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Elegestolepis and Its Kin, the Earliest Monodontode Chondrichthyans

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Running header—Earliest monodontode chondrichthyans

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ABSTRACT—Chondrichthyan-like scales with simple, single odontode crowns, reminiscent of those of euselachians, have been reported from Silurian strata in a number of previous studies. These specimens comprise the genera *Elegestolepis* (from Siberia, Mongolia and Tuva) and *Kannathalepis* (from the Canadian Arctic), and have been considered to exhibit contrasting patterns of ontogenetic development.

A study of elegestolepid microremains from the Chargat Formation of Mongolia (Llandovery–lower Wenlock) and the Baital Formation of Tuva (Wenlock–Ludlow) has been undertaken using SEM and micro-CT to examine scale canal system and hard tissue structure. These investigations revealed scales at different stages of development, whose morphogenesis is characterized by growth (elongation) of the crown odontode and formation of neck canals. This ontogenetic pattern (*Elegestolepis*-type morphogenesis) is also recognized in *Kannathalepis* and the Lower Devonian species *Ellesmereia schultzei*, and forms the basis for the unification of these taxa into a new chondrichthyan Order Elegestolepidida ordo nov. Similarities in crown vascularization (branching pulp, single neck canal) shared by *Elegestolepis*, *Ellesmereia* and *Deltalepis* gen. nov. (*D*. *magna* sp. nov. and *D*. *parva* sp. nov. erected here in for Mongolian specimens) require the erection of the Family Elegestolepididae fam. nov. that is distinguished from the mono-generic Kannathalepididae (non-branching pulp, multiple neck canals).

Elegestolepid scales exhibit characteristics (neck canal formation and lack of enamel and basal bone osteons) consistent with those of the chondrichthyan dermal skeleton. This establishes Elegestolepidida as the stratigraphically oldest chondrichthyan taxon to

develop monodontode scales, which, in contrast to the ‘placoid’ scales of euselachians, are growing structures.

INTRODUCTION

The type species of the genus *Elegestolepis* (*E. grossi*) was described by Karatajūtė-Talimaa (1973) from isolated scales from upper Ludlow–Pridoli strata (Elegest and Kadvoj outcrops, Tuva, Russian Federation) of the Tuva-Mongol terrane and, at the time of publication, was the earliest known taxon referred to the Chondrichthyes. Subsequent studies on microvertebrate fossils from the lower Paleozoic have led to the identification of stratigraphically older species attributed to *Elegestolepis*. These are represented by middle Llandovery–lower Wenlock *E.* sp. specimens from the Tuva-Mongol (Chargat Formation, north western Mongolia; Elegest Formation, Tuva, Russia (Karatajūtė-Talimaa et al., 1990; Sennikov et al., 2015)) and Altai terranes (Gornaya Shoriya, Altai Republic, Russia (Sennikov et al., 2015)) and the middle–upper Llandovery *E. conica* from the adjacent Siberian craton (Angara-Ilim, Niuya-Bresovo and Tchuna-Biriussa sections, Siberian District, Russia (Karatajūtė-Talimaa and Predtechenskyj, 1995)). The paleogeographical and stratigraphical range of *Elegestolepis*-like taxa was further expanded with the description (Vieth, 1980) of the Laurussian chondrichthyan scale species *Ellesmereia schultzei* (from the Lochkovian of Ellesmere Island, Nunavut Territory, Canada).

According to the categories of scale morphogenesis established by Karatajūtė-Talimaa (1992) for Paleozoic chondrichthyans, *Elegestolepis* and *Ellesmereia* belong to the *Elegestolepis* developmental type as the scales have a monodontode, non-growing crown enclosing a pulp canal that opens at the crown neck via a single foramen. Influenced by the lepidomorial theory put forward by Stensiö and Ørvig (Stensiö and

Ørvig, 1951–1957; Stensiö, 1961), Karatajūtė-Talimaa (Karatajūtė-Talimaa, 1992; Karatajūtė-Talimaa, 1998) proposed that elegestolepid scale crowns represent the simplest monodontode dermatoskeletal elements, exhibiting many of the characteristics of what were assumed to be the most elementary skeletal units of the integument (lepidomoria). Thus, the development of odontodes in elegestolepids was differentiated from other chondrichthyans with ‘placoid’ (monodontode) scales, where the crowns were considered to form through the coalescence of lepidomoria. Karatajūtė-Talimaa (1992, 1998) attributed this complex morphogenetic pattern to the *Polymerolepis* and *Heterodontus* (euselachian; Fig. 1C) scale types. A hypothesis of odontode evolution in stem chondrichthyans was founded upon these assumptions, placing lepidomorium-like elements as the phylogenetic precursors of all chondrichthyan scales (Karatajūtė-Talimaa, 1992).

In the years following the conceptualization of the lepidomorial theory, increasing evidence from studies on the development of the integumentary skeleton of Recent neoselachians (Reif, 1980b; Miyake et al., 1999; Johanson et al., 2008) has discredited the concrescence model of odontode morphogenesis, and this is now refuted by most authors (Smith and Coates, 1998; Donoghue, 2002 and references therein). The latter view is strengthened with the inclusion of ‘acanthodians’ bearing polyodontode scales with elaborately branching odontode pulps (e.g. in *Poracanthodes* Gross, 1956; Valiukevičius, 1992) within the chondrichthyan phylogenetic history (Zhu et al., 2013; Brazeau and Friedman 2015; Giles et al., 2015). This contradicts the evolutionary scenario predicted by the concrescence model, which claims origination of neoselachian placoid scales and their complex canal system via fusion of simple lepidomorial elements enclosing a single vascular loop (Stensiö and Ørvig, 1951–1957; Stensiö, 1961). Advances in developmental biology have revealed an apparently conserved gene regulatory network that maintains a variety of odontode morphogenetic pathways (Fraser et al. 2010). This further corroborates the notion that all structures resolvable into odontode units are, in a broad sense, homologous. In this context, a re-examination of *Elegestolepis* and *Elegestolepis*-like Silurian scale taxa (e.g. *Ellesmereia*, *Kannathalepis*) will enable a clearer understanding of the early evolution of single odontode integumentary skeletal elements in the Chondrichthyes. To meet this end, the present study investigates the histology, canal system and inferred development of *Elegestolepis grossi* scales and that of previously undescribed scales from the Lower Silurian of Mongolia referred to *Elegestolepis* (Karatajūtė-Talimaa et al., 1990). These new data permit a new systematic framework for *Elegestolepis*-like taxa and allow for the further evaluation of their likely chondrichthyan affinities.

MATERIALS AND METHODS

The isolated scales were extracted through dissolution of carbonate rock samples with dilute acetic acid. The specimens come from the Chargat Formation of north western Mongolia (Chargat outcrop, sample P-16/3 [2]) and the Baital Formation (Elegest River outcrop, samples from beds 236, 291, 293 and 295 [1]) of central Tuva, Russian Federation.

Scale morphology was documented using the Zeiss EVO LS and the JEOL JSM-6060 scanning electron microscopes at the School of Dentistry of the University of Birmingham, UK. Prior to imaging, the specimens were sputter-coated with a 25 nm-thick layer of gold/palladium alloy.

Hard tissue microstructure and internal architecture of thin-sectioned specimens was investigated by Nomarski differential interference contrast microscopy (using a ‘Zeiss Axioskop Pol’ polarization microscope) and scanning electron microscopy (with a JEOL JSM-6060 SEM at the School of Dentistry, University of Birmingham, UK).

Scale examination with X-ray radiation was conducted using the SkyScan 1172 microtomography scanner at the School of Dentistry of the University of Birmingham, UK. The acquired microradiographs (tomographic projections) were taken at 0.3° intervals over a 180° rotation cycle at exposure times of 400 ms, using a 0.5 mm thick X-ray attenuating Al filter. These image data were processed with the SkyScan NRecon reconstruction software in order to generate sets of microtomograms that were converted into volume renderings in Amira 5.4 3D analysis software.

Figured material is deposited in the Lapworth Museum of Geology, University of Birmingham, UK (BU prefix).

Definitions of Terms

Traditionally (Sykes, 1974; Duffin and Ward, 1993; Thies, 1995) the two main components (crown and base) of chondrichthyan scales have been identified on the basis of morphological and/or topological criteria without consideration of their developmental origin. This approach can lead to ambiguity when attempting to establish the extent of these structures and, more importantly, can result in homologizing scale parts with different tissue composition across taxa. To address the above issues, Andreev et al. (2015) provided revised definitions of terms used in literature to describe chondrichthyan scales, and these are followed in the present study.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880

Order ELEGESTOLEPIDIDA ordo nov.

Included Families—Kannathalepididae Märss and Gagnier 2001 and Elegestolepididae fam. nov.

Diagnosis—Chondrichthyan fish with monodontode scale crowns composed of a growing odontode that encloses neck-canal branches of the pulp cavity (Fig. 1B).

Remarks—The recent literature on putative basal chondrichthyan taxa (e.g. mongolepids, elegestolepids, kathemacanthids and polymerolepidiforms) from the lower Paleozoic expresses uncertainty regarding their systematic position relative to the major clades (Subclasses) of the Chondrichthyes (Karatajute-Talimaa and Novitskaya, 1997; Sansom et al., 2000; Märss et al., 2006; Hanke and Wilson, 2010; Hanke et al., 2013). This reflects an inadequate understanding of the phylogenetic significance of scale-derived characters, which have been employed to diagnose these taxa given the general absence of chondrichthyan endoskeletal and dental remains in the lower Paleozoic.

The odontode growth that typifies the ontogenesis of *Elegestolepis*-like scales is not seen within traditionally recognised chondrichthyan clades (*sensu* Grogan et al., 2012), yet the Elegestolepidida consistently falls inside stem-group Chondrichthyes when its affinities are tested via phylogenetic inference (Andreev et al., unpublished data; Fig. 2). The erection of a new Order draws together species that possess scales with growing single-odontode crowns whose morphogenesis can be differentiated from that of elasmobranch 'placoid' scales (the *Heterodontus* morphogenetic type of (Karatajūtė-Talimaa, 1992, 1998; Fig. 1C). The formal recognition of the *Elegestolepis*-type of scale development represents a change in concept from what was originally identified as a purely morphogenic category (Karatajūtė-Talimaa, 1992, 1998).

Family KANNATHALEPIDIDAE Märss and Gagnier, 2001

Included genera—*Kannathalepis* Märss and Gagnier, 2001

Revised diagnosis—Elegestolepids possessing dermal scales with vertically undivided pulp cavities from which multiple (up to five) horizontal neck canals emerge basally.

Remarks—The mono-generic Family Kannathalepididae was introduced by Märss and Gagnier (2001) to distinguish *Kannathalepis*, identified to exhibit a specialised type of scale morphogenesis, from other Silurian chondrichthyan scale taxa (mongolepid and elegestolepid). It was reported that the squamation of *Kannathalepis* consists of single-odontode scales along with more complex aggregates of fused ‘placoid’ scales that were thought to provide evidence for two separate modes of scale development within the genus (Märss and Gagnier, 2001: fig. 4f). The current study regards these compound scales of *Kannathalepis* as aberrant, formed by anomalous patterning that is thought to result from suppression of inter-scale domains in accordance with the inhibitory field model outlined by Reif (1980a, 1982). Localised suturing of scales has similarly been documented in stem (*Hybodus delabechei* (Reif, 1978: fig. 8 d, e) and *Lissodus sardiniensi* (Fischer et al., 2010: fig. 7l)) and crown (*Echinorhinus brucus* (Reif, 1985:pl. 15) and *Asterodermus platypterus* (Thies and Leidner, 2011:pl. 71)) euselachians with monodontode trunk scale cover that is known to be prevalent within the Order (Reif, 1985; Thies and Leidner, 2011; Dick, 1978; Dick and Maisey, 1980; Maisey, 1989; Wang et al., 2009).

Complexes of randomly sutured monodontode scales consequently cannot be considered equivalent to polyodontode scales (e.g. those of Mongolepidida (Karatajūtė-Talimaa, 1998)), since the odontodes of the latter are patterned as a unit in a particular manner and are given support by a common base/pedicle tissue. The scale development in *Kannathalepis* can thus be identified as that of ‘placoid’ scales with a growing odontode and base, corresponding to the *Elegestolepis* morphogenetic type (Fig. 1B) of Karatajūtė-Talimaa (1992). On that basis, Kannathalepididae is placed inside the new Order Elegestolepidida, and its validity is maintained by acknowledging the canal system characteristics (vertically undivided pulp cavity and multiple neck canals) diagnostic for the Family, recognized in the original description of the taxon.

Kannathalepididae was expanded subsequent to its erection to include the Wenlockian genus *Frigorilepis*, which was described from articulated body fossils (Märss et al., 2002, 2006). Nevertheless, crown morphogenesis in *Frigorilepis* has not been demonstrated to proceed in discrete growth phases as in elegestolepid taxa, which are further distinguished by the presence of scale-neck canal openings. The absence of characters diagnostic for Elegestolepidida results in treating *Frigorilepis* as Family and Order *incertae sedis* for the time being.

Family ELEGESTOLEPIDIDAE fam. nov.

Included genera—The type genus *Elegestolepis* Karatajūtė-Talimaa 1973, *Ellesmereia* Vieth, 1980 and *Deltalepis* gen. nov.

Diagnosis—Elegestolepids with scales that develop a vertically branched pulp cavity that gives off a single horizontal neck canal and dentine canals that originate at the lower neck/pedicle surface independently of the pulp (Fig. 9).

Genus *ELEGESTOLEPIS* Karatajūtė-Talimaa, 1973

Included species—The type species *E. grossi* Karatajūtė-Talimaa, 1973 and *E. conica* Novitskaya and Karatajūtė-Talimaa, 1986.

Revised diagnosis—Elegestolepidids possessing up to three unornamented scale crown lobes (Fig. 3A; Fig. 4A, B, D, E) incised by deep, linear grooves.

ELEGESTOLEPIS GROSSI Karatajūtė-Talimaa, 1973

(Figs. 1B, 3A, 4, 5, 9A–C)

Elegestolepis grossi Karatajūtė-Talimaa, 1973:figs. 1–5, pl. 3 (original description).

Elegestolepis grossi Karatajūtė-Talimaa, 1998:31, fig. 10.

Locality and horizon—Studied material comes from beds 236, 291, 293 and 295 of the Baital Formation (Wenlock–Ludlow (Vladimirskaya, 1978; Sennikov et al., 2015)) at the type locality on the Elegest River, central Tuva, Russia (Karatajūtė-Talimaa, 1973). *E*. *grossi* has also been reported from the Pridoli of Tuva, Russia (Khondergei Formation (Sennikov et al., 2015)) as well as from strata of the lower Wenlock Upper Tarkhata Subformation (Gorny Altai, Russia (Sennikov et al., 2015)).

Holotype—An ontogenetically mature scale (T-003) from the Baital Formation of Tuva, Russian Federation (Karatajūtė-Talimaa, 1973).

Referred material—Over 200 isolated scales that were examined for this study are deposited in the Lapworth Museum of Geology, University of Birmingham, UK.

Revised diagnosis—*Elegestolepis* species possessing small (up to c. 1 mm long) scales that have deltoid to lanceolate, trilobate crowns and develop moderately to strongly constricted necks and bulbous bases during their ontogenesis. Scale odontode composed of dentine tissue with multipolar odontocyte lacunae from which emerge canaliculi with dendroid branching. Cellular basal bone with layered mineralised-fibre organization.

Remarks—Certain differences were noted between the scale histology of *E. grossi* scales and the original descriptions of Karatajūtė-Talimaa (1973). Some of these concern the nature of the most superficial portion of the scale crown and neck, understood by Karatajūtė-Talimaa (1973) to consist of a type of hypermineralized dentine tissue, durodentine (one of the less commonly used synonyms of enameloid (Ørvig, 1967; Smith and Miles, 1971; Sire et al., 2009). This ‘enameloid’ layer is found not to be a persistent feature of *E*. *grossi* scales, and even when present it appears discontinuous across most of the upper crown surface (Fig. 5A–E), contrary to previous depictions (Karatajūtė-Talimaa, 1973: fig. 2a, b and Sire et al., 2009: fig. 10b). The layer is instead most prominent around the scale neck (Fig. 5A, C–E) and can extend all the way down to the level of the basal bone (Fig. 5C). This distribution is contrary to that of single crystalline enameloid in neoselachian scales, where it is confined mainly to the upper crown region (Johns et al., 1997). Furthermore, the architecture of the superficial crown region cannot be recognised in any of the known enameloid structural types (Johns et al., 1997; Sansom et al., 2005; Gillis and Donoghue, 2007; Guinot and Cappetta, 2011; Andreev and Cuny, 2012), but instead resembles that of the crown dentine and is regarded as such. The more porous appearance of the surface dentine is likely to be diagenetically induced and/or due to alteration of the original tissue microstructure by preparation of the specimens with unbuffered acetic acid (even in low concentration, the latter has been shown to damage the phosphatic tissues of conodont elements (Jeppsson et al., 1985; Jeppsson and Anehus, 1995).

This study also demonstrates the presence of not previously identified faint depositional lines (Fig. 5G) in the basal bone of *E*. *grossi* scales, although growth of the bone tissue has been inferred from specimens in different stages of development (Karatajūtė-Talimaa 1973, 1998). The lamellae, demarcated by the depositional lines produced by change in orientation of the matrix's crystalline fibres, have convex down profiles common for the scale bases of lower vertebrates (Ørvig, 1966; Zangerl, 1968; Denison, 1979; Burrow and Turner, 1998, 1999; Qu et al., 2013).

Genus *ELLESMEREIA* Vieth, 1980

Included species—*Ellesmereia schultzei* Vieth, 1980

Remarks—*Ellesmereia* (Fig. 3B) was assigned to the Elasmobranchii by Vieth (1980) despite being recognized to possess an *Elegestolepis*-type of scale morphogenesis (Reif, 1978; Karatajūtė-Talimaa, 1992) that is atypical for an elasmobranch, and consequently it is placed here within the Elegestolepidida. Mature *Ellesmereia* scales also possess a canal system architecture (Vieth, 1980: fig. 26) closely resembling the vascularization of *Elegestolepis* and *Deltalepis* gen. nov., and for these reasons the three taxa are united at a familial level.

Genus *DELTALEPIS* gen. nov.

Included species—*Deltalepis magna* gen. et sp. nov. (type species) and *Deltalepis parva* gen. et sp. nov.

Derivation of name—From ‘delta’ (alluding to the resemblance of the scale crown to the Greek letter Δ) and ‘lepis’, scale in Greek.

Diagnosis—Elegestolepidids whose scales possess lobed crowns ornamented by tuberculate ridges. Crown lobes and furrows extend down the anterior face of the scale neck (Figs. 7, 8).

Remarks—The material referred here to *Deltalepis* gen. nov. has not previously been formally described or figured, although was considered to belong to the genus *Elegestolepis* by Karatajūtė-Talimaa et al. (1990) and Karatajute-Talimaa and Novitskaya (1997) in their work on the mongolepid taxa from the Chargat Formation. *Deltalepis* gen. nov. scales possess crown morphology, ornamentation and pulp cavity branching pattern that differentiate them from *Elegestolepis* and *Ellesmereia*, and therefore require the erection of a new taxon. This distinction and the erection of two *Deltalepis* species is based on the documented intra- and inter-generic variation of trunk-scale morphology (e.g. crown shape, number of crown ridges/lobes and ornamentation) in Recent neoselachian Families (Reif, 1985; Compagno, 1988; Voigt and Weber, 2011). Comparable differences in ornament have also been used to distinguish taxa at genus level among thelodonts (e.g. *Erepsilepis* (Märss et al., 2006)) and mongolepid chondrichthyans (*Shiqianolepis* and *Rongolepis* (Sansom et al., 2000)). Ridged lobes are also a feature in the putative chondrichthyan taxon *Areyongalepis oervigi* (Young, 1997, 2000) known solely from micro-remains from the Darriwilian Stokes Siltstone (Amadeus Basin, Northern Territory, Australia). The crown necks and bases of elegestolepid scales, however, are not developed in *Areyongalepis* elements, and the latter do not demonstrate identifiable vertebrate mineralised tissues (Young, 1997), making their systematic position uncertain for the time being.

DELTALEPIS MAGNA sp. nov.

(Figs. 3C, 6, 8A–B, 9D–F)

Derivation of name—From the feminine form of the Latin word for large, referring to the scale size of the species relative to that of *D*. *parva* gen. et sp. nov.

Locality and horizon—The type and only known locality for *D. magna* is 80 km north of Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All specimens come from sample P-16/3 collected from the upper Llandovery–lower Wenlock (Salhit regional Stage) horizons of the Chargat Formation (Ørvig, 1977; Karatajūtė-Talimaa et al., 1990).

Holotype—An isolated, presumably trunk, scale BU5269 (Figs. 3C, 6A–C).

Referred material—Six isolated scales (BU5269–BU5274).

Diagnosis—*Deltalepis* species possessing scales with deltoid to elliptic crowns divided into three to five discrete lobes by posteriorly widening grooves. Parallel tuberculate ridges developed on the undersurface of the crown. The rami of the pulp cavity formed inside the scale crown connect directly to the main pulp canal.

Description

Morphology—Scales possess monodontode crowns with ovate to acuminate outlines (Fig. 6) that are 500–700 μm long and 400–700 μm wide. The crown surface displays a complex topography that is produced by three to five lobes separated by deeply recessed inter-lobe regions (Fig. 6A–C, E, G, H). The lobes are lanceolate-shaped and can exhibit slight divergence towards the posterior of the scale. Their surface is ornamented by sub-parallel tuberculate ridges (up to 8 per lobe) that are absent from the smooth-faced inter-lobe segments of the crown. Longitudinally directed ridges are similarly developed on the undersurface of the crown (Fig. 6F, I, J), and these demonstrate regular spacing across its width.

The crown transitions into an unornamented narrow neck (down to a third of the maximal crown width) that is located at the anterior of the scale, overhung on all sides by the crown. The lower portion of the neck is either gently curved outwards or flares out to form an ellipse-shaped pedicle. In specimens with a developed pedicle support (Fig. 6E–G, I, J) the posterior face of the neck is pierced by a single centrally positioned foramen (Fig. 6F) with a diameter of c. 30–40 μm. The lower pedicle surface of some specimens is deeply indented (Fig. 6I) and penetrated by the scale's canal system, whereas in others it is nearly flat (Fig. 6J), exhibiting only a greatly constricted opening of the pulp.

Histology—The scale odontodes are composed solely from a highly vascular tubular dentine (Fig. 8A, B). The canaliculi of the dentine have a coiled appearance and display a tangled organization as well as extensive ramification along their length (up to c. 20 μm). In the upper portion of the crown, the canalicular network emerges from a complex of horizontally and vertically branched, interconnected, small-calibre dentine canals (diameter of c. 5–25 µm; Fig. 9D). The latter are most prominent inside the crown lobes where they associate with and connect to branches (c. 30–60 µm in diameter) of the pulp canal. For most of their length the pulp branches extend parallel the crown surface, before curving basally to merge (Fig. 9F) into a single pulp canal (c. 60–90 µm wide) inside the scale neck. From the posterior of the pulp issues an unbranched horizontal canal (c. 70 µm long; Fig. 9F) that opens on the scale neck surface. Separate from the pulp cavity system, the posterior half of the scales houses numerous closely spaced (up to c. 10 µm apart) dentine canals (10–20 µm in diameter) whose paths parallel that of the lower crown surface (Fig. 9E). The lower ends of these canals ramify inside the scale neck before either exiting the scale basally (Fig. 9E) or ending blindly inside it.

The tissue (c. 40 µm thick) closing off the lower pedicle opening displays an optically discernable boundary with the overlying dentine (Fig. 8A), but it could not be ascertained whether it constitutes a distinct tissue type.

DELTALEPIS PARVA sp. nov.

(Figs. 3D, 7, 8C–D, 9G–J)

Derivation of name—From the feminine form of the Latin word for small, referring to the scale size of the species relative to that of *D. magna* gen. et sp. nov.

Locality and horizon—The type and only known locality situated 80 km north of Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All specimens come from the upper Llandovery–lower Wenlock (Salhit regional Stage) horizons (sample P-16/3) of the Chargat Formation (Karatajūtė-Talimaa et al., 1990; Žigaitė et al., 2011).

Holotype—An isolated, presumed trunk, scale BU5275 (Figs. 3D, 7A, B).

Referred material—Six isolated scales (BU5275, BU5277, BU5278–BU5280, BU5282).

Diagnosis—*Deltalepis* species with ovoid scale crowns compartmentalized into seven to ten lobes. The lateral crown branches of the pulp cavity do not connect directly to the main pulp canal.

Description

Morphology—The scale crowns are single odontode structures with ovoid outlines (Fig. 7) that are 200–500 μm long and 200–400 μm wide. Upper crown surface is divided into seven to ten antero-posteriorly aligned lobes (40–60 μm wide; Fig. 7A–F) separated by much narrower, deeply incised grooves that expand towards the posterior (up to c. 20 μm wide). Tubercles organized into parallel rows ornament the upper surface of the crown lobes (up to three rows per lobe), whereas all other scale surfaces are smooth.

The anterior of the crown is constricted into a vertically orientated neck that reaches a third to three-quarters of the maximal crown width, and which in some specimens expands basally to form a pedicle support (Fig. 7C–F, H, I). The posterior lower-neck/pedicle face of these scales is pierced by a single foramen (Fig. 7D, H, I) with a diameter of 20–35 µm. A canal opening is also present on the lower pedicle surface (Fig. 7H), while a row of elliptical foramina of laterally decreasing diameter (from 70 µm to 40 µm in Fig. 7G) mark the lower face of scales lacking a pedicle attachment.

Histology—Tubular dentine tissue (Fig. 8C, D) is the only component of the scale crown. The dentine canaliculi are less than 2 µm in diameter and up to c. 20 µm long, with arborescent branching (Fig. 8D) that gives the tubular system a tangled appearance. Inside the lobed regions of the crown, the tubules connect to a network of vertically (c. 5–10 µm wide and 25–40 µm long) and horizontally (c. 5 µm wide) oriented dentine canals (Fig. 8C; Fig. 9J) that are confluent with branches of the pulp cavity. These pulp branches (from c. 20 µm to c. 45 µm in diameter; Fig. 9G–J) occupy the crown lobes (one canal per lobe) before curving basally to merge with one another inside the scale neck. The three medial branches emerge from the main pulp canal—confined to the scale neck/pedicle—whereas the more lateral ones are only indirectly connected to it through the medial rami (Fig. 9I). Near its lower end, the main pulp canal gives off a short neck canal (Fig. 9I, J) that opens at the scale surface.

Posterior of the pulp-cavity canal system the scale houses a number (c. 15) of mutually parallel, ascending dentine canals (Fig. 9G) with diameters between c. 10 µm and 15 µm. These canals follow the posterior scale profile without establishing connections at any point with the pulp cavity and terminate basally at the lower pedicle surface.

DISCUSSION

Chondrichthyan Characteristics of Elegestolepid Scales

The odontogenic component of the vertebrate skeleton develops primarily as discrete elements (odontodes), each of which being the product of a single epithelia-mesenchymal cell condensation (Ørvig, 1977; Reif, 1982; Fraser et al., 2010). Odontodes are one of the main structural units of scales and in certain groups (e.g. in neoselachian chondrichthyans (Fig. 1C; Sire and Huysseune, 2003; Eames et al., 2007; Sire et al., 2009) can form the entire squamation in the absence of osteogenic contribution to the integumentary skeleton. In lower Paleozoic vertebrates, dermal odontodes are usually patterned in clusters (polyodontodia in Ørvig, 1977) that form compound scale crowns; these have been documented in pteraspidomorphs (Gross, 1961; Denison, 1967; Sansom et al., 2009; Keating et al., 2015), anaspids (Märss, 1968; Blom et al., 2002; Märss, 2002; Keating and Donoghue, 2016), galeaspids (Wang et al., 2005), osteostracans (Stensiö, 1932; Märss et al., 2014) and jawed gnathostomes (Schultze, 1968, 1977; Gross, 1969; Denison, 1979; Karatajūtė-Talimaa, 1995; Sansom et al., 1996; 2012; Burrow and Turner, 1998, 1999; Giles et al., 2013). The Thelodonti (Märss et al., 2007), Elegestolepidida (Karatajūtė-Talimaa, 1973, 1998 and this study) and some euchondrichthyans (*sensu* Janvier and Pradel, 2015)—e.g. iniopterygians (Zangerl R, Case, 1973; Grogan and Lund, 2009), petalodonts (Malzahn, 1968), symmoriiforms (Lund, 1985, 1986; Coates and Sequeira, 2001), living holocephalians (Patterson, 1965) and euselachians (Thies and Leidner, 2011)—are the exception, as their scale crowns form only from a single-odontode element.

The integumentary skeleton of thelodonts demonstrates perhaps the most phylogenetically primitive mode of monodontode scale morphogenesis (Figs. 1A, 2; Sire et al., 2009; Smith and Hall, 1990, 1993). In contrast to polyodontode scale development, where each of the component odontodes mineralizes in a single step, the scales of thelodonts go through several ontogenetic phases that result in gradual elongation of the crown in basal direction (Gross, 1967; Karatajūtė-Talimaa, 1978). Thelodonts can also possess basal bone tissue (Fig. 1A), the deposition of which commences only after cessation of odontode growth (Karatajūtė-Talimaa, 1978; Märss et al., 2007). It is argued here that a thelodont-like pattern of scale development evolved convergently in the early chondrichthyans (Fig. 2), with the appearance of Elegestolepida in the middle Llandovery. Nevertheless, during ontogenesis elegestolepid scales develop a more derived canal system architecture that features neck canal opening(s) of the odontode pulp (documented outside the Euchondrichthyes in ‘acanthodians’ (Denison, 1979) and stem osteichthyans (Gross, 1953, 1968; Qu et al., 2013) but absent from the dermal skeleton of the Thelodonti (Fig. 2; Gross, 1967; Karatajūtė-Talimaa, 1978; Märss et al., 2007). The depth of insertion of the scale into the integument has been suggested to influence the formation of neck canals (Hanke and Wilson, 2010) and this interpretation is supported by the position of scale necks inside the upper vascular layer (stratum spongiosum) of the dermis in Recent neoselachians (Reif, 1980b; Miyake et al., 1999). Similar topological relationship between scales and surrounding integumentary tissues is attributed here to the elegestolepids, whereas the dermal odontode papillae of thelodonts have been interpreted to form superficially at the epithelium-mesenchyme boundary and therefore not to intersect the vascular system (Karatajūtė-Talimaa, 1978; Märss et al., 2007).

Outside the Chondrichthyes, other derived gnathostomes regarded to possess monodontode body scales belong to the basal 'placoderm' Orders Stensioellida and Antiarcha (Fig. 2; also refer to Johanson, 2002; Giles et al., 2015; Brazeau and Friedman, 2015 and citations therein for recent vertebrate phylogenies) whose scale structure is still insufficiently investigated. The available data on the squamation of these taxa (e.g. *Stensioella* (Gross, 1962) and *Parayunnanolepis* (Upeniece, 2011; Zhu et al. 2012)) provides evidence for non-growing odontodes, implying this to be a plesiomorphic feature of the single-odontode scales of jawed gnathostomes. Histological descriptions of scale hard-tissues are presently not available for the above taxa, but known examples of 'placoderm' scale structure often demonstrate formation of an osteon-rich vascular layer inside the upper portion of the basal bone (Burrow and Turner 1998, 1999; Giles et al., 2013; Rücklin and Donoghue 2015). Osteon mediated bone remodeling and resorption is widespread in the dermal skeleton of 'placoderms' (Donoghue et al. 2006; Downs and Donoghue, 2009; Giles et al., 2013) and basal osteichthyans (Zhu et al., 2006), but, critically, is absent from the elegestolepid skeleton and in conventional chondrichthyans. Other characteristics placing elegestolepids with the Chondrichthyes among derived gnathostomes are the pattern of scale histogenesis and their hard tissue composition, both of which match those of polyodontode chondrichthyan scales by being two-component skeletal elements formed out of lamellar basal bone and crown dentine (Karatajūtė-Talimaa, 1992).

Elegestolepidida in the Context of Paleozoic Chondrichthyans

Although rare, elegestolepids are a significant component of pre-Devonian chondrichthyan faunas with five currently identified species grouped into two Families (Fig. 10), being second only in diversity to the Order Mongolepidida (Karatajūtė-Talimaa et al., 1990; Karatajute-Talimaa and Novitskaya, 1992, 1997; Sansom et al., 2000, 2001). Whilst the mongolepids (Sansom et al., 2001) and several other putative chondrichthyan lineages (represented by *Areyongalepis* (Young, 1997), *Tantalepis* (Sansom et al., 2012), *Tezakia* (Sansom et al., 1996; Andreev et al., 2015) and *Canyonlepis* (Sansom et al., 2001; Andreev et al., 2015)) have their origination in the Ordovician, no remains attributable to Elegestolepidida have yet to be reported from this period. These Ordovician taxa possess compound (polyodontode) scale crowns and lack neck canal openings; the latter are now understood not to develop in all basal chondrichthyans (Märss et al., 2007; Hanke and Wilson, 2010).

Neck pulp-canal openings stratigraphically first appear in the oldest elegestolepid species (*E. conica* Novitskaya and Karatajūtė-Talimaa, 1986; Karatajūtė-Talimaa and Predtechenskyj, 1995), in the Middle Llandovery, and can be recognized as a persistent feature of the canal system of mature elegestolepid scales (Fig. 10; Karatajūtė-Talimaa, 1973; Vieth, 1980; Märss and Gagnier, 2001). This condition is similarly developed in Silurian polyodontode chondrichthyan species (e.g. *Tuvalepis*, Žigaitė and Karatajūtė-Talimaa, 2008) and the monogolepids *Mongolepis*, *Teslepis* (Karatajūtė-Talimaa, 1998), *Shiqianolepis* and *Rongolepis* (Sansom et al., 2000). In monogolepids pulps exit the lower part of crown either by giving off short rami (termed ‘horizontal canals’ by Karatajūtė-Talimaa (1995) and considered equivalent to the neck canals of elegestolepid scales) or opening directly to the crown surface (in *Shiqianolepis* and *Rongolepis* (Sansom et al., 2000)).

Elegestolepidida and Mongolepidida might represent two distinct lineages of early chondrichthyans that provide an insight into the variability of scale characteristics within what appear to be monophyletic groups. Inside each of these clades the features shared by its member genera are those relating to the pattern of crown morphogenesis, whereas aspects of their scale vascularization and hard tissue structure can exhibit differences. Moreover, characters with a limited distribution in one of the Orders can have a constant presence in the other, as is the case with the neck canal openings of the elegestolepids. The identification of elegestolepid taxa is thus regarded to require the unique character combination of a growing monodontode scale crown (Order-grade character) and neck canal openings (plesiomorphy of crown-group gnathostomes).

Under the diagnosis formulated here, the Wenlockian species *Frigorilepis caldwelli*, placed inside Kannathalepididae by Märss et al. (2002, 2006), is removed from Elegestolepidida for not demonstrating recognisable stages of scale crown growth. As *Frigorilepis* does not develop neck canals (Fig. 10), the polygonal ultrasculptural pattern of the crown surface it shares with *Kannathalepis* has been used instead as a character to support its chondrichthyan affinity (Märss, 2006; Märss et al., 2006). Crown ornamentation is regarded non-diagnostic at higher taxonomic levels (see above) and at present no further evidence is available to unite *Frigorilepis* with basal chondrichthyans. As a consequence, the *Elegestolepis*-type of morphogenesis is the only mechanism of development recognised in monodontode chondrichthyan scales from the Silurian. The inclusion of *Ellesmereia* into Elegestolepidida also shows that odontode growth has persisted as a feature of the integumentary skeleton of chondrichthyans at least until the Early Devonian (Fig. 10). This last known appearance of an elegestolepid species coincides with a major diversification of chondrichthyans at the base of the Devonian (Ginter, 2004; Turner, 2004; Grogan et al., 2012) that sees the emergence of taxa with body cover of non-growing monodontode scales. Some of these species are known from body fossils and represent examples of the earliest recorded articulated chondrichthyan remains (Fig. 10; *Lupopsyrus pygmaeus* (Bernacsek and Dineley, 1977; Hanke and Davis, 2012) and *Obtusacanthus corroconis* (Hanke and Wilson, 2004)). *Polymerolepis whitei* (Karatajūtė-Talimaa, 1968, 1998; Hanke et al., 2013), is also added to the above by being identified on the basis of CT data (Andreev, 2014) to possess body scales with single odontode crowns that are randomly compartmentalized into chambered spaces. These scales lack the bony base component of the elegestolepid squamation, which within the Chondrichthyes has only been documented in scales with growing crowns (either mon- or poly-odontode). Moreover, *Lupopsyrus* and *Obtusacanthus*, a pair of genera that have been repeatedly recovered as stem chondrichthyans in recent hypotheses of early gnathostome phylogeny (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015) are resolved as sister taxa to Elegestolepidida (Fig. 2) and do not possess scale-neck openings of the pulp canal. A pattern of vascularization where the pulp opens only towards the lower surface of scales has a homoplastic distribution inside the stem group, and it is also a feature of the earliest recorded chondrichthyan polyodontode scales (Sansom et al., 1996; 2001; Donoghue and Sansom, 2002; Andreev et al., 2015).

CONCLUSIONS

The original concept of *Elegestolepis*-type scale morphogenesis (Karatajūtė-Talimaa, 1992) is re-interpreted here to feature a stepwise crown growth and neck canal formation as its diagnostic characteristics. The presence of neck canal openings in *Elegestolepis*-type scales is considered to distinguish them from the growing monodontode scales of the Thelodonti (Märss et al., 2007), whereas the absence of basal bone osteons and hard tissue resorption in these taxa are chondrichthyan apomorphies within crown gnathostomes. This implies that the total-group Chondrichthyes has evolved two distinct morphogenetic processes for generation of single odontode scales, one characteristic for the elegestolepids and the other producing the non-growing *Heterodontus*-type scales (sensu Karatajūtė-Talimaa, 1992), known in detail in euselachians. Consequently, the elegestolepid integumentary skeleton is seen to demonstrate one of the early forms of chondrichthyan scale development that are absent from more derived taxa of the clade. It is further speculated that the contribution of osteogenic tissues to elegestolepid scale units represents a phylogenetically basal state in relation to that of taxa with a solely odontogenically derived squamation.

The shared mode of scale morphogenesis unites *Elegestolepis* (Karatajūtė-Talimaa, 1973) with *Ellesmereia* (Vieth, 1980)*, Kannathalepis* (Märss and Gagnier, 2001) and *Deltalepis* gen. nov into the newly erected Order Elegestolepidida, extending the known stratigraphic range of elegestolepid taxa from the Lower Silurian (middle Llandovery) to the Lower Devonian (Lochkovian). Furthermore, a division of the Order into two

Families is established upon differences in pulp cavity architecture between *Kannathalepis* and all the other recognised elegestolepid genera.

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FIGURE CAPTIONS

FIGURE 1. Diagrammatic representation of monodontode scale types in **A**, the Thelodonti and (**B**, **C**) the Chondrichthyes. **A**, a *Thelodus calvus* scale (adapted from Märss and Karatajūtė-Talimaa 2002: fig. 15F) exemplifying the thelodont morphogenetic type; **B**, the *Elegestolepis* morphogenetic type represented by an *Elegestolepis grossi* scale (BU5284); **C**, the *Heterodontus* morphogenetic type represented by a *Triakis semifasciata* scale (BU5341). **Color-coded tissues**: **blue**, enameloid; **brown**, dentine; **gold**, bone. (2/3rd of a whole page width)

FIGURE 2. Distribution of relevant to the study scale characters among select groups of Paleozoic gnathostomes. Tree topology reconstructed from published phylogenies of total-group Chondrichthyes (Grogan et al., 2012) and vertebrates (Sire et al., 2009; Giles et al., 2013, 2015), with the position of Elegestolepidida on the chondrichthyan branch determined from yet to be published analysis by Andreev et al. (representative tree generated in TNT version 1.1 (Goloboff et al., 2008) using a data matrix of 68 equally weighted scale-based characters and 49 Paleozoic jawed-gnathostome taxa). (whole page width)

FIGURE 3. Line drawings depicting the range of crown-surface morphologies in elegestolepid scales. **A**, *Elegestolepis grossi* (BU5284); **B**, *Ellesmereia schultzei*

(adapted from Vieth 1980:pl. 9.2); **C**, *Deltalepis magna* (holotype BU5269); **D**, *Deltalepis parva* (holotype BU5275). Anterior towards the bottom. (column width)

FIGURE 4. Scales of *Elegestolepis grossi* from the Baital Formation of Tuva, Russian Federation; ontogenetically mature scales shown in **A**, antero-lateral (BU5285), **B**, lateral-crown (BU5285), **C**, lateral (BU5286) and (**D**, BU5286), (**E**, BU5287) crown views. **F**, postero-lateral view of BU5289 showing the single neck canal opening of the scale crown; **G**, postero-basal view of an ontogenetically young scale (BU5343) with not fully formed pedicle support; **H**, basal view of a scale (BU5343) with pedicle support at an advanced stage of formation; **I**, mature scale (BU5289) in basal view exhibiting bulbous basal bone. SEM micrographs. Anterior towards right in (B), towards left in (C), towards the bottom in (D, E) and towards the top in (H, I); arrows indicate neck canal openings, arrowhead indicates the basal opening of the main pulp canal. Scale bars represent 200 µm in (A–E, G, H) and 100 µm in (F, I). (whole page width)

FIGURE 5. Hard tissue structure of *Elegestolepis grossi* scales from the Baital Formation of Tuva, Russian Federation. **A**, vertical cross section of a scale (BU5290) in early stage of bony base formation, etched in 0.5% chromium sulphate solution for 2 hours; **B**, detail of **A**, showing the upper medial portion of the crown; **C**, vertical longitudinal section of a scale (BU5291) in advanced stage of basal bone developed (ontogenetically old), etched in 0.5% orthophosphoric acid for 10 minutes; **D**, detail of BU5291 depicting the lower posterior margin of the crown; **E**, detail of the anterior

portion of the crown of BU5291; **F**, vertical transverse section of an ontogenetically old scale (BU5292); **G**, basal bone of ontogenetically old scale (BU5293) in vertical longitudinal section. (B–E) SEM micrographs; (A, F, G) Nomarski interference contrast micrographs. Anterior towards the right in (C–E, G); (B), base; arrowheads in (B–E) demarcate the extent of artificially altered dentine, asterisks in (G) denote the borders of depositional bone lamellae. Scales bars represent 100 μm in (A, C, F, G) 50 μm in (B, E) and 20 μm in (D). (whole page width)

FIGURE 6. Scales of *Deltalepis magna* gen. et sp. nov. from the Chargat Formation of north-western Mongolia. Holotype specimen (BU5269, scale with a five-lobed crown and a gracile neck) in **A**, anterior, **B**, antero-lateral and **C**, crown view. **D**, scale (BU5270) with gracile neck in basal view. Scales with three-lobe crowns in **E**, anterior, **F**, posterior, **G**, lateral (E–G, BU5273) and **H**, crown (BU5271) views. **I**, BU5273 in basal view revealing the lower pedicle surface; **J**, basal view of a scale (BU5272) with fully formed pedicle support. (A–C, H–J**)** SEM micrographs; (D–G) volume renderings. Anterior towards the right in (B), towards the bottom in (C, H) towards the top in (D, **I**, J); arrow indicates a neck canal opening. Scale bars represent 200 μm. (whole page width)

FIGURE 7. Scales of *Deltalepis parva* gen. et sp. nov. from the Chargat Formation of north-western Mongolia. Holotype (BU5275) in **A**, crown and **B**, anterior-crown view. Scale (BU5280) with a gracile neck in **C**, anterior and **D**, posterior view. Scale (BU5277) in **E**, anterior and **F**, crown view. **G**, scale (BU5278) with a gracile neck in basal view,

exposing the rami of the pulp canal system. Scale (BU5279) with formed pedicle support in **H**, basal and **I**, postero-basal view. (A, B, E–I) SEM micrographs; (C, D) volume renderings. Anterior towards the bottom in (A, F) towards the top in (G–I); arrows indicate neck canal openings, arrowhead indicates the basal opening of the main pulp canal. Scale bars represent 200 μm in (A–D, G) and 100 μm in (E, F, H, I). (whole page width)

FIGURE 8. Hard tissue structure of *Deltalepis* gen. nov. **A**, longitudinal tomographic slice of a *Deltalepis magna* scale (BU5273); **B**, detail of the dentine tissue at the upper anterior margin of the crown of a longitudinally sectioned *Deltalepis magna* scale (BU5274); **C**, longitudinal tomographic slice of a *Deltalepis parva* scale (BU5280); **D**, view of the posterior portion of a *Deltalepis parva* scale (BU5282) crown immersed in clove oil. (B, D) Nomarski interference contrast micrographs; (A, C) volume renderings. Anterior towards the right in (A) and towards the left in (C). Scale bars represent 100 μm in (A, C, D) and 50 μm in (B). (whole page width)

FIGURE 9. Volume renderings of the scale canal system (in red) of examined elegestolepids. The scales are made translucent in all renderings, with the exception of (G). **A**–**C**, *Elegestolepis grossi* scale (BU5284) from the Baital Formation of Tuva (Russian Federation) in **A**, anterior, **B**, postero-lateral and **C**, crown (depicting the lower portion of the specimen that is transversely sliced through the neck region) view. **D**–**F**, *Deltalepis magna* scale (BU5273) from the upper Llandovery–lower Wenlock of north

western Mongolia in **D**, crown and **E**, posterior view and a **F**, crown view of the lower portion of the same specimen sliced through the neck region. **G**–**J**, *Deltalepis parva* specimens (BU5280 and BU5281) from the upper Llandovery–lower Wenlock of north western Mongolia; **G**, BU5280 sliced transversely through the crown in crown view; **H**, BU5280 in anterior view; **I**, **J**, BU5281 in **I** posterior and **J**, postero-lateral view. Anterior towards the left in (B), towards the top in (C, F, G) and towards the bottom in (D); arrows indicate neck canal openings, arrowheads point at the basal opening of the main pulp canal. Scale bars represent 100 µm. (whole page width)

FIGURE 10. Characteristics of monodontode scales of recognised lower Paleozoic chondrichthyans and their stratigraphic range. Pink rectangle designates elegestolepid taxa. *Elegestolepis* (Karatajūtė-Talimaa, 1973 and data from this study), *Deltalepis* (data from this study), *Kannathalepis* (Märss and Gagnier, 2001), *Ellesmereia* (Vieth, 1980), *Frigorilepis* (Märss et al., 2002, 2006), *Polymerolepis* Karatajūtė-Talimaa, 1998; Hanke et al., 2013), *Lupopsyrus* and *Obtusacanthus* (Hanke and Wilson, 2004; Hanke and Davis, 2012). (whole page width)

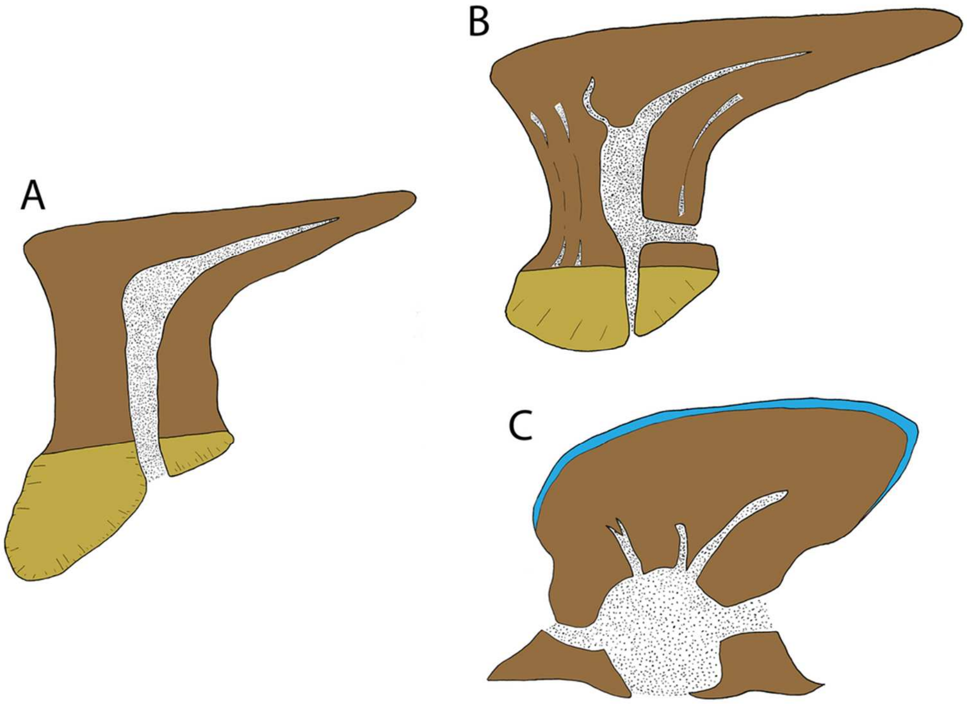
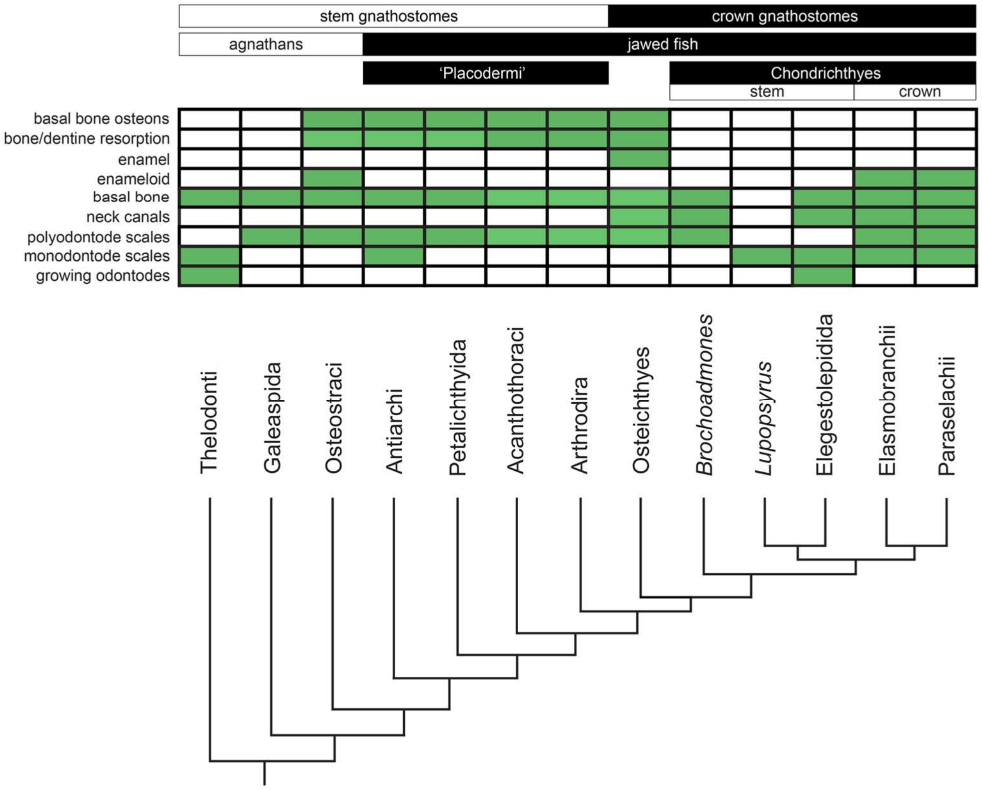


FIGURE 1. Diagrammatic representation of monodontode scale types in A, the Thelodonti and (B, C) the Chondrichthyes. A, a *Thelodus calvus* scale (adapted from Märss and Karatajūtė-Talimaa 2002: fig. 15F) exemplifying the thelodont morphogenetic type; B, the *Elegestolepis* morphogenetic type represented by an *Elegestolepis grossi* scale (BU5284); C, the *Heterodontus* morphogenetic type represented by a *Triakis semifasciata* scale (BU5341). Color-coded tissues: blue, enameloid; brown, dentine; gold, bone. [2/3 of a whole page width]

Fig1

91x69mm (300 x 300 DPI)



	Thelodonti	Galeaspida	Osteostraci	Antiarchi	Petalichthyida	Acanthothoraci	Arthrodira	Osteichthyes	*Brochoadmones*	*Lupopsyrus*	Elegestolepidida	Elasmobranchii	Paraselachii
basal bone osteons			🟩	🟩	🟩	🟩	🟩	🟩					
bone/dentine resorption			🟩	🟩	🟩	🟩	🟩	🟩					
enamel								🟩					
enameloid			🟩									🟩	🟩
basal bone	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩		🟩	🟩	🟩
neck canals								🟩	🟩		🟩	🟩	🟩
polyodontode scales		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩			🟩	🟩
monodontode scales	🟩			🟩						🟩	🟩	🟩	🟩
growing odontodes	🟩										🟩		

FIGURE 2. Distribution of relevant to the study scale characters among select groups of Paleozoic gnathostomes. Tree topology reconstructed from published phylogenies of total-group Chondrichthyes (Grogan et al., 2012) and vertebrates (Sire et al., 2009; Giles et al., 2013, 2015), with the position of Elegestolepidida on the chondrichthyan branch determined from yet to be published analysis by Andreev et al. (representative tree generated in TNT version 1.1 (Goloboff et al., 2008) using a data matrix of 68 equally weighted scale-based characters and 49 Paleozoic jawed-gnathostome taxa). [whole page width]

Fig2

145x116mm (300 x 300 DPI)

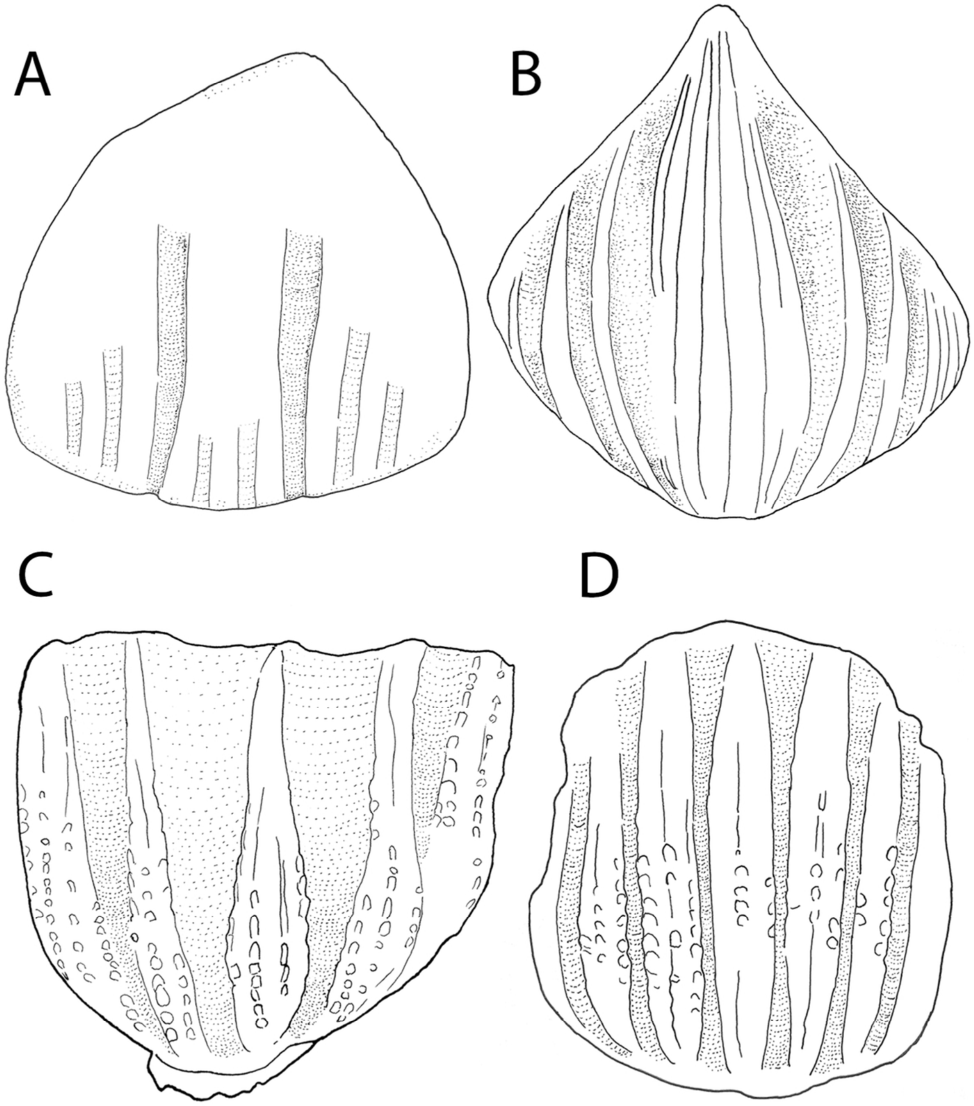


FIGURE 3. Line drawings depicting the range of crown-surface morphologies in elegestolepid scales. A, *Elegestolepis grossi* (BU5284); B, *Ellesmereia schultzei* (adapted from Vieth 1980:pl. 9.2); C, *Deltalepis magna* (holotype BU5269); D, *Deltalepis parva* (holotype BU5275). Anterior towards the bottom. (column width)‼ ┼

Fig. 3

101x116mm (300 x 300 DPI)

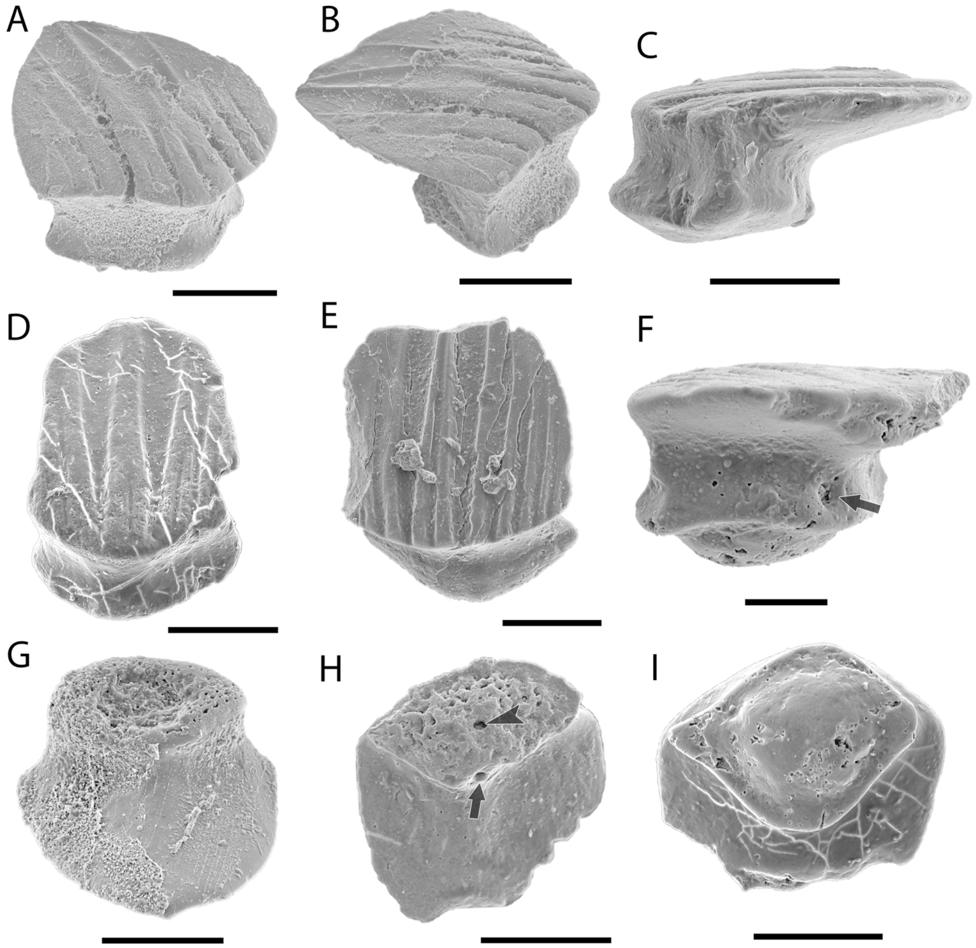


FIGURE 4. Scales of *Elegestolepis grossi* from the Baital Formation of Tuva, Russian Federation; ontogenetically mature scales shown in A, antero-lateral (BU5285), B, lateral-crown (BU5285), C, lateral (BU5286) and (D, BU5286), (E, BU5287) crown views. F, postero-lateral view of BU5289 showing the single neck canal opening of the scale crown; G, postero-basal view of an ontogenetically young scale (BU5343) with not fully formed pedicle support; H, basal view of a scale (BU5343) with pedicle support at an advanced stage of formation; I, mature scale (BU5289) in basal view exhibiting bulbous basal bone. SEM micrographs. Anterior towards right in (B), towards left in (C), towards the bottom in (D, E) and towards the top in (H, I); arrows indicate neck canal openings, arrowhead indicates the basal opening of the main pulp canal. Scale bars represent 200 μm in (A–E, G, H) and 100 μm in (F, I). [whole page width]

Fig. 4
180x178mm (300 x 300 DPI)

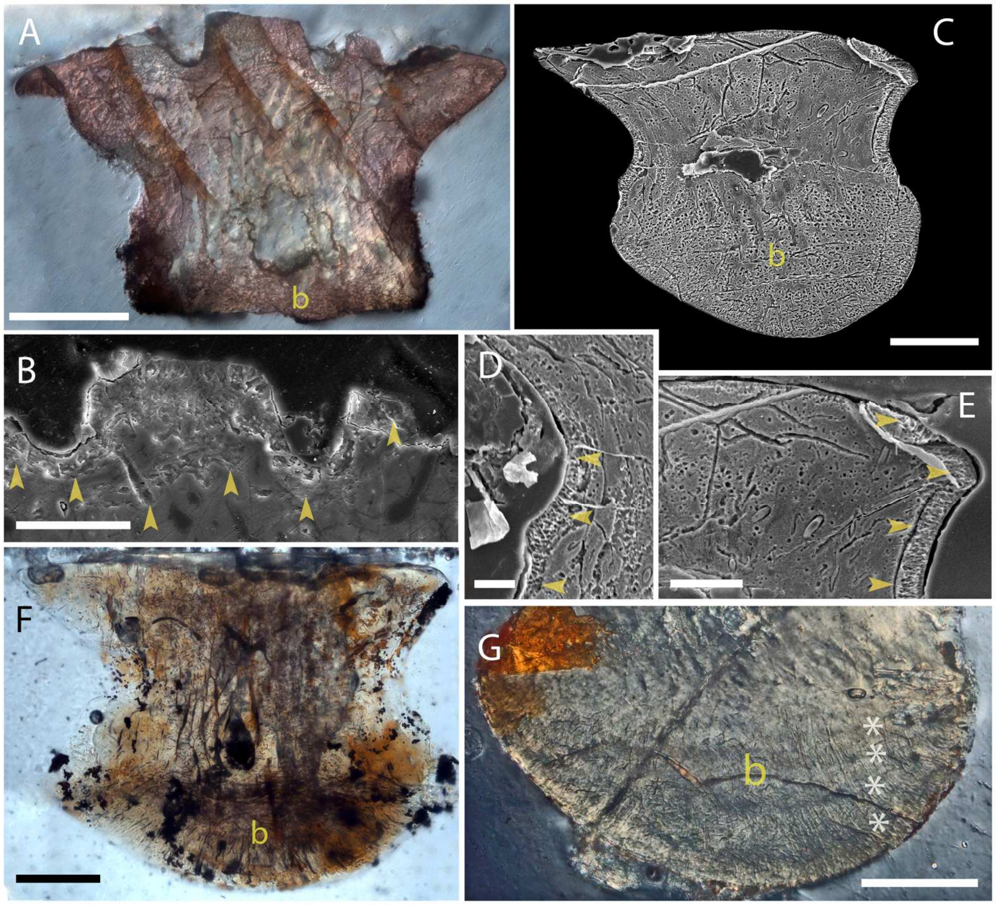


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Fig. 5
164x149mm (300 x 300 DPI)

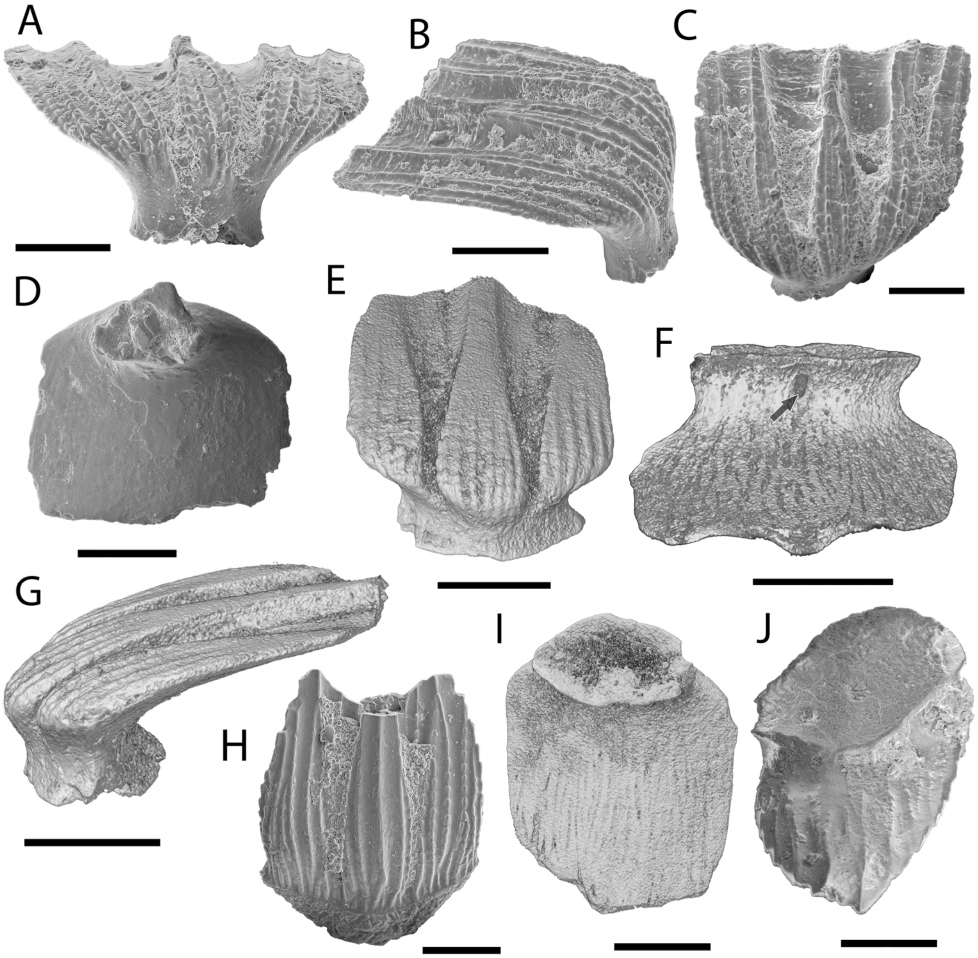

FIGURE 6. Scales of *Deltalepis magna* gen. et sp. nov. from the Chargat Formation of north-western Mongolia. Holotype specimen (BU5269, scale with a five-lobed crown and a gracile neck) in A, anterior, B, antero-lateral and C, crown view. D, scale (BU5270) with gracile neck in basal view. Scales with three-lobe crowns in E, anterior, F, posterior, G, lateral (E–G, BU5273) and H, crown (BU5271) views. I, BU5273 in basal view revealing the lower pedicle surface; J, basal view of a scale (BU5272) with fully formed pedicle support. (A–C, H–J) SEM micrographs; (D–G) volume renderings. Anterior towards the right in (B), towards the bottom in (C, H) towards the top in (D, I, J); arrow indicates a neck canal opening. Scale bars represent 200 µm. (whole page width)

Fig. 6
177x173mm (300 x 300 DPI)

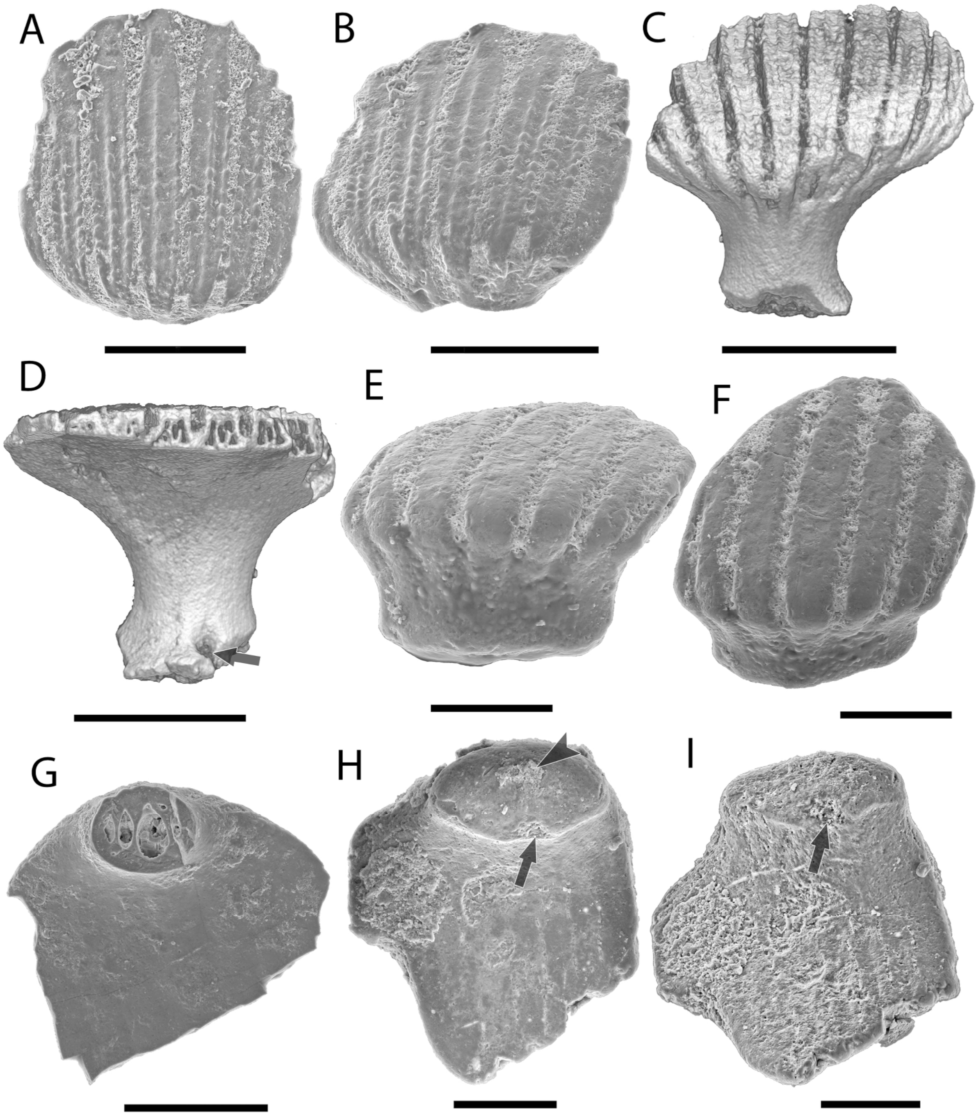

FIGURE 7. Scales of *Deltalepis parva* gen. et sp. nov. from the Chargat Formation of north-western Mongolia. Holotype (BU5275) in A, crown and B, anterior-crown view. Scale (BU5280) with a gracile neck in C, anterior and D, posterior view. Scale (BU5277) in E, anterior and F, crown view. G, scale (BU5278) with a gracile neck in basal view, exposing the rami of the pulp canal system. Scale (BU5279) with formed pedicle support in H, basal and I, postero-basal view. (A, B, E–I) SEM micrographs; (C, D) volume renderings. Anterior towards the bottom in (A, F) towards the top in (G–I); arrows indicate neck canal openings, arrowhead indicates the basal opening of the main pulp canal. Scale bars represent 200 μm in (A–D, G) and 100 μm in (E, F, H, I). [whole page width]

Fig. 7
204x229mm (300 x 300 DPI)

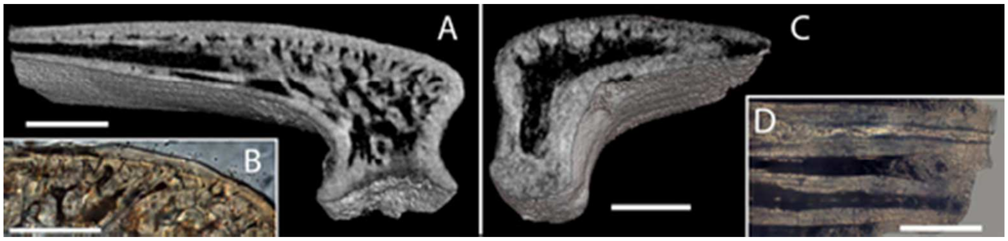

FIGURE 8. Hard tissue structure of *Deltalepis* gen. nov. A, longitudinal tomographic slice of a *Deltalepis magna* scale (BU5273); B, detail of the dentine tissue at the upper anterior margin of the crown of a longitudinally sectioned *Deltalepis magna* scale (BU5274); C, longitudinal tomographic slice of a *Deltalepis parva* scale (BU5280); D, view of the posterior portion of a *Deltalepis parva* scale (BU5282) crown immersed in clove oil. (B, D) Nomarski interference contrast micrographs; (A, C) volume renderings. Anterior towards the right in (A) and towards the left in (C). Scale bars represent 100 μm in (A, C, D) and 50 μm in (B). [whole page width]

Fig. 8
42x9mm (300 x 300 DPI)

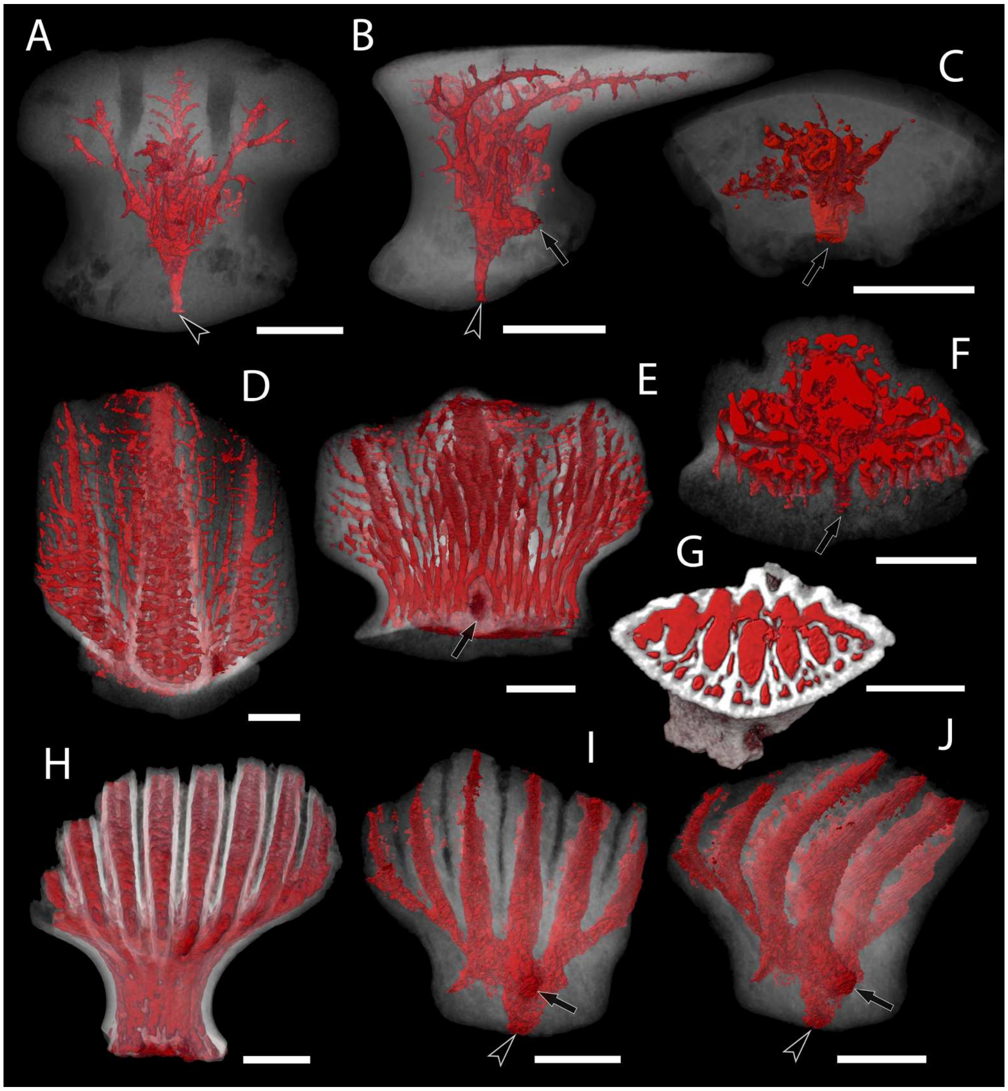

FIGURE 9. Volume renderings of the scale canal system (in red) of examined elegestolepids. The scales are made translucent in all renderings, with the exception of (G). A–C, *Elegestolepis grossi* scale (BU5284) from the Baital Formation of Tuva (Russian Federation) in A, anterior, B, postero-lateral and C, crown (depicting the lower portion of the specimen that is transversely sliced through the neck region) view. D–F, *Deltalepis magnus* scale (BU5273) from the upper Llandovery–lower Wenlock of north western Mongolia in D, crown and E, posterior view and a F, crown view of the lower portion of the same specimen sliced through the neck region. G–J, *Deltalepis parvus* specimens (BU5280 and BU5281) from the upper Llandovery–lower Wenlock of north western Mongolia; G, BU5280 sliced transversely through the crown in crown view; H, BU5280 in anterior view; I, J, BU5281 in I posterior and J, postero-lateral view. Anterior towards the left in (B), towards the top in (C, F, G) and towards the bottom in (D); arrows indicate neck canal openings, arrowheads point at the basal opening of the main pulp canal. Scale bars represent 100 μm. [whole page width]

Fig. 9
196x212mm (300 x 300 DPI)

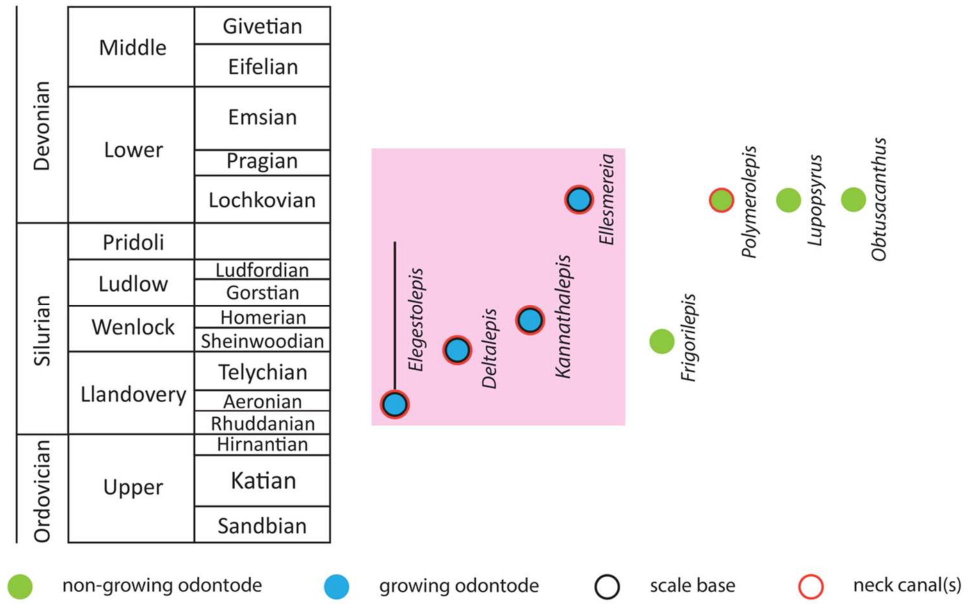

FIGURE 10. Characteristics of monodontode scales of recognised lower Paleozoic chondrichthyans and their stratigraphic range. Pink rectangle designates elegestolepid taxa. *Elegestolepis* (Karatajūtė-Talimaa, 1973 and data from this study), *Deltalepis* (data from this study), *Kannathalepis* (Märss and Gagnier, 2001), *Ellesmereia* (Vieth, 1980), *Frigorilepis* (Märss et al., 2002, 2006), *Polymerolepis* Karatajūtė-Talimaa, 1998; Hanke et al., 2013), *Lupopsyrus* and *Obtusacanthus* (Hanke and Wilson, 2004; Hanke and Davis, 2012). [whole page width]

Fig. 10
115x72mm (300 x 300 DPI)