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Late Silurian–Early Devonian tessellated heterostracan *Oniscolepis* Pander, 1856 from the East Baltic and North Timan

Tiiu Märss[a] and Valentina Karatajūtė-Talimaa[b]

[a] Institute of Geology at Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia; Tiiu.Marss@gi.ee
[b] Institute of Geology and Geography of Lithuania, Ševčenkos Street 13, LT 03223 Vilnius, Lithuania; vtalimaa@takas.lt

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Abstract. Pander (1856, *Monographie der fossilen Fische der silurischen Systems der Russisch–Baltischen Gouvernements. Obersilurische Fische*. Buchdruckerei Kaiserlichen Akademie des Wissenschaften, St. Petersburg, 91 pp.) first established four *Oniscolepis* and three *Strosipherus* species, which later, except *O. magna*, were referred to *Oniscolepis dentata*, the name fixed by Rohon (1893, *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg*, **41**, 1–124) as the senior synonym. Using modern techniques, we redescribe and illustrate morphological and histological varieties of its platelets, tesserae, and scales. No articulated specimen of *O. dentata* has ever been found. Fragments of head platelets, two branchial plates, an orbital plate (or tessera), and body ridge elements are described for the first time. The microstructure of scales of *O. dentata* specimens from the East Baltic and North Timan differs only slightly from that of scales from the type locality, Saaremaa Island, Ohesaare Cliff, which has fewer and finer dentine tubules and Sharpey's fibre tubules than the specimens from North Timan. *Oniscolepis* Pander and *Kallostrakon* Lankester are united into a new family Oniscolepididae fam. nov. with the type genus *Oniscolepis* Pander.

Key words: Silurian, Devonian, East Baltic, North Timan, Heterostraci, exoskeletal units.

INTRODUCTION

Oniscolepis (= *Strosipherus*) was introduced in the pioneer work of Pander (1856), but still only a few features of this taxon, such as the composition of the exoskeleton of two types of mesomeric elements (or units), tesserae and scales, and the histology of these elements, are known. Because of the complexity of the exoskeleton and variations in the ridged sculpture, the taxonomic content of the genus has been discussed since the first publication. Insufficient knowledge has hindered phylogenetic study of the group Heterostraci as a whole, so there has been uncertainty about its relationships with other tessellated heterostracans (e.g. with *Kallostrakon* Lankester) and its position in classifications.

The type locality for *Strosipherus* was indicated by Pander as Leo (present name Lõo), Saaremaa Island, Estonia. We have not succeeded to identify heterostracans either in Lõo Cliff or Kaugatuma Cliff (Kaugatuma Stage, Přidoli) situated nearby, although large samples of several kilograms of rock have been dissolved (for the list of vertebrate fossils found in outcrops see Märss 1986, fig. 26). In the rocks of these outcrops only rare acanthodian scales are present. As the acid dissolution method was not known at that time, it is highly improbable that Pander found *Strosipherus* on rock slabs from Lõo Cliff. Most likely Pander's specimens came from Ohesaare Cliff, which he gave as the locality for *Oniscolepis* species. However, in some drill cores (Kaavi-568, Kaavi-571, Sõrve-514, Ruhnu-500, and Kolka-54) rare specimens of this taxon do occur in the upper part of the Kaugatuma Stage. Stratigraphically *Oniscolepis dentata* ranges from Přidoli (Upper Silurian) to Lower Lochkovian (Lower Devonian), and so far it has been found in the East Baltic, North Timan (Fig. 1),

Fig. 1. Location of main study areas, East Baltic (1, Estonia; 2, Latvia; 3, Lithuania) and North Timan (Velikaya River).

and in the boulders of the North German Lowland (Gross 1961; Karatajūtė-Talimaa 1970; Märss 1986).

The aim of this publication is to redescribe and illustrate the microstructure and morphological variations of the exoskeleton elements of *O. dentata* and compare them with those of other tessellated agnathan taxa. The ontogenetic development of scales and tesserae is discussed. The material from the East Baltic is compared with that from North Timan.

HISTORICAL REVIEW

In his very detailed monograph of 1856 Pander distinguished four species of *Oniscolepis* in the Ohesaare locality, under the group name 'Ganoiden'. In his specimens isolated plates (herein called 'ridges'), covered with enamel, lie on the bony base of the scales. The shape of ridges from the middle or margins of scales is different. Pander (1856) also studied the microstructure of the exoskeletal elements of *Oniscolepis*. In his opinion all four species could belong to one taxon, whereas the scales possibly came from different parts of the body. Still, Pander considered the features of ridge margins, smooth or indented, and character of serration, the most important characteristics for establishing four *Oniscolepis* species.

Under 'Zähne' Pander (1856) described three *Strosipherus* species from the Leo locality (= Lõo), whose specimens carried isolated single ridges, and compared them with scales and teeth. He interpreted these elements as covering either a cartilaginous jaw or palate of a fish. For differentiation of his three species he again used the contour of ridge margins (whether and how these were structured) and the character of the upper surfaces of ridges (smooth or with a crest). He could not study the microstructure because of relatively poor preservation of the available material.

Rohon (1893) revised Upper Silurian fishes of Saaremaa, assigning *Oniscolepis* Pander in the family Pteraspidae, order Crossopterygii, subclass Ganoidei. He showed that *Oniscolepis magnus* should be included in *Tolypelepis* (*Tolypaspis*) *undulata* Pander and synonymized *Strosipherus* with *Oniscolepis*. He also corrected the gender of species names according to the generic name (*Oniscolepis*, gender feminine), chose *O. dentata* Pander from Ohesaare Cliff as a type species (*vorgehenden Art*), redescribed *O. serrata* Pander, and included all other Pander's species of *Oniscolepis* and *Strosipherus* in *O. serrata*. Rohon (*ibid*.) noted that the histological structure of the two species, *O. dentata* and *O. serrata*, was comparable to that of psammosteids. Incidentally, he (*ibid*., p. 93) wrote that *Strosipherus* described by Pander was collected by Acad. Fr. Schmidt from the Kaugatuma Cliff locality.

Gross (1947) studied fish microremains from the erratic boulders of the North German Lowland, among other agnathans and fishes also *Strosipherus indentatus*. Later on, he (Gross 1961) examined more thoroughly the fish material from Ohesaare Cliff, which he got from T. Ørvig, Stockholm. Gross (1961) gave a detailed description of the histology of *Oniscolepis* sp. indet. from the erratic boulders of the North German Lowland. In the lower layer of these specimens, Gross observed relatively few ascending canals and numerous Sharpey fibre tubules. In the middle layer, which was much thicker, he described numerous wide vascular canals, which became much narrower in the upper layer. The upper layer was composed of dentine ridges and tubercles (Gross 1961, figs 11, 12). Gross found that both *Strosipherus* and *Oniscolepis* had exactly the same microstructure, which convinced him to unite these two genera. As *Oniscolepis* came from the type locality, Ohesaare Cliff, he chose that generic name as senior, with *O. dentata* as its type species. Like Rohon (1893), he decided that the specimen of *O. magna* belonged to *Tolypelepis undulata*.

Obruchev (1964) treated *Oniscolepis* as a junior synonym of *Strosipherus*. Following his work, *Strosipherus* was accepted as the correct senior synonym by most palaeoichthyologists.

Karatajūtė-Talimaa (1970) distinguished six types of tesserae and two types of scales, and described the histology of *Strosipherus indentatus* Pander from North Timan, Velikaya River, Loc. 28 (= Loc. 32). She also explained the history of the generic name and concluded that as the name *Oniscolepis* (*O. magna*) was used for the scale which belonged to *Tolypelepis undulata* Pander, the name *Oniscolepis* could not be used any more, supposedly legitimizing the generic name *Strosipherus*, for which she picked the type species *S. indentatus* Pander.

The discovery of pores of the lateral line sensory system of *S. indentatus* allowed better understanding of the taxon (Märss 1986). Its sensory line system is composed of short vertical canals containing single neuromasts, and of short U-shaped canals connecting pores of one skeletal element, or those of adjacent tesserae or scales. Sensory line canals in *S. indentatus* were compared with those of *Tolypelepis undulata*, which also have U-shaped canals (Märss 1986). She described the material from the type locality, Ohesaare Cliff, gave the stratigraphic range of the taxon based on several drill core records, and chose a neotype specimen for *S. indentatus*.

In the last handbook on early agnathans and fishes (Novitskaya 2004), *Oniscolepis* was shortly discussed in the section on the order Tesseraspidiformes Halstead, family Tesseraspididae Berg, which contained two genera, *Tesseraspis* and ?*Kallostrakon*. The systematic position of *Oniscolepis* (the name preferred by Novitskaya) was not resolved.

In the late 1950s–1980s, data about the distribution of fishes were widely used for the subdivision and correlation of Lower and Middle Palaeozoic beds with the East Baltic as one of the key regions. Among other vertebrates, *S. indentatus* was used for that purpose, showing a rather limited stratigraphic range from the upper half of the Přidoli, Upper Silurian, to the lowermost Lochkovian, Lower Devonian (e.g. Obruchev 1958, 1973; Kossovoi & Obruchev 1962; Obruchev & Karatajūtė-Talimaa 1967, 1968; Karatajūtė-Talimaa 1968a, b, 1970; Kossovoi & Karatajūtė-Talimaa 1977; Valiukevičius et al. 1983; Märss 1986, 1989).

Continuous interest in the relationships of *Oniscolepis* with other heterostracans initiated studies of tessellated forms in the Baltic. The first results are available in Karatajūtė-Talimaa & Märss (2008).

MATERIAL AND METHODS

Both outcrop and drill core material from the East Baltic and North Timan was used in our study. The localities and intervals in drill cores containing *O. dentata* elements are listed below.

Estonia, Saaremaa Island, Ohesaare Cliff, Loode Cliff; Indu-653 core, depth 12.3 m; Ingelandi-615 core, depth 36.5–41.5 m; Ingelandi-618 core, depth 35.5–40.5 m; Kaavi-568 core, depth 24.8–48.2 m; Kaavi-571 core, depth 12.0–35.5 m; Mäebe-869 core, depth 31.0–55.7 m; Sõrve-514 core, depth 29.9–50.2 m; Tammuna-569 core, depth 1.1–4.9 m; Türju-620 core, depth 3.5–6.5 m; Ruhnu Island, Ruhnu-500 core, depth 148.1–177.4 m.

Latvia, Kolka-54 core, 158.3–205.6 m.

Lithuania, Stoniškiai, depth 1211–1217m.

North Timan, Velikaya River (see Valiukevičius et al. 1983, Loc. 8e; Kossovoi & Obruchev 1962; Karatajūtė-Talimaa 1970; Kossovoi & Karatajūtė-Talimaa 1977, Loc. 28, which at that time was numbered as 32). Sixty-four rock samples from the Velikaya River outcrop, North Timan, were given to V. Karatajūtė-Talimaa by L. S. Kossovoi. The richest ichthyofauna was found in the beds of localities 28 and 30. Drill core 379, depth 133.2–164.0 m; drill core 379a, depth 119.1–263.4 m; drill core 374, depth 37.2–50.6 m; drill core 81, depth 63.5–79.8 m; drill core 79, depth 79.7–81.7 m; drill core 385, depth 317.5–350.5 m.

Altogether, a couple of hundred samples with a few thousand specimens of *O. dentata* exoskeletal elements were available for this study. The material is housed in Tallinn and Vilnius. The illustrated specimens belonging to the Institute of Geology at Tallinn University of Technology carry the collection number GIT 570 + specimen number, and those in the Institute of Geology and Geography of Lithuania have the collection number LIGG 20 and LIGG 5 + specimen number.

The scales and tesserae were photographed under a scanning electron microscope, model JEOL JSM-840A, and optically with a Nikon AZ100 and camera Nikon Digital Sight DS-Fi1. Thin sections were photographed using the transmitted-light microscope Nikon Eclipse 50i and camera Nikon Digital Sight DS-Fi1.

SYSTEMATIC PALAEONTOLOGY

Class Pteraspidomorphi Goodrich, 1909
Subclass Heterostraci Lankester, 1868
Order Eriptychiida Ørvig, 1958
[Eriptychida, in error Stensiö, 1958]

Diagnosis. Exoskeleton of small, discrete units, the bases of which are not fused, covered with elongate ridges or roundish tubercles built from orthodentine of upper layer and aspidine of middle and lower layers.

Content. Eriptychiidae Tarlo, 1962; Oniscolepididae fam. nov.

Range. Ordovician to Devonian.

Family Oniscolepididae fam. nov.

Type genus. *Oniscolepis* Pander, 1856

Diagnosis. Exoskeleton of head region encased with small plates and platelets, partly possibly with tesserae; trunk and tail covered with tesserae and scales; upper layer of tubercles or elongate dentine ridges of fine dentine tubules arranged in bunches; dentine and pulp canals wide; middle and lower (basal) layers of spongiose aspidine; vascular canals either vertically or horizontally stretched.

Content. *Oniscolepis* Pander, 1856; *Kallostrakon* Lankester, 1870.

Stratigraphical and geographical range. Přidoli, Upper Silurian to Lochkovian, Lower Devonian of East Baltic, North Timan, British Isles, and North German Lowland (erratic boulders).

Genus *Oniscolepis* Pander, 1856

1856 Genus *Oniscolepis*; Pander, pp. 56–58.
1893 *Oniscolepis* Pander; Rohon, pp. 89–90.
1961 *Oniscolepis*; Gross, p. 28.
1856 Genus *Strosipherus*; Pander, p. 73.
1964 *Strosipherus* Pander, 1856; Obruchev, p. 55.
1970 *Strosipherus* Pander, 1856; Karatajūtė-Talimaa, p. 54.
1986 *Strosipherus* Pander, 1856; Märss, p. 48.

Type and only species. *Oniscolepis dentata* Pander, 1856.

Diagnosis. As for species.

Occurrence. Přidoli, Upper Silurian to Lochkovian, Lower Devonian of East Baltic and North Timan.

Remarks. Rohon (1893), the first revisor of the genera, synonymized *Strosipherus* Pander, 1856 under *Oniscolepis* Pander, 1856, i.e., he fixed *Oniscolepis* as the senior synonym. Obruchev (1964) chose *Strosipherus* as the senior generic synonym, but he was incorrect because the senior generic synonym was already chosen by the first revisor. Karatajūtė-Talimaa (1970) legitimized the generic name *Strosipherus*, for which she picked the type species *S. indentatus* Pander. This was unnecessary, because the synonymy of the species *O. magna* and *Tolypelepis undulata* Pander, 1856 (the former species is a junior synonym of the latter; the latter is a valid genus and a type species by monotypy) does not invalidate the generic name *Oniscolepis* Pander, which subsequently had its type species designated, before *Strosipherus*, by Rohon. Märss (1986) chose a neotype specimen for *S. indentatus*. However, that specimen does not automatically become the neotype specimen of *O. dentata*. A new specimen to be a lectotype for *O. dentata* should be picked from among Pander's specimens. As Pander's collection is lost, a neotype specimen should be chosen among new samples from what is believed to be the type locality for *O. dentata* (ICZN 1999, article 75) (letter K. Soehn, Edmonton, in June 2008).

Oniscolepis dentata Pander, 1856

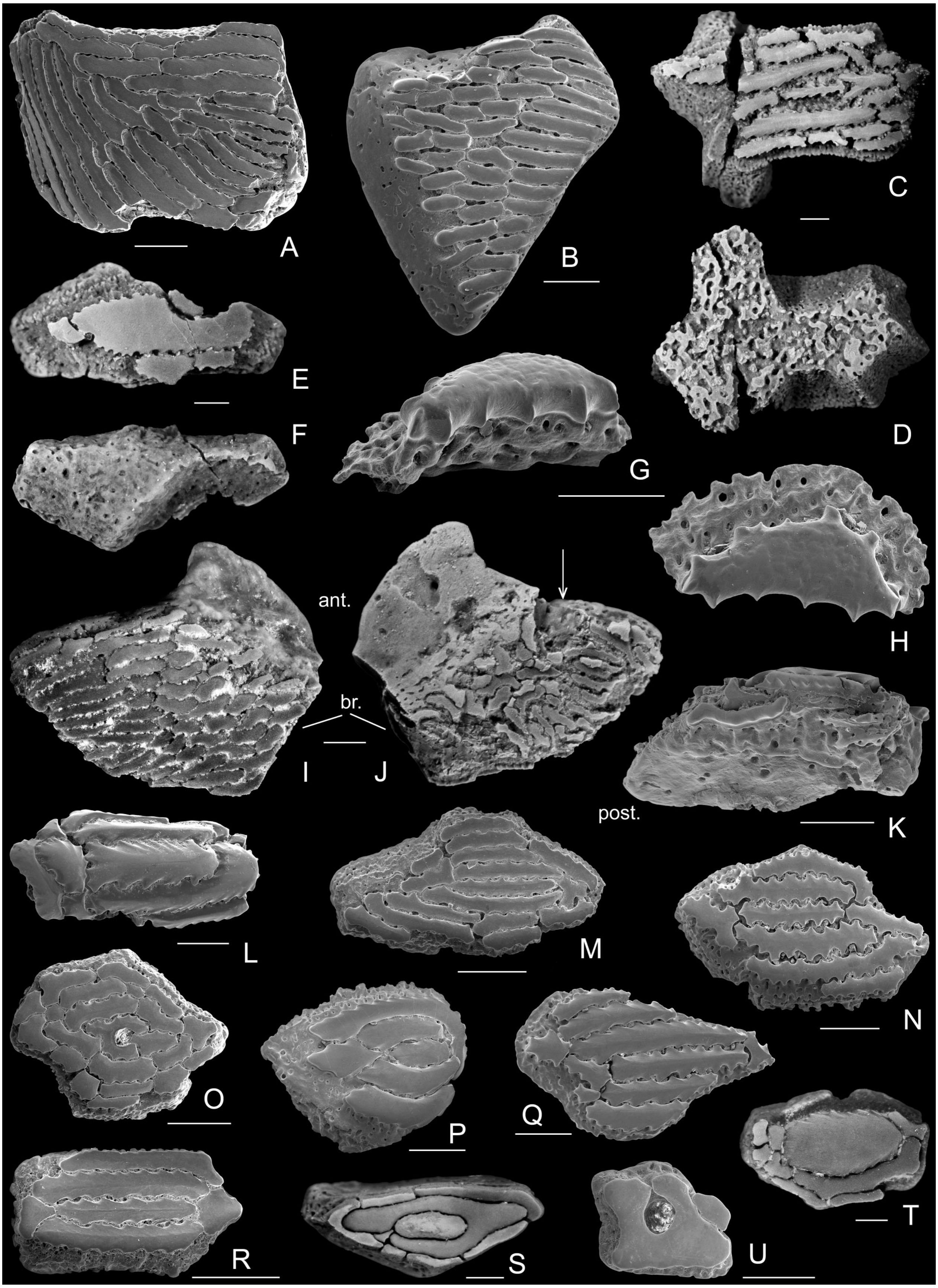
Figures 2–9

1856 *Oniscolepis dentatus*; Pander, p. 58; pl. 6, fig. 33.
1856 *Oniscolepis serratus*; Pander, p. 59; pl. 6, fig. 34.
1856 *Oniscolepis crenulatus*; Pander, p. 59; pl. 6, fig. 35.
1856 *Strosipherus indentatus*; Pander, p. 74; pl. 4, fig. 8a–g.
1856 *Strosipherus serratus*; Pander, p. 75; pl. 4, fig. 9a.
1856 *Strosipherus laevis*; Pander, p. 75; pl. 4, fig. 9b–d.
1893 *Oniscolepis dentata*; Rohon, pp. 90–93; pl. 1, fig. 46, pl. 3, fig. 59.
1893 *Oniscolepis serrata*; Rohon, pp. 93–94; text-fig. 19.
1947 *Strosipherus indentatus*; Gross, pp. 96–98; pl. 9, figs 1–4, text-fig. 2.
1961 *Oniscolepis* sp. indet.; Gross, pp. 28–36; figs 10, 11, 12A–L.
1964 *Strosipherus indentatus* Pander; Obruchev, p. 55, figs 14, 15.
1970 *Strosipherus indentatus* Pander; Karatajūtė-Talimaa, pp. 54–61, figs 11–14.
1986 *Strosipherus indentatus* Pander; Märss, pp. 48–49; pl. 25, figs 1–4, text-fig. 23.

Neotype. The specimen GIT 232-10 (= Pi 6180), Märss 1986, pl. 25, fig. 4, bed 3-VIII, Ohesaare Cliff, Saaremaa,

Fig. 2. Plates, platelets, and tesserae of *Oniscolepis dentata* Pander. **A**, platelet GIT 570-102; Ventspils core, depth 273.6 m. **B**, platelet GIT 570-82,Ventspils core, depth 302.4 m. **C**, **D**, platelet GIT 570-109 with lateral prongs, two overlapped areas anteriorly on the external side (C), and five overlapping areas on the visceral side (D), Ohesaare Cliff, bed 1-IX. **E**, **F**, small platelet or tessera with deep crescent-shaped cut on the side, GIT 570-110, Ohesaare Cliff. **G**, **H**, orbital plate (tessera), GIT 570-60, Ohesaare Cliff, bed 2-VIII. **I**, **J**, fragment of the branchial plate with an arrow showing the entrance of a canal, GIT 570-111, Ventspils core, depth 273.3 m. **K**, posterior part of another branchial plate, GIT 570-96, Ohesaare Cliff. **L**, body ridge tessera, GIT 570-65, Ventspils core, depth 268.4 m. **M–U**, tesserae; M, GIT 570-84, Ventspils core, depth 302.4 m; N, GIT 570-39, Ohesaare Cliff, bed 2-X; O, tessera with a pore of the lateral line system, GIT 570-66, Ventspils core, depth 268.7 m; P, GIT 570-43, Ohesaare Cliff, bed 2-X; Q, GIT 570-41, Ohesaare Cliff, bed 2-X; R, GIT 570-70, Ventspils core, depth 268.7 m; S, GIT 570-113, Ruhnu-500 core, depth 148.1 m; T, GIT 570-114, Ventspils core, depth 273.3 m; U, simple tessera with lateral line pore, GIT 570-76, Ventspils core, depth 268.7 m. All in external view except D, F, and J, which are in basal view, and G and K, which are in oblique side view. A–K, M, N, P, Q, S, T, Ohesaare Stage, Přidoli, Upper Silurian; L, O, R, U, Tilže Stage, Lower Lochkovian, Lower Devonian. Scale bar 0.5 mm.

Abbreviations: ant, anterior; br, broken margin; post, posterior.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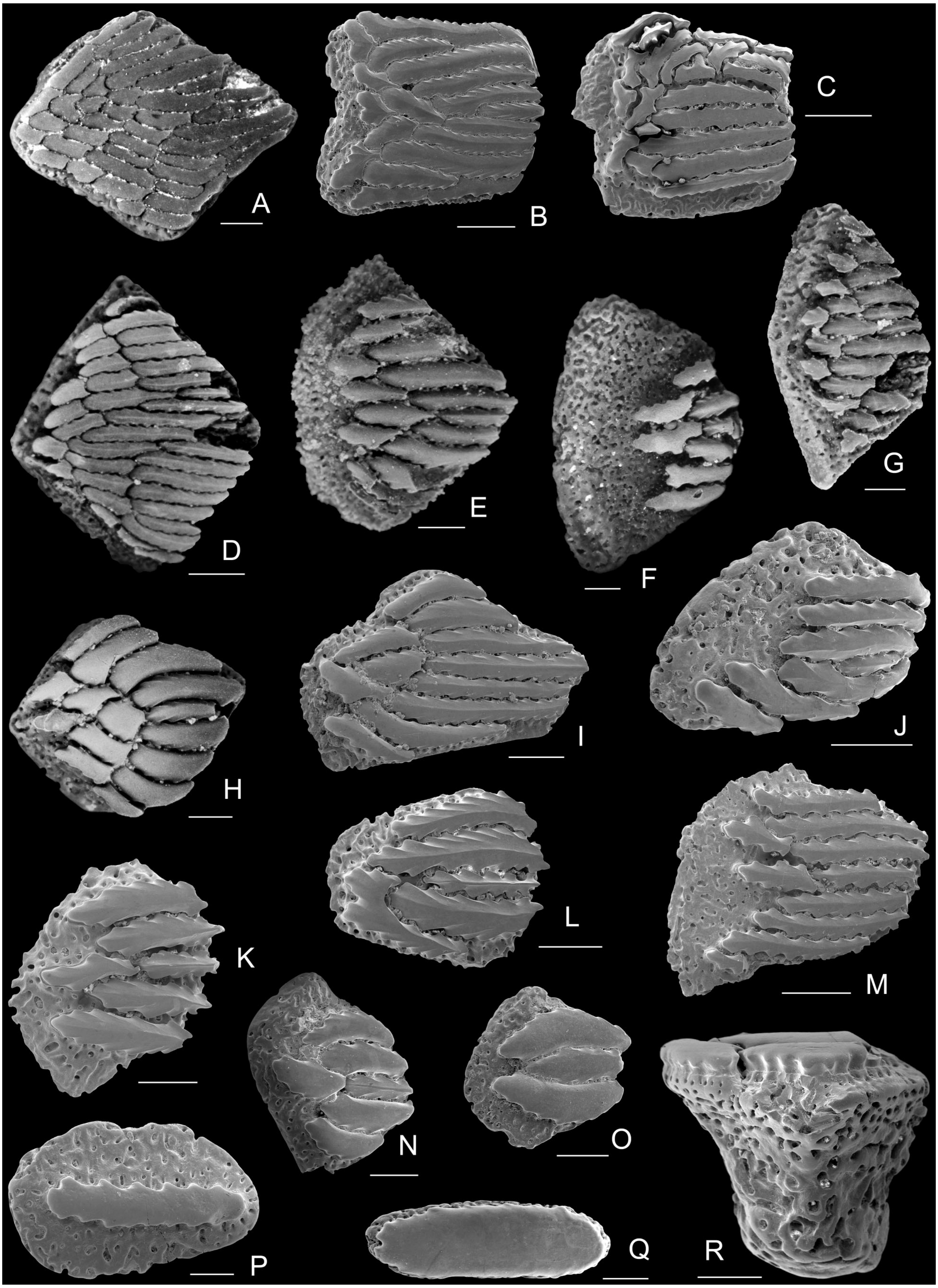
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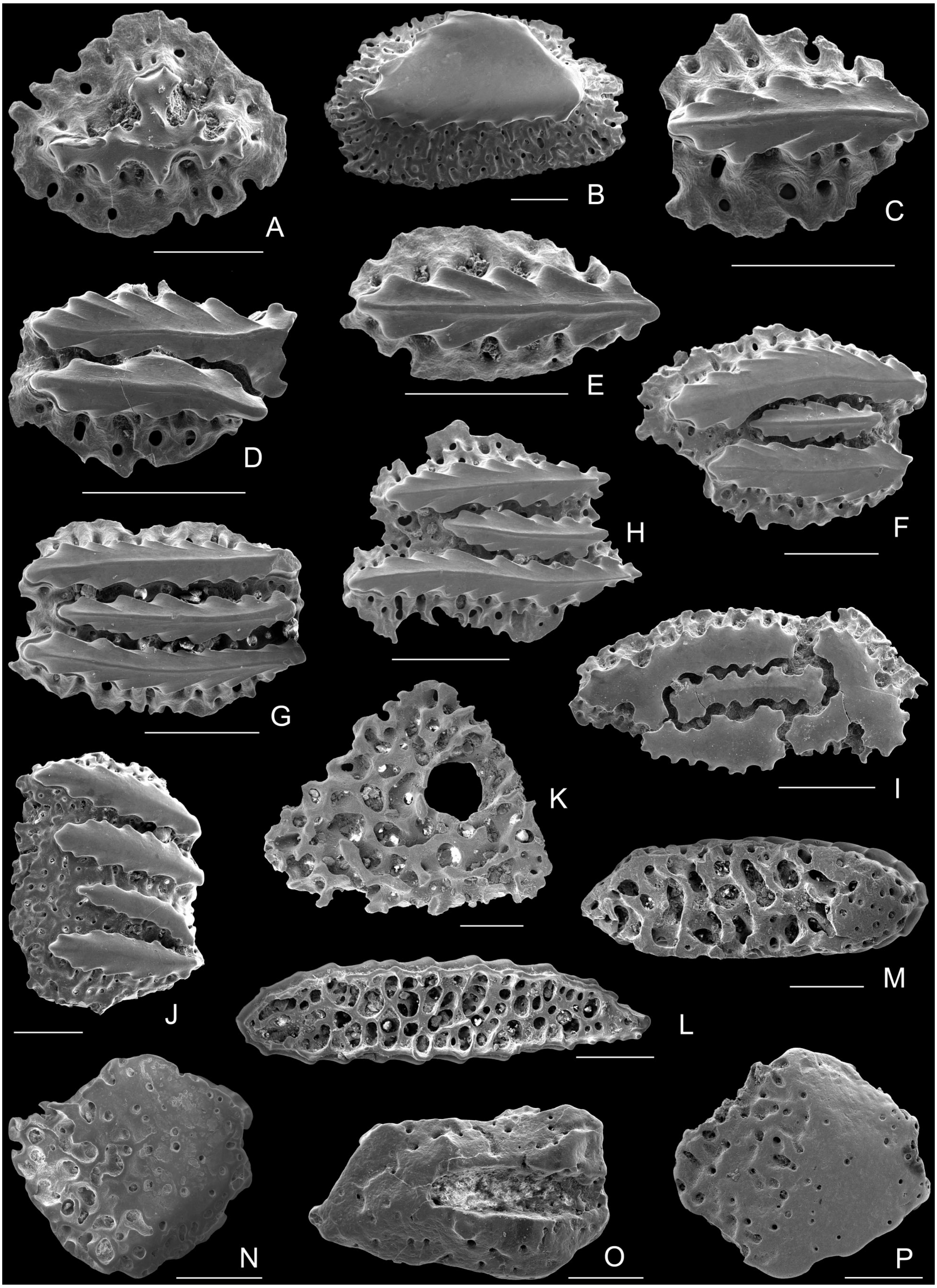
which was chosen as a neotype for *Strosipherus indentatus* Pander, is linked with this specific name; neotype for *O. dentata* is designated herein in Fig. 3H, the scale GIT 570-112, Ohesaare Cliff, Saaremaa; Ohesaare Stage, Přidoli, Upper Silurian.

Diagnosis. Plates, platelets, tesserae, and scales with dentine ridges overlying aspidine of middle and lower layers; ridges arranged concentrically on tesserae and longitudinally on scales; ridges with crenulated margins, flat-topped or having longitudinal crest; orbits surrounded by one or more rings of concentrically placed units (plates or tesserae); branchial area covered with small units (i.e., not with one single plate) whose anterior margin is smooth both externally and internally with openings of vascular canals; the rest of the external side covered with longitudinal dentine ridges, internal side has flattened, finer dentine ridges; anterior part of branchial plate elongate-oval, posterior part deltoid in transverse cross section; lateral line canals occur in tesserae as short simple vertical or U-shaped canals opening to the surface as pores.

Occurrence. Lõo Beds of Kaugatuma Stage and Ohesaare Stage, Přidoli, Upper Silurian of Estonia and Latvia, and Tilže Stage, Lower Lochkovian, Lower Devonian of Latvia; upper part of Jūra Stage, Přidoli of Lithuania; Eptarma Beds, Přidoli, Upper Silurian of North Timan; *Thelodus parvidens* Zone (erratic boulders) of North German Lowland.

Description. No articulated exoskeleton of *Oniscolepis dentata* is known. Morphology of the elements from the East Baltic is illustrated in Figs 2–4. Platelets from the dorsal side of the body (Fig. 2A, B) have quadrangular configuration, and fan-shaped or longitudinal pattern of dentine ridges. One platelet (Fig. 2A) is 3.3 mm long and 2.85 mm wide, the length of ridges is 0.1–0.2 mm; it has small tubercles along postero-lateral margins. Its ridges start immediately at the anterior corner, they are longer on the sides and shorter in the middle of the platelet. Another platelet is 2.5 mm long and 3.2 mm wide, with narrow, smooth ridges; anterior short ridges become longer posteriorly on the platelet (Fig. 2B). The anterior smooth margin of the platelet has small pores. The lower side of both platelets is relatively smooth. An asymmetrical cross-shaped platelet, 4.5 mm long and 3.25 mm wide (Fig. 2C, D), has one anteriomedial and two lateral prongs with two narrow articular areas anteriorly; ridges on the platelet (0.15–0.3 mm wide) are distributed longitudinally. Five incisions mark the overlapping areas on the posterior lower surface of the platelet. The lower surface is cavernous, with openings of vascular canals. An elongate platelet, 4 mm long and 1.8 mm wide (Fig. 2E, F), has one long and coarse (maximum width 0.95 mm) and four shorter and narrower ridges on its upper surface; it has a crescent-shaped incision in one of its margins, which is better seen from the visceral side (Fig. 2F). A small plate (or tessera) which we interpret as an orbital plate (tessera) has one, 1 mm long, rather wide arcuate crenulate dentine ridge on the porous basal plate (Fig. 2G, H). The maximum length of the plate is 1.35 mm and width 0.55 mm. The surface of the ridge is smoothly convex (Fig. 2H); the ridge surface is knobby. Its overlapped area is rather wide. The overlapping area on the visceral side is slanting outwards; it is uneven and porous. Two fragments of branchial plates were found (Fig. 2I–K). One fragment (Fig. 2I, J) is rather large (maximum measurements: 3.5 mm long and 3.55 mm wide). It seems rather complete with just a small piece broken off (in Fig. 2I, J marked by 'br'). The unit is streched-out oval in cross section, has longitudinal ridges externally, is shorter anteriorly and longer posteriorly. There are two spots of obliquely disposed ridges on the posterior end of the plate (Fig. 2I). The anterior margin with an articular area is without sculpture and is turned inwards. The internal side of this fragment carries very shiny, flattened, rather irregularly placed ridges with serrated margins (Fig. 2J). A deeper cut or groove, with diameter 0.75 mm, enters anteriorly into the lower side of the plate (in Fig. 2J indicated with an arrow). Another fragment of the branchial unit is from its posterior part (Fig. 2K). It is 2 mm long, deltoid in cross section, and with the smoothly pointed posterior end (to the left in the figure); the anterior end is broken. The plate carries ridges of average length and width on the external surface, and much finer ridges (0.1 mm wide) on the internal surface. Another part of the internal side is smooth, pierced by rare vascular canals.

Fig. 3. Tesserae and scales of *Oniscolepis dentata* Pander. **A**, a large scale GIT 570-106, Ventspils core, depth 273.3 m. **B**, mid-body scale, GIT 570-100,Ventspils core, depth 274.6 m. **C**, slightly asymmetrical scale with repaired anterior right part, GIT 570-37, Ohesaare Cliff, bed 2-VIII. **D**, large symmetrical scale GIT 570-107, Ventspils core, depth 273.9 m. **E**, scale GIT 570-116, Ohesaare Cliff, bed 1-VIII. **F**, large scale with a wide anterior overlapped area, GIT 507-115, Ohesaare Cliff. **G**, short and high scale, GIT 570-108, Ohesaare Cliff, bed 2-X. **H**, *neotype*, scale GIT 570-112, Ohesaare Cliff. **I**, scale GIT 570-35, Ohesaare Cliff, bed 1-VIII. **J**, scale GIT 570-8, Ohesaare Cliff. **K**, scale GIT 570-45, Ohesaare Cliff, bed 2-X. **L**, transitional form between scale and tessera, GIT 570-46, Ohesaare Cliff, bed 2-X. **M**, scale GIT 570-40, Ohesaare Cliff, bed 2-X. **N**, scale GIT 570-7. **O**, scale GIT 570-6. **P**, single ridge GIT 570-24. **Q**, single ridge GIT 570-5. **R**, tessera GIT 570-98, Ohesaare Cliff. All specimens in external view. Ohesaare Stage, Přidoli, Upper Silurian. Scale bar 0.5 mm.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The body ridge elements (one shown in Fig. 2L) are interpreted as coming from the dorsal side of the fish, with the medial ridge being finely crenulated by short ridgelets anteriorly and laterally. Two rows of short ridges occur anteriorly of the medial ridge. One lateral ridge turns posteriorly crosswise. The lower side of such elements is concave. The element is 2.45 mm long and 1 mm wide; the width of the medial ridge is 0.4 mm.

Tesserae (Fig. 2M–U) are of various sizes, with length between 0.9 and 3.35 mm and width between 0.6 and 1.65 mm; the width of ridges is 0.1–0.25 mm. The ridge patterns are concentric (Fig. 2M, O, P), consisting of the medial, and 1–4 longitudinal ridges on both sides of tesserae and a few rows of ridges (1–2) anteriorly. Always one or more ridges are present at the posterior end, which lie crosswise or at some angle to the medial ridge (Fig. 2Q, R). At the posterior end some medially-turned longitudinal ridges occur instead of short crosswise ridges (Fig. 2P, S, T). Ridges of tesserae are convex or flat in cross section. The base beneath the crown can be very deep, about eight times deeper than the height of the dentine ridge (Fig. 3R). There may be a very narrow

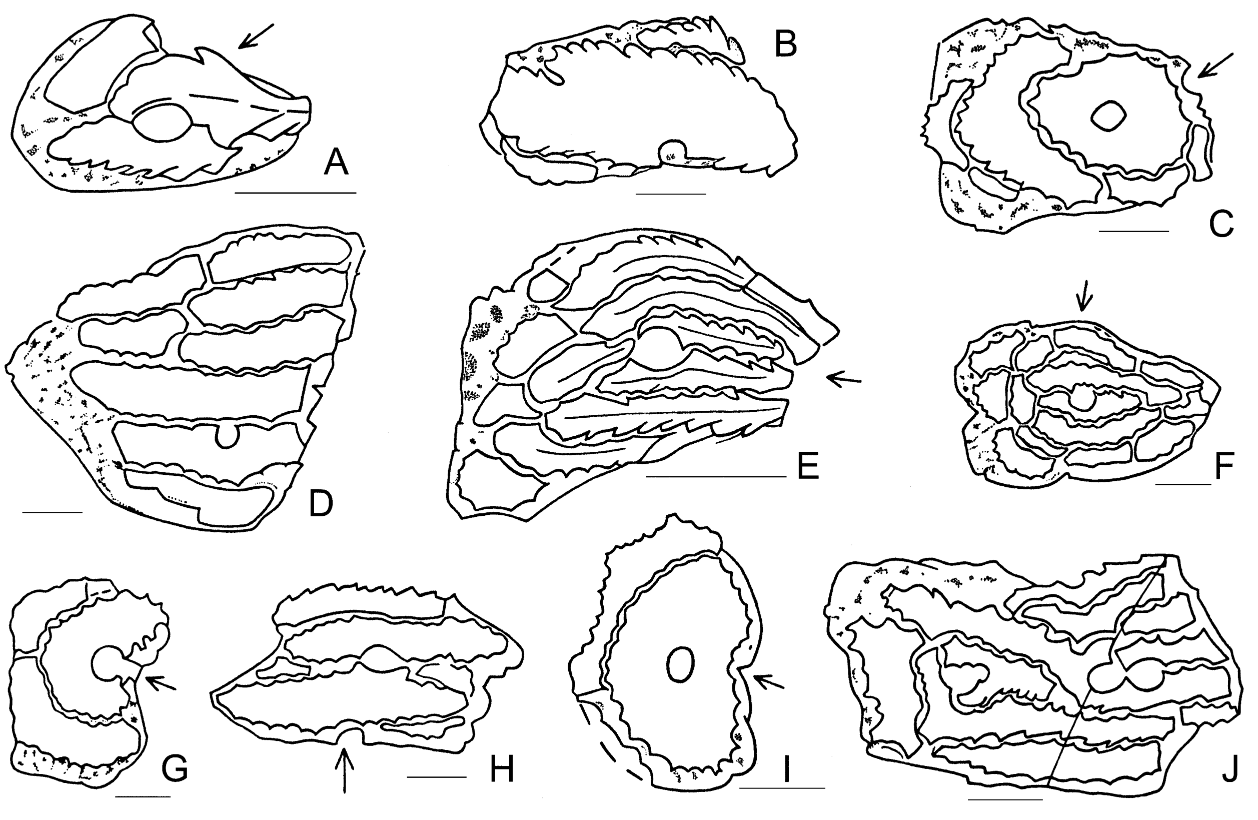
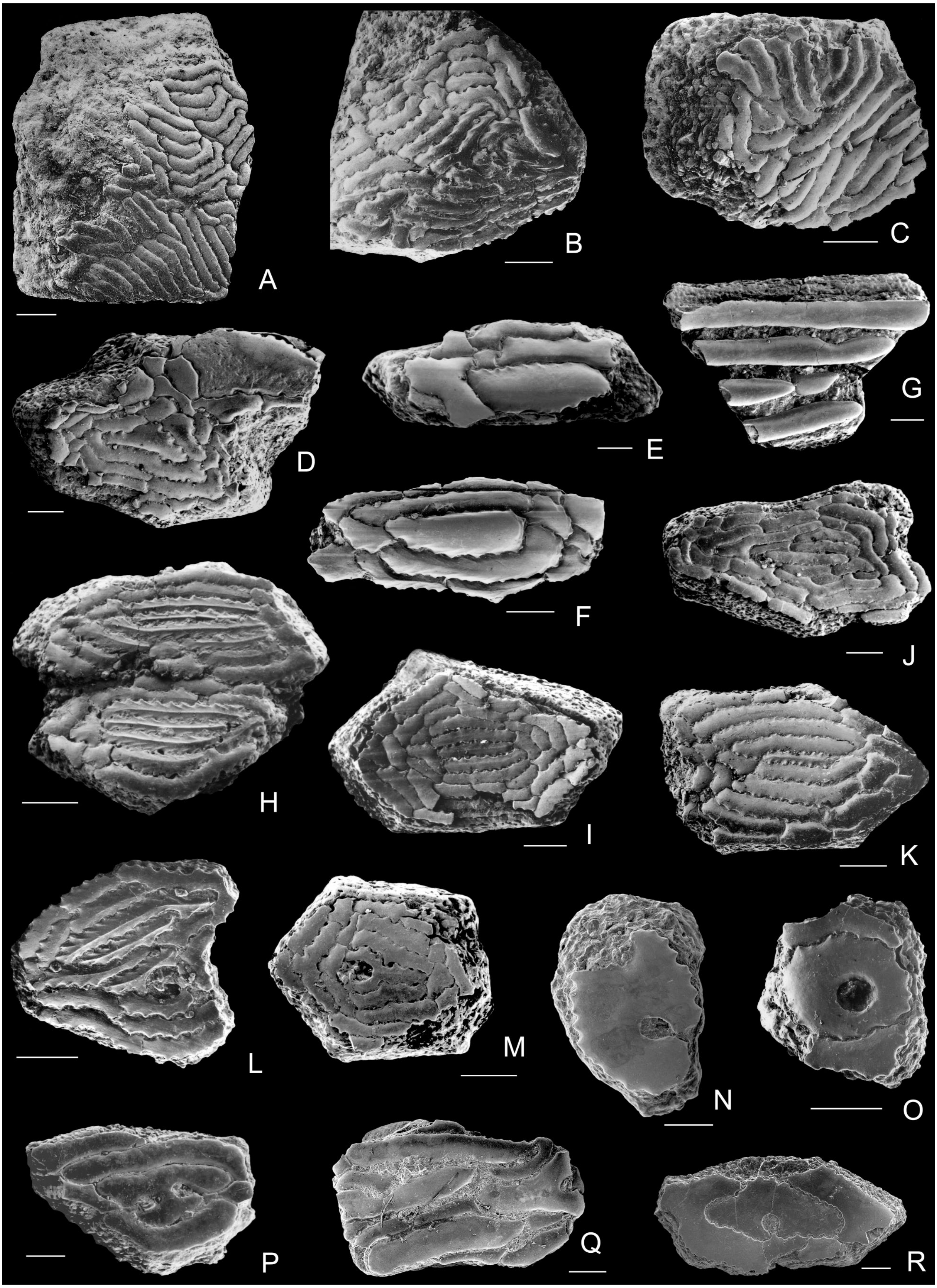


Fig. 5. Tesserae of *Oniscolepis dentata* Pander with lateral line canal openings (from Märss 1986, fig. 23). The arrows point to the side opening of canals. **A**, GIT 232-257 (Pi 6785; here and below the old collection numbers are given in brackets), Ruhnu-500, depth 165.2 m. **B**, GIT 232-260 (Pi 6788), Ohesaare Cliff, bed 4-XVIII. **C**, GIT 232-259 (Pi 6787), Ohesaare Cliff, bed I-IX. **D**, GIT 232-262 (Pi 6790), Ruhnu-500, depth 148.0 m. **E**, GIT 232-266 (Pi 6794), Ventspils core, depth 273.6 m. **F**, GIT 232-265 (Pi 6793), Ventspils core, depth 268.4 m. **G**, GIT 232-258 (Pi 6786), Ruhnu-500 core, depth 165.2 m. **H**, GIT 232-264 (Pi 6792), Kaavi-571 core, depth 23.1 m. **I**, GIT 232-263 (Pi 6791), Kolka-54 core, depth 180.2–181.0 m. **J**, GIT 232-261 (Pi 6789), Ohesaare Cliff, bed 2-VIII. A–E, G–J, Ohesaare Stage, Přidoli, Upper Silurian; F, Tilže Stage, Lower Lochkovian, Lower Devonian. Scale bar 0.5 mm.

Fig. 4. *Oniscolepis dentata* Pander. **A–J**, juvenile units in external view; **K–P**, development of the base; units in base view. A, GIT 570-59, Ohesaare Cliff, bed 2-VIII; B, GIT 570-47, Ohesaare Cliff, bed 2-X; C, GIT 570-58; D, GIT 570-57, Ohesaare Cliff, bed 2-VIII; E, GIT 570-50, Ohesaare Cliff, bed 2-X; F, GIT 570-23, Ohesaare Cliff; G, GIT 570-53; H, GIT 570-52, Ohesaare Cliff, bed 2-X; I, GIT 570-30, Ohesaare Cliff, bed 1-VIII; J, GIT 570-10; K, lateral line canal piercing the upper layer, GIT 570-95; L, GIT 570-92; M, GIT 570-97; N, GIT 570-89, Ohesaare Cliff; O, lateral line canal running deep in the base, GIT 570-38, Ohesaare Cliff, bed 2-X; P, GIT 570-87, Ohesaare Cliff. Ohesaare Stage, Přidoli, Upper Silurian. Scale bar 0.5 mm.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overlapped area anteriorly, but if the ridges are broken off the base, the upper surface can look like an articular area.

The scale size varies between 1.75 and 3.5 mm in length and 1.25 and 3.5 mm in width. The scales have on their main area longitudinal, slightly curved lateral ridges and a varying number of parallel medial ridges, which all terminate posteriorly with free points (Fig. 3B–G, I–K, M–O). The ridges have serrated margins; serrations can be rather deep (e.g. Fig. 3F) or hardly observable (Fig. 3D, H). The scales, as a rule, have an overlapped area anteriorly, which can reach noticeable width (Fig. 3F, J). There occur transitional elements from tesserae to scales (Fig. 3A, H, L), which

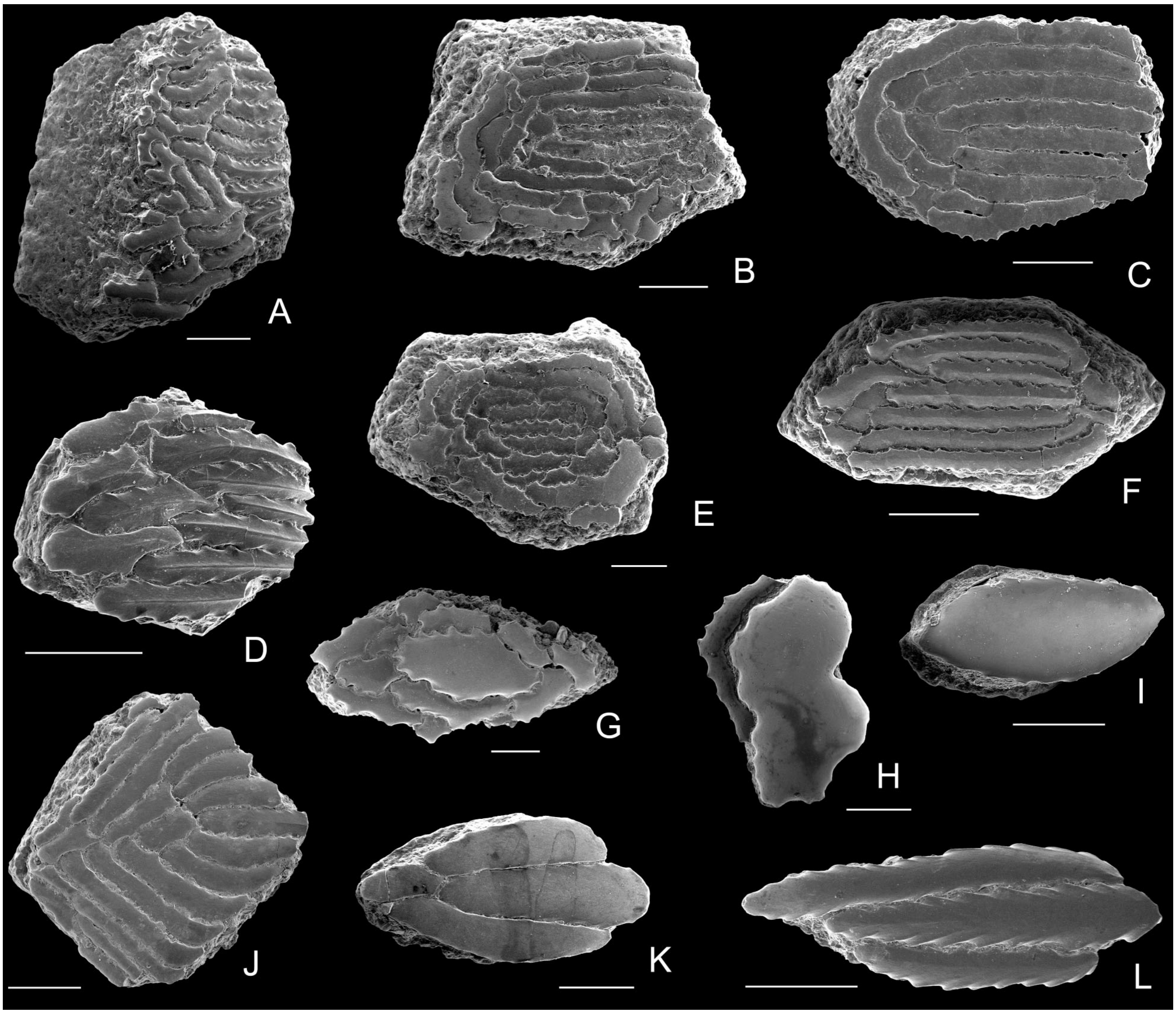


Fig. 7. *Oniscolepis dentata* Pander. **A**, **B**, **C?**, platelets; **D**, **J**, **K**, scales; **E–G**, tesserae; **H**, **I**, single sculpture elements which might have been situated on the tail; **L**, long tessera. A, LIGG 20-0-07; B, LIGG 20-0-20; C, LIGG 20-0-12; D, LIGG 20-0-37; E, LIGG 20-0-03; F, LIGG 20-0-04; G, LIGG 20-0-18; H, LIGG 20-0-17; I, LIGG 20-0-21; J, LIGG 20-0-08; K, LIGG 20-0-35; L, LIGG 20-0-36. Locality 32, Velikaya River, North Timan, Russia; Eptarma Formation, Přidoli, Upper Silurian. Scale bar 0.5 mm.

Fig. 6. *Oniscolepis dentata* Pander. **A–C**, **D?**, platelets from the anterior part of the body. **E**, **F**, body ridge tesserae. **G**, large platelet with high, smooth, and elongate ridges from the ?side of the body. **H–R**, tesserae; L–R tesserae with lateral line pore. A, LIGG 20-0-39; B, LIGG 20-0-40; C, LIGG 20-0-46; D, LIGG 20-0-43; E, LIGG 20-0-95; F, LIGG 20-0-96; G, LIGG 20-0-93; H, LIGG 20-0-74; I, LIGG 20-0-76; J, LIGG 20-0-72; K, LIGG 20-0-42; L, LIGG 20-0-81; M, LIGG 20-0-78; N, LIGG 20-0-14; O, LIGG 20-0-79; P, LIGG 20-0-84; Q, LIGG 20-0-09; R, LIGG 20-0-05. A–M, O, P, Locality 8e; N, Q, R, Locality 32, Velikaya River, North Timan, Russia; Eptarma Formation, Přidoli, Upper Silurian. Scale bar 0.5 mm.

have no or minimal overlapped area anteriorly, and whose ridges run not parallel, but arcuately.

Wide, smooth-topped single ridges with shallow serrations at the margins (Fig. 3P, Q) are always present in large samples but they are not numerous. They can have a wide base or a narrow rim. The specimen in Fig. 3P is 1.85 mm long and 1.0 mm wide; the specimen in Fig. 3Q is 2.75 mm long and 0.95 mm wide.

Juvenile units also have a medial longitudinal crest or a smooth, slightly convex surface (Fig. 4A–J). One to three, seldom more, short dentine ridges partly cover the base. The ridges are of different shapes: (1) irregular (Fig. 4A), (2) roundish, flat-topped (Fig. 4B), (3) straight, with crenulated margins, and with (Fig. 4C–E, G, H) or without (Fig. 4I) a medial longitudinal crest, (4) with curved ridges and a crest (Fig. 4F), or (5) with smooth, slightly convex ridges (Fig. 4J). Juvenile tesserae and scales usually have a very thin spongiose layer, with vascular canals piercing it (Fig. 4K). One can count the growth layers around the ridge (e.g. there are two such layers in Fig. 4A, C, F, three to four in Fig 4J). The units with one to two ridges are very small, less than 1 mm long (Fig. 4A, C–E); units with three ridges are 1.0–1.75 mm long and 0.75–1.35 mm wide. As a rule, the greater the number of ridges, the larger the tessera.

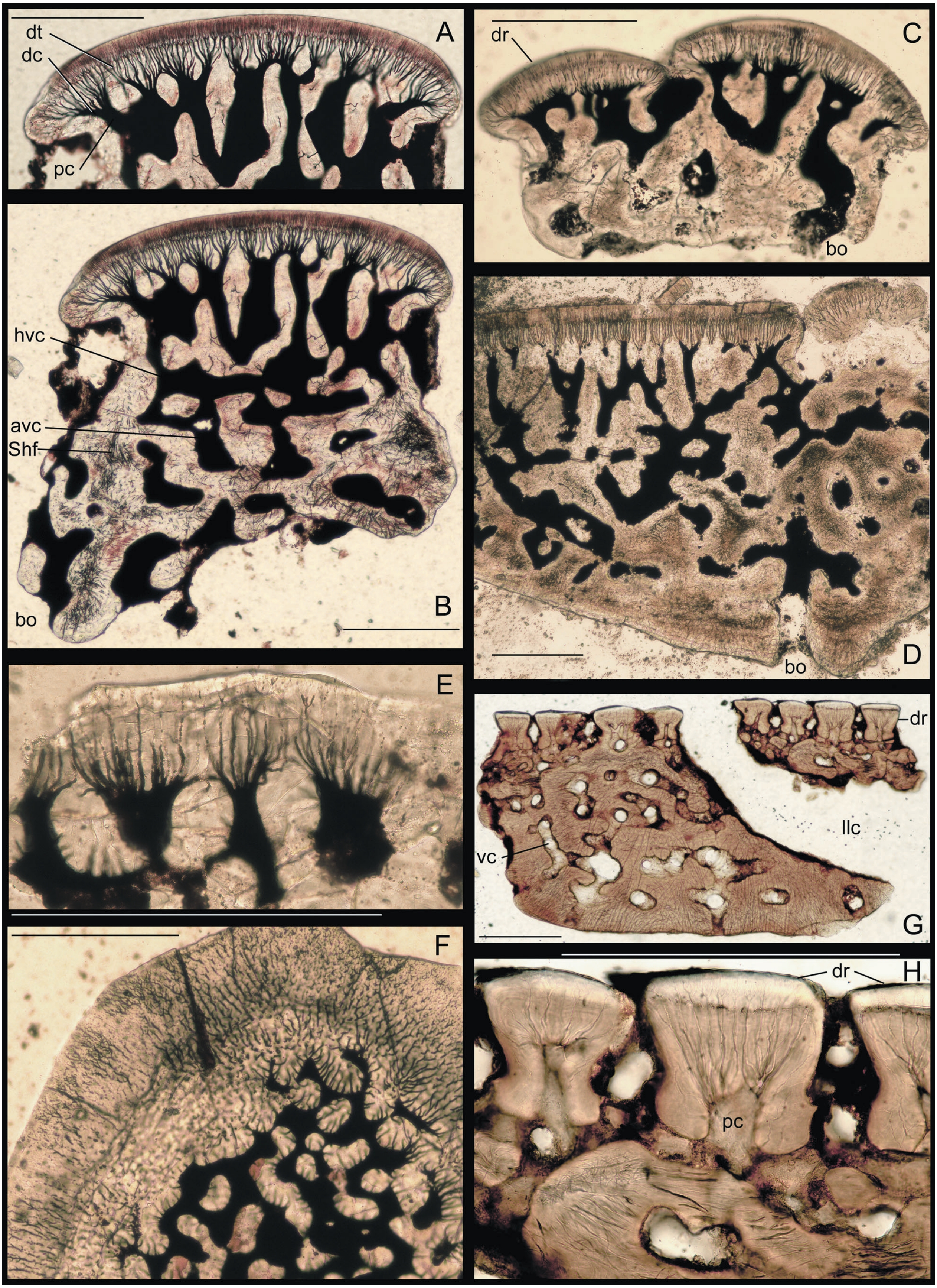
The lower surface of scales can be very uneven, containing holes and canals (Fig. 4L). The basal layer partly (Fig. 4M, N) or fully covers it (Fig. 4O, P). The lower surface of the scales reveals features which allow conclusions to be made about the scale ontogeny (Fig. 4L–N, P). The entire primary dentine cap of each scale was first underlain by a thin spongiose aspidine layer. In the course of time this layer thickened and the bottom of the posterior end of the scale was covered with a basal layer (Fig. 4L). The basal layer gradually expanded anteriorward until it covered the whole base, which became smooth, with rare vascular canals openings in it (Fig. 4M–P). Sharpey's fibres, which were for the attachment of the scale in the skin, were present already in early stages of the scale development. The scales never reached such thickness as the tesserae did, which might mean that the tesserae appeared in earlier life stages of the fish, and grew some time before the scales appeared. The growth of tesserae and scales differ in that the former grew more cyclomorially, the latter synchronomorially.

The pores and short canals in the tesserae belong to the lateral line system (Figs 2O, U; 4K, O; 5A–J). Such tesserae are not very common, and so far not a single true scale has been found with pores at any of the localities. Very thin to very thick, i.e. juvenile and adult tesserae with pores can be found. The pores (1–3) can be situated in the middle of the ridge, on the margin, or between the ridges. The pore diameter is between 0.1 and 0.4 mm. Short pore canals are directed down, but are often blind and do not pierce the basal surface of the tessera. In the juvenile scales with a thin middle layer, the canal is necessarily shorter and has an opening in the lower surface (Fig. 4K). Some scales with pores have a swollen base at the place where the canal runs, and from the side of this tessera the part of the canal directed to the adjacent tessera is visible. The openings of canals, marked with arrows in Fig. 5A, C, E–I, are directed obliquely, crosswise, or longitudinally in relation to the ridges. The canals can be open on the lower surface in young scales as mentioned above, or be entirely in the spongiose layer in adult scales.

Material from North Timan gives a more complete idea about the morphology of dermal units of *O. dentata*. The platelets (Figs 6A–C, D?; 7A, B, C?) which, we presume, were located anteriorly of the body, have at least one margin not covered by dentine ridges. The ridges are arranged irregularly (Figs 6A–C, D?; 7A) or longitudinally (Fig. 7B, C?). Platelets are usually broken. The preserved parts are commonly rather small, but there are also rather large platelets in samples, which have relatively high and elongate, straight and smooth dentine ridges (Fig. 6G). Body ridge tesserae (Fig. 6E, F)

Fig. 8. Microstructure of the scales and tesserae of *Oniscolepis dentata* Pander. **A**, **B**, vertical cross section of a single wide ridge with a deep base; A, close-up of B to show the upper dentine layer; B, section of the whole thick spongiose middle and lower layers, LIGG 20-1283. **C**, scale with two ridges in vertical cross section, showing the upper orthodentine layer and wide vertical canals, LIGG 20-1042. **D**, vertical cross section of a tessera with large dentine ridges, showing a vertical basal canal going up to the surface, LIGG 5-01262, Loc. 32 (= 28), Velikaya River, North Timan (see Karatajūtė-Talimaa 1970, fig. 14, fig. 2). **E**, **F**, horizontal section of a dentine ridge; E, close-up of orthodentine layer; F, part of the dentine ridge, LIGG 20-1044, Loc. 8e, Velikaya River, North Timan, Eptarma Formation, Přidoli, Upper Silurian. **G**, **H**, vertical cross section of a tessera along a short canal of the sensory line system; G, the canal opens in the middle of the crown between ridges and laterally in the base; H, close-up of G to show fine dentine tubules, wider dentine canals, and Sharpey's fibre tubules; GIT 232-348 (previous number Pi 6953); Ventspils-D3 core, depth 268.4 m, Tilže Stage, Lower Lochkovian, Lower Devonian. Scale bar 0.25 mm.

Abbreviations for Figs 8, 9: arc, arcade canal; avc, ascending vascular canal; bo, basal opening; dc, dentine canal; dr, dentine ridge; dt, dentine tubules; hvc, horizontal vascular canal; llc, lateral line canal; pc, pulp canal; Shf, Sharpey's fibre tubules; vc, vascular canals.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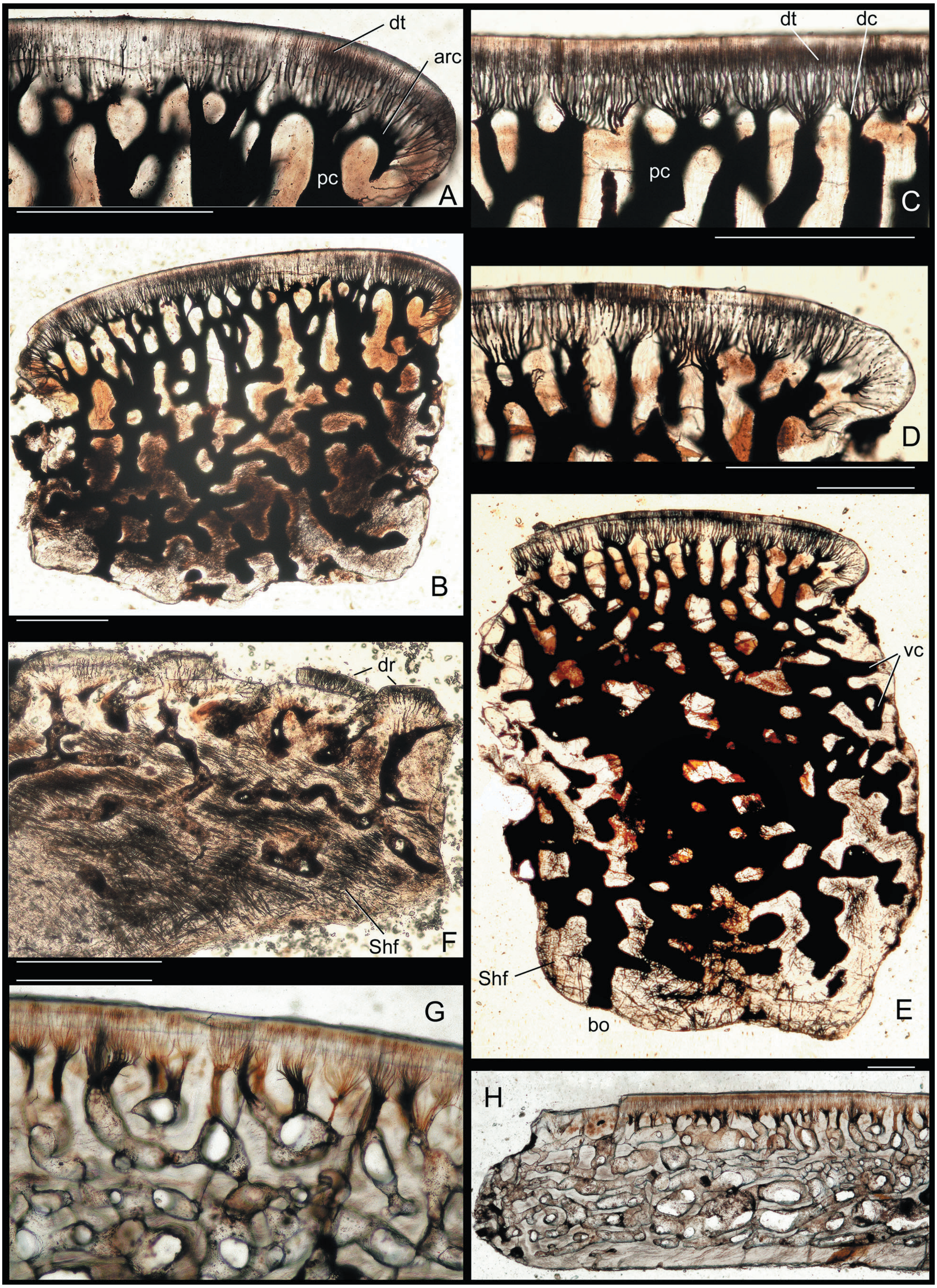
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are rather large relative to scales, with coarse sculpture. The main component of the material is still represented by tesserae (Figs 6H–R; 7E–G), among which rather often tesserae with lateral line canal openings can be found (Fig. 6L–R). Scales, rather big and multi-ridged (Fig. 7D), are also often found in the samples. Figure 7L shows an elongate unit with three ridges which may originate from the side of the body. The small scales composed of one single ridge (Fig. 7H, I) were probably situated on the tail, maybe on the tail lobes. Young or juvenile units of the exoskeleton were not found in the North Timan samples (for more descriptions see Karatajūtė-Talimaa 1970).

Histology. Material from North Timan (Figs 8A–F; 9A–F) and Estonia (Fig. 8G, H) suits for thin sectioning due to good preservation and colour of the units. In adult exoskeletal elements three layers can be distinguished: (1) the upper layer of the orthodentine of ridges and tubercles, (2) the middle spongiose layer, and (3) the denser basal layer. The middle and basal layers (Figs 8B–D; G; 9B, E–F) are both composed of spongiose aspidine pierced by vascular canals. The density of Sharpey's fibre tubules in the middle and basal layers can be high (Figs 8B; 9B, F); the fibre tubules are distributed irregularly or relatively horizontally. The middle spongiose layer can be very thick (Fig. 9E). The vascular canal system is disordered in the middle layer (Figs 8B–D; 9B, E) but distributed more vertically close to the boundary with the upper layer (Figs 8B; 9B, E). These vertical canals are followed by pulp canals and dentine canals. Higher in the ridges bunches of vertical dentine tubules spring from dentine canals (Figs 8A–D, H; 9A–E). Vertical sections of Fig. 8D and Fig. 9E were made at the level where vascular canals open through the basal layer. The horizontal section of a dentine ridge (Fig. 8E, F) reveals the relatively regular canal network of the upper part of the middle layer (Fig. 8F) and its transition into vertically running bunches of orthodentine tubules (Fig. 8E). The tubercles and ridges are composed of typical orthodentine (Figs 8A–E, H; 9A–E). The uppermost (?durodentine) layer is semitransparent and composed of a thin layer of dentine tubules, which are very fine or not visible at all (Figs 8D, G, H; 9A, C). Figure 8G represents a tessera that is pierced by a lateral line canal.

The middle layer, which is very thick in old tesserae, is of well-expressed spongiose aspidine tissue penetrated by vascular canals. The basal layer is not developed in juvenile scales and tesserae or is indistinct; in adult units the aspidine basal layer is rather dense but pierced by sparse, vertically-ascending vascular canals. Sharpey's fibre tubules occur in both the middle and the lower layer.

DISCUSSION

Exoskeleton

Articulated exoskeletons of *Oniscolepis dentata* are not known. We assumed that the body form of *Oniscolepis dentata*, as that of other heterostracans who lived just above the bottom of nearshore epicontinental seas, was somewhat flattened dorsoventrally. Probably the dorsal side of its body was more convex than the ventral side. For the differentiation of the dorsal and ventral sides of the exoskeletal elements or units, we used characteristics of dentine ridges. We supposed that dentine ridges on the elements of the dorsal side carry considerably stronger sculpture (to reinforce the laminar current of water) than those of the ventral side, and these ridges have a medial longitudinal crest and fine ridgelets laterally. This trend towards higher and more rugose dorsal sculpture versus flatter and wider ventral sculpture is often found in other heterostracans.

Oniscolepis dentata was covered with units of different shape and variable sculpture. No large plate or plate fragment with size over 5 mm has been discovered at the type locality or elsewhere. The morphological set of available elements includes (1) head platelets, (2) orbital plate (or tessera), (3) branchial plates, (4) tesserae of the dorsal and ventral sides, (5) tesserae with or without sensory line pores, (6) scales, and (7) body ridge (= crest) elements (body ridge tesserae).

The head was covered with platelets, which are larger than tesserae, sometimes somewhat stretched and convex, and often with irregular sculpture. Anterior and

Fig. 9. A–F, microstructure of the scales and tesserae of *Oniscolepis dentata* Pander. **A**, **B**, vertical cross section of a wide ridge and a relatively deep base, LIGG 20-1278; A, close-up of B showing arch-like dentine canals at the margin of ridge. **C**, vertical longitudinal section of a wide ridge, LIGG 20-1067. **D**, **E**, vertical cross section of a wide ridge with deep base; D, close-up of E; E shows three layers, upper orthodentine, middle spongiose, and lower relatively dense layer with Sharpey's fibre tubules, and a canal going through this layer, LIGG 20-1068. **F**, vertical cross section of an element showing tightly packed Sharpey's fibre tubules in the middle and lower layers, LIGG 20-1062; Loc. 8e, Velikaya River, North Timan, Eptarma Formation, Přidoli, Upper Silurian. **G**, **H**, *Kallostrakon podura* Lankester, vertical cross section of tessera, GIT 570-122; G, close-up of H; Targrove Dingle, Shropshire, Britain, Lower Lochkovian, Lower Devonian. Scale bar 0.25 mm. For abbreviations see Fig. 8.

anterolateral margins of platelets may have parts without sculpture. The eyes were surrounded by simple orbital plates (or tesserae), which had one crescent-shaped ridge following the curvature of the plate base; there was more than one (?three) concentric ring of these orbital units. The entire branchial plate is not known but we assume that it comprised a number of shorter units, in length being similar to the adjoining tesserae and/or platelets. They have longitudinal sculpture on the external surface and irregularly placed flattened dentine ridges on the internal one. The main part of the trunk was covered with tesserae which surrounded or followed platelets posteriorly and possibly laterally. The shape of tesserae can be (a) round or roundish; (b) polygonal or longitudinally elongate; or (c) elongate or roundish, solitary and single-ridged. The base of tesserae can be low or high. There are tesserae bearing pores of sensory line canals and tesserae without the pores. The body behind the tessellated area was covered with scales. According to their measurements, the scales are considered to be (a) large (4–5 mm in length and width), (b) of medium size (2–4 mm), and (c) small (1–2 mm). The scale shape can be (a) subequally rhomboidal, (b) stretched transversly, (c) stretched longitudinally, or (d) irregular. Often markedly asymmetrical right- and left-side scale forms can be found. Both the scales and tesserae can have different patterns of dentine ridges on the crown, with a varying number of ridges. The pattern of ridges on tesserae is concentric but longitudinal on scales. The units can have longitudinal crests on the dentine ridges from the dorsal side of the body or be without such crests on ridges from the ventral side of the body. The body-ridge (= crest) elements (or body-ridge tesserae) usually carry an elongate, longitudinal, primary dentine ridge and longitudinal ridgelets on the margins; cross-wise ridges occur on both the anterior and posterior parts of such elements. Judging from finely ridged and striated sculpture, the body-ridge units probably only occur dorsally. The scales and tesserae of *O. dentata* have a knobby surface. Such ultrasculpture is not seen in any other taxon.

The microstructure of *O. dentata* consisted of three layers: (1) orthodentine of ridges and tubercles, (2) well-expressed spongiose aspidine of the middle layer, and (3) somewhat denser aspidine of the basal layer. The orthodentine of tubercles and ridges resembles the dentine in the crown of katoporid thelodonts, and some other heterostracan scaled taxa. Vascular canals and Sharpey's fibre tubules occurred in both the middle and lower layers. The vascular canals change the direction, becoming connected and diverging again, thus giving the layers spongiose appearance; the location and number of these canals do not correspond to those of ridges.

Comparison

Oniscolepis dentata can be compared with some other tessellated forms. Several earlier authors have treated *Oniscolepis* and *Kallostrakon* within psammosteids (e.g. Bystrow 1955; Obruchev 1958; Tarlo 1964, 1965). We exclude psammosteids from this discussion, as the exoskeleton of Psammosteida is partly composed of large plates. No such plates or plate fragments have been found in *Oniscolepis*.

Some differences occur in the structure of the exoskeleton and microstructure of tesserae of *Tesseraspis* (*T. tessellata* Wills) and *O. dentata. Tesseraspis* Wills is known from tesserae associated into a large plate (Tarlo 1962), while in *Oniscolepis* there occurred small platelets and tesserae. In *Tesseraspis* the vertical chambers (cavities) in the lower layer were obviously not developed, the middle aspidine layer was more homogeneous (uniform?), and the orthodentine of the ridges had the same architecture as in *Oniscolepis* (Tarlo 1964, pl. VIII, figs 3–7; pl. IX, figs 1–4). The division of the exoskeleton into platelets, tesserae, and scales is difficult in *T. mosaica* Karatajūtė-Talimaa (1983). Variability of the shape of its tesserae is high like in *Oniscolepis*. *Tesseraspis mosaica* has some space between the sculpture elements, while in *Oniscolepis* the dentine ridges and tubercles lie rather close to each other. In *T. mosaica* the lateral tesserae are relatively thick, with fairly large ridges and tubercles along the lateral margins; in *Oniscolepis* the thickness of some tesserae can also be notable because of very deep bases, which can exceed eightfold the height of their ridges. Novitskaya (2004) included the genera *Tesseraspis* and ?*Kallostrakon* in the family Tesseraspididae Berg, order Tesseraspidiformes, but she did not discuss *Oniscolepis* because of too few data available about the taxon.

Oniscolepis units remind those of *Corvaspis* Woodward, in terms of symmetry, ridge numbers, crests and serrations, and the pattern and cross-sectional shape of ridges. That is why Stensiö (1958) included *Oniscolepis* (= *Strosipherus*) in the order Corvaspida. However, the histology of *Oniscolepis* and *Corvaspis* is different. For example, *C. kingi* has large vertical but irregular polygonal chambers in the middle cancellous layer, which are separated by vertical septae. In this respect this species is more similar to cyathaspidids than to *Oniscolepis* (Bystrow 1955). In both groups dentine tubules arise in clusters from the dentine or pulp canals.

In *Astraspis* Walcott the dorsal tesserae grade posteriorly into imbricated polygonal scales (Elliott 1987). The same is basically the case with *Oniscolepis* whose tesserae are replaced by scales posteriorly. At least one dorsal body ridge (= crest) was present in *O. dentata*.

It is not possible to speculate whether *Oniscolepis* had more than one dorsally placed body ridge (= crest) composed of tesserae as some other heterostracans or related taxa did (e.g. *Astraspis* and *Tesseraspis* Wills; see Obruchev 1964; Sansom et al. 1997). We found not a single ridge scale of *Oniscolepis* to attest to the occurrence of the body ridge behind the tessellated area. The features of the sculpture and histology of units substantially differ in *Astraspis* and *Oniscolepis*. The former has a star-shaped and smooth, circular to ovate tubercular ornament on fused units (Sansom et al. 1997), while *Oniscolepis* has elongate ridges on non-fused elements. Dentine tubules of *Astraspis* are much finer and simpler than those of *Oniscolepis*.

The ridge on the orbital plate (tessera) of *Oniscolepis* is 1.0 mm long and 0.3 mm wide, thus relatively coarser than those on the head plates (ridge width 0.1–0.2 mm). The overlapped area of the orbital plate is rather wide. The base of the overlapping area is uneven, porous, and slanting outwards. This suggests that there probably existed other plates as well, one more proximal, and the other more distal to the eye. The eye opening could be calculated as being about 2–3 mm in diameter. In the region of the orbit, the ornament is coarse in *Aserotaspis* Dineley & Loeffler, 1976 and *Aporemaspis* Elliott & Loeffler, 1989. The orbit in *Aporemaspis pholidata* is 2 mm in diameter and is surrounded by one to three concentrically placed units (Elliott & Loeffler 1989, text-fig. 2B). Sansom et al. (1997) interpreted a small arcuate plate as a possible circumorbital tessera in *Astraspis desiderata* and reconstructed the eye region consisting of four such tesserae forming one ring. We suggest that the orbital units of *O. dentata* were more similar to those of *A. pholidata*. In *Aporemaspis* the armour is composed of discrete elements (Elliott & Loeffler 1989) like in *Oniscolepis*. Still, the bases of *Aporemaspis* elements (units) form a continuous sheet in the lateral and anterior parts of the shield, the median aspidine layer consists of a regular system of vertical canals, and the layer above it consists of many fine canals rising from the apices of the vertical canals (*ibid*., pp. 886–888). *Aserotaspis* has mainly discrete, interlocking tesserae (Dineley & Loeffler 1976).

Fragments of the branchial plate, one from its posterior part, the other, bigger, from the more anterior part, are defined by some similarities with branchial plates of the cyathaspidids *Tolypelepis* (Märss 1977, fig. 6A, A1) and *Archegonaspis* (T. Märss, pers. obs.), and the thelodont *Phlebolepis elegans* Pander (Märss & Wilson 2008). The maximum width of the larger fragment of the branchial plate of *Oniscolepis* is 3.55 mm, in *Tolypelepis* about 4 mm. The plate is elongate-oval in cross section, with a groove in the visceral side. It carries predominantly longitudinal ridges of usual size on the external surface. Spots of obliquely disposed ridges on the posterior end may refer to the ventral part of the plate as seen in some cyathaspidids (Denison 1964, p. 319). One margin of the plate is smooth both externally and viscerally, with openings of vascular canals. The ridges are finer and flattened on the rest of the visceral surface. In *Oniscolepis*, as seen in the smaller fragment, the posterior unit is deltoid in cross section, as is the posterior part of the branchial plate of *Tolypelepis*. Similarity with the thelodont *P. elegans* is expressed in both species having a finely sculptured visceral surface (Märss & Wilson 2008) and possibly a branchial cover consisting of short units, but lacking any long plate.

The lateral line system in *O. dentata* was built of short vertical canals in which single neuromasts were located. However, there were developed also short U-shaped canals, which connected pores within tesserae or between adjacent tesserae. In that respect the lateral line system of *O. dentata* is comparable to that of *Tolypelepis undulata* Pander, which also had short U-shaped bits of canals (Märss 1977, 1986). In *T. undulata* pores occur also in the scales but not a single *Oniscolepis* scale with pores has been found so far. *Traquairaspis* Kiaer has a narrow row of cyclomorial units (tesserae) along the sensory canals in the ventral median plate, presumably to protect the sensory line canal (Tarlo 1962). In *Astraspis* the lateral line system apparently was developed only in the head region (Sansom et al. 1997), and in this sense *Astraspis* and *Oniscolepis* might be compared. Yet, it is hard to believe that such a large area of the body of a fish was devoid of sensory canals. Therefore we think that sensory line canals behind the head in *Oniscolepis* run in spaces between the scales. Another possibility is that because of different development of tesserae and scales (one developed cyclomorially, another synchronomorially), the pore-containing units on the posterior part of the body might have a different, non-scale like shape and complicate their recognition as scales (see Fig. 2U).

In *Lepidaspis* the cephalothorax consists of units whose basal plates are more or less fused (Dineley & Loeffler 1976), while in *Oniscolepis* the units are not fused. *Lepidaspis*, as a rule, has much simpler tesserae on the cephalothorax. The *Lepidaspis* tesserae have one serrated ridge on each basal plate and two or more ridges per basal plate on the tail (Dineley & Loeffler 1976), while in *Oniscolepis* usually the tesserae and scales are multi-ridged. The histology of *Lepidaspis* is not known.

The *Eriptychius* exoskeleton includes various small plates, scales, and arched ridge scales similar to *Oniscolepis*. Its sculpture is composed of ridges with rather smooth margins; the ridges are narrower anteriorly and widening posteriorly, while in *Oniscolepis* they are serrated and more-or-less of the same width. Some plates of *Eriptychius* seem to have concentrically arranged ridges (Denison 1967, figs 4D, 6C, 8D). The *Eriptychius* scales have a broad, anterior, unornamented, overlapped area, and a posterior exposed area with longitudinal ridges; the ridges can be short, like tubercles, or take up half the length of the scale. In *Oniscolepis* as well some scale types have a very wide anterior overlapped area; the basal layer of *Oniscolepis* adult scales is rather dense, with sparse canal openings. *Eriptychius* has elements of calcified cartilage (Denison 1967) which are not known in *Oniscolepis*. The basal layer, comprising one-third of the total plate thickness, is penetrated by a strikingly large number of vertical ascending vascular canals (Denison 1967) not found in *Oniscolepis* which has vertical canals in the upper part of the middle layer.

Kallostrakon Lankester is the closest form to *Oniscolepis*. The large sample of *Kallostrakon* material at our disposal originating from Targrove Dingle, Shropshire, Britain, shows a very wide variety of tesserae and scales like observed in *Oniscolepis*. Due to post-mortem preservational conditions juvenile units of *Kallostrakon* in Britain and *Oniscolepis* in North Timan have not been found. Still, *Kallostrakon* has more and larger fused units than *Oniscolepis*, which may have just twin-tesserae. The microstructure of *Oniscolepis* is of more vertically placed vascular canals in the lower and middle layers, while in *Kallostrakon* these canals are stretched horizontally (Fig. 9G, H).

In summary, on the basis of the features, such as the composition of the cephalothorax either from the associated plates or tesserae (*Astraspis*, *Tesseraspis*), or discrete but interlocking tesserae (*Aserotaspis*, *Lepidaspis*, ?*Aporemaspis*), or a variable number of plates (*Corvaspis*), we unite in the order Eriptychiida the genera *Eriptychius* Walcott, *Oniscolepis* Pander, and *Kallostrakon* Lankester, which all have discrete units. Relying on the similarities of histological features, we unite *Oniscolepis* and *Kallostrakon* to a new family Oniscolepididae fam. nov. We do not include in it the genus *Eriptychius* because of the histological features. The basal layer of *Eriptychius*, taking up one-third of the total plate thickness, is penetrated by a strikingly large number of vertical ascending vascular canals (Denison 1967) not found in *Oniscolepis* and *Kallostrakon*, which have vertical canals in the upper part of the middle layer.

CONCLUSIONS

In this study the valid taxonomic name *Oniscolepis dentata* Pander, 1856 is rehabilitated, and *Strosipherus indentatus* Pander is synonymized. The exoskeletal elements of *O. dentata* were examined using modern techniques. A significantly wide variability of the platelets, tesserae, and scales was determined; such units as ridge tesserae, orbital plate (or tessera), and fragments of branchial units (plates) were described for the first time. The ontogenetic development of tesserae and scales was considered in greater detail. Tesserae are characterized by the cyclomorial addition of ridges, while scales developed synchronomorially. The *Oniscolepis* materials from the East Baltic and North Timan were compared and only minor differences were detected. The microstructure of the scales from Ohesaare Cliff, Saaremaa, has finer and fewer dentine tubules and canals, and finer Sharpey's fibre tubules than the scales from North Timan, which have wider tubules and canals. *Oniscolepis* Pander was compared with other tessellated taxa. *Kallostrakon* turned out to be the closest form and these taxa are united into a new family Oniscolepididae fam. nov., into the order Eriptychiida Ørvig.

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Tessereeritud heterostraak *Oniscolepis* Pander, 1856 Baltikumi ja Põhja-Timaani Hilis-Silurist ning Vara-Devonist

Tiiu Märss ja Valentina Karatajūtė-Talimaa

Pander (1856) tuvastas esimesena neli *Oniscolepis*'e ja kolm *Strosipherus*'e liiki, mis hiljem, välja arvatud *O. magna*, leiti kuuluvaks *Oniscolepis dentata* alla (Rohon 1893). Artiklis on kirjeldatud uuesti ja illustreeritud *O. dentata* plaadikeste, tesseeride ning soomuste morfoloogilisi ja histoloogilisi variatsioone. Peaplaadikeste, kahe branhiaalplaadi ja ühe orbitaalplaadi (või tesseeri) fragmente ning kehal olnud kõrgemate pikiharjade elemente on kirjeldatud esmakordselt. Baltikumi ja Põhja-Timaani *Oniscolepis*'e eksemplarid erinevad üksteisest vähe: tüüpleiukohast Ohesaare pangalt Saaremaalt uuritud soomuste mikrostruktuuris eristub vähem dentiini- ning Sharpey-kiudude kanalikesi ja need on peenemad kui Põhja-Timaani eksemplarides. *Oniscolepis* Pander ja *Kallostrakon* Lankester on ühendatud uueks sugukonnaks Oniscolepididae fam. nov. tüüpperekonnaga *Oniscolepis* Pander.