Elegetolepis and its kin, the earliest monodontode chondrichthyans

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

DOI:

[10.1080/02724634.2017.1245664](https://doi.org/10.1080/02724634.2017.1245664)

Document Version

Peer reviewed version

Citation for published version (Harvard):

Andreev, P, Coates, M, Karatajute-Talimaa, V, Shelton, R, Cooper, P & Sansom, I 2017, 'Elegetolepis and its kin, the earliest monodontode chondrichthyans', *Journal of Vertebrate Paleontology*, vol. 37, no. 1, e1245664. <https://doi.org/10.1080/02724634.2017.1245664>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

Checked for eligibility: 27/09/2016.

This is an Accepted Manuscript of an article published by Taylor & Francis in *Journal of Vertebrate Paleontology* on 18/11/2016, available online:

<http://www.tandfonline.com/doi/abs/10.1080/02724634.2017.1245664>

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

***Elegestolepis* and its kin, the earliest monodontode chondrichthyans**

Journal:	<i>Journal of Vertebrate Paleontology</i>
Manuscript ID	JVP-2015-0108.R2
Manuscript Type:	Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Andreev, Plamen; University of Birmingham, School of Geography, Earth and Environmental Sciences Coates, Michael; University of Chicago, Karatajūtė-Talimaa, Valentina; Institute of Geology and Geography, ; Home address, Shelton, Richard; University of Birmingham, The School Of Dentistry Cooper, Paul; University of Birmingham, The School Of Dentistry Sansom, Ivan; University of Birmingham, Earth Sciences
Key Words:	Chondrichthyes, scales, Paleozoic, morphogenesis

SCHOLARONE™
Manuscripts

Elegestolepis and Its Kin, the Earliest Monodontode Chondrichthyans

PLAMEN S. ANDREEV,^{1*} MICHAEL I. COATES,² VALENTINA KARATAJŪTĖ-
TALIMAA,³ RICHARD M. SHELTON,⁴ PAUL R. COOPER,⁴ and IVAN J. SANSOM^{1*}

¹School of Geography, Earth and Environmental Sciences, University of Birmingham,
Birmingham, B15 2TT, U.K., p.andreev@bham.ac.uk, i.j.sansom@bham.ac.uk;

²Department of Organismal Biology and Anatomy, University of Chicago, Chicago,
Illinois 60637-1508, USA, mcoates@uchicago.edu;

³Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania;

⁴School of Dentistry, College of Medical and Dental Sciences, University of Birmingham,
St Chad's Queensway, Birmingham, B4 6NN, UK, r.m.shelton@bham.ac.uk,
p.r.cooper@bham.ac.uk

Running header—Earliest monodontode chondrichthyans

*Corresponding author

1
2
3
4 20 ABSTRACT—Chondrichthyan-like scales with simple, single odontode crowns,
5
6 21 reminiscent of those of euselachians, have been reported from Silurian strata in a
7
8 22 number of previous studies. These specimens comprise the genera *Elegestolepis* (from
9
10 23 Siberia, Mongolia and Tuva) and *Kannathalepis* (from the Canadian Arctic), and have
11
12 24 been considered to exhibit contrasting patterns of ontogenetic development.
13
14
15
16 25 A study of elegestolepid microremains from the Chargat Formation of Mongolia
17
18 26 (Llandovery–lower Wenlock) and the Baital Formation of Tuva (Wenlock–Ludlow) has
19
20 27 been undertaken using SEM and micro-CT to examine scale canal system and hard
21
22 28 tissue structure. These investigations revealed scales at different stages of
23
24 29 development, whose morphogenesis is characterized by growth (elongation) of the
25
26 30 crown odontode and formation of neck canals. This ontogenetic pattern (*Elegestolepis*-
27
28 31 type morphogenesis) is also recognized in *Kannathalepis* and the Lower Devonian
29
30 32 species *Ellesmereia schultzei*, and forms the basis for the unification of these taxa into a
31
32 33 new chondrichthyan Order Elegestolepidida ordo nov. Similarities in crown
33
34 34 vascularization (branching pulp, single neck canal) shared by *Elegestolepis*,
35
36 35 *Ellesmereia* and *Deltalepis* gen. nov. (*D. magna* sp. nov. and *D. parva* sp. nov. erected
37
38 36 here in for Mongolian specimens) require the erection of the Family Elegestolepididae
39
40 37 fam. nov. that is distinguished from the mono-generic Kannathalepididae (non-
41
42 38 branching pulp, multiple neck canals).
43
44
45
46
47
48
49
50 39 Elegestolepid scales exhibit characteristics (neck canal formation and lack of enamel
51
52 40 and basal bone osteons) consistent with those of the chondrichthyan dermal skeleton.
53
54
55 41 This establishes Elegestolepidida as the stratigraphically oldest chondrichthyan taxon to
56
57
58
59
60

1
2
3 42 develop monodontode scales, which, in contrast to the ‘placoid’ scales of euselachians,
4
5
6 43 are growing structures.
7
8
9 44
10
11
12 45
13
14
15 46
16
17
18 47
19
20
21 48
22
23
24 49
25
26
27 50
28
29
30 51
31
32
33 52
34
35
36 53
37
38
39 54
40
41
42 55
43
44
45 56
46
47
48 57
49
50
51 58
52
53
54 59
55
56
57 60
58
59
60

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

1
2
3 84 Ørvig, 1951–1957; Stensiö, 1961), Karatajūtė-Talimaa (Karatajūtė-Talimaa, 1992;
4
5
6 85 Karatajūtė-Talimaa, 1998) proposed that elegendolepid scale crowns represent the
7
8 86 simplest monodontode dermatoskeletal elements, exhibiting many of the characteristics
9
10 87 of what were assumed to be the most elementary skeletal units of the integument
11
12 88 (lepidomoria). Thus, the development of odontodes in elegendolepids was differentiated
13
14
15 89 from other chondrichthyans with ‘placoid’ (monodontode) scales, where the crowns
16
17
18 90 were considered to form through the coalescence of lepidomoria. Karatajūtė-Talimaa
19
20 91 (1992, 1998) attributed this complex morphogenetic pattern to the *Polymerolepis* and
21
22 92 *Heterodontus* (euselachian; Fig. 1C) scale types. A hypothesis of odontode evolution in
23
24 93 stem chondrichthyans was founded upon these assumptions, placing lepidomorium-like
25
26
27 94 elements as the phylogenetic precursors of all chondrichthyan scales (Karatajūtė-
28
29 95 Talimaa, 1992).

30
31
32 96 In the years following the conceptualization of the lepidomorial theory, increasing
33
34 97 evidence from studies on the development of the integumentary skeleton of Recent
35
36
37 98 neoselachians (Reif, 1980b; Miyake et al., 1999; Johanson et al., 2008) has discredited
38
39 99 the concrescence model of odontode morphogenesis, and this is now refuted by most
40
41
42 100 authors (Smith and Coates, 1998; Donoghue, 2002 and references therein). The latter
43
44 101 view is strengthened with the inclusion of ‘acanthodians’ bearing polyodontode scales
45
46
47 102 with elaborately branching odontode pulps (e.g. in *Poracanthodes* Gross, 1956;
48
49 103 Valiukevičius, 1992) within the chondrichthyan phylogenetic history (Zhu et al., 2013;
50
51 104 Brazeau and Friedman 2015; Giles et al., 2015). This contradicts the evolutionary
52
53
54 105 scenario predicted by the concrescence model, which claims origination of
55
56 106 neoselachian placoid scales and their complex canal system via fusion of simple
57
58
59
60

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.

1
2
3 128 Scale morphology was documented using the Zeiss EVO LS and the JEOL JSM-
4
5 129 6060 scanning electron microscopes at the School of Dentistry of the University of
6
7
8 130 Birmingham, UK. Prior to imaging, the specimens were sputter-coated with a 25 nm-
9
10 131 thick layer of gold/palladium alloy.
11
12
13 132 Hard tissue microstructure and internal architecture of thin-sectioned specimens was
14
15 133 investigated by Nomarski differential interference contrast microscopy (using a 'Zeiss
16
17 134 Axioskop Pol' polarization microscope) and scanning electron microscopy (with a JEOL
18
19 135 JSM-6060 SEM at the School of Dentistry, University of Birmingham, UK).
20
21
22
23 136 Scale examination with X-ray radiation was conducted using the SkyScan 1172
24
25 137 microtomography scanner at the School of Dentistry of the University of Birmingham,
26
27 138 UK. The acquired microradiographs (tomographic projections) were taken at 0.3°
28
29 139 intervals over a 180° rotation cycle at exposure times of 400 ms, using a 0.5 mm thick
30
31 140 X-ray attenuating Al filter. These image data were processed with the SkyScan NRecon
32
33 141 reconstruction software in order to generate sets of microtomograms that were
34
35 142 converted into volume renderings in Amira 5.4 3D analysis software.
36
37
38
39 143 Figured material is deposited in the Lapworth Museum of Geology, University of
40
41 144 Birmingham, UK (BU prefix).
42
43
44
45
46 145
47
48

49 **Definitions of Terms**
50
51

52 147 Traditionally (Sykes, 1974; Duffin and Ward, 1993; Thies, 1995) the two main
53
54 148 components (crown and base) of chondrichthyan scales have been identified on the
55
56 149 basis of morphological and/or topological criteria without consideration of their
57
58
59
60

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, kathermacanthids 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-

1
2
3 171 derived characters, which have been employed to diagnose these taxa given the
4
5 172 general absence of chondrichthyan endoskeletal and dental remains in the lower
6
7
8 173 Paleozoic.
9
10
11 174 The odontode growth that typifies the ontogenesis of *Elegestolepis*-like scales is
12
13 175 not seen within traditionally recognised chondrichthyan clades (*sensu* Grogan et al.,
14
15 176 2012), yet the *Elegestolepidida* consistently falls inside stem-group Chondrichthyes
16
17 177 when its affinities are tested via phylogenetic inference (Andreev et al., unpublished
18
19 178 data; Fig. 2). The erection of a new Order draws together species that possess scales
20
21 179 with growing single-odontode crowns whose morphogenesis can be differentiated from
22
23 180 that of elasmobranch ‘placoid’ scales (the *Heterodontus* morphogenetic type of
24
25 181 (Karatajūtė-Talimaa, 1992, 1998; Fig. 1C). The formal recognition of the *Elegestolepis*-
26
27 182 type of scale development represents a change in concept from what was originally
28
29 183 identified as a purely morphogenic category (Karatajūtė-Talimaa, 1992, 1998).
30
31
32
33
34
35
36
37
38

39 184
40
41
42 185 Family KANNATHALEPIDIDAE Märss and Gagnier, 2001
43
44

45 186 **Included genera**—*Kannathalepis* Märss and Gagnier, 2001
46
47

48 187 **Revised diagnosis**—*Elegestolepids* possessing dermal scales with vertically
49
50 188 undivided pulp cavities from which multiple (up to five) horizontal neck canals emerge
51
52 189 basally.
53

54 190 **Remarks**—The mono-generic Family Kannathalepididae was introduced by Märss
55
56 191 and Gagnier (2001) to distinguish *Kannathalepis*, identified to exhibit a specialised type
57
58
59
60

1
2
3 192 of scale morphogenesis, from other Silurian chondrichthyan scale taxa (mongolepid and
4
5
6 193 elegestolepid). It was reported that the squamation of *Kannathalepis* consists of single-
7
8 194 odontode scales along with more complex aggregates of fused 'placoid' scales that
9
10 195 were thought to provide evidence for two separate modes of scale development within
11
12 196 the genus (Märss and Gagnier, 2001: fig. 4f). The current study regards these
13
14 197 compound scales of *Kannathalepis* as aberrant, formed by anomalous patterning that is
15
16 198 thought to result from suppression of inter-scale domains in accordance with the
17
18 199 inhibitory field model outlined by Reif (1980a, 1982). Localised suturing of scales has
19
20 200 similarly been documented in stem (*Hybodus delabechei* (Reif, 1978: fig. 8 d, e) and
21
22 201 *Lissodus sardiniensi* (Fischer et al., 2010: fig. 7l)) and crown (*Echinorhinus brucus* (Reif,
23
24 202 1985:pl. 15) and *Asterodermus platypterus* (Thies and Leidner, 2011:pl. 71))
25
26 203 euselachians with monodontode trunk scale cover that is known to be prevalent within
27
28 204 the Order (Reif, 1985; Thies and Leidner, 2011; Dick, 1978; Dick and Maisey, 1980;
29
30 205 Maisey, 1989; Wang et al., 2009).

31
32
33
34
35
36
37 206 Complexes of randomly sutured monodontode scales consequently cannot be
38
39 207 considered equivalent to polyodontode scales (e.g. those of Mongolepidida (Karatajūtė-
40
41 208 Talimaa, 1998)), since the odontodes of the latter are patterned as a unit in a particular
42
43 209 manner and are given support by a common base/pedicle tissue. The scale
44
45 210 development in *Kannathalepis* can thus be identified as that of 'placoid' scales with a
46
47 211 growing odontode and base, corresponding to the *Elegestolepis* morphogenetic type
48
49 212 (Fig. 1B) of Karatajūtė-Talimaa (1992). On that basis, Kannathalepididae is placed
50
51 213 inside the new Order Elegestolepidida, and its validity is maintained by acknowledging
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

1
2
3 255 canaliculi with dendroid branching. Cellular basal bone with layered mineralised-fibre
4
5
6 256 organization.
7
8
9 257 **Remarks**—Certain differences were noted between the scale histology of *E.*
10
11 258 *grossi* scales and the original descriptions of Karatajūtė-Talimaa (1973). Some of these
12
13 259 concern the nature of the most superficial portion of the scale crown and neck,
14
15
16 260 understood by Karatajūtė-Talimaa (1973) to consist of a type of hypermineralized
17
18 261 dentine tissue, durodentine (one of the less commonly used synonyms of enameloid
19
20 262 (Ørvig, 1967; Smith and Miles, 1971; Sire et al., 2009). This ‘enameloid’ layer is found
21
22 263 not to be a persistent feature of *E. grossi* scales, and even when present it appears
23
24 264 discontinuous across most of the upper crown surface (Fig. 5A–E), contrary to previous
25
26 265 depictions (Karatajūtė-Talimaa, 1973: fig. 2a, b and Sire et al., 2009: fig. 10b). The layer
27
28 266 is instead most prominent around the scale neck (Fig. 5A, C–E) and can extend all the
29
30 267 way down to the level of the basal bone (Fig. 5C). This distribution is contrary to that of
31
32 268 single crystalline enameloid in neoselachian scales, where it is confined mainly to the
33
34 269 upper crown region (Johns et al., 1997). Furthermore, the architecture of the superficial
35
36 270 crown region cannot be recognised in any of the known enameloid structural types
37
38 271 (Johns et al., 1997; Sansom et al., 2005; Gillis and Donoghue, 2007; Guinot and
39
40 272 Cappetta, 2011; Andreev and Cuny, 2012), but instead resembles that of the crown
41
42 273 dentine and is regarded as such. The more porous appearance of the surface dentine is
43
44 274 likely to be diagenetically induced and/or due to alteration of the original tissue
45
46 275 microstructure by preparation of the specimens with unbuffered acetic acid (even in low
47
48 276 concentration, the latter has been shown to damage the phosphatic tissues of conodont
49
50 277 elements (Jeppsson et al., 1985; Jeppsson and Anehus, 1995).
51
52
53
54
55
56
57
58
59
60

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.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

364 canals (diameter of c. 5–25 μm ; Fig. 9D). The latter are most prominent inside the
365 crown lobes where they associate with and connect to branches (c. 30–60 μm in
366 diameter) of the pulp canal. For most of their length the pulp branches extend parallel
367 the crown surface, before curving basally to merge (Fig. 9F) into a single pulp canal (c.
368 60–90 μm wide) inside the scale neck. From the posterior of the pulp issues an
369 unbranched horizontal canal (c. 70 μm long; Fig. 9F) that opens on the scale neck
370 surface. Separate from the pulp cavity system, the posterior half of the scales houses
371 numerous closely spaced (up to c. 10 μm apart) dentine canals (10–20 μm in diameter)
372 whose paths parallel that of the lower crown surface (Fig. 9E). The lower ends of these
373 canals ramify inside the scale neck before either exiting the scale basally (Fig. 9E) or
374 ending blindly inside it.

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

378

379 *DELTALEPIS PARVA* sp. nov.

380 (Figs. 3D, 7, 8C–D, 9G–J)

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

383 **Locality and horizon**—The type and only known locality situated 80 km north of
384 Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All specimens
385 come from the upper Llandovery–lower Wenlock (Salhit regional Stage) horizons

1
2
3 386 (sample P-16/3) of the Chargat Formation (Karatajūtė-Talimaa et al., 1990; Žigaitė et
4
5 387 al., 2011).

6
7
8 388 **Holotype**—An isolated, presumed trunk, scale BU5275 (Figs. 3D, 7A, B).

9
10
11 389 **Referred material**—Six isolated scales (BU5275, BU5277, BU5278–BU5280,
12
13 390 BU5282).

14
15
16
17 391 **Diagnosis**—*Deltalepis* species with ovoid scale crowns compartmentalized into
18
19 392 seven to ten lobes. The lateral crown branches of the pulp cavity do not connect directly
20
21 393 to the main pulp canal.

22
23
24
25 394
26
27
28 395 **Description**

29
30
31 396 **Morphology**—The scale crowns are single odontode structures with ovoid
32
33 397 outlines (Fig. 7) that are 200–500 µm long and 200–400 µm wide. Upper crown surface
34
35 398 is divided into seven to ten antero-posteriorly aligned lobes (40–60 µm wide; Fig. 7A–F)
36
37 399 separated by much narrower, deeply incised grooves that expand towards the posterior
38
39 400 (up to c. 20 µm wide). Tubercles organized into parallel rows ornament the upper
40
41 401 surface of the crown lobes (up to three rows per lobe), whereas all other scale surfaces
42
43 402 are smooth.

44
45
46
47
48 403 The anterior of the crown is constricted into a vertically orientated neck that
49
50 404 reaches a third to three-quarters of the maximal crown width, and which in some
51
52 405 specimens expands basally to form a pedicle support (Fig. 7C–F, H, I). The posterior
53
54 406 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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

429

430 **Chondrichthyan Characteristics of Elegestolepid Scales**

431 The odontogenic component of the vertebrate skeleton develops primarily as
432 discrete elements (odontodes), each of which being the product of a single epithelia-
433 mesenchymal cell condensation (Ørvig, 1977; Reif, 1982; Fraser et al., 2010).
434 Odontodes are one of the main structural units of scales and in certain groups (e.g. in
435 neoselachian chondrichthyans (Fig. 1C; Sire and Huysseune, 2003; Eames et al., 2007;
436 Sire et al., 2009) can form the entire squamation in the absence of osteogenic
437 contribution to the integumentary skeleton. In lower Paleozoic vertebrates, dermal
438 odontodes are usually patterned in clusters (polyodontodia in Ørvig, 1977) that form
439 compound scale crowns; these have been documented in pteraspidomorphs (Gross,
440 1961; Denison, 1967; Sansom et al., 2009; Keating et al., 2015), anaspids (Märss,
441 1968; Blom et al., 2002; Märss, 2002; Keating and Donoghue, 2016), galeaspids (Wang
442 et al., 2005), osteostracans (Stensiö, 1932; Märss et al., 2014) and jawed
443 gnathostomes (Schultze, 1968, 1977; Gross, 1969; Denison, 1979; Karatajūtė-Talimaa,
444 1995; Sansom et al., 1996; 2012; Burrow and Turner, 1998, 1999; Giles et al., 2013).
445 The Thelodonti (Märss et al., 2007), Elegestolepidida (Karatajūtė-Talimaa, 1973, 1998
446 and this study) and some euchondrichthyans (*sensu* Janvier and Pradel, 2015)—e.g.
447 iniopterygians (Zangerl R, Case, 1973; Grogan and Lund, 2009), petalodonts (Malzahn,
448 1968), symmoriiforms (Lund, 1985, 1986; Coates and Sequeira, 2001), living
449 holocephalians (Patterson, 1965) and euselachians (Thies and Leidner, 2011)—are the
450 exception, as their scale crowns form only from a single-odontode element.

1
2
3 451 The integumentary skeleton of thelodonts demonstrates perhaps the most
4
5
6 452 phylogenetically primitive mode of monodontode scale morphogenesis (Figs. 1A, 2; Sire
7
8 453 et al., 2009; Smith and Hall, 1990, 1993). In contrast to polyodontode scale
9
10 454 development, where each of the component odontodes mineralizes in a single step, the
11
12 455 scales of thelodonts go through several ontogenetic phases that result in gradual
13
14 456 elongation of the crown in basal direction (Gross, 1967; Karatajūtė-Talimaa, 1978).
15
16
17 457 Thelodonts can also possess basal bone tissue (Fig. 1A), the deposition of which
18
19 458 commences only after cessation of odontode growth (Karatajūtė-Talimaa, 1978; Märss
20
21 459 et al., 2007). It is argued here that a thelodont-like pattern of scale development evolved
22
23 460 convergently in the early chondrichthyans (Fig. 2), with the appearance of
24
25 461 Elegestolepida in the middle Llandovery. Nevertheless, during ontogenesis
26
27 462 elegestolepid scales develop a more derived canal system architecture that features
28
29 463 neck canal opening(s) of the odontode pulp (documented outside the Euchondrichthyes
30
31 464 in 'acanthodians' (Denison, 1979) and stem osteichthyans (Gross, 1953, 1968; Qu et
32
33 465 al., 2013) but absent from the dermal skeleton of the Thelodonti (Fig. 2; Gross, 1967;
34
35 466 Karatajūtė-Talimaa, 1978; Märss et al., 2007). The depth of insertion of the scale into
36
37 467 the integument has been suggested to influence the formation of neck canals (Hanke
38
39 468 and Wilson, 2010) and this interpretation is supported by the position of scale necks
40
41 469 inside the upper vascular layer (stratum spongiosum) of the dermis in Recent
42
43 470 neoselachians (Reif, 1980b; Miyake et al., 1999). Similar topological relationship
44
45 471 between scales and surrounding integumentary tissues is attributed here to the
46
47 472 elegestolepids, whereas the dermal odontode papillae of thelodonts have been
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

473 interpreted to form superficially at the epithelium-mesenchyme boundary and therefore
474 not to intersect the vascular system (Karatajūtė-Talimaa, 1978; Märss et al., 2007).

475 Outside the Chondrichthyes, other derived gnathostomes regarded to possess
476 monodontode body scales belong to the basal ‘placoderm’ Orders Stensioellida and
477 Antiarcha (Fig. 2; also refer to Johanson, 2002; Giles et al., 2015; Brazeau and
478 Friedman, 2015 and citations therein for recent vertebrate phylogenies) whose scale
479 structure is still insufficiently investigated. The available data on the squamation of
480 these taxa (e.g. *Stensioella* (Gross, 1962) and *Parayunnanolepis* (Upeniec, 2011; Zhu
481 et al. 2012)) provides evidence for non-growing odontodes, implying this to be a
482 plesiomorphic feature of the single-odontode scales of jawed gnathostomes.

483 Histological descriptions of scale hard-tissues are presently not available for the above
484 taxa, but known examples of ‘placoderm’ scale structure often demonstrate formation of
485 an osteon-rich vascular layer inside the upper portion of the basal bone (Burrow and
486 Turner 1998, 1999; Giles et al., 2013; Rücklin and Donoghue 2015). Osteon mediated
487 bone remodeling and resorption is widespread in the dermal skeleton of ‘placoderms’
488 (Donoghue et al. 2006; Downs and Donoghue, 2009; Giles et al., 2013) and basal
489 osteichthyans (Zhu et al., 2006), but, critically, is absent from the elegestolepid skeleton
490 and in conventional chondrichthyans. Other characteristics placing elegestolepids with
491 the Chondrichthyes among derived gnathostomes are the pattern of scale histogenesis
492 and their hard tissue composition, both of which match those of polyodontode
493 chondrichthyan scales by being two-component skeletal elements formed out of
494 lamellar basal bone and crown dentine (Karatajūtė-Talimaa, 1992).

495

496 **Elegestolepidida in the Context of Paleozoic Chondrichthyans**

497 Although rare, elegestolepids are a significant component of pre-Devonian
498 chondrichthyan faunas with five currently identified species grouped into two Families
499 (Fig. 10), being second only in diversity to the Order Mongolepidida (Karatajūtė-Talimaa
500 et al., 1990; Karatajute-Talimaa and Novitskaya, 1992, 1997; Sansom et al., 2000,
501 2001). Whilst the mongolepids (Sansom et al., 2001) and several other putative
502 chondrichthyan lineages (represented by *Areyongalepis* (Young, 1997), *Tantalepis*
503 (Sansom et al., 2012), *Tezakia* (Sansom et al., 1996; Andreev et al., 2015) and
504 *Canyonlepis* (Sansom et al., 2001; Andreev et al., 2015)) have their origination in the
505 Ordovician, no remains attributable to Elegestolepidida have yet to be reported from this
506 period. These Ordovician taxa possess compound (polyodontode) scale crowns and
507 lack neck canal openings; the latter are now understood not to develop in all basal
508 chondrichthyans (Märss et al., 2007; Hanke and Wilson, 2010).

509 Neck pulp-canal openings stratigraphically first appear in the oldest elegestolepid
510 species (*E. conica* Novitskaya and Karatajūtė-Talimaa, 1986; Karatajūtė-Talimaa and
511 Predtechenskyj, 1995), in the Middle Llandovery, and can be recognized as a persistent
512 feature of the canal system of mature elegestolepid scales (Fig. 10; Karatajūtė-Talimaa,
513 1973; Vieth, 1980; Märss and Gagnier, 2001). This condition is similarly developed in
514 Silurian polyodontode chondrichthyan species (e.g. *Tuvalepis*, Žigaitė and Karatajūtė-
515 Talimaa, 2008) and the monogolepids *Mongolepis*, *Teslepis* (Karatajūtė-Talimaa, 1998),
516 *Shiqianolepis* and *Rongolepis* (Sansom et al., 2000). In monogolepids pulps exit the
517 lower part of crown either by giving off short rami (termed 'horizontal canals' by
518 Karatajūtė-Talimaa (1995) and considered equivalent to the neck canals of

1
2
3 519 elegestolepid scales) or opening directly to the crown surface (in *Shiqianolepis* and
4
5
6 520 *Rongolepis* (Sansom et al., 2000)).
7
8
9 521 Elegestolepidida and Mongolepidida might represent two distinct lineages of
10
11 522 early chondrichthyans that provide an insight into the variability of scale characteristics
12
13 523 within what appear to be monophyletic groups. Inside each of these clades the features
14
15
16 524 shared by its member genera are those relating to the pattern of crown morphogenesis,
17
18 525 whereas aspects of their scale vascularization and hard tissue structure can exhibit
19
20 526 differences. Moreover, characters with a limited distribution in one of the Orders can
21
22
23 527 have a constant presence in the other, as is the case with the neck canal openings of
24
25 528 the elegestolepids. The identification of elegestolepid taxa is thus regarded to require
26
27
28 529 the unique character combination of a growing monodontode scale crown (Order-grade
29
30 530 character) and neck canal openings (plesiomorphy of crown-group gnathostomes).
31
32

33 531 Under the diagnosis formulated here, the Wenlockian species *Frigorilepis*
34
35 532 *caldwelli*, placed inside Kannathalepididae by Märss et al. (2002, 2006), is removed
36
37
38 533 from Elegestolepidida for not demonstrating recognisable stages of scale crown growth.
39
40 534 As *Frigorilepis* does not develop neck canals (Fig. 10), the polygonal ultrasculptural
41
42
43 535 pattern of the crown surface it shares with *Kannathalepis* has been used instead as a
44
45 536 character to support its chondrichthyan affinity (Märss, 2006; Märss et al., 2006). Crown
46
47 537 ornamentation is regarded non-diagnostic at higher taxonomic levels (see above) and at
48
49
50 538 present no further evidence is available to unite *Frigorilepis* with basal chondrichthyans.
51
52 539 As a consequence, the *Elegestolepis*-type of morphogenesis is the only mechanism of
53
54 540 development recognised in monodontode chondrichthyan scales from the Silurian. The
55
56
57 541 inclusion of *Ellesmereia* into Elegestolepidida also shows that odontode growth has
58
59
60

1
2
3 542 persisted as a feature of the integumentary skeleton of chondrichthyans at least until the
4
5 543 Early Devonian (Fig. 10). This last known appearance of an elegestolepid species
6
7
8 544 coincides with a major diversification of chondrichthyans at the base of the Devonian
9
10 545 (Ginter, 2004; Turner, 2004; Grogan et al., 2012) that sees the emergence of taxa with
11
12 546 body cover of non-growing monodontode scales. Some of these species are known
13
14 547 from body fossils and represent examples of the earliest recorded articulated
15
16 548 chondrichthyan remains (Fig. 10; *Lupopsyrus pygmaeus* (Bernacsek and Dineley, 1977;
17
18 549 Hanke and Davis, 2012) and *Obtusacanthus corroconis* (Hanke and Wilson, 2004)).
19
20 550 *Polymerolepis whitei* (Karatajūtė-Talimaa, 1968, 1998; Hanke et al., 2013), is also
21
22 551 added to the above by being identified on the basis of CT data (Andreev, 2014) to
23
24 552 possess body scales with single odontode crowns that are randomly compartmentalized
25
26 553 into chambered spaces. These scales lack the bony base component of the
27
28 554 elegestolepid squamation, which within the Chondrichthyes has only been documented
29
30 555 in scales with growing crowns (either mon- or poly-odontode). Moreover, *Lupopsyrus*
31
32 556 and *Obtusacanthus*, a pair of genera that have been repeatedly recovered as stem
33
34 557 chondrichthyans in recent hypotheses of early gnathostome phylogeny (Brazeau, 2009;
35
36 558 Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015) are resolved as sister taxa to
37
38 559 Elegestolepidida (Fig. 2) and do not possess scale-neck openings of the pulp canal. A
39
40 560 pattern of vascularization where the pulp opens only towards the lower surface of scales
41
42 561 has a homoplastic distribution inside the stem group, and it is also a feature of the
43
44 562 earliest recorded chondrichthyan polyodontode scales (Sansom et al., 1996; 2001;
45
46 563 Donoghue and Sansom, 2002; Andreev et al., 2015).
47
48
49
50
51
52
53
54
55
56 564
57
58
59
60

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

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

ACKNOWLEDGMENTS

593 Funding for this study was provided by the School of Geography, Earth and
594 Environmental Sciences, University of Birmingham (P. A. studentship).

595 The authors wish to acknowledge Z. Johanson (Natural History Museum, London) and
596 R. Bulter (University of Birmingham) for their comments on the manuscript in the
597 capacity of examiners of P. A.'s PhD thesis. M. Smith (King's College, London) is
598 thanked for discussions on the nature of this material over many years.

599 R. Sammons and M. Sandholzer provided technical assistance during SEM and micro-
600 CT imaging of *Elegestolepis* and *Deltalepis* specimens at the School of Dentistry,
601 University of Birmingham.

602 The two undisclosed reviewers of the manuscript are thanked for their comprehensive
603 comments and recommendations.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

608

609

610

611

612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629

LITERATURE CITED

Andreev, P. S. 2014. The early evolutionary history of sharks and shark-like fishes: In *School of Geography, Earth and Environmental Science*, Vol. Ph.D. thesis. University of Birmingham, Birmingham.

Andreev, P. S., M. I. Coates, R. M. Shelton, P. R. Cooper, M. P. Smith, and I. J. Sansom. 2015. Upper Ordovician chondrichthyan-like scales from North America. *Palaeontology* 58:691–704.

Andreev, P. S., and G. Cuny. 2012. New Triassic stem selachimorphs (Chondrichthyes, Elasmobranchii) and their bearing on the evolution of dental enameloid in Neoselachii. *Journal of Vertebrate Paleontology* 32:255–266.

Bernacsek, G. M., and D. L. Dineley. 1977. New acanthodians from the Delorme Formation (Lower Devonian) of NWT Canada. *Palaeontographica Abteilung A* 158:1–25.

Blom, H., T. Marss, and C. G. Miller. 2002. Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere. *Transactions of the Royal Society of Edinburgh-Earth Sciences* 92:263–323.

Brazeau, M. D. 2009. The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. *Nature* 457:305–308.

Brazeau, M. D., and M. Friedman. 2015. The origin and early phylogenetic history of

- 630 jawed vertebrates. *Nature* 520:490–497.
- 631 Burrow, C., and S. Turner. 1998. Devonian placoderm scales from Australia. *Journal of*
632 *Vertebrate Paleontology* 18:677–695.
- 633 Burrow, C. J., and S. Turner. 1999. A review of placoderm scales, and their significance
634 in placoderm phylogeny. *Journal of Vertebrate Paleontology* 19:204–219.
- 635 Coates, M., and S. Sequeira. 2001. A new stethacanthid chondrichthyan from the Lower
636 Carboniferous of Bearsden, Scotland. *Journal of Vertebrate Paleontology*
637 21:438–459.
- 638 Compagno, L. J. 1988. *Sharks of the order Carcharhiniformes*. 486 pp. Princeton
639 University Press Princeton, New Jersey.
- 640 Davis, S. P., J. A. Finarelli, and M. I. Coates. 2012. *Acanthodes* and shark-like
641 conditions in the last common ancestor of modern gnathostomes. *Nature*
642 486:247–250.
- 643 Denison, R. H. 1967. Ordovician vertebrates from western United States. *Fieldiana:*
644 *Geology* 16:131–192.
- 645 Denison, R. H. 1979. *Acanthodii*. 62 pp. Gustav Fischer Verlag, Stuttgart, New York.
- 646 Dick, J. R. 1978. On the Carboniferous shark *Tristychius arcuatus* Agassiz from
647 Scotland. *Transactions of the Royal Society of Edinburgh* 70:63–108.
- 648 Dick, J., and J. Maisey. 1980. The Scottish Lower Carboniferous shark *Onychoselache*
649 *traquairi*. *Palaeontology* 23:363–374.
- 650 Donoghue, P. C. 2002. Evolution of development of the vertebrate dermal and oral
651 skeletons: unraveling concepts, regulatory theories, and homologies.
652 *Paleobiology* 28:474–507.

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

- 676 Giles, S., M. Rücklin, and P. C. Donoghue. 2013. Histology of "placoderm" dermal
677 skeletons: Implications for the nature of the ancestral gnathostome. *Journal of*
678 *Morphology* 274:627–644.
- 679 Gillis, J. A., and P. C. Donoghue. 2007. The homology and phylogeny of chondrichthyan
680 tooth enameloid. *Journal of Morphology* 268:33–49.
- 681 Ginter, M. 2004. Devonian sharks and the origin of Xenacanthiformes; pp. 473–486 in
682 G. Arratia, M. V. H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin*
683 *and Early Radiation of Vertebrates*. Verlag Friedrich Pfeil, Munich.
- 684 Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for
685 phylogenetic analysis. *Cladistics* 24:774–786.
- 686 Grogan, E. D., and R. Lund. 2009. Two new inioptrygians (Chondrichthyes) from the
687 Mississippian (Serpukhovian) Bear Gulch Limestone of Montana with evidence of
688 a new form of chondrichthyan neurocranium. *Acta Zoologica* 90:134–151.
- 689 Grogan, E. D., R. Lund, and E. Greenfest-Allen. 2012. The origin and relationships of
690 early chondrichthyans; pp. 3–29 in J. C. Carrier, Musick J. A., Heithaus M. R.
691 (ed.), *Biology of sharks and their relatives*. Taylor & Francis, New York.
- 692 Gross, W. 1953. Devonische Palaeonisciden-Reste in Mittel-und Osteuropa.
693 *Paläontologische Zeitschrift* 27:85–112.
- 694 Gross, W. 1956. Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im
695 Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems
696 paläozoischer Agnathen und Fische. *Kungliga Svenska vetenskapsakademiens*
697 *handlingar* 5:1–140.
- 698 Gross, W. 1961. Aufbau des Panzers obersilurischer Heterostraci und Osteostraci

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

1
2
3 745 and patterned scales in the embryonic catshark tail. *Biology letters* 4:87–90.
4
5
6 746 Johns, M. J., C. R. Barnes, and M. J. Orchard. 1997. Taxonomy and biostratigraphy of
7
8 747 Middle and Late Triassic elasmobranch ichthyoliths from northeastern British
9
10 748 Columbia. 235 pp. Geological Survey of Canada.
11
12
13 749 Karatajūtė-Talimaa, V. 1968. New thelodonts, heterostracans and arthrodires from the
14
15 750 Chortkov Stage of Podolia; pp. 33–42 in D. V. Obruchev (ed.), *Sketches in*
16
17 751 *phylogenesis and taxonomy of fossil fishes and agnatha*. Nauka, Moscow.
18
19
20 752 Karatajūtė-Talimaa, V. 1973. *Elegestolepis grossi* gen. et sp. nov., ein neuer Typ der
21
22 753 Placoidschuppe aus dem Oberen Silur der Tuwa. *Palaeontographica* Abt. A
23
24 754 143:35–50.
25
26
27 755 Karatajūtė-Talimaa, V. 1978. Silurian and Devonian thelodonts of the U.S.S.R. and
28
29 756 Spitsbergen. 334 pp. Mokslas, Vilnius.
30
31
32 757 Karatajūtė-Talimaa, V. 1992. The early stages of the dermal skeleton formation in
33
34 758 chondrichthyans; pp. 223–231 in E. Mark-Kurik (ed.), *Fossil fishes as living*
35
36 759 *animals*. Institute of Geology, Tallinn.
37
38
39 760 Karatajūtė-Talimaa, V. 1998. Determination methods for the exoskeletal remains of
40
41 761 early vertebrates. *Mitteilungen aus dem Museum für Naturkunde in Berlin*,
42
43 762 *Geowissenschaftliche Reihe* 1:21–51.
44
45
46 763 Karatajūtė-Talimaa, V., L. Novitskaya, K. S. Rozman, and Z. Sodov. 1990.
47
48 764 *Mongolepis*—a new lower Silurian genus of elasmobranchs from Mongolia.
49
50 765 *Paleontologicheskii Zhurnal* 1990:76–86.
51
52
53 766 Karatajūtė-Talimaa, V., and L. Novitskaya. 1992. *Teslepis*—a new representative of
54
55 767 mongolepid elasmobranchs from the Lower Silurian of Mongolia.
56
57
58
59
60

- 768 Paleontologicheskii Zhurnal 4:36–46.
- 769 Karatajūtė-Talimaa, V., and L. Novitskaya. 1997. *Sodolepis*—a new representative of
770 Mongolepidida (Chondrichthyes?) from the Lower Silurian of Mongolia.
771 Paleontologicheskii Zhurnal 1997:96–103.
- 772 Karatajūtė-Talimaa, V. 1995. The Mongolepidida: scale structure and systematic
773 position. Geobios 19:35–37.
- 774 Karatajūtė-Talimaa, V., and N. Predtechenskyj. 1995. The distribution of the vertebrates
775 in the Late Ordovician and Early Silurian palaeobasins of the Siberian Platform.
776 Bulletin du Muséum National d'Histoire Naturelle 17:39–55.
- 777 Keating, J. N., C. L. Marquart, and P. C. Donoghue. 2015. Histology of the
778 heterostracan dermal skeleton: Insight into the origin of the vertebrate
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
782 Society B 283: No. 1826, p. 20152917.
- 783 Lund, R. 1985. The morphology of *Falcatus falcatus* (St. John and Worthen), a
784 Mississippian stethacanthid chondrichthyan from the Bear Gulch Limestone of
785 Montana. Journal of Vertebrate Paleontology 5:1–19.
- 786 Lund, R. 1986. On *Damocles serratus*, nov. gen. et sp. (Elasmobranchii: Cladodontida)
787 from the Upper Mississippian Bear Gulch Limestone of Montana. Journal of
788 Vertebrate Paleontology 6:12–19.
- 789 Maisey, J. G. 1989. *Hamiltonichthys mapesi*, g. & sp. nov. (Chondrichthyes,
790 Elasmobranchii), from the Upper Pennsylvanian of Kansas. American Museum

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

- 814 thelodonts and putative chondrichthyans from the Canadian Arctic Archipelago.
815 144 pp. The Palaeontological Association, London.
- 816 Miyake, T., J. L. Vaglia, L. H. Taylor, and B. K. Hall. 1999. Development of dermal
817 denticles in skates (Chondrichthyes, Batoidea): patterning and cellular
818 differentiation. *Journal of Morphology* 241:61–81.
- 819 Novitskaya, L. I., and V. Karatajūtė-Talimaa. 1986. Remarks about the cladistic analysis
820 in connection with myopterygian hypothesis and the problem of the origin of
821 gnathostomes; pp. 102–125 in E. Vorobyeva, and N. Lebedkina (eds.),
822 *Morphology and Evolution of Animals*. Nauka, Moscow.
- 823 Ørvig, T. 1966. Histologic studies of ostracoderms, placoderms and fossil
824 elasmobranchs. 2. On the dermal skeleton of two late Palaeozoic
825 elasmobranchs. *Arkiv för Zoologi* 19:1–39.
- 826 Ørvig, T. 1967. Phylogeny of tooth tissues: evolution of some calcified tissues in early
827 vertebrates; pp. 45–110 in A. E. W. Miles (ed.), *Structural and chemical*
828 *organization of teeth*, Volume 1. Academic Press New York.
- 829 Ørvig, T. 1977. A survey of odontodes ('dermal teeth') from developmental, structural,
830 functional, and phyletic points of view; pp. 53–75 in M. Andrews, R. S. & Walker,
831 A. D. (ed.), *Problems in Vertebrate Evolution*. Academic Press, London, New
832 York.
- 833 Patterson, C. 1965. The phylogeny of the chimaeroids. *Philosophical Transactions of*
834 *the Royal Society B: Biological Sciences* 249:101-219.
- 835 Qu, Q., M. Zhu, and W. Wang. 2013. Scales and dermal skeletal histology of an early
836 bony fish *Psarolepis romeri* and their bearing on the evolution of rhombic scales

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

- 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 in E. Ahlberg (ed.), *Major Events in Early Vertebrate*
866 *Evolution, Systematics Association Special Volume*. Taylor & Francis, London
867 and New York.
- 868 Schultze, H.-P. 1968. Palaeoniscoidea-Schuppen aus dem Unterdevon Australiens und
869 Kanadas und aus dem Mitteldevon Spitzbergens. 16:341–368.
- 870 Schultze, H.-P. 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

1
2
3 883 skeletogenic and odontogenic tissues. *Biological Reviews* 65:277–373.
4
5
6 884 Smith, M. M., and B. K. Hall. 1993. A developmental model for evolution of the
7
8 885 vertebrate exoskeleton and teeth. The role of cranial and trunk neural crest; pp.
9
10 886 387–448 in M. K. Hecht, R. J. Macintyre, and M. Clegg (eds.), *Evolutionary*
11
12 887 *biology*. Plenum Press, New York.
13
14
15 888 Smith, M. M., and A. Miles. 1971. The ultrastructure of odontogenesis in larval and adult
16
17 889 urodeles; differentiation of the dental epithelial cells. *Zeitschrift für Zellforschung*
18
19 890 *und mikroskopische Anatomie* 121:470–498.
20
21
22 891 Stensiö, E. A. 1932. The cephalaspids of Great Britain. 220 pp. The British Museum
23
24 892 (Natural History), London.
25
26
27 893 Stensiö, E. A. 1961. Permian vertebrates; pp. 231–247 in G. Raasch (ed.), *Geology of*
28
29 894 *the Arctic*. University of Toronto, Toronto.
30
31
32 895 Stensiö, E., and T. Ørvig. 1951–1957. On the scales of the elasmobranchs. Swedish
33
34 896 Museum of Natural History, Stockholm.
35
36
37 897 Sykes, J. 1974. On elasmobranch dermal denticles from the Rhaetic bone bed at
38
39 898 Barnstone, Nottinghamshire. *Mercian Geologist* 5:49–64.
40
41
42 899 Thies, D. 1995. Placoid scales (Chondrichthyes: Elasmobranchii) from the late Jurassic
43
44 900 (Kimmeridgian) of northern Germany. *Journal of Vertebrate Paleontology*
45
46 901 15:463–481.
47
48
49 902 Thies, D., and A. Leidner. 2011. Sharks and guitarfishes (Elasmobranchii) from the Late
50
51 903 Jurassic of Europe. *Palaeodiversity* 4:63–184.
52
53
54 904 Turner, S. 2004. Early vertebrates: analysis from microfossil evidence; pp. 67–94 in G.
55
56 905 Arratia, M. V. H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin*
57
58
59
60

- 906 and Early Radiation of Vertebrates. Verlag Dr. Friedrich Pfeil, Munich.
- 907 Upeniece, I. 2011. Palaeoecology and juvenile individuals of the Devonian placoderm
908 and acanthodian fishes from Lode site, Latvia: In *Department of Geology*, Vol.
909 Doctoral Thesis, pp. 221. University of Latvia, Riga.
- 910 Vieth, J. 1980. Thelodontier-, Acanthodier-und Elasmobranchier-Schuppen aus dem
911 Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). 69 pp. Im Selbstverlag
912 des Geologisch-Paläontologischen Institut der Georg-August-Universität
913 Göttingen, Göttingen.
- 914 Valiukevičius, J. 1992. First articulated *Poracanthodes* from the Lower Devonian of
915 Severnaya Zemlya; pp. 193-214 in E. Mark-Kurik (ed.), Fossil Fishes as Living
916 Animals. Academy of Sciences of Estonia, Tallinn.
- 917 Vladimirkaya, E. V. 1978. Brachiopods of the Silurian in Tuva. *Ezhegodnik*
918 *Vsesoyuznogo Paleontologicheskogo Obshchestva* 21:148–167.
- 919 Voigt, M., and D. Weber. 2011. Field Guide for Sharks of the Genus *Carcharhinus*. 151
920 pp. Verlag Dr. Friedrich Pfeil, Munich.
- 921 Wang, N.-Z., P. C. Donoghue, M. M. Smith, and I. J. Sansom. 2005. Histology of the
922 galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of
923 the vertebrate cranial endoskeleton. *Journal of Vertebrate Paleontology* 25:745–
924 756.
- 925 Wang, N.-Z., X. Zhang, M. Zhu, and W. J. Zhao. 2009. A new articulated hybodontoid
926 from Late Permian of northwestern China. *Acta Zoologica* 90:159–170.
- 927 Young, G. 1997. Ordovician microvertebrate remains from the Amadeus Basin, central
928 Australia. *Journal of Vertebrate Paleontology* 17:1–25.

1
2
3 929 Young, G. 2000. *Areyongalepis*, a replacement name for *Areyonga* Young 1997
4
5 930 (preoccupied name). Journal of Vertebrate Paleontology 20:611–611.
6
7
8 931 Zangerl, R. 1968. The morphology and the developmental history of the scales of the
9
10 932 Paleozoic sharks *Holmesella?* sp. and *Orodus*; pp. 399–412 in T. Ørvig (ed.),
11
12 933 Current Problems of Lower Vertebrate Phylogeny. Almquist & Wiksell,
13
14 934 Stockholm.
15
16
17 935 Zangerl, R., and G. R. Case. 1973. Iniopterygia: A new order of chondrichthyan fishes
18
19 936 from the Pennsylvanian of North America. 67 pp. Field Museum of Natural
20
21 937 History, Chicago.
22
23
24 938 Zhu, M., X. Yu, P. E. Ahlberg, B. Choo, J. Lu, T. Qiao, Q. Qu, W. Zhao, L. Jia, and H.
25
26 939 Blom. 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones.
27
28 940 Nature 502:188–193.
29
30
31 941 Zhu, M., X. Yu, B. Choo, J. Wang, and L. Jia. 2012. An antiarch placoderm shows that
32
33 942 pelvic girdles arose at the root of jawed vertebrates. Biology letters 8:453–456.
34
35
36 943 Zhu, M., X. Yu, W. Wang, W. Zhao, and L. Jia. 2006. A primitive fish provides key
37
38 944 characters bearing on deep osteichthyan phylogeny. Nature 441:77–80.
39
40
41 945 Žigaitė, Ž., and V. Karatajūtė-Talimaa. 2008. New genus of chondrichthyans from the
42
43 946 Silurian–Devonian boundary deposits of Tuva (Russia). Evolution and diversity of
44
45 947 chondrichthyans. Acta Geologica Polonica 58:127–131.
46
47
48 948 Žigaitė, Ž., V. Karatajūtė-Talimaa, and A. Blieck. 2011. Vertebrate microremains from
49
50 949 the Lower Silurian of Siberia and Central Asia: palaeobiodiversity and
51
52 950 palaeobiogeography. Journal of Micropalaeontology 30:97–106.
53
54
55 951

952

953

954 Submitted: September 21, 2015

955 Revisions received: MM, DD, YYYY

956 Accepted: Month DD, YYYY

957

958

959

960

961

962

963

964

965

966

967

968

969

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 *Elegetolepis* morphogenetic type represented by an *Elegetolepis 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 Elegetolepidida 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 elegetolepid scales. **A**, *Elegetolepis grossi* (BU5284); **B**, *Ellesmereia schultzei*

991 (adapted from Vieth 1980:pl. 9.2); **C**, *Deltalepis magna* (holotype BU5269); **D**,
 992 *Deltalepis parva* (holotype BU5275). Anterior towards the bottom. (column width)
 993
 994 FIGURE 4. Scales of *Elegestolepis grossi* from the Baital Formation of Tuva, Russian
 995 Federation; ontogenetically mature scales shown in **A**, antero-lateral (BU5285), **B**,
 996 lateral-crown (BU5285), **C**, lateral (BU5286) and (**D**, BU5286), (**E**, BU5287) crown
 997 views. **F**, postero-lateral view of BU5289 showing the single neck canal opening of the
 998 scale crown; **G**, postero-basal view of an ontogenetically young scale (BU5343) with not
 999 fully formed pedicle support; **H**, basal view of a scale (BU5343) with pedicle support at
 1000 an advanced stage of formation; **I**, mature scale (BU5289) in basal view exhibiting
 1001 bulbous basal bone. SEM micrographs. Anterior towards right in (B), towards left in (C),
 1002 towards the bottom in (D, E) and towards the top in (H, I); arrows indicate neck canal
 1003 openings, arrowhead indicates the basal opening of the main pulp canal. Scale bars
 1004 represent 200 µm in (A–E, G, H) and 100 µm in (F, I). (whole page width)

1006 FIGURE 5. Hard tissue structure of *Elegestolepis grossi* scales from the Baital
 1007 Formation of Tuva, Russian Federation. **A**, vertical cross section of a scale (BU5290) in
 1008 early stage of bony base formation, etched in 0.5% chromium sulphate solution for 2
 1009 hours; **B**, detail of **A**, showing the upper medial portion of the crown; **C**, vertical
 1010 longitudinal section of a scale (BU5291) in advanced stage of basal bone developed
 1011 (ontogenetically old), etched in 0.5% orthophosphoric acid for 10 minutes; **D**, detail of
 1012 BU5291 depicting the lower posterior margin of the crown; **E**, detail of the anterior

1
2
3 1013 portion of the crown of BU5291; **F**, vertical transverse section of an ontogenetically old
4
5 1014 scale (BU5292); **G**, basal bone of ontogenetically old scale (BU5293) in vertical
6
7
8 1015 longitudinal section. (B–E) SEM micrographs; (A, F, G) Nomarski interference contrast
9
10 1016 micrographs. Anterior towards the right in (C–E, G); (B), base; arrowheads in (B–E)
11
12 1017 demarcate the extent of artificially altered dentine, asterisks in (G) denote the borders of
13
14 1018 depositional bone lamellae. Scales bars represent 100 µm in (A, C, F, G) 50 µm in (B,
15
16 1019 E) and 20 µm in (D). (whole page width)
17
18
19
20
21 1020
22
23

24 1021 FIGURE 6. Scales of *Deltalepis magna* gen. et sp. nov. from the Chargat Formation of
25
26 1022 north-western Mongolia. Holotype specimen (BU5269, scale with a five-lobed crown
27
28 1023 and a gracile neck) in **A**, anterior, **B**, antero-lateral and **C**, crown view. **D**, scale
29
30 1024 (BU5270) with gracile neck in basal view. Scales with three-lobe crowns in **E**, anterior,
31
32 1025 **F**, posterior, **G**, lateral (E–G, BU5273) and **H**, crown (BU5271) views. **I**, BU5273 in basal
33
34 1026 view revealing the lower pedicle surface; **J**, basal view of a scale (BU5272) with fully
35
36 1027 formed pedicle support. (A–C, H–J) SEM micrographs; (D–G) volume renderings.
37
38 1028 Anterior towards the right in (B), towards the bottom in (C, H) towards the top in (D, I, J);
39
40 1029 arrow indicates a neck canal opening. Scale bars represent 200 µm. (whole page width)
41
42
43
44
45
46 1030
47

48 1031 FIGURE 7. Scales of *Deltalepis parva* gen. et sp. nov. from the Chargat Formation of
49
50 1032 north-western Mongolia. Holotype (BU5275) in **A**, crown and **B**, anterior-crown view.
51
52 1033 Scale (BU5280) with a gracile neck in **C**, anterior and **D**, posterior view. Scale (BU5277)
53
54 1034 in **E**, anterior and **F**, crown view. **G**, scale (BU5278) with a gracile neck in basal view,
55
56
57
58
59
60

1035 exposing the rami of the pulp canal system. Scale (BU5279) with formed pedicle
 1036 support in **H**, basal and **I**, postero-basal view. (A, B, E–I) SEM micrographs; (C, D)
 1037 volume renderings. Anterior towards the bottom in (A, F) towards the top in (G–I);
 1038 arrows indicate neck canal openings, arrowhead indicates the basal opening of the
 1039 main pulp canal. Scale bars represent 200 μm in (A–D, G) and 100 μm in (E, F, H, I).
 1040 (whole page width)

1042 FIGURE 8. Hard tissue structure of *Deltalepis* gen. nov. **A**, longitudinal tomographic
 1043 slice of a *Deltalepis magna* scale (BU5273); **B**, detail of the dentine tissue at the upper
 1044 anterior margin of the crown of a longitudinally sectioned *Deltalepis magna* scale
 1045 (BU5274); **C**, longitudinal tomographic slice of a *Deltalepis parva* scale (BU5280); **D**,
 1046 view of the posterior portion of a *Deltalepis parva* scale (BU5282) crown immersed in
 1047 clove oil. (B, D) Nomarski interference contrast micrographs; (A, C) volume renderings.
 1048 Anterior towards the right in (A) and towards the left in (C). Scale bars represent 100 μm
 1049 in (A, C, D) and 50 μm in (B). (whole page width)

1051 FIGURE 9. Volume renderings of the scale canal system (in red) of examined
 1052 elegestolepids. The scales are made translucent in all renderings, with the exception of
 1053 (G). **A–C**, *Elegestolepis grossi* scale (BU5284) from the Baital Formation of Tuva
 1054 (Russian Federation) in **A**, anterior, **B**, postero-lateral and **C**, crown (depicting the lower
 1055 portion of the specimen that is transversely sliced through the neck region) view. **D–F**,
 1056 *Deltalepis magna* scale (BU5273) from the upper Llandovery–lower Wenlock of north

1
2
3 1057 western Mongolia in **D**, crown and **E**, posterior view and a **F**, crown view of the lower
4
5
6 1058 portion of the same specimen sliced through the neck region. **G–J**, *Deltalepis parva*
7
8 1059 specimens (BU5280 and BU5281) from the upper Llandovery–lower Wenlock of north
9
10 1060 western Mongolia; **G**, BU5280 sliced transversely through the crown in crown view; **H**,
11
12 1061 BU5280 in anterior view; **I**, **J**, BU5281 in **I** posterior and **J**, postero-lateral view. Anterior
13
14
15 1062 towards the left in (B), towards the top in (C, F, G) and towards the bottom in (D);
16
17 1063 arrows indicate neck canal openings, arrowheads point at the basal opening of the main
18
19
20 1064 pulp canal. Scale bars represent 100 µm. (whole page width)
21
22
23 1065
24
25
26 1066 FIGURE 10. Characteristics of monodontode scales of recognised lower Paleozoic
27
28 1067 chondrichthyans and their stratigraphic range. Pink rectangle designates elegestolepid
29
30 1068 taxa. *Elegestolepis* (Karatajūtė-Talimaa, 1973 and data from this study), *Deltalepis*
31
32
33 1069 (data from this study), *Kannathalepis* (Märss and Gagnier, 2001), *Ellesmereia* (Vieth,
34
35 1070 1980), *Frigorilepis* (Märss et al., 2002, 2006), *Polymerolepis* Karatajūtė-Talimaa, 1998;
36
37
38 1071 Hanke et al., 2013), *Lupopsyrus* and *Obtusacanthus* (Hanke and Wilson, 2004; Hanke
39
40 1072 and Davis, 2012). (whole page width)
41
42
43 1073
44
45
46 1074
47
48
49 1075
50
51
52 1076
53
54
55 1077
56
57
58
59
60

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 *Egestolepis* morphogenetic type represented by an *Egestolepis 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)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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 μ m in (A–E, G, H) and 100 μ m 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. Scale 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 μ m in (A-D, G) and 100 μ m 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 elegetolepid taxa. *Elegetolepis* (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)