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A redescription of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (Vertebrata: †Pteraspidomorphi: Heterostraci) from the Lochkovian (Lower Devonian) of Severnaya Zemlya, Russia, with a review of tessellated heterostracan taxa

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ABSTRACT:

Blieck, A., Elliott, D.K. and Karatajūtė-Talimaa, V.N. 2018. A redescription of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (Vertebrata: †Pteraspidomorphi: Heterostraci) from the Lochkovian (Lower Devonian) of Severnaya Zemlya, Russia, with a review of tessellated heterostracan taxa. *Acta Geologica Polonica*, **68** (3), 275–306. Warszawa.

Material of tesseraspids (Tesseraspidiformes) is reported from the uppermost Severnaya Zemlya Formation (Lochkovian, Lower Devonian) of the Severnaya Zemlya archipelago, in the Russian Arctic, where it is associated with other vertebrate remains, including corvaspids, acanthodians, and large but rare specimens of osteostracans. The tesseraspid material is not abundant, and most often preserved as a "patchwork" of bony platelets (tesserae), except for a few partly articulated specimens. We redescribe the holotype of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983, whose head carapace is preserved as a flattened tube of adjacent tesserae. This material is compared to the already published tesseraspid taxa, i.e., *T. tessellata* Wills, 1935, *T. toombsi* Tarlo, 1964, *T. mutabilis* (Brotzen, 1934), *T. oervigi* Tarlo, 1964 emend. Dineley and Loeffler, 1976, *T. denisoni* Tarlo, 1964, and *T. talimaae* Tarlo, 1965. All species are based upon rare and incomplete material, as no head carapaces associated with trunk and tail are known, and so, the intraspecific variability is also unknown. Distinction between "species" is based on the detail of the superficial sculpture of the tesserae of the head carapaces, which is unsatisfactory. It is concluded that only four of the nominal species can be retained. A review of all other known tessellated pteraspidomorphs indicates that our knowledge of tessellated heterostracans is currently insufficient to support a meaningful classification.

Key words: Tessellated heterostracans; Tesseraspidiformes; Lochkovian; Severnaya Zemlya; Comparative anatomy; Systematic review.

This paper is dedicated to our colleague and friend Dr. Elga Mark-Kurik (26.12.1928–06.11.2016), an active expert in Palaeozoic vertebrates, who participated in expeditions to the Russian Arctic regions, and in particular to Severnaya Zemlya.

Text-fig. 1. Members of the 1978 Soviet summer expedition to Severnaya Zemlya: base camp along the Matusevich River, with, from left to right: Juozas J. Valiukevičius (Vilnius, Lithuania), Nikolai Kolotov (Novosibirsk, Russia), the driver, Rostislav G. Matukhin (Novosibirsk, Russia), Vladimir V. Menner (Moscow, Russia), Valentina N. Karatajūtė-Talimaa (Vilnius, Lithuania), the radio operator, and Avo Kärber (Estonia, cook). They stand in front of the Severnaya Zemlya Formation that shows a homoclinal structure

INTRODUCTION

This paper is part of a series of publications on Silurian–Devonian vertebrate faunas from the Severnaya Zemlya archipelago, on the northern margin of Russian Arctic regions. This program is part of a French-Lithuanian collaboration, including study of the collections of the Lithuanian Institute of Geology and Geography from 1997 to 2005 (Karatajūtė-Talimaa and Blieck 1999; Blieck and Karatajūtė-Talimaa 2001; Blieck *et al.* 2002). This activity was part of IGCP projects 406 "Circum-Arctic Palaeozoic Vertebrates" (1996–2000) and 491 "Middle Palaeozoic Vertebrate Biogeography, Palaeogeography and Climate" (2003–2008), and later of the French-Lithuanian exchange programme Gilibert (2005–2008). The material was originally collected by Drs. V.N. Karatajūtė-Talimaa, E. Mark-Kurik, and J.J. Valiukevičius from expeditions to the archipelago in 1978 and 1979. The Silurian–Devonian sedimentary sequence of Severnaya Zemlya yields rich assemblages of heterostracan vertebrates, providing important information on their taxonomy, phylogeny, biostratigraphy and palaeobiogeography.

In this paper, we focus on tesseraspidid heterostracans, a group of vertebrates that is rarely represented in the Silurian–Devonian. Heterostracans were first collected on the October Revolution Island of Severnaya Zemlya in 1978 during an expedition with Drs. V.V. Menner, R.G. Matukhin, V.M. Kuršs, J.J. Valiukevičius and V.N. Karatajūtė-Talimaa (Text-fig. 1), and subsequently in 1979 during an expedition when Dr. E. Mark-Kurik collected additional material (Karatajūtė-Talimaa 1983, p. 22). The tesseraspidid material comes from four localities in the uppermost Severnaya Zemlya Formation of October Revolution Island (Matukhin and Menner 1999). Their faunal lists are provided in the Appendix.

The original paper on *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 comprised a preliminary paper on the material presented here, with a rather short description of the holotype. It is more precisely described and figured herein. New specimens have been prepared both mechanically with needles, and by etching in dilute formic acid. Palaeohistological thin sections have been prepared and are also described and figured. All specimens are curated at the Lithuanian Institute of Geology and Geography (prefix LIG = Geologijos ir geografijos institutas in Lithuanian), Nature Research Centre, Akademijos 2, Vilnius, Lithuania (new address and information provided by Dr. Gražina Skridlaitė, e-mail on 21.04.2017).

COMMENTS ON TAPHONOMY

The material is not abundant and is most often preserved as a "patchwork" of broken fragments of carapaces, except for a few partly articulated specimens. This probably means that the conditions of deposition and/or transportation of specimens after death were quite different in the different localities. The articulated head carapace of *T. mosaica* from the Matusevich River (locality 1-21 of Matukhin and Menner 1999; Text-fig. 1 and Appendix, locality 1 herein) may be used as an argument for a short transportation, if any, in this locality. But it should be noted that the degree of articulation is most strongly related to the level of decomposition of the organism before it is transported. Fresh specimens can be transported some distance without disarticulation. The state of preservation of the disarticulated tesserae found with the articulated head carapace is very good and allowed thin sections to be made for histological studies (see the corresponding section below). This probably also means that the material was buried quickly and suffered little diagenetic alteration. However, this head carapace is nearly totally flattened indicating compaction of the sediment. The other three localities that have yielded *Tesseraspis* Wills, 1935 remains also come from the uppermost Severnaya Zemlya Formation, in a sequence which corresponds to the same level as the Matusevich River locality (VNKT's personal field observations; J.J. Valiukevičius, pers. comm., 2005; and see Männik *et al.* 2002, p. 111). However, the material of *Tesseraspis* from these three localities consists of disarticulated and fragmentary specimens, either separated tesserae, broken pieces of head and/or trunk carapaces, or only partially articulated parts of head carapaces. This probably corresponds either to higher energy conditions of deposition at these localities or a longer transportation of the material after death.

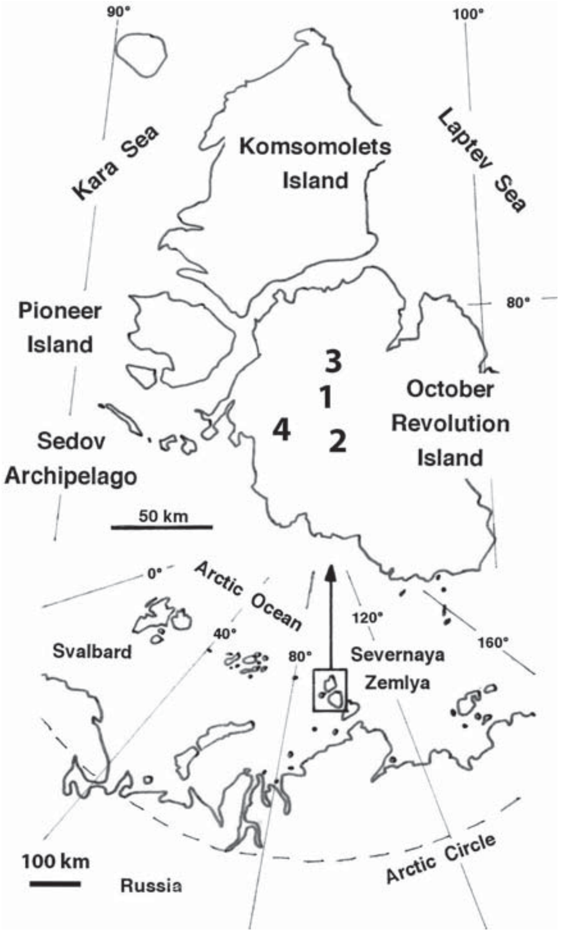
The Matusevich River locality (locality 1-21 of Matukhin and Menner 1999; Männik *et al.* 2002, fig. 12) containing *T. mosaica* is also the locality where an articulated specimen of *Corveolepis elgae* Blieck and Karatajūtė-Talimaa, 2001 was discovered. Numerous specimens of acanthodians have also been collected at this locality, namely *Acritolepis ushakovi* Valiukevičius, 2003, *Nostolepis fragilis* Valiukevičius, 2003, and *Acanthopora transitans* Valiukevičius, 2003 (Valiukevičius 2003, figs 1, 19, 4, respectively). At the other three localities, partly articulated specimens of acanthodians have been collected, namely *Acritolepis ushakovi*, *Poracanthodes* sp. cf. *P. subporosus* Valiukevičius, 1998, and *Acanthacanthus ornatus* Valiukevičius, 2003 at the Spokoinaya River locality (41-12 of Matukhin and Menner 1999; Valiukevičius 2003, figs 2, 28E, 30A); *Acritolepis urvantsevi* Valiukevičius, 2003, *Nostolepis decora* Valiukevičius, 2003, and *Acanthospina irregulare* Valiukevičius, 2003 at the Pod'emnaya River locality (67-12 of Matukhin and Menner 1999; Valiukevičius 2003, figs 13, 17, 46); and *Acanthopora transitans* at the Ushakov River locality (21-9 of Matukhin and Menner 1999; Valiukevičius 2003, fig. 41A–C). Valiukevičius (2003, table 2) analysed the distribution and abundance of the different acanthodian species in all four localities: the two localities richest in acanthodian specimens are undoubtedly those at the Matusevich River and Pod'emnaya River (localities 1-21 and 67-12), but, much more articulated material has been collected at the Matusevich River (locality 1-21) than in the other three. This result for the acanthodians is in agreement with the observations on the *Tesseraspis* material.

In the Matusevich locality (1-21) all the articulated specimens are preserved in carbonate concretions within the uppermost part of the Severnaya Zemlya Formation, which is composed of predominantly dark grey, thinly laminated, non-carbonate argillites with thin limestone interlayers (Matukhin and Menner 1999, p. 39). The occurrence of concretions is certainly related to the state of preservation of the fossil material. At this locality, there is only one layer with fish-bearing concretions, constituting a good field marker. The lithology of the other localities differs from that at the Matusevich River. The Pod'emnaya River locality (67-12), in the upper member of the formation (22 m), is composed of greenish red argillites with limestone interlayers and contains two layers with fish-bearing concretions, separated from each other by c. 1.30 m in the field. The Spokoinaya River locality (41-12), in the clayey member of the formation (c. 17 m), which is transitional to the overlying Pod'emnaya Formation, is composed of dark argillites with fish-bearing concretions. So, it seems that there were differences in the local conditions of deposition and preservation. The more reduced uppermost member of the Severnaya Zemlya Formation at the Matusevich locality (10.5 m in thickness, as compared to 22 m at the Pod'emnaya River locality, and to 17 m at the Spokoinaya River), made of darker and more thinly laminated clayey deposits, may correspond to quieter, dysaerobic conditions of deposition and preservation. The taphonomic conditions at the Matusevich River locality were much better, which makes this locality a potential Fossil-Lagerstätte.

STRATIGRAPHY WITH COMMENTS ON THE AGE OF THE SEVERNAYA ZEMLYA FORMATION

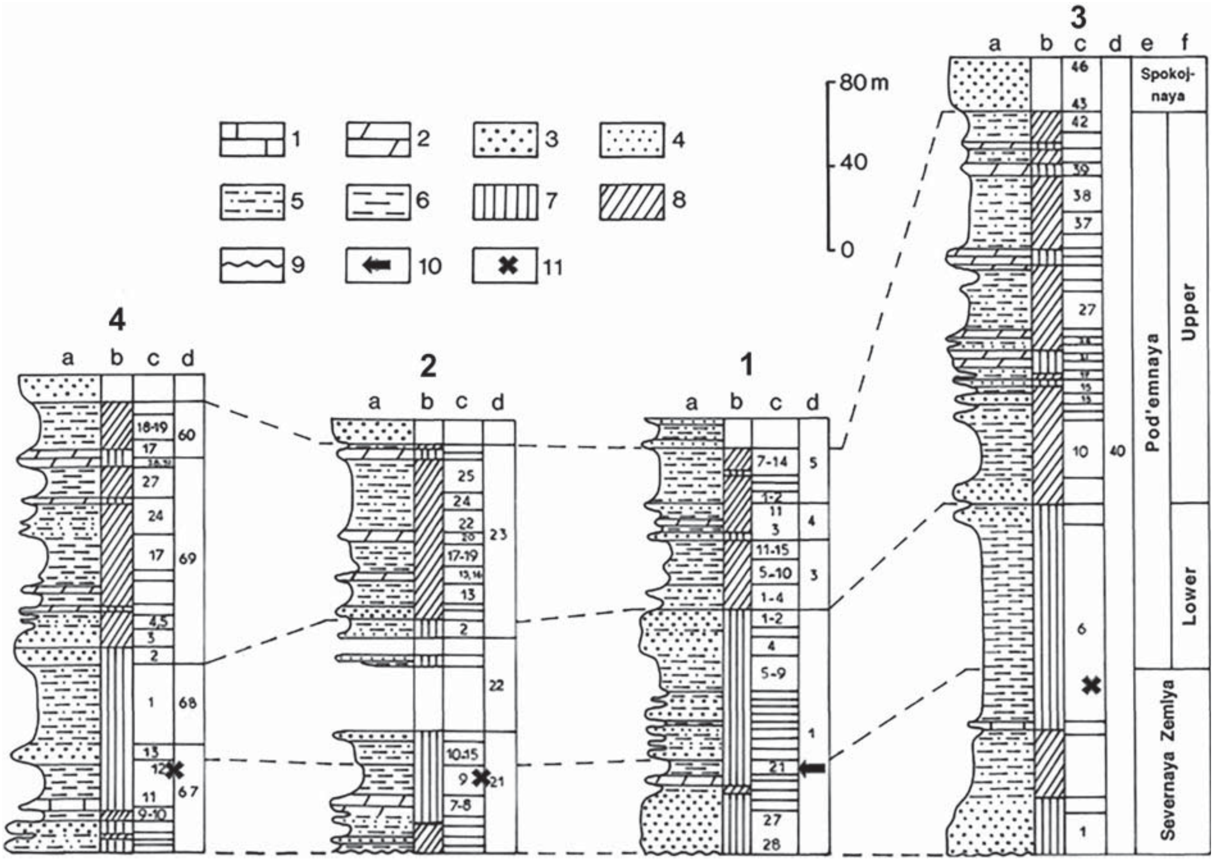
All tesseraspid specimens described here were collected in the uppermost Severnaya Zemlya Formation from four sections on October Revolution Island, described by Matukhin and Menner (1999, fig. 8), namely the Pod'emnaya River, Ushakov River, Matusevich River and Spokoinaya River sites (Text-figs 2, 3). The localities show an assemblage of heterostracans, with tesseraspids and corvaspids, associated with osteostracans, acanthodians and rare elasmobranch? remains (see section 'Comments on taphonomy' below and the Appendix). This assemblage is probably linked to a lithofacies that mostly consists of carbonate siltstones with many concretions (see section 'Comments on taphonomy' below).

The Severnaya Zemlya Formation is classically dated as "Dittonian" (Karatajūtė-Talimaa 1983), or Lochkovian in the standard Lower Devonian Series, and more precisely as lower Lochkovian (Matukhin and Menner 1999, table 2; Karatajūtė-Talimaa and Blieck 1999, table 20; Blieck *et al.* 2002, figs 3–5; Männik *et al.* 2002, fig. 3). This age is based upon its heterostracan assemblage with *Anglaspis*, *Corvaspis*, *Ctenaspis*, *Lepidaspis*, *Phialaspis*, *Protopteraspis*, *Tesseraspis*, and *Unarkaspis*? (Männik *et al.* 2002, p. 111, citing Karatajūtė-Talimaa and Blieck 1999). However, this is incorrect because, apart from tesseraspids and corvaspids, the other cited genera do not occur in the Severnaya Zemlya Formation (see Karatajūtė-Talimaa 1983, p. 22; Karatajūtė-Talimaa and Blieck 1999, table 20). Additionally, *T. mosaica* and *C. elgae*, both from the uppermost Severnaya Zemlya Formation (see Blieck and Karatajūtė-Talimaa 2001), are endemic to Severnaya Zemlya. The age of the Severnaya Zemlya Formation is in fact constrained by its over- and under-lying formations, and its acanthodian content.



Text-fig. 2. Map of the Russian Arctic regions (bottom) with enlargement of the northern Severnaya Zemlya archipelago (top). Numbers 1–4 refer to the stratigraphical logs described in Text-fig. 3 (see Blieck and Karatajūtė-Talimaa 2001, fig. 1)

The overlying Pod'emnaya Formation yielded the richest heterostracan assemblage of the whole archipelago, including *Phialaspis* Wills, 1935, *Ctenaspis* Kiær, 1930, *Anglaspis* Jækel, 1927, *Poraspis* Kiær, 1930, *Irregulareaspis* Zych, 1931, *Homalaspidella* Strand, 1934 and *Unarkaspis*? Elliott, 1983. This correlates with the late Lochkovian Ben Nevis Formation, and perhaps the uppermost part of the underlying Frænkelryggen Formation of Spitsbergen (Blieck *et al.* 2002, fig. 5). An age that is supported by the ostracode content of the Pod'emnaya Formation (references in Männik *et al.* 2002, p. 113). The acanthodian assemblage of the Severnaya Zemlya Formation (with its articulated specimens corresponding to several species endemic to Severnaya Zemlya) is attributed to the *Poracanthodes menneri* Subzone as a lower part of the *Nostolepis minima* Zone, "only based on the occurrence of *Nostolepis minima*", and of *Poracanthodes menneri* (Valiukevičius, 1992) (Valiukevičius 2003, p. 197 and table 3). With regard to the Devonian standard conodont zonation, the *Poracanthodes menneri* Subzone "is related to the *woschmidti* Zone … indirectly based on correlations of several studied regions" (such as Belarus and Podolia in Ukraine; Valiukevičius 2003, p. 199), thus lower Lochkovian. As noted by Karatajūtė-Talimaa (2002), thelodonts are extremely rare in the Severnaya Zemlya Formation which has only yielded "doubtful Thelodontida indet.", and no turiniid species, which is most probably due to the lithofacies. Thelodonts are more abundant and



Text-fig. 3. Stratigraphical logs of the Severnaya Zemlya and Pod'emnaya formations on October Revolution Island, Severnaya Zemlya, after Matukhin and Menner (1999, fig. 8). Logs 1 to 4 refer to localities 1–4 of Text-fig. 2, and of Blieck and Karatajūtė-Talimaa (2001, fig. 2). 1, Matusevich River; 2, Ushakov River; 3, Spokoinaya River; 4, Pod'emnaya River. Each tesseraspid-bearing bed is referenced by the number of the outcrop section along one of the rivers of October Revolution Island (d), and the number of the bed in the section (c) (Matukhin and Menner 1999, fig. 2; Männik *et al.* 2002). Key: a, lithostratigraphic log; b, colour of rock; c, beds, with tesseraspid-bearing beds indicated by symbols; d, outcrop; e, formation; f, 'subformation'; 1, limestones; 2, dolomitic marls; 3, sandstones with conglomerates; 4, sandstones; 5, siltstones; 6, shales; 7, grey; 8, red and variegated; 9, erosional surface; 10, *Tesseraspis mosaica* + *Tesseraspis* sp.; 11, *Tesseraspis* sp.

diversified in the overlying Pod'emnaya Formation, with scales of *Turinia composita* Karatajūtė-Talimaa, 2002, *Boreania minima* Karatajūtė-Talimaa, 1985, *Nikolivia aligera* Karatajūtė-Talimaa, 2002, *Canonia* sp. cf. *C. grossi* Vieth, 1980, and *Turinia pagei* (Powrie, 1870). The co-occurrence of *T. pagei* and *B. minima* in the Matusevich River section, locality 4-3, gives a Lochkovian (and probably early Lochkovian) age to the middle Pod'emnaya Formation (Matukhin and Menner 1999, p. 43; Karatajūtė-Talimaa 2002, pp. 796, 802, 803). So, as for acanthodians, this constrains the age of the Severnaya Zemlya Formation to the early Lochkovian. The rarity of thelodonts in the Severnaya Zemlya Formation, and in particular of the index species *T. pagei*, shows that the latter cannot be used to define the base of the Devonian here (contrary to most basal Devonian sequences over the Old Red Sandstone Continent; see references in Blieck *et al.* 2000).

Constraining the age of the Severnaya Zemlya Formation by its underlying formation(s) is more difficult, due to an almost general unconformity at its base. In the four sections dealt with here, the Severnaya Zemlya Formation unconformably rests on the late Silurian Krasnaya Bukhta (Pridoli) or Ust'Spokoinaya (Ludlow) formations (Matukhin and Menner 1999, figs 8, 14; Männik *et al.* 2002, p. 111). In the Matusevich and Ushakov River sections, the whole Pridoli is lacking. In the Spokoinaya River section, the Severnaya Zemlya Formation rests disconformably on the Pridoli Krasnaya Bukhta Formation (Matukhin and Menner 1999, figs 7, 8). This is perhaps not the case in the Pod'emnaya River section, but this section was not visited by VNKT in 1978. It is probable that the base of the Devonian is absent in the sections we are concerned with here.

The stratigraphic occurrence of tesseraspids is very restricted in the Lower Devonian of Severnaya Zemlya. *Tesseraspis mosaica* and *Tesseraspis* sp. were collected in the topmost part of the Severnaya Zemlya Formation, in locality 1-21 of the Matusevich River section, while *Tesseraspis* sp. was collected in localities 21-9 of the Ushakov River section, 41-12 of the Spokoinaya River section (equivalent to outcrops '40' described by Matukhin and Menner 1999, fig. 8; see Matukhin and Menner 1999, fig. 2-III; Männik *et al.* 2002, fig. 9), and 67-12 of the Pod'emnaya River section (Text-fig. 3 and Appendix). Tesseraspids are thus dated as early Lochkovian in the Severnaya Zemlya archipelago. This very restricted stratigraphic distribution may make *T. mosaica* a potential index heterostracan taxon for the Lower Devonian of the Arctic regions if further work supports this.

A QUESTION OF SEMANTICS: WHAT ARE TESSERAE?

A short historical survey

There is uncertainty as to the meaning of the word 'tessera' used to describe small bony platelets that constitute part or whole of the head carapace of some heterostracans. It is classically used for, e.g., the Ordovician genus *Astraspis* Walcott, 1892 to which *Tesseraspis* is sometimes compared (see section 'Preliminary nomenclatorial and taxonomic remarks' below). It seems that "it will be difficult to find the earliest usage for such a common term because it is used outside fish studies and much earlier than for fossil fishes (agnathans, placoderms…)" (H.-P. Schultze, e-mail on 5.06.2017). For instance, in his book "The Pattern of Vertebrate Evolution", Halstead (1969) does not say who coined the term or first discussed the concept (S. Turner, e-mail on 12.08.2017). For Gross (1963, p. 141): "… Tesserae, [sind] kleine, polygonale Plättchen…" (small polygonal platelets). Tarlo (1962, 1964, a.k.a. Halstead or Halstead Tarlo) who made a thorough review of heterostracans with tesserae (or what were supposed to be tesserae), does not seem to have given a strict definition of the term. He simply says that in *Astraspis* and *Eriptychius* Walcott, 1892 the "Carapace [is] composed of discrete polygonal tesserae" (Tarlo 1962, pp. 252, 254), that in *Tesseraspis* it is "composed of independent polygonal plates or tesserae which may be fused to form discrete larger plates" (Tarlo 1962, p. 258), and that tesserae are 'small polygonal plates' (Tarlo 1964, p. 2), although he distinguishes the 'independent tesserae' of *Tesseraspis* (Tarlo 1964, p. 41) from the 'superficial tesserae' of, e.g., *Psammosteus megalopteryx* (Trautschold, 1880) (Tarlo 1964, pl. 1, fig. 5; also his fig. 14A 'superficial polygonal cyclomorial tesserae'). The latter can in fact not be considered as actual tesserae (see here below the paragraph devoted to psammosteids). Tarlo (1967) did not give a definition of tesserae, but proposed a series of growth stages leading to a tessellated pattern for the heterostracan carapace in which small independent bony elements form by accretion of concentric tubercle rings around a central primordial tubercle, as is observed on *Astraspis* (Tarlo 1967, fig. 2; also Halstead 1973, fig. 6a–c; what was called cyclomorial growth by, e.g., Ørvig 1951 – *fide* Tarlo 1967). For Dineley and Loeffler (1976, p. 137) "… tesserae … are separate in their deep and superficial layers". Reif (1982, p. 297) mentions that "In Drepanaspidae [i.e., psammosteids] the large, probably growing head plates are separated by a mosaic of small plates ("tesserae")". For Francillon-Vieillot *et al.* (1990, p. 486): "Tesserae are either small plates of dermal armor in fossil ostracoderms and placoderms … or prisms or small blocks of calcified tissue belonging to the cartilaginous endoskeleton of elasmobranchs and holocephalans …". They and Moss (1968) argue that the term tesserae should be used for bony structures and not for prismatic cartilage. Janvier (1996, p. 87) defines tesserae as "loosely attached polygonal units of spongy aspidine". For Dean *et al.* (2010, p. 263): "Each tessera is a geometric block (hundreds of microns deep and wide in adults), comprised of hydroxyapatite crystals on a collagen scaffold". These definitions do not say what is the size limit of a tessera or small polygonal platelet.

What can be retained

Tesserae are small plates of dermal bony armour of fossil ostracoderms (and gnathostomes); they are independent of other bony dermal elements, not being fused with their surrounding tesserae, platelets or plates (*sensu* Dineley and Loeffler 1976; Francillon-Vieillot *et al.* 1990). They are distinguished from scales of the trunk and tail by the absence of overlapping or overlapped areas.

Tesserae have been considered to occur in corvaspids (see e.g., Tarlo 1960, 1964, 1965, and thus classified as psammosteids). However, as Tarlo (1965, p. 16 and pl. 3) says in the diagnosis of *Corvaspis kingi*, its dermal armour has an "Ornamentation of short, longitudinally aligned dentine ridges arranged in superficial tesserae, generally separated from one another by a narrow groove.” In such conditions, the external elements seen on the head carapace of corvaspid heterostracans, being fused at their basal lamellar layer, are not tesserae. They were named ‘small tesseriform units’ by Blieck and Karatajūtė-Talimaa (2001). It should be noted here that the term ‘ornamentation’, frequently used for describing the superficial structure of most early vertebrate dermal bony elements such as plates, platelets, tesserae, and scales, may be considered as inappropriate. This word means ‘a thing used or serving to adorn’, and relates to decoration; so, it is probably worth using the term ‘sculpture’ or ‘superficial sculpture’ (see discussion by Märss 2006, p. 235).

Lepidaspis serrata Dineley and Loeffler, 1976, originally classified as an *incertae sedis* vertebrate, is often considered as an heterostracan (by e.g., Janvier 1996; Keating *et al.* 2015). Keating *et al.* (2015) showed that the histology of *Lepidaspis* Dineley and Loeffler, 1976 is four-layered as in typical heterostracans with a superficial layer of dentine tubercles capped by enameloid, a compact reticular layer with canals, a middle cancellous layer of aspidin, and a basal isopedin-like lamellar layer [illustrated by thin sections through a portion of a head shield where the ‘scale-units’ are fused, Keating *et al.* 2015, fig. 2, erroneously attributed to ‘*Loricopteraspis*’ *serrata*]. Its head carapace is entirely covered with "small scale-units with basal plates more or less fused” and 3–14 mm long (Dineley and Loeffler 1976, pp. 175, 176). These so-called scale-units are typically not fused on some specimens where they could be called tesserae (see Dineley and Loeffler 1976, fig. 77B, pl. 31, fig. 2, pl. 32, figs 2–8). On some other parts, they are fused and “the sutures between individual basal plates are not distinguishable” (Dineley and Loeffler 1976, p. 176), although on others they are, that is, the individual elements are fused basally, and the external margins of their outer faces are or are not visible.

Therefore, these cannot be called tesserae but could perhaps be referred to as ‘fused tesserae’. Another tessellated heterostracan, *Aporemaspis pholidata* Elliott and Loeffler, 1989, shows a carapace that is composed of “discrete elements, 0.5–1.5 mm long (thus much smaller than the scale-units of *Lepidaspis*)… the bases of which are normally not fused” (Elliott and Loeffler 1989, p. 884 and fig. 2A) although “[on] the lateral margin of the dorsal surface … the elements are joined together at the base” (Elliott and Loeffler 1989, p. 884) as in *Lepidaspis*. The unfused elements of *Aporemaspis* Elliott and Loeffler, 1989 could thus be called tesserae (unless they are just odontodes because they resemble thelodont scales: S. Turner, e-mail, 26.08.2017). Elliott and Loeffler (1989, pl. 107, fig. 5) described the histology of an isolated element of *Aporemaspis*, which is composed of a basal, partially lamellar layer, a middle aspidin layer with thick canals, an upper more compact layer with finer canals, and a superficial layer that they interpret as made of dentine, and thus could well be of enameloid. This is consistent with a general heterostracan histology. Both taxa, *Lepidaspis* and *Aporemaspis*, and others will be commented on further in the section ‘Discussion’ below.

Psammosteids

Another group of heterostracans, the psammosteids, is well known for bearing tesserae. However, two different kinds of tesserae must be considered here: a first type which consists of independent polygonal platelets or ‘actual tesserae’, and a second type which does not correspond to independent elements and cannot be called tesserae. The first type comprises small polygonal plates that occur between the main plates of the head carapace. These platelets are usually called tesserae. They typically occur on articulated specimens of *Drepanaspis* Schlüter, 1887 (the only psammosteid known from fully articulated specimens; see e.g., Gross 1963, figs 6, 9, pl. 6–8; Obruchev and Mark-Kurik 1965, pl. 1–4), considered as a ‘primitive’ genus for psammosteids [e.g., Obruchev 1945 (*fide* Tarlo 1964, p. 21); Glinskiy 2017, but *contra* Pernègre and Elliott 2008 who resolved *Drepanaspis* as basal within the pteraspids, as did also Randle and Sansom 2017 but with a different phylogenetic scheme). *Drepanaspis* tesserae have various shapes from quadrangular or rhombic, to polygonal; they are more or less elongated, and sometimes imbricated, and are 7 to 30 mm long (Gross 1963, p. 142 and fig. 9C–M). They clearly appear to be independent from each other, that is not fused with their neighbouring bony elements, either other tesserae or plates. Tesserae have also been found in other psammosteids, but have rarely been illustrated (e.g., by Obruchev and Mark-Kurik 1965, figs 23, 41, 67a, 90; Tarlo 1965, pl. 8, fig. 2, pl. 19, fig. 6; Moloshnikov 2009, pl. 8, figs 6, 8; however, in the latter case, the tessera at the posterior end of a dorsal median plate of *Schizosteus shkurlatensis* Moloshnikov, 2009 might well be interpreted as a small dorsal spine or first dorsal fulcral scale). These ‘first type’ tesserae appear to be a “special feature of psammosteids” (“ein besonderes Merkmal der Psammosteiden”; Gross 1963, p. 141). They could certainly be interpreted as a synapomorphy of the group when considered as derived from pteraspids [Obruchev 1945 (*fide* Tarlo 1964, p. 21); Blieck 1984], but *contra* Halstead 1973, who considered pteraspids as derived from a 'stock' of tessellated (or supposedly tessellated) heterostracans that Tarlo (1964, 1965) classified within the order Psammosteiformes. This included *Tesseraspis*, *Oniscolepis* Pander, 1856, *Kallostrakon* Lankester, 1868, *Corvaspis* Woodward, 1934, *Weigeltaspis* Brotzen, 1933 and all psammosteids, that is all heterostracans with tesserae or supposed tesserae. Psammosteids (*sensu* Obruchev 1964: order Psammosteida; or Glinskiy 2017: monophyletic group [Drepanaspididae [Guerichosteidae [[Obrucheviidae + Pycnosteidae] ['Psammolepididae' + Psammosteidae]]]]) and pteraspids share a series of apomorphic characters, including radiating sensory canals on the dorsal median plate (or disc), the occurrence of paired cornual plates, and an unpaired dorsal spine (or spinal plate) (Blieck 1984, p. 97). Additionally, the smallest known (thus supposedly the youngest) *Drepanaspis gemuendenensis* Schlüter, 1887 specimen has a head carapace that is made only of plates, without tesserae (Kutscher 1933, pl. 34, fig. 2; Gross 1963, pl. 9, fig. 3), contrary to all adult specimens which show plates and intermediate tesserae (e.g., Gross 1963). So, it has been suggested that these 'first type', intermediate tesserae are secondary for psammosteids, they appear during ontogenic development and their number is important in allowing the adult individuals to grow larger (Blieck 1984, p. 97). They are considered as non-homologous to the tesserae of e.g., *Tesseraspis* that are supposedly primary.

The second type of 'tesserae' in psammosteids has been illustrated by Mark-Kurik (1999), Blom *et al.* (2006), Glinskiy and Mark-Kurik (2016), Glinskiy (2017), and Glinskiy and Nilov (2017). Mark-Kurik (1999) has published a series of dermal skeletal microremains of *Psammosteus* sp. from Essi, in SE Estonia, collected in the Givetian (Middle Devonian) Abava Substage of the Burtnieki Stage. "The elements described … are small independent ones, both single and complex. Some of them resemble turiniid thelodont scales, the others chondrichthyan scales." (Mark-Kurik 1999, p. 5). "The single elements may be very small, 0.3–0.5 mm high, but they can also reach 1.0 mm in height. In the larger complex elements, forming tiny platelets ("tesserae") or scales, the size range varies from 1.0 to 2.1 mm in length and from 0.8 to 2.5 mm in width" (Mark-Kurik 1999, p. 9 and figs 3–6), thus much smaller than the 'first type tesserae' of psammosteids. Mark-Kurik (1999, p. 7) clearly says that "The detachment of the "tesserae" is the reason why a fragment of the dorsal plate of *Psammosteus* sp. (Figure 8a), … found from the Essi locality, is completely lacking ornamentation" and "Loose attachment characterizes the platelets ("tesserae") and tubercles of the carapace plates, particularly the median plates of representatives of this genus [*Psammosteus*]". She refers to a vertical thin section of a bony plate of *Psammosteus megalopteryx* figured by Gross (1933, fig. 4B) showing "that the fusion of the vascular canals in the upper part of the "spongiosa" enables the detachment of the "tesserae" from a median plate" (Mark-Kurik 1999, p. 7).

Glinskiy (2017, poster fig. 3F) also shows such "cavities between the tessera and the plate" of *Psammosteus megalopteryx* and *P. asper* Obruchev in Obruchev and Mark-Kurik, 1965. Tarlo (1964, fig. 14A) also figured part of the superficial sculpture ('ornamentation') of a plate of *Psammosteus megalopteryx* with "superficial polygonal cyclomorial tesserae showing cavity due to loss of tessera" (compare with Tarlo 1964, pl. 1, figs 2, 5 where the 'superficial tesserae' are *in situ*). Keating *et al.* (2015, p. 673 and fig. 10A: *P. megalopteryx*) say that "A discontinuity exists between these layers [that is, between their reticular Layer L1 and trabecular Layer L2 (the 'spongiosa' of Gross)], which is interpreted as a line of arrested growth demarking two distinct phases of mineralisation (Fig. 10A)." So, all the *Psammosteus* Agassiz, 1844 microremains described by Mark-Kurik (1999) seem to correspond to detached elements from head plates of the carapace. They are either 'single' (one tubercle with a pulp cavity, thus corresponding to an odontode) or 'complex' (with two or more tubercles). They most often lack a base (Mark-Kurik 1999, p. 10 and fig. 3a, b). Similar elements, that Blom *et al.* (2006, fig. 2A–D) have attributed to *Psammosteus* sp., have been described from the late Frasnian of a locality on Ymer Ø in East Greenland. Other 'complex elements' with a "high cone-shaped central tubercle, surrounded by circles of smaller ones" and 3.1×2.2 mm in size, have been published by Glinskiy and Mark-Kurik (2016, fig. 7C, D) from the ventral side of a branchial plate of *Psammosteus livonicus* Obruchev in Obruchev and Mark-Kurik, 1965 (Amata Stage, lower Frasnian, Latvia). These are interpreted as 'cyclomorial tesserae' by Glinskiy and Mark-Kurik (2016). Glinskiy and Nilov (2017), while describing various *Psammosteus* species from the early Frasnian Amata Stage of eastern Latvia and NW Russia, defined several types of what they call micromeric elements: (i) discrete, single elements (*sensu* Mark-Kurik 1999) with a crown, a neck and a cancellous aspidin layer

(Glinskiy and Nilov 2017, e.g., fig. 5R, S) corresponding to 'solitary primordial odontode[s]'; (ii) discrete complex elements (*sensu* Mark-Kurik 1999) with two or more odontodes, interpreted as growing synchronomorially; and (iii) 'tesserae' (*sensu* Mark-Kurik 1999), with a main central tubercle and concentric rows of smaller tubercles, interpreted as growing cyclomorially (called "discrete concentric 'islands', separated by an intersecting network of grooves" by Keating *et al*. 2015). Among the latter 'tesserae' they distinguish a 'basic type' where "tubercles are similar both in general shape and in inner structure" (Glinskiy and Nilov 2017, p. 67, and e.g., fig. 5E–J), and a 'progressive type' with a larger central primordial tubercle that "can have one or several pulp cavities, usually filled in by aspidin trabeculae", and 'satellite tubercles' "arranged in concentric zones on the neck" (Glinskiy and Nilov 2017, p. 67 and fig. 6). Again, on all these elements, a basal lamellar layer is lacking (see Glinskiy and Nilov 2017, figs 5J, N, Q, 6M, and 7A), and they are detached from bony plates of the head carapace of *Psammosteus* spp. Some of the 'discrete single elements' or the 'tesserae' are described as being 'rooted', that is "recognized by a missing neck, and a large base area" (Glinskiy and Nilov 2017, p. 65 and fig. 5A–F); they do in fact come from surface areas of branchial plates as indicated on fig. 3B, E, G, H of Glinskiy and Nilov (2017). In summary, all these separated bony elements described on various *Psammosteus* species do in fact correspond to detached outer portions of bigger plates of the head carapace. They cannot be called 'tesserae' as defined here above. We suggest that these dermal bony superficial structures are called 'tesseriform units' as in corvaspids (*sensu* Blieck and Karatajūtė-Talimaa 2001). However, the capacity of having such areas of detached 'micromeric elements' in psammosteids seem to be restricted to the family Psammosteidae (*sensu* Novitskaya 2004) that Glinskiy (2017) interprets as being the most derived among psammosteids.

Other lower vertebrates

This discussion about tesserae should not be restricted to heterostracans. For instance, Ørvig (1968) recognised a difference between 'tesserae' in early osteostracans, and 'polygonal plates' in advanced osteostracans of Miguasha (Frasnian of eastern Québec, Canada). He says: "In the early representatives of the Osteostraci, the dermal skeleton (Fig. 2A [the 'Downtonian' *Hemicyclaspis murchisoni* (Egerton, 1857)]) is well known from earlier descriptions (…); it consists of (a) a single, large cephalic shield which, although subdivided into polygonal tesserae, is nevertheless a continuous, macromeric formation, and (b) a squamation of comparatively large, mesomeric scutes on the trunk. In one of the earliest cephalaspids, the Lower Upper Devonian *Alaspis macrotuberculata* Ørvig (Fig. 2B), the cephalic shield in contrast is modified in such a way that it consists throughout of small, independently growing, suturally interconnected, polygonal plates (Fig. 2C), which correspond to the tesserae in the shield of earlier forms, although they are not in this case continuous with each other." (Ørvig 1968, p. 382 and fig. 2). So, Ørvig clearly distinguishes between (1) polygonal, basally fused dermal elements in *Hemicyclaspis* Lankester in Powrie, 1870, and (2) discrete, basally unfused, polygonal elements in *Alaspis* Ørvig, 1957. But we disagree with his terminology: former elements of *Hemicyclaspis*, after our definition here above, cannot be called tesserae ('units formed of fused tesserae' perhaps), although the independent elements of *Alaspis* are tesserae.

In *Superciliaspis gabrielsei* (Dineley and Loeffler, 1976) (Hawthorn *et al*. 2008) an ontogenetic series from juvenile to adult shows that although paired elements in the head were the first to ossify, the dermoskeleton grew through a combination of the formation of new tesserae and the enlargement of existing tesserae through centrifugal growth. The progression of fusion over the entire animal combined anterior to posterior with lateral to median fields of ossification. This contrasts with the situation in cyathaspidid heterostracans (Greeniaus and Wilson 2003) in which ossification of the dermoskeleton took place along the midline with posteromedial primordia of the dorsal and ventral shields ossifying first.

Another example is given by placoderms. Janvier (1996, p. 153) mentions that "In some placoderms (petalichthyids, rhenanids, some acanthothoracids), there are, in addition to the larger plates, a number of minute platelets often referred to as 'tesserae'. These are superimposed on the large dermal plates, and probably represent a derived condition … ." These cannot be considered as tesserae after our definition, except if they are proved to be basally unfused. For instance, contrary to what Janvier says, the rhenanid placoderm *Ohioaspis* Wells, 1944 (originally classified within the Osteostraci by Wells 1944) is defined as having "Small isolated tuberculated tesserae up to 3 mm in diameter, oval to subpolygonal in outline" (Wells 1944, p. 15, fig. 2, pl. 2, figs 1–16, pl. 5, figs 5–8). "They are constructed of a laminated basal layer, a thin, vascular median layer, both of bone, and a superficial layer consisting of one or several superimposed generations of tubercles composed of semidentine" and might well be tesserae of *Asterosteus* Newberry, 1875 (Denison 1978, p. 26 and fig. 13).

SYSTEMATIC PALAEONTOLOGY

Authorship of suprageneric names and higher rank assignments

The authorship, year and name of this group of heterostracans have been variously attributed through nearly 80 years of publications. In the original paper on tesseraspids, *Tesseraspis tessellata* was attributed to ?Drepanaspida by Wills (1935) who described this species as "Large, probably skate-like Drepanaspid Ostracoderms with the anterior part of the body covered with more or less anchylosed polygonal plates forming a large shield" (Wills 1935, p. 436). Two years later, Gross (1937, p. 12) considered that "In den Kreis dieser Familie [Psammosteidae] gehören wahrscheinlich auch die kürzlich beschriebenen neuen Gattungen *Tesseraspis* Wills und *Phialaspis* Wills (Downtonian von Shropshire) und *Weigeltaspis* Brotzen (Gotlandium und unterstes Unterdevon Podoliens)", that is, "The recently described new genera *Tesseraspis* Wills, *Phialaspis* Wills (Downtonian of Shropshire) and *Weigeltaspis* Brotzen ('Gotlandium' [= Silurian], and lowermost Devonian of Podolia) belong probably also in the "group" of this family [Psammosteidae]." (translated by Prof. H.-P. Schultze, e-mail on 15.03.2017).

Berg (1940), in his "Class IV. †PTERASPIDES (*Heterostraci*)" [*sic*], did not create any name for the tesseraspids, contrary to Obruchev's (1964, p. 56), Dineley and Loeffler's (1976, p. 138), Karatajūtė-Talimaa's (1983, p. 25), Novitskaya's (2004, p. 196), and Voichyshyn's (2011, p. 82) opinions. It is in a later paper that Berg (1955, p. 28) created the family Tesseraspididae as follows: "Inc. sedis. sem. 24. Tesseraspidae" ['sem.' is for the Russian 'semeistvo', that is, family]. This attribution was known by Tarlo (1962, p. 259; 1964, p. 110; 1965, p. 2).

Ørvig (1961) was convinced that "*Tesseraspis* is certainly in many ways reminiscent of the early forms which are the direct predecessors of *Drepanaspis* and the post-Emsian Drepanaspida in general, though of course not necessarily identical with any of these" (Ørvig 1961, p. 518). He described and figured fragments of exoskeletal plates from Jagielnica Stara [Jagilnytsia Stara] in Podolia, Ukraine, as 'Drepanaspida gen. et sp. indet.' (Ørvig 1961, fig. 4), that were subsequently attributed to a new species, *Tesseraspis orvigi* [*sic*] by Tarlo (1964, p. 110; see also Tarlo 1965, p. 7; Novitskaya 2004, p. 197), among his Psammosteiformes (the Drepanaspida of Wills and Ørvig). According to the International Code of Zoological Nomenclature (ICZN 1999), "No diacritic or other mark (such as an apostrophe), or ligature of the letters *a* and *e* (æ) or *o* and *e* (œ) is to be used in a scientific name" (ICZN 1999, Article 27). So, the specific name introduced by Tarlo (1964) should be emended as *Tesseraspis oervigi* Tarlo, 1964 (see ICZN 1999, Article 19.2 for authorship of emended species-name).

Obruchev (1964, pp. 55, 56) included the tesseraspids in the order Eriptychiida (without authorship); he was followed by e.g., Karatajūtė-Talimaa (1983, p. 25: order Eriptychiformes [*sic*]), and Dineley and Metcalf (1999, p. 70, 111: Eriptychiformes [*sic*] Tesseraspididae), but not by Novitskaya (2004, p. 196) who included the tesseraspids in their own order, Tesseraspidiformes (without authorship). Novitskaya (2004) gives the following definition ('diagnosis') for the order Tesseraspidiformes (and the family Tesseraspididae): "The carapace consists of separate tesserae of polygonal or irregular shape, which can both join into big separate plates. Sometimes tesserae differentiate without joining, forming very big flat plates, consisting of the tesserae which are all of one type" (translated from Russian by Ž. Žigaite, Vilnius in 2005). However, it seems that Voichyshyn (2011, p. 82) who indicates "Tesseraspidiformes Halstead, 1962" [*sic* – in place of Tarlo, 1962] is correct. Tarlo (1962, p. 258) first created the name Tesseraspidida which was then raised to Tesseraspidiformes by Novitskaya (2004). As the ending only was changed Tarlo (1962) remains the author of the taxon.

Tarlo (1962, 1965) included *T. tessellata* in the family Tesseraspididae Berg, 1955, suborder Tesseraspidida Tarlo, 1962, within the order Psammosteiformes (which also includes the drepanaspids), with the following definition ('diagnosis' in Tarlo's papers) for the family Tesseraspididae: "Carapace composed of discrete tesserae differentiated into separate areas foreshadowing dorsal and ventral median plates, branchials and fields of tesserae of later forms. Ornamentation of crenulated dentine tubercles which vary in different parts of the carapace" (Tarlo, 1962, p. 259). Tarlo (1964, 1965) recognised six different species in the genus *Tesseraspis*, namely *T. tessellata* Wills, 1935; *T. toombsi* Tarlo, 1964; *T. mutabilis* (Brotzen, 1934); *T. orvigi* [*sic*] Tarlo, 1964; *T. denisoni* Tarlo, 1964; *T. talimaae* Tarlo, 1965 (see Novitskaya 2004, p. 196; Voichyshyn 2011, p. 82). When Tarlo (1964) created the new species name *T. toombsi*, he gave a diagnosis of the taxon (as required by ICZN 1999, Article 13.1.1 and Recommendation 13A), and designated name-bearing-type material (identified as holotype: Tarlo 1964, p. 110; also 1965, p. 6), but this was not figured (contrary to ICZN 1999, Appendix B, General recommendation 3, p. 125). This material was illustrated later by Tarlo (1965, pl. 1, figs 7–10).

However, several years later, Tarlo changed his mind and considered that "*Tesseraspis* is structurally close to *Eriptychius* (as Obruchev 1964 thought) and heralds the formation of discrete plates in the heterostracans" (Halstead 1973, p. 281), leading him to classify the tesseraspids (suborder Tesseraspidida, family Tesseraspididae) within the Eriptychiiformes (Halstead 1973, p. 325).

These different assessments testify to the fact that the taxonomic and phylogenetic position of *Tesseraspis* is unclear. We follow here Novitskaya's (2004) use of the name Tesseraspidiformes as formal ordinal rank for this group of fossil agnathans.

†Class Pteraspidomorphi Goodrich, 1909
Subclass Heterostraci Lankester, 1868

COMMENT: We cannot be sure that *Tesseraspis* is an heterostracan proper. Its tesserae do show a typical heterostracan histology (see corresponding section here below), but the occurrence of a pair of common external branchial openings on either side of the head carapace cannot be proved (see Janvier 1996, p. 89). However, as described here below, the right and left marginal tesserae of the head carapace of *T. mosaica* do not show any trace of small external openings as is seen on *Astraspis* (Elliott 1987), and thus a row of branchial openings on either side of the head is not demonstrated either for *T. mosaica*.

"Heterostraci tessellati"

COMMENT: We propose to provisionally create this informal group for tessellated heterostracans (*sensu* Elliott and Loeffler 1989, sometimes named 'tessellate heterostracans' e.g., in Nelson *et al.* 2016, p. 28). Its name is derived from the Latin word '*tessellatus*' (plural '*tessellati*'), made of small square stones (*tessellae* or *tesserae* in Latin) (from Dictionary.com, based on the Random House Dictionary, © Random House, Inc. 2017). This group is certainly paraphyletic, and perhaps polyphyletic, but this will have to be strictly demonstrated after a thorough phylogenetic analysis. Its content is not precisely defined yet (see Discussion below). We provisionally include the following genera in it: *Aporemaspis*, *Aserotaspis* Dineley and Loeffler, 1976, *Kallostrakon*, *Lepidaspis*, *Oniscolepis* (syn. *Strosipherus* Pander, 1856), *Tesseraspis*, and *Weigeltaspis*.

Order Tesseraspidiformes Tarlo, 1962
Family Tesseraspididae Berg, 1955 [non Berg, 1940]
Genus *Tesseraspis* Wills, 1935

TYPE SPECIES: *Tesseraspis tessellata* Wills, 1935.

CORRECTED DIAGNOSIS: Fully tessellated head carapace; contiguous, discrete polygonal tesserae, form a continuous cylindrical element; thicker tesserae on lateral margins of carapace; longitudinal crests formed of thicker tesserae on rear part of (supposed) dorsal surface of carapace; variable superficial sculpture of individual tubercles of dentine on tesserae; large coarse tubercles on marginal tesserae; small rhombic trunk scales; tesserae have four-layered structure, external tubercles composed of a superficial layer of orthodentine capped by an avascular layer of enameloid tissue, a layer of columnar dentine below, overlying middle aspidin 'cancellous' layer, and basal laminated isopedin layer.

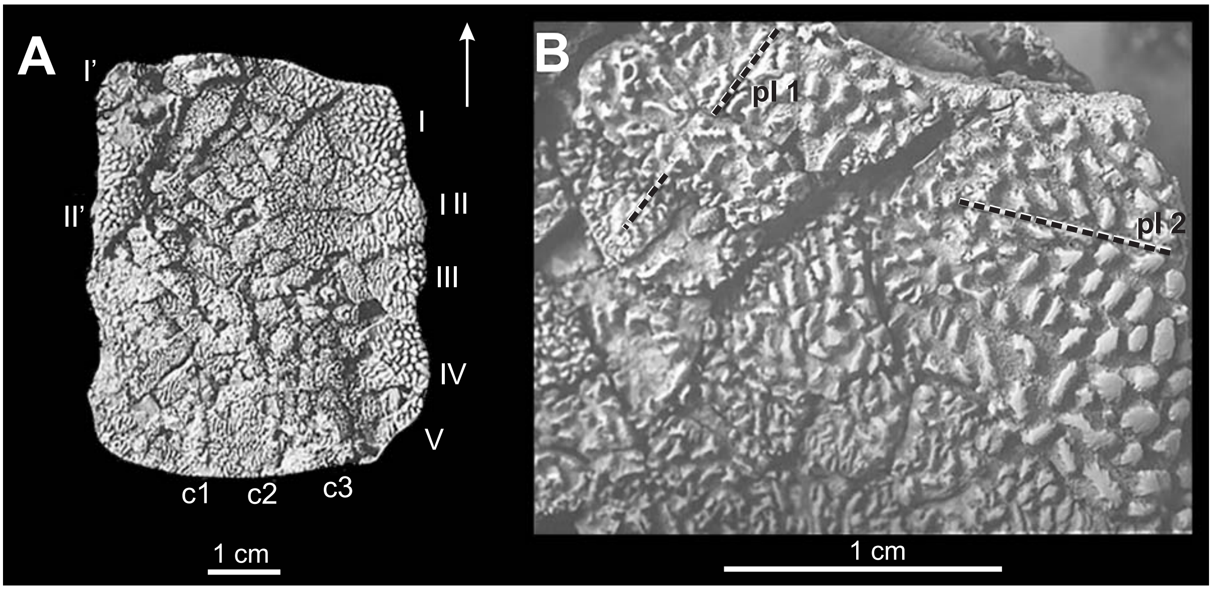
Tesseraspis mosaica Karatajūtė-Talimaa, 1983
(Text-figs 4–10)

ORIGIN OF NAME: "From Latin *mosaica*, in mosaic" after Karatajūtė-Talimaa (1983, p. 25). In fact, this word does not exist in Classical Latin. It seems to come from the Latin *musaicus*, an inlay of small pieces of various colours and geometric patterns (Brown 1956).

SYNONYMY LIST: This species has unaccountably been forgotten in most recent papers on heterostracans in which tesseraspids were described and/or figured (e.g., Novitskaya 2004; Voichyshyn 2011). So, its synonymy list is short.

1983. *Tesseraspis mosaica* Talimaa, sp. nov. [*sic*]; Karatajūtė-Talimaa, p. 25, fig. 1.
1986. *Tesseraspis mosaica*; Karatajūtē-Talimaa *et al.*, p. 255.
2001. *Tesseraspis mosaica*; Blieck and Karatajūtė-Talimaa, p. 650.
2002. *Tesseraspis mosaica*; Blieck *et al.*, p. 811, fig. 4.

HOLOTYPE: Specimen LIG 35-324a (Karatajūtė-



Text-fig. 4. Presumed dorsal surface of specimen LIG 35-324a, holotype of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983. Severnaya Zemlya archipelago, October Revolution Island, Matusevich River section, uppermost Severnaya Zemlya Formation, locality 1-21, Lower Devonian, lower Lochkovian. A – General view; B – Detail of its right anterior part. Abbreviations: c1, c2, c3 – posterior longitudinal crests; I to V – five bigger and thicker marginal tesserae (right side); I' to II' – two bigger and thicker marginal tesserae (left side). Arrow indicates the front part

Talimaa 1983, fig. 1), a flattened tubular cephalic carapace made of a patchwork of separate bony platelets (tesserae) (Text-figs 4, 5). Its anterior and posterior parts are apparently lacking.

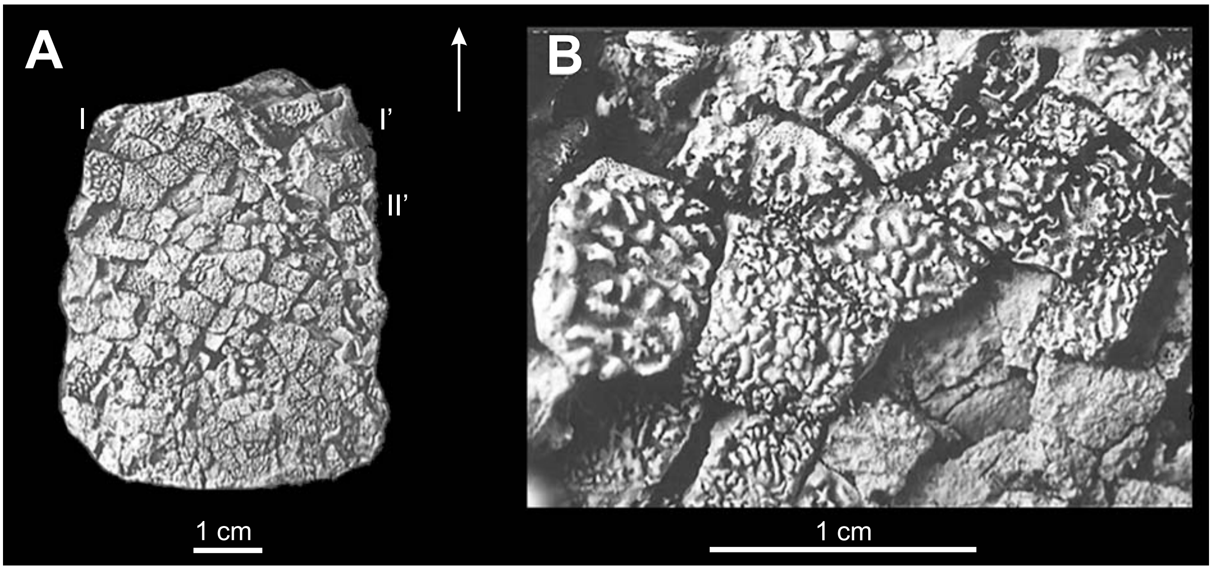
OTHER MATERIAL: Paratypes LIG 35-324 b-f, isolated tesserae extracted from the same sample as the holotype (Text-fig. 6).

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION: Severnaya Zemlya archipelago, October Revolution Island, Matusevich River section, uppermost Severnaya Zemlya Formation, locality 1-21 (= outcrop 1, bed 21), Lower Devonian, lower Lochkovian, *Nostolepis minima* acanthodian Zone, *Poracanthodes menneri* Subzone ("Dittonian" in Karatajūtė-Talimaa 1983; locality 1-21 of Matukhin and Menner 1999, figs 2-I, 8; Männik *et al.* 2002, figs 2, 12; Valiukevičius 2003, p. 197 and table 3).

CORRECTED DIAGNOSIS: Small (c. 75 to 80 mm long) head carapace, composed of contiguous, discrete, irregularly shaped tesserae, forming a continuous flattened tubular element; series of at least five marginal tesserae on both edges of the carapace; these are two to five times bigger than tesserae of the central part of the carapace, and apparently with no trace of external branchial openings; three slight longitudinal crests of thicker tesserae on rear part of the (supposed) dorsal face of carapace; superficial sculpture ('ornamentation') of tesserae made of tubercles that are highly variable in size and shape; typical four-layered heterostracan histology where the middle 'cancellous' layer shows a dense network of small cavities giving a spongy structure.

DESCRIPTION: This material was prepared by one of us (VNKT) both mechanically with needles and chemically with dilute formic acid. This was a very long process on the holotype, a unique specimen which is very fragile. The following description is based on the French translation of the original paper (Karatajūtė-Talimaa 1983) made by our colleague Bernard Battail (while in the Muséum National d'Histoire Naturelle, in Paris, France, on 25.06.1984). It is complemented with morphological and histological observations made directly from the specimens curated in Vilnius.

Head carapace. The single articulated specimen, and holotype of the species, is a 3D-preserved head carapace showing both dorsal and ventral surfaces. It is flattened, slightly distorted (probably due to diagenesis and tectonics), and both anterior and posterior parts are lacking, so oral region, orbits, and



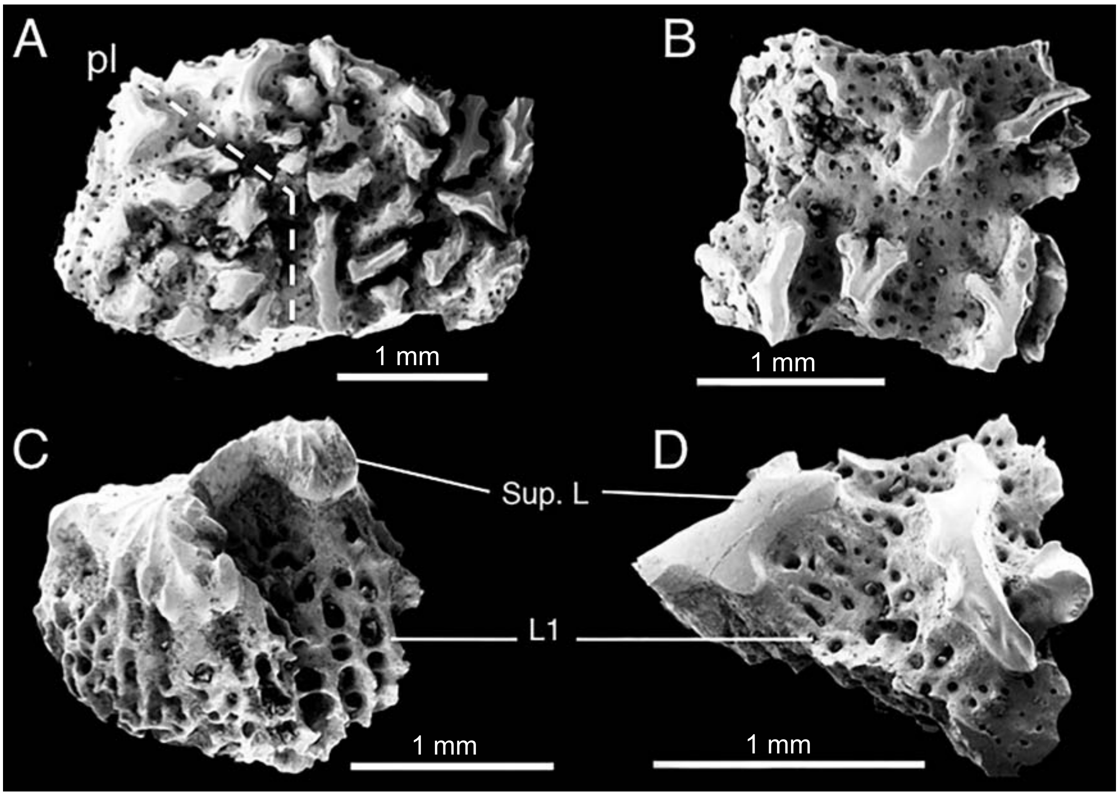
Text-fig. 5. Presumed ventral surface of specimen LIG 35-324a, holotype of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (same specimen as in Text-fig. 4). A – General view; B – Detail of its right anterior part. Abbreviations: I, I’, II’ – marginal tesserae as numbered on Text-fig. 4. Arrow indicates the front part

branchial openings are missing. Slight longitudinal ridges on presumed dorsal surface distinguish it from presumed ventral (Text-fig. 4A, c1, c2 and c3). Median (presumed) dorsal length is 65 mm, maximum dorsal width is 50 mm (as also for ventral measurements). Original length estimated as 75 to 80 mm (Karatajūtė-Talimaa 1983). Entirely composed of adjacent tesserae (or platelets).

Rear part of dorsal surface shows a set of three, slight, longitudinal ridges or crests, a central (Text-fig. 4A, c2) and two lateral (c1 and c3). Ridges identified by tesserae that are thicker, more externally developed, and narrower than the others. Right anterior shows three tesserae with an open ‘canal’ bordered by narrower, small, elongated tubercles delineating probable pit-line (Text-fig. 4B, pl 1). Right side of dorsal face is a series of five bigger tesserae (11–16 mm long, 8–10 mm wide, noted I to V on Text-fig. 4A) with superficial sculpture of higher and slightly convex tubercles, coarser than other tesserae, most anterior with another possible pit-line (Text-fig. 4B, pl 2). Central tesserae are irregular in shape and not organised. Dorsal surface does not show median larger tesserae and lateral margins with regularly arranged hexagonal tesserae, as reconstructed for *T. tessellata* by Tarlo (1962, fig. 5; 1964, fig. 4). Tesserae are square, diamond-shaped, or polygonal, 4–6 mm long. Smallest antero-posteriorly shorter than wide, 4–5 mm wide, 3 mm long, covered by numerous small tubercles, which are variable, sometimes narrow and oak-leaf-like, or ovoid with small lateral denticulations, or very small and tri-or multi-furcate (Text-fig. 4B). They show no regular arrangement on dorsal surface.

The right marginal tesserae I, IV and V are partly broken externally, tesserae II and III seem complete (Text-fig. 4A). No concave unornamented zones for possible branchial openings are seen (as in *Astraspis*, see Elliott 1987, fig. 2). Tessera I shows smaller tubercles to left, bigger more ovoid tubercles to right. Anteriorly some tubercles seem organised along pit-line (Text-fig. 4B, pl 2). Left anterior part of dorsal face shows only two bigger tesserae (noted I’ and II’), more posterior ones apparently lacking. Posterior tesserae also lacking on left ventral surface of carapace (Text-fig. 5A**)**. Placing those three posterior tesserae *in situ* indicates dorsal surface wider posteriorly than anteriorly, thus trapezoid in outline.

Ventral surface also a patchwork of irregular tesserae, quadrangular, lozenge-shaped, or rectangular, 3–8 mm long (Text-fig. 5A). Variability of tubercles as great as on dorsal surface; small oak-leaf-like tubercles, wider and slightly convex ones, some very densely arranged, with vermiculate pattern in some places (Text-fig. 5B). Tesserae and sculpture irregularly arranged. Posterior part of surface shows smaller tesserae, does not seem to correspond to natural rear edge of carapace; no rows of ridged tesserae.

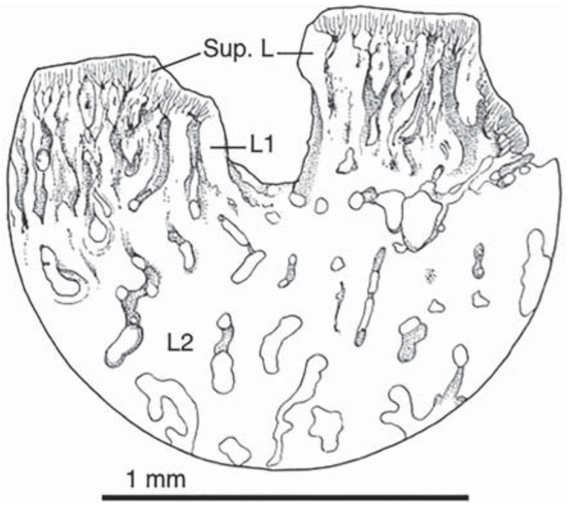


Text-fig. 6. Broken isolated tesserae, paratypes of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (same origin as holotype, Text-figs 4, 5). A – specimen LIG 35-324b; B – specimen LIG 35-324c; C – specimen 35-324d; D – specimen 35-324f. Abbreviations: L1 – reticular Layer 1 (*sensu* Keating *et al*. 2015); pl – pit-line; Sup. L – Superficial layer (*sensu* Keating *et al*. 2015)

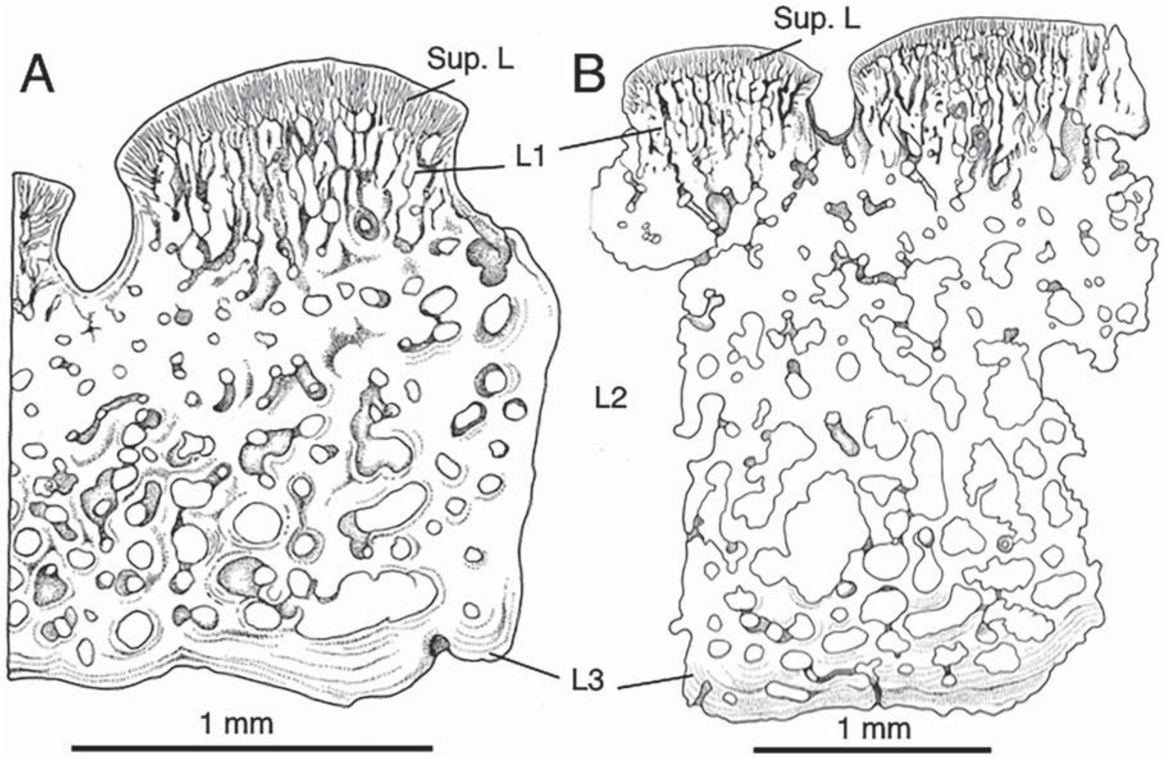
Isolated tesserae. About twenty isolated tesserae have been chemically prepared from the same sample as holotype, only a few scanned (SEM). Very fragile, mostly incomplete (partially broken). Only nearly complete one is LIG 35-324b (Text-fig. 6A). Irregularly hexagonal, 3.4 mm long, 2.4 mm wide. Bears variously shaped tubercles similar to those on dorsal and ventral faces of holotype (Text-figs 4, 5). Some short and narrow, others wider and bifurcated, the longest is c. 1 mm in length (lower part of Text-fig. 6A). Other elements are fragments, mostly have outer mineralised layers preserved. All show tubercles longer than wide; most denticulated. One shows terminal bifurcation with bifid endings (Text-fig. 6B, lower part in the middle). Specimen LIG-35-324d (Text-fig. 6C) has two bigger tubercles with small superficial ridges radiating from centre of tubercles. All these tubercles correspond to what Keating *et al.* (2015, e.g., fig. 3) called the 'superficial layer' made of dentine tubercles with enameloid capping (see section 'Histology' below; Sup. L on Text-fig. 6). Under this superficial layer is a reticular layer corresponding to 'Layer 1' of Keating *et al.* (2015), composed of an "anastomosing network of canals" which "open externally via numerous pores between tubercles" (Keating *et al.* 2015, fig. 3B; Text-fig. 6).

Histology. Thin sections on which this section is based were made by (VNKT) in 2003 in Vilnius, using specimens from the same sample as the holotype of *T. mosaica*, the type-locality 1-21 along the Matusevich River. One has been taken directly from the holotype, specimen LIG 35-324a (Text-fig. 7). All the others, can be securely attributed to the same species. Thin section No. 1304 (collection of VNKT) corresponds to marginal part of small tessera extracted from holotype during acid etching preparation. It shows the extremity of a longitudinal tubercle (on the left of Text-fig. 7), and a small marginal tubercle (on the right). Tubercles composed of an outer layer with thin canaliculi of the dentine layer capped by an avascular layer of enameloid tissue (Sup. L on Text-fig. 7; nomenclature of Keating *et al.* 2015). Under this Sup. L, Layer 1 (L1) composed of a series of compact wider, pulp canals that open externally between tubercles as in Text-fig. 6. Under L1 a layer with a mesh of canals and some wider chambers (cancellae) corresponding to Layer 2 (L2, Text-fig. 7) can be seen. The latter is also usually called the middle 'cancellous' layer and is interpreted as aspidin by Keating *et al*. (2015 and references therein).

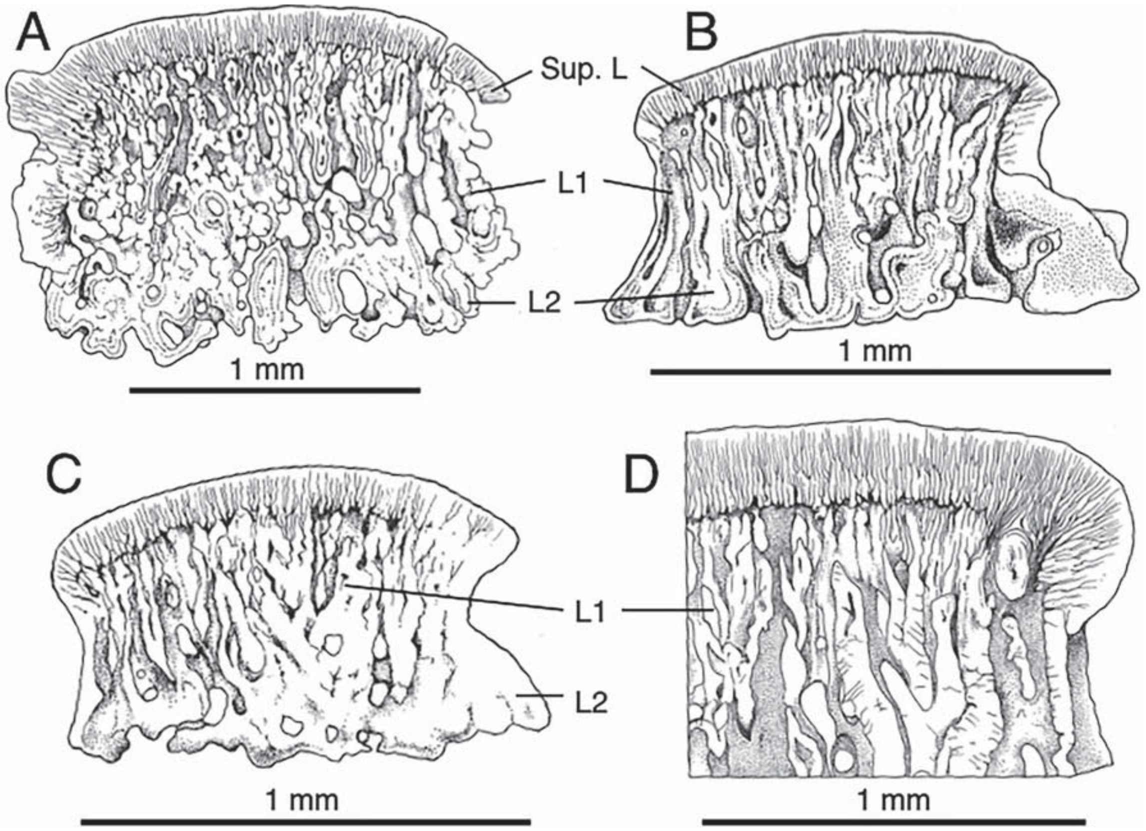
Two thin sections show tesserae with a thick middle layer L2 (Text-fig. 8). Section No. 1431 (Text-fig. 8A) shows natural unbroken margin of a tessera bearing a longitudinal section of a tubercle with typical dentine layer with dense series of thin canaliculi (Sup. L) capped by enameloid layer. It lies over a layer with much thicker canals, intercalated between thick vertical pillars (L1), that we interpret as 'columnar' dentine, contrary to Keating *et al*. (2015) who interpret this layer as a compact "anastomosing network of vascular canals" "circumscribed by osteon-like centripetal lamellar walls" (Keating *et al*. 2015, p. 662). The middle, spongiose ("cancellous") Layer 2 (L2, Text-fig. 8A) is thick (> 1 mm) with larger chambers in lower part. Basal Layer 3 (L3) is clearly laminated. Section No. 1435 shows two tubercles (Text-fig. 8B) with an even thicker middle Layer 2 (c. 2 mm thick) and again a laminated basal Layer 3. The chambers (cancellae) of Layer 2 are wider in the lower part as on section No. 1431.



Text-fig. 7. Thin section of a tessera taken from specimen LIG 35-324a, holotype of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (same as in Text-figs 4, 5), showing part of a longitudinal tubercle (left) and a marginal tubercle (right). The lower circular boundary corresponds to the limit of binocular microscope field. Abbreviations: Sup. L – Superficial layer of dentine (with thin canaliculi) capped by enameloid, L1 – reticular Layer 1 with thicker canals, L2 – middle 'cancellous' Layer 2

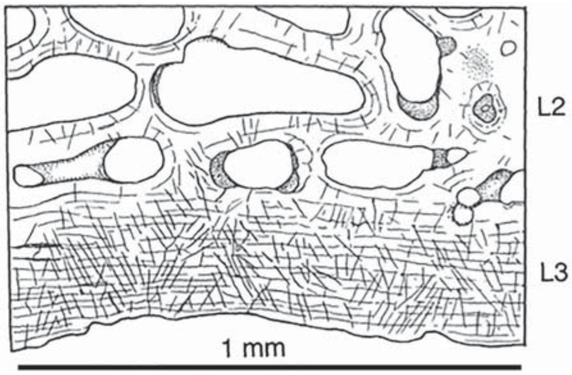


Text-fig. 8. Thin sections of two tesserae of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (same origin as holotype, Text-figs 4, 5). A – section No. 1431; B – section No. 1435. Abbreviations: same as in Text-fig. 7; L3 – basal lamellar Layer 3 (*sensu* Keating *et al*. 2015)



Text-fig. 9. Thin sections of isolated tubercles from tesserae of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (same origin as holotype, Text-figs 4, 5). A – section No. 1429; B – section No. 1422; C – section No. 1423; D – section No. 1432. Abbreviations: same as in Text-figs 7, 8. These sections show enlargements of the 'columnar' dentine layer L1

A series of thin sections has been made through discrete isolated tubercles, detached from tesserae, and showing only outer mineralised layers, mostly superficial layer of tubercles (Sup. L), Layer 1 of columnar dentine (L1) and outermost part of Layer 2 or middle 'cancellous' layer (L2, Text-fig. 9). Isolated tubercles clearly resemble the discrete micro-elements detached from bony plates of psammosteids described and illustrated by Glinskiy (2017, poster), and Glinskiy and Nilov (2017, fig. 7). However, on our *Tesseraspis* tubercles, the compact anastomosed Layer 1, interpreted as 'columnar' dentine, is typically organised as vertical, 60–100 µm thick pillars, more or less undulating. Canals of Layer 1 are in continuity with those of the superficial dentine layer on one side (Text-fig. 9D) and seem also to communicate with canals of Layer 2 on the other side (Text-fig. 9A, C), as already observed by Keating *et al.* (2015, p. 662). Section No. 1429 (Text-fig. 9A), when observed at ×280 shows the canaliculi of the superficial dentine layer (Sup. L) nearly join the external surface of the tubercle, where the enameloid layer is very thin or absent. On sections Nos. 1422 and 1432 (Text-fig. 9B, D), Layer 1 of 'columnar' dentine shows growth lines inside pillars, and superficial layer (Sup. L) has a very thin enameloid capping that looks like what Ørvig (1989, fig. 18) called 'orthodentine' on *Pycnaspis* (*Astraspis*) *splendens* (also Sansom *et al.* 2005, fig. 1h: "fine calibre tubules penetrating through the enameloid layer"). This nomenclature is probably due to a possible enameloid structure with very fine tubule-like elements perpendicular to the external surface of tubercles, called 'tubular' structure by Sansom *et al.* (2005, fig. 1g, i), or 'fibrous' fabric by Keating *et al.* (2015, fig. 3C) on *T. tessellata*. Finally, an isolated tessera shows wide chambers of the lowermost part of Layer 2, and an unusually thick, isopedin-like basal Layer 3 (section No. 1430, L3, Text-fig. 10). The latter shows a superimposed series of lamellae, parallel to basal layer of tessera, and numerous short, interlaced fibres, perpendicular or subperpendicular to the base. For



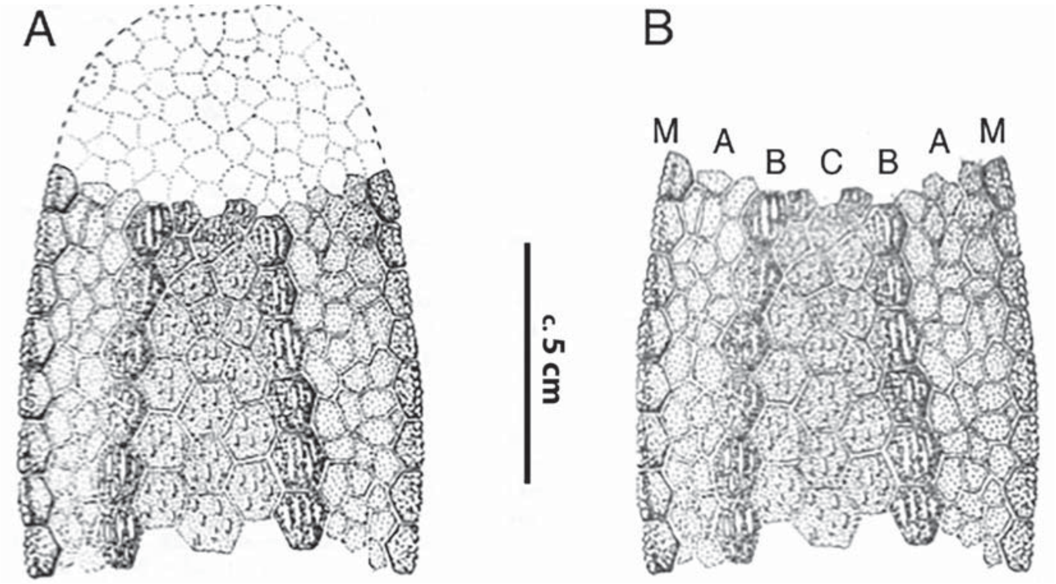
Text-fig. 10. Thin section through the basal part of an isolated tessera of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983 (same origin as holotype, Text-figs 4, 5). Section No. 1430. Abbreviations: same as in Text-figs 7, 8. This section shows an unusually thick basal lamellar Layer 3 with isopedin-like structure

this reason these interlaced fibres are not Sharpey's fibers, but the structure of L3 does correspond well to an "acellular, plywood-like, lamellar tissue compatible with isopedin" (Keating *et al.* 2015, fig. 3F, G, p. 677, and references herein).

COMPARISONS, WITH A REVIEW OF *TESSERASPIS* SPECIES: Apart from *T. mosaica*, six other nominal species were attributed to the genus *Tesseraspis*, *viz.* the type-species *T. tessellata*, and five others: *T. toombsi*, *T. mutabilis*, *T. orvigi* [*sic*], *T. denisoni*, and *T. talimaae* (Novitskaya 2004). *Tesseraspis tessellata* is the most abundantly described and figured of the series. The diagnosis of the genus *Tesseraspis* was given by Novitskaya (2004, p. 196; translated by Ž. Žigaite in 2005) as follows : "Elongated carapace, consisting of tesserae, which are differentiated into three groups: thicker tesserae, forming longitudinal medial zone/part; tesserae, forming lateral edges of the carapace; and comparatively thinner tesserae in between the medial zone and lateral edges. Scales are small, rhombic (diamond-shaped)." This is evidently based upon Wills' (1935) description and Tarlo's (1962, fig. 5) reconstruction of *T. tessellata*. It does not take into consideration the morphology of *T. mosaica*, which was, however, published as coming from "adjacent countries" of Russia when Novitskaya (2004) published her handbook. Apart from *T. mosaica*, *T. tessellata* is the only other species known from partly articulated specimens, the five other species being known from fragmentary material and corresponding possibly to 'parataxa' (Novitskaya 2004, p. 196; in the sense of taxa based on incomplete material; see a critical discussion of this term by Bengtson 1985, pp. 1352–1354).

Tesseraspis tessellata Wills, 1935. This species was mostly described from two large specimens collected from Earnstrey Hall Farm brook on the western slope of Brown Clee Hill in Shropshire, England (Wills 1935, pp. 427, 435, pl. 4, figs 1, 5; for stratigraphy, see here below). Both specimens show articulated 'thick tuberculated plates' "being polygonal and fitting into one another [and] resembled tessellated pavements" (Wills 1935, p. 436). One of these specimens shows the natural "cast of inner surface showing polygonal outlines of the plates" (Wills 1935, IS on pl. 4, fig. 5; lectotype of *T. tessellata*, specimen of Birmingham University no. 113, after Tarlo 1965, pl. 1, fig. 1 [photograph reversed]). This demonstrated that these 'plates' are discrete, independent elements of the carapace, that is, tesserae, thus embodied in the name of the genus.

These two large specimens are interpreted as being symmetrical and organised into a central area with 'polygonal moderately thick plates' (Wills 1935, C on pl. 4, figs 1, 5) and two lateral areas with 'thin lateral plates' (Wills 1935, A on pl. 4, figs 1, 5), and with longitudinal rows of 'very thick oblong plates' between A and C (Wills 1935, B on pl. 4, figs 1, 5). The tesserae are 0.66 to 1.12 cm wide, depending on their place on the carapace, coarsely tuberculated tesserae of the central area being wider than the finely tuberculated ones of the lateral areas (compare Wills 1935, pl. 4, figs 3, 5 and 6). For Wills (1935, p. 437), *T. tessellata* "is suggestive of a dorso-ventrally flattened body" and "probably having had a skate-like shape comparable with that of *Drepanaspis*." Tarlo (1965, pp. 3–5, fig. 1B, and pl. 1, fig. 2) added the description of marginal 'plates' being "thick ridge plates with large oval tubercles at ridge". It is these descriptions that enabled Tarlo (1962, 1964; Halstead 1973) to propose a reconstruction of the head carapace (Text-fig. 11), but without "mouth, orbits, branchial opening, or electric fields" none of which have been observed (Wills 1935, p. 437). *Tesseraspis tessellata* shows big oval or ovoid tubercles with or without lateral crenulations on tesserae of the central area (Wills 1935, pl. 4, fig. 3; Tarlo 1964, pl. 4, figs 1, 2), small stellate or knucklebone-shaped tubercles on tesserae of the lateral areas (Wills 1935, pl. 4, fig. 7; Tarlo 1964, pl. 4, fig. 4), small elongated "fleur-de-lys"-shaped tubercles (*sensu* Tarlo 1965, p. 3) on small rhombic scales of the trunk (Wills 1935, pl. 4, fig. 2; Tarlo 1964, pl. 4, fig. 3), and all intermediate morphologies, so that the variability of shape and size of tubercles is as important on *T. tessellata* as on *T.*



Text-fig. 11. Reconstruction of *Tesseraspis tessellata* Wills, 1935. A – by Tarlo (1962, fig. 5), and B – by Tarlo (1964, fig. 4), with addition of a metric scale (deduced from Wills 1935, pl. 4, fig. 5, lectotype – see Tarlo 1965), and the longitudinal areas of tesserae as described by Wills (1935) and Tarlo (1965). Abbreviations: C, central area; B, intermediate area of very thick oblong tesserae; A, lateral areas; M, marginal tesserae

mosaica. The main difference between *T. tessellata* and *T. mosaica* is that the former has a carapace which is organised into longitudinal, differentiated bands of tesserae that are not seen on *T. mosaica*. The latter only shows three longitudinal rows of slightly thicker tesserae on the rear part of the dorsal surface of its carapace (Text-fig. 4A). The *T. tessellata* dorsal shield is wider (c. 83 mm) than the dorsal surface of the head carapace in *T. mosaica* (c. 50 mm) (compare Text-figs 4A and 11). However, because of the very small number of specimens collected, we do not know what the variability of both species was, and this size difference may not be significant.

Wills (1935) described several thin sections of tesserae of *T. tessellata* which are 2–2.5 mm thick, with a clear superficial layer of dentine tubercles capped by enameloid (‘e’ on Wills 1935, pl. 5, fig. 2), a compact reticulated Layer 1 (both being united into ‘el’ by Wills 1935, pl. 5, fig. 1), a middle cancellous Layer 2 (‘ml’ of Wills 1935), and a basal strongly laminated Layer 3 (‘bl’ of Wills 1935, pl. 5, fig. 1). This corresponds well to the histology of *T. mosaica* as figured here (Text-fig. 8). Tarlo (1964, fig. 19A, and pl. 8, figs 3–7, pl. 9, figs 1, 3, 4) illustrated several thin sections through elements of *T. tessellata*, with the same arrangement of mineralised tissues (but with different interpretations as to the origin of these tissues, particularly concerning the aspidin of Layer 2). There are some differences in the type of dentine in tubercles of *T. mosaica* and *T. tessellata*. The dentine of the superficial layer (Sup. L) of tubercles of *T. mosaica* is more regularly organised into small, closely packed, parallel canaliculi, perpendicular to the outer edge of the tubercles (Text-figs 8, 9), forming a typical orthodentine. On *T. tessellata*, this superficial layer is made of packs of dentine canaliculi branching from the wider canals of Layer 1 (the ‘complex pulp cavity’ of Tarlo 1964, pl. 9). Sansom *et al.* (2005, fig. 1g, i) and Keating *et al.* (2015, fig. 3C) mostly brought new information on the ‘tubular’ or ‘fibrous’ structure of the enameloid capping of tubercles of *T. tessellata*, which is perforated by very thin branches generating from the dentine canaliculi of Layer 1.

The type-locality of *T. tessellata* is Earnstrey Hall Farm brook on the western slope of Brown Clee Hill in Shropshire, England (Wills 1935, pp. 427, 435), a.k.a. Earnstrey Brook (Leath 3) in the “Downton Series, Red Downton Formation, c. 70 ft. [c. 21 m] below the “*Psammosteus* Limestone” (Ball and Dineley 1961, locality 25; White 1961, p. 245). The associated vertebrate fauna includes ‘*Traquairaspis*’ *symondsi* Lankester, 1870 (*Phialaspis symondsi sensu* Tarrant 1991), *Anglaspis macculloughi* Woodward, 1891, *Corvaspis kingi* Woodward, 1934, cf. *Ctenaspis* sp., *Cephalaspis* sp. and *Onchus* sp. (Wills 1935; Ball and Dineley 1961) as well as *Turinia pagei*

(Turner *et al*. 2017, table 1). This is in the Zone of '*Traquairaspis*' *symondsi sensu* Ball and Dineley (1961, p. 201 and table 1), in the Upper Ledbury Formation, Upper Downton Group, and dated as lowermost Lochkovian (Blieck and Janvier 1989, fig. 11, '*Traquairaspis*' Zone, and references therein; now within the Daugleddau Group, Milford Haven Subgroup, Moor Cliffs Formation [Raglan Mudstone Formation], where the '*Psammosteus*' Limestone is renamed Chapel Point Limestone; see Barclay *et al*. 2015, fig. 4; Turner *et al*. 2017, fig. 2). We must recall here that this uppermost part of the Moor Cliffs Formation, with its '*Traquairaspis*' *symondsi* vertebrate assemblage including *Turinia pagei*, is, by correlation based upon vertebrates and miospores, equivalent to the lowermost Lochkovian (Blieck and Janvier 1989), not to the upper Pridoli (as indicated in Barclay *et al*. 2015, table 4 and fig. 4; Turner *et al*. 2017, fig. 2; however, the latter authors indicate a Lochkovian age for the "Daugleddau Gp *symondsi* Zone", in their appendix 1, p. 3). The Silurian–Devonian (Pridoli–Lochkovian) boundary does not coincide with the Chapel Point Limestone (formerly '*Psammosteus*' Limestone, at the former Downton–Ditton boundary), but lies lower in the succession, at least below the '*Traquairaspis*' Zone. So, *T. tessellata* in its type-locality is lowermost Lochkovian in age.

Tarlo (1964, 1965) described and figured *T. tessellata* specimens from the type-locality (Earnstrey Hall), some of which were already studied by Wills (1935; see Tarlo 1964, pl. 4, figs 1–4, pl. 7, figs 5, 6, pl. 8, figs 3–7, pl. 9, figs 1, 3, 4; and Tarlo 1965, fig. 1 and pl. 1, figs 1–6). *Tesseraspis tessellata* was also recorded in two sites of the UK Geological Conservation Review programme by Dineley and Metcalf (1999):

– Lydney, in Gloucestershire (locality 15, Dineley and Metcalf 1999, fig. 3.19, table 1.2 and p. 101) in the Fish Conglomerate of the Raglan Marl Group, in association with *Anglaspis macculloughi*, *Corvaspis kingi*, *Protopteraspis leathensis* White, 1935 [synonym of *P. gosseleti* (Leriche, 1906), see Blieck and Tarrant 2001], and *Turinia pagei*, thus equivalent to the *Protopteraspis* Zone *sensu* Blieck and Janvier (1989, fig. 11, lower Lochkovian; not Silurian as indicated by Dineley and Metcalf 1999);
– Devil's Hole, in Shropshire, NE of Brown Clee Hill (locality 18 of Dineley and Metcalf 1999, table 1.2, fig. 4.8) in two lower fish horizons of a section along the Lye Brook (LB1 and LB3 of Dineley and Metcalf 1999; Lye Brook 1 and 3 of Ball and Dineley 1961, localities 55, 57, p. 229 and geological map; 'Traquairaspis Band' and 'Arthrodire Band' of Rowlands and Cleal 1985), in association with '*Traquairaspis*' *symondsi*, *Turinia pagei*, cephalaspid, arthrodire and acanthodian remains (Ball and Dineley 1961; Rowlands and Cleal 1985; Dineley and Metcalf 1999), thus equivalent to the '*Traquairaspis*' Zone *sensu* Blieck and Janvier (1989, fig. 11, lowermost Lochkovian).

Tesseraspis toombsi Tarlo, 1964. This species is based upon a single specimen, its holotype. It was not figured in the original publication (contrary to ICZN 1999, Appendix B, General recommendation 3, p. 125), but briefly described (Tarlo 1964, p. 110). This material was illustrated by Tarlo (1965). It does correspond to "part of an articulated carapace which has been broken up into patches of associated tesserae" (Tarlo 1965, p. 6) and was poorly figured (Tarlo 1965, pl. 1, figs 7–10). It is distinguished from *T. tessellata* by the 'sculpture' of the (supposed) different parts of the carapace, with "Tesserae of median areas ornamented by large flat tubercles, usually with larger elongated, oval tubercle ringed with smaller ones. Some tesserae ornamented by short dentine ridges or elongated tubercles, arranged on either side of a similar median one. Scales ornamented by short, longitudinally aligned ridges." (Tarlo 1965, p. 6). So, this "Species [is] very close to *Tesseraspis tessellata*" although "the ornamentation of the different parts of the carapace [mostly of the trunk scales] … seems to be quite distinct from *Tesseraspis tessellata*" after Tarlo (1965, pp. 6, 7). *Tesseraspis toombsi* being based upon its 'sculpture' of tubercles on one side, and the variability of this sculpture on both *T. tessellata* and *T. mosaica* being important on another side, *T. toombsi* does not seem to be clearly distinguished from either of the others, and may not be different from *T. tessellata* (Dineley and Loeffler 1976, p. 138). *Tesseraspis toombsi* comes from the "Lower Devonian (Gedinnian), Lower Dittonian; Mad Bay, Skokholm Island, Pembrokeshire, Wales" (Tarlo 1964, p. 110), now "LORS/Devonian: Lochkovian Daugleddau Gp *symondsi* Zone" in Turner *et al*. (2017, appendix 1, p. 3), thus lower Lochkovian as are *T. tessellata* and *T. mosaica*.

Tesseraspis mutabilis (Brotzen, 1934) nov. comb. Tarlo, 1965. This species was created by Tarlo (1965, p. 7) for fragments of plates with superficial tubercles, coming from the "Lower Devonian (Gedinnian), Beyrichienkalk, *Traquairaspis* zone; Rauhen Bergen, near Steglitz (Berlin), Germany" (*fide* Tarlo 1965). These fragments were originally attributed to *Lophaspis crenulata* (as 'Aspiphoridae', i.e., Heterostraci) and to *Lophosteus mutabilis* (as *Incertae sedis* vertebrates) by Brotzen (1934, figs 2 and 5, 6 respectively), and considered as being of the same taxon by Gross (1947,

p. 111: "typische Heterostracenschilder"). These remains are 1.2 to 3.1 mm long fragmentary plates with c. 0.7 to 1.0 mm long superficial tubercles. These tubercles are typically oak-leaf-shaped (Brotzen 1934, fig. 2 right), or 'fleur-de-lys'-like (Brotzen 1934, fig. 5D), or oval with slightly crenulated edges (Brotzen 1934, fig. 2 left). On the latter specimen, narrower 1 mm long tubercles are intercalated between wider 1 mm long ones, that resemble the superficial sculpture of several traquairaspidids described and illustrated by Dineley and Loeffler (1976, e.g., figs 4, 8), with no trace of superficial grooves between tesserae. Ørvig (1969) already recognised that "the '*Lophosteus mutabilis*' Brotzen from this erratic rock, recently referred to *Tesseraspis* by Tarlo, has presumably to be classified as *Traquairaspis* sp. together with '*Orthaspis plana*' Brotzen [1934, fig. 1] and '*Lophaspis crenulata*' Brotzen", and if this appears to be a separate species of *Traquairaspis*, "the name *T. plana* is of course available for it" (Ørvig 1969, p. 226; also Ørvig 1961, p. 523), '*plana*' being the first of these three species names to appear in Brotzen's (1934) paper. So, it seems probable that *T. mutabilis* is a traquairaspidid (Dineley and Loeffler 1976, p. 138). The few specimens published by Brotzen (1934) have nothing in common with *T. mosaica* when considering their detailed superficial sculpture.

Tesseraspis oervigi Tarlo, 1964 emend. Dineley and Loeffler, 1976. Based on ICZN 1999, Article 27, the specific name introduced by Tarlo (1964, p.110) in honour of Dr. T. Ørvig, should be emended to *Tesseraspis oervigi* Tarlo, 1964, as written by Dineley and Loeffler (1976, p. 138, perhaps in error). This 'species' was created for a single "fragment of exoskeletal plate" (Ørvig 1961, fig. 4: Drepanaspida gen. et sp. indet.), re-interpreted as a "fragment of tessera" by Tarlo (1964, p. 110; 1965, pp. 7, 8). This fragment is 1.15 mm wide and 1.9 mm long, so much smaller than *T. mosaica* (Text-figs 4, 5) and *T. tessellata* (Text-fig. 11) tesserae. It bears superficial tubercles with a nearly flat top and crenulated margins, and "situated close to each other" (Ørvig 1961, p. 523 and fig. 4). This 'sculpture' is very similar to that of some psammosteids illustrated by Bystrov (1955, fig. 26: *Psammolepis paradoxa* Agassiz, 1844, cf. Ørvig 1961, p. 523), Tarlo (1964, pl. 14, fig. 1, *Guerichosteus kozlowskii* Tarlo, 1964), or Obruchev and Mark-Kurik (1965, pl. 7, fig. 2, *Schizosteus toriensis* Mark-Kurik in Obruchev and Mark-Kurik, 1965; pl. 19, fig. 2, *Schizosteus asatkini* Obruchev, 1940). The tubercles on *T. oervigi* are 0.66×0.4 to 0.66×0.73 mm large *vs.* 1.5×1.12 to 2.18×1.25 mm on *P. paradoxa*, c. 0.8×1.0 mm on *G. kozlowskii*, and c. 0.6×0.6 mm on *S. toriensis*, that is, in a similar size range as *T. oervigi* and *S. toriensis*. Additionally, the original figure of Ørvig (1961, fig. 4) clearly shows that the unique specimen of *T. oervigi* presents only the outer tuberculated and middle spongiose (L2) layers of bone, but that the basal laminated layer (L3) is lacking. This is reminiscent of the psammosteid micro-elements figured by Glinskiy and Mark-Kurik (2016) and Glinskiy and Nilov (2017) (see section 'Psammosteids' above). So, as expressed by Ørvig himself, "the material on which this 'species' [*T. oervigi*] is based (Ørvig 1961, fig. 4) is appropriately classified as Psammosteida (= Drepanaspidida) gen. et sp. indet." (Ørvig 1969, p. 225), an opinion retained by Dineley and Loeffler [1976, p. 138: "*T. oervigi* [*sic*] was a psammosteid (*sensu stricto*)"]. However, this is the opinion of neither Novitskaya (2004, p. 197) nor Voichyshyn (2011, p. 82) who both maintain *T. oervigi* within the Tesseraspidiformes. This 'species' was collected in the "Upper part of Czortków Group, Jagielnica Stara, Western Podolia" (Ørvig 1961), dated as "Lower Devonian (Gedinnian) … *Traquairaspis* zone" by Tarlo (1964, 1965), now "Jagilnytsia Stara, Lochkovian (Ivanie Stage of the Tyver formation) of Podolia (Ukraine)" (Voichyshyn 2011, p. 82). As stated by Ørvig (1961, p. 523), if it is confirmed that the fragmentary bony plate that he described is of a "psammosteid (*sensu stricto*)" (Dineley and Loeffler 1976, that is *sensu* Obruchev 1964, Obruchev and Mark-Kurik 1965, or Novitskaya 2004), it is among the earliest psammosteids ever described.

Tesseraspis denisoni Tarlo, 1964. This 'species' was created by Tarlo (1964, p. 111) for three specimens originally attributed to 'Heterostraci indet., Type D' by Denison (1963, figs 81D and 82C: specimen considered as holotype of *T. denisoni* by Tarlo 1964; plus two other unfigured specimens). The specimen figured by Denison (1963) is a 24×33 mm large fragment of bony plate, covered with "short, broad, ovoid [and denticulated] tubercles" grading into narrower tubercles "with very prominent side processes" toward one edge of the fragment. There are no intermediate fine ridges between these tubercles, contrary to what Denison (1963, fig. 82A, B) described on other specimens from the same locality. No trace of superficial or deep grooves is seen between the tubercles of *T. denisoni*, so that no tessera or superficial 'scale unit' is visible. Its tuberculated 'ornamentation' is compared by Denison (1963, p. 138) to *T. oervigi*'s 'ornamentation' (Drepanaspida gen. et sp. indet. of Ørvig 1961, fig. 4) although tubercles are not so closely situated on *T. denisoni*, where they are well separated (Tarlo 1964, p. 111; 1965, p. 8). Denison (1963) also compared his 'Heterostraci indet., Type D' with marginal plates of *Cardipeltis* Branson and Mehl, 1931 which, however, mostly show longitudinal wide dentine ridges with irregularly undulating edges and series of marginal closely packed tubercles (see Denison 1966, figs 3, 7, 8). The specimen of Denison (1963) does in fact better compare with some of the traquairaspidids of the Western District of Mackenzie, N. W. T. of Canada, in particular ?*Traquairaspis* cf. ?*T. pustulata* Dineley and Loeffler, 1976 (Dineley and Loeffler 1976, fig. 7, and pl. 2, figs 2, 4) which shows an 'ornamentation' of circular, irregular and oval tubercles on the central part of shields, passing toward longer, narrower, sometimes lachrymiform tubercles on their marginal parts. On the central part tubercles are more closely packed than on the marginal parts where they show only rare interstitial fine ridges (Dineley and Loeffler 1976, p. 28). So, "*T. denisoni* is probably a traquairaspidid" (Dineley and Loeffler 1976, p. 138; note that Ørvig 1969, p. 225 already cast doubt on the validity of Tarlo's species *T. denisoni*). Its structure and superficial sculpture do not fit with *T. mosaica* tesserae. Its size is c. twice as big as that of *T. mosaica* marginal tesserae (Text-figs 4, 5). Additionally, its age being estimated as "Late Silurian, either Early or Middle Ludlow" (Denison 1963, p. 140), is more in accordance with the age of Dineley and Loeffler's (1976) traquairaspidids such as ?*Traquairaspis* cf. ?*T. pustulata* and ?*Traquairaspis pustulata* (which are dated as Silurian and Ludlow respectively: localities GSC 58497 and 69017 in Dineley and Loeffler 1976, pp. 4–8) than with the age of *Tesseraspis tessellata* and *T. mosaica* which is Lochkovian. Nevertheless, Novitskaya (2004) and Voichyshyn (2011) keep *T. denisoni* as a valid *Tesseraspis* species.

Tesseraspis talimaae Tarlo, 1965. This species was created for three specimens originally attributed to *Traquairaspis* sp. and *Tesseraspis* sp. by Karatajūtė-Talimaa (1962). The first one "consists of two naturally articulated tesserae which are roughly hexagonal in outline, with six and eight tubercles on them, respectively", and are 3.16×3.33 mm and 3.16×4 mm large (Tarlo 1965, p. 9 = *Traquairaspis* sp. of Karatajūtė-Talimaa 1962, fig. 2.4 and pl. 1, fig. 21; holotype of *T. talimaae* according to Tarlo 1965, p. 8), and the two others are tesserae, c. 4×4 mm large with a dozen of small tubercles each (Tarlo 1965, p. 8 = *Tesseraspis* sp. of Karatajūtė-Talimaa 1962, fig. 2.6 and pl. 1, fig. 15). The size of these tesserae is within the size variability of *T. mosaica* (Text-figs 4–6) and of the lateral tesserae of *T. tessellata* (zone A on Text-fig. 11; see Tarlo's 1965 comment, p. 9). The tubercles on *T. talimaae* tesserae are well separated and small (0.6×0.8 to 1.5×0.8 mm large on the holotype, Karatajūtė-Talimaa 1962, pl. 1, fig. 21; 0.6×0.4 to 0.6×1.6 mm large on the isolated tesserae, Karatajūtė-Talimaa 1962, pl. 1, fig. 15) as are *T. mosaica* (Text-fig. 6) and *T. tessellata* tubercles (Wills 1935, pl. 4). The shape of *T. talimaae* tubercles varies from small narrow, elongated, with apparently smooth edges on the isolated tesserae (Karatajūtė-Talimaa 1962, fig. 2.6 and pl. 1, fig. 15) to small, slightly wider tubercles, with two, three or four marginal denticulations and bifurcate or trifurcate endings (Karatajūtė-Talimaa 1962, fig. 2.4 and pl. 1, fig. 21) as can be seen on some *T. mosaica* tesserae (Text-figs 4, 6; this feature is not so visible on *T. tessellata* in Wills' 1935 illustrations). From the very small sample of *T. talimaae* tesserae it is thus difficult to decide whether or not this species differs from *T. tessellata* and *T. mosaica*. *Tesseraspis mosaica* shows very small, vermiculated tubercles on many of its tesserae (particularly on Text-fig. 5) that we see neither on *T. tessellata* nor on *T. talimaae*. So, it might be that *T. talimaae* is indistinguishable from *T. tessellata* as hypothesised by Ørvig (1969, p. 226; also Dineley and Loeffler 1976, p. 138), contrary to Tarlo's (1965) opinion. More material is necessary to be sure. *Tesseraspis talimaae* was collected from two boreholes in Lithuania, *viz.*, Krekenava at -540 m and Ukmergė at -301.25–-301.50 m, in the Tilžė Formation, correlated with the "Upper Downtonian of the Welsh Borderland" by Karatajūtė-Talimaa (1962, table 1 and p. 58), and after its faunal list with the *Traquairaspis* Zone (*sensu* Blieck and Janvier 1989; see Tarlo 1965, p. 8: "Lower Devonian (Gedinnian), Lower Dittonian, *Traquairaspis* zone"). So, *T. talimaae* is of early Lochkovian age as is *T. tessellata*.

Tesseraspis sp. In the Brown Clee Hill region of Welsh Borderland, *Tesseraspis* sp. was mentioned by White (1961, p. 245) in a series of localities "from 50 ft. [c. 15 m] below the '*Psammosteus*' Limestone to 400 ft. (? 600 ft.) [c. 120 m (? 180 m)] above it", that is from the uppermost Downton Series ('*Traquairaspis*' *symondsi* Zone) to the 'middle' Ditton Series ('*Belgicaspis*' *crouchi*; now *Rhinopteraspis crouchi* Zone) (Ball and Dineley 1961, table 1). This sequence is dated to the lower and middle Lochkovian in the standard Devonian stratigraphy (Blieck and Janvier 1989, and references therein) where the thelodont *Turinia pagei* is an index species for the base of the Devonian (base of Lochkovian) having its first occurrence in the Upper Ledbury Formation, Upper Downton Group (Turner 1973, p. 567 and fig. 9; Märss and Miller 2004, fig. 3; now in the Daugleddau Group, Milford Haven Subgroup, Moor Cliffs Formation = Raglan Mudstone Formation – see above).

‘*Tesseraspis* (?) sp. ind.’ was mentioned by Obruchev and Karatajūtė-Talimaa (1967, table 2) in the First Zone of the Old Red of Podolia (Ukraine). Ørvig (1969, p. 225) cites this mention, but specifies that he has never been able to identify this taxon in the Podolian material at his disposal in the collections of the Swedish Museum of Natural History. Moreover, it is shown that *T. oervigi* is most probably not a *Tesseraspis*, but more probably a psammosteid (*sensu stricto*, see above), so that no *Tesseraspis* material has ever been described from Podolia (*contra* Novitskaya 2004 and Voichyshyn 2011).

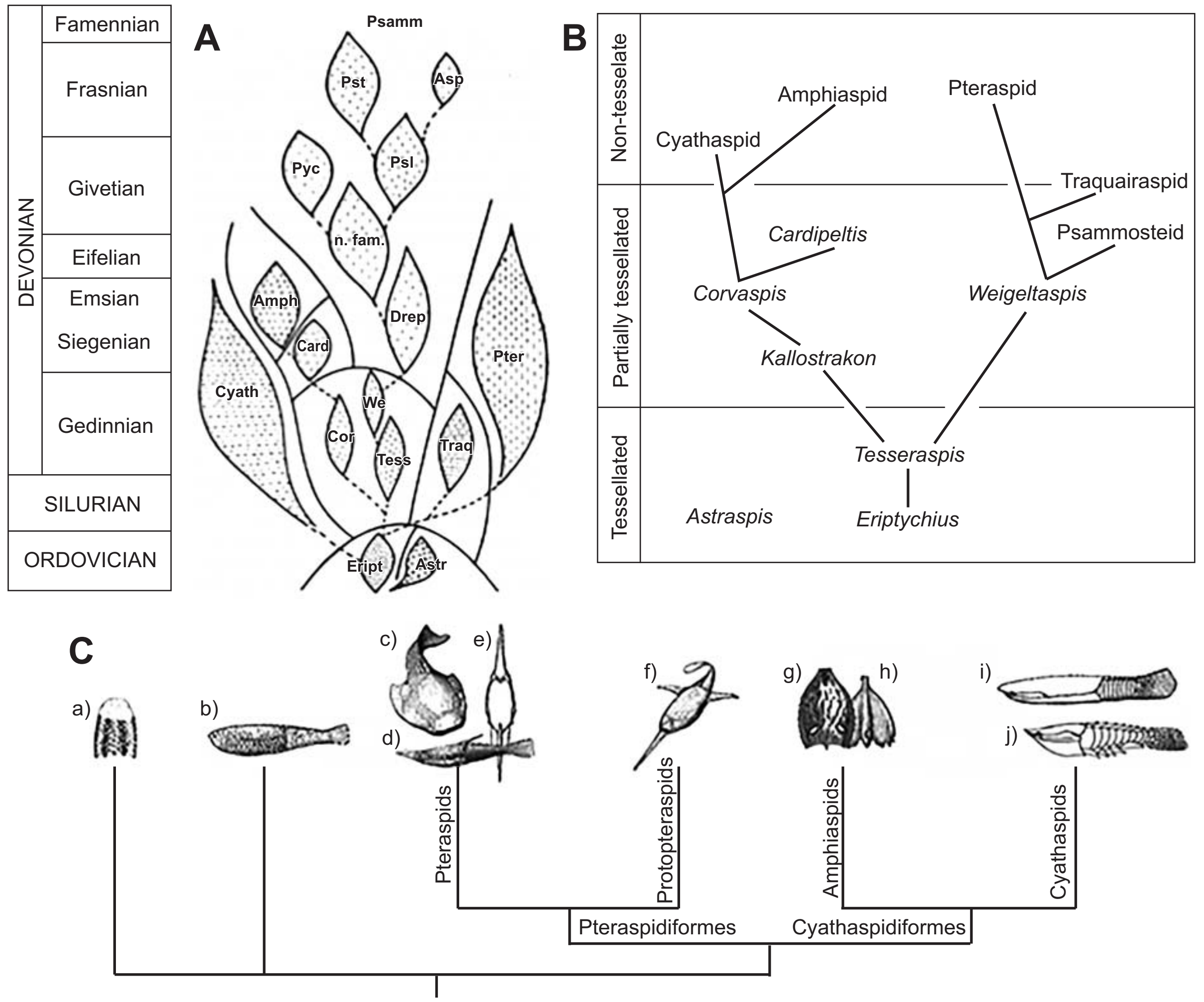
“Tesserae resembling those of *Tesseraspis* species” were mentioned by Gupta and Turner (1973, pl. 1g: ‘*Tesseraspis* ?’) among “oldest Indian fish” from the Naubug Beds in Anantnag District of Kashmir (Upper Silurian to lower Middle Devonian); however, Talent *et al.* (1988; also Talent 1989, 1990) have shown that this mention is part of the “greatest paleontological fraud of all time” (Lewin 1989), and must be rejected.

Mark-Kurik and Novitskaya (1977, figs 3, 4 and p. 149) briefly described and figured “an indeterminate form with tubercles of the *Tesseraspis* type” collected in Lower Devonian terrigenous rocks of the northern island of Novaya Zemlya Archipelago (Schmidt Peninsula, Russkaya Gavan region in Russia; cited by Blieck 1984, fig. 74, locality 45); the few figured tubercles are 1 to 2.4 mm long, with lateral sharp denticulations, as seen on *T. mosaica* (Text-figs 4, 5), but not clearly on *T. tessellata* (e.g., Wills 1935; Tarlo 1965). If *Tesseraspis* is confirmed on Novaya Zemlya, it would not be astonishing to find a species related to *T. mosaica* or even *T. mosaica* itself, due to the close palaeobiogeographic relationships between Novaya Zemlya and Severnaya Zemlya in Early Devonian time (see e.g., Mark-Kurik *et al.* 2013, fig. 11: The Arctic Province of Blieck and Janvier 1999, fig. 9.14).

DISCUSSION

A tessellated state of the head carapace is generally viewed as plesiomorphous for heterostracans. Tessellated heterostracans have been variously interpreted as related to either eriptychiids (e.g., Obruchev 1964), or psammosteids (e.g., Tarlo 1964, 1965), or even traquairaspids (Blieck 1983; Tarrant 1991). Tarlo (1962, fig. 15) tentatively produced a phylogeny of all Pteraspidomorphi (that is, Ordovician taxa such as *Eriptychius* and *Astraspis*, plus Silurian–Devonian taxa – the whole being called ‘Heterostraci’ by Tarlo) where Tesseraspididae derive from Eriptychiiformes and are basal to all Psammosteiformes (*sensu* Tarlo 1962–1965) (Text-fig. 12A). Halstead (1973, fig. 12) derived *Tesseraspis* from *Eriptychius*, and placed it at the root of all Silurian–Devonian taxa (Text-fig. 12B). Keating (2013, fig. 4), interpreted both tessellated genera *Tesseraspis* and *Lepidaspis* as basal to all heterostracans (Text-fig. 12C). In the latter scheme, *Tesseraspis* and *Lepidaspis* are in the same place as *Lepidaspis* and ‘*Traquairaspis*’ *mackensiensis* in Janvier’s (1996, fig. 4.8; also 1997) scheme. In such hypotheses the authors define a general evolutionary trend from fully tessellated to partially tessellated, and then to non-tessellated taxa (Text-fig. 12). If this is correct (but has still to be strictly demonstrated after a phylogenetic analysis of all pteraspidomorphs), it is important to have a precise overview of all tessellated pteraspidomorphs other than *Tesseraspis* itself, i.e., *Astraspis*, *Eriptychius*, and Heterostraci: *Aporemaspis*, *Aserotaspis*, *Kallostrakon* (see e.g., Tarlo 1965; Märss and Karatajūtė-Talimaa 2009); *Lepidaspis*, *Oniscolepis* (synonym: *Strosipherus*; see Märss and Karatajūtė-Talimaa 2009); and *Weigeltaspis* (see e.g., Tarlo 1965; Blieck 1983). These are briefly reviewed hereafter.

Astraspis. *Astraspis desiderata* was described by Walcott (1892) from fragments from the Harding Sandstone, Colorado. He added an articulated headshield in a postscript (Walcott 1892, p. 167) but did not illustrate it or designate a type. Eastman (1917, pl. 12, figs 5, 6) and Bryant (1936, pl. 1) illustrated and described it and Sansom *et al.* (1997) designated it as the lectotype. Ørvig (1958) erected *Pycnaspis splendens* for material from the Bighorn Mts., Wyoming that he differentiated from *A. desiderata* based on the morphology of the tubercles. Denison (1967) accepted the two species but considered them to be con-generic, and Sansom *et al.* (1997) showed that the morphological differences formed a continuum and considered *P. splendens* to be a junior synonym of *A. desiderata*. In overall appearance the dorsal shield of *A. desiderata* is very similar to that of *T. mosaica*, the dorsal aspect consisting of a shield of polygonal tesserae, with three ridges posteriorly, one central and two lateral. The shield (USNM 8121) is 69 mm long and 51 mm broad and thus is similar in size to that of *T. mosaica*. Along the margins of *A. desiderata* are a series of large plates that form the margins of the eight branchial openings (Elliott 1987). No such openings are visible in *T. mosaica* although a similar series of marginal plates is present. The ventral shield appears to be formed of a series of irregular plates (Elliott 1987; Sansom *et al.* 1997). The histology of the tesserae shows tubercles with two tissues (Denison 1967), an outer cap of clear dense tissue identified as modified dentine, and



Text-fig. 12. Three phylogenetic hypotheses that include the genus *Tesseraspis*. A – after Tarlo (1962, fig. 15). Amph, Amphiaspidiformes; Astr, Astraspidiformes; Card, Cardipeltiformes; Cyath, Cyathaspidiformes; Eript, Eriptychiiformes; Psamm, Psammosteiformes; Pter, Pteraspidiformes; Traq, Traquairaspidiformes; Asp, Aspidosteidae; Cor, Corvaspididae; Drep, Drepanaspididae; Psl, Psammolepididae; Pst, Psammosteidae; Pyc, Pycnosteidae; Tess, Tesseraspididae; We, Weigeltaspididae. B – after Halstead (1973, fig. 12). C – after Keating (2013, fig. 4). a), *Tesseraspis*; b), *Lepidaspis*; c), *Psammolepis* (erroneously attributed to *Drepanaspis* by Keating); d), *Errivaspis*; e), *Rhinopteraspis*; f), *Doryaspis*; g), *Kureykaspis* (erroneously attributed to *Eglonaspis* by Keating); h), *Eglonaspis* (erroneously attributed to *Ctenaspis* by Keating); i), *Torpedaspis*; j), *Anglaspis* (reconstructions are not to scale)

a pulp chamber with fine tubules radiating from the pulp cavity identified as orthodentine (Denison 1967). Below that is a middle layer distinguished by its complex meshwork of canals and a horizontally laminated basal layer (Denison 1967). The Harding Sandstone is middle Mohawkian, lower–middle Caradoc in British terms (Sansom *et al.* 1997), that is, late Sandbian in the new standard Ordovician stratigraphic scale (Cooper *et al.* 2012, fig. 20.9). Additional material of *Astraspis desiderata* has also been reported from the Gull River Formation in Québec (Darby 1982) which is dated to the middle and lower part of the Black River Stage, which is also Caradoc. As currently understood *Astraspis desiderata* is restricted to the Middle and Upper Ordovician of North America (Sansom *et al.* 1997).

Eriptychius. *Eriptychius americanus* Walcott, 1892 consists of isolated plates and scales showing varied sculpture but distinctive histology (Walcott 1892; Bryant 1936). The only associated material is the rostral portion of a headshield (Field Museum, PF 179500), which is split through the middle and shows the presence of several large elements of globular calcified cartilage that are evidently part of the internal skeleton (Denison 1967, figs 1–3). Some of these were recognised as rostral and orbital cartilages by Denison (1967). Rostral and marginal plates frequently show sculpture of short broad ridges that may be arranged around an apparent centre (Denison 1967, fig. 6), while those from the centre of the shield are covered by narrow elongated ridges (Denison 1967, fig. 8). *Eriptychius* is found often with *Astraspis desiderata* over most of its range, however, the specimens illustrated by Darby (1982, pl. 1, figs 4, 5) do not appear to be *Eriptychius* and may represent fragments of lingulate brachiopods.

Aporemaspis. This taxon was briefly described above in the section 'A question of semantics: what are tesserae?'. Its partially articulated head carapace does show isolated tesserae which may be fused on some parts of the head, and have an heterostracan-like histology (Elliott and Loeffler 1989). It seems that *Aporemaspis*, originally defined from material from the late Lochkovian of Cornwallis Island in the Canadian Arctic Archipelago, is also present in the Lochkovian of Spitsbergen. For T. Märss indeed (pers. comm. to AB, 16.05.2000, in Flagstaff, AZ) small scales attributed to '*Corvaspis* sp. indet. (type A)' by Blieck (1982, pl. 10, figs 4, 5) are indistinguishable from *Aporemaspis* tesserae (Elliott and Loeffler 1989, fig. 2D and pl. 107, fig. 4). If confirmed, this co-occurrence increases the resemblance between Early Devonian vertebrate assemblages of both Spitsbergen and the Canadian Arctic, and their belonging to a common palaeobiological Arctic province (*sensu* Blieck and Janvier 1999; Mark-Kurik *et al.* 2013). The detailed superficial structure of *Aporemaspis* tesserae is quite different from that of *Tesseraspis* tesserae. In particular they do not show the long, slender, denticulated tubercles that are so uniformly distributed on *Tesseraspis* head shields.

Aserotaspis. *Aserotaspis canadensis* Dineley and Loeffler, 1976 from the Delorme Formation, N. W. T. of Canada consists of tesserae that are separate in their deep and superficial layers but interlock to form a complete cover, and bear an 'ornament' of flat- topped, noodle-like dentine ridges. The dimensions of the holotype are incomplete but suggest an animal that was at least 75 mm wide and 60 mm long (Dineley and Loeffler 1976). Dineley and Loeffler (1976) note that isolated tesserae of *Aserotaspis* resemble tesserae that have been referred to *Tesseraspis*, *Kallostrakon*, *Oniscolepis*, and *Strosipherus* in the past, but that these genera are poorly understood. The *Aserotaspis* material comes from GSC locality 69014, a.k.a. the MOTH locality (Adrain and Wilson 1994) which is middle Lochkovian based on conodonts (R. Thorsteinsson, pers. comm. to AB, Calgary, 1987; see also Zorn *et al.* 2005).

Kallostrakon. There has been little interest in *Kallostrakon* since Tarlo's (1964, 1965) review of the genus. This author created three new species, *viz*., *K. macanuffi* Tarlo, 1964, *K. grindrodi* Tarlo, 1964 and *K. alleni* Tarlo, 1964, leading to a total of four nominal species for the genus, that is, the latter three species plus the type-species *K. podura* Lankester, 1870 (Tarlo 1965, pp. 10–15). For Tarlo (1965, pp. 10, 11), the *Kallostrakon* head carapace is characterised by the occurrence of both isolated tesserae and fused plates, but the arrangement of these bony elements is unknown, due to the absence of articulated specimens. It is this co-occurrence of tesserae and plates that led Tarlo to include *Kallostrakon* within the family Tesseraspididae. However, as seen on *T. tessellata* and *T. mosaica*, this co-occurrence is unproved for *Tesseraspis* and, thus, there is no reason to include *Kallostrakon* and *Tesseraspis* in the same family. The superficial sculpture of *Kallostrakon* tesserae is composed of c. 2.4–4.8 mm long, longitudinally aligned tubercles, with occasional smaller, ovoid, intersticial tubercles (e.g., Tarlo 1965, pl. 2). The bigger tubercles may be narrow or wide, and thus have an ovoid shape (Tarlo 1965, pl. 2, figs 1, 13–16). The variability of this superficial structure is rather important. For instance, *K. macanuffi* shows tesserae with either small, slender tubercles, sometimes with a more ovoid one in the centre of tesserae, or with wide, ovoid, sometimes irregularly shaped tubercles (Tarlo 1964, pl. 5; 1965, pl. 2). This variability seems to include various patterns illustrated for the other three species with the result that all four species of *Kallostrakon* might well correspond to a single one. Additionally it must be noted that all four species come from the Upper Silurian and Lower Devonian (Lochkovian) of Herefordshire, England (Tarlo 1964, 1965), except a single (apparently still undescribed and unfigured) plate from the Upper Read Bay Formation, Somerset Island, Arctic Canada (*fide* Tarlo 1965, p. 11).

For Märss and Karatajūtė-Talimaa (2009, p. 60) "*Kallostrakon* Lankester is the closest form to *Oniscolepis*". They have a "large sample of *Kallostrakon* material at [their] disposal originating from Targrove Dingle, Shropshire, Britain" that shows "more and larger fused units than *Oniscolepis*" (Märss and Karatajūtė-Talimaa 2009, p. 60). On the basis of the head carapace ('cephalothorax') which is composed of 'discrete units', Märss and Karatajūtė-Talimaa (2009) included *Eriptychius* (family Eriptychiidae), *Oniscolepis* and *Kallostrakon* (family Oniscolepididae) in the same order Eriptychiida; contrary to Novitskaya (2004) who doubtfully included *Kallostrakon* inside the Tesseraspididae.

Lepidaspis. *Lepidaspis serrata* is well known from a series of partially complete specimens from the Delorme Formation, N. W. T. of Canada and is dated as early Dittonian (Lochkovian) (Dineley and Loeffler 1976). It is large, with a cephalothorax about 70 mm wide and 110 mm long, and a caudal region approximately 30 mm wide and 80 mm long. It is composed of elements showing varying degrees of fusion that consist of an oval basal plate with a single longitudinal barbed ridge (Dineley and Loeffler 1976, fig. 73, pl. 29). Secondary ridges are short and bulbous and are associated with abraded primary ridges (Dineley and Loeffler 1976, fig. 76). On the lateral and anterior margins of the cephalothorax the ridges are more closely spaced and the bone is relatively thick, although adjacent elements are not fused (Dineley and Loeffler 1976, pl. 28, fig. 2, pl. 29). The position of the branchial openings could not be determined and histological study of *L. serrata* was prevented by the opacity and extreme flattening of the bone. However, Keating *et al.* (2015) have shown that the histology of *Lepidaspis* is four-layered as in typical heterostracans (see section ‘A question of semantics: what are tesserae?’). Similar elements have been reported from the Cape Phillips Formation, Arctic Canada (Thorsteinsson 1973) named by him *Pilolepis margaritifera*; the Pernes Formation, northern France (Goujet and Blieck 1979, fig. 3G); the Windmill Limestone of the northern Simpson Park Range, Nevada (Turner and Murphy 1988, fig. 1.36–1.39); the Beartooth Butte Formation at an outcrop near Grandview Canyon, western Idaho (Dehler *et al.* 1995); and the Tonnel’nyj Brook, De Long Strait coastal section, Chukotka, Arctic far-eastern Russia (Mark-Kurik *et al.* 2013, fig. 6D); suggesting a fairly wide range for this organism.

Oniscolepis. This genus was revised by Märss and Karatajūtė-Talimaa (2009). It is based upon disarticulated material such as scales, tesserae, platelets and fragments of plates (branchial, orbital). Märss and Karatajūtė-Talimaa (2009) consider all the nominal species previously attributed to both *Oniscolepis* and *Strosipherus* as synonyms of *O. dentata* Pander, 1856, the type and only species of *Oniscolepis*. They show the very wide variability of the sculpture of its bony elements, mostly body scales and tesserae, which are composed of “ridges arranged concentrically on tesserae and longitudinally on scales; … with crenulated margins, flat-topped or having longitudinal crest” (Märss and Karatajūtė-Talimaa 2009, p. 49). These ridges are closely or very closely arranged on all the figured elements (Märss and Karatajūtė-Talimaa 2009, figs 2–7).

Some of these have a simpler structure with either a single or a few tubercles or ridges that are reminiscent of *Aporemaspis* (Märss and Karatajūtė-Talimaa 2009, figs 3Q, 7I, although larger than *Aporemaspis* tesserae), or *Lepidaspis* (Märss and Karatajūtė-Talimaa 2009, figs 3P, 4E, although smaller than most *Lepidaspis* tesserae). They may also look like corvaspid elements (Märss and Karatajūtė-Talimaa 2009, fig. 3H). The histology of *O. dentata* is very similar to the histology of *T. mosaica* with the same four-layered arrangement of mineralised tissues in both scales and tesserae (Märss and Karatajūtė-Talimaa 2009, figs 8, 9). As no articulated specimen has ever been collected, we do not know how all the bony elements of *O. dentata* were related to each other. Märss and Karatajūtė-Talimaa (2009) interpret some isolated platelets or fragments of plates as head platelets, orbital and branchial plates, which are unknown on *Tesseraspis*. They classify *Oniscolepis* within its own family Oniscolepididae, together with *Kallostrakon*, as a component of the order Eriptychiida, thus following Obruchev (1964). *Oniscolepis* is Pridoli (latest Silurian) to Lochkovian (earliest Devonian) in age.

Weigeltaspis. This is another ‘enigmatic’ heterostracan genus, classified as ‘Incerti ordinis’ in its own monogeneric family Weigeltaspididae by Novitskaya (2004, pp. 198, 199). This family was retained by Tarlo (1964, 1965) among his wide-ranging Psammosteiformes. As for *Kallostrakon*, Tarlo defined *Weigeltaspis* on the basis of its type-species (*W. alta* Brotzen, 1933) and a series of newly defined species (*W. brotzeni* Tarlo, 1964, *W. godmani* Tarlo, 1964, and *W. heintzi* Tarlo, 1964). The latter were based upon fragments of plates or ventral or dorsal median plates of the head carapace. These elements have little in common with *Tesseraspis* isolated tesserae, except in the detailed structure of tubercles and small dentine ridges adorning the superficial layer of *Weigeltaspis* plates. It must be noted that Tarlo (1965) figured a specimen of *W. heintzi* representing a “carapace in ventral view showing convex ventral median plate, laterally projecting branchial plate, and intervening field of tesserae” (Tarlo 1965, fig. 2B and pl. 4, fig. 1), a pattern which is psammosteid-like. However, while describing *Weigeltaspis* material from Podolia, Voichyshyn (2011, pp. 136–140) did not mention any tessellated part attributed to this genus, but only isolated median dorsal plates or fragments of plates, and an orbital plate (Voichyshyn 2011, figs 81, 82). Isolated tesserae with oak-leaf-like tubercles were all determined as "*Lepidaspis*" sp. by Voichyshyn (2011, p. 136 and fig. 80). *Weigeltaspis* has been reported from the Canadian Arctic (Elliott 1983) where plates have been recorded from the Peel Sound Formation at Baring Channel, Prince of Wales Island, and the Snowblind Bay Formation of Cornwallis Island. A specimen with disarticulated orbital plates, dorsal plates and tesserae was collected by DKE from Baring Channel in 1990, and a partially articulated specimen showing lateral areas of articulated tesserae continuing over the dorsal plate was collected from the same locality by H.-P. Schultze in 1975 (DKE, pers. obs.). This leads to the conclusion that *Weigeltaspis* was probably a tessellated organism with a median dorsal plate, but, as with all other tessellated heterostracans, needs to be fully revised.

CONCLUSIONS

The diagnosis of *Tesseraspis* was based upon a reconstruction of its type-species *T. tessellata* made by Tarlo (e.g., 1962, fig. 5; 1964, fig. 4; Halstead 1973, fig. 1c) and showing the dorsal shield composed of symmetrical longitudinal areas with different kinds of tesserae: thicker tesserae in the central area and along the lateral edges, thinner and smaller tesserae in between (Text-fig. 11). This diagnosis was reproduced with some rewording by Novitskaya (2004) and Voichyshyn (2011). However, as noted in the section 'Synonymy list' above, the latter authors did not take into account *T. mosaica*, which does not show such a longitudinal pattern on its head carapace, neither on its dorsal nor on its ventral face (Text- figs 4, 5). So, following the redescription of *T. mosaica* and a review of *Tesseraspis* species, a corrected diagnosis of the genus is proposed.

From the seven nominal species of *Tesseraspis* (the six ones listed by Tarlo 1965 plus *mosaica* Karatajūtė-Talimaa, 1983), it seems that only four may be retained: the type-species *Tesseraspis tessellata* Wills, 1935; *T. toombsi* Tarlo, 1964, which may not be different from *T. tessellata*; *T. talimaae* Tarlo, 1965, which might be indistinguishable from *T. tessellata*; and *T. mosaica* Karatajūtė-Talimaa, 1983. These species are all early Lochkovian in age, making *Tesseraspis* another good biostratigraphic marker for the Old Red Sandstone series. Additionally, some other material was attributed to undetermined *Tesseraspis*, namely: *Tesseraspis* sp. in the Brown Clee Hill region of the Welsh Borderland, England; '*Tesseraspis* type' tubercles on the northern Island of the Novaya Zemlya archipelago, Russia; and *Tesseraspis* sp. from October Revolution Island in the Severnaya Zemlya archipelago, Russia (to be described in a separate paper). All the latter three taxa are Early Devonian in age, *T.* sp. from England and Severnaya Zemlya being Lochkovian.

The following items are not *Tesseraspis*: *T. mutabilis* (Brotzen, 1934) nov. comb. Tarlo, 1965 is probably a traquairaspidid; *T. oervigi* Tarlo, 1964 emend. Dineley and Loeffler, 1976 is probably a psammosteid (*sensu stricto*); *T. denisoni* Tarlo, 1964 is probably a traquairaspidid; '*Tesseraspis* (?) sp. ind.' mentioned in the First Zone of the Old Red of Podolia (Ukraine) has not been confirmed, implying that no *Tesseraspis* material has ever been described from Podolia; '*Tesseraspis* ?' from the Naubug Beds in Anantnag District of Kashmir, India must be rejected, due to the suspicious origin of the fossil material concerned. It seems that some of Tarlo's (1964, 1965) *Tesseraspis* species names are *nomina dubia* (*sensu* ICZN 1999, and see comments of Chorn and Whetstone 1978; Mones 1989), that is, *T. toombsi* Tarlo, 1964, and *T. talimaae* Tarlo, 1965. The non-tesseraspid items will have to be evaluated separately, in their own groups, traquairaspidids or psammosteids.

After comparison with all other known tessellated heterostracans, "… it is concluded that at present our knowledge for the group [tessellated heterostracans] is insufficient to support a meaningful classification, although it is clear that the Ordovician genera should not be considered to be heterostracans " (Elliott and Loeffler 1989).

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APPENDIX

List of localities with their faunal lists

As stated here in the taphonomical and stratigraphical sections, all the material of *Tesseraspis* spp. described in this paper comes from the uppermost Severnaya Zemlya Formation (Text-fig. 3, same localities and numbering as in Blieck and Karatajūtė-Talimaa 2001, fig. 2). Localities are described by Matukhin and Menner (1999, fig. 8); locality 41-12 along the Spokoinaya River (Matukhin and Menner 1999, figs 2, 3; also Männik *et al*. 2002, fig. 9) is equivalent to locality '40' of Matukhin and Menner (1999, fig. 8; 3 in Text-fig. 3 herein). Collection numbers of specimens are indicated (prefix LIG). Note that neither thelodonts nor placoderms are present. The lists here below may be compared to the provisional lists published by Matukhin and Menner (1999, pp. 39, 40) and Karatajūtė-Talimaa and Blieck (1999, pp. 127–129 and table 20).

Matusevich River, locality 1-21: *Tesseraspis mosaica* (LIG 35-324a, holotype, and 35-324 b–f, paratypes); *Tesseraspis* sp. (LIG 35-545, 35-961, 35-964, 35-965); *Corveolepis elgae*; Corvaspididae gen. et sp. indet.; Osteostraci; *Acritolepis ushakovi*, *Nostolepis fragilis*, *Acanthopora transitans* (see Valiukevičius 2003).

Ushakov River, locality 21-9: *Tesseraspis* sp. (unnumbered small fragments); Corvaspididae gen. et sp. indet.; Elasmobranchii?; *Acanthopora transitans* (see Valiukevičius 2003).

Spokoinaya River, locality 41-12: *Tesseraspis* sp. (LIG 35-962 and 35-963); Corvaspididae gen. et sp. indet.; "*Ateleaspis* sp."; *Acritolepis ushakovi*; *Poracanthodes* sp. cf. *P. subporosus*; *Acanthacanthus ornatus* (see Valiukevičius 2003).

Pod'emnaya River, locality 67-12: *Tesseraspis* sp. (LIG 35-547 and 35-548); *Corveolepis elgae*; Corvaspididae gen. et sp. indet.; Osteostraci; Anaspida; Elasmobranchii?; *Acritolepis urvantsevi*; *Nostolepis decora*; *Acanthospina irregulare* (see Valiukevičius 2003).