

Elegetolepis and its kin, the earliest monodontode chondrichthyans

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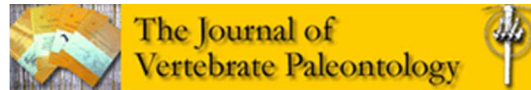
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***Elegestolepis* and its kin, the earliest monodontode chondrichthyans**

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4 1 *Elegestolepis* and Its Kin, the Earliest Monodontode Chondrichthyans
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41 14 Running header—Earliest monodontode chondrichthyans
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4 20 ABSTRACT—Chondrichthyan-like scales with simple, single odontode crowns,
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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.

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16 25 A study of elegestolepid microremains from the Chargat Formation of Mongolia
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18 26 (Llandovery–lower Wenlock) and the Baital Formation of Tuva (Wenlock–Ludlow) has
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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
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30 32 species *Ellesmereia schultzei*, and forms the basis for the unification of these taxa into a
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32 33 new chondrichthyan Order Elegestolepidida ordo nov. Similarities in crown
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34 34 vascularization (branching pulp, single neck canal) shared by *Elegestolepis*,
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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
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40 37 fam. nov. that is distinguished from the mono-generic Kannathalepididae (non-
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42 38 branching pulp, multiple neck canals).

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50 39 Elegestolepid scales exhibit characteristics (neck canal formation and lack of enamel
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52 40 and basal bone osteons) consistent with those of the chondrichthyan dermal skeleton.
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55 41 This establishes Elegestolepidida as the stratigraphically oldest chondrichthyan taxon to
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42 develop monodontode scales, which, in contrast to the 'placoid' scales of euselachians,
43 are growing structures.

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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

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

32 96 In the years following the conceptualization of the lepidomorial theory, increasing
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34 97 evidence from studies on the development of the integumentary skeleton of Recent
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36 98 neoselachians (Reif, 1980b; Miyake et al., 1999; Johanson et al., 2008) has discredited
37
38 99 the concrescence model of odontode morphogenesis, and this is now refuted by most
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40 100 authors (Smith and Coates, 1998; Donoghue, 2002 and references therein). The latter
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42 101 view is strengthened with the inclusion of ‘acanthodians’ bearing polyodontode scales
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44 102 with elaborately branching odontode pulps (e.g. in *Poracanthodes* Gross, 1956;
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46 103 Valiukevičius, 1992) within the chondrichthyan phylogenetic history (Zhu et al., 2013;
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48 104 Brazeau and Friedman 2015; Giles et al., 2015). This contradicts the evolutionary
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50 105 scenario predicted by the concrescence model, which claims origination of
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52 106 neoselachian placoid scales and their complex canal system via fusion of simple
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3 107 lepidomerial elements enclosing a single vascular loop (Stensiö and Ørvig, 1951–1957;
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5 108 Stensiö, 1961). Advances in developmental biology have revealed an apparently
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7
8 109 conserved gene regulatory network that maintains a variety of odontode morphogenetic
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11 110 pathways (Fraser et al. 2010). This further corroborates the notion that all structures
12
13 111 resolvable into odontode units are, in a broad sense, homologous. In this context, a re-
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15 112 examination of *Elegestolepis* and *Elegestolepis*-like Silurian scale taxa (e.g.
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17 113 *Ellesmereia*, *Kannathalepis*) will enable a clearer understanding of the early evolution of
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19 114 single odontode integumentary skeletal elements in the Chondrichthyes. To meet this
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21
22 115 end, the present study investigates the histology, canal system and inferred
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24 116 development of *Elegestolepis grossi* scales and that of previously undescribed scales
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27 117 from the Lower Silurian of Mongolia referred to *Elegestolepis* (Karatajūtė-Talimaa et al.,
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29 118 1990). These new data permit a new systematic framework for *Elegestolepis*-like taxa
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32 119 and allow for the further evaluation of their likely chondrichthyan affinities.
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38 121 MATERIALS AND METHODS

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44 123 The isolated scales were extracted through dissolution of carbonate rock
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46 124 samples with dilute acetic acid. The specimens come from the Chargat Formation of
47
48 125 north western Mongolia (Chargat outcrop, sample P-16/3 [2]) and the Baital Formation
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50 126 (Elegest River outcrop, samples from beds 236, 291, 293 and 295 [1]) of central Tuva,
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53 127 Russian Federation.
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3 128 Scale morphology was documented using the Zeiss EVO LS and the JEOL JSM-
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6 129 6060 scanning electron microscopes at the School of Dentistry of the University of
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8 130 Birmingham, UK. Prior to imaging, the specimens were sputter-coated with a 25 nm-
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10 131 thick layer of gold/palladium alloy.

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13 132 Hard tissue microstructure and internal architecture of thin-sectioned specimens was
14
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16 133 investigated by Nomarski differential interference contrast microscopy (using a 'Zeiss
17
18 134 Axioskop Pol' polarization microscope) and scanning electron microscopy (with a JEOL
19
20 135 JSM-6060 SEM at the School of Dentistry, University of Birmingham, UK).

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23 136 Scale examination with X-ray radiation was conducted using the SkyScan 1172
24
25
26 137 microtomography scanner at the School of Dentistry of the University of Birmingham,
27
28 138 UK. The acquired microradiographs (tomographic projections) were taken at 0.3°
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30 139 intervals over a 180° rotation cycle at exposure times of 400 ms, using a 0.5 mm thick
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33 140 X-ray attenuating Al filter. These image data were processed with the SkyScan NRecon
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35 141 reconstruction software in order to generate sets of microtomograms that were
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37 142 converted into volume renderings in Amira 5.4 3D analysis software.

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40 143 Figured material is deposited in the Lapworth Museum of Geology, University of
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43 144 Birmingham, UK (BU prefix).

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47 48 49 146 **Definitions of Terms**

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52 147 Traditionally (Sykes, 1974; Duffin and Ward, 1993; Thies, 1995) the two main
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54 148 components (crown and base) of chondrichthyan scales have been identified on the
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57 149 basis of morphological and/or topological criteria without consideration of their
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3 150 developmental origin. This approach can lead to ambiguity when attempting to establish
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6 151 the extent of these structures and, more importantly, can result in homologizing scale
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8 152 parts with different tissue composition across taxa. To address the above issues,
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11 153 Andreev et al. (2015) provided revised definitions of terms used in literature to describe
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13 154 chondrichthyan scales, and these are followed in the present study.
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19 156 SYSTEMATIC PALEONTOLOGY

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25 158 Class CHONDRICHTHYES Huxley, 1880

27 159 Order ELEGESTOLEPIDIDA ordo nov.

30 160 **Included Families**—Kannathalepididae Märss and Gagnier 2001 and
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32 161 Elegestolepididae fam. nov.
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38 163 **Diagnosis**—Chondrichthyan fish with monodontode scale crowns composed of a
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41 164 growing odontode that encloses neck-canal branches of the pulp cavity (Fig. 1B).
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44 165 **Remarks**—The recent literature on putative basal chondrichthyan taxa (e.g.
45
46 166 mongolepids, elegestolepids, kathermacanthids and polymerolepidiforms) from the lower
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48 167 Paleozoic expresses uncertainty regarding their systematic position relative to the major
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51 168 clades (Subclasses) of the Chondrichthyes (Karatajute-Talimaa and Novitskaya, 1997;
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53 169 Sansom et al., 2000; Märss et al., 2006; Hanke and Wilson, 2010; Hanke et al., 2013).
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56 170 This reflects an inadequate understanding of the phylogenetic significance of scale-

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3 171 derived characters, which have been employed to diagnose these taxa given the
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6 172 general absence of chondrichthyan endoskeletal and dental remains in the lower
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8 173 Paleozoic.
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11 174 The odontode growth that typifies the ontogenesis of *Elegestolepis*-like scales is
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14 175 not seen within traditionally recognised chondrichthyan clades (*sensu* Grogan et al.,
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16 176 2012), yet the *Elegestolepida* consistently falls inside stem-group Chondrichthyes
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18 177 when its affinities are tested via phylogenetic inference (Andreev et al., unpublished
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21 178 data; Fig. 2). The erection of a new Order draws together species that possess scales
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23 179 with growing single-odontode crowns whose morphogenesis can be differentiated from
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26 180 that of elasmobranch ‘placoid’ scales (the *Heterodontus* morphogenetic type of
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28 181 (Karatajūtė-Talimaa, 1992, 1998; Fig. 1C). The formal recognition of the *Elegestolepis*-
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30 182 type of scale development represents a change in concept from what was originally
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33 183 identified as a purely morphogenic category (Karatajūtė-Talimaa, 1992, 1998).
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39 185 Family KANNATHALEPIDIDAE Märss and Gagnier, 2001
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42 186 **Included genera**—*Kannathalepis* Märss and Gagnier, 2001
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45 187 **Revised diagnosis**—*Elegestolepids* possessing dermal scales with vertically
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48 188 undivided pulp cavities from which multiple (up to five) horizontal neck canals emerge
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50 189 basally.
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53 190 **Remarks**—The mono-generic Family *Kannathalepididae* was introduced by Märss
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55 191 and Gagnier (2001) to distinguish *Kannathalepis*, identified to exhibit a specialised type
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3 192 of scale morphogenesis, from other Silurian chondrichthyan scale taxa (mongolepid and
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5 193 elegestolepid). It was reported that the squamation of *Kannathalepis* consists of single-
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8 194 odontode scales along with more complex aggregates of fused 'placoid' scales that
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10 195 were thought to provide evidence for two separate modes of scale development within
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12 196 the genus (Märss and Gagnier, 2001: fig. 4f). The current study regards these
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14 197 compound scales of *Kannathalepis* as aberrant, formed by anomalous patterning that is
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16 198 thought to result from suppression of inter-scale domains in accordance with the
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18 199 inhibitory field model outlined by Reif (1980a, 1982). Localised suturing of scales has
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20 200 similarly been documented in stem (*Hybodus delabechei* (Reif, 1978: fig. 8 d, e) and
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22 201 *Lissodus sardiniensi* (Fischer et al., 2010: fig. 7l)) and crown (*Echinorhinus brucus* (Reif,
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24 202 1985:pl. 15) and *Asterodermus platypterus* (Thies and Leidner, 2011:pl. 71))
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26 203 euselachians with monodontode trunk scale cover that is known to be prevalent within
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28 204 the Order (Reif, 1985; Thies and Leidner, 2011; Dick, 1978; Dick and Maisey, 1980;
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30 205 Maisey, 1989; Wang et al., 2009).

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37 206 Complexes of randomly sutured monodontode scales consequently cannot be
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39 207 considered equivalent to polyodontode scales (e.g. those of Mongolepidida (Karatajūtė-
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41 208 Talimaa, 1998)), since the odontodes of the latter are patterned as a unit in a particular
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43 209 manner and are given support by a common base/pedicle tissue. The scale
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45 210 development in *Kannathalepis* can thus be identified as that of 'placoid' scales with a
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47 211 growing odontode and base, corresponding to the *Elegestolepis* morphogenetic type
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49 212 (Fig. 1B) of Karatajūtė-Talimaa (1992). On that basis, Kannathalepididae is placed
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51 213 inside the new Order Elegestolepidida, and its validity is maintained by acknowledging
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3 214 the canal system characteristics (vertically undivided pulp cavity and multiple neck
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6 215 canals) diagnostic for the Family, recognized in the original description of the taxon.
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9 216 Kannathalepididae was expanded subsequent to its erection to include the
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11 217 Wenlockian genus *Frigorilepis*, which was described from articulated body fossils
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13 218 (Märss et al., 2002, 2006). Nevertheless, crown morphogenesis in *Frigorilepis* has not
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15
16 219 been demonstrated to proceed in discrete growth phases as in elegendolepid taxa,
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18 220 which are further distinguished by the presence of scale-neck canal openings. The
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20 221 absence of characters diagnostic for Elegendolepidida results in treating *Frigorilepis* as
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22 222 Family and Order *incertae sedis* for the time being.
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29 224 Family ELEGESTOLEPIDIDAE fam. nov.
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32 225 **Included genera**—The type genus *Elegendolepis* Karatajūtė-Talimaa 1973,
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34 226 *Ellesmereia* Vieth, 1980 and *Deltalepis* gen. nov.
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37 227 **Diagnosis**—Elegendolepids with scales that develop a vertically branched pulp cavity
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39 228 that gives off a single horizontal neck canal and dentine canals that originate at the
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41 229 lower neck/pedicle surface independently of the pulp (Fig. 9).
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48 231 Genus *ELEGESTOLEPIS* Karatajūtė-Talimaa, 1973
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51 232 **Included species**—The type species *E. grossi* Karatajūtė-Talimaa, 1973 and *E.*
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53 233 *conica* Novitskaya and Karatajūtė-Talimaa, 1986.
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3 234 **Revised diagnosis**—Elegestolepidids possessing up to three unornamented
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6 235 scale crown lobes (Fig. 3A; Fig. 4A, B, D, E) incised by deep, linear grooves.
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11 237 *ELEGESTOLEPIS GROSSI* Karatajūtė-Talimaa, 1973

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13 238 (Figs. 1B, 3A, 4, 5, 9A–C)

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17 239 *Elegestolepis grossi* Karatajūtė-Talimaa, 1973:figs. 1–5, pl. 3 (original description).

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19 240 *Elegestolepis grossi* Karatajūtė-Talimaa, 1998:31, fig. 10.

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21 241 **Locality and horizon**—Studied material comes from beds 236, 291, 293 and
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23 242 295 of the Baital Formation (Wenlock–Ludlow (Vladimirskaya, 1978; Sennikov et al.,
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25 243 2015)) at the type locality on the Elegest River, central Tuva, Russia (Karatajūtė-
26
27 244 Talimaa, 1973). *E. grossi* has also been reported from the Pridoli of Tuva, Russia
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29 245 (Khondergei Formation (Sennikov et al., 2015)) as well as from strata of the lower
30
31 246 Wenlock Upper Tarkhata Subformation (Gorny Altai, Russia (Sennikov et al., 2015)).
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36 247 **Holotype**—An ontogenetically mature scale (T-003) from the Baital Formation of
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38 248 Tuva, Russian Federation (Karatajūtė-Talimaa, 1973).
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41 249 **Referred material**—Over 200 isolated scales that were examined for this study
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43 250 are deposited in the Lapworth Museum of Geology, University of Birmingham, UK.
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47 251 **Revised diagnosis**—*Elegestolepis* species possessing small (up to c. 1 mm
48
49 252 long) scales that have deltoid to lanceolate, trilobate crowns and develop moderately to
50
51 253 strongly constricted necks and bulbous bases during their ontogenesis. Scale odontode
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53 254 composed of dentine tissue with multipolar odontocyte lacunae from which emerge
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3 255 canaliculi with dendroid branching. Cellular basal bone with layered mineralised-fibre
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6 256 organization.

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9 257 **Remarks**—Certain differences were noted between the scale histology of *E.*
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11 258 *grossi* scales and the original descriptions of Karatajūtė-Talimaa (1973). Some of these
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13 259 concern the nature of the most superficial portion of the scale crown and neck,
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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
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20 262 (Ørvig, 1967; Smith and Miles, 1971; Sire et al., 2009). This ‘enameloid’ layer is found
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22
23 263 not to be a persistent feature of *E. grossi* scales, and even when present it appears
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25 264 discontinuous across most of the upper crown surface (Fig. 5A–E), contrary to previous
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28 265 depictions (Karatajūtė-Talimaa, 1973: fig. 2a, b and Sire et al., 2009: fig. 10b). The layer
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30 266 is instead most prominent around the scale neck (Fig. 5A, C–E) and can extend all the
31
32 267 way down to the level of the basal bone (Fig. 5C). This distribution is contrary to that of
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35 268 single crystalline enameloid in neoselachian scales, where it is confined mainly to the
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37 269 upper crown region (Johns et al., 1997). Furthermore, the architecture of the superficial
38
39 270 crown region cannot be recognised in any of the known enameloid structural types
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42 271 (Johns et al., 1997; Sansom et al., 2005; Gillis and Donoghue, 2007; Guinot and
43
44 272 Cappetta, 2011; Andreev and Cuny, 2012), but instead resembles that of the crown
45
46 273 dentine and is regarded as such. The more porous appearance of the surface dentine is
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49 274 likely to be diagenetically induced and/or due to alteration of the original tissue
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51 275 microstructure by preparation of the specimens with unbuffered acetic acid (even in low
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54 276 concentration, the latter has been shown to damage the phosphatic tissues of conodont
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56 277 elements (Jeppsson et al., 1985; Jeppsson and Anehus, 1995).

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3 278 This study also demonstrates the presence of not previously identified faint
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5
6 279 depositional lines (Fig. 5G) in the basal bone of *E. grossi* scales, although growth of the
7
8 280 bone tissue has been inferred from specimens in different stages of development
9
10 281 (Karatajūtė-Talimaa 1973, 1998). The lamellae, demarcated by the depositional lines
11
12 282 produced by change in orientation of the matrix's crystalline fibres, have convex down
13
14 283 profiles common for the scale bases of lower vertebrates (Ørvig, 1966; Zangerl, 1968;
15
16 284 Denison, 1979; Burrow and Turner, 1998, 1999; Qu et al., 2013).
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21 285

22
23
24 286 Genus *ELLESMEREIA* Vieth, 1980

25
26
27 287 **Included species**—*Ellesmereia schultzei* Vieth, 1980

28
29
30 288 **Remarks**—*Ellesmereia* (Fig. 3B) was assigned to the Elasmobranchii by Vieth
31
32 289 (1980) despite being recognized to possess an *Elegestolepis*-type of scale
33
34 290 morphogenesis (Reif, 1978; Karatajūtė-Talimaa, 1992) that is atypical for an
35
36 291 elasmobranch, and consequently it is placed here within the *Elegestolepidida*. Mature
37
38 292 *Ellesmereia* scales also possess a canal system architecture (Vieth, 1980: fig. 26)
39
40 293 closely resembling the vascularization of *Elegestolepis* and *Deltalepis* gen. nov., and for
41
42 294 these reasons the three taxa are united at a familial level.
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49
50 296 Genus *DELTALEPIS* gen. nov.

51
52
53 297 **Included species**—*Deltalepis magna* gen. et sp. nov. (type species) and
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55 298 *Deltalepis parva* gen. et sp. nov.
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3 299 **Derivation of name**—From ‘delta’ (alluding to the resemblance of the scale
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5
6 300 crown to the Greek letter Δ) and ‘lepis’, scale in Greek.

7
8
9 301 **Diagnosis**—Elegestolepidids whose scales possess lobed crowns ornamented
10
11 302 by tuberculate ridges. Crown lobes and furrows extend down the anterior face of the
12
13 303 scale neck (Figs. 7, 8).

14
15
16 304 **Remarks**—The material referred here to *Deltalepis* gen. nov. has not previously
17
18
19 305 been formally described or figured, although was considered to belong to the genus
20
21 306 *Elegestolepis* by Karatajūtė-Talimaa et al. (1990) and Karatajute-Talimaa and
22
23 307 Novitskaya (1997) in their work on the mongolepid taxa from the Chargat Formation.
24
25 308 *Deltalepis* gen. nov. scales possess crown morphology, ornamentation and pulp cavity
26
27 309 branching pattern that differentiate them from *Elegestolepis* and *Ellesmereia*, and
28
29 310 therefore require the erection of a new taxon. This distinction and the erection of two
30
31 311 *Deltalepis* species is based on the documented intra- and inter-generic variation of
32
33 312 trunk-scale morphology (e.g. crown shape, number of crown ridges/lobes and
34
35 313 ornamentation) in Recent neoselachian Families (Reif, 1985; Compagno, 1988; Voigt
36
37 314 and Weber, 2011). Comparable differences in ornament have also been used to
38
39 315 distinguish taxa at genus level among thelodonts (e.g. *Erepsilepis* (Märss et al., 2006))
40
41 316 and mongolepid chondrichthyans (*Shiqianolepis* and *Rongolepis* (Sansom et al., 2000)).
42
43 317 Ridged lobes are also a feature in the putative chondrichthyan taxon *Areyongalepis*
44
45 318 *oervigi* (Young, 1997, 2000) known solely from micro-remains from the Darrivilian
46
47 319 Stokes Siltstone (Amadeus Basin, Northern Territory, Australia). The crown necks and
48
49 320 bases of elegestolepid scales, however, are not developed in *Areyongalepis* elements,
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3 321 and the latter do not demonstrate identifiable vertebrate mineralised tissues (Young,
4
5 322 1997), making their systematic position uncertain for the time being.
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9 323

10 324 *DELTALEPIS MAGNA* sp. nov.

11
12 325 (Figs. 3C, 6, 8A–B, 9D–F)
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16 326 **Derivation of name**—From the feminine form of the Latin word for large,
17
18 327 referring to the scale size of the species relative to that of *D. parva* gen. et sp. nov.
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21 328 **Locality and horizon**—The type and only known locality for *D. magna* is 80 km
22
23 329 north of Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All
24
25 330 specimens come from sample P-16/3 collected from the upper Llandovery–lower
26
27 331 Wenlock (Salhit regional Stage) horizons of the Chargat Formation (Ørvig, 1977;
28
29 332 Karatajūtė-Talimaa et al., 1990).
30
31

32
33 333 **Holotype**—An isolated, presumably trunk, scale BU5269 (Figs. 3C, 6A–C).
34
35

36 334 **Referred material**—Six isolated scales (BU5269–BU5274).
37
38

39 335 **Diagnosis**—*Deltalepis* species possessing scales with deltoid to elliptic crowns
40
41 336 divided into three to five discrete lobes by posteriorly widening grooves. Parallel
42
43 337 tuberculate ridges developed on the undersurface of the crown. The rami of the pulp
44
45 338 cavity formed inside the scale crown connect directly to the main pulp canal.
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53 340 **Description**
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3 341 **Morphology**—Scales possess monodontode crowns with ovate to acuminate
4
5
6 342 outlines (Fig. 6) that are 500–700 μm long and 400–700 μm wide. The crown surface
7
8 343 displays a complex topography that is produced by three to five lobes separated by
9
10 344 deeply recessed inter-lobe regions (Fig. 6A–C, E, G, H). The lobes are lanceolate-
11
12 345 shaped and can exhibit slight divergence towards the posterior of the scale. Their
13
14
15 346 surface is ornamented by sub-parallel tuberculate ridges (up to 8 per lobe) that are
16
17 347 absent from the smooth-faced inter-lobe segments of the crown. Longitudinally directed
18
19
20 348 ridges are similarly developed on the undersurface of the crown (Fig. 6F, I, J), and
21
22 349 these demonstrate regular spacing across its width.
23
24

25 350 The crown transitions into an unornamented narrow neck (down to a third of the
26
27 351 maximal crown width) that is located at the anterior of the scale, overhung on all sides
28
29 352 by the crown. The lower portion of the neck is either gently curved outwards or flares
30
31 353 out to form an ellipse-shaped pedicle. In specimens with a developed pedicle support
32
33 354 (Fig. 6E–G, I, J) the posterior face of the neck is pierced by a single centrally positioned
34
35 355 foramen (Fig. 6F) with a diameter of c. 30–40 μm . The lower pedicle surface of some
36
37 356 specimens is deeply indented (Fig. 6I) and penetrated by the scale’s canal system,
38
39 357 whereas in others it is nearly flat (Fig. 6J), exhibiting only a greatly constricted opening
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41
42 358 of the pulp.
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47 359 **Histology**—The scale odontodes are composed solely from a highly vascular
48
49 360 tubular dentine (Fig. 8A, B). The canaliculi of the dentine have a coiled appearance and
50
51 361 display a tangled organization as well as extensive ramification along their length (up to
52
53 362 c. 20 μm). In the upper portion of the crown, the canalicular network emerges from a
54
55 363 complex of horizontally and vertically branched, interconnected, small-calibre dentine
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3 364 canals (diameter of c. 5–25 μm ; Fig. 9D). The latter are most prominent inside the
4
5 365 crown lobes where they associate with and connect to branches (c. 30–60 μm in
6
7
8 366 diameter) of the pulp canal. For most of their length the pulp branches extend parallel
9
10
11 367 the crown surface, before curving basally to merge (Fig. 9F) into a single pulp canal (c.
12
13 368 60–90 μm wide) inside the scale neck. From the posterior of the pulp issues an
14
15 369 unbranched horizontal canal (c. 70 μm long; Fig. 9F) that opens on the scale neck
16
17
18 370 surface. Separate from the pulp cavity system, the posterior half of the scales houses
19
20 371 numerous closely spaced (up to c. 10 μm apart) dentine canals (10–20 μm in diameter)
21
22 372 whose paths parallel that of the lower crown surface (Fig. 9E). The lower ends of these
23
24 373 canals ramify inside the scale neck before either exiting the scale basally (Fig. 9E) or
25
26 374 ending blindly inside it.

27
28
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30 375 The tissue (c. 40 μm thick) closing off the lower pedicle opening displays an
31
32 376 optically discernable boundary with the overlying dentine (Fig. 8A), but it could not be
33
34 377 ascertained whether it constitutes a distinct tissue type.

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41 379 *DELTALEPIS PARVA* sp. nov.

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43 380 (Figs. 3D, 7, 8C–D, 9G–J)

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46 381 **Derivation of name**—From the feminine form of the Latin word for small,
47
48 382 referring to the scale size of the species relative to that of *D. magna* gen. et sp. nov.

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51 383 **Locality and horizon**—The type and only known locality situated 80 km north of
52
53 384 Lake Khar-Us, north-western Mongolia (Karatajūtė-Talimaa et al., 1990). All specimens
54
55 385 come from the upper Llandovery–lower Wenlock (Salhit regional Stage) horizons
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3 386 (sample P-16/3) of the Chargat Formation (Karatajūtė-Talimaa et al., 1990; Žigaitė et
4
5 387 al., 2011).

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9 388 **Holotype**—An isolated, presumed trunk, scale BU5275 (Figs. 3D, 7A, B).

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

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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.

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25 394
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28 395 **Description**

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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.

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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)

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3 407 with a diameter of 20–35 μm . A canal opening is also present on the lower pedicle
4
5
6 408 surface (Fig. 7H), while a row of elliptical foramina of laterally decreasing diameter (from
7
8 409 70 μm to 40 μm in Fig. 7G) mark the lower face of scales lacking a pedicle attachment.
9

10
11 410 **Histology**—Tubular dentine tissue (Fig. 8C, D) is the only component of the
12
13 411 scale crown. The dentine canaliculi are less than 2 μm in diameter and up to c. 20 μm
14
15 412 long, with arborescent branching (Fig. 8D) that gives the tubular system a tangled
16
17 413 appearance. Inside the lobed regions of the crown, the tubules connect to a network of
18
19 414 vertically (c. 5–10 μm wide and 25–40 μm long) and horizontally (c. 5 μm wide) oriented
20
21 415 dentine canals (Fig. 8C; Fig. 9J) that are confluent with branches of the pulp cavity.
22
23 416 These pulp branches (from c. 20 μm to c. 45 μm in diameter; Fig. 9G–J) occupy the
24
25 417 crown lobes (one canal per lobe) before curving basally to merge with one another
26
27 418 inside the scale neck. The three medial branches emerge from the main pulp canal—
28
29 419 confined to the scale neck/pedicle—whereas the more lateral ones are only indirectly
30
31 420 connected to it through the medial rami (Fig. 9I). Near its lower end, the main pulp canal
32
33 421 gives off a short neck canal (Fig. 9I, J) that opens at the scale surface.
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40 422 Posterior of the pulp-cavity canal system the scale houses a number (c. 15) of
41
42 423 mutually parallel, ascending dentine canals (Fig. 9G) with diameters between c. 10 μm
43
44 424 and 15 μm . These canals follow the posterior scale profile without establishing
45
46 425 connections at any point with the pulp cavity and terminate basally at the lower pedicle
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48 426 surface.
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DISCUSSION

429

430 Chondrichthyan Characteristics of Elegendolepid 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), Elegendolepidida (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.

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3 451 The integumentary skeleton of thelodonts demonstrates perhaps the most
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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).
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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 Egestolepida in the middle Llandovery. Nevertheless, during ontogenesis
26
27 462 egestolepid 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 egestolepids, whereas the dermal odontode papillae of thelodonts have been
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3 473 interpreted to form superficially at the epithelium-mesenchyme boundary and therefore
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5
6 474 not to intersect the vascular system (Karatajūtė-Talimaa, 1978; Märss et al., 2007).
7
8

9 475 Outside the Chondrichthyes, other derived gnathostomes regarded to possess
10
11 476 monodontode body scales belong to the basal 'placoderm' Orders Stensioellida and
12
13 477 Antiarcha (Fig. 2; also refer to Johanson, 2002; Giles et al., 2015; Brazeau and
14
15
16 478 Friedman, 2015 and citations therein for recent vertebrate phylogenies) whose scale
17
18 479 structure is still insufficiently investigated. The available data on the squamation of
19
20
21 480 these taxa (e.g. *Stensioella* (Gross, 1962) and *Parayunnanolepis* (Upeniec, 2011; Zhu
22
23 481 et al. 2012)) provides evidence for non-growing odontodes, implying this to be a
24
25 482 plesiomorphic feature of the single-odontode scales of jawed gnathostomes.
26
27
28 483 Histological descriptions of scale hard-tissues are presently not available for the above
29
30 484 taxa, but known examples of 'placoderm' scale structure often demonstrate formation of
31
32
33 485 an osteon-rich vascular layer inside the upper portion of the basal bone (Burrow and
34
35 486 Turner 1998, 1999; Giles et al., 2013; Rücklin and Donoghue 2015). Osteon mediated
36
37 487 bone remodeling and resorption is widespread in the dermal skeleton of 'placoderms'
38
39
40 488 (Donoghue et al. 2006; Downs and Donoghue, 2009; Giles et al., 2013) and basal
41
42 489 osteichthyans (Zhu et al., 2006), but, critically, is absent from the elegendolepid skeleton
43
44
45 490 and in conventional chondrichthyans. Other characteristics placing elegendolepids with
46
47 491 the Chondrichthyes among derived gnathostomes are the pattern of scale histogenesis
48
49 492 and their hard tissue composition, both of which match those of polyodontode
50
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).
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57 495

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

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3 519 elegestolepid scales) or opening directly to the crown surface (in *Shiqianolepis* and
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5
6 520 *Rongolepis* (Sansom et al., 2000)).
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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
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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
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20
21 526 differences. Moreover, characters with a limited distribution in one of the Orders can
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
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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).
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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
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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
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54
55 540 development recognised in monodontode chondrichthyan scales from the Silurian. The
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57 541 inclusion of *Ellesmereia* into Elegestolepidida also shows that odontode growth has
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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 elegendolepid species
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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 elegendolepid 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 Elegendolepidida (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).
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CONCLUSIONS

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

583 The shared mode of scale morphogenesis unites *Elegestolepis* (Karatajūtė-Talimaa,
584 1973) with *Ellesmereia* (Vieth, 1980), *Kannathalepis* (Märss and Gagnier, 2001) and
585 *Deltalepis* gen. nov into the newly erected Order Elegestolepidida, extending the known
586 stratigraphic range of elegestolepid taxa from the Lower Silurian (middle Llandovery) to
587 the Lower Devonian (Lochkovian). Furthermore, a division of the Order into two

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3 588 Families is established upon differences in pulp cavity architecture between
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6 589 *Kannathalepis* and all the other recognised elegestolepid genera.
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970 FIGURE CAPTIONS

971

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

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

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

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3 991 (adapted from Vieth 1980:pl. 9.2); **C**, *Deltalepis magna* (holotype BU5269); **D**,
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6 992 *Deltalepis parva* (holotype BU5275). Anterior towards the bottom. (column width)
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11 994 FIGURE 4. Scales of *Elegestolepis grossi* from the Baital Formation of Tuva, Russian
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14 995 Federation; ontogenetically mature scales shown in **A**, antero-lateral (BU5285), **B**,
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16 996 lateral-crown (BU5285), **C**, lateral (BU5286) and (**D**, BU5286), (**E**, BU5287) crown
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19 997 views. **F**, postero-lateral view of BU5289 showing the single neck canal opening of the
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21 998 scale crown; **G**, postero-basal view of an ontogenetically young scale (BU5343) with not
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23 999 fully formed pedicle support; **H**, basal view of a scale (BU5343) with pedicle support at
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26 1000 an advanced stage of formation; **I**, mature scale (BU5289) in basal view exhibiting
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28 1001 bulbous basal bone. SEM micrographs. Anterior towards right in (B), towards left in (C),
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30 1002 towards the bottom in (D, E) and towards the top in (H, I); arrows indicate neck canal
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32 1003 openings, arrowhead indicates the basal opening of the main pulp canal. Scale bars
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34 1004 represent 200 μm in (A–E, G, H) and 100 μm in (F, I). (whole page width)
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41 1006 FIGURE 5. Hard tissue structure of *Elegestolepis grossi* scales from the Baital
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44 1007 Formation of Tuva, Russian Federation. **A**, vertical cross section of a scale (BU5290) in
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46 1008 early stage of bony base formation, etched in 0.5% chromium sulphate solution for 2
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48 1009 hours; **B**, detail of **A**, showing the upper medial portion of the crown; **C**, vertical
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51 1010 longitudinal section of a scale (BU5291) in advanced stage of basal bone developed
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53 1011 (ontogenetically old), etched in 0.5% orthophosphoric acid for 10 minutes; **D**, detail of
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55 1012 BU5291 depicting the lower posterior margin of the crown; **E**, detail of the anterior
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3 1013 portion of the crown of BU5291; **F**, vertical transverse section of an ontogenetically old
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5 1014 scale (BU5292); **G**, basal bone of ontogenetically old scale (BU5293) in vertical
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8 1015 longitudinal section. (B–E) SEM micrographs; (A, F, G) Nomarski interference contrast
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10 1016 micrographs. Anterior towards the right in (C–E, G); (B), base; arrowheads in (B–E)
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12 1017 demarcate the extent of artificially altered dentine, asterisks in (G) denote the borders of
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14 1018 depositional bone lamellae. Scales bars represent 100 μm in (A, C, F, G) 50 μm in (B,
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16 1019 E) and 20 μm in (D). (whole page width)
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23 1021 **FIGURE 6.** Scales of *Deltalepis magna* gen. et sp. nov. from the Chargat Formation of
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25 north-western Mongolia. Holotype specimen (BU5269, scale with a five-lobed crown
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27 and a gracile neck) in **A**, anterior, **B**, antero-lateral and **C**, crown view. **D**, scale
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29 (BU5270) with gracile neck in basal view. Scales with three-lobe crowns in **E**, anterior,
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31 1024 **F**, posterior, **G**, lateral (E–G, BU5273) and **H**, crown (BU5271) views. **I**, BU5273 in basal
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33 1025 view revealing the lower pedicle surface; **J**, basal view of a scale (BU5272) with fully
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35 1026 formed pedicle support. (A–C, H–J) SEM micrographs; (D–G) volume renderings.
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37 1027 Anterior towards the right in (B), towards the bottom in (C, H) towards the top in (D, I, J);
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39 1028 arrow indicates a neck canal opening. Scale bars represent 200 μm . (whole page width)
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48 1031 **FIGURE 7.** Scales of *Deltalepis parva* gen. et sp. nov. from the Chargat Formation of
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50 north-western Mongolia. Holotype (BU5275) in **A**, crown and **B**, anterior-crown view.
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52 1032 Scale (BU5280) with a gracile neck in **C**, anterior and **D**, posterior view. Scale (BU5277)
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54 1033 in **E**, anterior and **F**, crown view. **G**, scale (BU5278) with a gracile neck in basal view,
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3 1035 exposing the rami of the pulp canal system. Scale (BU5279) with formed pedicle
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6 1036 support in **H**, basal and **I**, postero-basal view. (A, B, E–I) SEM micrographs; (C, D)
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8 1037 volume renderings. Anterior towards the bottom in (A, F) towards the top in (G–I);
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10 1038 arrows indicate neck canal openings, arrowhead indicates the basal opening of the
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12 1039 main pulp canal. Scale bars represent 200 μm in (A–D, G) and 100 μm in (E, F, H, I).
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14 1040 (whole page width)
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21 1042 FIGURE 8. Hard tissue structure of *Deltalepis* gen. nov. **A**, longitudinal tomographic
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23 1043 slice of a *Deltalepis magna* scale (BU5273); **B**, detail of the dentine tissue at the upper
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25 1044 anterior margin of the crown of a longitudinally sectioned *Deltalepis magna* scale
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27 1045 (BU5274); **C**, longitudinal tomographic slice of a *Deltalepis parva* scale (BU5280); **D**,
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29 1046 view of the posterior portion of a *Deltalepis parva* scale (BU5282) crown immersed in
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31 1047 clove oil. (B, D) Nomarski interference contrast micrographs; (A, C) volume renderings.
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33 1048 Anterior towards the right in (A) and towards the left in (C). Scale bars represent 100 μm
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35 1049 in (A, C, D) and 50 μm in (B). (whole page width)
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44 1051 FIGURE 9. Volume renderings of the scale canal system (in red) of examined
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46 1052 elegestolepids. The scales are made translucent in all renderings, with the exception of
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48 1053 (G). **A–C**, *Elegestolepis grossi* scale (BU5284) from the Baital Formation of Tuva
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50 1054 (Russian Federation) in **A**, anterior, **B**, postero-lateral and **C**, crown (depicting the lower
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52 1055 portion of the specimen that is transversely sliced through the neck region) view. **D–F**,
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54 1056 *Deltalepis magna* scale (BU5273) from the upper Llandovery–lower Wenlock of north
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3 1057 western Mongolia in **D**, crown and **E**, posterior view and a **F**, crown view of the lower
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5 1058 portion of the same specimen sliced through the neck region. **G–J**, *Deltalepis parva*
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8 1059 specimens (BU5280 and BU5281) from the upper Llandovery–lower Wenlock of north
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10 1060 western Mongolia; **G**, BU5280 sliced transversely through the crown in crown view; **H**,
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12 1061 BU5280 in anterior view; **I**, **J**, BU5281 in **I** posterior and **J**, postero-lateral view. Anterior
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15 1062 towards the left in (B), towards the top in (C, F, G) and towards the bottom in (D);
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17 1063 arrows indicate neck canal openings, arrowheads point at the basal opening of the main
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20 1064 pulp canal. Scale bars represent 100 μm . (whole page width)
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26 1066 FIGURE 10. Characteristics of monodontode scales of recognised lower Paleozoic
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28 1067 chondrichthyans and their stratigraphic range. Pink rectangle designates elegendolepid
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30 1068 taxa. *Elegendolepis* (Karatajūtė-Talimaa, 1973 and data from this study), *Deltalepis*
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33 1069 (data from this study), *Kannathalepis* (Märss and Gagnier, 2001), *Ellesmereia* (Vieth,
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35 1070 1980), *Frigorilepis* (Märss et al., 2002, 2006), *Polymerolepis* Karatajūtė-Talimaa, 1998;
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38 1071 Hanke et al., 2013), *Lupopsyrus* and *Obtusacanthus* (Hanke and Wilson, 2004; Hanke
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40 1072 and Davis, 2012). (whole page width)
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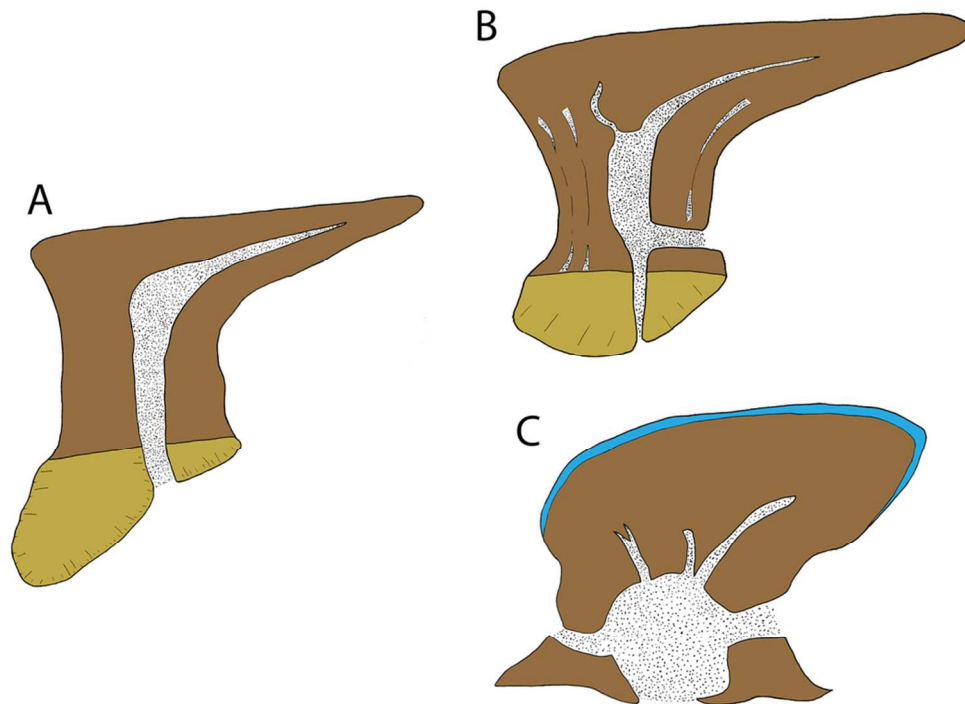


FIGURE 1. Diagrammatic representation of monodontode scale types in A, the Thelodonti and (B, C) the Chondrichthyes. A, a *Thelodus calvus* scale (adapted from Märss and Karatajūtė-Talimaa 2002: fig. 15F) exemplifying the thelodont morphogenetic type; B, the *Egestolepis* morphogenetic type represented 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)

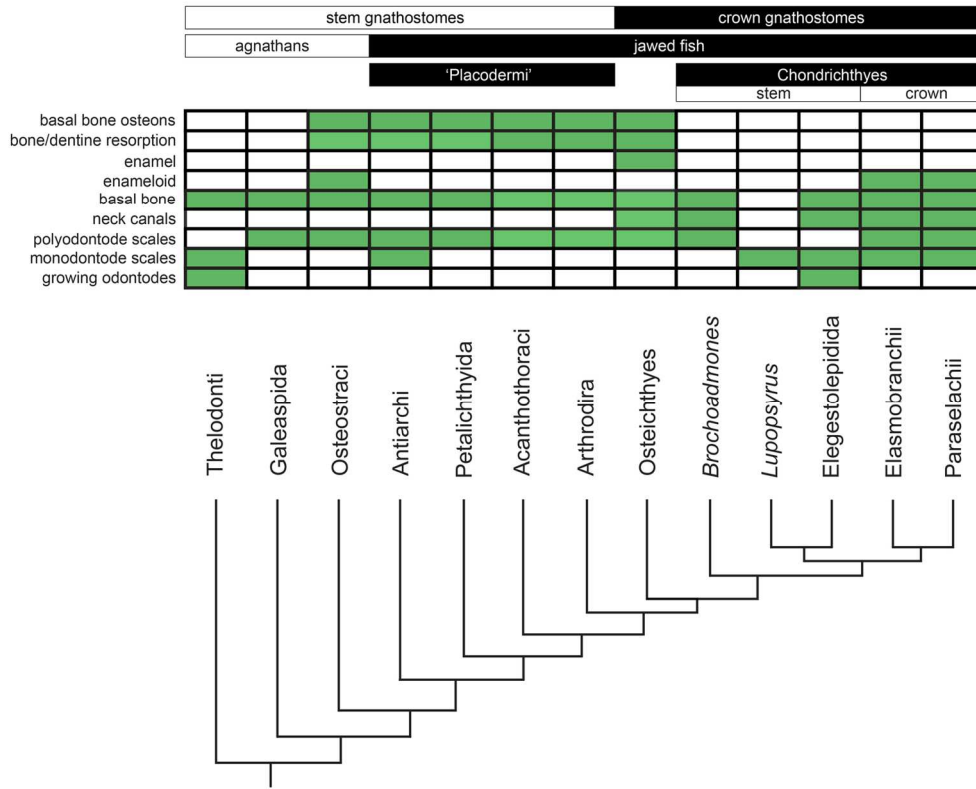


FIGURE 2. Distribution of relevant to the study scale characters among select groups of Paleozoic gnathostomes. Tree topology reconstructed from published phylogenies of total-group Chondrichthyes (Grogan et al., 2012) and vertebrates (Sire et al., 2009; Giles et al., 2013, 2015), with the position of 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
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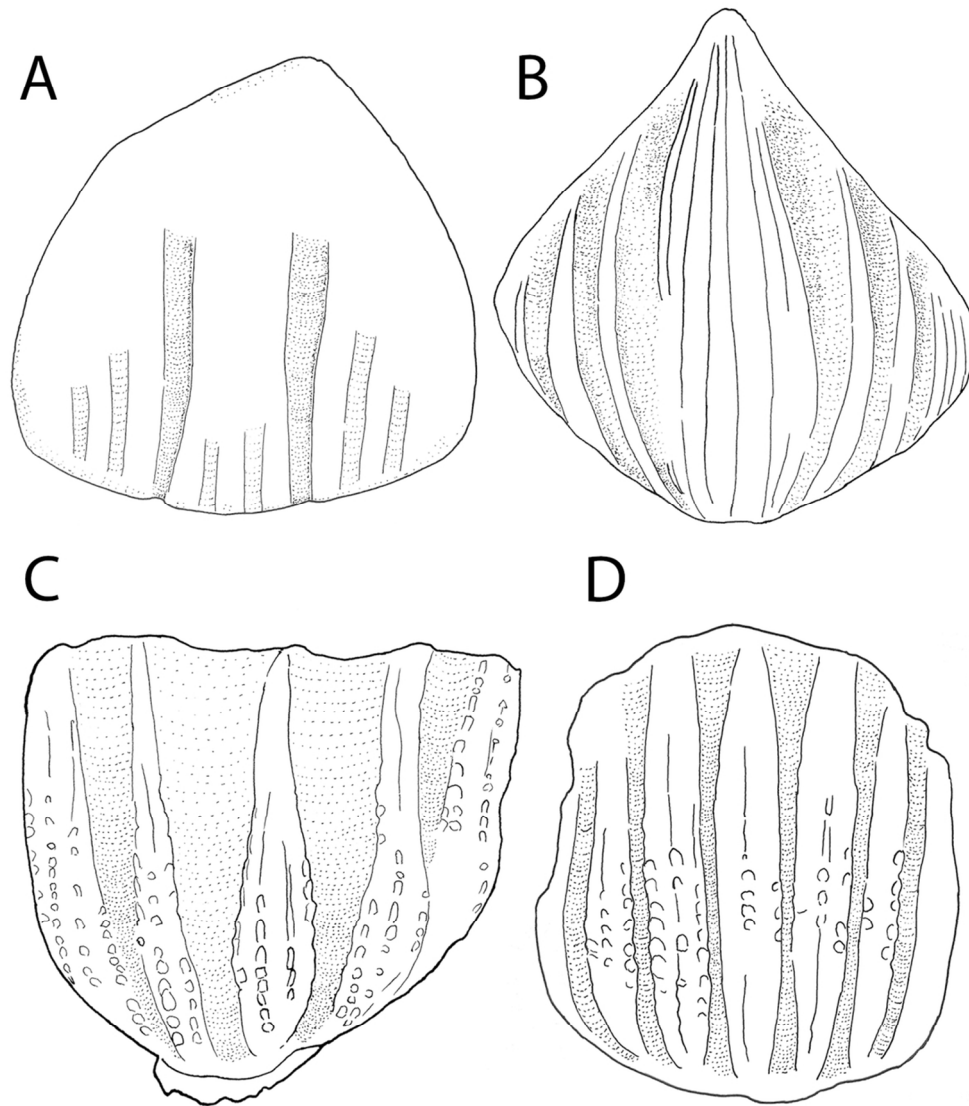


FIGURE 3. Line drawings depicting the range of crown-surface morphologies in egestolepid scales. A, *Elegestolepis grossi* (BU5284); B, *Ellesmereia schultzei* (adapted from Vieth 1980:pl. 9.2); C, *Deltalepis magna* (holotype BU5269); D, *Deltalepis parva* (holotype BU5275). Anterior towards the bottom.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

Fig. 3

101x116mm (300 x 300 DPI)

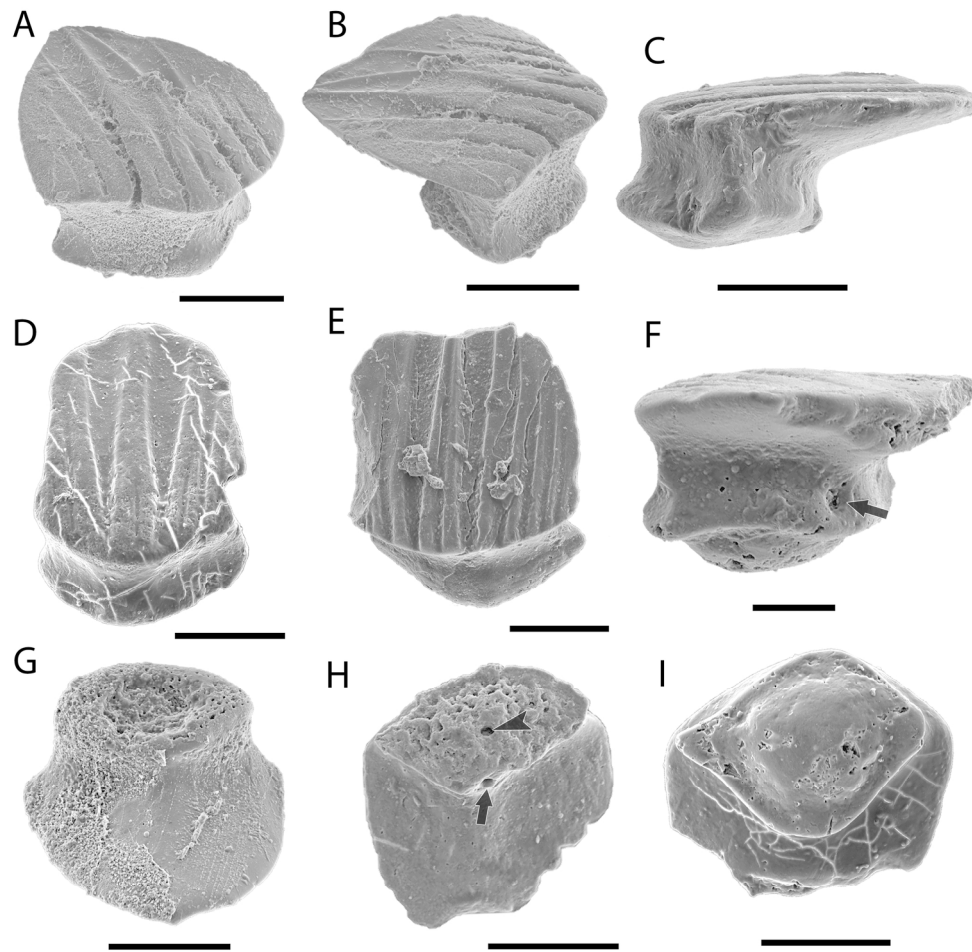


FIGURE 4. Scales of *Elegestolepis grossi* from the Baital Formation of Tuva, Russian Federation; ontogenetically mature scales shown in A, antero-lateral (BU5285), B, lateral-crown (BU5285), C, lateral (BU5286) and (D, BU5286), (E, BU5287) crown views. F, postero-lateral view of BU5289 showing the single 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)

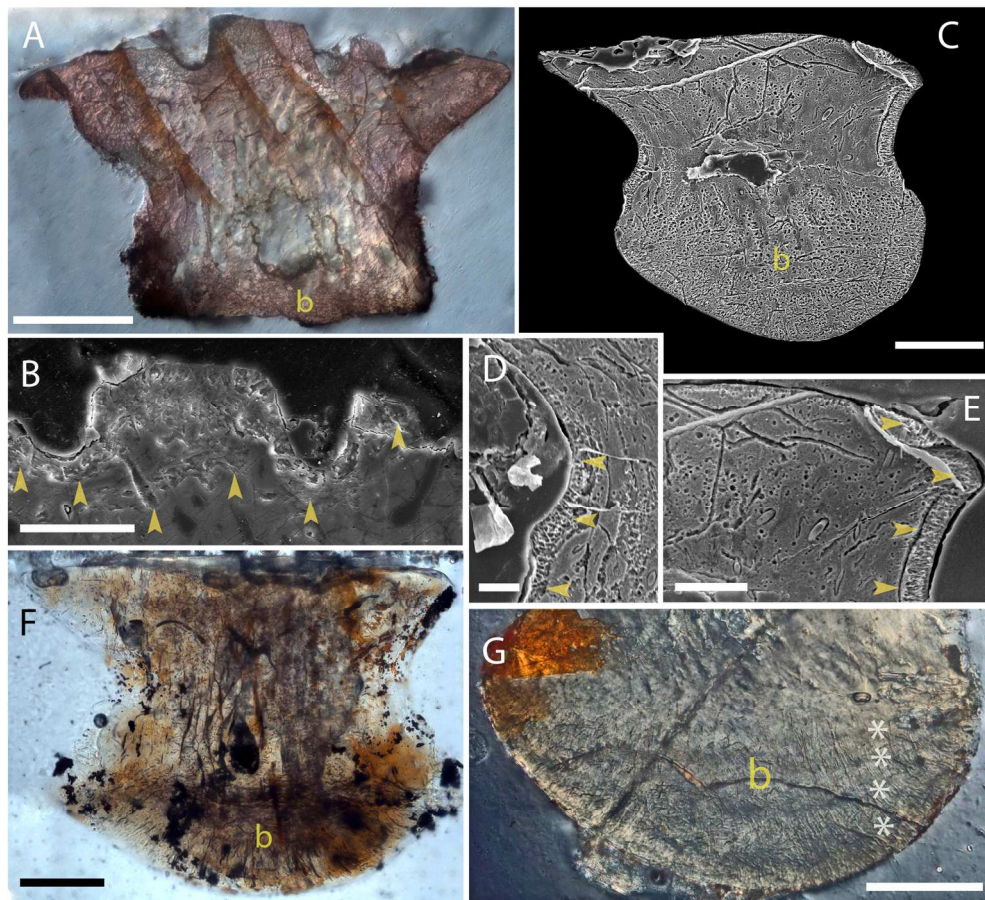


FIGURE 5. Hard tissue structure of *Elegestolepis grossi* scales from the Baital Formation of Tuva, Russian Federation. A, vertical cross section of a scale (BU5290) in early stage of bony base formation, etched in 0.5% chromium sulphate solution for 2 hours; B, detail of A, showing the upper medial 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. 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)

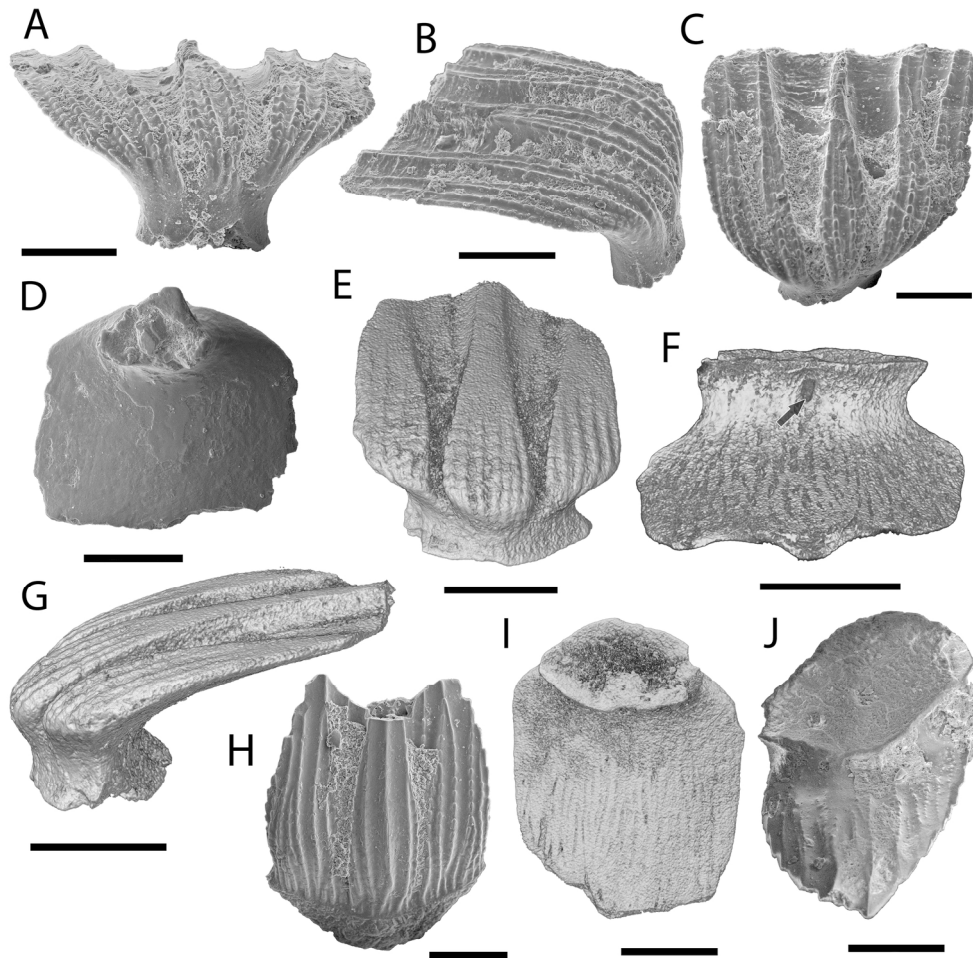


FIGURE 6. Scales of *Deltalepis magna* gen. et sp. nov. from the Chargat Formation of north-western Mongolia. Holotype specimen (BU5269, scale with a five-lobed crown and a gracile neck) in A, anterior, B, antero-lateral and C, crown view. D, scale (BU5270) with gracile neck in basal view. Scales with 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)

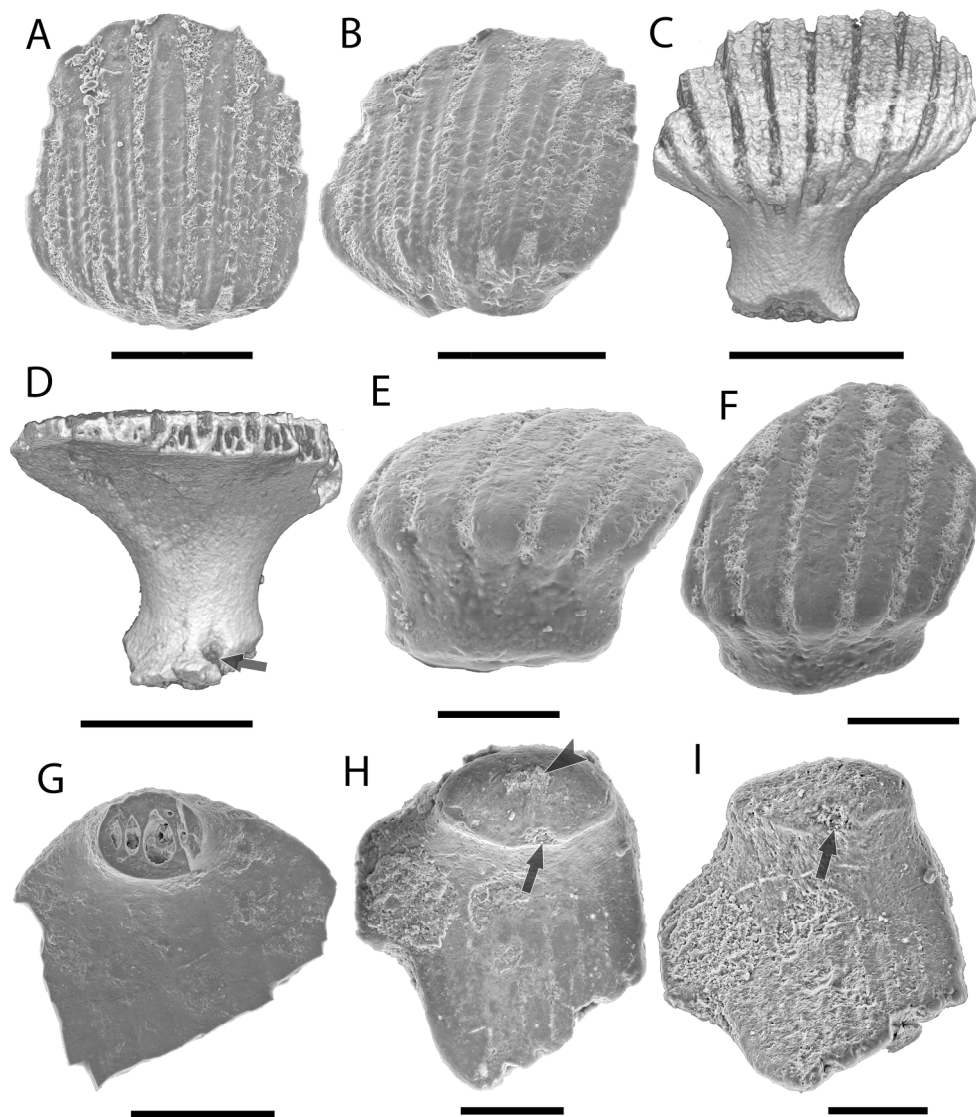


FIGURE 7. Scales of *Deltalepis parva* gen. et sp. nov. from the Chagat Formation of north-western Mongolia. Holotype (BU5275) in A, crown and B, anterior-crown view. Scale (BU5280) with a gracile neck in C, anterior and D, posterior view. Scale (BU5277) in E, anterior and F, crown view. G, scale (BU5278)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

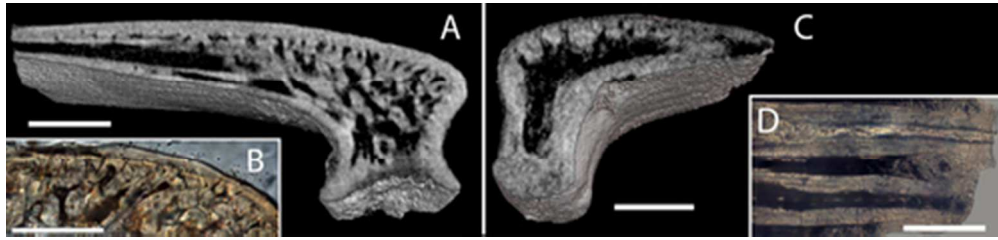


FIGURE 8. Hard tissue structure of *Deltalepis* gen. nov. A, longitudinal tomographic slice of a *Deltalepis magna* scale (BU5273); B, detail of the dentine tissue at the upper anterior margin of the crown of a longitudinally sectioned *Deltalepis magna* scale (BU5274); C, longitudinal tomographic slice 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)

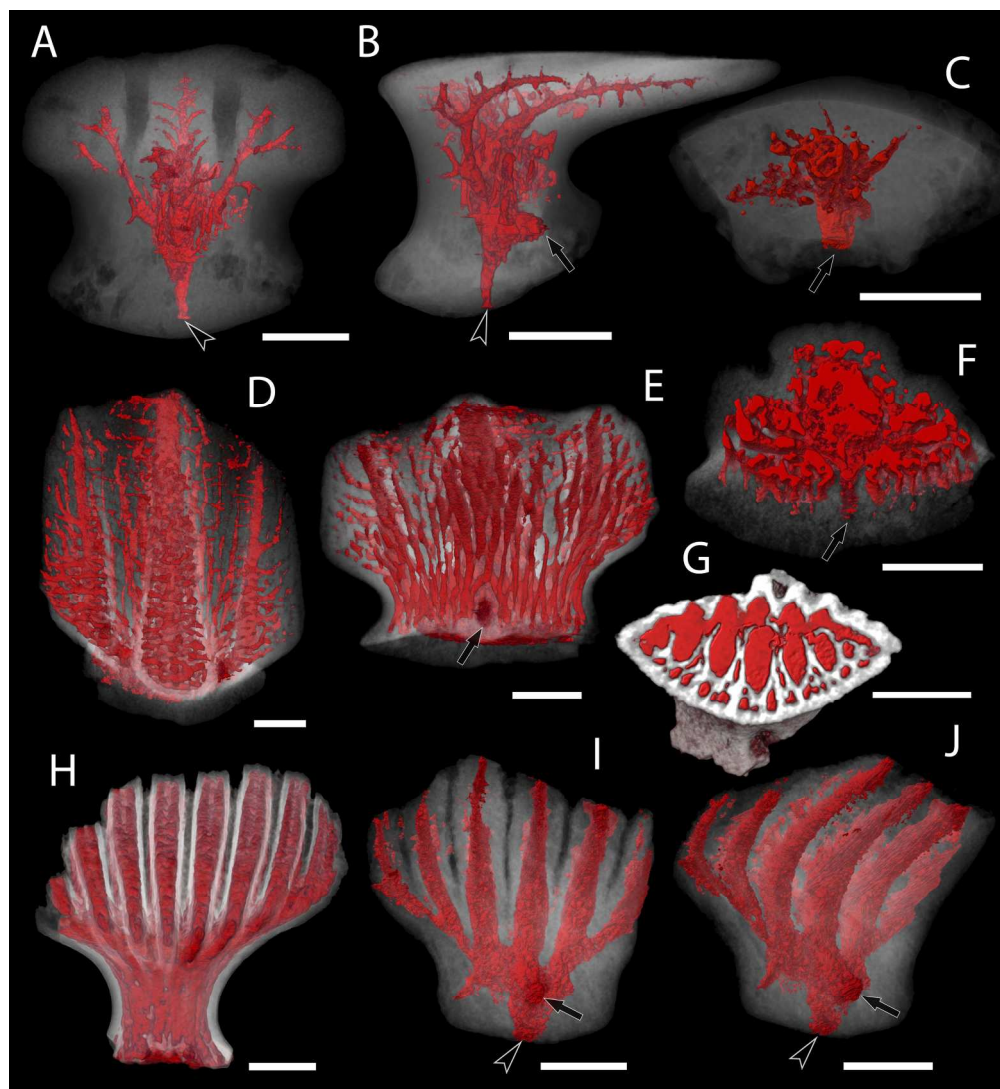


FIGURE 9. Volume renderings of the scale canal system (in red) of examined elegestolepids. The scales are made translucent in all renderings, with the exception of (G). A–C, *Elegestolepis grossi* scale (BU5284) from the Baital Formation of Tuva (Russian Federation) in A, anterior, B, postero-lateral 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)

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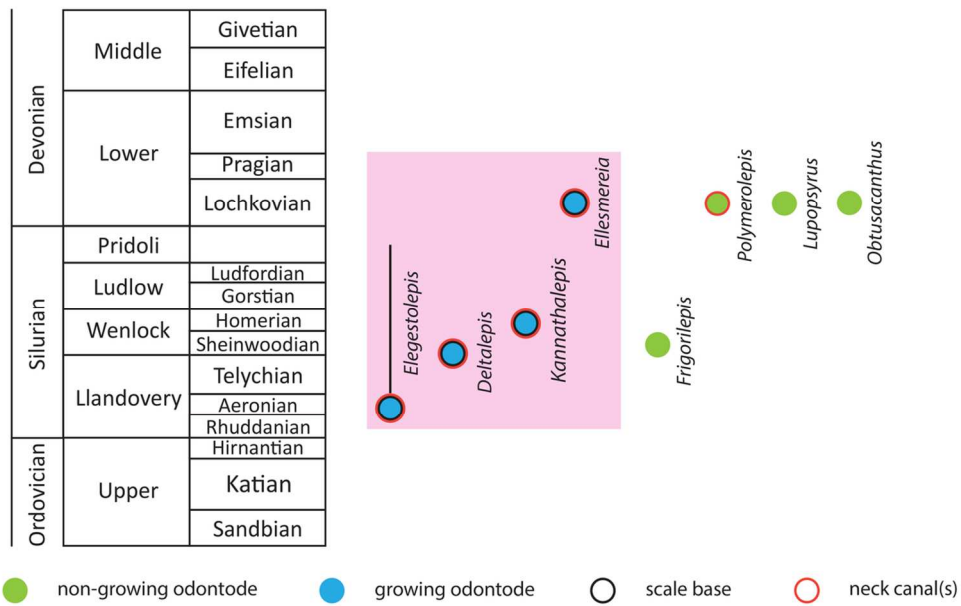


FIGURE 10. Characteristics of monodontode scales of recognised lower Paleozoic chondrichthyans and their stratigraphic range. Pink rectangle designates elegestolepid taxa. *Elegestolepis* (Karatajūtė-Talimaa, 1973 and data from this study), *Deltalepis* (data from this study), *Kannathalepis* (Märss 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)