed; trunk with five rows of long and narrow scales, head covered with small plates; postbranchial and pectoral plate present; scales and plates sculptured externally with tubercles, ridges, ridgelets and spines; eight to 15 small branchial openings; well-developed long or short anal fin; dermal skeleton of compact lamellar or spongy aspidin; scales with one to two visceral ribs along longer axis.

Content: Birkeniidae Traquair, 1899; Pterygolepididae Obruchev, 1964; Rhyncholepididæ Kiær, 1924; Pharyngolepididae Kiær, 1924; Tahulalepididae fam. nov.; Septentrioniidae fam. nov.

Distribution. Late Wenlock: Ringerike, Norway. Early Wenlock–late Ludlow: Gotland, Sweden. Early Wenlock–Přídolí: Saaremaa, Estonia. Late Llandovery–early Wenlock: Scotland, U.K. Přídolí: Welsh Borderland, U.K. Early Wenlock: Ireland. Přídolí: Central Urals, Russia. Wenlock–Lochkovian: Severnaya Zemlya Archipelago, Russia. Late Llandovery–early Lochkovian: N Greenland. Early Wenlock–early Lochkovian: Arctic Canada Archipelago. Late Llandovery: Mackenzie Mountains, northwestern Canada.

Family Birkeniidae Traquair, 1899

Diagnosis. Dorsal ridge scales anteriorly large and flat, and posteriorly as spines; one or two rows of dorso-lateral scales that can be inclined to posterior or anterior; eight branchial openings; anal fin short without or with modified anteriorly bordering spine; scales and plates with tuberculated sculpture and compact laminar aspidine.

Content. *Birkenia* Traquair, 1898; *Hoburgilepis* gen. nov.

Distribution. Late Llandovery–early Wenlock: Scotland, U.K.Late Wenlock: Saaremaa, Estonia. Late Ludlow: Gotland, Sweden. Early Wenlock–early Lochkovian: Arctic Canada Archipelago. Late Llandovery: Mackenzie Mountains, northwestern Canada.

Genus *Birkenia* Traquair, 1898

Type species. *Birkenia elegans* Traquair, 1898.

Diagnosis. Scales and plates with regular tuberculate sculpture; tubercles evenly sized and spaced.

Species content. *B. elegans* Traquair, 1898; *B.* sp. Ritchie, 1985 (fig. 5); *B. robusta* sp. nov.

Distribution. Late Llandovery–early Wenlock: Scotland, U.K. Late Wenlock: Saaremaa, Estonia.

Birkenia elegans Traquair, 1898
(Figs 11–14)

Syntypes. Specimens GSE 5980 (Traquair 1898, pl. V, fig 1), GSE 5982 (Traquair 1898, pl. V, fig. 2) and GSE 1145 (Traquair 1898, pl. V, fig. 3) from Birkenhead Burn, Lesmahagow inlier, Scotland, U.K.; Waterhead Group, early Wenlock, Early Silurian. Small scale figured by Traquair (1898, fig. 4) from Lyneslie Burn, Pentland Hills, Scotland U.K.; Early Silurian. Traquair (1898) did not specify a holotype but noted that the specimen he figured in plate V, figure 1 was the most complete.

Material. Many of the illustrations here are taken from two latex casts (Fig. 11) from the part and counterpart of a specimen (KIMMG: Vf6/7) from Slot Burn, Seggholm, Ayr, Lesmahagow Inlier, Scotland, U.K.; Slot Burn Formation, Waterhead Group, early Wenlock, Early Silurian. Other specimens studied are from Slot Burn (NHM P9637 and NHM P11032–11035) and Smithy Burn (NHM P52386 and NHM P52387), Hagshaw Hills Inlier, Scotland, U.K.; Fish Bed Formation, Glenbuck Group, Hagshaw Hills Inlier, early Wenlock, Early Silurian.

Diagnosis. Small species of *Birkenia*, up to 10 cm long, with double-headed mid-dorsal spine; dorso-lateral scales inclined to the anterior anteriorly and to the posterior posteriorly; whole body covered with similar, regular granular to finely tuberculate sculpture; mid-part of lateral scales, double-headed dorsal spine and scales on anal fin, showing regular dorso-ventral arrangement of sculpture; lateral scales towards articulation sockets show similar regular but not linearly arranged sculpture as do all ventral and dorsal plates, and rostral and pineal plates of the head; sculpture in anterior-posterior arrangement on pineal plates and postbranchial spine.

Description. All parts of the body have similar, regular finely tuberculate sculpture. The spacing and arrangement of the tubercles is variable across the body but generally more widely spaced on plates and spines than on scales (Figs 12, 13).

Scales and plates of the head (Fig. 12A–D) are represented by broader and more quadrangular rostral scales (Fig. 12A) and the lanceolate to lenticular postpineal scales (Fig. 12D). Both types of scale have sculpture following the long, anterior–posterior axis of the scale. Towards the margins of scales and plates the sculptural arrangement is not always as regular. The median rostral plate (Fig. 12B) and ?pineal plate (Fig. 12C) have a typical granular sculpture that is regularly spaced but unoriented. Occasionally the tubercles merge forming small ridgelets.

The postbranchial region (Fig. 12G–I) has branchial openings pentagonal to hexagonal in outline so that surrounding plates and scales have triangular extensions (Fig. 12G, H) with unoriented sculpture. The branchial spine (Fig. 12I) is V-shaped in outline with the sculpture of the central area arranged along the long axis. Towards the margins the tubercles are not so regular.

The lateral scales (Figs 12E, K, L, 13E, G, 14A, C, F, G) vary
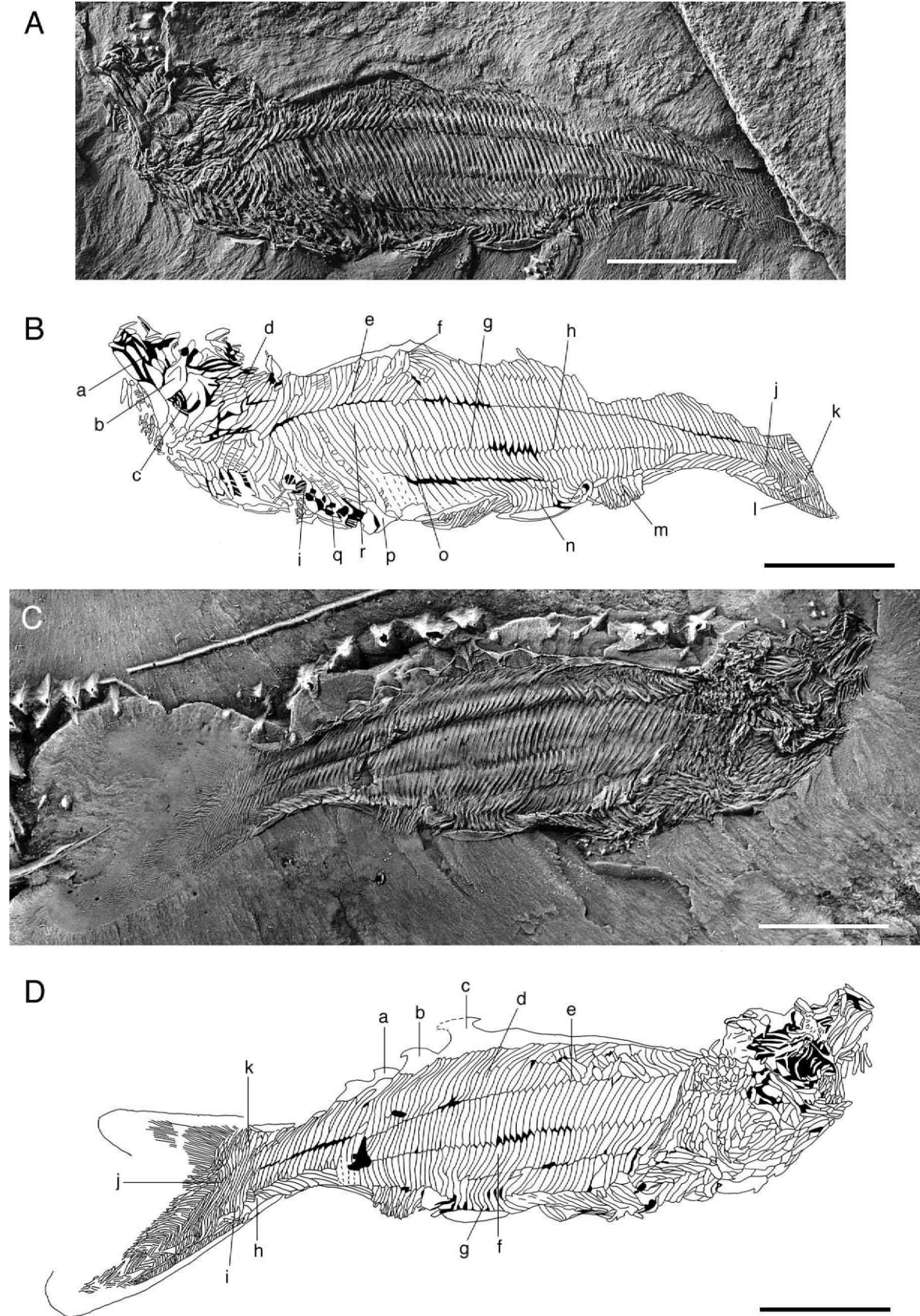
Figure 11 *Birkenia elegans* Traquair, 1898: body morphology with scale and plate positions. Latex casts of part and counterpart of specimen KIMMG: Vf6/7 from Slot Burn, Seggholm, Lesmahagow inlier, Scotland, U.K.; Slot Burn Formation, Waterhead Group, Wenlock, Early Silurian. Scale bars 10 mm. (A) Latex cast of specimen in lateral view. (B) Drawing showing position on body of scales, plates and spines illustrated in other figures. a = Figure 12A; b = Figure 12B; c = Figure 12C; d = Figure 12D; e = Figure 12E; f = Figure 12F; g = Figure 12K; h = Figure 12L; i = Figure 12G; j = Figure 12N; k = Figure 12B; l = Figure 12O; m = Figure 12M; n = Figure 12J; o = Figure 12G; p = Figure 12I; q = Figure 12H; r = Figure 14F. (C) Latex cast of counterpart in lateral view. (D) Drawing of counterpart, showing position on body of spines, scales and plates in other figures: a = Figure 13A; b = Figure 13B; c = Figure 13C; d = Figure 14A; e = Figure 13E; f = Figure 13G; g = Figure 13F; h = Figure 13J; i = Figure 13I; j = Figure 13H; k = Figure 13D.
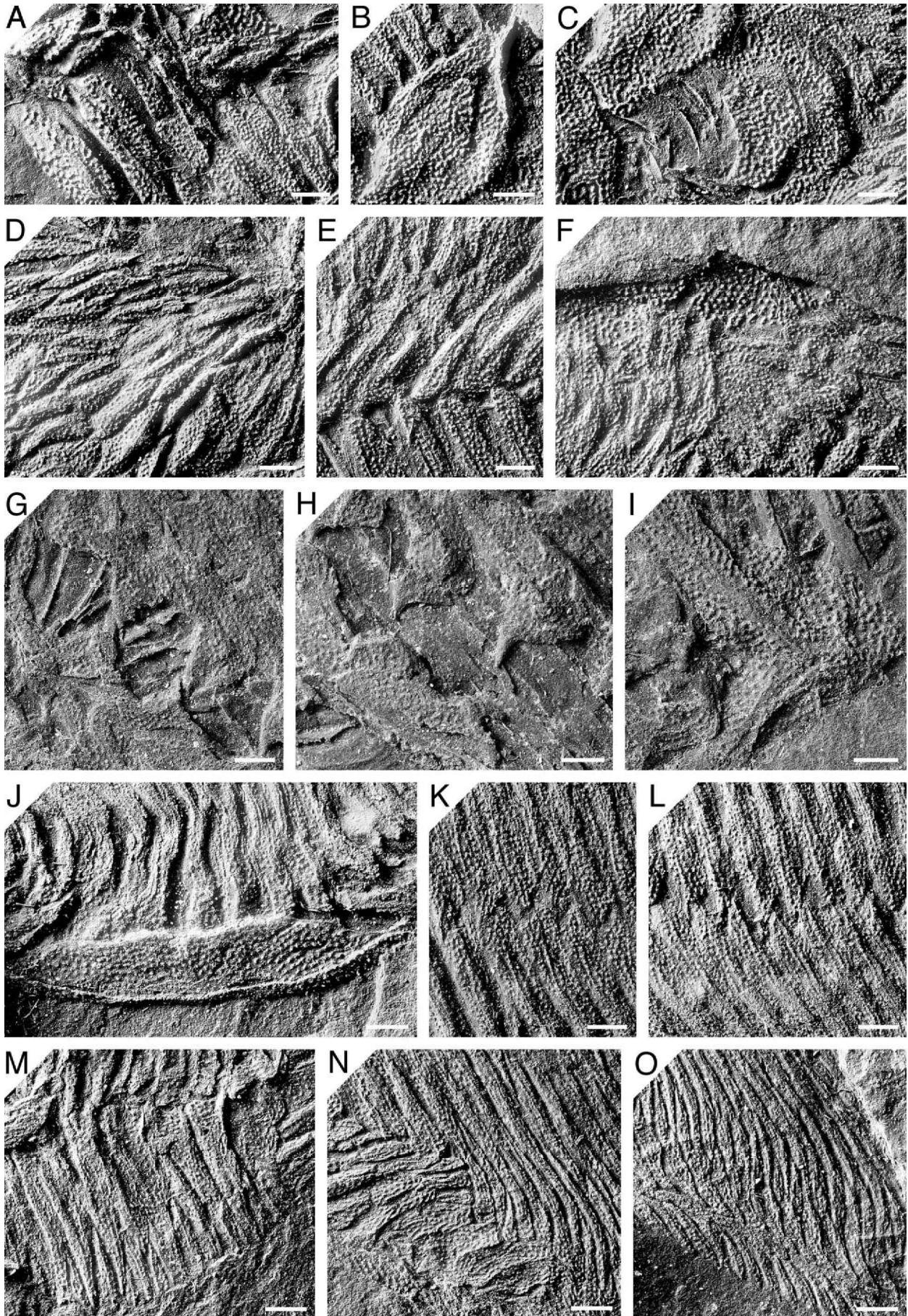
Figure 12 *Birkenia elegans* Traquair, 1898: SEM photographs of latex cast illustrated in Figure 11A; scale bars 0·5 mm. (A) Lateral rostral plate; (B) median rostral plate; (C) pineal plate? (D) postpineal plates; (E) lateral scales; (F) dorsal ridge scale; (G, H) branchial openings; (I) postbranchial spine; (J) preanal plate; (K, L) lateral scales; (M) anal fin. (N, O) caudal fin.
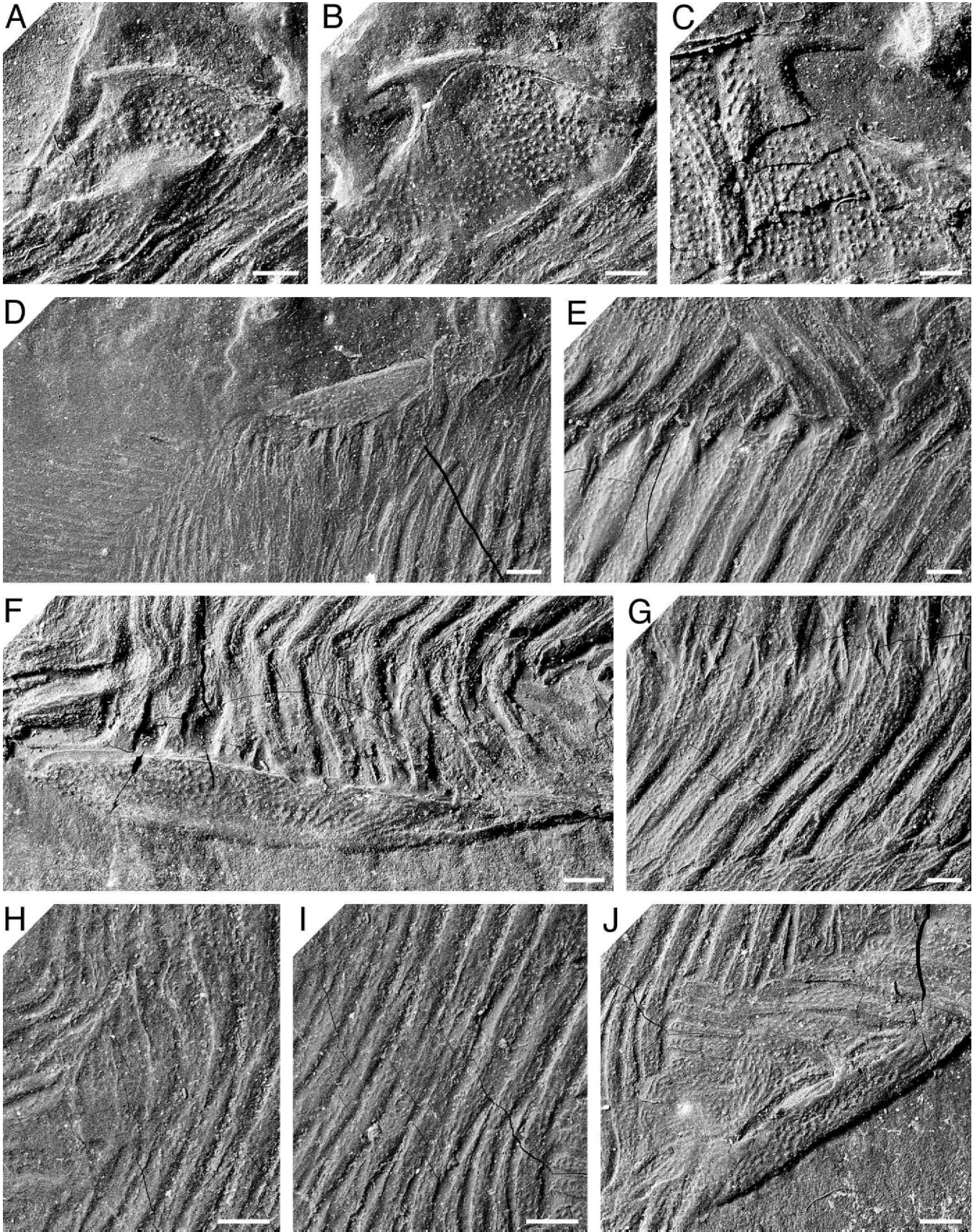
Figure 13 *Birkenia elegans* Traquair, 1898: SEM photographs of latex cast illustrated in Figure 11C; scale bars 0·5 mm. (A–C) dorsal ridge scales; (D) scales from dorsal part of caudal fin; (E) lateral scales; (F) preanal plate; (G) lateral scales; (H–J) scales from caudal fin.
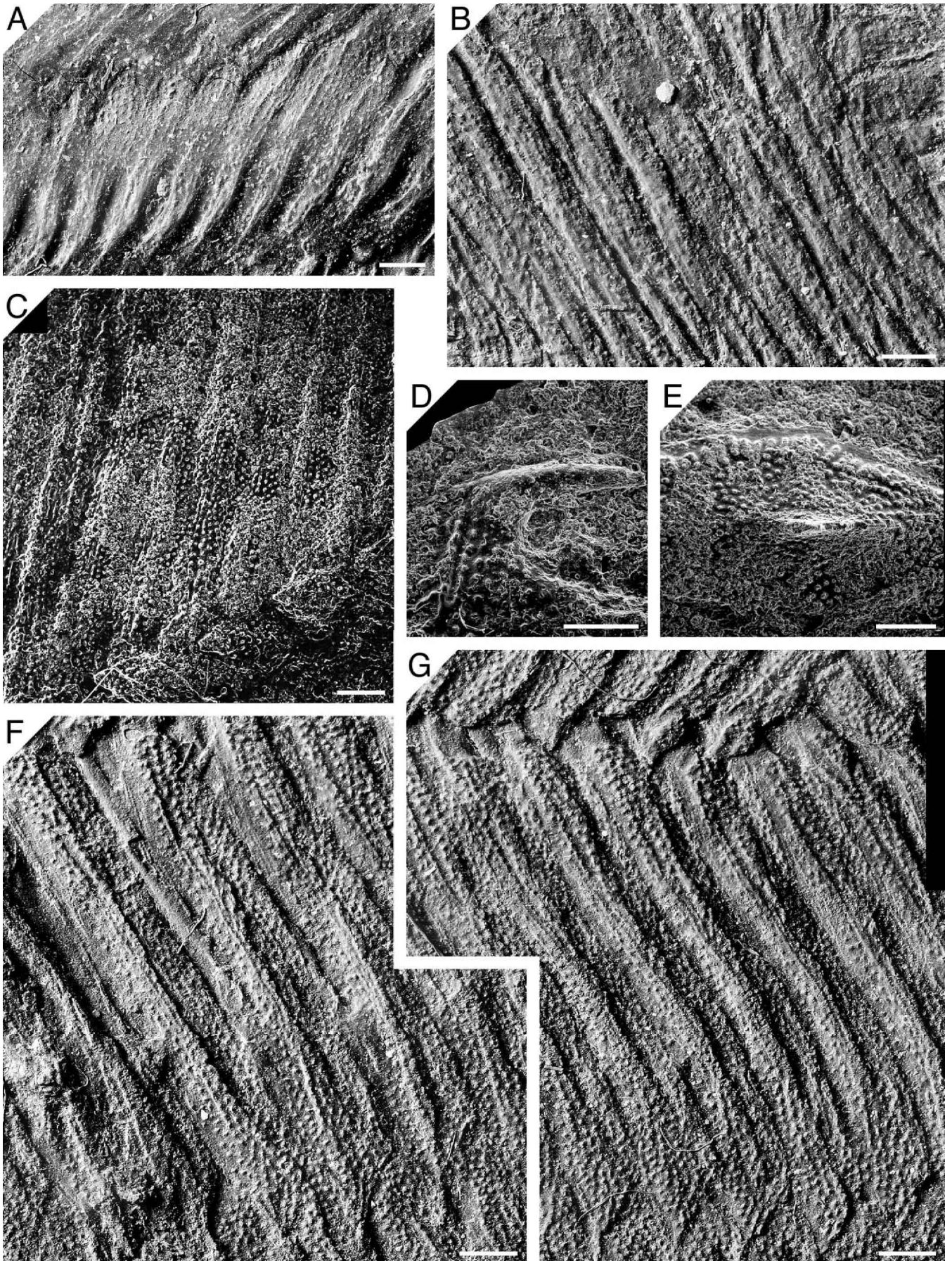
Figure 14 *Birkenia elegans* Traquair, 1898: SEM photographs of latex casts. (A, B, F, G) From specimen in Figure 11. (C, D, E) Specimen NHM P11033 from Slot Burn, Seggholm, Lesmahagow inlier, Scotland, U.K.; Slot Burn Formation, Waterhead Group, Wenlock, Early Silurian; scale bars 0·5 mm. (A) Dorso-lateral scales; (B) scales from tail; (C) lateral scales; (D) part of double headed dorsal ridge scale; (E) dorsal view of dorsal ridge scale; (F, G) lateral scales.

greatly in shape, size and outline. Lower dorso-lateral scales in the most extensive row taper to both extremities, forming zig-zag articulation with neighbouring scale rows (Figs 12K, L, 13G, 14F, G). Other lateral scales, particularly in the lower dorso-lateral and lower ventro-lateral regions, have blunter terminations (Figs 12E, 13E), are more curved along their long axis (Fig. 13G) and occasionally almost sigmoidal in outline (Fig. 14A).

In places, and below the double-headed spine in particular (Fig. 11B, D), there appear to be two rows of scales in the dorso-lateral region (Fig. 14A).

Along the length of the lateral scales the sculpture is variable. In the middle part, the tuberculated sculpture is well developed, oriented parallel to the long axis and occasionally merged into extensive ridges (Fig. 14F, G) or shorter ridgelets (Fig. 14C, F, G). Towards the articulation processes, the ridges/ridgelets converge to an apex or the sculpture is regular but unoriented and granular (Figs 12I, J, 13E, G, 14C, F, G).

Among the ventral plates, both pre- and post-anal plates are lenticular with typical granular sculpture that is mostly unoriented and rarely amalgamated into ridgelets (Figs 12J, 13F, J).

The anal fin scales have blunt to concave dorsal margins and taper slowly to a pointed ventral margin (Fig. 12M). Tiny dorsally pointed accessory scales fill the gaps between them. The sculpture is characterised by dorso-ventrally oriented tubercles and ridgelets.

Most tubercles of the dorsal spines and plates are well spaced and unoriented with the exception of those of the double-headed mid-dorsal spines (Figs 12F, 13A–D, 14D, E). These tubercles are dorso-ventrally oriented and may occasionally merge into ridges.

The fin scales (Figs 12N, O, 13H, I, 14B) are elongate, narrow and taper to a point (Fig. 14B). Sub dorso-ventrally arranged scales have a typical granular sculpture that has one to three tubercles across the width of the scale. Towards the posterior part of the fin, the anterior-posteriorly arranged scales are smooth or with a single row of tubercles.

Remarks. The sculpture of individual scales and plates of *B. elegans* has been described on the material available. However, the preservation of the specimens studied varies greatly. For example, the NHM specimens are not as well-preserved as the best specimen available (Fig. 11). Even this specimen has been preserved with a twisted head because scales and plates supposedly on the mid-line (Fig. 12B, D) are displaced and are at an angle to the margin of the preserved specimen. Ritchie (1963) remarked that this particular specimen is superbly preserved, having been found in an olive mudstone matrix rather than the laminated siltstone from which fish have usually been recovered in this region. For this reason this specimen has been studied and illustrated in detail, and because it shows some features not present on the other NHM material studied. It appears that the dorso-lateral row of scales is divided into two on this specimen (as in reconstruction in Fig. 5D). This does not appear to correspond with any articulation in the scales apart from in the area just below the double-headed spine (Fig. 11B, D). Most of the NHM specimens show that the surfaces of the lateral scales were tuberculate but relatively flat (Fig. 14C) rather than possessing ridges towards the centre of scales (Fig. 14A, F, G). From the single exceptionally well-preserved specimen, it appears that the sculpture is more coarsely developed on the dorsal ridge spines/scales and plates in the head region. This cannot be shown on the other material present in the NHM collections. Unfigured material typical of the specimens held at the National Museum of Scotland, Edinburgh shows some thermally mature phosphatic remains in the matrix giving the specimens a dark coloration. Attempts to extricate some of this

material for sectioning have not been successful. These detailed studies on the sculpture of *B. elegans* scales are therefore essential for taxonomic identification within the Birkeniida.

Distribution. Early Wenlock: Scotland, U.K.

Birkenia elegans? Traquair, 1898
(Fig. 15)

Material. Apart from the illustrated specimens, there are about five badly preserved fragments (NRM) from one Ranberget Member sample, Ringerike, Norway; Steinfjorden Formation, late Wenlock. Five small fragments (UALVP) from the Sheinwoodian, Baillie-Hamilton and Cornwallis islands, Arctic Canada. Some fragments (LIG) from Severnaya Zemlya Archipelago, Russia. Some fragments (UALVP) from late Llandovery of Avalanche Lake section, Mackenzie Mountains, northwestern Canada.

Remarks. Several fragments of possible *B. elegans* have been found in the residue of the Ranberget Member in Ringerike, Norway. They are badly preserved and show on the external surface round, evenly distributed tubercles (Fig. 15A). Their identification is uncertain and they could be modified scales of *Pterygolepis nitida* (Kiær) 1911, since this taxon has a regular set of small tubercles on its head scales and dorsal ridge scales.

Fragments of similar scale sculpture have also been found in Sheinwoodian, early Wenlock, strata on Baillie-Hamilton and Cornwallis islands (Fig. 15B, C). They also possess fine round tubercles, as well as a fine external medial ridge running from the upper to lower end of the scales (Fig. 15C). Small evenly spaced tubercles are also visible on poorly preserved material from the late Wenlock and Ludlow of Severnaya Zemlya (Fig. 15D). All scales from these areas with small tuberculated sculpture have a very compact inner structure without vascular canals and visible pore openings.

Some fragments of *B. elegans*? have recently been found in the Avalanche Lake section (AV-1G), Mackenzie Mountains, northwestern Canada.

Birkenia robusta sp. nov.
(Figs 16, 17)
1986 Birkeniida sp. ind.; Märss, pl. 26, fig. 3.

Derivation of name. From the Latin word *robustus*, meaning robust or strong, referring to the robust, compact scales with large tubercles.

Holotype. Trunk scale fragment GI Pi 7680 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian (Fig. 16C, D).

Material. More than 100 fragments (GI) from several different samples collected at Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. Several fragments (NHM) from Viita Trench, Saaremaa, Estonia; Viita Beds, Rootsiküla Stage, late Wenlock, Early Silurian.

Diagnosis. Short and robust scales of *Birkenia* with very large tubercles; large anterior and medial visceral ribs of equal width.

Description. The scales are mostly dark brown to black in colour and very weakly worn on the delicate sculptured parts. Although the material is usually very robust and well-preserved, typical trunk scales are never found complete. All fragments of these more elongated trunk scales represent either the dorsal or ventral end (Fig. 16A–D), often having the articulation process well-preserved (Fig. 16A). No fragments are found exclusively representing the middle part of the trunk scales. This and the robust nature suggest that the scales are not very dorso-ventrally elongate. On the visceral side a large wide anterior and a medial rib are both well developed and almost equal in width (Fig. 16B).
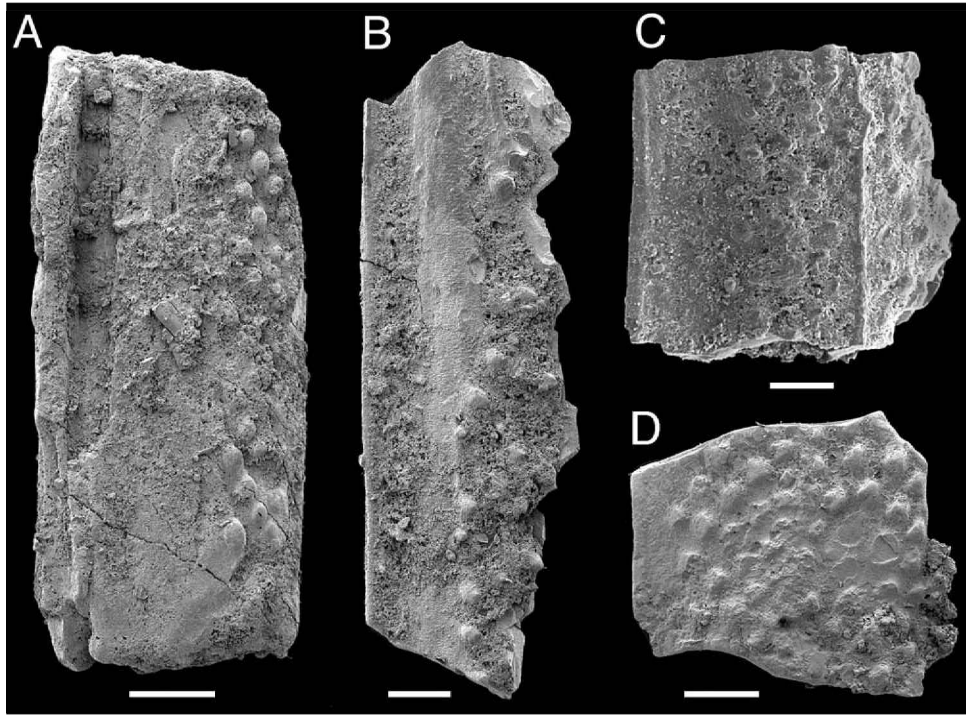
Figure 15 Birkenia *elegans*? Traquair, 1898: SEM photographs of disarticulated lateral scale fragments in external view; scale bars 0·2 mm. (A) NRM P.9478 from 9g Beds, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian. (B) UALVP 44987 from Baillie-Hamilton section 1 at 85·5 m, Arctic Canada; early Wenlock, Early Silurian. (C) UALVP 44613 from Baillie-Hamilton section 1 at 85·5 m, Canadian Arctic; early Wenlock, Early Silurian. (D) LIG 35–925 from Ushakov River, locality 30-1, October Revolution Island, Severnaya Zemlya Archipelago, Arctic Russia; lower part of Ust-Spokoinaya Formation, Ludlow, Late Silurian.

The median dorsal ridge scales (Fig. 16E), post branchial spines (Fig. 16F) and other questionable fragments (Fig. 16G, H), all show the same robust nature and low tendency to break as seen in the trunk scales.

The external sculpture is similar in all fragments with large round tubercles, varying in diameter between 0·05 mm and 0·1 mm. They are arranged in an even unoriented pattern and separated by inter tubercle smooth areas approximately equal to the tubercle diameter. The tubercles cover almost the whole external surface with the exception of the smooth surface of the scale articulation process (Fig. 16A), the overlapped area and the main protruding part of the spines (Fig. 16F). In the middle part, the tuberculated sculpture is well developed, oriented parallel to the long axis and occasionally merged into extensive ridges. A row of coarser tubercles runs dorsoventrally on the medial part of the scale (Fig. 16C).

The scales and plates are very compact and pore openings are neither visible in the external nor in the visceral surfaces. In thin section the tissue shows very compact aspidine without a developed vascular canal system (Fig. 17). Most scales are rather thick with many growth layers and thick basal tissue, which is rich in very irregularly oriented spaces for Sharpey's fibres, sensu Gross (1958, 1968).

Remarks. The sculpture of *B. robusta* sp. nov. and *B. elegans* is very similar in the general shape and arrangement of the tubercles. However, the tubercles of the younger species, *B. robusta,* are much larger and the scales much shorter and more compact. This feature is visible in all scales of this type found at the Vesiku Brook locality, indicating a taxonomic validity rather than being an ontogenetic effect in *B. elegans*. No scale with typical *B. elegans* sculpture type has been found at Vesiku Brook or other localities of similar age.

B. robusta sp. nov. is found as fragments of scales and plates from almost all positions on the body. Many of the more specialised types are badly preserved, but some of them still have diagnostic features left. One example is the fragment that shows traces of being triradiate, which suggests a post-branchial position (Fig. 16F).

Distribution. Late Wenlock: Saaremaa, Estonia.

Genus *Hoburgilepis* gen. nov.

Derivation of name. From the locality Hoburgen 2 and the Greek word *lepis*, meaning scale.

Type species. *Hoburgilepis papillata* gen. et sp. nov.

Diagnosis. Very thin, narrow scales with small, irregularly arranged tubercles of variable size.

*Hoburgilepis papillata* gen. et sp. nov.
(Fig. 18)

Derivation of name. From the Latin word *papillatus*, meaning bud-like, referring to the bud-like tubercles on the external surface.

Holotype. Specimen NRM P.9479 from Hoburgen 2, Gotland, Sweden; Hamra Beds, late Ludlow, Late Silurian (Fig. 18).

Material. Three scale fragments (NRM) from Hoburgen 2, Gotland, Sweden; Burgsvik/Hamra beds, late Ludlow, Late Silurian.

Diagnosis. As for the genus.

Description. At present, material of *H. papillata* is rare. Only the holotype shows all the features required to establish this
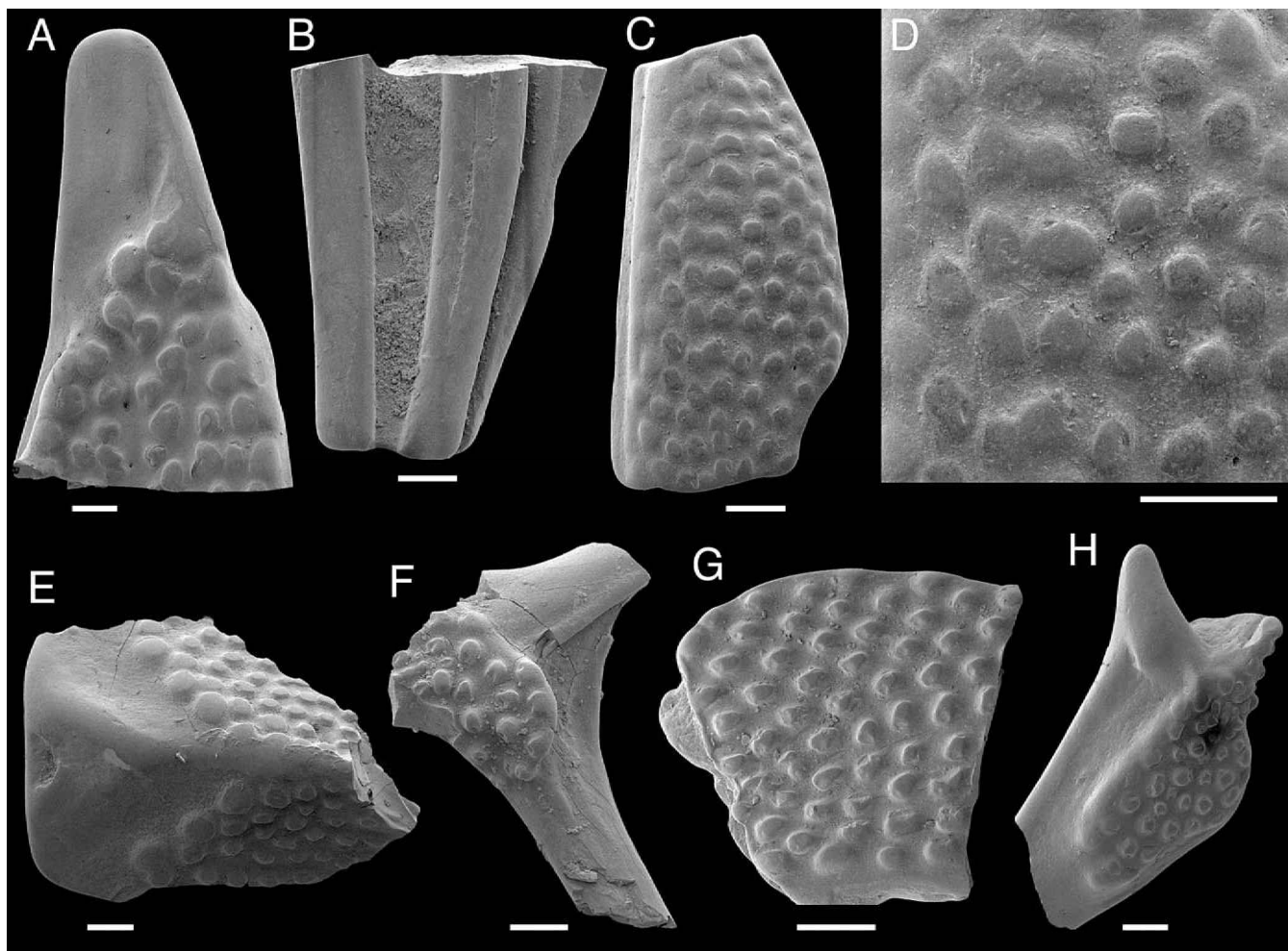
Figure 16 *Birkenia robusta* sp. nov.: SEM photographs of fragments of disarticulated scales, spines and plates; scale bars 0·2 mm. (A) Lateral? scale fragment in external view, GI Pi 7678; (B) scale fragment in visceral view, GI Pi 7679; (C, D) holotype, lateral scale fragment in external view, GI Pi 7680, (D) close up; (E) median dorsal ridge scale in dorsal view, GI Pi 7681; (F) post branchial scale in lateral view, GI Pi 7682; (G) plate fragment in external view, GI Pi 7683; (H) anal fin spine fragment in lateral view, GI Pi 6208. All specimens from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian.

new taxon (Fig. 18). This fragment is composed of two pieces and probably represents the upper dorsal part of a trunk scale. The external side is characterised by a wide, elevated and sculptured main scale area, and a low and smooth overlapped area. There is a step-like transition between these two areas. The sculpture is represented by very small, irregularly arranged tubercles of different sizes. Because of the scarcity, of material it has only been possible to see the histology of one specimen immersed in aniseed oil. It shows a compact acellular tissue with a large portion of irregularly shaped tubules of Sharpey's fibres.

Distribution. Late Ludlow: Gotland, Sweden.

Family Pterygolepididae Obruchev, 1964

Diagnosis. Large dorsal ridge scales bent upwards and to posterior, forming spines; anterior dorsal ridge scales less curved and less spiny than posterior ones; ten branchial openings; anal fin short with long anal fin spine; scales and plates with elongated tuberculated sculpture; dermal skeleton of compact lamellar aspidine.

Remarks. The family was originally named Pterolepididae by Kiær (1924) following the type genus *Pterolepis*. After *Ptero-*

lepis was replaced by *Pterygolepis,* Obruchev (1964) changed the family name to Pterygolepididae.

Genus *Pterygolepis* Cossmann, 1920

Type species. *Pterolepis nitidus* Kiær, 1911.
Diagnosis. As for the family.
Remarks. *Pterolepis* Kiær, 1911 is preoccupied by the insect *Pterolepis* Rambur, 1838 and replaced with *Pterygolepis* Cossmann (1920). The genera *Pterygolepis* and *Birkenia* both have dorsal ridges that are more spiny and curved in the posterior part of the body. However, *Birkenia* differs in having flatter dorsal plates anteriorly and dorso-lateral scales that incline both to anterior and posterior. The sculpture of the two genera is similar with small rather simple tubercles that are evenly spaced. In the head region and on specialised plates, the tubercles of *Pterygolepis* are very similar to *Birkenia* but on the scales they are more elongated and antero-posteriorly oriented. Also the anal fin and their associated plates and spines are different between these two genera (Fig. 5B, D).
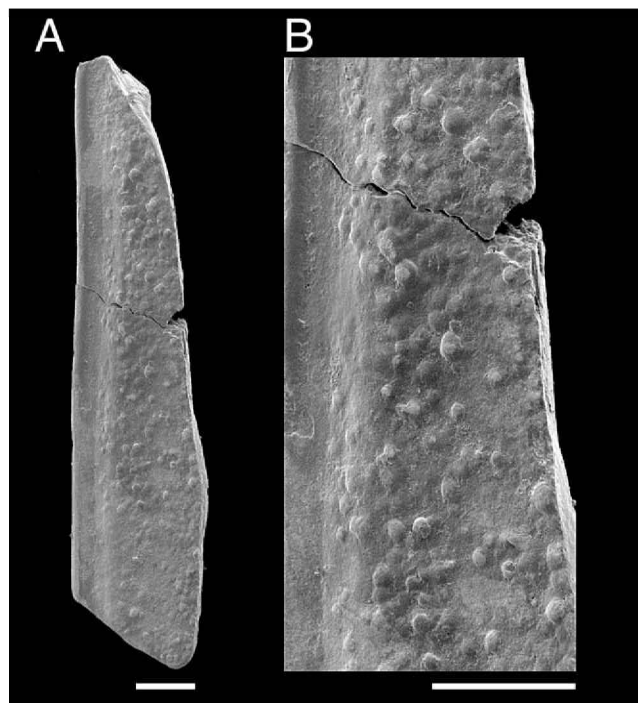
Pterygolepis nitida (Kiær, 1911)
(Figs 5B, 19–22, 23B, b, β)
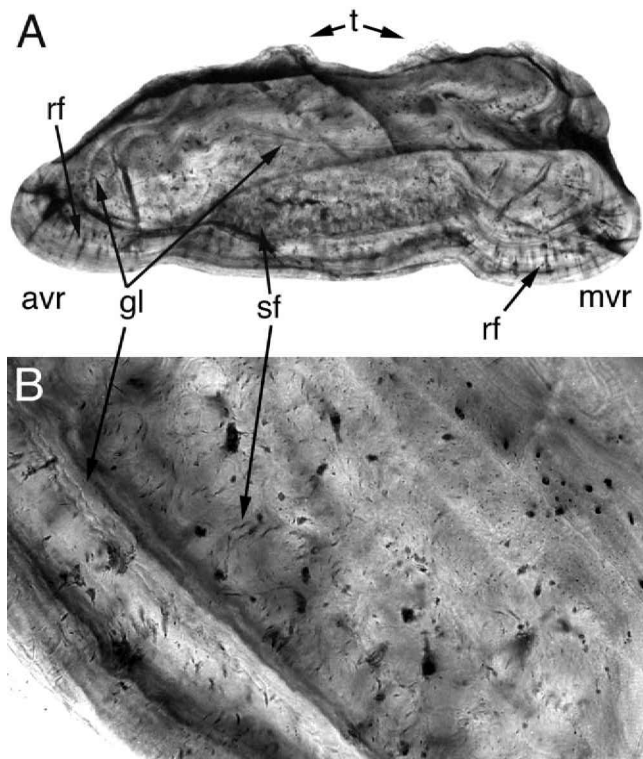
Figure 17 *Birkenia robusta* sp. nov.: (A, B) histology of scale fragment GI Pi 7685 in vertical cross section, (A) ×81, (B) ×324. Specimen from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian.

Figure 18 *Hoburgilepis papillata* gen. et sp. nov.: (A, B) SEM photograph of holotype NRM P.9479, scale fragment in external view; scale bars 0·2 mm. Specimen from Hoburgen 2, Gotland, Sweden; Burgsvik/Hamra beds, late Ludlow, Late Silurian.

1911 *Pterolepis nitidus* nov. gen. et sp.; Kiær, pp. 18–19.
1920 *Pterygolepis*; Cossmann, p. 83.
1924 *Pterolepis nitidus* Kiær; Kiær, p. 135; pls 1–7; figs 12, 14–19, 26a, 27–31, 34a, 35, 47, 48a.
1957 *Pterygolepis nitidus* (Kiær); Smith, pl. 5, fig. 3; pl. 6.

In accordance with the International Code of Zoological Nomenclature, Article 34b, the species-group name must agree in gender with the generic name. Since *Pterygolepis* is feminine the correct species-group name spelling is *nitida* instead of *nitidus*.

Syntypes. Articulated specimens, PMO E1037, E1041, E1042, E1057, E1063, E1123, E1131, E1150, E1151, E197,

E215, E309 and E424, from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian (Kiær 1924). Kiær (1924) did not specify a holotype but illustrated a series of well-preserved specimens, showing different important features. Some of the specimens illustrated by Kiær have not been recognised and therefore have no museum number.

Material. More than 100 articulated specimens (PMO) from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian. Tens of disarticulated scales and plates (NRM) from a Ranberget Member sample at Ringerike, Norway; Steinfjorden Formation, late Wenlock, Early Silurian. Large collections of more than 100 fragments have been found in residues (NRM, PMU) from Gothemshammar, Gotland; Halla Beds, unit c, late Wenlock, Early Silurian. About 70 broken scales (LIG) from Severnaya Zemlya, Arctic Russia;
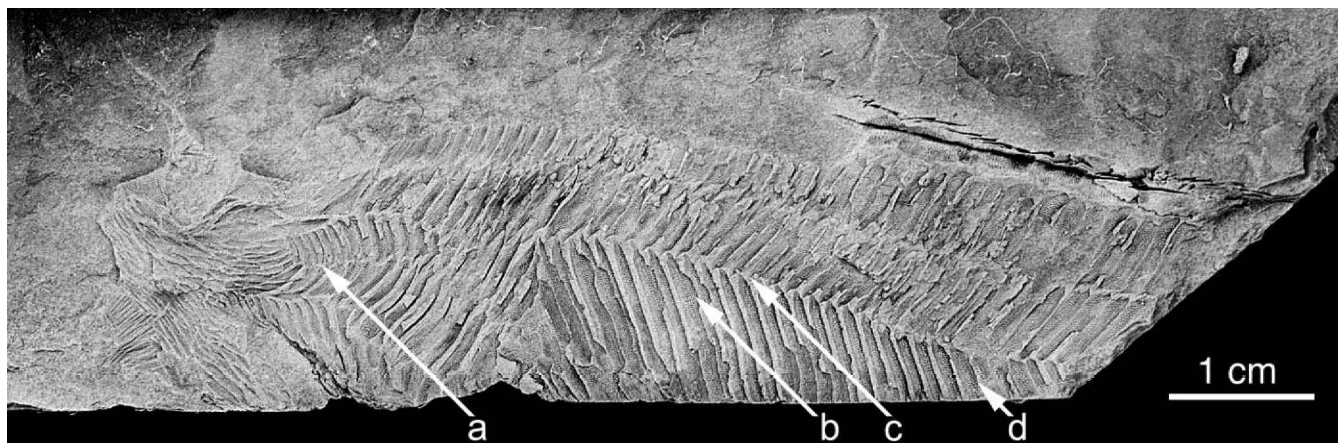
Figure 19 *Pterygolepis nitida* (Kiær, 1911): head and anterior part of trunk used for detailed study of the sculpture of the dermal skeleton; specimen PMO E0318 from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian; a = Figure 20E, F; b = Figure 20A; c = Figure 20C; d = 20 B, D.
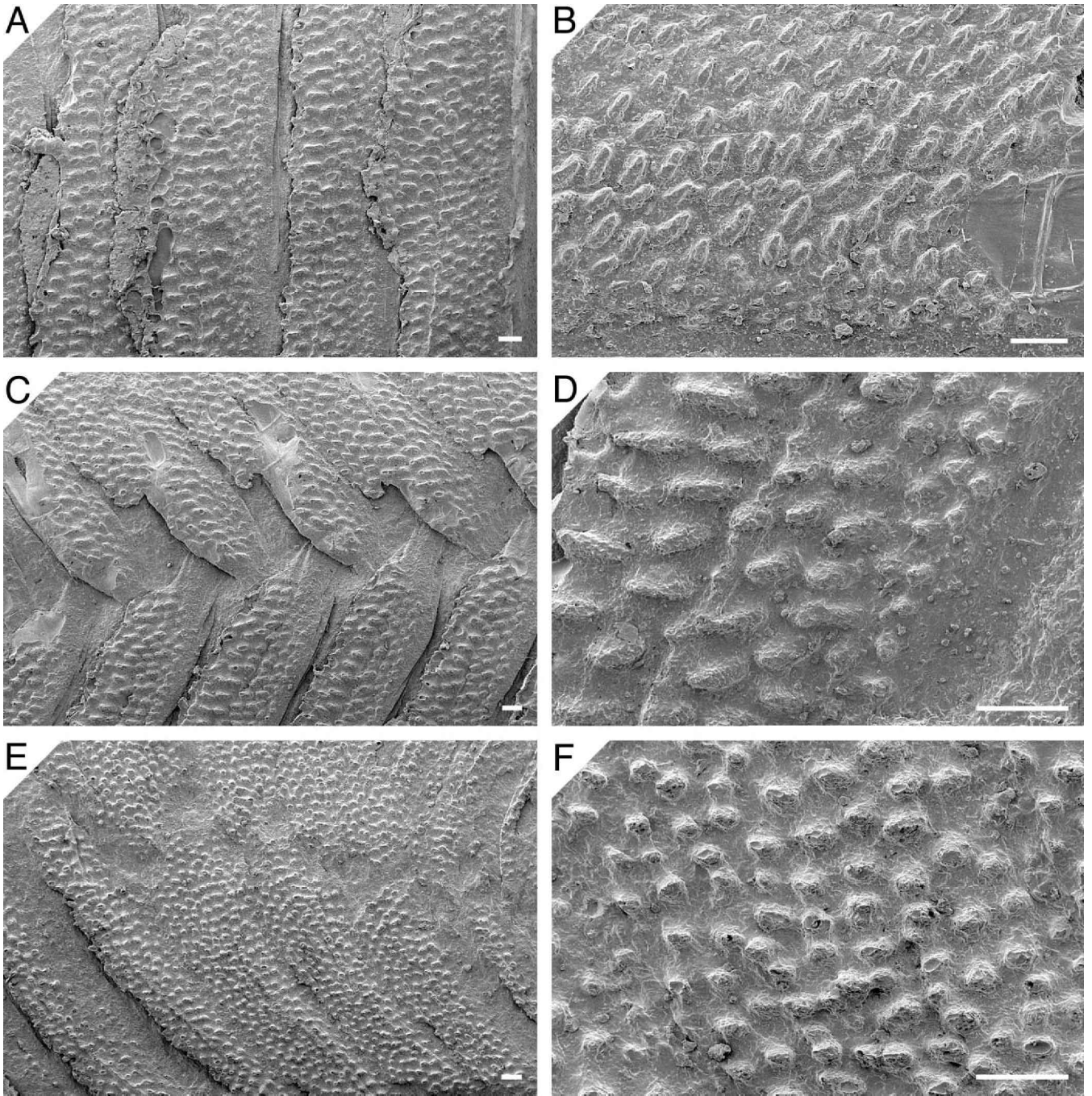
Figure 20 *Pterygolepis nitida* (Kiær, 1911): SEM photographs of latex casts of specimen in Figure 19; scale bars 0·2 mm. (A) Upper ventro-lateral scales; (B) close up on one lower dorso-lateral scale; (C) articulation area of lower dorso-lateral and upper ventro-lateral scales; (D) close up on one lower dorso-lateral scale close to the articulation area; (E) head scales and plates; (F) close up on head plates.

sample 31-208, Ushakov River, October Revolution Island, Samoilovich Formation and sample 5d, Pioneer Island, late Wenlock, Early Silurian; sample 47-14, Spokoinaya River and samples 30, 30-1, Ushakov River, lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian. A few fragments (GI) from Ohesaare Borehole, core at 163·30–163·55 m, Saaremaa, Estonia; Maasi Beds, Jaagarahu Stage, late Wenlock, Early Silurian. Several fragments (NHM) from Viita Trench, Saaremaa, Estonia; Viita Beds, Rootsiküla Stage, late Wenlock, Early Silurian.

Diagnosis. As for the family.

Description. *P. nitida* is the only species from Ringerike that has not been the object of major revision or restudy since

Kiær's original descriptive work in 1924. For a detailed description of the general anatomy of the animal, see Kiær (1924).

Scales of *P. nitida* are characterised by regularly arranged elongated tubercles on the upper surface (Fig. 20). The best details were found in the lower dorso-lateral scales (Fig. 20 B, D) but the upper ventro-lateral scales (Fig. 20A, C) also show the same sculpture. In the anterior part, close to the margin, the tubercles are round with a diameter of about 0·04 mm. Towards the posterior part, the tubercles become longer and posteriorly pointed. They reach their greatest length and width in the middle part of the scale, but decrease in the same towards the posterior margin. The tubercles are arranged in regular antero-posterior rows, or often diagonally depending
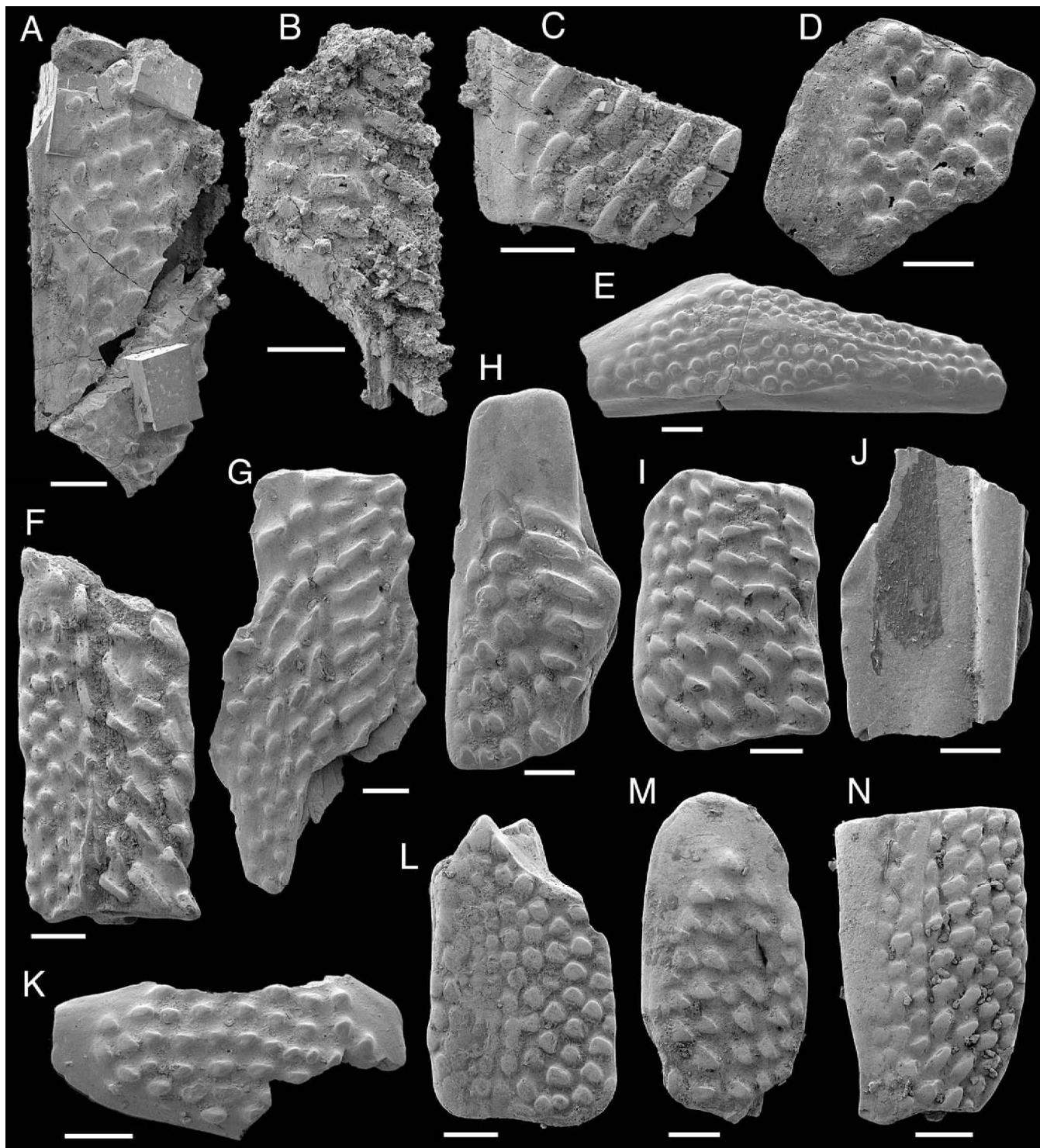
Figure 21 *Pterygolepis nitida* (Kiær, 1911): SEM photographs of disarticulated fragments of lateral scales and plates showing variation in sculpture; all are scale fragments in external view unless stated; scale bars 0·2 mm. (A) NRM P.9480; (B) NRM P.9481; (C) NRM P.9482; (D) plate, NRM P.9483; (E) plate, NRM P.9484; (F) PMU G1021; (G) PMU G1022; (H) NRM P.9485; (I) PMU G1023; (J) scale fragment in visceral view, PMU G1024; (K) plate, GI Pi 7684; (L) LIG 35-918; (M) LIG 35-921; (N) LIG 35-922. NRM P.9480-948 3 from Ringerike, Norway; Ranberget Member, Steinfjorden Formation, late Wenlock, Early Silurian. NRM P.9484, 9485, PMU G1021–G1024 from Gothemshammar, Gotland Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. GI Pi 7684 from Ohesaare Borehole, core at depth 163·30–163·55 mm, Saaremaa, Estonia; Maasi Beds of Jaagarahu Stage, Wenlock, Early Silurian. LIG 35–918, 921, 922 from sample 30, 30–1, Ushakov River, October Revolution Island, Severnaya Zemlya, Arctic Russia; lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian.
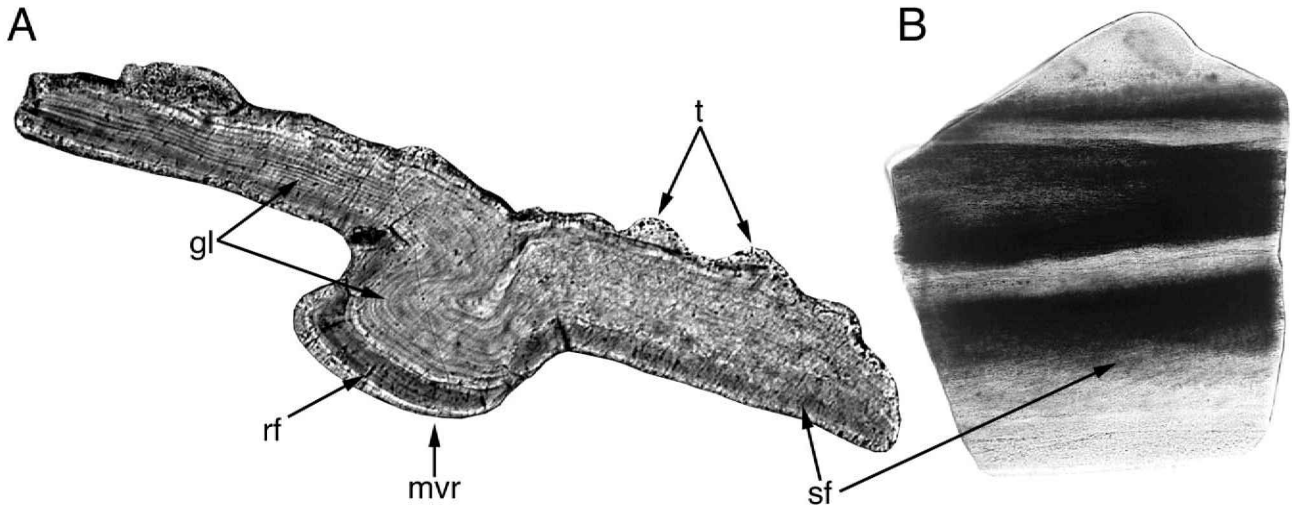
Figure 22 *Pterygolepis nitida* (Kiær, 1911): histology of scales. (A) Scale in vertical cross section, PMU G1025, ×108; (B) scale in external view, immersed in aniseed oil, NRM P.9486, ×64. Both specimens from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian.

on body position. Occasionally this arrangement is disrupted by a few elongated tubercles that point at a slightly different angle. There is a clear gap between each tubercle in each row. The larger tubercles are usually about 0.15 mm long and 0.06 mm wide, but may reach 0·2 mm and 0·08 mm, respectively. The smaller tubercles on the posterior part of the scales have the same proportions as the larger and characteristic middle tubercles, but can be as small as 0·08 mm in length and 0·04 mm in width. Just to the anterior of the mid-line the scales often have a little depression or furrow along the longer axis of the scales (Fig. 20B, D). This depression sometimes disrupts the arrangement of the tubercles, with tubercles sometimes lining this furrow, giving it a more ridged appearance.

Scales and plates from the head region, to the anterior of the branchial openings, have a slightly different surface sculpture. The anterior area is usually smoother and the tubercles are developed as round knobs, with a diameter of about 0·06 mm, which are often arranged in regular rows (Fig. 20F). Sometimes these knob-like tubercles are slightly elongated. More elongated tubercles are also typical of the dorsal spines.

The large characteristic upper ventral lateral scales can be 13 mm long and 1·2 mm wide. On the visceral side there is a high, and about 0·26 mm wide, medial rib and a slightly narrower, about 0·21 mm wide, anterior rib. Both become smaller and taper toward the dorsal end. At the ventral end, the medial rib fades out while the anterior rib merges with the medial thickening that is developed at the ventral end. This articulation socket is curved to enable overlap with the neighbouring scales. The dorsal end has a thickening that forms a short articulation process, which is variable in size as is the overlapping area. Some scales have processes at both ends and some have only one at one end.

No type material was made available for thin sectioning, but Smith (1957, pl. 6) illustrated a section taken from Norwegian specimen PMO E1041, showing compact tissue of acellular laminar bone without a vascular canal system. The tissue morphology observed fits well with the histology found in Gotland specimens (Fig. 22). Kiær (1924) had predicted that all species of the Ringerike fauna should have the same histological structure. He claimed this despite the lack of histological data for all taxa from the Rudstangen locality. A few sections have been made from fragments found in the Ranberget Member at

Ringerike. They were heavily pyritised, so no clear histological feature was detected. Well-preserved forms from Gothemshammar (Fig. 22) show a very compact tissue of acellular bone, with thin and regular growth layers and tightly packed fine tubules of Sharpey's fibres *sensu* Gross (1958, 1968).

Remarks. A few poorly preserved fragments of isolated scales and plates occur in the Ranberget Member at Ringerike (Fig. 21A–D). The elongated tubercles are rather worn and it is also difficult to detect the typical dorso-ventral medial furrow on the exteral scale surface seen in the articulated type material.

Material from Gothemshammar, Gotland (Fig. 21E–J), differs slightly from the type material in gross morphology by not showing such a distinct anterior visceral rib.

Several specimens from Severnaya Zemlya, Arctic Russia, fall within the same morphological range of sculpture. However, the ornamentation is slightly more compact with tubercles closer to each other than in the type material (Fig. 21L–N).

Distribution. Late Wenlock: Ringerike, Norway; Gotland, Sweden and Saaremaa, Estonia. Late Wenlock–early Ludlow: Severnaya Zemlya, Russia.

Family Rhyncholepididae Kiær, 1924

Diagnosis. Dorsal ridge scales small and low, pointed posteriorly; relatively large rostral plates and large plates on cranial roof; anal fin long and low, with long scales; shortened paired ventro-lateral fin; eight branchial openings; scales and plates with regular rows of triangular or modified triangular sculptural elements; vascular canal system well developed.

Content. *Rhyncholepis* Kiær, 1911; *Rytidolepis* Pander, 1856; *Schidiosteus* Pander, 1856; *Silmalepis* gen. nov.; *Vesikulepis* gen. nov.; *Maurylepis* gen. nov.

Distribution. Late Wenlock: Ringerike, Norway; Gotland, Sweden and Arctic Canada Archipelago. Late Wenlock–early Ludlow: Saaremaa, Estonia and Severnaya Zemlya Archipelago, Russia. Ludlow: Central Urals, Russia.

Genus *Rhyncholepis* Kiær, 1911

Type species. *Rhyncholepis parvulus* Kiær, 1911.
Diagnosis. Scales and plates with regular, widely and evenly spaced ridges formed from rows of triangular sculptural elements.

Species content. *R. parvula* Kiær, 1911; *R. butriangula* sp. nov.

Distribution. Late Wenlock: Ringerike, Norway and Gotland, Sweden. Late Wenlock: Saaremaa, Estonia.

Rhyncholepis parvula Kiær, 1911
(Figs 5C, 6, 23C, c, γ, 24–27)

1911 *Rhyncholepis parvulus* nov. gen. et sp.; Kiær, p. 19.
1924 *Rhyncholepis parvulus* Kiær; Kiær, p. 136; pl. 13, 14; figs 23–5, 26c, 34b, 36.
1957 *Rhyncholepis parvulus* Kiær; Smith, pl. 5, fig. 2; pl. 6.
1980 *Rhyncholepis parvulus* Kiær; Ritchie, figs 6, 8–11.

In accordance with the International Code of Zoological Nomenclature, Article 34b, the species-group name must agree in gender with the generic name. Since *Rhyncholepis* is feminine, the correct species-group name spelling is *parvula* instead of *parvulus*.

Syntypes. Articulated specimens PMO E1049, E1059, E1060, E1128, E1129, E1153, E1154 and E0127 from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian (Kiær 1924).

Material. About 100 specimens (PMO) from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian. About 20 fragments of scales and plates (NRM) from a Ranberget Member sample, Ringerike, Norway; Steinfjorden Formation, late Wenlock, Early Silurian. More than 100 fragments of scales and plates (NRM, PMU) from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. More than 100 fragments of scales and plates (GI) from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. Two scale fragments (GI) from the Ohesaare Borehole, Saaremaa, Estonia; core at a depth of 163·3 m, Maasi Beds of Jaagarahu Stage, early Wenlock, Early Silurian. 13 fragmentary scales (LIG) from Severnaya Zemlya, Arctic Russia; samples 5d and 8g-1, Pioneer Island, late Wenlock, Early Silurian; sample MF 157-4, Spokoinaya River, October Revolution Island, sample 30-1, Ushakov River, lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian.

Diagnosis. Scale sculpture very fine with narrow, less than 0·04 mm wide, triangular sculptural elements in widely spaced rows.

Description. The original description and reconstruction of *Rhyncholepis parvula* Kiær, 1924 is accurate. Some complementary data were provided by Ritchie (1980) and description of the scales and plates is augmented here.

The specimen PMO E 0177, after acid preparation and latex casting, shows very well-preserved sculpture from the scale and plate surfaces. This specimen is preserved with an almost complete head and half of the full body length (Fig. 24). The area around the preanal plate is well-preserved with sculpture (Fig. 25A). The ventral scales closest to the preanal plate (Fig. 25A, B) show very narrow rows of fine ridges, formed by small, overlapping, elongated, triangle-like sculptural elements. The posterior part of each triangle is low, with its posterior apex joining the wider part of the next triangular sculptural element in a small depression, giving the appearance
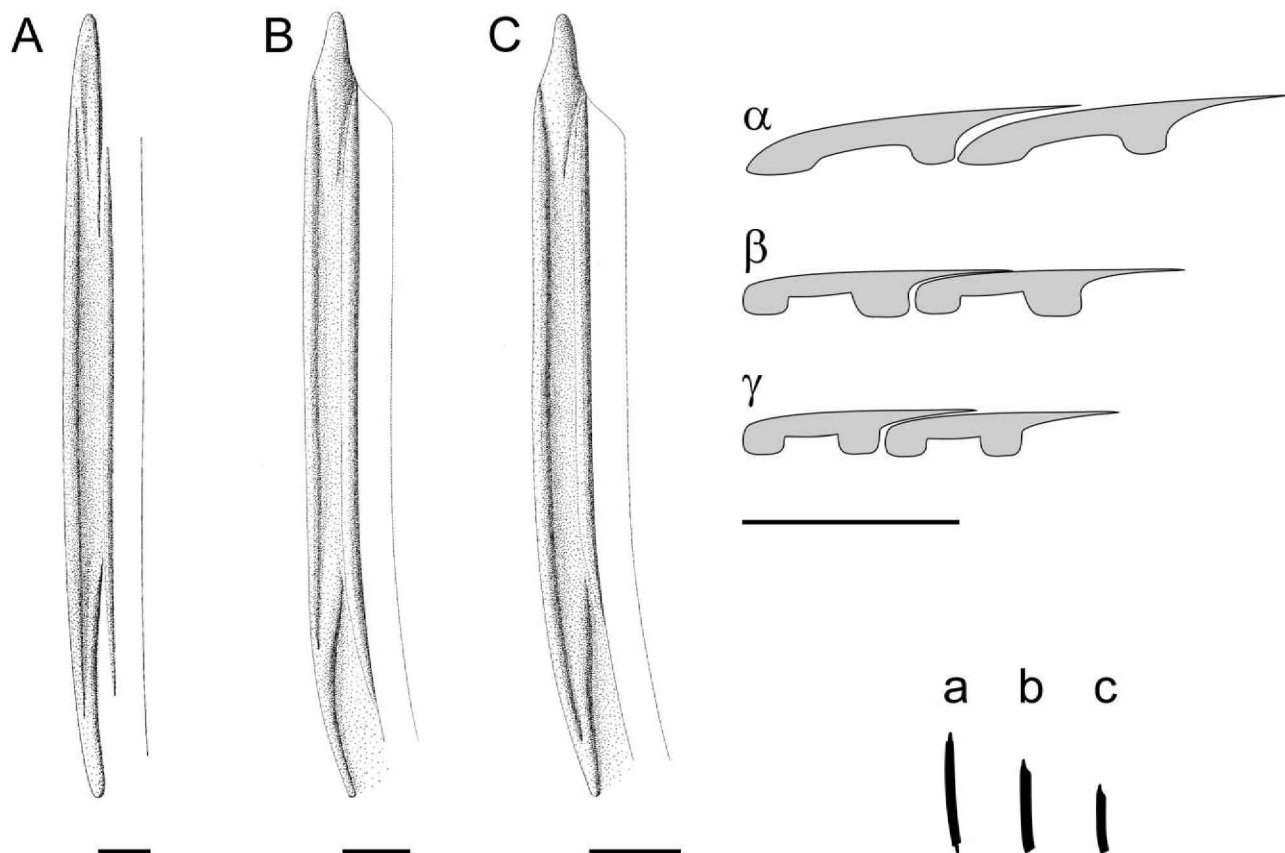
Figure 23 Reconstruction of lateral scales of birkeniids from Rudstangen, Ringerike, Norway. (A, a, α) *Pharyngolepis oblonga* Kiær, 1911; (B, b, β) *Pterygolepis nitida* (Kiær, 1911); (C, c, γ) *Rhyncholepis parvula* Kiær, 1911. (A, B, C) In visceral view; scale bar 1 mm. (a, b, c) In natural size. (α, β, γ) In vertical cross-section; scale bar 1 mm.
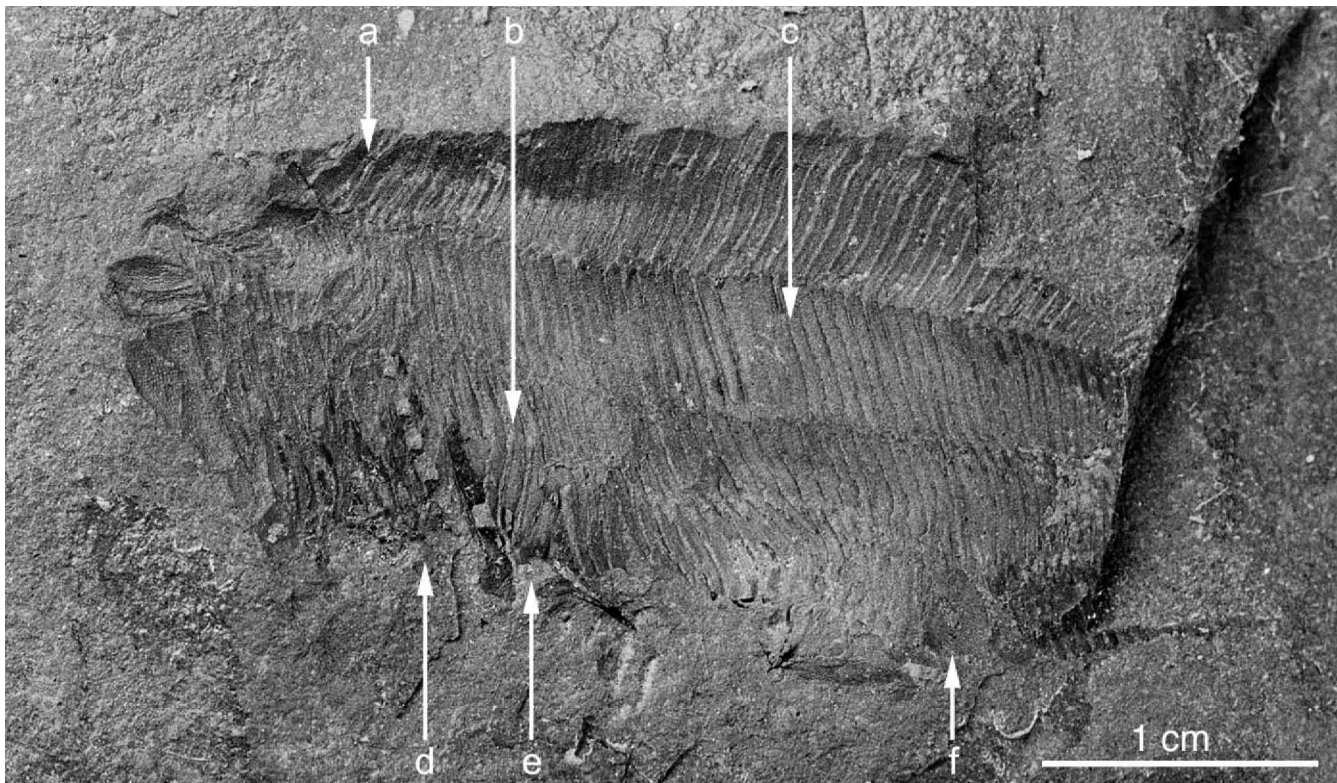
Figure 24 *Rhyncholepis parvula* Kiær, 1911: part of head and anterior part of trunk of prepared specimen used for detailed sculptural study; scale bar 10 mm; specimen PMO E0177 from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian; a = Figure 25H; b = Figure 25E; c = 25C, D; d = Figure 25F; e = Figure 25G; f = Figure 25A, B.

that the elements have grown together into antero-posterior continuous ridges. The sculptural elements are about 0·07–0·1 mm long and reach a width of about 0·04 mm at their widest anterior part. The intermediate furrows are as wide as or wider than the rows of tubercles that they clearly separate. In the anterior part of each scale where the overlapped area bends down, the sculptural elements are shorter, less triangular, almost tubercle-like and more irregularly oriented.

PMO E 0177 also has well-preserved upper ventro-lateral scales (Fig. 25C, D). In this area of the body, it is possible to see the articulation of the scales and the same general sculpture as in scales from the area around the preanal plate. Here the rows of triangular sculptural elements are slightly more irregularly aligned. The visceral side of these scales was reconstructed (Fig. 23C) from PMO E 0177 before the bone was dissolved, and from information taken from other articulated specimens. The largest upper ventro-lateral scale is about 1·1 mm wide and 9 mm long. On the visceral side there is one anterior and one medial rib developed. Both are fairly distinct and almost of the same width and height. The medial rib becomes narrower and less well developed towards the scale upper and lower termination, where it finally fades out. The anterior visceral rib fades in the same way in the dorsal end, where a swollen articulation process is developed. At the ventral scale end, a small posterior socket allows the articulation process of the middle ventral lateral scale to be housed. Scale termination features differ depending on where on the body the scales are located.

Well-preserved sculpture from the lower ventro-lateral scales of PMO E 0177 (Fig. 25E), the head plates just in front of the branchial area (Fig. 25F), the pectoral spine (Fig. 25G) and the head plates (Fig. 25H) shows that the sculpture of *R. parvula* is basically the same over the whole body. The only variation is in the orientation and regularity of the rows. The rows on the 'gular' plates are slightly wider than on the other scales, reaching a width of about 0·05 mm.

A few fragmentary isolated scales from the Ranberget Member of the Steinfjorden Formation, Ringerike, Norway, have similar sculpture on the external side (Fig. 26A, B). Each triangular sculptural element is up to 0·1 mm long and 0·05 mm wide, and clearly shows less oriented rows in the anterior part and more distinct rows to the posterior. A scale with very regular rows of equally sized triangular sculptural elements has also been found in the Jaagarahu Stage on Saaremaa, Estonia (Fig. 26E).

At Gothemshammar on Gotland and Vesiku Brook on Saaremaa, scales and plates have very narrow rows of elongated triangular sculptural elements with wide spaces in between (Fig. 26C, D, F–I, L–O). The scales are large with a sculpture that differs slightly from the Norwegian type material. In the anterior part of the scales, the sculptural elements are rounded like tubercles and become more triangle-shaped posteriorly. Further to the posterior the elements are more irregular, elongated and arrow-shaped, with a distinct smooth, wide, anterior notch for the next scale to overlap. In some scales the sculptural elements tightly overlap each other (Fig. 26C, D). Viscerally, the scales have a very weakly developed anterior rib (Fig. 26H) or no rib at all (Fig. 26N). There are also a few forms with similar sculpture from Severnaya Zemlya (Fig. 26J, K). They differ slightly by having more tightly packed rows and a more distinct overlap of sculptural elements.

Description of the histology of *R. parvula* is based on material from Gotland and Saaremaa, because the type material from Rudstangen is not well-enough preserved. Scales from the Ranberget Member, Ringerike, were also poorly
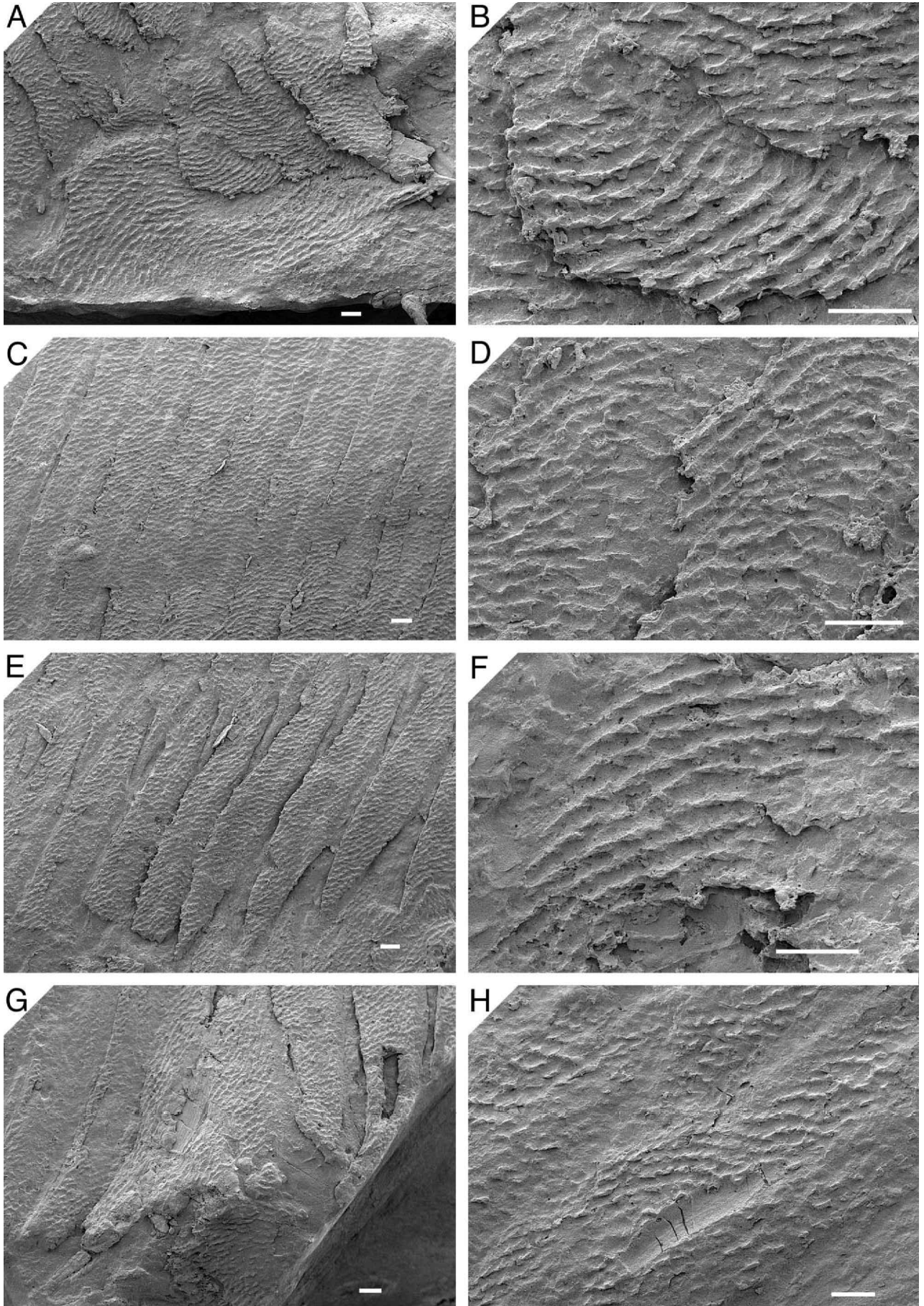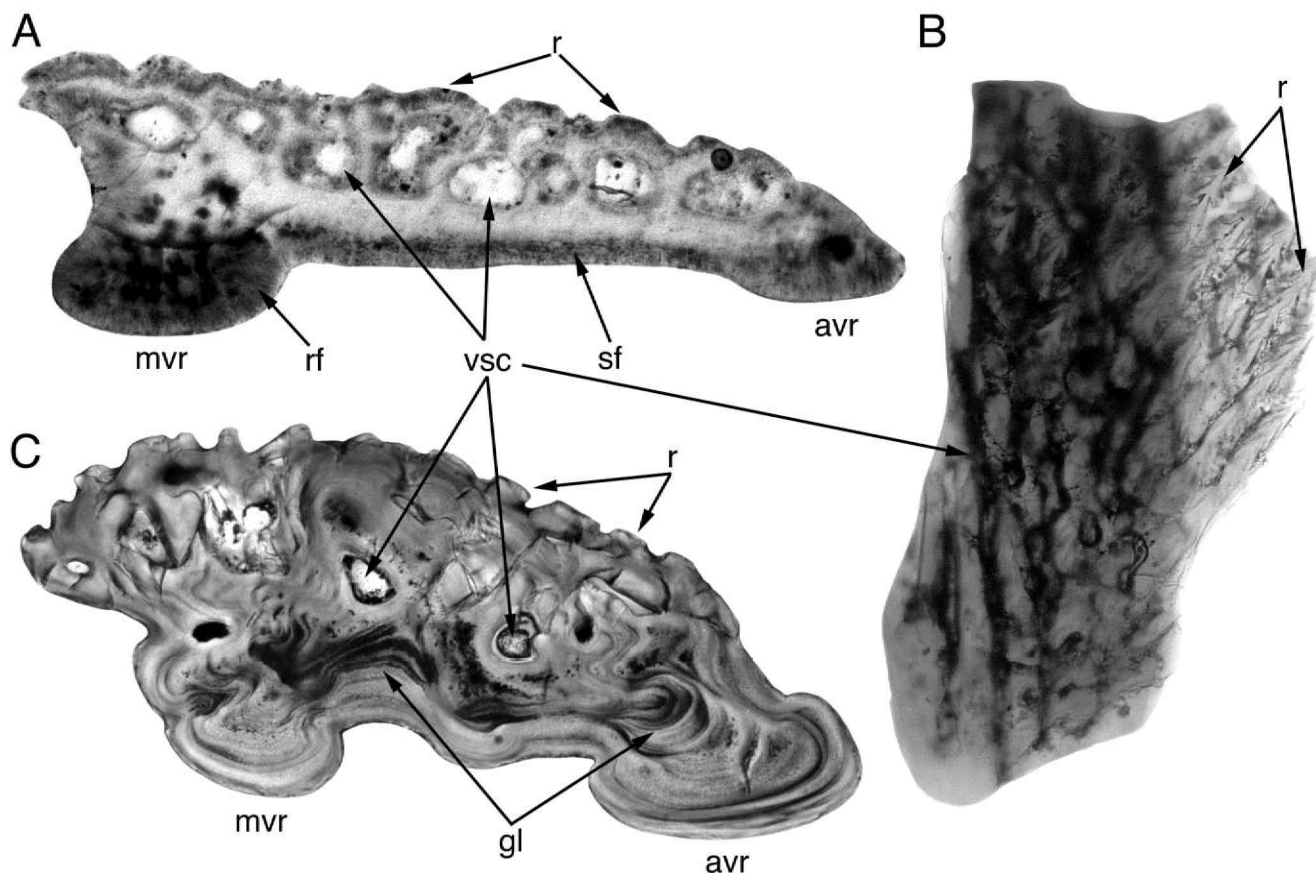
Figure 25 *Rhyncholepis parvula* Kiær, 1911: SEM photographs of latex casts of specimen in Figure 24; scale bars 0·2 mm. (A) Anal fin spine area; (B) close up of one anterior anal fin plate; (C) upper ventro-lateral scales; (D) close up of upper ventro-lateral scales; (E) lower ventro-lateral scales from the anterior region; (F) close up of head plates to anterior of the pectoral spine; (G) pectoral spine area; (H) head plate from behind the eye.
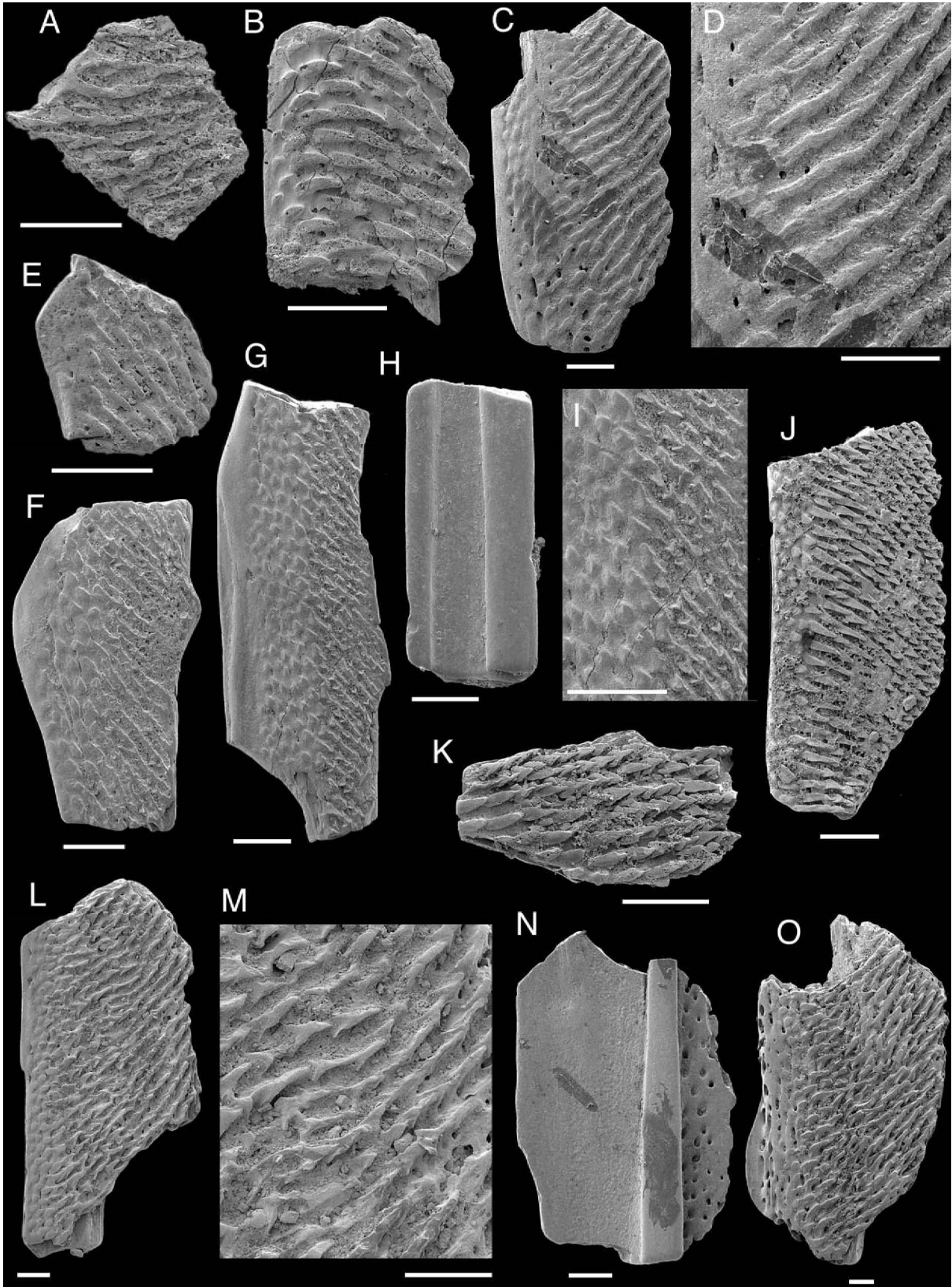
Figure 26 *Rhyncholepis parvula* Kiær, 1911: SEM photographs of disarticulated lateral scale fragments in external view unless stated; scale bars 0·2 mm. (A) NRM P.9487; (B) NRM P.9488; (C, D) NRM P.9489; (D) close up; (E) GI Pi 7720; (F) GI Pi 7686; (G, I) GI Pi 7687; (I) close up; (H) visceral view, GI Pi 7688; (J) LIG 35-925; (K) LIG 35-916; (L, M) PMU G1026; (M) close up; (N) visceral view, PMU G1027; (O) NRM P.9490. NRM P.9487, 9488 from Ringerike, Norway; Ranberget Member, Steinfjorden Formation, late Wenlock, Early Silurian. NRM P.9489, 9490, PMU G1026, G1027, from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. GI Pi 7686-7688 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. GI Pi 7720 from Ohesaare Borehole, core depth 163·3 m, Saaremaa, Estonia; Maasi Beds, Jaagarahu Stage, early Wenlock, Early Silurian. LIG 35-925 from 30-1, Ushakov River, October Revolution Island, Severnaya Zemlya, Arctic Russia; lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian. LIG 35–916 from sample 5d/76, Pioneer Island, Severnaya Zemlya Archipelago, Arctic Russia; Wenlock, Early Silurian.

Figure 27 *Rhyncholepis parvula* Kiær, 1911: Histology of scales. (A) Scale in vertical cross-section, NRM P.9491, ×167; (B) scale in external view, immersed in aniseed oil, GI Pi 7689, ×105; (C) scale in vertical cross-section, GI Pi 7690, ×138. NRM P.9491 from Gothemshammar, Gotland Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. GI Pi 7689, 7690 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, Homerian, late Wenlock, Early Silurian.

preserved. Scales from Gotland and Saaremaa are characterised by a well-developed vascular canal system with larger main canals running along the elongation of the scales (Fig. 27). They all occur at one level and are distributed across the whole scale (Fig. 27A). In more mature scales the canals become narrower because of osteon infilling. The main vascular canals are also interconnected with narrower canals.

Distribution. Late Wenlock: Ringerike, Norway; Gotland, Sweden and Saaremaa, Estonia. Late Wenlock–early Ludlow: Severnaya Zemlya, Arctic Russia.

Rhyncholepis butriangula sp. nov.
(Figs 28, 29A)
1968 Anaspida gen. et sp. indet; Gross, fig. 14B.
1990 Birkeniida sp. C; Fredholm, fig. 7A, B.
1990 Birkeniida sp. D; Fredholm, fig. 7C, D.

Derivation of name. From the Latin words *bu*, prefix for large, and *triangulus*, meaning triangular, referring to the larger size of triangular sculptural elements in comparison with the type species of the genus.

Holotype. Trunk scale fragment NRM P.9493 from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian (Fig. 28B).

Material. More than 100 specimens, mostly scale fragments (NRM, PMU) from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. About 100 specimens, mostly scale fragments (GI) from Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian.

Diagnosis. *Rhyncholepis* species with coarse scale sculpture with wide, greater than 0·06 mm wide, triangular sculptural elements in widely spaced rows.

Description. Many scale and plate fragments of *R. butriangula* are rather complete. They are robust and vary within the same sample in colour between yellow or pale brown to dark brown and almost black. The sculpture is characterised by dominant regular rows of elongate triangles, mostly running slightly oblique to the antero-posterior axis of the scale (Fig. 28B–E, H, I). In some scales, the direction of the ridges changes slightly across the scale (Fig. 28E–I). The width of grooves between the rows usually equals the width of the rows or is slightly less. In the anterior part of the scales, the elongate sculptural elements are shorter, more irregular in shape, and sometimes isolated as round tubercles (Fig. 28B). In some rare forms, the triangular sculptural elements have an anterior furrow or depression (Fig. 28F, G), giving them a more arrow-like outline. Pores of the vascular canals are located on the external surface between ridges.

On the visceral side the openings of the vascular canals are only visible on the surface to the anterior of the relatively narrow medial rib (Fig. 28A). The anterior visceral rib is often very indistinct (Fig. 28A), but sometimes can be as large as the medial rib.
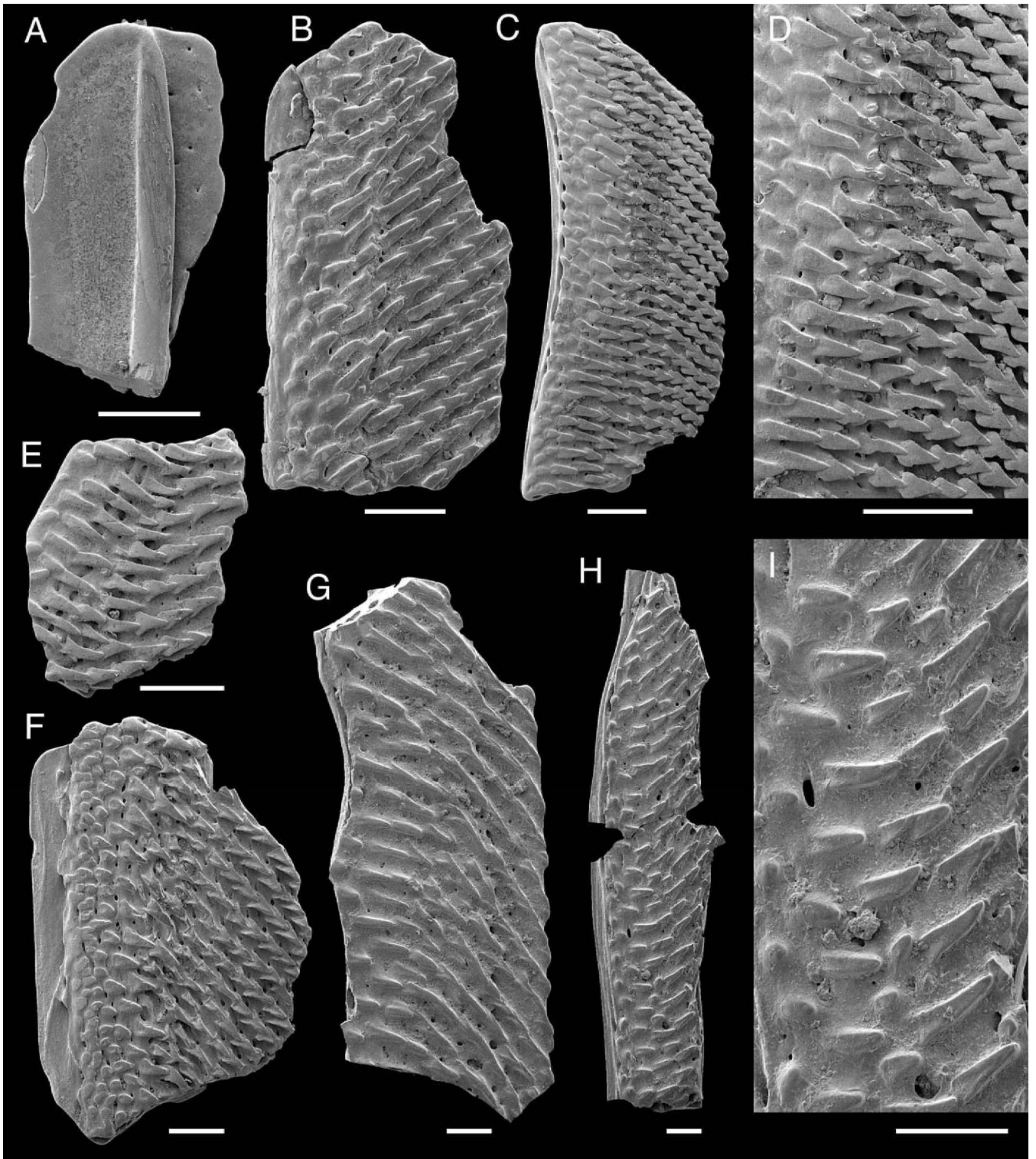
Figure 28 *Rhyncholepis butriangula* sp. nov.: SEM photographs of disarticulated lateral scale fragments in external view unless stated; scale bars 0·2 mm. (A) Visceral view, NRM P.9492; (B) Holotype, NRM P.9493; (C, D) NRM P.9494, (D) close up; (E) NRM P.9495; (F) NRM P.9496; (G) GI Pi 7691; (H, I) GI Pi 7692, (I) close up. NRM P.9492–9496 from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. GI Pi 7691, 7692 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian.
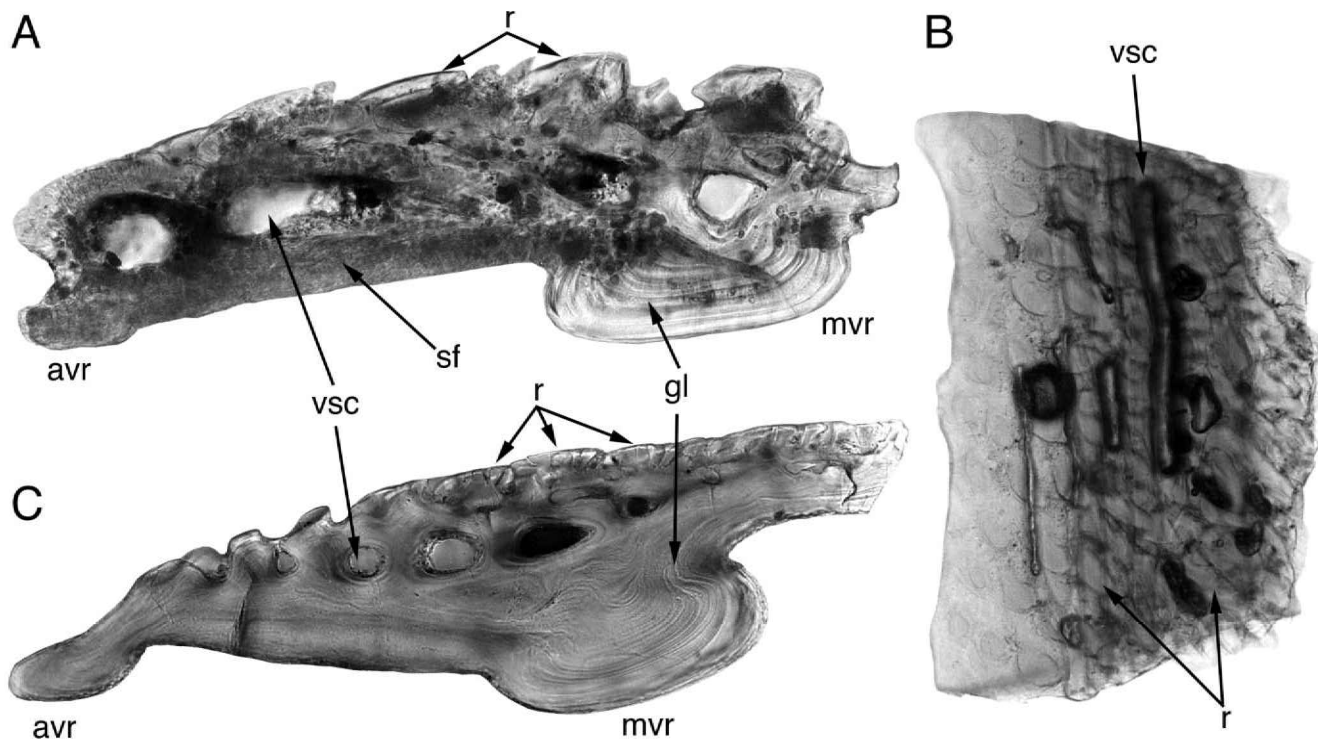
Figure 29 Histology of scales: (A) *Rhyncholepis butriangula* sp. nov. scale in vertical cross-section, NRM P.9497, ×202; (B, C) *Schidiosteus mustelensis* Pander, 1856: (B) scale in external view, immersed in aniseed oil, GI Pi 7693, ×95; (C) scale in vertical cross-section, GI Pi 7694, ×171. NRM P.9497 from Gothemshammar, Gotland Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. GI Pi 7693, 7694 from Silma Cliff, Saaremaa, Estonia; Himmiste Beds, middle Ludlow, Late Silurian.

These scales and plates have a relatively coarse vascular canal system, distributed all over the scale but mainly on one level (Fig. 29A). The larger vascular canals run almost straight along the long axis of the scale.

Remarks. *R. butriangula* differs from *R. parvula* in the size of the sculptural elements, which are substantially larger in this new taxon. We do not consider this to be an ontogenetic feature because other known taxa do not show substantial size variation of the elements within species.

Distribution. Late Wenlock: Gotland, Sweden and Saaremaa, Estonia.

Genus *Schidiosteus* Pander, 1856

Type species. *Schidiosteus mustelensis* Pander, 1856.

Diagnosis. Scales and plates with fine sculpture; short, wide triangular or heart-shaped sculptural elements in closely spaced or overlapping regular rows.

Remarks. The name *Schidiosteus mustelensis* was used by Pander in 1856 for the fragments of scales he treated as 'Ganoiden'. Although the original material is lost, it is possible to identify the same type of sculpture as described in the present paper and *S. mustelensis* is retained for reasons of priority. *S. mustelensis* was originally referred to the locality Mustelpank (= Mustjala Pank = Panga Cliff). However, this is almost certainly not the type locality for that species because no anaspid scales have been found there since. Pander was given material by many geologists and amateurs, and it is a reasonable assumption that the sample comes from another locality situated on western Saaremaa, most probably Silma Cliff.

Schidiosteus mustelensis Pander, 1856
(Figs 29B, C, 30)

1856 *Schidiosteus mustelensis*; Pander, p. 49; pl. 5, fig. 13. (reproduced as Fig. 3C in the present paper)
1968 Anaspida gen. et sp. indet; Gross, pp. 395–397; fig. 14A.
1980 *Rhyncholepis (Saarolepis) oeselensis* (Robertson); Ritchie, fig. 1a, b.
1986 Birkeniida sp. C; Märss, pp. 53, 88; pl. 26, figs 4–6; pl. 27, fig. 3.
1988 ?Birkeniida sp. D; Fredholm, p. 174; fig. 12D.

Neotype. Trunk scale fragment GI Pi 6192 from Silma Cliff, Saaremaa, Estonia; Himmiste Beds, Paadla Stage, middle Ludlow, Late Silurian (Fig. 30A–C). The type specimen (Pander, 1856, pl. 5, fig. 13) is lost but most probably also came from Silma Cliff.

Material. Hundreds of scale and plate fragments (GI) from Silma Cliff, Himmiste Quarry and bore holes of Saaremaa, Estonia; Himmiste Beds, Paadla Stage, middle Ludlow, Late Silurian. Hundreds of fragments (NRM, PMU, LO) from Gothemshammar and Möllbos 1, Gotland, Sweden; Halla Beds, units b and c; late Wenlock, Early Silurian. About 25 fragmentary scales (LIG) from Severnaya Zemlya, Arctic Russia: sample 5m-d, Pioneer Island, Ludlow, Late Silurian; samples 30, 30-1, Ushakov River and sample 47-14, Spokoinaya River, lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian; samples 2-12, 2-14, Matusevich River, middle part of Ust-Spokoinaya Formation, middle Ludlow, Late Silurian. One specimen (GI) from Central Urals, Russia; Ludlow, Late Silurian.

Diagnosis. As for the genus.

Description. Most of the external scale surface is covered by small but wide triangular, v-shaped, arrow-shaped or heart-shaped sculptural elements. They are arranged in regular rows with each element overlapping the posterior in the row.
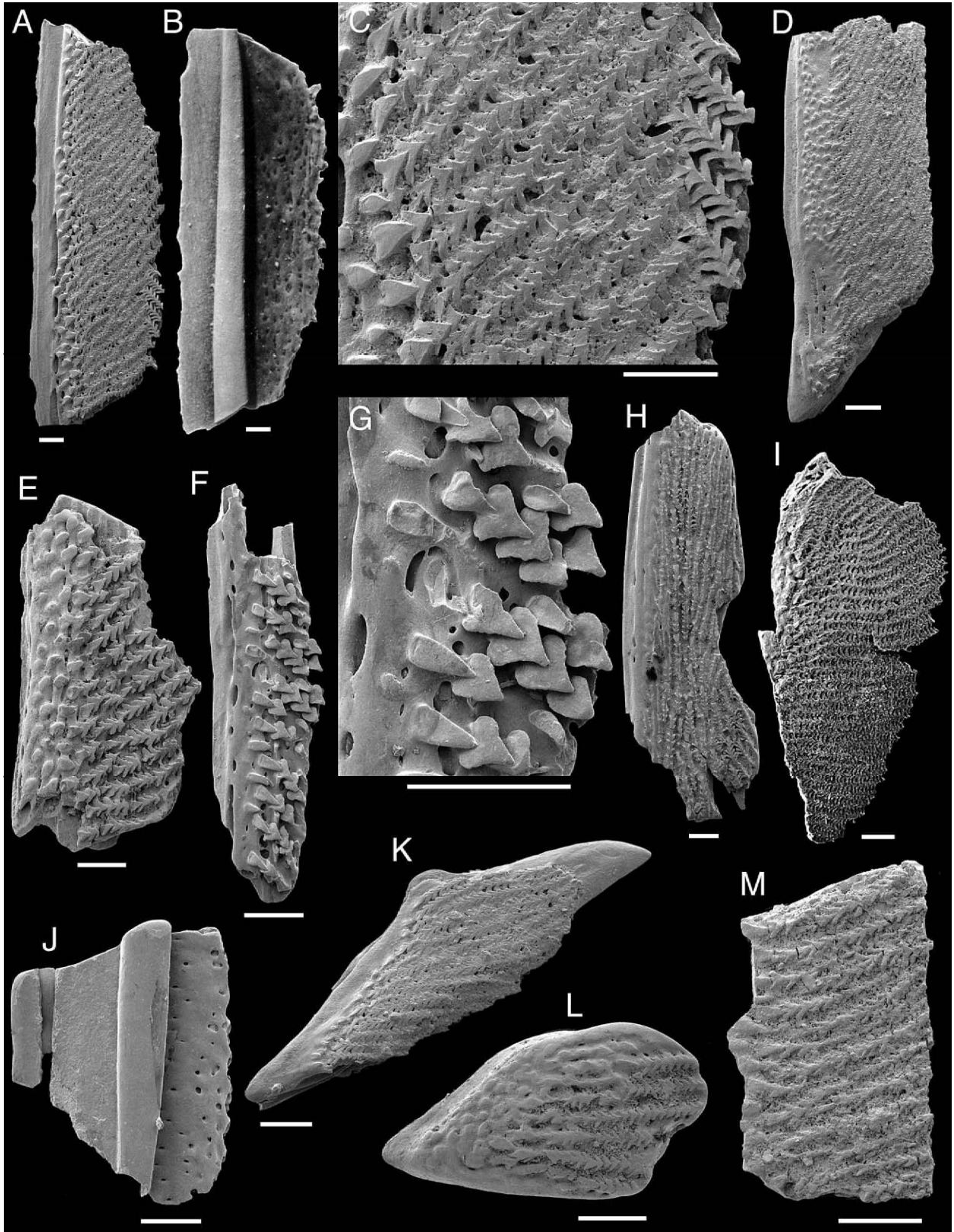
Figure 30 *Schidiosteus mustelensis* Pander, 1856: SEM photographs of disarticulated fragments of lateral scales, spines and plates; all are lateral scale fragments in external view unless stated; scale bars 0·2 mm. (A–C) Neotype, GI Pi 6192; (B) visceral view; (C) close up; (D) GI Pi 6205; (E) NRM P.9498; (F, G) NRM P.9499; (G) close up; (H) GI Pi 7695; (I) GI Pi 7225; (J) visceral view, NRM P.9500; (K) medial dorsal ridge spine in lateral view, GI Pi 6190; (L) plate in lateral view, LIG 35-919; (M) LIG 35-913. NRM P.9498-9500, Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. GI Pi 6192, 7695, 6205, 6190, Silma Cliff, Saaremaa, Estonia; Himmiste Beds, middle Ludlow, Late Silurian. LIG 35-919 from sample 30-1, Ushakov River, October Revolution Island, Severnaya Zemlya, Arctic Russia; lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian. LIG 35–913 from sample MF 157–4, Spokoinaya River, October Revolution Island, Severnaya Zemlya, Arctic Russia; Ust-Spokoinaya Formation, early Ludlow, Late Silurian, GI Pi 7225 from sample 85–042, section on the right bank of the Ufa River, downstream from the mouth of the Tabuska River, Central Urals, Russia; Tabuska Beds, Ludlow, Late Silurian.

The rows are most often tightly packed without any obvious inter-ridge groove or furrow, but with some scales there is more space between the rows (Fig. 30E, F). Most rows are straight with antero-posterior orientation, but some change growth angle posteriorly (Fig. 30C) or are slightly curved (Fig. 30M). Rare scales have rows in a completely different dorso-ventral direction (Fig. 30H), thus parallel to the anterior rim of the scales. Towards the anterior margin, the sculpture is smaller, occasionally tuberculate and more widely spaced (Fig. 30E). In some scales the marginal anterior overlapped area is smooth without any clear ornamentation (Fig. 30A). Dorsal ridge spines have the same typical external sculpture seen in lateral scales (Fig. 30K).

The visceral side is usually characterised by a large medial rib and a less developed (Fig. 30J), or reduced (Figs 29C, 30B) narrower anterior rib. Openings for the vascular canal system are visible on both the external and visceral surface of the scales. *S. mustelensis* has a well-developed vascular canal system distributed at one level over the whole scale (Fig. 29B, C).

Remarks. The scale from the Central Urals (Fig. 30I) is very similar to the type material, while scales from Severnaya Zemlya are slightly different in having more space between the rows of sculpture (Fig. 30L, M).

Specimen GI Pi 6192 shows an interesting feature in the change in direction of the sculpture rows at the posterior margin (Fig. 30A, C). This may be an example of local physical damage of dermal skeleton, perhaps self caused or due to predatory attack, followed by healing of wound and change in growth direction.

Schidiosteus and *Rhyncholepis* are similar in the dominating regular rows of triangular sculptural elements and in having smaller rounded tubercles in the anterior overlapped area of the external surface. The modification from narrow, posteriorly pointing triangles in *Rhyncholepis* to wider v-shaped or heart-shaped triangles in *Schidiosteus* is clearly detectable, and distinguishes these two genera while supporting the position of *Schidiosteus* within the family Rhyncholepididae. This position is also further supported by the histology of the well-developed vascular canal system. The variation in packing of the rows between tightly packed (Fig. 30A–D, H–M) and not so tightly packed (Fig. 30E, F) is considered to be an ontogenetic variation with sculptural elements becoming more closely spaced through ontogeny.

Two large fragments described by Robertson (1937, 1941, 1945), as *Saarolepis oeselensis* (or *Rhyncholepis oeselensis* (Robertson) by Ritchie 1980) have been studied. In his re-examination Ritchie (1980) assigned the best-preserved specimens, AMNH 6698, AMNH 6699 and AMNH 6777a, b (part and counterpart of two specimens) to the same species of the genus *Rhyncholepis*. In the present paper, these two specimens are regarded as two different species for two reasons. Firstly, although the head plates behind the orbits are broken, it appears that the much larger specimen, AMNH 6777, has a higher number of plate units behind the eye than the smaller one. The higher number of units and their orientation pattern in the large specimen does not indicate an ontogenetic change from the smaller to the larger specimen. Secondly, the scale and plate sculpture is completely different in these two specimens. AMNH 6777 has a much larger and irregular sculpture, more similar to that found in *Pharyngolepis oblonga*. The preservation of the dermal skeleton in AMNH 6698 and 6699 is good, but it is difficult to study the sculpture because the external surface lies face down into the matrix and further preparation has not been allowed. Under some light conditions the scales become slightly transluscent and it is possible to see the overlapping v-shaped elements of sculpture characteristic

for *S. mustelensis*. Taking good photographs that showed this feature were not possible. These two arguments also suggest that neither of the AMNH specimens belongs to the genus *Rhyncholepis*.

Distribution. Middle Ludlow: Saaremaa, Estonia. Late Wenlock–early Ludlow: Gotland, Sweden and Severnaya Zemlya, Russia. Ludlow: Central Urals, Russia.

Genus *Vesikulepis* gen. nov.

Derivation of name. After the type locality Vesiku Brook, Saaremaa, Estonia, and the Greek word *lepis,* meaning scale.

Type species. *Vesikulepis funiforma* gen. et sp. nov.

Diagnosis. Scales and plates with coarse external sculpture, wide interrupted ridges with crosswise-cutting needle-like serrations.

Vesikulepis funiforma gen. et sp. nov.
(Figs 31A–G, 32A, B)

1986 Birkeniida sp. C?; Märss, p. 53; pl. 26, fig. 10; pl. 27, fig. 5.

Derivation of name. From the Latin word *funis*, meaning rope, referring to the rope-like appearance of the rows in the sculpture, and *forma*, meaning shape.

Holotype. Trunk scale fragment GI Pi 6204 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian (Fig. 19A, C).
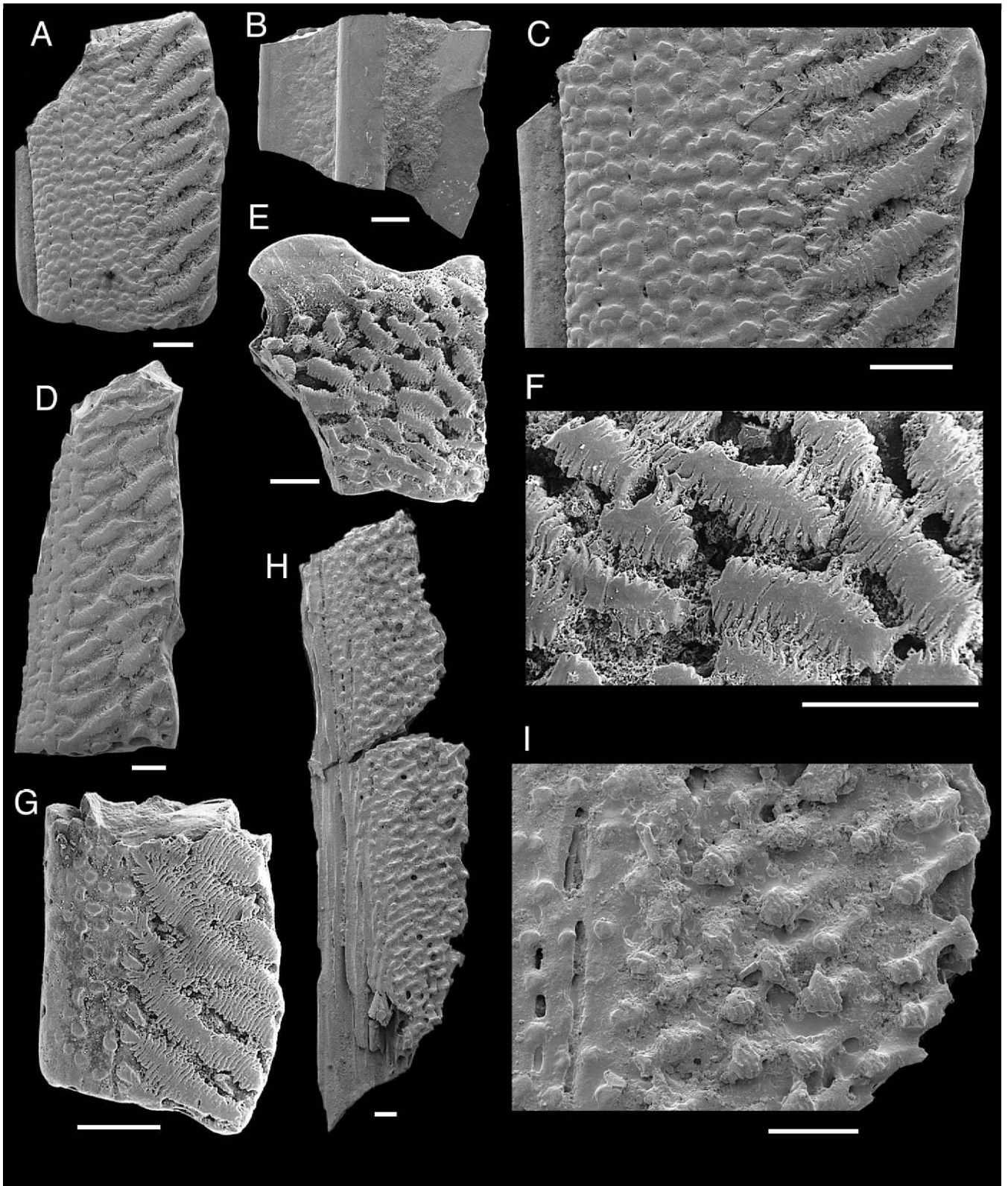
Material. Tens of broken scales (GI) from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. A few fragments (NHM) from Viita Trench, Saaremaa, Estonia; Viita Beds, Rootsiküla Stage, late Wenlock, Early Silurian. Seven fragmentary scales (LIG) from Severnaya Zemlya, Arctic Russia: samples 30, 30-1, Ushakov River and sample 47-14, Spokoinaya River, lower part of Ust-Spokoinaya Formation; early Ludlow, Late Silurian.

Diagnosis. As for the genus.

Description. *V. funiforma* is mainly found as fragments of thick and robust scales with characteristic sculpture. The upper surface can be divided into two areas, the anterior over-lapped area with rounded tubercles and the posterior main scale area with elongate serrated ridges. Ridge size varies between specimens. The anterior area is characterised by tightly packed and irregularly arranged rounded tubercles of low relief. They vary in diameter between 0·025 mm and 0·03 mm and can often be slightly irregular in shape. The anterior area can cover from one-third to two-thirds of the external surface of the scale. The external surface curves gently anteriorwards until, at the margin, it curves viscerally, forming in some scales a clear anterior lip (Figs 31A, C; 32A). The sculpture of the main scale area, by contrast, has large and very wide ridges that run obliquely to the posterior and can be closely spaced or tightly packed. Each ridge, which can be up to 0·15 mm wide and 0·5 mm long, is composed of smaller sculp-tural elements that look like a tightly packed row of needles. To the anterior, the needles give the ridges a serrated appearance, but to the posterior, the needles are more tightly packed and amalgamate into ridges. The medial part of these tightly packed ridges is often smooth and flat or slightly convex, with serrated margins. Specimens from Severnaya Zemlya (Fig. 31E, F) show similar sculpture and include a dorsal ridge scale (Fig. 31E).

On the visceral side, one well-developed medial rib and a narrower, much thinner anterior rib is present; the latter is located on the anterior margin and curves slightly toward the external surface (Fig. 32A).

Figure 31 *Vesikulepis* gen. nov.: SEM photographs of disarticulated lateral and ridge scale fragments; all are lateral scale fragments in external view unless stated; scale bars 0·2 mm. (A–G) *Vesikulepis funiforma* gen. et sp. nov.: (A, C) holotype, GI Pi 6204; (C) close up; (B) visceral view, GI Pi 7696; (D) GI Pi 7697; (E, F) dorsal ridge scale in lateral view, LIG 35-928; (F) close up; (G) LIG 35-929. (H, I) *Vesikulepis funiforma*? gen. et sp. nov.: (H, I) GI Pi 7698, (I) close up. GI Pi 6204, 7696, 7697 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. GI Pi 7698 from Silma Cliff, Saaremaa, Estonia; Himmiste Beds, middle Ludlow, Late Silurian. LIG 35-928, 929 from sample 47-14, Spokoinaya River, October Revolution Island, Severnaya Zemlya, Arctic Russia; lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian.
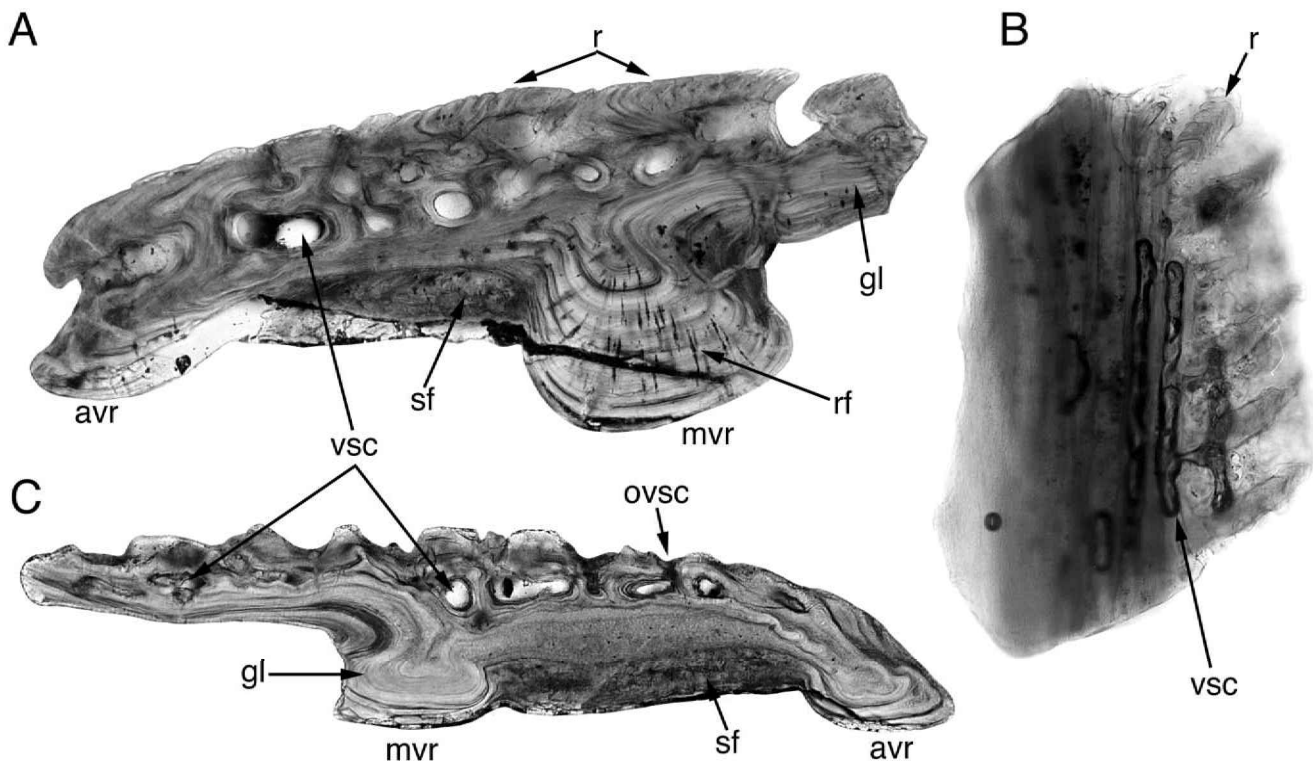
Figure 32 Histology of scales: (A, B) *Vesikulepis funiforma* gen. et sp. nov.: (A) scale in vertical cross-section, GI Pi 7699, ×110; (B) scale in external view, immersed in aniseed oil, GI Pi 7700, ×95. (C) *Rytidolepis quenstedtii* Pander, 1956 scale in vertical cross section, GI Pi 7701, ×96. All specimens from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian.

The histology is of rhyncholepid type, with a well-developed vascular canal system (Fig. 32A, B). The scales also show other typical anaspid structures, such as growth lines and tubules of Sharpey's and radial fibres.

Remarks. *V. funiforma* is regarded as closely related to *S. mustelensis*, since the elongate tubercles of *V. funiforma* may be regarded as a modification of the tightly packed rows of short, triangular sculptural elements seen in *S. mustelensis*. However, *V. funiforma* has interrupted ridges and space between the ridges, while *S. mustelensis* has long, even rows with no space between rows in adult scales.

Distribution. Late Wenlock: Saaremaa, Estonia. Early Ludlow: Severnaya Zemlya, Arctic Russia.

Vesikulepis funiforma? gen. et sp. nov.
(Fig. 31H, I)

Remarks. One specimen from Silma Cliff, Saaremaa, differs slightly by having short and rounded tubercles with the posterior part of them fading out gradually. This may be a preservational feature with sculpture worn by transportation or etching. However, tubercles on the overlapped area and the tightly packed ridgelets to the anterior of the ridges are here considered common features with *V. funiforma*, but the specimens are different enough for this identification to be questioned.

Distribution. Middle Ludlow: Saaremaa, Estonia.

Genus *Rytidolepis* Pander, 1856

Diagnosis. Scales with large and long, slightly irregular to meandering ridges of coalescent triangular elements.

Type species. *Rytidolepis quenstedtii* Pander, 1856.

Rytidolepis quenstedtii Pander, 1856
(Figs 3B, 32C, 33)

1856 *Rytidolepis quenstedtii*; Pander, p. 50, pl. 5, fig. 2 (see Fig. 3B herein)
1958 *Saarolepis oeselensis* (Robertson); Gross, pp. 30–34, pl. 3.
1986 Birkeniida sp. D; Märss, pl. 26, figs 7–9; pl. 27, fig. 6.
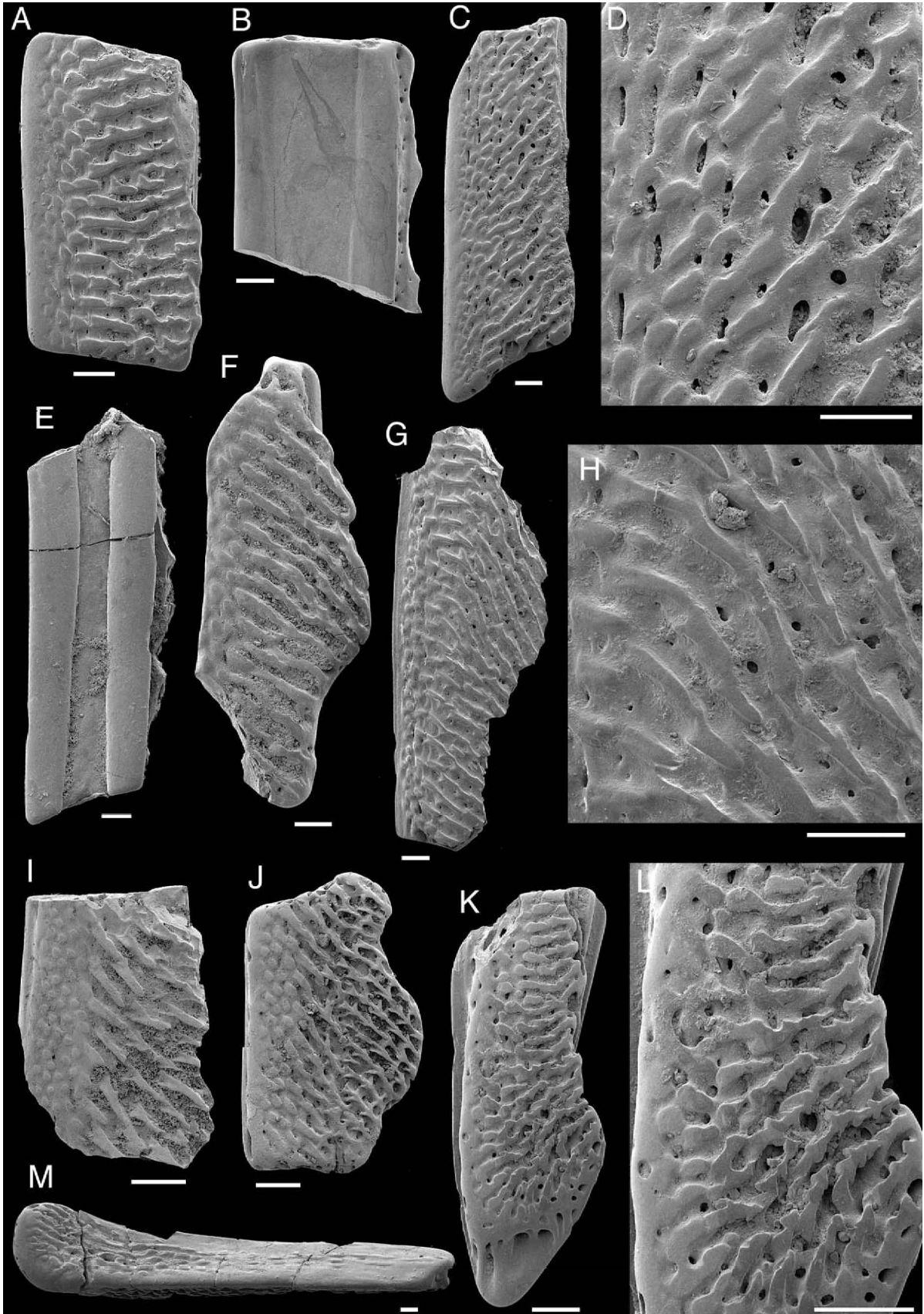1988 ?Birkeniida sp. D; Fredholm, fig. 12C.

Neotype. Trunk scale fragment GI Pi 6201 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian (Fig. 33C, D). The type material illustrated by Pander (1856, pl. 5, fig. 2a–f) is lost; the locality referred to as Rootsiküla is situated in the vicinity of Rootsiküla village and probably corresponds to the Vesiku Brook locality.

Material. More than 100 fragments (GI) from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. Tens of fragments of scales and plates (NRM, PMU) from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. About 15 fragments (LIG) from Severnaya Zemlya, Arctic Russia: sample 5d, Pioneer Island, late Wenlock, Early Silurian; sample 30, 30-1, Ushakov River, sample 2-21, Matusevich River and sample MF 157-4, Spokoinaya River; lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian.

Diagnosis. As for the genus.

Description. Scales and plates of *R. quenstedtii* are mostly preserved as large, thick robust fragments with a coarse sculpture. The overlapped area is tuberculated. To the posterior, ridges are composed of shorter elongated triangular sculptural elements, which occasionally have anterior bifurcations but generally are pointed to the posterior. Each element joins

Figure 33 *Rytidolepis quenstedtii* Pander, 1856: SEM photographs of disarticulated lateral scale and spine fragments; all specimens are lateral scale fragments and in external view unless stated; scale bars 0·2 mm. (A) GI Pi 7702; (B) visceral view, GI Pi 7703; (C, D) neotype, GI Pi 6201; (D) close up; (E) visceral view, GI Pi 7704; (F) GI Pi 7705; (G, H) GI Pi 7706; (H) close up; (I) LIG 35-926; (J) LIG 35-924; (K, L) NRM P.9502; (L) close up; (M) anal fin spine, NRM P.9501. GI Pi 7702-7706, 6201 from Vesiku Brook, Saaremaa, Estonia; Vesiku Beds, Rootsiküla Stage, late Wenlock, Early Silurian. NRM P.9501, 9502 from Gothemshammar, Gotland Sweden; Halla Beds, unit c, late Wenlock, Early Silurian. LIG 35-924, 926 from sample 30-1, Ushakov River, October Revolution Island, Severnaya Zemlya, Arctic Russia; lower part of Ust-Spokoinaya Formation, early Ludlow, Late Silurian.

with the next one at the bifurcation, giving the appearance of a continuous ridge. The grooves between the ridges are nearly as wide as the ridges and are quite frequently pierced by pores of the vascular canal system, giving the external surface a pock-marked appearance. Fragments of scales are most common, but plates from different parts of the body and anal fin spines (Fig. 33M) are not uncommon. Viscerally, the medial and anterior ribs are well developed and approximately of equal width and thickness (Fig. 33E). Vascular pores are visible to the posterior of the medial rib.

The vascular canal system is well developed (Fig. 32C) and perforates the scales with large canals and pores both viscerally and externally (Fig. 33 D, H, L).

Remarks. The most distinctive feature of *R. quenstedtii* is the presence of anterior tubercles and ridges of modified triangular sculptural elements. This and the well-developed vascular canal system suggest a position for this taxon in the Family Rhyncholepididae. However, *R. quenstedtii* has some similarities, such as coarseness and irregular arrangement of sculpture, with representatives of *Pharyngolepis*, although the members of the Pharyngolepididae do not have anterior tubercles or a well-developed vascular canal system.

The figured and described material in this study comes mainly from the Vesiku Brook locality, Vesiku Beds, Rootsiküla Stage and supports the notion that Pander's material also came from Vesiku Brook.

Fragments from the Severnaya Zemlya islands have modified ornamentation that might fall within *R. quenstedtii* (Fig. 33 I, J). The sculptural elements are of similar size with more rounded tubercles anteriorly, but they show a less worn sculpture and each element is more triangular or triradiate.

Distribution. Late Wenlock: Saaremaa, Estonia and Gotland, Sweden. Late Wenlock–early Ludlow: Severnaya Zemlya, Arctic Russia.

Genus *Silmalepis* gen. nov.

Derivation of name. From the type locality at Silma Cliff, Saaremaa, Estonia, and the Greek word *lepis,* meaning scale.

Type species. *Silmalepis erinacea* gen. et sp. nov.

Diagnosis. Medium-sized scales with spines, up to 0·5 mm long, inclined with a low angle to the main scale area; well-developed vascular canal system.

Remarks. *Silmalepis* differs from all other genera of the family in having scales with long posteriorly pointing spines projecting at a low angle to the main scale area. The tubercles on the anterior overlapped area and the well-developed vascular canal system make it comparable with other genera in Family Rhyncholepididae.

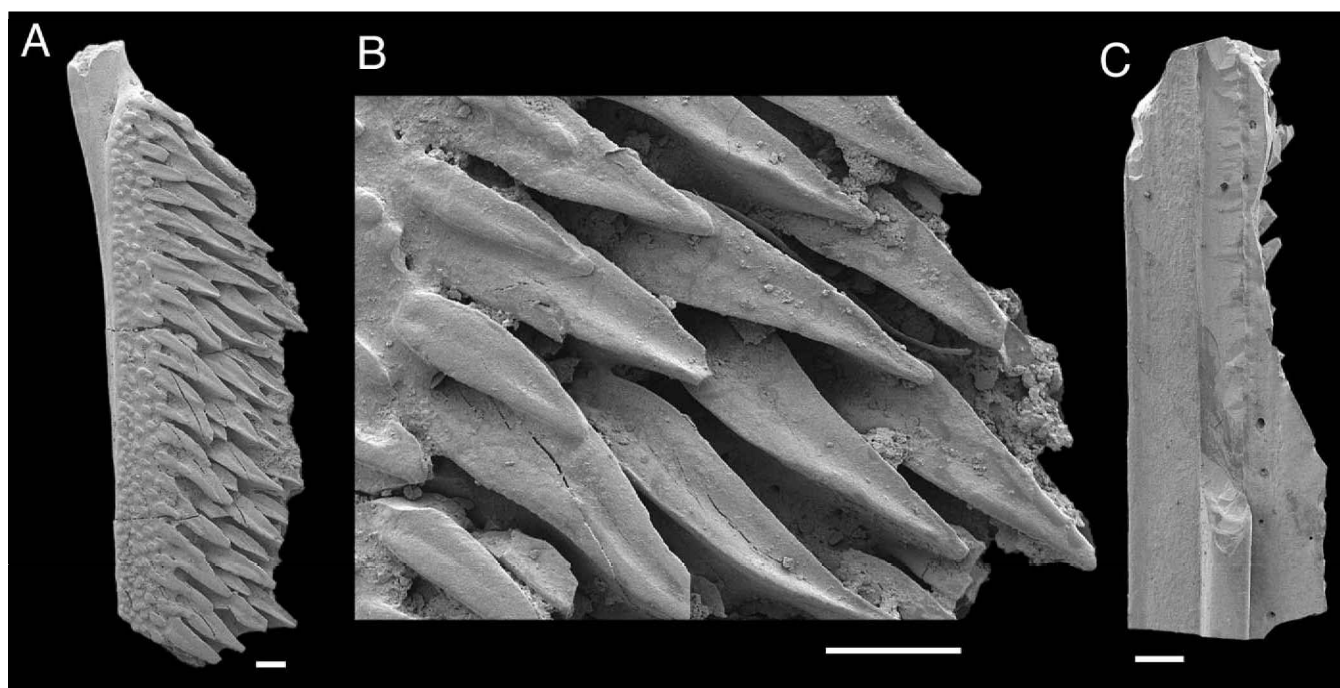## *Silmalepis erinacea* gen. et sp. nov.
(Figs 34, 35)

Derivation of name. From the Latin word *erinaceus*, meaning hedgehog, referring to the spiny appearance of the sculpture.

Holotype. Trunk scale fragment GI Pi 7707 from Silma Cliff, Saaremaa, Estonia; Himmiste Beds, Paadla Stage, middle Ludlow, Late Silurian (Fig. 34A, B).

Material. About ten scale fragments (GI) from Silma Cliff Saaremaa, Estonia; Himmiste Beds, Paadla Stage, middle Ludlow, Late Silurian.

Diagnosis. As for the genus.

Description. Scales very fragile, such that the external sculpture and the posterior margin are usually broken. A lack of complete plate and scale specimens makes it difficult to estimate scale size. Best-preserved specimens indicate a width of about 1·4 mm and a length of at least 4·5 mm (Fig 34A). One-third of the external surface of the scales consists of an overlapping

Figure 34 *Silmalepis erinacea* gen. et sp. nov.: SEM photographs of disarticulated lateral scale fragments; scale bars 0·2 mm. (A, B) Holotype, external view, GI Pi 7707; (B) close up; (C) visceral view, GI Pi 7708. Both specimens from Silma Cliff, Saaremaa, Estonia; Himmiste Beds, middle Ludlow, Late Silurian.
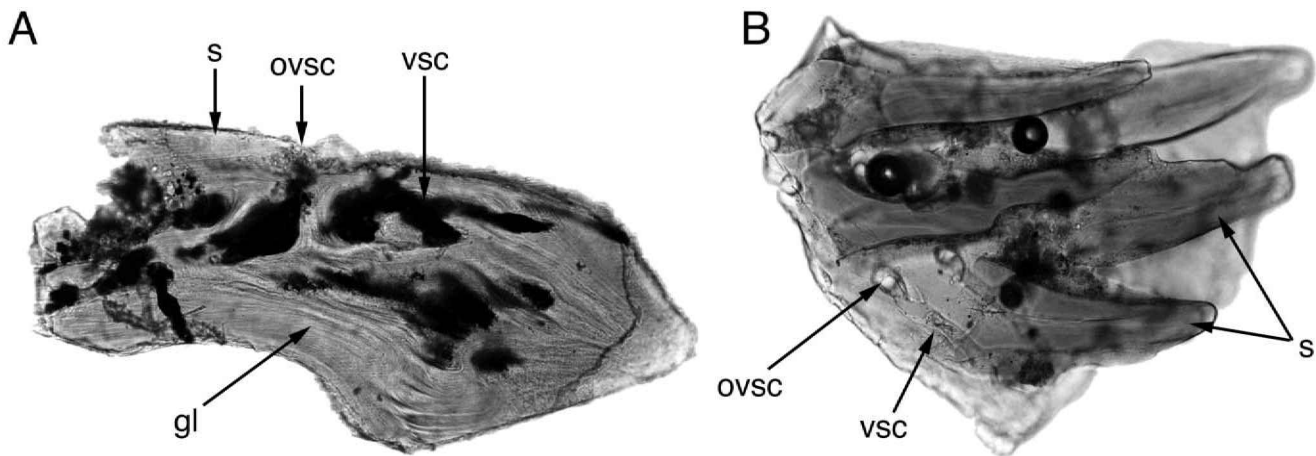
Figure 35 *Silmalepis erinacea* gen. et sp. nov:. histology of scales. (A) Scale in vertical cross-section, GI Pi 7709, ×89; (B) scale in external view, immersed in aniseed oil, GI Pi 7710, ×82. GI Pi 7709 from Uduvere-958 Borehole, core depth 4·5 m, and GI Pi 7710 from Silma Cliff, both from Saaremaa, Estonia; Himmiste Beds, middle Ludlow, Late Silurian.

area covered with small and rounded tubercles, about 0·07 mm in diameter. The main scale area has large posteriorly pointed elongate spines at a low angle that is flat or with a medial furrow. These spines vary in length between 0·2 mm and 0·7 mm, but most are around 0·5 mm long. Spines may reach a width of about 0·2 mm in their proximal part; but to the anterior they are not as wide. The spines are tightly packed (Fig. 34B), and are inclined at a low angle so that the tip of the spine is above the widest part of the following spine but without actually joining it. Many spines are slightly bent and some have an indistinct median furrow or depression along their full length. The best-preserved specimen, which probably is a ventral lateral scale, has an articulation process for attachment with neighbouring scale at the dorsal end (Fig. 34A). The visceral side is characterised by a large, 0·2 mm wide, well-developed medial rib (Fig. 34C). Along the anterior margin, the anterior rib is present as a very weak and low elevation. On the overlapping area, a few rounded openings of vascular canals are sometimes visible.

The few scales available for histological studies show a well-developed vascular canal system with many external openings between the spines (Fig. 35).

Distribution. Middle Ludlow: Saaremaa, Estonia.

Genus *Maurylepis* gen. nov.

Derivation of name. After the Maury Channel situated between Baillie-Hamilton and Cornwallis islands, Arctic Canada, and the Greek word *lepis,* meaning scale.

Type species. *Maurylepis lacrimans* gen. et sp. nov.

Diagnosis. Scales wide with overlapped area comparatively wide; main scale area covered with smooth, flat or slightly convex tubercles that are tear-shaped in outline; tubercles can partly overlap each other or be isolated; viscerally, the medial rib is situated to the posterior part of the scale.

Remarks. The distinctive tear-shaped tubercles separate this genus from all others, but show similarities with the specialised sculpture seen in the Rhyncholepididae.

Maurylepis lacrimans gen. et sp. nov.
(Fig. 36)

1998 Birkeniida gen. et sp. 2, Märss *et al*. p. 58, fig. 2.

Derivation of name. From the Latin word *lacrimo,* meaning flowing tears, because the surface of the scale is covered with tear-drop-like tubercles.

Holotype. Trunk scale fragment UALVP 44622 from 73·5 m level, BH-2 section, southern coast of Baillie-Hamilton Island, Arctic Canada Archipelago; Cape Phillips Formation, late Wenlock, Early Silurian (Fig. 36C).

Material. Three broken scales from the same level as the holotype.

Diagnosis. As for the genus.

Description. These scales have a smooth anterior overlapped area, but in one scale this anterior overlapped area is covered with fine tubercles (Fig. 36C). The anterior part of the main scale area has sparse tubercles, but to the posterior, tubercles are more tightly packed and arranged in oblique rows. The tubercles are flat and tear-shaped in outline, with a posteriorly pointing apex. These apices overhang the anterior margin of the next scale so that the row margin appears serrated. Over the
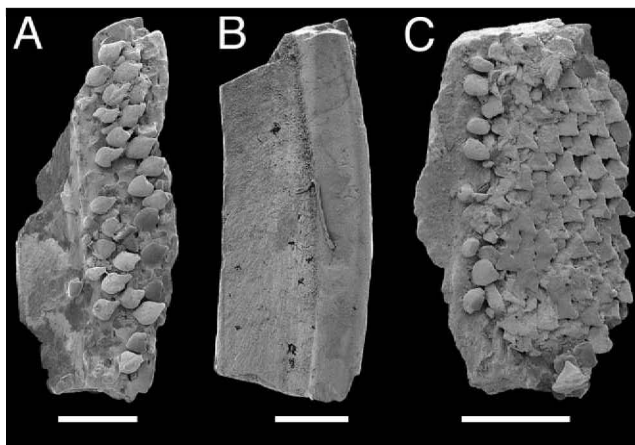
Figure 36 *Maurylepis lacrimans* gen. et sp. nov.: SEM photographs of disarticulated lateral scale fragments; scale bars 0·2 mm. (A) External view, UALVP 44620; (B) visceral view, UALVP 44621; (C) holotype, external view, UALVP 44622. Specimens from 73·5 m level, BH-2 section, southern coast of Baillie-Hamilton Island, Arctic Canada Archipelago; Cape Phillips Formation, upper Wenlock, Early Silurian.

main scale area tubercles show variable density and on some scales they are sparsely packed. Pores of vascular canals are observed on the external surface, beneath and between the tubercles. The visceral side has a posteriorly located relatively narrow medial visceral rib (Fig. 36B), no pores of the vascular canals have been identified due to the poor preservation of most scales. The histology cannot be studied because of the small number of specimens available.

Remarks. All other described birkeniid anaspids from Arctic Canada are similar to *Maurylepis* in having a wide and smooth overlapped area without anterior rib and groove.

Distribution. Late Wenlock: Arctic Canada Archipelago.

Family Pharyngolepididae Kiær, 1924

Diagnosis. Dorsal ridge scales very small with posterior apex poorly developed; 12–15 branchial openings; anal fin short with long anteriorly bordering spine; no or reduced preanal spine; very coarse and irregular scale and plate sculpture.

Remarks. Since this study has used a fixed number of branchial openings as a character for defining families, it is questionable whether *Pharyngolepis heintzi* Ritchie, 1964 with 12 openings belongs to this family and its type genus.

Genus *Pharyngolepis* Kiær, 1911

Type species. *Pharyngolepis oblongus* Kiær, 1911.
Diagnosis. As for family.
Species content. *P. oblonga* Kiær, 1911; *P.? heintzi* Ritchie, 1964.
Remarks. Three species have been described, but Ritchie (1964) did not regard the supposed differences in the cranial roof of *P. kiaeri* Smith, 1956 sufficient for establishing a new species.

Pharyngolepis oblonga Kiær, 1911
(Figs 23A, a, α, 37, 38)

1911 *Pharyngolepis oblongus* nov. gen. et sp.; Kiær, p. 19.
1924 *Pharyngolepis oblongus* Kiær; Kiær, p. 135; pls 8–12; figs 20–22, 26b, 34c, 37.
1956 *Pharyngolepis kiaeri* n. sp.; Smith, pl. 1.
1957 *Pharyngolepis oblongus* Kiær; Smith, pp. 380–84; pls 1–3, 5, fig. 1; figs 1, 3A, 4A, 5, 6.
1957 *Pharyngolepis kiaeri* sp. nov.; Smith, pp. 384–9; pl. 4; figs 2, 3B, 4B, 8, 10.
1964 *Pharyngolepis oblongus* Kiær; Ritchie, pp 18–19; pls 1–4; figs 1a, b, 2.

In accordance with the International Code of Zoological Nomenclature, Article 34b, the species-group name must agree in gender with the generic name. Since *Pharyngolepis* is feminine the correct species-group name spelling is *oblonga* instead of *oblongus*.

Lectotype. PMO E 1152 with counterpart PMO E 0122 (see Kiær 1924, pl. 8, fig. 1; pl. 9, fig. 1, and Smith 1957, pl. 1) from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian. Lectotype was designated by Smith (1957).

Material. About ten articulated specimens from the same locality as the lectotype.

**Diagnosis.** 15 branchial openings; scales and plates with irregular rows of large and high ridges and spines.

Description. The general anatomy was treated by Kiær (1924), Smith (1956, 1957) and Ritchie (1964), and will not be repeated here. Specimen PMO E0090 produced the scale sculpture described below, following acid treatment.

Typical body scales in the medial and lower ventro-lateral regions (Fig. 38A–D) are long and wide with sculpture characterised by short and well-developed ridges arranged in irregular rows. These ridges are 0·06–0·1 mm wide and separated by deep inter-ridge grooves of equivalent width to the ridges. Their length may reach 0·5 mm, but is usually not that long. The rows of short ridges have an overall meandering or slightly irregular arrangement with each short ridge separated by a
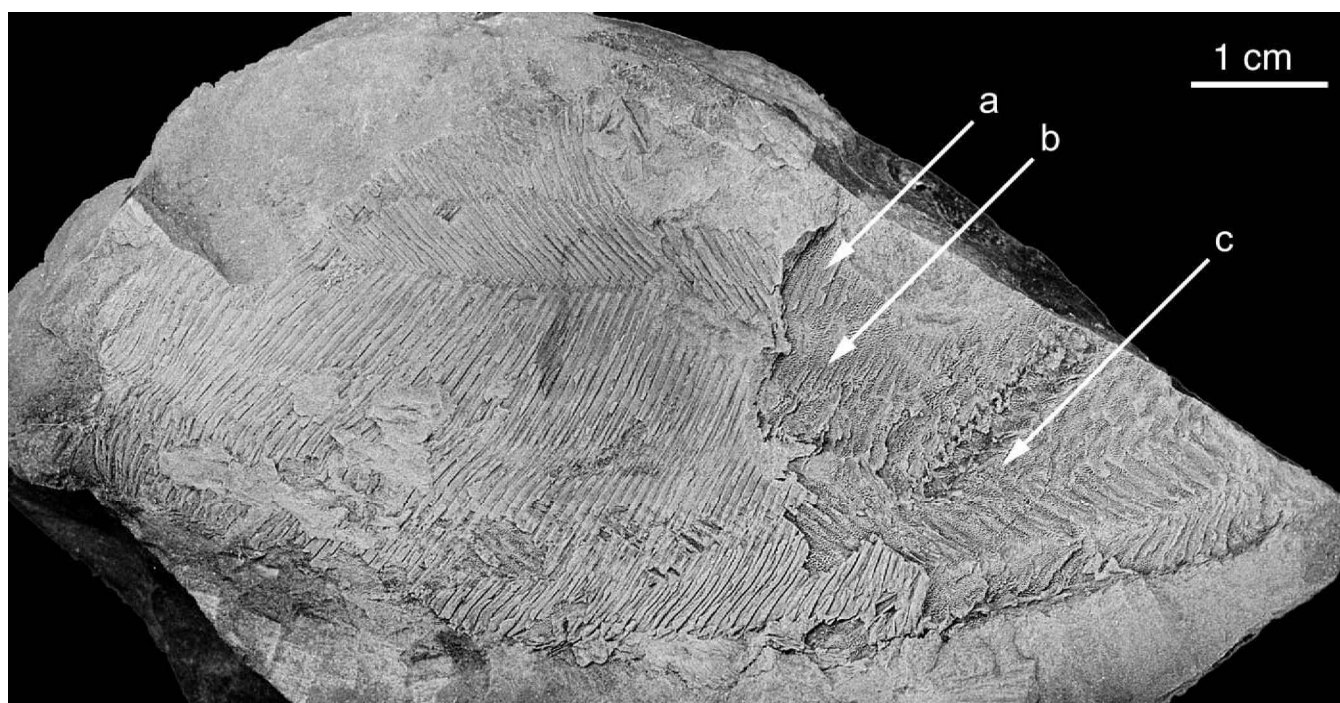
Figure 37 *Pharyngolepis oblonga* Kiær, 1911: branchial region and trunk behind it, used for detailed study of the sculpture of the dermal skeleton. Specimen PMO E0090 from Rudstangen, Ringerike, Norway; Sundvollen Formation, late Wenlock, Early Silurian; a = Figure 38A, B; b = Figure 38C, D; c = Figure 38E, F.
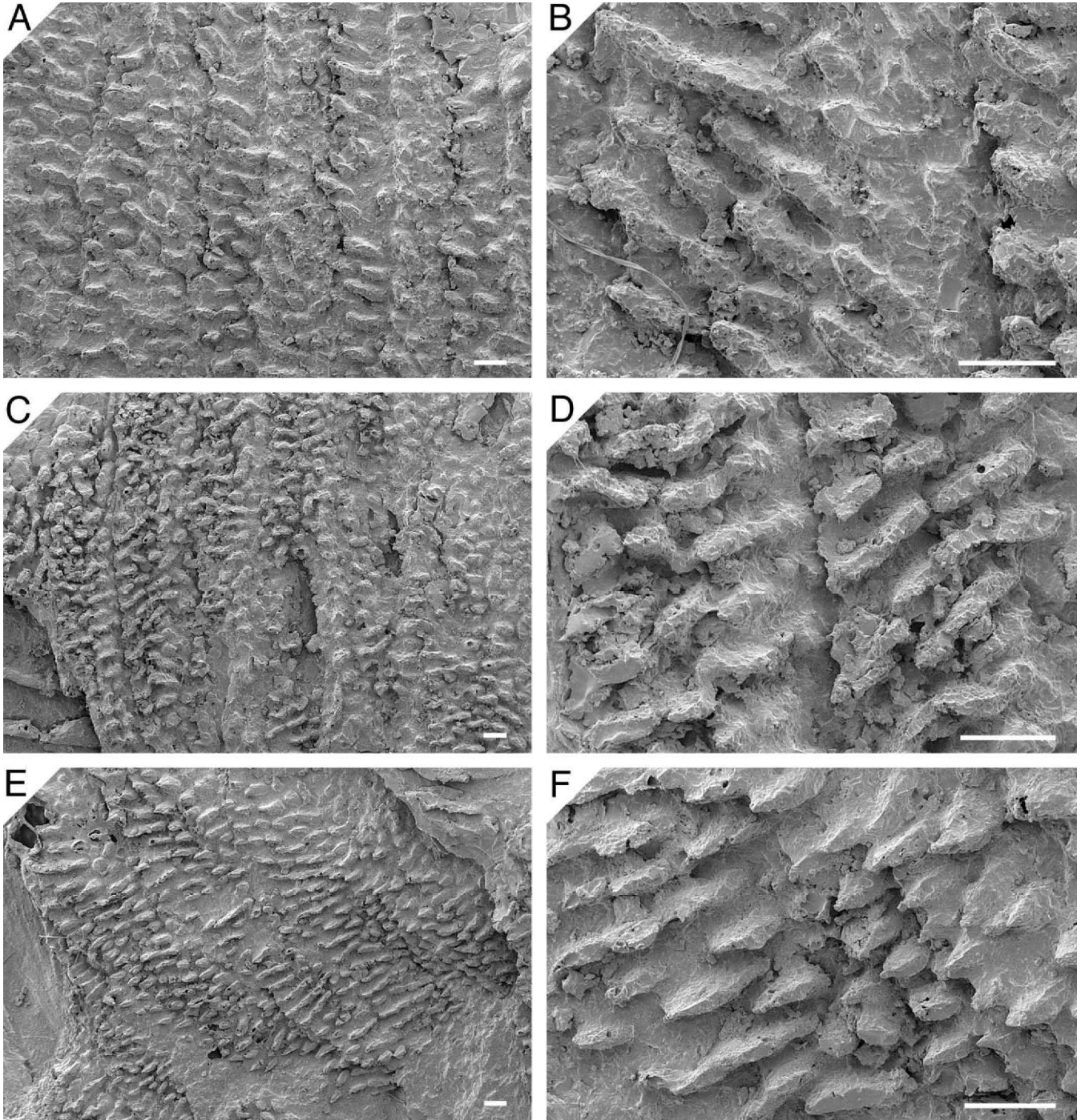
Figure 38 *Pharyngolepis oblonga* Kiær, 1911: SEM photographs of latex casts of specimen in Figure 37; scale bars 0·2 mm. (A) Middle ventro-lateral scales; (B) close up of Figure 38A; (C) lower ventro-lateral scales around branchial spine; (D) close up of Figure 38C; (E) ventral scales anterior of branchial openings; (F) close up of Figure 38E.

distinct but narrow gap. Sometimes these gaps are not distinct, giving the row a more continuous appearance.

Scale and plate sculpture on the external surface can vary to some degree between the different areas of the body. Anterior to the branchial openings, on smaller plates and ventral scales (Fig. 38E–F), the short ridges are less regularly arranged in rows, slightly narrower, and sometimes with a posteriorly pointed spine-like apex.

The largest scales, the upper ventro-lateral scales, can reach a length of about 16 mm and a width of about 1·5 mm. The visceral side of *Pharyngolepis oblonga* scales shows one

narrow medial rib and a wider anterior rib which slopes gently toward the medial rib, forming a wide anterior visceral groove (Fig. 23A). The medial rib fades out toward the ends of the scales, while the anterior rib welds with another short anterior rib at both terminations (Fig. 23A). A narrow and thick articulation process with a shallow furrow is developed at the dorsal end. The junction of ribs at the ventral end forms a thicker slightly bent rib with a posteriorly lying socket-like space for overlapping and attachment for the articulation process of the medial ventro-lateral scale.

The histology of type material was not studied. Identification
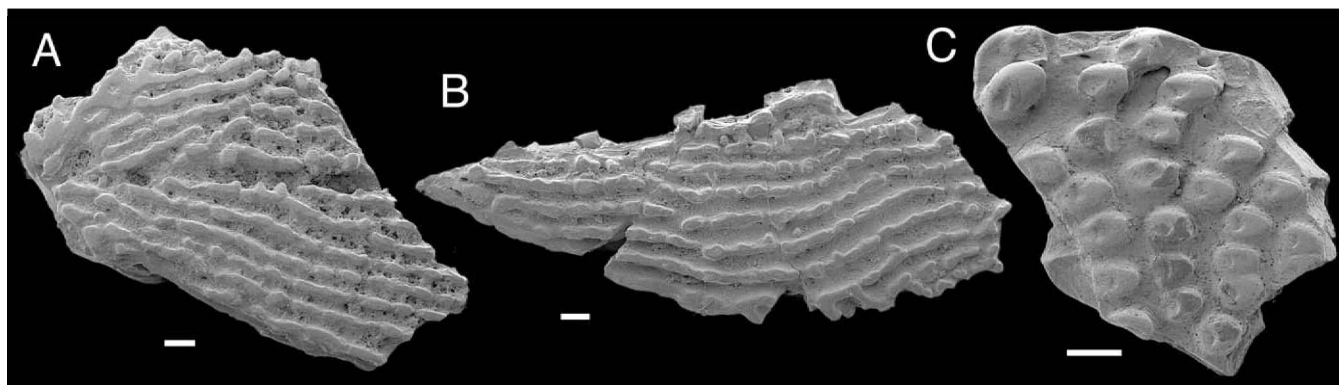
Figure 39 *Pharyngolepis*? sp.: SEM photographs of disarticulated plates in external view; scale bars 0·2 mm. (A) GI Pi 7711; (B) GI Pi 7712; (C) PMU G1028. GI Pi 7711, 7712 from Silma Cliff, Saaremaa, Estonia; Himmiste Beds, middle Ludlow, Late Silurian. PMU G1028 from Gothemshammar, Gotland, Sweden; Halla Beds, unit c, late Wenlock, Early Silurian.

of other fragments of *P. oblonga* found from other areas is taxonomically uncertain and therefore their histology has not been considered here.

Remarks. There are only two specimens known of *P.*? *heintzi* Ritchie, 1964 and these could not be prepared by acid for detailed description of scale and plate sculptures. From some areas it appears that the sculpture of *P.*? *heintzi* is similar to *P. oblonga*.

The single specimen, PMO E 0090, prepared and used for the latex cast did not have a complete row of branchial openings preserved and does not show any lateral fin. Therefore, it cannot be proved that this specimen is certainly *P. oblonga* rather than *P.*? *heintzi*. However, the larger size (interpolated to a length of about 200 mm) suggests *P. oblonga* since none of the *P.*? *heintzi* specimens reach such a size.

Few disarticulated scales or plates with typical characters of *Pharyngolepis* have been found, but some possible fragments with very large and coarse sculpture (Fig. 39A, B) are known from Silma Cliff, Saaremaa, Himmiste Beds, Paadla Stage, middle Ludlow, from the same stratigraphical level as AMNH 6777, figured by Ritchie (1980). This very well-preserved specimen was considered by Ritchie (1980) to be *R. oeselensis*, based on its large head plates, particularly the 'gular' plates. He also included the other well-preserved specimen AMNH 6698 and 6699 (part and counterpart) from Himmiste Quarry, Saaremaa, in this species. In the present study AMNH 6698 and 6699 (part and counterpart) are placed within *S. mustelensis* on the basis of their external sculpture. The external sculpture of AMNH 6777 is mainly preserved face down in the matrix, but it is possible to see a *Pharyngolepis* affinity with respect to the large, high and irregularly arranged short ridges. If this sculpture is diagnostic for the genus *Pharyngolepis*, then the size and shape of the 'gular' plates suggest a new species for AMNH 6777. The overall size and sculpture, consisting of large short ridges, suggest that this Estonian specimen should be treated as a new possible species of *Pharyngolepis*, but the relative size of the head plates suggests similarities with *Rhyncholepis* as Ritchie (1980) suggested, or another genus within the family Rhyncholepididae.

Distribution. Late Wenlock: Ringerike, Norway.

Family Tahulalepididae fam. nov.

Diagnosis. Scales and plates with large, well-spaced tubercles on the main scale area; smooth unsculptured anterior overlapped area on a lower level, sometimes with one or two narrow external ribs; weakly developed vascular canal system with rare pore openings on external and visceral surfaces.

Remarks. The presence of a vascular canal system with pore openings has supported the establishment of a new family. The representatives of the Family Birkeniidae also have a tuberculated sculpture but a histology of compact lamellar aspidine.

Genus *Tahulalepis* gen. nov.

Derivation of name. After Tahula Village, Saaremaa, Estonia, and the Greek word *lepis,* meaning scale.

Type species. *Tahulalepis elongituberculata* gen. et sp. nov.

Diagnosis. As for the family.

Species content. *T. elongituberculata* gen. et sp. nov.; *T. kingi* (Woodward, 1947).

Distribution. Late Ludlow: Saaremaa, Estonia and Skåne, Sweden. Přídolí: Herefordshire, U.K.

Tahulalepis elongituberculata gen. et sp. nov.
(Figs 40, 41)

1986 Birkeniida sp. A; Märss, pp. 52–3, 88; pl. 26, fig. 1a, b; pl. 27, figs 2, 4.

Derivation of name. *Elongituberculata* refers to scales with elongate tubercles.

Holotype. Trunk scale fragment Pi 6207 from Tahula-709 Borehole, core at depth 8·4 m, Saaremaa Island; Tahula Beds, Kuressaare Stage, late Ludlow, Late Silurian (Fig. 40A, B, H).

Material. About 100 fragmentary scales (GI). Estonian Boreholes: Varbla-502, 19·1–22·0 m; Kaugatuma, 52·5 m; Kuressaare, 14·50–18·38 m; Kihnu-526, 90·1 m; Lahetaguse-573, 14·00–14·50 m; Ohesaare, 92·27–95·17 m; Sakla, 7·88–13·40 m; Sutu-605, 21·4–23·7 m; Sõrve-514, 143·4–144·4 m; Tahula-709 m, 7·6–10·0 m. Estonian outcrop at Laadjala Bridge. Latvian Kolka-54 Borehole, core at depth 284·2–284·5 m. All Kuressaare Stage, late Ludlow, Late Silurian. Tens of scales (NRM) from Ramsåsa, Skåne, Sweden; late Ludlow?, Late Silurian.

Diagnosis. *Tahulalepis* species with scales up to 1·8 mm in length; sculpture with large, elongate smooth tubercles arranged in irregular rows; main scale area between tubercles smooth with rounded to elongated pores of vascular canals.

Description. Scales are up to 5 mm in length and 1·8 mm in width (holotype 3·1 mm and 1·8 mm, respectively). The anterior unsculptured overlapped area is wide, with one
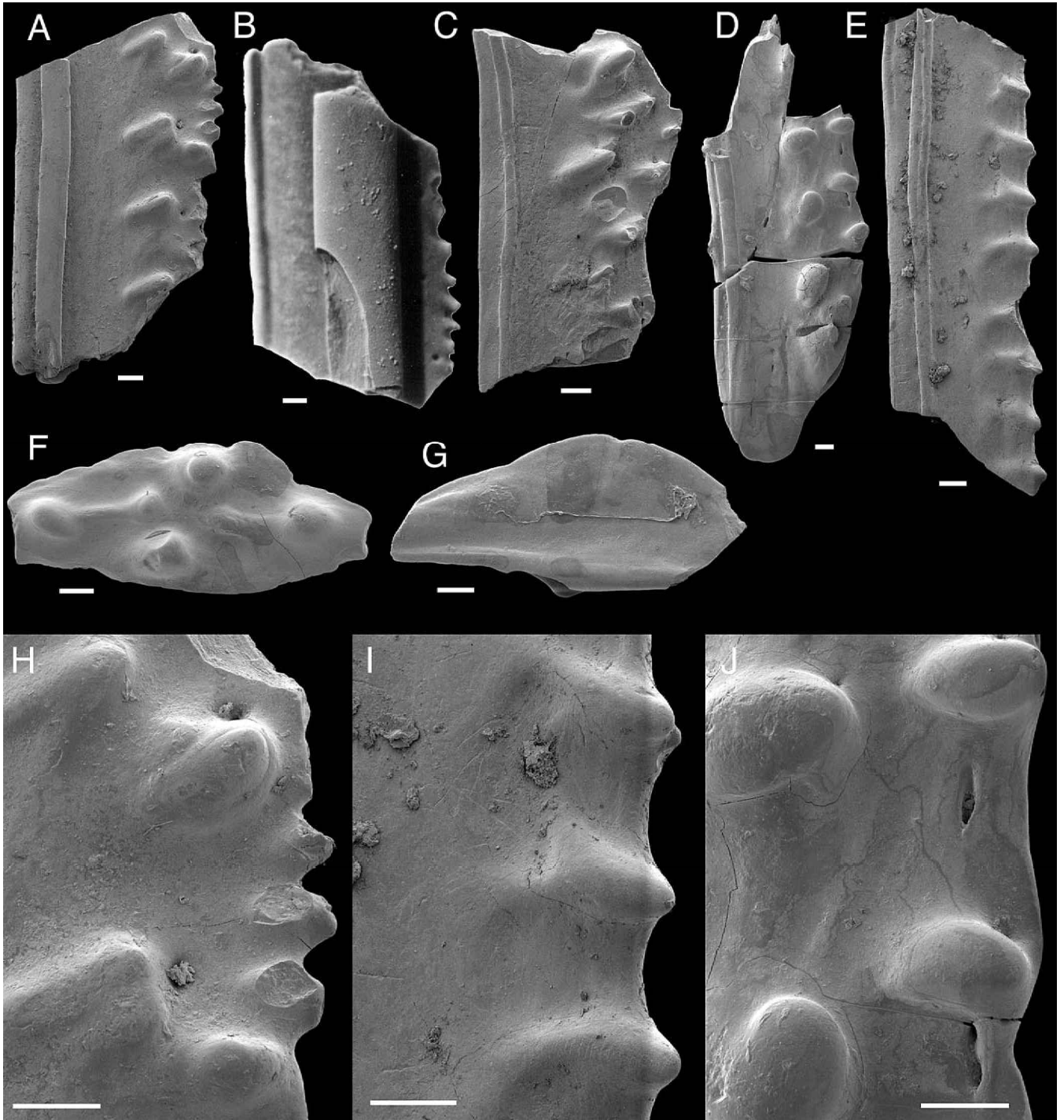
Figure 40 *Tahulalepis elongituberculata* gen. et sp. nov.: SEM photographs of disarticulated lateral scale fragments and plates; scale fragments in external view unless stated; scale bars 0·2 mm. (A, B, H) Holotype, GI Pi 6207; (B) visceral view; (H) close up; (C) GI Pi 7713; (D, J) GI Pi 7714; (J) close up; (E, I) NRM P.9503; (I) close up; (F) plate, GI Pi 7715; (G) plate in visceral view, GI Pi 7716. GI Pi 6207, 7713, 7714 from Tahula-709 Borehole, core depth 8·4 m, GI Pi 7715 from Laadjala Bridge, and GI Pi 7716 from Lahetaguse-573 Borehole, core depth 14·00–14·50 m. All GI Pi specimens from Saaremaa, Estonia; Tahula Beds, Kuressaare Stage, early Ludlow, Late Silurian. NRM P.9503 from Ramsåsa, Skåne, Sweden; Öved Sandstone Formation, late Ludlow, Late Silurian.

narrow rib on a smooth scale surface, parallel to the margin, and occasionally another less-developed rib running along the anterior margin of the scale. The sculpture is characterised by sparse slightly elongate tubercles on the posterior half of the scale and with a smooth surface between the tubercles. One to four rows of tubercles are arranged obliquely to the anterior margin (parallel to the axis of the animal). The tubercle length is up to 0·4 mm and the width is generally half of the length.

Most tubercles are rather uniform in size, except when small tubercles are developed on the posterior margin. Because of the overhanging tubercles, the posterior margin is undulated. Small pores of vascular canals open between the tubercles (Fig. 40H, I). The anteriormost pores pierce the surface behind the first row of tubercles. On the visceral surface, a narrow rib runs along the anterior margin and a strong medial rib follows the long axis of the scale (Fig. 40B). Both
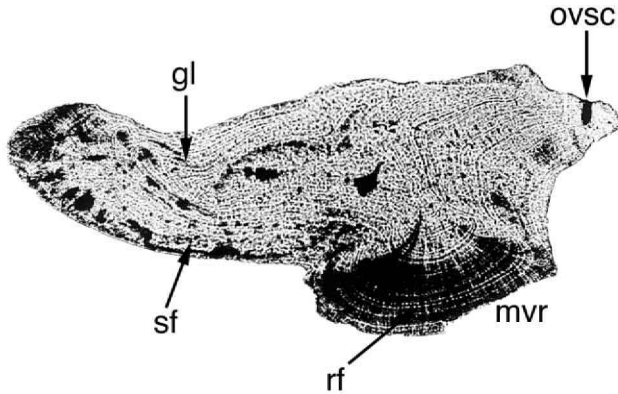
Figure 41 *Tahulalepis elongituberculata* gen. et sp. nov.: histology of scale GI Pi 6961 in vertical cross-section, ×71; specimen from Laadjala Bridge, Saaremaa, Estonia; Tahula Beds, Kuressaare Stage, early Ludlow, Late Silurian.

ribs become narrower or disappear towards the ventral or dorsal terminations of the scale.

Plates are lanceolate in outline with irregularly arranged smooth tubercles and ridgelets. The visceral surface is slightly concave, smooth and with no rib.

The vascular canal system is poorly developed and only present in the more posterior part of the scales, where rare openings are visible on the external and posterior surface (Fig. 41). Very small, rounded pores of vascular canals open to the posterior of the medial rib. Scales of aspidine contain fine radial fibres, especially in the medial visceral rib.

Remarks. The large and irregularly spaced tubercles on the external surface of the scales are different from the finely tuberculated scales of Birkeniidae. The plates (Fig. 40F, G) are considered to belong to this species because the irregular arrangement and size of lanceolate tubercles is similar to the trunk scales. We suggest that they may come from the head region.

Distribution. Late Ludlow: Saaremaa, Estonia. Late Ludlow?: Skåne, Sweden.

Tahulalepis kingi (Woodward, 1947)
(Fig. 42)
1947 *Birkenia kingi* sp. n.; Woodward, pp. 876–8; fig. 1.

Holotype. Woodward (1947, fig. 1). University Museum, Oxford, D202a–d from Ledbury, Herefordshire, U.K.; Grey Grit, Ledbury Passage Beds, Přídolí, Late Silurian (Fig. 42).

Material. One articulated specimen (holotype) in four pieces with original phosphatic scales and moulds of visceral surfaces. Locality and horizon as above.

Diagnosis. Large *Tahulalepis* species with scales up to 2·5 mm in width; sculpture of large, tightly packed and rounded tubercles arranged in irregular rows. Pores of vascular canals not visible.

Description. The upper cheek scales just above the branchial openings comprise five short lanceolate scales with six longer scales to the anterior. No sculpture preserved on any of these. The possible branchial area has eight circular to sub-circular structures up to 5 mm in diameter, trending at a low angle to the ventral mid-line. No plates are visible on either side of these structures. The dorso- and ventro-lateral scales are large, up to 2·5 mm in width and arranged in a regular manner oblique to the ventral mid-line. The anterior overlapped area is wide and smooth with a thin medial rib. The main scale area is irregularly and densely tuberculated with

the tubercle tops rounded, flattened or slightly concave. The visceral surface has a single medial rib, and is slightly concave.

Remarks. Woodward (1947) interpreted the articulated remains described herein as belonging to the anterior ventral region of an anaspid trunk and based this on comparison with articulated specimens of *B. elegans*. It is here suggested that the scales are from the left anterior part of the trunk just behind the head of a birkeniid anaspid but the specimen is not placed in *Birkenia* for two reasons. Firstly, it is much larger than a typical *Birkenia* specimen, which reaches a maximum of 10 cm. Secondly, the sculpture is formed by much larger tubercles which are not arranged in a regular manner as is the case for trunk scales of *B. elegans* (Fig. 42E). Woodward's (1947) species is placed within the new genus *Tahulalepis* because the trunk scales have a coarsely tuberculate ornament and a wide unsculptured overlapped area with rib. Comparison with articulated specimens of *B. elegans* suggests that the arrangement of scales of *Tahulalepis* and *Birkenia* is partly similar, but with the dorso-lateral scales of *Tahulalepis* trending in only one direction while *Birkenia* has a zig-zag arrangement of anterior dorso-lateral scales. The type species, *T. elongituberculata* gen. et sp. nov., differs from *T. kingi* in having more elongate and widely spaced tubercles that are often drawn out into a cusp.

Distribution. Přídolí: Herefordshire, U.K.

Family Septentrioniidæ fam. nov.

Diagnosis. Birkeniida with predominantly ridged sculpture on scales; intra-scale variations in style and size of sculpture; weakly developed vascular canal system with few main canals in medial and rare openings in the posterior part of scales.

Content. *Septentrionia* gen. nov.; *Liivilepis* gen. nov.; *Spokoinolepis* gen. nov.; *Manbrookia* gen. nov.

Remarks. This family is based only on disarticulated scales and plates and is established on the basis of the predominantly ridged sculpture of the scales and the vascular canal system. In Rhyncholepididae this system is distributed all over the scale, while the canals in Septentrioniidae are only developed in the medial or posterior part of the scales.

Distribution. Přídolí: Welsh Borderland, U.K.; erratics from the Netherlands; Skåne, Sweden and Ruhnu and Saaremaa islands, Estonia. Early Ludlow–Early Devonian: Arctic Canada. Ludlow: Gotland, Sweden and Central Urals, Russia. Late Přídolí–early Lochkovian: N Greenland. Late Ludlow–Přídolí: Severnaya Zemlya Archipelago, Arctic Russia.

Genus *Septentrionia* gen. nov.

Derivation of name. *Septentrionia* (f.) from the Latin word *septentrionalis*, meaning northern, referring to the fact that the species of this genus are found in several areas of the Northern Hemisphere.

Type species. *Septentrionia lancifera* gen. et sp. nov.

Diagnosis. Scales and plates with sculpture of ridges with flattened or rounded surfaces; length and style of ridges variable across scale. Very strongly developed medial visceral rib; area posterior to medial visceral rib and between ridges on main scale area covered with many openings of vascular canals.

Species content. *S. lancifera* gen. et sp. nov.; *S. mucronata* gen. et sp. nov.; *S. dissimilis* gen. et sp. nov.; *S. seducta* gen. et sp. nov.

Distribution. Late Přídolí: Welsh Borderland, U.K. Early Ludlow–Early Devonian: Arctic Canada. Ludlow: Gotland, Sweden and Central Urals, Russia. Late Přídolí–early Lochkovian: N Greenland. Přídolí: erratics from the Netherlands.
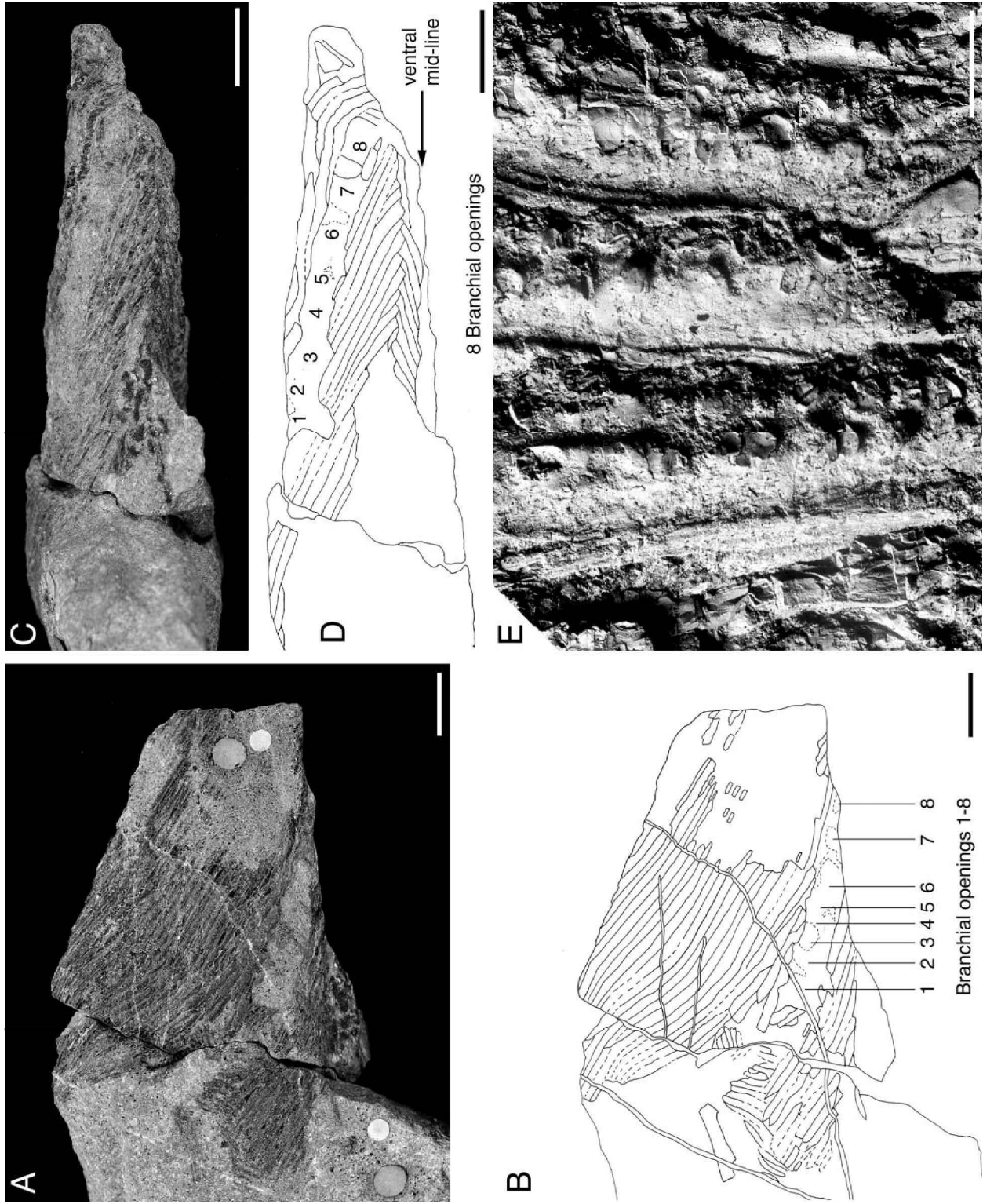
Figure 42 *Tabulalepis kingi* (Woodward, 1947; articulated specimen D202a–d, holotype; scale bars 10 mm (A–D) and 5 mm (E). (A) Photograph of specimen in lateral view; (B) camera lucida drawing of specimen in lateral view showing positions of branchial openings; (C) photograph of specimen in ventral view; (D) camera lucida drawing of specimen in ventral view; (E) SEM close up of scales. Specimen from Grey Grit, Ledbury, Ledbury Passage Beds, Přídolí, Late Silurian.

Septentrionia lancifera gen. et sp. nov.
(Figs 43, 44A, B)

1998 Birkeniida gen. et sp. 4, Märss *et al.*, p. 62, fig. 4.
1999 Birkeniid, Vergoossen, p. 233; pl. 1, figs 8–10.

Derivation of name. From the Latin words *lancea*, meaning lance, and *fere*, meaning almost, because of the lancet-like sculpture.

Holotype. Trunk scale fragment NHM P65550 from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian (Fig. 43T).

Material. More than 100 broken scales (NHM) from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian. A few scales (UALVP) from Cornwallis Island, Arctic Canada, collected from talus, at 61·5 m in Read Bay southern section of Märss *et al.* (1998); early Lochkovian?, Early Devonian.

Diagnosis. Species of *Septentrionia* whose scales have a relatively narrow overlapped area with narrow, deep groove; transitional series of well to closely spaced ribs that taper posteriorly, abut or sometimes incise following rib to posterior; narrow anterior visceral rib and well-developed medial visceral rib.

Description. The scales are 0·30–0·74 mm wide, with a well developed anterior external rib and a deep groove on the narrow, 0·09–0·20 mm wide, overlapped area. To the posterior of the groove, the main scale area starts at a slightly higher level except at the dorsal and ventral extremities, where the groove is also absent (Fig. 43C, F). An unsculptured margin is often present anteriorly to the main scale area and followed by a series of oblique ridges. On the mid-part, the scales have a main scale area/overlapped area width ratio of between 1:2·9 and 1:5·5, but toward the extremities of the scale, the overlapped area becomes wider (Fig. 43C, F, G, S).

Between the ridges, openings of vascular canals occur, occasionally piercing the edges of the ridges (Fig. 43C). Three styles of ribbed sculpture are present on some scales (Fig. 43F, J, R, S), showing a transition between styles along the length of scale. Scales of the first type (Fig. 43A–D, F) have well-spaced long ridges that extend across the whole or most of the main area of the scale. Short intercalated ridges occur only at the posterior part of the scale (Fig. 43L). The second type shows a transitional style of sculpture where the anteriormost ridges are well spaced, but midway to the posterior margin, accessory ridges fill the gaps. The main ridges are followed posteriorwards by single shorter ridges (Fig. 43I, J, M). Scales of the third type (Fig. 43N, O, Q, T, U) have closely spaced short ridges that taper posteriorwards and abut against or even cut into the following rib so that the anterior part of the following rib is forked (Fig. 43N). Up to three successive small ridges can traverse the main area of the scales. Occasionally these scales have a row of fine tubercles on the anteriormost part of the main area (Fig. 43O, Q, S, U). This species exhibits a wide variety of scale sculptures with some transitional ones, the common feature being that each successive ridge follows directly on from the previous one. Scale fragments considered to be from the dorsal and ventral extremities of the scales (Fig. 43A, C, F) are generally of type 1. Other scales show transitions in sculpture types which suggest that the ridges may become more widely spaced towards the dorsal and ventral extremities (Fig. 43R, S) and more tightly packed towards the middle of the scales.

All scales with an anterior visceral rib and groove have a well-developed medial visceral rib (Fig. 43E, K, P). Posterior to the medial rib, the overlapping area is pierced by numerous rounded pores of vascular canals. Plates are flattened with no overlapping area and show similar lanceolate ridges. These ridges are occasionally curved and of variable length (Fig. 43V, Y). The visceral surface has one well-developed visceral rib (Fig. 43W, X) and regularly spaced circular pores of vascular canals. The internal structure is characterised by typical aspidine tissue and a few small vascular canals in the posterior part (Fig. 44A, B).

Distribution. Late Přídolí: U.K., Arctic Canada and erratics from the Netherlands.

Septentrionia mucronata gen. et sp. nov.
(Figs 44C, D, 45A–I)

Derivation of name. From the Latin word *mucronatus*, meaning sharp-pointed, because of posteriorly pointed ridges.

Holotype. Scale fragment NRM P.9511 from Uddvide, Gotland, Sweden; Burgviks Beds, late Ludlow, Late Silurian (Fig. 45G, H).

Material. About 50 broken scales (NRM) from Uddvide, Hoburgen 2 and Hoburgen 3 localities, Gotland, Sweden; Burgsvik/Hamra beds, late Ludlow, Late Silurian.

Diagnosis. *Septentrionia* species with relatively wide and smooth overlapped area of scales; low, narrow, anterior and posterior external ribs; ridges on main area of scale smooth, elongate and sharply pointed posteriorly; ridges extend to area between following ridges; inter-ridge area with elongate pores; weakly developed anterior visceral rib, medial rib well developed.

Description. The overlapped area of the scales is relatively wide and smooth with two weak and narrow external ribs sometimes developed. The anterior rib is situated slightly to the posterior of the margin. The posterior rib is smooth or finely tuberculated (Fig. 45G) and the anterior external groove relatively wide.

The main scale area is covered with ridges that have a flat smooth surface and are developed at the same level as the anterior part of the overlapped area. The ridges vary in length from those that cover the whole of the main area of the scale, to short ones with a rounded anterior and sharply pointed posterior apex. The ridges point into the gap between the next row of ridges with up to four rows of ridges crossing the main area. On the visceral side (Fig. 44C, I), the anterior rib is very weak and the overlapping area perforated by round openings of vascular canals. Elliptical vascular canal openings are visible on the external surface in the inter-ridge area. Histology is characterised by a weakly developed vascular canal system with the main canals only developed in the medial or posterior part of the scale (Fig. 44C, D).

Remarks. Like scales of *S. lancifera*, *S. mucronata* exhibits a wide variety of scale sculpture that can be shown to be transitional along the scale (Figs 43, 45). They differ from scales of *S. lancifera* by having a wider overlapped area lacking a deep groove. The style of densely packed ridge sculpture of the two species is also quite different; *S. mucronata* has short ridges that taper posteriorly into the gap between the succeeding row of ridges, while in *S. lancifera* the ridges are arranged so that they usually follow one after the other. The sculpture of *S. mucronata* is developed at the same level as the anterior overlapped area while most scales of *S. lancifera* have the sculpture developed at a slightly higher level. Both mentioned taxa are also similar to *Silmalepis erinacea*, but differ by having ribs and grooves instead of tubercles on the overlapped area. *Silmalepis* also differs in having a well-developed vascular canal system and larger projecting spines.

Distribution. Late Ludlow: Gotland, Sweden.
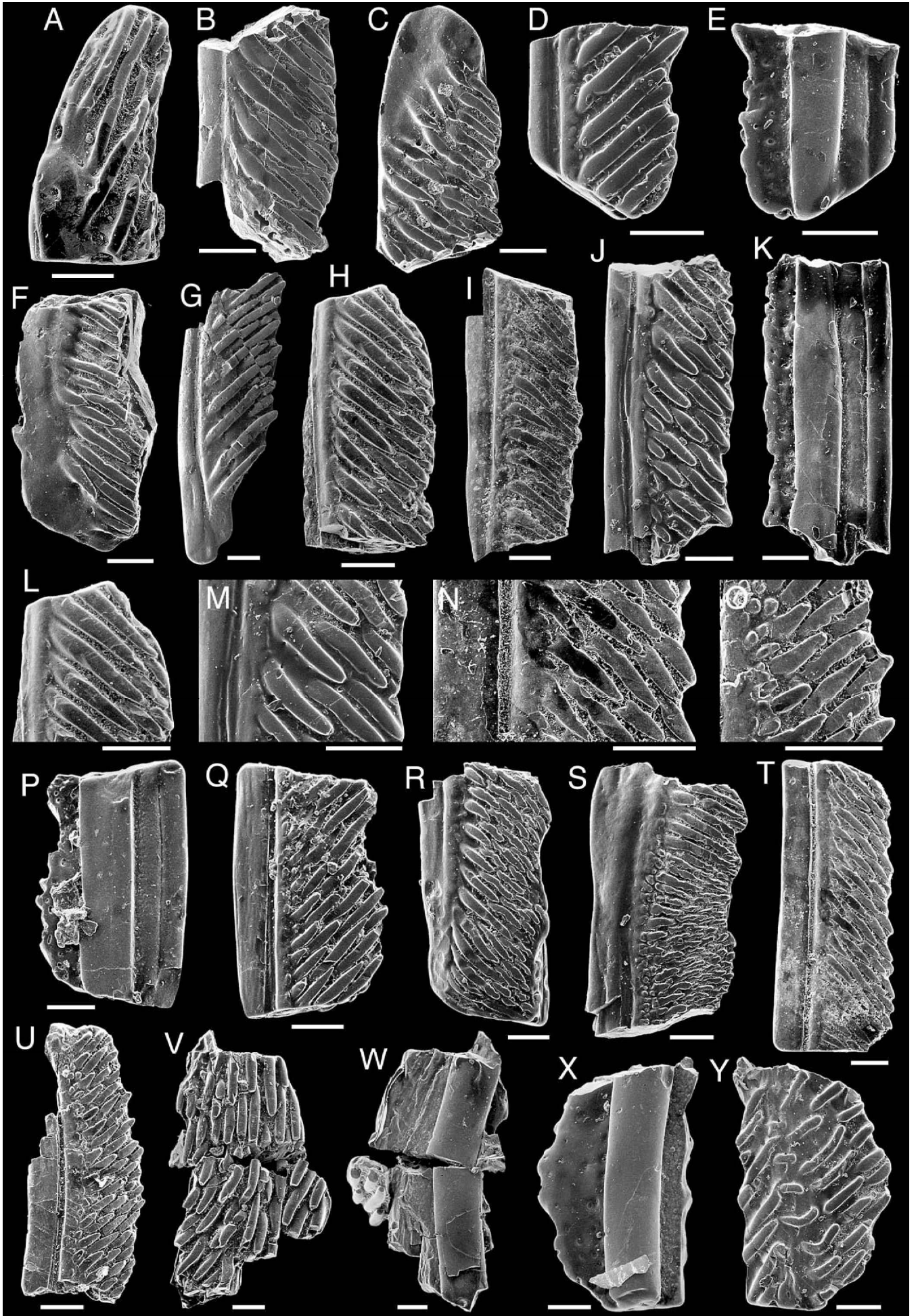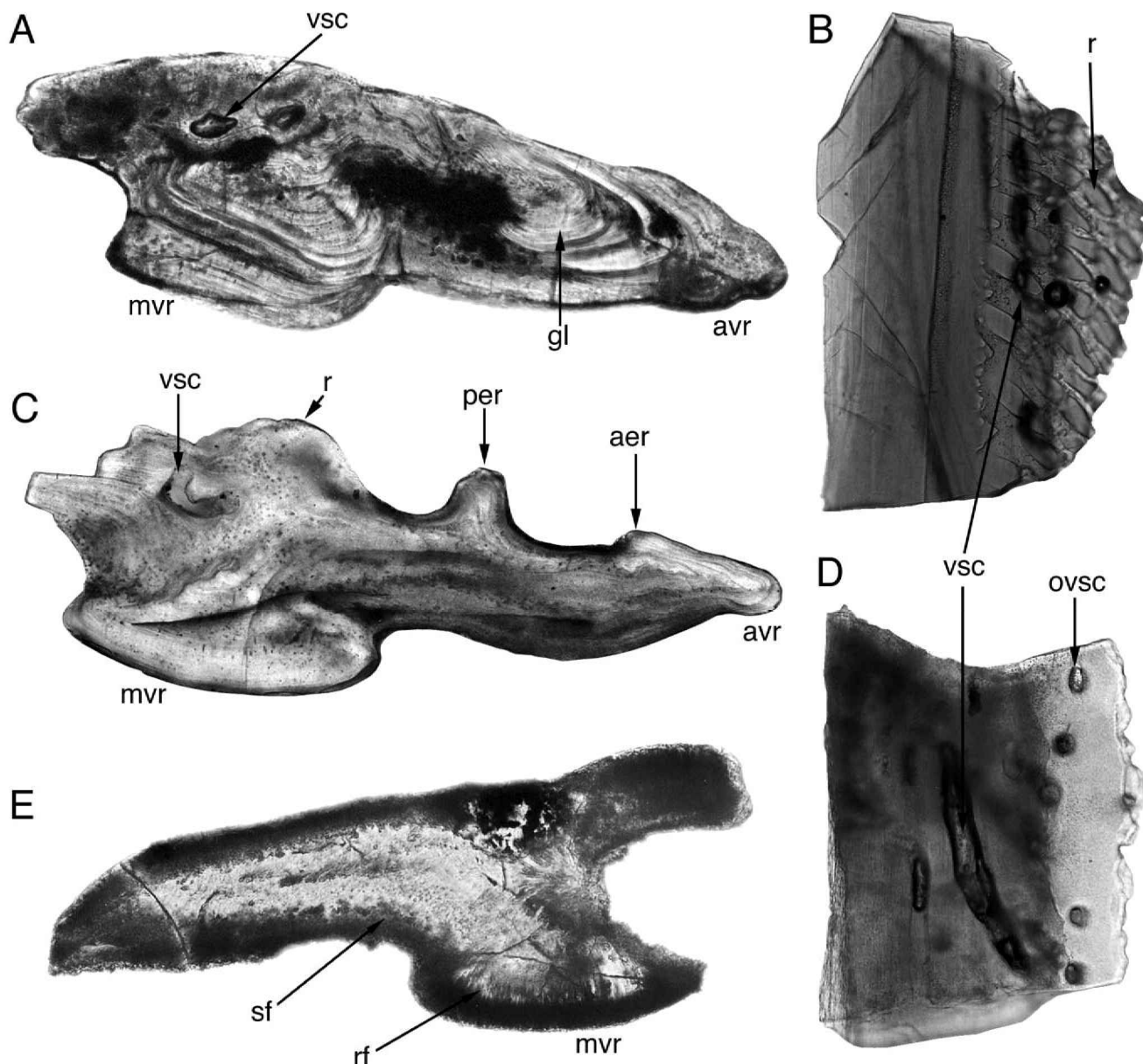
Figure 44 Histology of *Septentrionia* gen. nov. lateral scales. (A–B) *Septentrionia lancifera* gen. et sp. nov.: (A) scale in vertical cross-section, NHM P65666, ×162; (B) scale in external view, immersed in aniseed oil, NHM P65667, ×56; (C–D) *Septentrionia mucronata* gen. et sp. nov:. (C) scale in vertical cross-section, NRM P.9504, ×146; (D) scale in external view, immersed in aniseed oil, NRM P.9505, ×97. (E) *Septentrionia seducta* gen. et sp. nov. scale in vertical cross-section, MGUH VP 3546, ×221. NHM P65666 and NHM P65667 from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian. NRM P.9504, 9505 from Uddvide, Gotland, Sweden; Burgsvik Beds, late Ludlow, Late Silurian. MGUH VP 3546 from GGU sample 82738, Halls Grav, Hall Land, N Greenland; Chester Bjerg Formation, late Přídolí, Late Silurian.

Figure 43 *Septentrionia lancifera* gen. et sp. nov.: SEM photographs of fragments of disarticulated lateral scales and plates; all fragments of lateral scales in external view unless stated; scale bars 0·2 mm. (A) Type 1 sculpture, NHM P.65575; (B) type 1 sculpture, NHM P.65559; (C) type 1 sculpture, NHM P.65552;. (D, E) NHM P.65529; (D) type 1 sculpture; (E) visceral view; (F) type 1 sculpture, NHM P.65632; (G) type 1-2 sculpture, UALVP 44806; (H, L) NHM P.65560; (H) type 1-2 sculpture; (L) close up, type 1 sculpture; (I) type 2 sculpture; NHM P.65555; (J, K, M) NHM P.65628; (J) type 2 sculpture; (K) visceral view; (M) close up, type 2 sculpture; (N, T) holotype, NHM P.65550; (N) close up, type 3 sculpture; (T) type 3 sculpture; (O, U) NHM P.65551; (O) close up, type 3 sculpture; (U) type 3 sculpture; (P, Q) NHM P.65636; (P) visceral view; (Q) type 3 sculpture; (R) type 1-3 sculpture, NHM P.65638; (S) type 1-3 sculpture, NHM P.65635; (V, W) plate, NHM P.65623; (W) visceral view; (X, Y) plate, NHM P.65624; (X) visceral view. All NHM specimens from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian. UALVP 44806 from Read Bay southern section, level 61·5 m talus, Cornwallis Island, Arctic Canada; Lochkovian, Early Devonian.

Septentrionia mucronata? gen. et sp. nov.
(Fig. 45J)
2002 Birkeniida gen. et sp. K, Chekhovich *et al*.

Description. Scales of this type are found in sample 85-042 from a section on the right bank of the Ufa River, downstream from the mouth of the Tabuska River, the Central Urals, from the Tabuska Beds, Ludlow, Late Silurian. They are similar to *S. mucronata* gen. et sp. nov. in their arrangement of ridges, but the ridges are rounded in cross-section and have fine longitudinal striae. The overlapped area also lacks the ribs of *S. mucronata*.

Remarks. Tubercles anterior to the ridges in *S. mucronata* are arranged on a rib (Fig. 45F–H), while in *S. mucronata*?

they occur on the surface of the overlapped area (Fig. 45J), as they are in a few specimens of *S. lancifera* (Fig. 43O, S, U).

Septentrionia dissimilis gen. et sp. nov.
(Fig. 46A–C)
1998 Birkeniida gen. et sp. 3, Märss *et al*. pp. 58–9, fig. 2, partim.

Derivation of name. From the Latin word *dissimilis*, meaning different, because the sculpture is different from the European species of *Septentrionia*.

Holotype. Trunk scale fragment UALVP 44628 from sample at 371·0 m, section BH-2, Baillie-Hamilton Island, Arctic
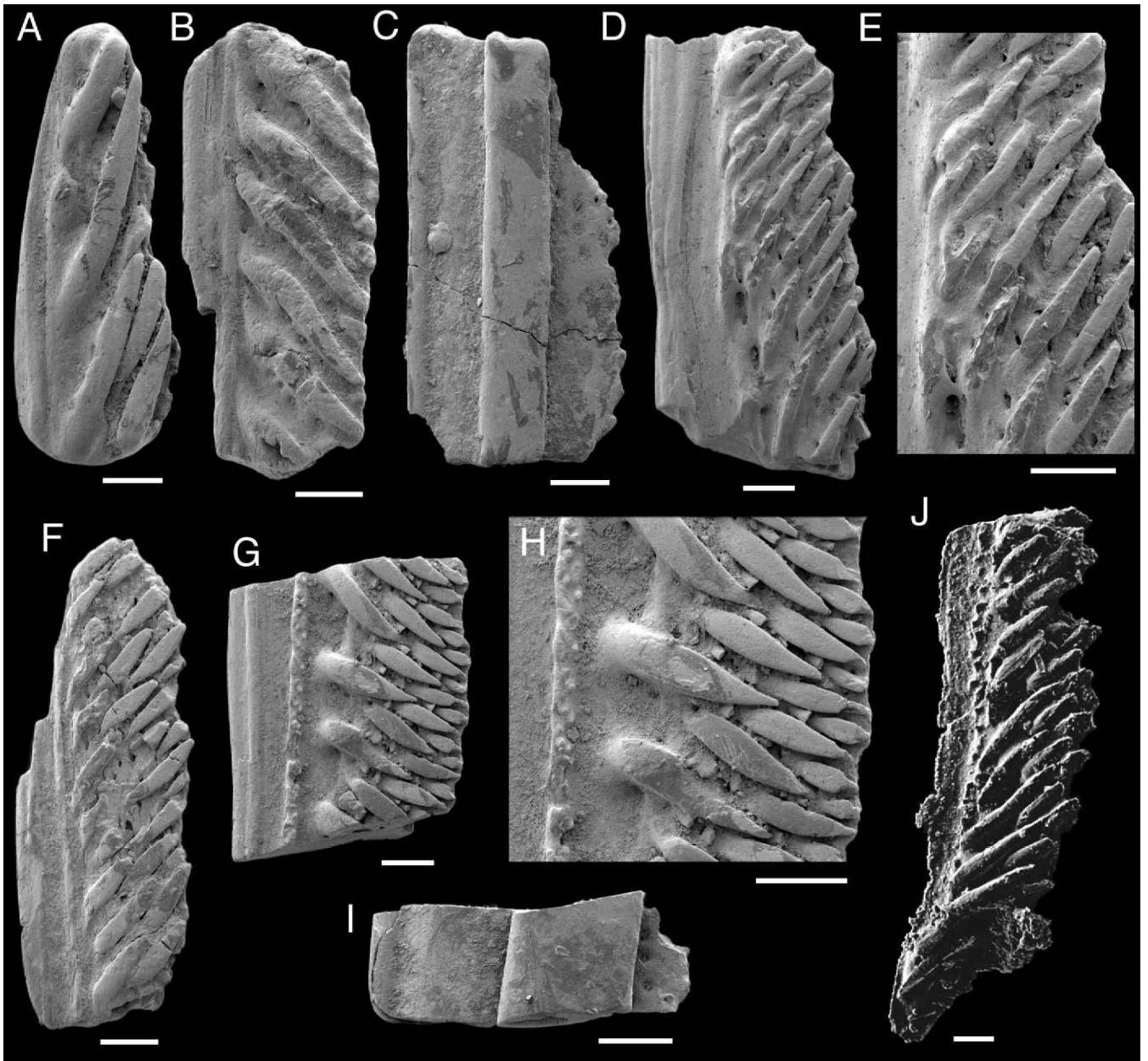
Figure 45 *Septentrionia* gen. nov.: SEM photographs of disarticulated lateral scale fragments in external view unless stated; scale bars 0·2 mm. (A–I) *Septentrionia mucronata* gen. et sp. nov.: (A) NRM P.9506; (B) NRM P.9507; (C) visceral view, NRM P.9508; (D) NRM P.9509; (E) NRM P.9509; (F) NRM P.9510; (G, H) holotype, NRM P.9511; (H) close up; (I) visceral view, NRM P.9512. (J) *Septentrionia mucronata*? gen. et sp. nov., GI Pi 7724. NRM P.9506–9510 from Uddvide, Gotland, Sweden; Burgsvik Beds, late Ludlow, Late Silurian. NMR P.9511, 9512 from Hoburgen 2/3 Gotland, Sweden; Hamra Beds, late Ludlow, Late Silurian. GI Pi 7724 from sample 85–042, section on the right bank of the Ufa River, downstream from the mouth of the Tabuska River, Central Urals, Russia; Tabuska Beds, Ludlow, Late Silurian.
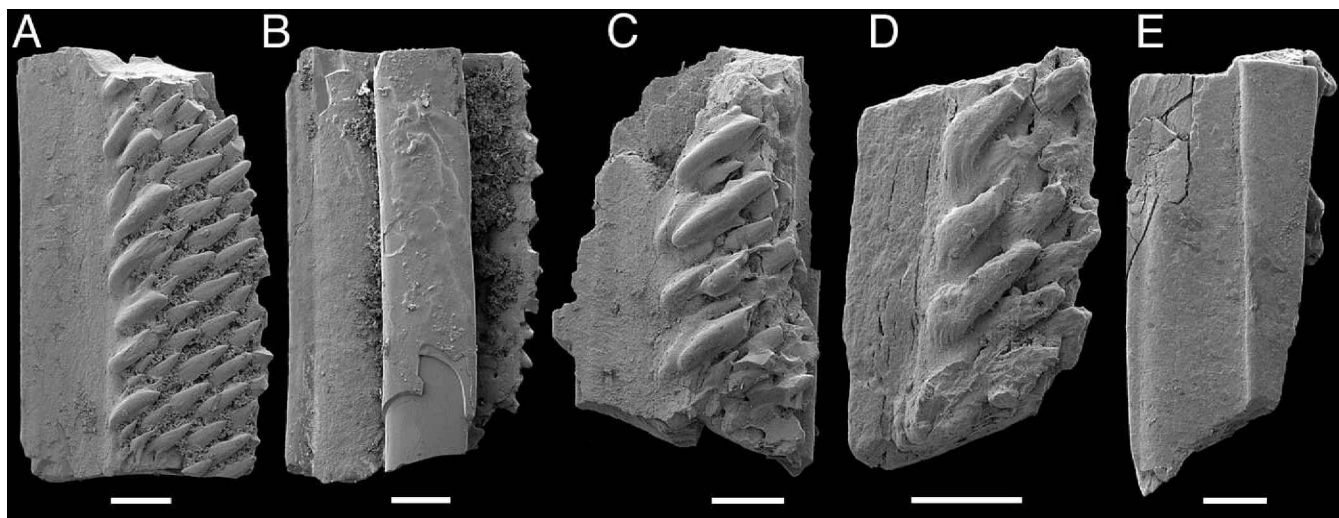
Figure 46 *Septentrionia dissimilis* gen. et sp. nov.: SEM photographs of disarticulated scale fragments in external view unless stated; scale bars 0·2 mm. (A–B) Holotype, UALVP 44628; (B) visceral view; (C) UALVP 44627. *Septentrionia dissimilis?* gen. et sp. nov.: (D) UALVP 44625; (E) UALVP 44988. All specimens on this figure from Baillie-Hamilton Island section 2, Arctic Canada, Ludlow, Late Silurian. UALVP 44627 and 44628 from 371·0 m; UALVP 44625, 270·5 m; UALVP 44988 from 249·0 m.

Canada; Cape Phillips Formation, late Ludlow, Late Silurian, (Fig. 46A, B).

Material. Four broken scales from horizon as holotype.

Diagnosis. Scales with similarly sized short striated ridges, rounded in cross-section; overlapped area wide and completely smooth.

Description. The scales have a wide, smooth overlapped area and an anterior external rib as an indistinct rim. Most parts of the external surface are covered by short ridges, rounded in cross-section and finely striated longitudinally. The striae converge to the posterior. The comparatively smooth convex ridges in the first row have blunt posterior ends at a slightly higher level than succeeding ridges, which all point to the posterior. The short ridges are all of a similar size. Sometimes, larger anteriormost ridges appear partly to cover some of the smaller striated ridges (Fig. 46A, C). Between the ridges rare openings of the vascular canals are visible, but further studies of the internal structure were not possible because of the few specimens available.

Remarks. *S. dissimilis* differs from all other species of this genus because it has striated convex ridges and a smooth, wide, anterior overlapped area. Some ridges appear finely striated (Fig. 46A) and reminiscent of *S. mucronata?* from the Central Urals. However, *S. mucronata?* has flattened ridges and *S. dissimilis* has rounded ridges. *S. lancifera* is similar to *S. dissimilis* in having the sculpture developed at a slightly higher level, but it also has a well-developed groove in the overlapped area and the ridges are much more variable in length.

Septentrionia dissimilis? gen. et sp. nov.
(Fig. 46D, E)
1998 Birkeniida gen. et sp. 3, Märss *et al.*, p. 58, fig. 2, partim.

Remarks. In the Baillie-Hamilton 2 section, Arctic Canada, at levels 249·0 m and 270·5 m (early Ludlow), three scales have been found which have a relatively smooth anterior overlapped area. However, this area is narrower than in *S. dissimilis*, and the ridges have a flat surface, with no striations visible. Pores of vascular canals are slightly larger than in *S. dissimilis*. Until more material is found, we prefer to leave this taxon as *S. dissimilis?*.

Septentrionia seducta gen. et sp. nov.
(Figs 44E, 47)
1999b Anaspida indet.; Blom, p. 50, fig. 25.

Derivation of name. From the Latin word *seductus*, meaning remote or apart, referring to the widely spaced external ridges of the sculpture.

Holotype. Trunk scale MGUH VP 3541 from GGU sample 319264 from the Monument, Hall Land, N Greenland; Chester Bjerg Formation, early Lochkovian, Early Devonian (Fig. 47A, D).

Material. About 50 fragments (MGUH) of variable preservation and size from GGU samples 82734, 82736, 82738 and 298937 from the Halls Grav locality and GGU samples 319264 from the Monument, Hall Land, N Greenland; Chester Bjerg Formation, Late Silurian–Early Devonian (Přídolí–Lochkovian).

Diagnosis. Scales and plates with extremely widely spaced elongate ridges, and small interstitial, rounded tubercles.

Description. Only small fragments of scales and plates are preserved, with a maximum preserved size of about 1·5 mm in length in some and 1 mm in width in others (Fig. 47A). They are characterised by having an external sculpture of coarse elongated ridges, some of which are elongate drop-shaped and clearly separated from each other. Some specimens also have small, round tubercles between the larger elongate ridges (Fig. 47D). Rounded pores occur between the ridges and the tubercles on the slightly elevated external main scale area in the middle part of the scale. This elevated area merges with the slightly concave anterior overlapped area which is almost totally smooth with rare wide discontinuous grooves (Fig. 47C). Some scales have a smoother transition from the anterior overlapped area to the posterior main scale area. This type lacks the pores on the upper surface seen in the first type, but the sculpture is otherwise almost identical.

Scales have one large, smooth, longitudinal medial visceral rib which is almost square in cross-section (Fig. 47B). The rib becomes wider and lower before merging with the main visceral surface at the dorsal or ventral termination. At the opposite termination the rib becomes narrower, forming the main part of the articulation process. A wide and low
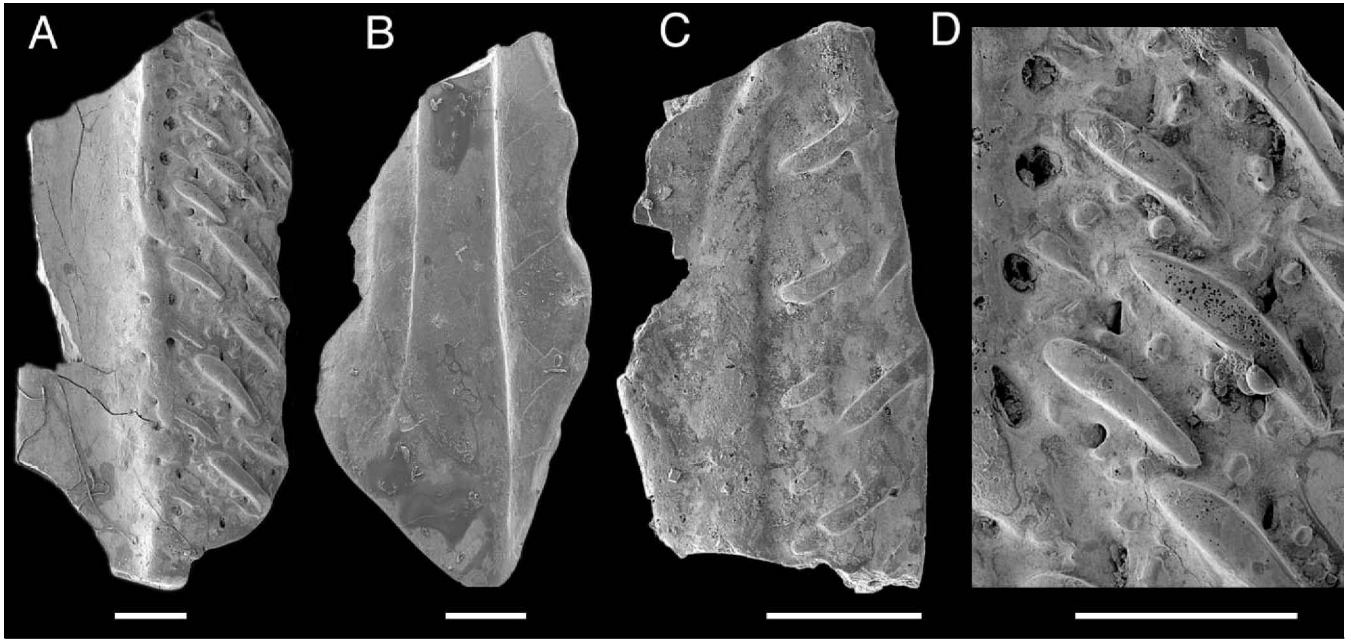
Figure 47 *Septentrionia seducta* gen. et sp. nov.: SEM photographs of fragments of disarticulated lateral scales in external view unless stated; scale bars 0·2 mm. (A, D) holotype, MGUH VP 3541; (D) close up; (B) visceral view, MGUH VP 3543; (C) MGUH VP 3544. MGUH VP 3541, 3543 from GGU sample 319264, Monument, Hall Land, N Greenland; Chester Bjerg Formation, lower Lochkovian, Early Devonian. MGUH VP 3544 from GGU sample 82736, Halls Grav, Hall Land, N Greenland; Chester Bjerg Formation, late Přídolí, Late Silurian.

longitudinal medial rib may be developed in the junction between these two areas (Fig. 47C). Due to poor preservation and the lack of material, only remnants of tubules of Sharpey's fibres and radial fibres in the basal medial rib have been seen (Fig. 44E).

Distribution. Přídolí–Lochkovian: Hall Land, N Greenland.

Genus *Liivilepis* gen. nov.

Derivation of name. After Liivi Bay where Ruhnu Island, Estonia is situated—the type species is from a borehole drilled on Ruhnu Island— and the Greek word *lepis,* meaning scale.

Type species. *Liivilepis curvata* gen. et sp. nov.

Diagnosis. Anterior overlapped area smooth or with very narrow rib at anterior margin; sculpture of tubercles and ridges, straight to slightly curved, short ridges that are broader in the first row than those situated posteriorly; tubercles and ridges do not form regular anterior to posterior rows; external surface around tubercles, and visceral surface of both sides of medial visceral rib pierced by numerous openings of vascular canals.

Liivilepis curvata gen. et sp. nov.
(Figs 48A–K, 49)

1958　Anaspidae gen. et sp. indet.; Gross, pp. 25–30, Abb. 1, 2; pl. 1, 2.
1986　Birkeniida sp. E; Märss, pp. 54, 88, pl. 26, fig. 12; pl. 27, fig. 8.

Derivation of name. From the Latin word *curvatus,* meaning curved, after curved ridges of the scales.

Holotype. Trunk scale fragment Pi 6197 from Ruhnu Borehole, core at depth 172·6 m, Ruhnu Island, Estonia; Ohesaare Stage, Přídolí, Late Silurian (Fig. 48A, B).

Material. Six broken scales (GI) from Ruhnu Borehole, core at depth 172·6 m, Ruhnu Island, Estonia and Lahetaguse

Borehole, core depth 14·0–14·5 m, Saaremaa, Estonia; Ohesaare Stage, Přídolí, Late Silurian. 14 scales (NRM) from Ramsåsa, Skåne, Sweden; Öved Sandstone Formation, early Přídolí, Late Silurian. Two scales (GI) from the right bank of the Ufa River, downstream from the mouth of the Tabuska River, Central Urals; Tabuska Beds, Ludlow, Late Silurian. A few scales (NRM) from Hoburgen 3, Gotland, Sweden; Hamra Beds, late Ludlow, Late Silurian.

Diagnosis. As for the genus.

Description. The scales have an overlapped area which is usually smooth and flat with a narrow rib at the anterior margin. The main area of scale is at a slightly higher level with a sculpture of tubercles and ridges of various sizes. The spiny ridges in the anteriormost row are wider than the following ones; they may be of the same length but are usually slightly longer. Occasional small ridgelets or tubercles can be found between the ridges (Fig. 48G, H). The ridges have smooth surfaces, tapered to the posterior and are either straight or usually slightly curved. The inter-ridge area is narrower than the width of ridges themselves and perforated by numerous pores of vascular canals. On the visceral side of the scales, pores are visible to the posterior of a well-developed visceral medial rib, and a granular sculpture occurs in front of it. Thin scales have numerous elliptical pores, while thicker and more robust scales have fewer, circular and smaller openings. There is a weakly developed, but distinct, vascular canal system in the middle and posterior part of the scale (Fig. 49).

Remarks. Smooth, curved ridges on the main scale area are characteristic for *L. curvata*. Another sculpture type with less variation in ridge size found in the Tahula Beds of the Kuressaare Stage in the Lahetaguse Borehole, core at depth 14·0–14·5 m, and in the Öved Sandstone Formation in Ramsåsa, Skåne, is included in *L. curvata* because it has curved ridges as well. This type is represented by fragments from both the end part and the medial part (Fig. 48J–K). However, in other septentrioniids, these types of scale generally have longer

ridges at the ends of scales. The well-developed medial visceral rib has meant that most of the material recovered (e.g. material from calcareous sandstone of Ramsåsa, Skåne) is from the central part of the scale. This could account for the relative scarcity of head plates or material with this type of sculpture. Thin scales with numerous elliptical pores are probably juvenile, while thicker, more robust scales with fewer, circular and smaller openings represent adult scales.

Distribution. Late Ludlow: Central Urals; Gotland and erratic boulders of the North German Lowland. Přídolí: Skåne, Sweden, and Ruhnu and Saaremaa islands, Estonia.

Liivilepis curvata? gen. et sp. nov.
(Fig. 48L, M)
1986 Birkeniida sp. E; Märss, pp. 54, 88, pl. 26, fig. 11.

Remarks. Material from the same horizon as the type specimen has distinctive curved ridges, but it is tentatively included in *L. curvata*? because it has a very wide overlapped area with wide anterior external rib.

Genus *Spokoinolepis* gen. nov.

Derivation of name. After the Spokoinaya River on October Revolution Island, Severnaya Zemlya Archipelago, Russia, and the Greek word *lepis,* meaning scale.

Type species. *Spokoinolepis alternans* gen. et sp. nov.

Diagnosis. Sculpture of wide and elongate ridges surrounded on both sides by short and narrow weakly developed ridges; medial visceral rib well developed; microstructure of compact lamellar aspidine.

Spokoinolepis alternans gen. et sp. nov.
(Fig. 50)
2002 Birkeniida sp. J, Märss.

Derivation of name. From the Latin word *alternans*, meaning alternating; because of the alternating sculpture of large and small ridges on the scales.

Holotype. Trunk scale fragment GI Pi 7573 from the upper part of Ust-Spokoinaya Formation, Spokoinaya River, October Revolution Island, Severnaya Zemlya Archipelago, Russia; late Ludlow, Late Silurian (Fig. 50).

Material. Five broken scales (LIG) in samples MF 157-3, Spokoinaya River, upper part of Ust-Spokoinaya Formation, late Ludlow, Late Silurian and MF 157-2, Spokoinaya River, Krasnaya Bukhta Formation, Přídolí, Late Silurian.

Diagnosis. As for the genus.

Description. Fragments of scales, reddish in colour, with very wide, elongate ridges that start almost at the anterior margin and run obliquely almost to the posterior margin. Small narrow, weakly developed ridges occur on both sides of these dominant ridges, with the inter-ridge area often as wide as the ridges. The medial visceral rib is well developed. On the broken edges of three scale fragments aspidine lamellae are present, but no vascular canals are visible. A few fine pores of the vascular canals occur on both visceral and external surfaces of the scales.

Remarks. *S. alternans* differs in general from other species within Septentrioniidae by the robust nature of the scales. The wide, elongated ridges and the surrounding weakly developed ridges show a larger relative size variation than in, for instance, *Liivilepis*. The apparent lack of an overlapping area is possibly a preservational feature.

Distribution. Late Ludlow–Přídolí: Severnaya Zemlya Archipelago, Arctic Russia.

Genus *Manbrookia* gen. nov.

Derivation of name. After Man Brook, near Trimpley, Worcestershire, U.K.

Type species. *Manbrookia asperella* gen. et sp. nov.

Diagnosis. Wide, overlapping area of scales smooth or with one to two indistinct, discontinuous anterior ribs; main area of scale with or without short ridges; small tubercles irregular in shape and variable in size and density cover main area of scale; well-developed medial visceral rib; microstructure of compact aspidine layers.

Manbrookia asperella gen. et sp. nov.
(Figs 51, 52)

Derivation of name. From the Latin word *asper*, meaning rough, referring to the knobbly nature of the sculpture.

Holotype. Trunk scale fragment NHM P65617 from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian (Fig. 51A, B, G).

Material. More than 100 broken scales of type 1 and 2, and a few dorsal ridge scales (NRM) from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian.

Diagnosis. As for the genus.

Description. Scale type 1 (Fig. 51A–D, G, H) has a wide anterior overlapped area (0·2–0·32 mm) that can be smooth or with one to two indistinct and discontinuous ribs and grooves (Fig. 51C). The anterior margin is straight and rarely irregular. The sculpture of the main area consists of well-spaced and parallel ridges which are at 45 degrees to but do not reach the posterior margin (Fig. 51A, C). Usually the ridges are very well developed but they can be indistinct or present over only part of the scale (Fig. 51J, M). Fine tubercles fill the inter-ridge areas and are of irregular shape, density and size (Fig. 51A, C, G, H). Pores of vascular canals are visible in the inter-ridge areas (Fig. 51G). The visceral surface of scales has a well-developed medial rib (Fig. 51B, D) and the area just to the anterior of the rib is smooth or finely granular. A thin rib is developed along the anterior margin (Fig. 51D).

Very narrow scales (Fig. 51E, F, I) have the same general sculpture as for type 1 scales but with no overlapping area. The main area is convex over the well-developed medial visceral rib (Fig. 51F). Pores of vascular canals occur next to the ribs (Fig. 51I).

Scale type 2 has an anterior overlapping area generally narrower (0·06–0·20 mm) than for type 1 scales, and with one distinct rib and up to two more indistinct and discontinuous ribs (Fig. 51L, O, Q, T). The anterior margin is convex or rarely concave. The sculpture of the main area has irregular granular tubercles circular to crescentic in outline that vary greatly in size and spacing (Fig. 51P, Q, T). These tubercles are less well developed toward the termination of scales (Fig. 51L). The visceral surface is almost the same as for type 1 scales, but no pores of vascular canals are visible (Fig. 51R, S).

The histology is of compact structure with rare vascular canals and distinct thin aspidine growth layers (Fig. 52).

Remarks. The scales of this taxon are similar to those of *B. elegans* in having tubercles. However, the tubercles on scales of *B. elegans* are of the same size and spaced equally, while in *M. asperella* they vary greatly in size and are often interspersed with well-developed ridges. Both type 1 and type 2 scales are included in the same species because they both possess the same granular sculpture. There is a definite size difference between the two types of scale with type 1 scales having a wider overlapping area and main area (Fig. 51). Some type 1
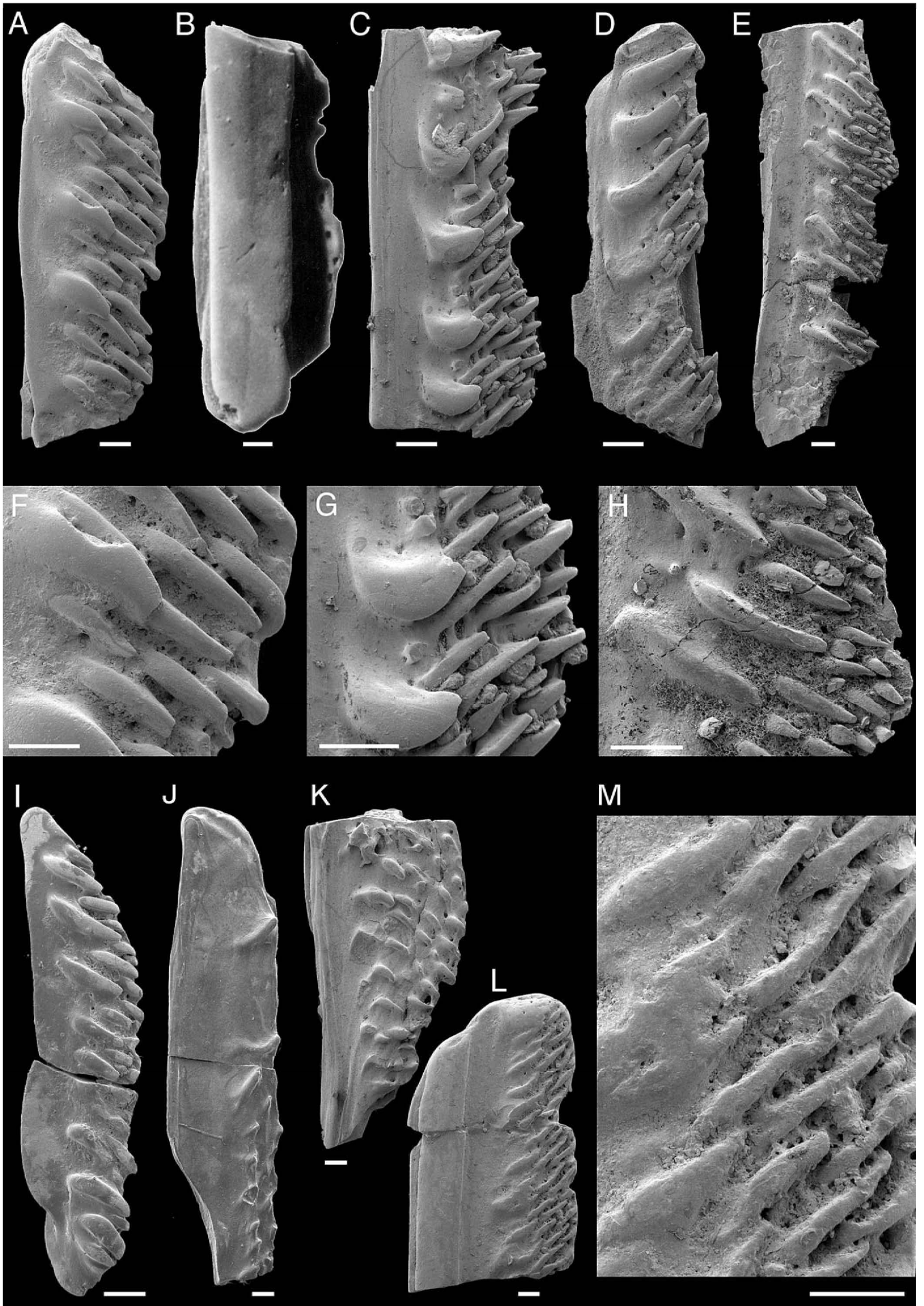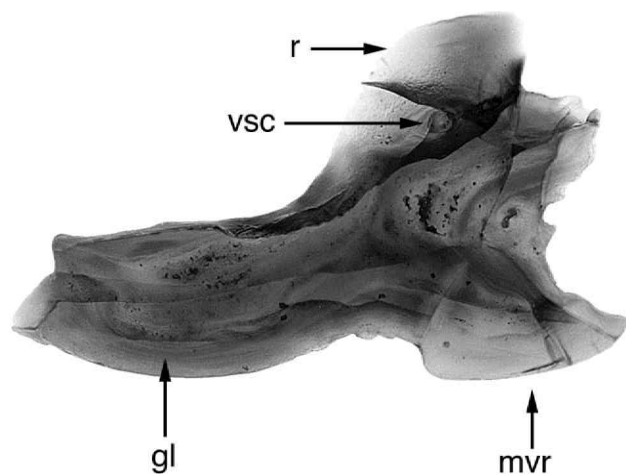
Figure 49 *Liivilepis curvata* gen. et sp. nov.: histology of scale GI Pi 7719; scale in vertical cross-section, ×83; specimen from Ruhnu-500 Borehole, core depth 172·6 m, Ruhnu Island, Saaremaa; Ohesaare Stage, Přídolí, Late Silurian.

Figure 50 *Spokoinolepis alternans* gen. et sp. nov.: SEM photographs of holotype lateral scale fragment GI Pi 7573; scale bar 0·2 mm. (A) external view; (B) visceral view. Specimen from Spokoinaya River, October Revolution Island, Severnaya Zemlya Archipelago, Arctic Russia; upper part of Ust-Spokoinaya Formation, Late Ludlow, Late Silurian.

scales could also be considered as intermediate between the two varieties, as the ridges are only poorly developed (Figs 51J, N).

Distribution. Late Přídolí: Worcestershire, U.K.

Family indet.
Genus *Ruhnulepis* gen. nov.

Derivation of name. After Ruhnu Island in western Estonia, and the Greek word *lepis,* meaning scale.

Type species. Ruhnulepis *longicostata* gen. et sp. nov.

Diagnosis. Scale with uniform, long, narrow and subparallel sharp-crested ridges; flat overlapped area with small tubercles; anterior visceral rib much wider than the medial rib.

Remarks. This new genus has a very distinct external and visceral scale sculpture, but it still shows some similarities with *Birkenia*, *Pterygolepis* and *Rhyncholepis* in having round anterior tubercles and regular ridges on the main scale area, which in *Ruhnulepis* gen. nov. are modified as long narrow uniform subparallel ridges. This type of sculpture is not found in any of the other known groups, so a new family might be considered when more material is available for comparison.

Ruhnulepis longicostata gen. et sp. nov.
(Fig. 53)
1986 Birkeniida sp. B; Märss, pp. 53, 88, pl. 26, fig. 2a,b.

Derivation of name. From the Latin words *longus*, meaning long, and *costatus* meaning bearing a rib, because of long ridges that cover the main scale area.

Holotype. Lateral scale GI Pi 6182 from Ruhnu-500 Borehole, core at depth 163·2 m, Ruhnu Island, Estonia; Ohesaare Stage, Přídolí, Late Silurian (Fig. 53).

Material. Only one well-preserved scale in three parts (the holotype).

Diagnosis. As for the genus.

Description. This single scale is 4·3 mm long and 1·1 mm wide, and very fragile (Fig. 53). The narrow anterior overlapped area has very fine, rounded, tubercles. To the posterior of the tubercles, narrow, smooth and sharp-crested transparent ridges, of regular width, extend obliquely across the whole of the main area of the scale. Some of the ridges extend only part way to the posterior. Those ridges that reach the posterior margin form cusps on the undulatory edge. Viscerally, two ribs of variable width are developed. The anterior rib is much wider than the posterior rib, which becomes narrower and converges with the anterior rib at the dorsal and ventral ends of the scale (Fig. 53B). A few, tiny pores of vascular canals are visible on the external surface in the middle part of the scale, but not on the visceral surface.
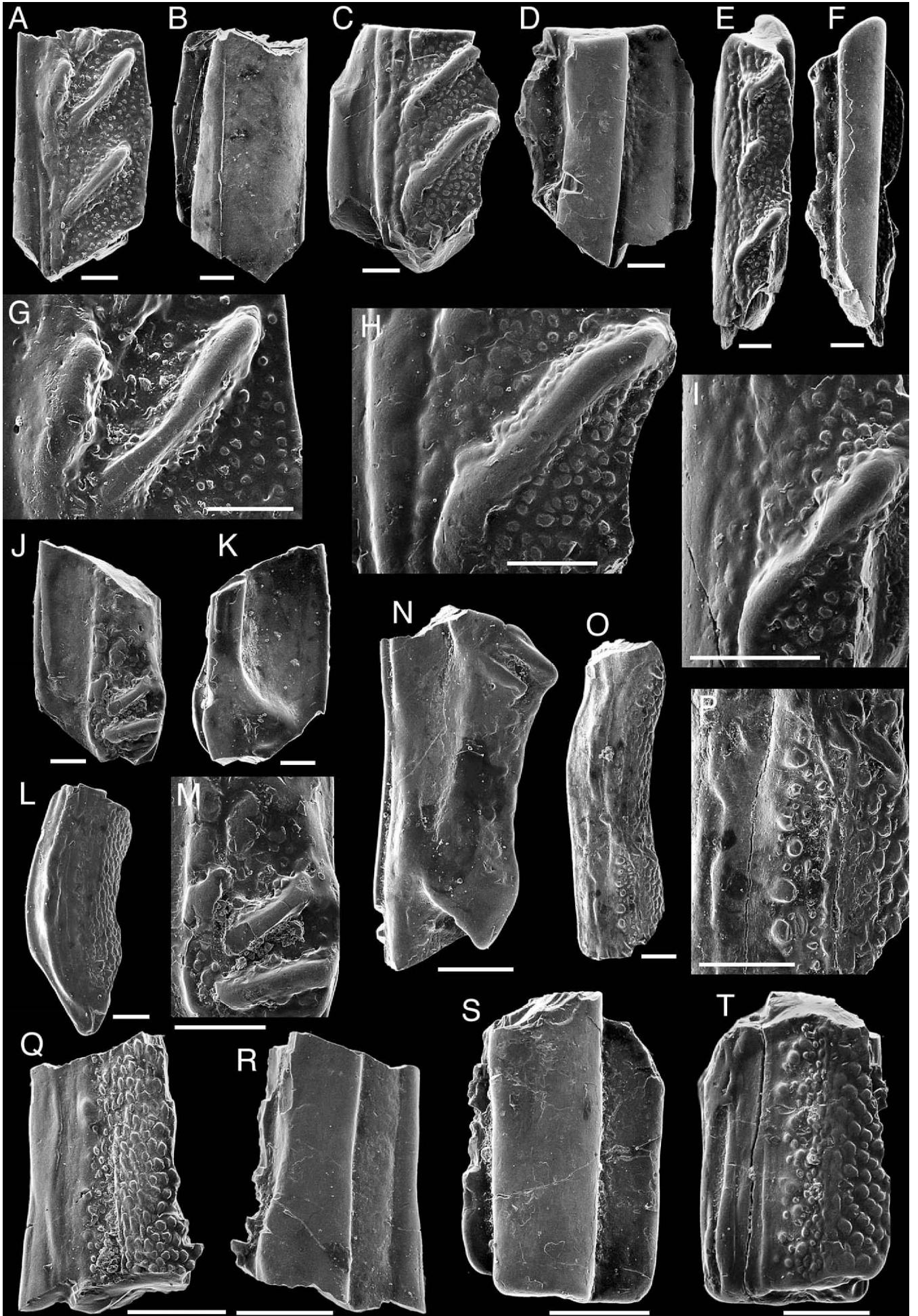
The single scale has not been examined histologically. The tiny holes on the surface might belong to the vascular canal system or be a preservational feature.

Remarks. *R. longicostata* differs from all other birkeniids in having nearly parallel, uniform, long narrow ridges extending over the whole scale. It is also unusual to have an anterior visceral rib much wider than the medial rib.
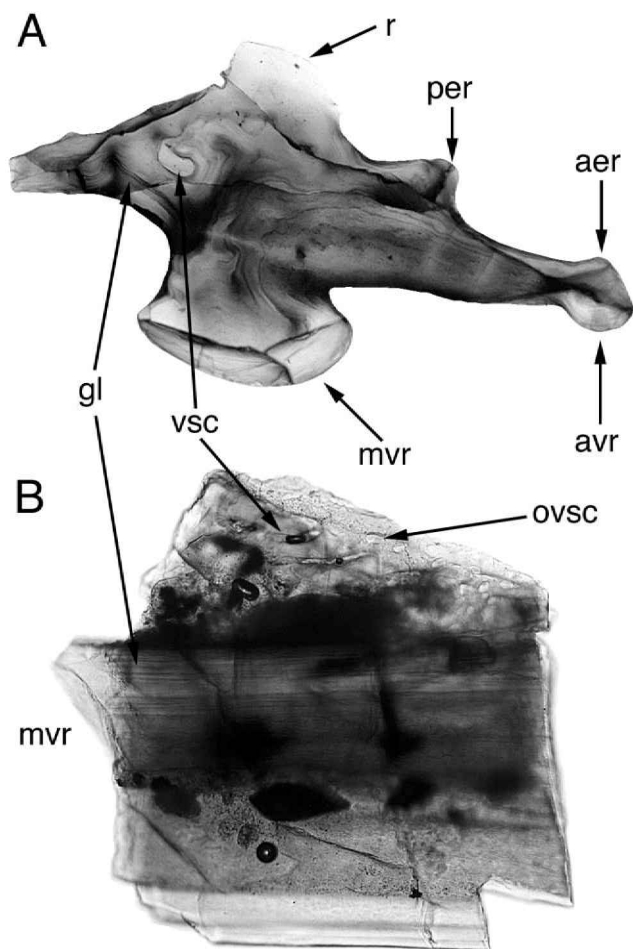
Distribution. Přídolí: Ruhnu Island, Estonia.

Figure 48 *Liivilepis* gen. nov.: SEM photographs of fragments of disarticulated lateral scales in external view unless stated; scale bars 0·2 mm. (A–K) *Liivilepis curvata* gen. et sp. nov.: (A, B, F) holotype, GI Pi 6197; (B) visceral view; (F) close up; (C, G) NRM P.9513; (G) close up; (D) NRM P.9514; (E, H) GI Pi 7717; (H) close up; (I) NRM P.9515; (J) GI Pi 7718; (K) NRM P.9516. (L, M) *Liivilepis curvata*? gen. et sp. nov.: (L, M) GI Pi 6181, (M) close up. GI Pi 6181 and 6197 from Ruhnu Borehole, core depth 172·6 m, Ruhnu Island, Estonia; Ohesaare Stage, Přídolí, Late Silurian. NMR P.9513 and 9516 from Ramsåsa, Skåne, Sweden; Öved Sandstone Formation, early Přídolí, Late Silurian. NMR P.9514 and 9515 from Hoburgen 3, Gotland, Sweden; Hamra Beds, late Ludlow, Late Silurian. GI Pi 7718 from Lahetaguse Borehole, core depth 14·0–14·5 m, Saaremaa, Estonia; Kuressaare Stage, late Ludlow, Late Silurian. GI Pi 7717 from right bank of the Ufa River, downstream from the mouth of the Tabuska River, Central Urals, Russia; Tabuska Beds, Ludlow, Late Silurian.

Figure 52 *Manbrookia asperella* gen. et sp. nov.: histology of scales. (A) Scale in vertical cross-section, NHM P65668, ×107; (B) scale in external view, immersed in aniseed oil, NHM P65669, ×74; both specimens from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian.

- Family Birkeniidae Traquair, 1899 includes *Birkenia elegans*, *B. robusta* sp. nov. and *Hoburgilepis papillata* gen. et sp. nov.
- Pterygolepididae Kiær 1924 is a monospecific family, containing *Pterygolepis nitida*. Pharyngolepididae Kiær 1924 contains *Pharyngolepis oblonga* and *Pharyngolepis? heintzi* Ritchie, 1964.
- Rhyncholepididae Kiær, 1924 includes *Rhyncholepis parvula*, *R. butriangula* sp. nov., *Silmalepis erinacea* gen. et sp. nov., *Vesikulepis funiforma* gen. et sp. nov., *Maurylepis lacrimans* gen. et sp. nov., and the revised *Schidiosteus mustelensis* Pander, 1856 and *Rytidolepis quenstedtii* Pander, 1856.
- Tahulalepididae fam. nov. is represented by *Tahulalepis elongituberculata* gen. et sp. nov. and the revised *T. kingi* (Woodward 1947).
- Septentrioniidae fam. nov. contains *Septentrionia lancifera* gen. et sp. nov., *S. mucronata* gen. et sp. nov., *S. dissimilis* gen. et sp. nov., *S. seducta* gen. et sp. nov., *Liivilepis curvata* gen. et sp. nov., *Spokoinolepis alternans* gen. et sp. nov. and *Manbrookia asperella* gen. et sp. nov.
- The position of *Ruhnulepis longicostata* gen. et sp. nov. is uncertain.
- Three distinct faunas with characteristic sculpture are defined: the Llandovery–early Wenlock *Birkenia* fauna, the late Wenlock–middle Ludlow Rhyncholepididae fauna and the late Ludlow–early Lochkovian Septentrioniidae fauna.
- Three main types of histology are identified: compact scales without vascular canal system, including genera such as *Birkenia*, *Pterygolepis*, *Hoburgilepis*; well-developed vascular canal system found in *Rhyncholepis*, *Silmalepis*, *Vesikulepis* *Schidiosteus* and *Rytidolepis*; weakly developed vascular canal system as seen in *Septentrionia*, *Tahulalepis*, *Liivilepis* and *Manbrookia*.
- Biostratigraphy of birkeniid anaspids has been treated; they range from late Llandovery (Early Silurian) up to the Lochkovian (Early Devonian).
- Their correlative value is evaluated: most useful for interregional correlation are *Birkenia elegans* (late Llandovery–early Wenlock), *Septentrionia lancifera* (late Přídolí), *Tahulalepis* (late Ludlow–early Přídolí) and *Schidiosteus mustelensis* (late Wenlock–late Ludlow).

6. Conclusions

- Birkeniid anaspids from the Baltic Sea area (Estonia, Latvia and Gotland, Sweden), Scandinavia (Ringerike, Norway and Skåne, Sweden), British Isles, N Greenland, Arctic Canada, Arctic Russia, northwestern Canada and the Central Urals of Russia have been described.
- *Birkenia elegans* Traquair, 1898 from Scotland and articulated specimens of *Rhyncholepis parvula* Kiær, 1911, *Pterygolepis nitida* (Kiær, 1911) and *Pharyngolepis oblonga* Kiær, 1911 from Norway clearly define four types of sculpture.
- The distinct sculpture of these four taxa is used to establish a taxonomy based on both articulated and disarticulated material, and includes 22 species (15 new), 16 genera (ten new) and six families (two new).

7. Acknowledgements

Figure 51 *Manbrookia asperella* gen. et sp. nov.: SEM photographs of fragments of disarticulated lateral and ridge scales; fragments of lateral scales in external view unless stated; scale bars 0·2 mm. (A, B, G) Holotype, type 1, NHM P65617; (B) visceral view; (G) close up; (C, D, H) type 1 NHM P65614; (H) close up; (D) visceral view; (E, F, I) ridge scale fragment, NHM P65615; (I) close up; (F) ridge scale fragment in visceral view; (J, K, M) transitional type, NHM P65618; (M) close up; (K) transitional type in visceral view; (L) type 2, NHM P65565; (N) transitional type, NHM P65564; (O, P) type 2 in visceral view, NHM P65561; (O) close up; (Q, R) type 2, NHM P65619; (R) type 2, visceral view; (S, T) type 2, visceral view, NHM P65620. All specimens from Man Brook, near Trimpley, Worcestershire, U.K.; late Přídolí, Late Silurian.
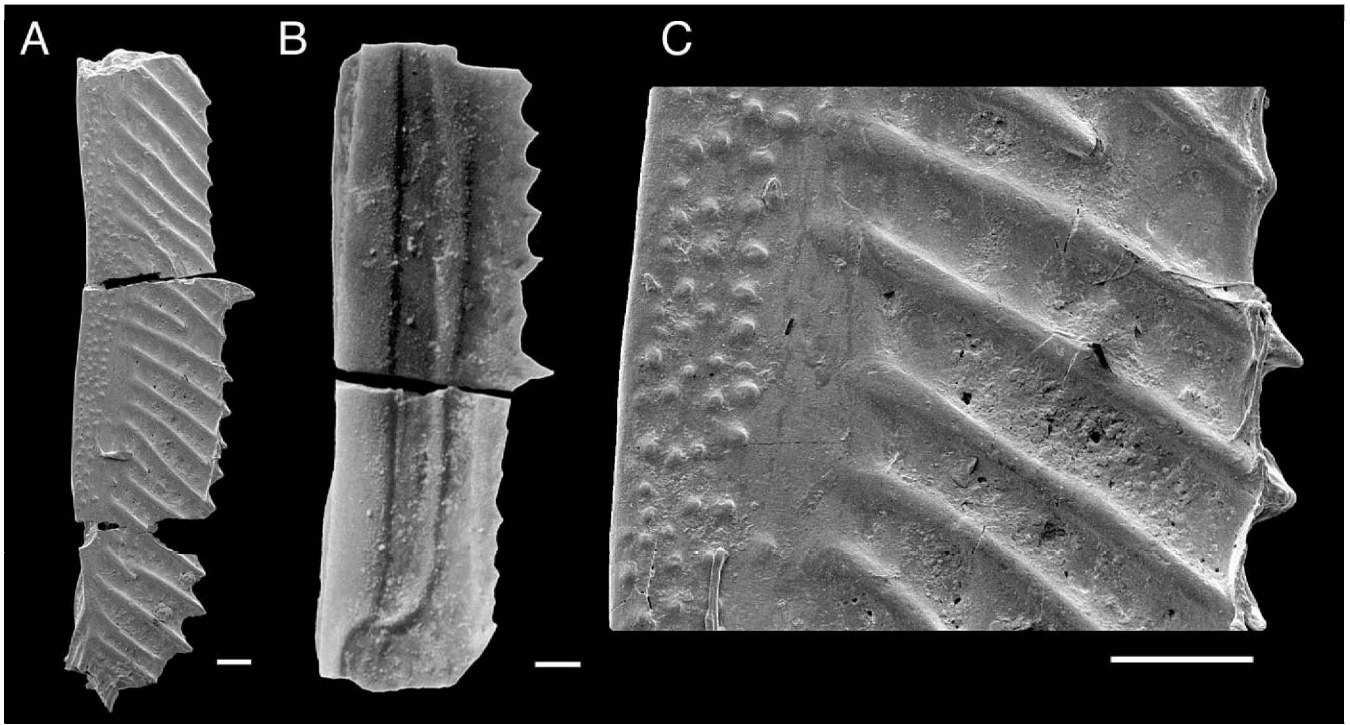
Figure 53 *Ruhnulepis longicostata* gen. et sp. nov.: SEM photographs of fragmentary lateral scale, holotype, GI Pi 6182; scale bars 0·2 mm. (A) External view; (B) visceral view; (C) close up, external view. Ruhnu-500 Borehole, core depth 163·2 m, Ruhnu Island, Estonia; Ohesaare Stage, Přídolí, Late Silurian.

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HENNING BLOM, Department of Earth Sciences, Historical Geology and Palaeontology, Norbyvägen 22, SE-752 36 Uppsala, Sweden. (Current address: Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.)
e-mail: H.Blom@nhm.ac.uk
TIIU MÄRSS, Institute of Geology at Tallinn Technical University, Estonia Avenue 7, Tallinn EE-0001, Estonia.
e-mail: marss@gi.ee
C. GILES MILLER, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.
e-mail: G.Miller@nhm.ac.uk