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Elegestolepis and its kin, the earliest monodontode chondrichthyans

Andreev, Plamen; Coates, Michael; Karatajute-Talimaa, Valentina; Shelton, Richard; Cooper, Paul; Sansom, Ivan

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Elegestolepis and its kin, the earliest monodontode chondrichthyans

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10	3	PLAMEN S. ANDREEV, ^{1*} MICHAEL I. COATES, ² VALENTINA KARATAJŪTĖ-
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12 13	4	TALIMAA, 3 RICHARD M. SHELTON, 4 PAUL R. COOPER, 4 and IVAN J. SANSOM
14		
15	5	¹ School of Geography, Earth and Environmental Sciences, University of Birmingham,
16 17		
18	6	Birmingham, B15 2TT, U.K., <u>p.andreev@bham.ac.uk</u> , i.j.sansom@bham.ac.uk;
19		
20 21	7	² Department of Organismal Biology and Anatomy, University of Chicago, Chicago
22	/	Department of Organismal biology and Anatomy, Oniversity of Onicago, Chicago,
23	8	Illinois 60637-1508. USA. mcoates@uchicago.edu:
24 25	-	
26		
27	9	³ Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania;
28		
29 30	10	⁴ School of Dentistry, College of Medical and Dental Sciences, University of Birmingham
31	10	School of Demistry, Conege of Medical and Demai Ociences, Oniversity of Dirmingham,
32	11	St Chad's Queensway, Birmingham, B4 6NN, UK, r.m.shelton@bham.ac.uk,
33 34		
35	12	p.r.cooper@bham.ac.uk
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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

 42 develop monodontode scales, which, in contrast to the 'placoid' scales of euselachians, 43 are growing structures. 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 50 50 51 52 54 55 56 57 58 59 60 50 50 51 52 54 55 56 57 58 59 60 50 51 52 54 55 56 57 58 59 59 50 50 51 52 54 55 56 57 58 59 59 50 50 51 52 54 55 56 57 58 59 59 50 50 51 54 55 56 57 58 59 59 50 50 51 52 54 55 55 56 57 58 59 59 50 50 51 52 54 55 55 56 57 58 59 59 50 50 51 52 54 55 55 56 57 58 59 59 50 50 51 51 52 54 55 56 57 57 58 59 59 50 51 51 52 54 55 56 57 57 58 59 59 50 51 51 52 54 55 56 57 57 58 59 59 50 50 51 51 51<th>1</th><th></th><th></th>	1		
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2 3 4	61	INTRODUCTION
5 6 7 8	62	
9 10	63	The type species of the genus <i>Elegestolepis</i> (<i>E. grossi</i>) was described by
11 12 12	64	Karatajūtė-Talimaa (1973) from isolated scales from upper Ludlow–Pridoli strata
13 14 15	65	(Elegest and Kadvoj outcrops, Tuva, Russian Federation) of the Tuva-Mongol terrane
16 17	66	and, at the time of publication, was the earliest known taxon referred to the
18 19 20	67	Chondrichthyes. Subsequent studies on microvertebrate fossils from the lower
20 21 22	68	Paleozoic have led to the identification of stratigraphically older species attributed to
23 24	69	Elegestolepis. These are represented by middle Llandovery–lower Wenlock E. sp.
25 26 27	70	specimens from the Tuva-Mongol (Chargat Formation, north western Mongolia; Elegest
28 29	71	Formation, Tuva, Russia (Karatajūtė-Talimaa et al., 1990; Sennikov et al., 2015)) and
30 31	72	Altai terranes (Gornaya Shoriya, Altai Republic, Russia (Sennikov et al., 2015)) and the
32 33 34	73	middle–upper Llandovery E. conica from the adjacent Siberian craton (Angara-Ilim,
35 36	74	Niuya-Bresovo and Tchuna-Biriussa sections, Siberian District, Russia (Karatajūtė-
37 38	75	Talimaa and Predtechenskyj, 1995)). The paleogeographical and stratigraphical range
39 40 41	76	of Elegestolepis-like taxa was further expanded with the description (Vieth, 1980) of the
42 43	77	Laurussian chondrichthyan scale species Ellesmereia schultzei (from the Lochkovian of
44 45 46	78	Ellesmere Island, Nunavut Territory, Canada).
47 48 49	79	According to the categories of scale morphogenesis established by Karatajūtė-
50 51	80	Talimaa (1992) for Paleozoic chondrichthyans, Elegestolepis and Ellesmereia belong to
52 53	81	the Elegestolepis developmental type as the scales have a monodontode, non-growing
54 55 56	82	crown enclosing a pulp canal that opens at the crown neck via a single foramen.
57 58 59	83	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

2		
3 4	107	lepidomorial elements enclosing a single vascular loop (Stensiö and Ørvig, 1951–1957;
5 6 7 8 9 10 11 12 13 14 15 16	108	Stensiö, 1961). Advances in developmental biology have revealed an apparently
	109	conserved gene regulatory network that maintains a variety of odontode morphogenetic
	110	pathways (Fraser et al. 2010). This further corroborates the notion that all structures
	111	resolvable into odontode units are, in a broad sense, homologous. In this context, a re-
	112	examination of <i>Elegestolepis</i> and <i>Elegestolepis</i> -like Silurian scale taxa (e.g.
17 18	113	Ellesmereia, Kannathalepis) will enable a clearer understanding of the early evolution of
19 20 21	114	single odontode integumentary skeletal elements in the Chondrichthyes. To meet this
21 22 23 24 25 26 27 28 29 30 31 32 33	115	end, the present study investigates the histology, canal system and inferred
	116	development of <i>Elegestolepis grossi</i> scales and that of previously undescribed scales
	117	from the Lower Silurian of Mongolia referred to <i>Elegestolepis</i> (Karatajūtė-Talimaa et al.,
	118	1990). These new data permit a new systematic framework for <i>Elegestolepis</i> -like taxa
	119	and allow for the further evaluation of their likely chondrichthyan affinities.
33 34 35 36	120	
37 38 39	121	MATERIALS AND METHODS
40 41 42	122	
43 44 45 46 47 48 49 50 51 52	123	The isolated scales were extracted through dissolution of carbonate rock
	124	samples with dilute acetic acid. The specimens come from the Chargat Formation of
	125	north western Mongolia (Chargat outcrop, sample P-16/3 [2]) and the Baital Formation
	126	(Elegest River outcrop, samples from beds 236, 291, 293 and 295 [1]) of central Tuva,
53 54	127	Russian Federation.
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- 3 4	128	Scale morphology was documented using the Zeiss EVO LS and the JEOL JSM-
5 6 7	129	6060 scanning electron microscopes at the School of Dentistry of the University of
7 8 9	130	Birmingham, UK. Prior to imaging, the specimens were sputter-coated with a 25 nm-
10 11 12	131	thick layer of gold/palladium alloy.
12 13 14	132	Hard tissue microstructure and internal architecture of thin-sectioned specimens was
15 16 17	133	investigated by Nomarski differential interference contrast microscopy (using a 'Zeiss
18 19	134	Axioskop Pol' polarization microscope) and scanning electron microscopy (with a JEOL
20 21 22	135	JSM-6060 SEM at the School of Dentistry, University of Birmingham, UK).
23 24	136	Scale examination with X-ray radiation was conducted using the SkyScan 1172
25 26 27	137	microtomography scanner at the School of Dentistry of the University of Birmingham,
28 29	138	UK. The acquired microradiographs (tomographic projections) were taken at 0.3°
30 31 32	139	intervals over a 180° rotation cycle at exposure times of 400 ms, using a 0.5 mm thick
33 34	140	X-ray attenuating AI filter. These image data were processed with the SkyScan NRecon
35 36	141	reconstruction software in order to generate sets of microtomograms that were
37 38 39	142	converted into volume renderings in Amira 5.4 3D analysis software.
40 41 42	143	Figured material is deposited in the Lapworth Museum of Geology, University of
43 44 45	144	Birmingham, UK (BU prefix).
45 46 47	145	
48 49 50 51 52 53 54 55	146	Definitions of Terms
	147	Traditionally (Sykes, 1974; Duffin and Ward, 1993; Thies, 1995) the two main
	148	components (crown and base) of chondrichthyan scales have been identified on the
57 58 50	149	basis of morphological and/or topological criteria without consideration of their
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2 3	150	developmental origin. This approach can lead to ambiguity when attempting to establish
4 5		
6 7	151	the extent of these structures and, more importantly, can result in homologizing scale
8 9	152	parts with different tissue composition across taxa. To address the above issues,
10 11	153	Andreev et al. (2015) provided revised definitions of terms used in literature to describe
12 13 14	154	chondrichthyan scales, and these are followed in the present study.
15 16 17	155	
18 19 20	156	SYSTEMATIC PALEONTOLOGY
21 22 23	157	
24 25 26	158	Class CHONDRICHTHYES Huxley, 1880
20 27 28	159	Order ELEGESTOLEPIDIDA ordo nov.
29 30 31	160	Included Families—Kannathalepididae Märss and Gagnier 2001 and
32 33 34	161	Elegestolepididae fam. nov.
35 36 37	162	
38 39	163	Diagnosis—Chondrichthyan fish with monodontode scale crowns composed of a
40 41 42	164	growing odontode that encloses neck-canal branches of the pulp cavity (Fig. 1B).
43 44 45	165	Remarks—The recent literature on putative basal chondrichthyan taxa (e.g.
46 47 48 49 50 51 52	166	mongolepids, elegestolepids, kathemacanthids and polymerolepidiforms) from the lower
	167	Paleozoic expresses uncertainty regarding their systematic position relative to the major
	168	clades (Subclasses) of the Chondrichthyes (Karatajute-Talimaa and Novitskaya, 1997;
53 54 55	169	Sansom et al., 2000; Märss et al., 2006; Hanke and Wilson, 2010; Hanke et al., 2013).
56 57 58	170	This reflects an inadequate understanding of the phylogenetic significance of scale-
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derived characters, which have been employed to diagnose these taxa given the L71 general absence of chondrichthyan endoskeletal and dental remains in the lower L72 Paleozoic. L73

The odontode growth that typifies the ontogenesis of *Elegestolepis*-like scales is L74 not seen within traditionally recognised chondrichthyan clades (sensu Grogan et al., L75 2012), yet the Elegestolepidida consistently falls inside stem-group Chondrichthyes L76 when its affinities are tested via phylogenetic inference (Andreev et al., unpublished L77 data; Fig. 2). The erection of a new Order draws together species that possess scales L78 with growing single-odontode crowns whose morphogenesis can be differentiated from L79 that of elasmobranch 'placoid' scales (the *Heterodontus* morphogenetic type of L80 L81 (Karatajūtė-Talimaa, 1992, 1998; Fig. 1C). The formal recognition of the *Elegestolepis*-L82 type of scale development represents a change in concept from what was originally identified as a purely morphogenic category (Karatajūtė-Talimaa, 1992, 1998). L83 L84 Family KANNATHALEPIDIDAE Märss and Gagnier, 2001 L85 Included genera—Kannathalepis Märss and Gagnier, 2001 186 **Revised diagnosis**—Elegestolepids possessing dermal scales with vertically L87 undivided pulp cavities from which multiple (up to five) horizontal neck canals emerge L88 basally. L89 Remarks—The mono-generic Family Kannathalepididae was introduced by Märss 190 191 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. 7I)) 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

206 Complexes of randomly sutured monodontode scales consequently cannot be
207 considered equivalent to polyodontode scales (e.g. those of Mongolepidida (Karatajūtė208 Talimaa, 1998)), since the odontodes of the latter are patterned as a unit in a particular
209 manner and are given support by a common base/pedicle tissue. The scale
210 development in *Kannathalepis* can thus be identified as that of 'placoid' scales with a
211 growing odontode and base, corresponding to the *Elegestolepis* morphogenetic type
212 (Fig. 1B) of Karatajūtė-Talimaa (1992). On that basis, Kannathalepididae is placed
213 inside the new Order Elegestolepidida, and its validity is maintained by acknowledging

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- 3 4 5 6 7 8 9 10 11 2 3 4 5 6 7 8 9 10 11 2 3 4 5 6 7 8 9 10 11 2 3 4 5 6 7 8 9 10 11 2 13 14 5 6 7 8 9 10 11 2 14 5 10 10 10 10 10 10 10 10 10 10 10 10 10	214	the canal system characteristics (vertically undivided pulp cavity and multiple neck	
	215	canals) diagnostic for the Family, recognized in the original description of the taxon.	
	216	Kannathalepididae was expanded subsequent to its erection to include the	
	217	Wenlockian genus Frigorilepis, which was described from articulated body fossils	
	218	(Märss et al., 2002, 2006). Nevertheless, crown morphogenesis in Frigorilepis has not	
	219	been demonstrated to proceed in discrete growth phases as in elegestolepid taxa,	
18 19	220	which are further distinguished by the presence of scale-neck canal openings. The	
20 21	221	absence of characters diagnostic for Elegestolepidida results in treating Frigorilepis as	
22 23 24	222	Family and Order incertae sedis for the time being.	
25 26 27	223		
20 29 30 31	224	Family ELEGESTOLEPIDIDAE fam. nov.	
32 33	225	Included genera—The type genus <i>Elegestolepis</i> Karatajūtė-Talimaa 1973,	
34 35 36 37 38 39 40 41	226	Ellesmereia Vieth, 1980 and Deltalepis gen. nov.	
	227	Diagnosis—Elegestolepids with scales that develop a vertically branched pulp cavity	
	228	that gives off a single horizontal neck canal and dentine canals that originate at the	
42 43 44	229	lower neck/pedicle surface independently of the pulp (Fig. 9).	
45 46 47	230		
48 49 50 51 52	231	Genus ELEGESTOLEPIS Karatajūtė-Talimaa, 1973	
	232	Included species—The type species <i>E. grossi</i> Karatajūtė-Talimaa, 1973 and <i>E.</i>	
53 54 55 56 57	233	<i>conica</i> Novitskaya and Karatajūtė-Talimaa, 1986.	
58 59 60		11	
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2 3 4	234	Revised diagnosis—Elegestolepidids possessing up to three unornamented
5	235	scale crown lobes (Fig. 3A; Fig. 4A, B, D, E) incised by deep, linear grooves.
7 8 9 10	236	
11 12	237	ELEGESTOLEPIS GROSSI Karatajūtė-Talimaa, 1973
13 14 15	238	(Figs. 1B, 3A, 4, 5, 9A–C)
16 17 18	239	Elegestolepis grossi Karatajūtė-Talimaa, 1973:figs. 1–5, pl. 3 (original description).
19 20	240	Elegestolepis grossi Karatajūtė-Talimaa, 1998:31, fig. 10.
21 22	241	Locality and horizon—Studied material comes from beds 236, 291, 293 and
23 24 25	242	295 of the Baital Formation (Wenlock–Ludlow (Vladimirskaya, 1978; Sennikov et al.,
25 26 27	243	2015)) at the type locality on the Elegest River, central Tuva, Russia (Karatajūtė-
28 29 30 31 32	244	Talimaa, 1973). E. grossi has also been reported from the Pridoli of Tuva, Russia
	245	(Khondergei Formation (Sennikov et al., 2015)) as well as from strata of the lower
33 34 25	246	Wenlock Upper Tarkhata Subformation (Gorny Altai, Russia (Sennikov et al., 2015)).
35 36 37	247	Holotype—An ontogenetically mature scale (T-003) from the Baital Formation of
38 39 40	248	Tuva, Russian Federation (Karatajūtė-Talimaa, 1973).
41 42 42	249	Referred material—Over 200 isolated scales that were examined for this study
43 44 45	250	are deposited in the Lapworth Museum of Geology, University of Birmingham, UK.
46 47 48	251	Revised diagnosis—Elegestolepis species possessing small (up to c. 1 mm
49 50	252	long) scales that have deltoid to lanceolate, trilobate crowns and develop moderately to
51 52 53	253	strongly constricted necks and bulbous bases during their ontogenesis. Scale odontode
55 54 55 56 57	254	composed of dentine tissue with multipolar odontocyte lacunae from which emerge
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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).

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8	This study also demonstrates the presence of not previously identified faint
9	depositional lines (Fig. 5G) in the basal bone of <i>E. grossi</i> scales, although growth of the
0	bone tissue has been inferred from specimens in different stages of development
1	(Karatajūtė-Talimaa 1973, 1998). The lamellae, demarcated by the depositional lines
2	produced by change in orientation of the matrix's crystalline fibres, have convex down
3	profiles common for the scale bases of lower vertebrates (Ørvig, 1966; Zangerl, 1968;
4	Denison, 1979; Burrow and Turner, 1998, 1999; Qu et al., 2013).
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6	Genus ELLESMEREIA Vieth, 1980
7	Included species—Ellesmereia schultzei Vieth, 1980
8	Remarks—Ellesmereia (Fig. 3B) was assigned to the Elasmobranchii by Vieth
9	(1980) despite being recognized to possess an <i>Elegestolepis</i> -type of scale
0	morphogenesis (Reif, 1978; Karatajūtė-Talimaa, 1992) that is atypical for an
1	elasmobranch, and consequently it is placed here within the Elegestolepidida. Mature
2	Ellesmereia scales also possess a canal system architecture (Vieth, 1980: fig. 26)
3	closely resembling the vascularization of <i>Elegestolepis</i> and <i>Deltalepis</i> gen. nov., and for
4	these reasons the three taxa are united at a familial level.
5	
6	Genus DELTALEPIS gen. nov.
7	Included species—Deltalepis magna gen. et sp. nov. (type species) and
8	<i>Deltalepis parva</i> gen. et sp. nov.

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

301 **Diagnosis**—Elegestolepidids whose scales possess lobed crowns ornamented 302 by tuberculate ridges. Crown lobes and furrows extend down the anterior face of the 303 scale neck (Figs. 7, 8).

Remarks—The material referred here to *Deltalepis* gen. nov. has not previously)4 been formally described or figured, although was considered to belong to the genus)5 Elegestolepis by Karatajūtė-Talimaa et al. (1990) and Karatajute-Talimaa and)6 Novitskaya (1997) in their work on the mongolepid taxa from the Chargat Formation.)7 Deltalepis gen. nov. scales possess crown morphology, ornamentation and pulp cavity)8)9 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 10 Deltalepis species is based on the documented intra- and inter-generic variation of 1 12 trunk-scale morphology (e.g. crown shape, number of crown ridges/lobes and ornamentation) in Recent neoselachian Families (Reif, 1985; Compagno, 1988; Voigt 13 and Weber, 2011). Comparable differences in ornament have also been used to 4 distinguish taxa at genus level among thelodonts (e.g. *Erepsilepis* (Märss et al., 2006)) ۱5 and mongolepid chondrichthyans (Shigianolepis and Rongolepis (Sansom et al., 2000)). 16 Ridged lobes are also a feature in the putative chondrichthyan taxon Areyongalepis 17 oervigi (Young, 1997, 2000) known solely from micro-remains from the Darriwilian 18 Stokes Siltstone (Amadeus Basin, Northern Territory, Australia). The crown necks and 19 20 bases of elegestolepid scales, however, are not developed in Areyongalepis elements,

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3 4	321	and the latter do not demonstrate identifiable vertebrate mineralised tissues (Young,
5 6 7	322	1997), making their systematic position uncertain for the time being.
8 9	323	
10 11	324	DELTALEPIS MAGNA sp. nov.
12 13 14	325	(Figs. 3C, 6, 8A–B, 9D–F)
15 16 17	326	Derivation of name —From the feminine form of the Latin word for large,
18 19	327	referring to the scale size of the species relative to that of <i>D. parva</i> gen. et sp. nov.
20 21 22	328	Locality and horizon—The type and only known locality for <i>D. magna</i> is 80 km
23 24 25	329	north of Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All
25 26 27	330	specimens come from sample P-16/3 collected from the upper Llandovery-lower
28 29	331	Wenlock (Salhit regional Stage) horizons of the Chargat Formation (Ørvig, 1977;
30 31 32	332	Karatajūtė-Talimaa et al., 1990).
33 34 35	333	Holotype—An isolated, presumably trunk, scale BU5269 (Figs. 3C, 6A–C).
36 37 38	334	Referred material—Six isolated scales (BU5269–BU5274).
39 40 41	335	Diagnosis—Deltalepis species possessing scales with deltoid to elliptic crowns
42 43	336	divided into three to five discrete lobes by posteriorly widening grooves. Parallel
44 45 46	337	tuberculate ridges developed on the undersurface of the crown. The rami of the pulp
40 47 48	338	cavity formed inside the scale crown connect directly to the main pulp canal.
49 50 51	339	
52 53 54 55 56 57 58	340	Description
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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 μ m). In the upper portion of the crown, the canalicular network emerges from a complex of horizontally and vertically branched, interconnected, small-calibre dentine

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- 3 4	364	canals (diameter of c. 5–25 $\mu\text{m};$ Fig. 9D). The latter are most prominent inside the
5 6 7	365	crown lobes where they associate with and connect to branches (c. 30–60 μm in
8 9	366	diameter) of the pulp canal. For most of their length the pulp branches extend parallel
10 11	367	the crown surface, before curving basally to merge (Fig. 9F) into a single pulp canal (c.
12 13	368	60–90 μ m wide) inside the scale neck. From the posterior of the pulp issues an
14 15 16	369	unbranched horizontal canal (c. 70 μm long; Fig. 9F) that opens on the scale neck
17 18	370	surface. Separate from the pulp cavity system, the posterior half of the scales houses
19 20 21	371	numerous closely spaced (up to c. 10 μm apart) dentine canals (10–20 μm in diameter)
22 23	372	whose paths parallel that of the lower crown surface (Fig. 9E). The lower ends of these
24 25	373	canals ramify inside the scale neck before either exiting the scale basally (Fig. 9E) or
26 27 28	374	ending blindly inside it.
29 30 31	375	The tissue (c. 40 μ m thick) closing off the lower pedicle opening displays an
32 33	376	optically discernable boundary with the overlying dentine (Fig. 8A), but it could not be
34 35 26	377	ascertained whether it constitutes a distinct tissue type.
30 37 38	378	
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40 41 42	379	DELTALEPIS PARVA sp. nov.
42 43 44	380	(Figs. 3D, 7, 8C–D, 9G–J)
45 46	381	Derivation of name—From the feminine form of the Latin word for small,
47 48 49	382	referring to the scale size of the species relative to that of <i>D</i> . magna gen. et sp. nov.
49 50		
51 52	383	Locality and horizon—The type and only known locality situated 80 km north of
53 54 55	384	Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All specimens
56 57	385	come from the upper Llandovery-lower Wenlock (Salhit regional Stage) horizons
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(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)

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- 3 4	407	with a diameter of 20–35 $\mu m.$ A canal opening is also present on the lower pedicle
5 6 7	408	surface (Fig. 7H), while a row of elliptical foramina of laterally decreasing diameter (from
7 8 9	409	70 μm to 40 μm in Fig. 7G) mark the lower face of scales lacking a pedicle attachment.
10 11 12	410	Histology—Tubular dentine tissue (Fig. 8C, D) is the only component of the
13 14	411	scale crown. The dentine canaliculi are less than 2 μm in diameter and up to c. 20 μm
15 16 17	412	long, with arborescent branching (Fig. 8D) that gives the tubular system a tangled
18 19	413	appearance. Inside the lobed regions of the crown, the tubules connect to a network of
20 21	414	vertically (c. 5–10 μm wide and 25–40 μm long) and horizontally (c. 5 μm wide) oriented
22 23 24	415	dentine canals (Fig. 8C; Fig. 9J) that are confluent with branches of the pulp cavity.
25 26	416	These pulp branches (from c. 20 μm to c. 45 μm in diameter; Fig. 9G–J) occupy the
27 28 20	417	crown lobes (one canal per lobe) before curving basally to merge with one another
29 30 31	418	inside the scale neck. The three medial branches emerge from the main pulp canal—
32 33	419	confined to the scale neck/pedicle—whereas the more lateral ones are only indirectly
34 35 36	420	connected to it through the medial rami (Fig. 9I). Near its lower end, the main pulp canal
37 38 39	421	gives off a short neck canal (Fig. 9I, J) that opens at the scale surface.
40 41	422	Posterior of the pulp-cavity canal system the scale houses a number (c. 15) of
42 43	423	mutually parallel, ascending dentine canals (Fig. 9G) with diameters between c. 10 μm
44 45 46	424	and 15 μ m. These canals follow the posterior scale profile without establishing
47 48	425	connections at any point with the pulp cavity and terminate basally at the lower pedicle
49 50 51	426	surface.
52 53 54	427	
55 56 57	428	DISCUSSION
58 59 60		20
		Society of Vertebrate Paleontology

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3 4	429	
5 6 7 8	430	Chondrichthyan Characteristics of Elegestolepid Scales
9 10	431	The odontogenic component of the vertebrate skeleton develops primarily as
11 12 13	432	discrete elements (odontodes), each of which being the product of a single epithelia-
14 15	433	mesenchymal cell condensation (Ørvig, 1977; Reif, 1982; Fraser et al., 2010).
16 17 18	434	Odontodes are one of the main structural units of scales and in certain groups (e.g. in
19 20	435	neoselachian chondrichthyans (Fig. 1C; Sire and Huysseune, 2003; Eames et al., 2007;
21 22	436	Sire et al., 2009) can form the entire squamation in the absence of osteogenic
23 24 25	437	contribution to the integumentary skeleton. In lower Paleozoic vertebrates, dermal
26 27	438	odontodes are usually patterned in clusters (polyodontodia in Ørvig, 1977) that form
28 29 20	439	compound scale crowns; these have been documented in pteraspidomorphs (Gross,
30 31 32	440	1961; Denison, 1967; Sansom et al., 2009; Keating et al., 2015), anaspids (Märss,
33 34	441	1968; Blom et al., 2002; Märss, 2002; Keating and Donoghue, 2016), galeaspids (Wang
35 36 37	442	et al., 2005), osteostracans (Stensiö, 1932; Märss et al., 2014) and jawed
38 39	443	gnathostomes (Schultze, 1968, 1977; Gross, 1969; Denison, 1979; Karatajūtė-Talimaa,
40 41	444	1995; Sansom et al., 1996; 2012; Burrow and Turner, 1998, 1999; Giles et al., 2013).
42 43 44	445	The Thelodonti (Märss et al., 2007), Elegestolepidida (Karatajūtė-Talimaa, 1973, 1998
45 46	446	and this study) and some euchondrichthyans (sensu Janvier and Pradel, 2015)—e.g.
47 48 40	447	iniopterygians (Zangerl R, Case, 1973; Grogan and Lund, 2009), petalodonts (Malzahn,
49 50 51	448	1968), symmoriiforms (Lund, 1985, 1986; Coates and Sequeira, 2001), living
52 53	449	holocephalians (Patterson, 1965) and euselachians (Thies and Leidner, 2011)—are the
54 55 56 57 58 59	450	exception, as their scale crowns form only from a single-odontode element.

The integumentary skeleton of the lodonts 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 the lodonts go through several ontogenetic phases that result in gradual elongation of the crown in basal direction (Gross, 1967; Karatajūtė-Talimaa, 1978). The lodonts 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

2 3	473	interpreted to form superficially at the epithelium-mesenchyme boundary and therefore
4 5	474	not to interport the vector (Karatajūtė Talimae, 1079; Märze et al. 2007)
6 7	474	not to intersect the vascular system (Karatajute-railmaa, 1976, Marss et al., 2007).
8 9 10	475	Outside the Chondrichthyes, other derived gnathostomes regarded to possess
11 12	476	monodontode body scales belong to the basal 'placoderm' Orders Stensioellida and
13 14	477	Antiarcha (Fig. 2; also refer to Johanson, 2002; Giles et al., 2015; Brazeau and
15 16 17	478	Friedman, 2015 and citations therein for recent vertebrate phylogenies) whose scale
18 19	479	structure is still insufficiently investigated. The available data on the squamation of
20 21	480	these taxa (e.g. Stensioella (Gross, 1962) and Parayunnanolepis (Upeniece, 2011; Zhu
22 23 24	481	et al. 2012)) provides evidence for non-growing odontodes, implying this to be a
25 26	482	plesiomorphic feature of the single-odontode scales of jawed gnathostomes.
27 28	483	Histological descriptions of scale hard-tissues are presently not available for the above
29 30 31	484	taxa, but known examples of 'placoderm' scale structure often demonstrate formation of
32 33	485	an osteon-rich vascular layer inside the upper portion of the basal bone (Burrow and
34 35 36	486	Turner 1998, 1999; Giles et al., 2013; Rücklin and Donoghue 2015). Osteon mediated
37 38	487	bone remodeling and resorption is widespread in the dermal skeleton of 'placoderms'
39 40	488	(Donoghue et al. 2006; Downs and Donoghue, 2009; Giles et al., 2013) and basal
41 42 43	489	osteichthyans (Zhu et al., 2006), but, critically, is absent from the elegestolepid skeleton
44 45	490	and in conventional chondrichthyans. Other characteristics placing elegestolepids with
46 47	491	the Chondrichthyes among derived gnathostomes are the pattern of scale histogenesis
48 49 50	492	and their hard tissue composition, both of which match those of polyodontode
51 52	493	chondrichthyan scales by being two-component skeletal elements formed out of
53 54	494	lamellar basal bone and crown dentine (Karatajūtė-Talimaa, 1992).
55 56 57 58	495	

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496 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 Predtechensky, 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).

1 2 3 4 5	565	CONCLUSIONS
6 7 8	566	
9 10	567	The original concept of <i>Elegestolepis</i> -type scale morphogenesis (Karatajūtė-
11 12 13	568	Talimaa, 1992) is re-interpreted here to feature a stepwise crown growth and neck canal
14 15	569	formation as its diagnostic characteristics. The presence of neck canal openings in
16 17	570	Elegestolepis-type scales is considered to distinguish them from the growing
18 19 20	571	monodontode scales of the Thelodonti (Märss et al., 2007), whereas the absence of
21 22	572	basal bone osteons and hard tissue resorption in these taxa are chondrichthyan
23 24	573	apomorphies within crown gnathostomes. This implies that the total-group
25 26 27	574	Chondrichthyes has evolved two distinct morphogenetic processes for generation of
28 29	575	single odontode scales, one characteristic for the elegestolepids and the other
30 31 32	576	producing the non-growing <i>Heterodontus</i> -type scales (sensu Karatajūtė-Talimaa, 1992),
33 34	577	known in detail in euselachians. Consequently, the elegestolepid integumentary
35 36	578	skeleton is seen to demonstrate one of the early forms of chondrichthyan scale
37 38 39	579	development that are absent from more derived taxa of the clade. It is further
40 41	580	speculated that the contribution of osteogenic tissues to elegestolepid scale units
42 43	581	represents a phylogenetically basal state in relation to that of taxa with a solely
44 45 46	582	odontogenically derived squamation.
47 48 49	583	The shared mode of scale morphogenesis unites <i>Elegestolepis</i> (Karatajūtė-Talimaa,
50 51	584	1973) with Ellesmereia (Vieth, 1980), Kannathalepis (Märss and Gagnier, 2001) and
52 53	585	Deltalepis gen. nov into the newly erected Order Elegestolepidida, extending the known
55 56	586	stratigraphic range of elegestolepid taxa from the Lower Silurian (middle Llandovery) to
57 58	587	the Lower Devonian (Lochkovian). Furthermore, a division of the Order into two
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1 2		
3 4	588	Families is established upon differences in pulp cavity architecture between
5 6 7	589	Kannathalepis and all the other recognised elegestolepid genera.
8 9 10	590	
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46 47 48	604	
49 50 51	605	
52 53 54	606	
55 56 57 58	607	
59 60		28

1 2		
2 3 4 5	608	
6 7 8	609	
9 10 11	610	LITERATURE CITED
12 13	611	
15 16	612	Andreev, P. S. 2014. The early evolutionary history of sharks and shark-like fishes: In
17 18 19	613	School of Geography, Earth and Environmental Science, Vol. Ph.D. thesis.
20 21	614	University of Birmingham, Birmingham.
22 23	615	Andreev, P. S., M. I. Coates, R. M. Shelton, P. R. Cooper, M. P. Smith, and I. J.
24 25 26	616	Sansom. 2015. Upper Ordovician chondrichthyan-like scales from North
27 28	617	America. Palaeontology 58:691–704.
29 30	618	Andreev, P. S., and G. Cuny. 2012. New Triassic stem selachimorphs (Chondrichthyes,
31 32 33	619	Elasmobranchii) and their bearing on the evolution of dental enameloid in
34 35	620	Neoselachii. Journal of Vertebrate Paleontology 32:255–266.
36 37	621	Bernacsek, G. M., and D. L. Dineley. 1977. New acanthodians from the Delorme
30 39 40	622	Formation (Lower Devonian) of NWT Canada. Palaeontographica Abteilung A
41 42	623	158:1–25.
43 44 45	624	Blom, H., T. Marss, and C. G. Miller. 2002. Silurian and earliest Devonian birkeniid
46 47	625	anaspids from the Northern Hemisphere. Transactions of the Royal Society of
48 49	626	Edinburgh-Earth Sciences 92:263–323.
50 51 52	627	Brazeau, M. D. 2009. The braincase and jaws of a Devonian 'acanthodian' and modern
53 54	628	gnathostome origins. Nature 457:305–308.
55 56 57	629	Brazeau, M. D., and M. Friedman. 2015. The origin and early phylogenetic history of
58 59 60		29

1 2		
- 3 4	630	jawed vertebrates. Nature 520:490–497.
5 6 7	631	Burrow, C., and S. Turner. 1998. Devonian placoderm scales from Australia. Journal of
7 8 9	632	Vertebrate Paleontology 18:677–695.
10 11	633	Burrow, C. J., and S. Turner. 1999. A review of placoderm scales, and their significance
12 13	634	in placoderm phylogeny. Journal of Vertebrate Paleontology 19:204–219.
14 15 16	635	Coates, M., and S. Sequeira. 2001. A new stethacanthid chondrichthyan from the Lower
17 18	636	Carboniferous of Bearsden, Scotland. Journal of Vertebrate Paleontology
19 20 21	637	21:438–459.
21 22 23	638	Compagno, L. J. 1988. Sharks of the order Carcharhiniformes. 486 pp. Princeton
24 25	639	University Press Princeton, New Jersey.
26 27 28	640	Davis, S. P., J. A. Finarelli, and M. I. Coates. 2012. Acanthodes and shark-like
29 30	641	conditions in the last common ancestor of modern gnathostomes. Nature
31 32	642	486:247–250.
33 34 35	643	Denison, R. H. 1967. Ordovician vertebrates from western United States. Fieldiana:
36 37	644	Geology 16:131–192.
38 39 40	645	Denison, R. H. 1979. Acanthodii. 62 pp. Gustav Fischer Verlag, Stuttgart, New York.
40 41 42	646	Dick, J. R. 1978. On the Carboniferous shark Tristychius arcuatus Agassiz from
43 44	647	Scotland. Transactions of the Royal Society of Edinburgh 70:63–108.
45 46 47	648	Dick, J., and J. Maisey. 1980. The Scottish Lower Carboniferous shark Onychoselache
48 49	649	traquairi. Palaeontology 23:363–374.
50 51 52	650	Donoghue, P. C. 2002. Evolution of development of the vertebrate dermal and oral
52 53 54	651	skeletons: unraveling concepts, regulatory theories, and homologies.
55 56	652	Paleobiology 28:474–507.
57 58 59		
60		30

Page 31 of 59

1 2		
- 3 4	653	Donoghue, P. C. J., and I. J. Sansom. 2002. Origin and early evolution of vertebrate
5 6 7	654	skeletonization. Microscopy research and technique 59:352–372.
8 9	655	Donoghue, P. C. J., I. J. Sansom, and J. P. Downs. 2006. Early evolution of vertebrate
10 11	656	skeletal tissues and cellular interactions, and the canalization of skeletal
12 13 14	657	development. Journal of Experimental Zoology Part B: Molecular and
15 16	658	Developmental Evolution 306:278-294.
17 18	659	Downs, J. P., and P. C. Donoghue. 2009. Skeletal histology of Bothriolepis canadensis
19 20 21	660	(Placodermi, Antiarchi) and evolution of the skeleton at the origin of jawed
22 23	661	vertebrates. Journal of Morphology 270:1364–1380.
24 25 26	662	Duffin, C., and D. Ward. 1993. The Early Jurassic palaeospinacid sharks of Lyme
20 27 28	663	Regis, southern England. Professional Paper of the Belgian Geological Survey,
29 30	664	Elasmobranches et stratigraphie 264:53–102.
31 32 33	665	Eames, B. F., N. Allen, J. Young, A. Kaplan, J. A. Helms, and R. A. Schneider. 2007.
33 34 35	666	Skeletogenesis in the swell shark Cephaloscyllium ventriosum. Journal of
36 37	667	anatomy 210:542–554.
38 39 40	668	Fischer, J., J. W. Schneider, and A. Ronchi. 2010. New hybondontoid shark from the
40 41 42	669	Permocarboniferous (Gzhelian-Asselian) of Guardia Pisano (Sardinia, Italy). Acta
43 44 45	670	Palaeontologica Polonica 55:241–264.
45 46 47	671	Fraser, G. J., R. Cerny, V. Soukup, M. Bronner-Fraser, and J. T. Streelman. 2010. The
48 49	672	odontode explosion: The origin of tooth-like structures in vertebrates. Bioessays
50 51	673	32:808–817.
52 53 54	674	Giles, S., M. Friedman, and M. D. Brazeau. 2015. Osteichthyan-like cranial conditions in
55 56 57 58	675	an Early Devonian stem gnathostome. Nature 520:82–85.
59 60		31

3 4	676	Giles, S., M. Rücklin, and P. C. Donoghue. 2013. Histology of "placoderm" dermal
5 6	677	skeletons: Implications for the nature of the ancestral gnathostome. Journal of
7 8 9	678	Morphology 274:627–644.
10 11	679	Gillis, J. A., and P. C. Donoghue. 2007. The homology and phylogeny of chondrichthyan
12 13	680	tooth enameloid. Journal of Morphology 268:33–49.
14 15 16	681	Ginter, M. 2004. Devonian sharks and the origin of Xenacanthiformes; pp. 473–486 in
17 18	682	G. Arratia, M. V. H. Wilson, and R. Cloutier (eds.), Recent Advances in the Origin
19 20 21	683	and Early Radiation of Vertebrates. Verlag Friedrich Pfeil, Munich.
22 23	684	Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for
24 25	685	phylogenetic analysis. Cladistics 24:774-786.
26 27 28	686	Grogan, E. D., and R. Lund. 2009. Two new iniopterygians (Chondrichthyes) from the
29 30	687	Mississippian (Serpukhovian) Bear Gulch Limestone of Montana with evidence of
31 32	688	a new form of chondrichthyan neurocranium. Acta Zoologica 90:134–151.
33 34 35	689	Grogan, E. D., R. Lund, and E. Greenfest-Allen. 2012. The origin and relationships of
36 37	690	early chondrichthyans; pp. 3–29 <i>i</i> n J. C. Carrier, Musick J. A., Heithaus M. R.
38 39 40	691	(ed.), Biology of sharks and their relatives. Taylor & Francis, New York.
40 41 42	692	Gross, W. 1953. Devonische Palaeonisciden-Reste in Mittel-und Osteuropa.
43 44	693	Paläontologische Zeitschrift 27:85–112.
45 46 47	694	Gross, W. 1956. Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im
48 49	695	Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems
50 51	696	paläozoischer Agnathen und Fische. Kungliga Svenska vetenskapsakademiens
52 53 54	697	handlingar 5:1–140.
55 56 57	698	Gross, W. 1961. Aufbau des Panzers obersilurischer Heterostraci und Osteostraci
58 59 60		32

Page 33 of 59

1 2		
2 3 4	699	Norddeutschlands (Geschiebe) und Oesels. Acta Zoologica 42:73–150.
5 6 7	700	Gross, W. 1962. Neuuntersuchung der Stensioellida (Arthrodira, Unter- devon).
8 9	701	Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden
10 11	702	90:48–86.
12 13 14	703	Gross, W. 1967. Über Thelodontier-Schuppen. Palaeontographica Abteilung A 127:1-
15 16	704	67.
17 18	705	Gross, W. 1968. Fragliche Actinopterygier-Schuppen aus dem Silur Gotlands. Lethaia
19 20 21	706	1:184–218.
22 23	707	Gross, W. 1969. Lophosteus superbus Pander, ein Teleostome aus dem Silur Oesels.
24 25 26	708	Lethaia 2:15–47.
20 27 28	709	Guinot, G., and H. Cappetta. 2011. Enameloid microstructure of some Cretaceous
29 30	710	Hexanchiformes and Synechodontiformes (Chondrichthyes, Neoselachii): new
31 32 33	711	structures and systematic implications. Microscopy research and technique
34 35	712	74:196–205.
36 37	713	Hanke, G. F., and S. P. Davis. 2008. Redescription of the acanthodian Gladiobranchus
38 39 40	714	probaton Bernacsek & Dineley, 1977, and comments on diplacanthid
41 42	715	relationships. Geodiversitas 30:303–330.
43 44 45	716	Hanke, G. F., and S. P. Davis. 2012. A re-examination of Lupopsyrus pygmaeus
45 46 47 48 49 50 51 52 53 54	717	Bernacsek & Dineley, 1977 (Pisces, Acanthodii). Geodiversitas 34:469–487.
	718	Hanke, G. F., and M. V. H. Wilson. 2004. New teleostome fishes and acanthodian
	719	systematics; pp. 189–216 <i>i</i> n G. Arratia, Wilson, M. V. H. & R. Cloutier (ed.),
	720	Recent advances in the origin and early radiation of vertebrates. Verlag Dr.
55 56 57 58	721	Friedrich Pfeil, Munich.
59 60		33

1	
2	
3	
4	
5	
6	
7	
2 2	
a	
3	
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11	
12	
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45	
46	
47	
48	
49	
50	
51	
52	
53	
54	
55	
56	
57	
58	
59	
60	

722	Hanke, G. F., and M. V. H. Wilson. 2010. The putative stem-group chondrichthyans
723	Kathemacanthus and Seretolepis from the Lower Devonian MOTH locality,
724	Mackenzie Mountains, Canada.; pp. 159–182 <i>i</i> n J. G. M. D. K. Elliott, X. Yu & D.
725	Miao (ed.), Morphology, phylogeny and paleobiogeography of fossil fishes.
726	Verlag Dr. Friedrich Pfiel, Munich.
727	Hanke, G. F., M. V. Wilson, and F. J. Saurette. 2013. Partial articulated specimen of the
728	Early Devonian putative chondrichthyan Polymerolepis whitei Karatajute-
729	Talimaa, 1968, with an anal fin spine. Geodiversitas 35:529–543.
730	Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the
731	Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological
732	Society of London 43:649–662.
733	Janvier, P. and A. Pradel. 2015. Elasmobranchs and their extinct relatives: diversity,
734	relationships, and adaptations through time; pp. 1–17 <i>i</i> n R. E. Shadwick, Farrell
735	A. P., Brauner C. J. (ed.), Physiology of Elasmobranch Fishes: Structure and
736	Interaction with Environment: Fish Physiology 34 A. Academic Press Inc.
737	Jeppsson, L., and R. Anehus. 1995. A buffered formic acid technique for conodont
738	extraction. Journal of Paleontology 69:790–794.
739	Jeppsson, L., D. Fredholm, and B. Mattiasson. 1985. Acetic acid and phosphatic
740	fossils—a warning. Journal of Paleontology 59:952–956.
741	Johanson, Z. 2002. Vascularization of the osteostracan and antiarch (Placodermi)
742	pectoral fin: similarities, and implications for placoderm relationships. Lethaia
743	35:169–186.
744	Johanson, Z., M. Tanaka, N. Chaplin, and M. Smith. 2008. Early Palaeozoic dentine

Page 35 of 59

1 2		
3 4	745	and patterned scales in the embryonic catshark tail. Biology letters 4:87–90.
5 6 7	746	Johns, M. J., C. R. Barnes, and M. J. Orchard. 1997. Taxonomy and biostratigraphy of
, 8 9	747	Middle and Late Triassic elasmobranch ichthyoliths from northeastern British
10 11	748	Columbia. 235 pp. Geological Survey of Canada.
12 13	749	Karatajūtė-Talimaa, V. 1968. New thelodonts, heterostracans and arthrodires from the
15 16	750	Chortkov Stage of Podolia; pp. 33–42 in D. V. Obruchev (ed.), Sketches in
17 18	751	phylogenesis and taxonomy of fossil fishes and agnatha. Nauka, Moscow.
19 20 21	752	Karatajūtė-Talimaa, V. 1973. <i>Elegestolepis grossi</i> gen. et sp. nov., ein neuer Typ der
22 23	753	Placoidschuppe aus dem Oberen Silur der Tuwa. Palaeontographica Abt. A
24 25	754	143:35–50.
26 27 28	755	Karatajūtė-Talimaa, V. 1978. Silurian and Devonian thelodonts of the U.S.S.R. and
29 30	756	Spitsbergen. 334 pp. Mokslas, Vilnius.
31 32	757	Karatajūtė-Talimaa, V. 1992. The early stages of the dermal skeleton formation in
33 34 35	758	chondrichthyans; pp. 223–231 <i>i</i> n E. Mark-Kurik (ed.), Fossil fishes as living
36 37	759	animals. Institute of Geology, Tallinn.
38 39	760	Karatajūtė-Talimaa, V. 1998. Determination methods for the exoskeletal remains of
40 41 42	761	early vertebrates. Mitteilungen ausdem Museum für Naturkunde in Berlin,
43 44	762	Geowissenschaftliche Reihe 1:21–51.
45 46	763	Karatajūtė-Talimaa, V., L. Novitskaya, K. S. Rozman, and Z. Sodov. 1990.
47 48 49	764	Mongolepis—a new lower Silurian genus of elasmobranchs from Mongolia.
50 51	765	Paleontologicheskii Zhurnal 1990:76–86.
52 53 54	766	Karatajūtė-Talimaa, V., and L. Novitskaya. 1992. Teslepis—a new representative of
55 56	767	mongolepid elasmobranchs from the Lower Silurian of Mongolia.
57 58		
59 60		35

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2		
3 4	768	Paleontologicheskii Zhurnal 4:36–46.
5 6 7	769	Karatajūtė-Talimaa, V., and L. Novitskaya. 1997. Sodolepis—a new representative of
7 8 9	770	Mongolepidida (Chondrichthyes?) from the Lower Silurian of Mongolia.
10 11	771	Paleontologicheskii Zhurnal 1997:96–103.
12 13	772	Karatajūtė-Talimaa, V. 1995. The Mongolepidida: scale structure and systematic
14 15 16	773	position. Geobios 19:35–37.
17 18	774	Karatajūtė-Talimaa, V., and N. Predtechenskyj. 1995. The distribution of the vertebrates
19 20 21	775	in the Late Ordovician and Early Silurian palaeobasins of the Siberian Platform.
22 23	776	Bulletin du Muséum National d'Histoire Naturelle 17:39–55.
24 25	777	Keating, J. N., C. L. Marquart, and P. C. Donoghue. 2015. Histology of the
26 27 28	778	heterostracan dermal skeleton: Insight into the origin of the vertebrate
28 29 30 31 32 33 34 35	779	mineralised skeleton. Journal of Morphology 276:657-680.
	780	Keating, J.N. and P.C. Donoghue. 2016. Histology and affinity of anaspids, and the
	781	early evolution of the vertebrate dermal skeleton. Proceedings of the Royal
36 37	782	Society B 283: No. 1826, p. 20152917.
38 39	783	Lund, R. 1985. The morphology of <i>Falcatus falcatus</i> (St. John and Worthen), a
40 41 42	784	Mississippian stethacanthid chondrichthyan from the Bear Gulch Limestone of
43 44	785	Montana. Journal of Vertebrate Paleontology 5:1–19.
45 46 47	786	Lund, R. 1986. On Damocles serratus, nov. gen. et sp. (Elasmobranchii: Cladodontida)
48 49	787	from the Upper Mississippian Bear Gulch Limestone of Montana. Journal of
50 51	788	Vertebrate Paleontology 6:12–19.
52 53 54	789	Maisey, J. G. 1989. Hamiltonichthys mapesi, g. & sp. nov. (Chondrichthyes,
55 56	790	Elasmobranchii), from the Upper Pennsylvanian of Kansas. American Museum
57 58 50		
60		36

2 3 4	791	novitates 2931:1–42.
5 6	792	Malzahn, E., 1968. Über neue Funde von <i>Janassa bituminosa</i> (Schloth.) im
7 8 9	793	niederrheinischen Zechstein. Geologisches Jahrbuch 85: 67–96.
10 11	794	Märss, T. 1986. Silurian vertebrates of Estonia and west Latvia. 104 pp. Valgus, Tallinn.
12 13	795	Märss, T. 2002. Silurian and Lower Devonian anaspids (Agnatha) from Severnaya
14 15 16	796	Zemlya (Russia). Geodiversitas 24:123–137.
17 18	797	Märss, T. 2006. Exoskeletal ultrasculpture of early vertebrates. Journal of Vertebrate
19 20 21	798	Paleontology 26:235–252.
22 23	799	Märss, T., O. Afanassieva, and H. Blom. 2014. Biodiversity of the Silurian osteostracans
24 25	800	of the East Baltic. Earth and Environmental Science Transactions of the Royal
26 27 28 29 30	801	Society of Edinburgh 105: 73–148.
	802	Märss, T., and P. Y. Gagnier. 2001. A new chondrichthyan from the Wenlock, Lower
31 32 33	803	Silurian, of Baillie-Hamilton Island, the Canadian Arctic. Journal of Vertebrate
33 34 35 36 37 38 39 40	804	Paleontology 21:693–701.
	805	Märss, T., and V. Karatajūtė-Talimaa. 2002. Ordovician and Lower Silurian thelodonts
	806	from Severnaya Zemlya Archipelago (Russia). Geodiversitas 24:381-404.
41 42	807	Märss, T., V. Karatajūtė-Talimaa, and S. Turner. 2007. Agnatha II. Thelodonti. 143 pp.
43 44	808	Verlag Dr. Friendrich Pfeil, Munich.
45 46 47	809	Märss, T., M. V. Wilson, and R. Thorsteinsson. 2002. New thelodont (Agnatha) and
48 49	810	possible chondrichthyan (Gnathostomata) taxa established in the Silurian and
50 51 52	811	Lower Devonian of the Canadian Arctic Archipelago. Proceedings of the Estonian
53 54	812	Academy of Sciences, Geology 51:88–120.
55 56 57	813	Märss, T., M. Wilson, and R. Thorsteinsson. 2006. Silurian and Lower Devonian
58 59 60		37

2		
3 4	814	thelodonts and putative chondrichthyans from the Canadian Arctic Archipelago.
5 6 7	815	144 pp. The Palaeontological Association, London.
7 8 9	816	Miyake, T., J. L. Vaglia, L. H. Taylor, and B. K. Hall. 1999. Development of dermal
10 11	817	denticles in skates (Chondrichthyes, Batoidea): patterning and cellular
12 13	818	differentiation. Journal of Morphology 241:61–81.
14 15 16	819	Novitskaya, L. I., and V. Karatajūtė-Talimaa. 1986. Remarks about the cladistic analysis
17 18	820	in connection with myopterygian hypothesis and the problem of the origin of
19 20	821	gnathostomes; pp. 102–125 <i>i</i> n E. Vorobyeva, and N. Lebedkina (eds.),
21 22 23	822	Morphology and Evolution of Animals. Nauka, Moscow.
24 25	823	Ørvig, T. 1966. Histologic studies of ostracoderms, placoderms and fossil
26 27	824	elasmobranchs. 2. On the dermal skeleton of two late Palaeozoic
28 29 30	825	elasmobranchs. Arkiv för Zoologi 19:1–39.
31 32	826	Ørvig, T. 1967. Phylogeny of tooth tissues: evolution of some calcified tissues in early
33 34 25	827	vertebrates; pp. 45–110 in A. E. W. Miles (ed.), Structural and chemical
35 36 37	828	organization of teeth, Volume 1. Academic Press New York.
38 39	829	Ørvig, T. 1977. A survey of odontodes ('dermal teeth') from developmental, structural,
40 41 42	830	functional, and phyletic points of view; pp. 53–75 in M. Andrews, R. S. & Walker,
42 43 44	831	A. D. (ed.), Problems in Vertebrate Evolution. Academic Press, London, New
45 46	832	York.
47 48 ⊿q	833	Patterson, C. 1965. The phylogeny of the chimaeroids. Philosophical Transactions of
50 51	834	the Royal Society B: Biological Sciences 249:101-219.
52 53	835	Qu, Q., M. Zhu, and W. Wang. 2013. Scales and dermal skeletal histology of an early
54 55 56	836	bony fish Psarolepis romeri and their bearing on the evolution of rhombic scales
57 58		
59 60		38

1 2		
2 3 4	837	and hard tissues. PloS one 8:e61485.
5 6	838	Reif, W. E. 1978. Types of morphogenesis of the dermal skeleton in fossil sharks.
7 8 9	839	Paläontologische Zeitschrift 52:110–128.
10 11	840	Reif, W. 1980a. A model of morphogenetic processes in the dermal skeleton of
12 13	841	elasmobranchs. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen
14 15 16	842	159:339–359.
17 18	843	Reif, W. E. 1980b. Development of dentition and dermal skeleton in embryonic
19 20	844	Scyliorhinus canicula. Journal of Morphology 166:275–288.
21 22 23	845	Reif, W. E. 1982. Evolution of dermal skeleton and dentition in vertebrates - the
24 25	846	odontode regulation theory. Evolutionary Biology 15:287–368.
26 27 28	847	Reif, WE. 1985. Squamation and ecology of sharks. 255 pp. Senckenbergische
20 29 30	848	Naturforschende Gesellschaft, Frankfurt am Main.
31 32	849	Rücklin, M., and P. C. Donoghue. 2015. <i>Romundina</i> and the evolutionary origin of teeth.
33 34 35	850	Biology letters 11:20150326.
36 37	851	Sansom, I. J., R. Aldridge, and M. Smith. 2000. A microvertebrate fauna from the
38 39	852	Llandovery of South China. Transactions of the Royal Society of Edinburgh:
40 41 42	853	Earth Sciences 90:255–272.
43 44	854	Sansom, I. J., N. S. Davies, M. I. Coates, R. S. Nicoll, and A. Ritchie. 2012.
45 46 47	855	Chondrichthyan-like scales from the Middle Ordovician of Australia.
47 48 49	856	Palaeontology 55:243–247.
50 51	857	Sansom, I. J., P. C. Donoghue, and G. Albanesi. 2005. Histology and affinity of the
52 53 54	858	earliest armoured vertebrate. Biology letters 1:446–449.
55 56 57 58	859	Sansom, I. J., C. G. Miller, A. Heward, N. S. Davies, G. A. Booth, R. A. Fortey, and F.
59 60		39

860	Paris. 2009. Ordovician fish from the Arabian Peninsula. Palaeontology 52:337-
861	342.
862	Sansom, I. J., M. M. Smith, and M. P. Smith. 1996. Scales of thelodont and shark-like
863	fishes from the Ordovician of Colorado. Nature 379:628–630.
864	Sansom, I. J., M. M. Smith, and M. P. Smith. 2001. The Ordovician radiation of
865	vertebrates; pp. 156–171 <i>i</i> n E. Ahlberg (ed.), Major Events in Early Vertebrate
866	Evolution, Systematics Association Special Volume. Taylor & Francis, London
867	and New York.
868	Schultze, HP. 1968. Palaeoniscoidea-Schuppen aus dem Unterdevon Australiens und
869	Kanadas und aus dem Mitteldevon Spitzbergens. 16:341–368.
870	Schultze, HP. 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der
871	Osteichthyes (Pisces). Paläontologische Zeitschrift 51:152–168.
872	Sennikov, N., O. Rodina, N. Izokh, and O. Obut. 2015. New data on Silurian vertebrates
873	of southern Siberia. Palaeoworld 24:231–242.
874	Sire, J. Y., P. C. J. Donoghue, and M. K. Vickaryous. 2009. Origin and evolution of the
875	integumentary skeleton in non-tetrapod vertebrates. Journal of anatomy
876	214:409–440.
877	Sire, J. Y., and A. Huysseune. 2003. Formation of dermal skeletal and dental tissues in
878	fish: a comparative and evolutionary approach. Biological Reviews 78:219–249.
879	Smith, M., and M. Coates. 1998. Evolutionary origins of the vertebrate dentition:
880	phylogenetic patterns and developmental evolution. European journal of oral
881	sciences 106:482–500.
882	Smith, M. M., and B. K. Hall. 1990. Development and evolutionary origins of vertebrate
	40
	 860 861 862 863 864 865 866 867 868 869 870 871 872 873 874 875 876 877 878 879 880 881 882

Page 41 of 59

2 3 4	883	skeletogenic and odontogenic tissues. Biological Reviews 65:277–373.
5 6	884	Smith, M. M., and B. K. Hall. 1993. A developmental model for evolution of the
7 8 9	885	vertebrate exoskeleton and teeth. The role of cranial and trunk neural crest; pp.
10 11	886	387–448 in M. K. Hecht, R. J. Macintyre, and M. Clegg (eds.), Evolutionary
12 13 14	887	biology. Plenum Press, New York.
15 16	888	Smith, M. M., and A. Miles. 1971. The ultrastructure of odontogenesis in larval and adult
17 18	889	urodeles; differentiation of the dental epithelial cells. Zeitschrift für Zellforschung
19 20 21	890	und mikroskopische Anatomie 121:470–498.
22 23	891	Stensiö, E. A. 1932. The cephalaspids of Great Britain. 220 pp. The British Museum
24 25 26	892	(Natural History), London.
27 28	893	Stensiö, E. A. 1961. Permian vertebrates; pp. 231247 in G. Raasch (ed.), Geology of
29 30	894	the Arctic. University of Toronto, Toronto.
31 32 33	895	Stensiö, E., and T. Ørvig. 1951–1957. On the scales of the elasmobranchs. Swedish
34 35	896	Museum of Natural History, Stockholm.
36 37 38	897	Sykes, J. 1974. On elasmobranch dermal denticles from the Rhaetic bone bed at
39 40	898	Barnstone, Nottinghamshire. Mercian Geologist 5:49–64.
41 42	899	Thies, D. 1995. Placoid scales (Chondrichthyes: Elasmobranchii) from the late Jurassic
43 44 45	900	(Kimmeridgian) of northern Germany. Journal of Vertebrate Paleontology
46 47	901	15:463–481.
48 49	902	Thies, D., and A. Leidner. 2011. Sharks and guitarfishes (Elasmobranchii) from the Late
50 51 52	903	Jurassic of Europe. Palaeodiversity 4:63–184.
53 54	904	Turner, S. 2004. Early vertebrates: analysis from microfossil evidence; pp. 67–94 in G.
55 56 57 58	905	Arratia, M. V. H. Wilson, and R. Cloutier (eds.), Recent Advances in the Origin
59 60		41

2		
3 4	906	and Early Radiation of Vertebrates. Verlag Dr. Friedrich Pfeil, Munich.
5 6 7	907	Upeniece, I. 2011. Palaeoecology and juvenile individuals of the Devonian placoderm
7 8 9	908	and acanthodian fishes from Lode site, Latvia: In Department of Geology, Vol.
10 11	909	Doctoral Thesis, pp. 221. University of Latvia, Riga.
12 13	910	Vieth, J. 1980. Thelodontier-, Acanthodier-und Elasmobranchier-Schuppen aus dem
14 15 16	911	Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). 69 pp. Im Selbstverlag
17 18	912	des Geologisch-Paläontologischen Institut der Georg-August-Universität
19 20	913	Göttingen, Göttingen.
21 22 23	914	Valiukevičius, J. 1992. First articulated Poracanthodes from the Lower Devonian of
24 25	915	Severnaya Zemlya; pp. 193-214 <i>i</i> n E. Mark-Kurik (ed.), Fossil Fishes as Living
26 27 28	916	Animals. Academy of Sciences of Estonia, Tallinn.
29 30	917	Vladimirskaya, E. V. 1978. Brachiopods of the Silurian in Tuva. Ezhegodnik
31 32	918	Vsesoyuznogo Paleontologicheskogo Obshchestva 21:148–167.
33 34 35	919	Voigt, M., and D. Weber. 2011. Field Guide for Sharks of the Genus Carcharhinus. 151
36 37	920	pp. Verlag Dr. Friedrich Pfeil, Munich.
38 39 40	921	Wang, NZ., P. C. Donoghue, M. M. Smith, and I. J. Sansom. 2005. Histology of the
40 41 42	922	galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of
43 44	923	the vertebrate cranial endoskeleton. Journal of Vertebrate Paleontology 25:745-
45 46 47	924	756.
48 49	925	Wang, NZ., X. Zhang, M. Zhu, and W. J. Zhao. 2009. A new articulated hybodontoid
50 51	926	from Late Permian of northwestern China. Acta Zoologica 90:159–170.
52 53 54	927	Young, G. 1997. Ordovician microvertebrate remains from the Amadeus Basin, central
55 56	928	Australia. Journal of Vertebrate Paleontology 17:1–25.
57 58 59		
60		42

2		
3 4 5 6 7 8 9 10 11 12 13 14 15 6 7 8 9 10 11 23 4 5 21 22 23 4 5 22 24 5 22	929	Young, G. 2000. Areyongalepis, a replacement name for Areyonga Young 1997
	930	(preoccupied name). Journal of Vertebrate Paleontology 20:611–611.
	931	Zangerl, R. 1968. The morphology and the developmental history of the scales of the
	932	Paleozoic sharks Holmesella? sp. and Orodus; pp. 399–412 in T. Ørvig (ed.),
	933	Current Problems of Lower Vertebrate Phylogeny. Almqvist & Wiksell,
	934	Stockholm.
	935	Zangerl, R., and G. R. Case. 1973. Iniopterygia: A new order of chondrichthyan fishes
	936	from the Pennsylvanian of North America. 67 pp. Field Museum of Natural
	937	History, Chicago.
	938	Zhu, M., X. Yu, P. E. Ahlberg, B. Choo, J. Lu, T. Qiao, Q. Qu, W. Zhao, L. Jia, and H.
26 27 28	939	Blom. 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones.
28 29 30 31 32 33 34 35	940	Nature 502:188–193.
	941	Zhu, M., X. Yu, B. Choo, J. Wang, and L. Jia. 2012. An antiarch placoderm shows that
	942	pelvic girdles arose at the root of jawed vertebrates. Biology letters 8:453–456.
36 37	943	Zhu, M., X. Yu, W. Wang, W. Zhao, and L. Jia. 2006. A primitive fish provides key
38 39	944	characters bearing on deep osteichthyan phylogeny. Nature 441:77-80.
40 41 42	945	Žigaitė, Ž., and V. Karatajūtė-Talimaa. 2008. New genus of chondrichthyans from the
43 44	946	Silurian–Devonian boundary deposits of Tuva (Russia). Evolution and diversity of
45 46 47 48 49 50 51	947	chondrichthyans. Acta Geologica Polonica 58:127–131.
	948	Žigaitė, Ž., V. Karatajūtė-Talimaa, and A. Blieck. 2011. Vertebrate microremains from
	949	the Lower Silurian of Siberia and Central Asia: palaeobiodiversity and
52 53 54	950	palaeobiogeography. Journal of Micropalaeontology 30:97–106.
55 56	951	
57 58		
59 60		43
		Society of Vertebrate Paleontology

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2 3 4 5	970	FIGURE CAPTIONS
6 7 8	971	
9 10 11	972	FIGURE 1. Diagrammatic representation of monodontode scale types in A , the
12 13	973	Thelodonti and (B , C) the Chondrichthyes. A , a <i>Thelodus calvus</i> scale (adapted from
14 15	974	Märss and Karatajūtė-Talimaa 2002: fig. 15F) exemplifying the thelodont morphogenetic
16 17 18	975	type; B , the <i>Elegestolepis</i> morphogenetic type represented by an <i>Elegestolepis grossi</i>
19 20	976	scale (BU5284); C , the <i>Heterodontus</i> morphogenetic type represented by a <i>Triakis</i>
21 22	977	semifasciata scale (BU5341). Color-coded tissues: blue, enameloid; brown, dentine;
23 24 25	978	gold, bone. (2/3rd of a whole page width)
26 27 28	979	
29 30 31	980	FIGURE 2. Distribution of relevant to the study scale characters among select groups of
32 33	981	Paleozoic gnathostomes. Tree topology reconstructed from published phylogenies of
34 35 36	982	total-group Chondrichthyes (Grogan et al., 2012) and vertebrates (Sire et al., 2009;
37 38	983	Giles et al., 2013, 2015), with the position of Elegestolepidida on the chondrichthyan
39 40	984	branch determined from yet to be published analysis by Andreev et al. (representative
41 42 43	985	tree generated in TNT version 1.1 (Goloboff et al., 2008) using a data matrix of 68
44 45	986	equally weighted scale-based characters and 49 Paleozoic jawed-gnathostome taxa).
46 47 48	987	(whole page width)
49 50 51	988	
52 53 54	989	FIGURE 3. Line drawings depicting the range of crown-surface morphologies in
55 56 57 58	990	elegestolepid scales. A , <i>Elegestolepis grossi</i> (BU5284); B , <i>Ellesmereia schultzei</i>
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(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

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L013	portion of the crown of BU5291; \mathbf{F} , vertical transverse section of an ontogenetically old
L014	scale (BU5292); \mathbf{G} , basal bone of ontogenetically old scale (BU5293) in vertical
L015	longitudinal section. (B–E) SEM micrographs; (A, F, G) Nomarski interference contrast
L016	micrographs. Anterior towards the right in (C–E, G); (B), base; arrowheads in (B–E)
L017	demarcate the extent of artificially altered dentine, asterisks in (G) denote the borders of
L018	depositional bone lamellae. Scales bars represent 100 μm in (A, C, F, G) 50 μm in (B,
L019	E) and 20 μm in (D). (whole page width)
1020	
L021	FIGURE 6. Scales of Deltalepis magna gen. et sp. nov. from the Chargat Formation of
L022	north-western Mongolia. Holotype specimen (BU5269, scale with a five-lobed crown
L023	and a gracile neck) in A , anterior, B , antero-lateral and C , crown view. D , scale
L024	(BU5270) with gracile neck in basal view. Scales with three-lobe crowns in E , anterior,
L025	F, posterior, G, lateral (E–G, BU5273) and H, crown (BU5271) views. I, BU5273 in basal
L026	view revealing the lower pedicle surface; ${f J}$, basal view of a scale (BU5272) with fully
L027	formed pedicle support. (A–C, H–J) SEM micrographs; (D–G) volume renderings.
L028	Anterior towards the right in (B), towards the bottom in (C, H) towards the top in (D, I, J);
L029	arrow indicates a neck canal opening. Scale bars represent 200 μ m. (whole page width)
1030	
L031	FIGURE 7. Scales of Deltalepis parva gen. et sp. nov. from the Chargat Formation of
L032	north-western Mongolia. Holotype (BU5275) in A , crown and B , anterior-crown view.
L033	Scale (BU5280) with a gracile neck in C , anterior and D , posterior view. Scale (BU5277)
L034	in E , anterior and F , crown view. G , scale (BU5278) with a gracile neck in basal view,

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3 4	1035	exposing the rami of the pulp canal system. Scale (BU5279) with formed pedicle
5 6 7	1036	support in H , basal and I, postero-basal view. (A, B, $E-I$) SEM micrographs; (C, D)
7 8 9	1037	volume renderings. Anterior towards the bottom in (A, F) towards the top in (G–I);
10 11	1038	arrows indicate neck canal openings, arrowhead indicates the basal opening of the
12 13	1039	main pulp canal. Scale bars represent 200 μm in (A–D, G) and 100 μm in (E, F, H, I).
14 15 16 17	1040	(whole page width)
17 18 19 20	1041	
20 21 22	1042	FIGURE 8. Hard tissue structure of <i>Deltalepis</i> gen. nov. A , longitudinal tomographic
23 24	1043	slice of a <i>Deltalepis magna</i> scale (BU5273); B , detail of the dentine tissue at the upper
25 26 27	1044	anterior margin of the crown of a longitudinally sectioned Deltalepis magna scale
28 29	1045	(BU5274); C , longitudinal tomographic slice of a <i>Deltalepis parva</i> scale (BU5280); D ,
30 31 32	1046	view of the posterior portion of a <i>Deltalepis parva</i> scale (BU5282) crown immersed in
32 33 34	1047	clove oil. (B, D) Nomarski interference contrast micrographs; (A, C) volume renderings.
35 36	1048	Anterior towards the right in (A) and towards the left in (C). Scale bars represent 100 μm
37 38 30	1049	in (A, C, D) and 50 μm in (B). (whole page width)
40 41 42	1050	
43 44 45	1051	FIGURE 9. Volume renderings of the scale canal system (in red) of examined
46 47	1052	elegestolepids. The scales are made translucent in all renderings, with the exception of
48 49	1053	(G). A–C, Elegestolepis grossi scale (BU5284) from the Baital Formation of Tuva
50 51 52	1054	(Russian Federation) in A , anterior, B , postero-lateral and C , crown (depicting the lower
53 54	1055	portion of the specimen that is transversely sliced through the neck region) view. $D-F$,
55 56 57 58	1056	Deltalepis magna scale (BU5273) from the upper Llandovery–lower Wenlock of north
59 60		48

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3 4	1057	western Mongolia in D , crown and E , posterior view and a F , crown view of the lower
5 6 7	1058	portion of the same specimen sliced through the neck region. G–J , <i>Deltalepis parva</i>
, 8 9	1059	specimens (BU5280 and BU5281) from the upper Llandovery–lower Wenlock of north
10 11	1060	western Mongolia; G , BU5280 sliced transversely through the crown in crown view; H ,
12 13	1061	BU5280 in anterior view; I, J, BU5281 in I posterior and J, postero-lateral view. Anterior
15 16	1062	towards the left in (B), towards the top in (C, F, G) and towards the bottom in (D);
17 18	1063	arrows indicate neck canal openings, arrowheads point at the basal opening of the main
19 20 21	1064	pulp canal. Scale bars represent 100 μ m. (whole page width)
22 23 24	1065	
25 26 27	1066	FIGURE 10. Characteristics of monodontode scales of recognised lower Paleozoic
28 29	1067	chondrichthyans and their stratigraphic range. Pink rectangle designates elegestolepid
30 31 32	1068	taxa. Elegestolepis (Karatajūtė-Talimaa, 1973 and data from this study), Deltalepis
33 34	1069	(data from this study), Kannathalepis (Märss and Gagnier, 2001), Ellesmereia (Vieth,
35 36	1070	1980), <i>Frigorilepis</i> (Märss et al., 2002, 2006), <i>Polymerolepis</i> Karatajūtė-Talimaa, 1998;
37 38 39	1071	Hanke et al., 2013), Lupopsyrus and Obtusacanthus (Hanke and Wilson, 2004; Hanke
40 41	1072	and Davis, 2012). (whole page width)
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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)





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)



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]

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 (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)

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