

Chondrenchelys problematica (Traquair, 1888) redescribed: a Lower Carboniferous, eel-like holocephalan from Scotland

John A. Finarelli¹ and Michael I. Coates²

¹ School of Biology and Environmental Science, Science Centre West and UCD Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland
Email: john.finarelli@ucd.ie

² Department of Organismal Biology and Anatomy, University of Chicago, 1027 E 57th St, Chicago, IL 60637, USA
Email: mcoates@uchicago.edu

ABSTRACT: *Chondrenchelys problematica*, from the Viséan (Holverian) of Scotland, is the earliest holocephalan known from extensive cranial and postcranial material. Here, we provide a comprehensive new description of this taxon using three new specimens, in which we observe many morphological features for the first time. Much of the cranial morphology is closer to that of living chimaeroid holocephalans than was previously appreciated. For this reason, we provide original figures illustrating the chondrocranium of a hatchling *Callorhynchus milii* demonstrating these similarities. In *Chondrenchelys*, although the jaw articulation is positioned at the posterior margin of the orbit, the high-walled lamina orbitonasalis and densely-mineralised antorbital crest provide evidence for forward rotation of the jaw adductor musculature. Preserved foramina for the efferent superficial ophthalmic nerves show that the sensory organs on the rostrum were enervated in a manner similar to modern sharks, with the ophthalmic nerves not enclosed in an ethmoid canal, as in modern holocephalans. The conjunction of numerous distinctly holocephalan features with those that are otherwise general to Chondrichthyes demonstrates a decoupling of several of the structural conditions that characterise the distinctive morphological complex of the extant holocephalan skull. The anguilliform postcranium is more elongate than previously reconstructed, and it is now clear that the axial skeleton extended beyond the posterior extremity of the elongate dorsal fin. Morphological characters are reviewed with a view to further phylogenetic analyses. We recommend using the appearance of *Chondrenchelys* at 336.5 Ma as a hard minimum age for the last common ancestor of elasmobranchs and chimaeroids, because of its secure association with other holocephalans, and current uncertainties concerning elasmobranch stem lineage membership.



KEY WORDS: Chondrichthyes, Holocephali, node calibration, Palaeozoic

In this study, we provide a new, comparative description of *Chondrenchelys problematica* (Traquair 1888b) (Fig. 1) from the Lower Carboniferous (Viséan) of Scotland. *C. problematica* is the earliest undoubted holocephalan (Moy-Thomas 1935; Patterson 1965) known from both substantial cranial and postcranial material. Three exceptionally preserved specimens, discovered by Mr. S. P. Wood, are central to our project. Two of the specimens are new to science, while the third was previously misidentified as an actinopterygian. The principal pair of specimens derives from the Mumbie Quarry exposure (Coates & Gess 2007) of the Glencartholm fish beds (Schram 1983; Dineley & Metcalf 1999). Each of the fossils has been prepared to a higher standard than previously described specimens of *C. problematica* (Traquair 1888b; Moy-Thomas 1935), facilitating a more detailed analysis of this remarkable fish. Such data-rich material contributes directly to our broader aims of improving the understanding of early chondrichthyan diversity, and broadening the range of morphological data available for phylogenetic analyses of early chondrichthyans.

Extant Chondrichthyes (cartilaginous fish) comprises two reciprocally monophyletic clades, Elasmobranchii (sharks, skates, and rays) and Holocephali (chimaeras: including ratfish, rabbitfish, spookfish and elephant sharks) (Maisey 1984; Winchell *et al.* 2002; Inoue *et al.* 2010; Licht *et al.* 2012). Crown-clade holocephalans (chimaeroids) are characterised by a suite of highly

distinctive apomorphies, including the complete fusion of the palatoquadrate with the neurocranium (holostyly), a dentition of large tooth plates, a “complete” hyoid arch possessing a pharyngohyal cartilage (but see: Maisey 1984; Didier 1995), branchial arches positioned under the otic capsule with an associated anterior displacement of the mandible, large, narrowly-separated orbits positioned high on the cranium, and a polyspondylous axial skeleton composed of chordacentra (Dean 1906; de Beer & Moy-Thomas 1935; de Beer 1937; Patterson 1965; Didier 1995, Stahl 1999; Gillis *et al.* 2011). There is also a high degree of sexual dimorphism in holocephalans, with pre- and postpelvic claspers and a frontal clasper organ (tenaculum) in males (Stahl 1999).

Monophyly of the crown clades of Chondrichthyes, Elasmobranchii and Holocephali is not in doubt: unequivocal support from both molecular and morphological data exists for each of these clades. However, the early fossil membership of each of these groups, especially as concerns the stem lineages preceding the crown-clade radiations, is uncertain. This ambiguity is linked to a more general problem in early chondrichthyan phylogeny: fossil shark-like fishes that are not holostylic have historically been classified as elasmobranchs. The result of this circular criterion for taxonomic assignment is an elasmobranch–holocephalan split that is deep within the chondrichthyan tree (Maisey 2012).

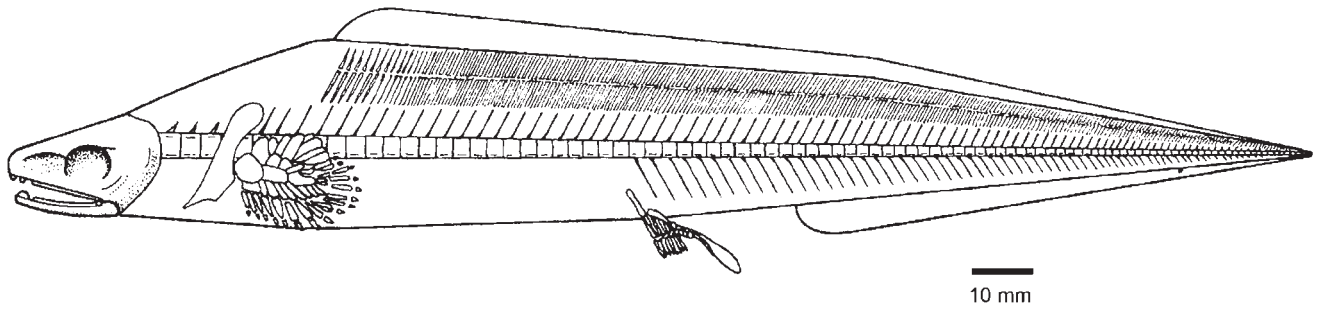


Figure 1 Traditional reconstruction of *Chondrenchelys problematica*, from Moy-Thomas (1935, text-fig.12), as used and adapted in many standard references.

Lack of any substantial evidence to support such a profound divergence led Maisey (2012) to conclude that “Elasmobranchii” should refer solely to the crown-clade and its immediate fossil relatives, while also commenting, “considerable progress has been made in elucidating the evolution of holocephalans.” In fact, published phylogenies of fossil holocephalans show little agreement. Grogan *et al.*'s (2012) tree of chimaeriforms and their fossil relatives differs profoundly from Stahl (1999), and both conflict with the topology of the holocephalan taxa in Pradel *et al.* (2011). This problem persists at deeper phylogenetic levels. Symmoriids (Zangerl 1981; Maisey 2007), a distinctive and diverse group of Palaeozoic chondrichthyans, might be stem-holocephalans (Janvier 1996; Coates & Sequeira 2001), stem-elasmobranches (Coates & Sequeira 2001; Grogan *et al.* 2012) or even stem chondrichthyans (Pradel *et al.* 2011; Davis *et al.* 2012). Moreover, recent conjectures about plesiomorphic holocephalan conditions include revived comparisons with placoderm-grade fishes (Trinajstić *et al.* 2012), perhaps including *Stensioella* (Janvier 1996; Pradel *et al.* 2009b), as well as speculation that the apparent Devonian chondrichthyan *Gladbachus* might be a stem-holocephalan (Heidtke & Krätschmer 2001).

This is not to say that the current state of affairs is entirely negative. New and detailed data on Palaeozoic chondrichthyans are becoming increasingly available (Maisey 2005, 2007; Pradel *et al.* 2009a, 2011, 2014; Maisey & Lane 2010; Pradel 2010), complementing the extraordinary diversity of holocephalans from the Upper Mississippian of Bear Gulch (see: Grogan *et al.* 2012 and references therein; and classic studies by Stahl (1999) and Patterson (1965)). Additionally, the recent publication of the elephant shark genome (*Callorhynchus milii*) (Venkatesh *et al.* 2014) has promoted interest in holocephalans as a potential model system for comparative genomics (Venkatesh *et al.* 2007; Larsson *et al.* 2009), evolutionary physiology (Baker 2010, Kakumura *et al.* 2009), sensory system evolution (Davies *et al.* 2009; Niimura 2009; Callaway 2012) and the evolution of developmental regulatory mechanisms (Gillis *et al.* 2009; Mulley *et al.* 2009; Ravi *et al.* 2009; MacDonald *et al.* 2010; Oulion *et al.* 2010).

It is commonly assumed that holocephalans represent primitive conditions for jawed vertebrates, both morphologically (Carroll 1997) and genomically (Ravi *et al.* 2009; Inoue *et al.* 2010; Venkatesh *et al.* 2014). Yet, long internal branches separate the most recent common ancestor of the holocephalan crown clade from that of the chondrichthyan crown (Maisey 1984; Inoue *et al.* 2010; Licht *et al.* 2012), and the degree of lost morphologic and taxonomic diversity along each branch is unknown. Living chimaeroids are anatomically conservative, in the sense that we observe low morphologic disparity within the clade today, but this modern body plan is not representative of the morphologic diversity in early holocephalans (Patterson 1965; Pradel 2010; Finarelli & Coates 2012; Grogan *et al.* 2012). A better understanding of the skeletal anatomy of

early holocephalans, such as *Chondrenchelys*, is needed to shed further light on the evolution of chondrichthyan body plans; to corroborate inferences drawn from fossils preserved in contrasting conditions (Lund 1982; Lund & Grogan 2004); to resolve phylogenetic relationships (Brazeau 2009; Davis *et al.* 2012; Grogan *et al.* 2012; Zhu *et al.* 2013); to test hypotheses of tempo and mode of morphological and molecular evolution (Inoue *et al.* 2010; Davis *et al.* 2012; Licht *et al.* 2012; Venkatesh *et al.* 2014); and to inform hypotheses of evolutionary developmental biology (Gillis *et al.* 2009; Ravi *et al.* 2009; Oulion *et al.* 2011) in this species-poor, but fundamental division of living vertebrate diversity.

1. History and context

1.1. History of discovery, previous interpretations and likely related fossil material

Traquair (1888b) erected *Chondrenchelys problematica* on the basis of specimens from Glencartholm, Scotland. Moy-Thomas (1935) re-described *Chondrenchelys* in detail, providing the standard reconstruction (Fig. 1). This was reviewed briefly by Patterson (1965), and has subsequently been reproduced in numerous texts, notably Stahl's (1999) handbook on the Holocephali. *Chondrenchelys* is allied with holocephalans based on its fused tooth plates and holostylic skull (Moy-Thomas 1935; Patterson 1965; Stahl 1999). Lund (1982) re-described key anatomical features of *Chondrenchelys* in his comparative description of the slightly younger holocephalan *Harpagofututor völselhorhinus* from the Bear Gulch fauna, placing both genera in the Family Chondrenchelyidae (Berg 1940), based on their anguilliform (eel-like) body plans, and general similarities in the morphologies of the pectoral fin and tooth plates.

To date, *Chondrenchelys* remains monotypic, although Ginter & Sun (2007) provisionally assigned isolated tooth plates from China to *Chondrenchelys* sp. The morphology of the dentition and inferred mode of dental growth in *Chondrenchelys* was completely revised (Finarelli & Coates 2012), based upon specimens that we further describe here. In addition, isolated tooth plates matching known chondrenchelyids include those of the ichthyolith genus *Platyxystrodus* (Hay 1899), as reviewed by Lund (1982, table 1) and Stahl (1999, fig. 46 A–J). These range stratigraphically from the Lower to Upper Carboniferous of Great Britain, Northern Ireland, Belgium, North America and Russia. *Xystrodus striatus* (McCoy 1855) (now *Platyxystrodus*), specimens GS 48785–48788 of the British Geological Survey collections at Keyworth (UK), originating from the Carboniferous Limestone series of Cumbria and Northumberland, England, are strikingly similar to the lower posterior tooth plates of *Chondrenchelys*.

1.2. Geological context and age of Mumbie Quarry

The two new *Chondrenchelys* specimens, NMS 1998.35.1 and NMS 2002.68.1, originate from the Mumbie Quarry locality

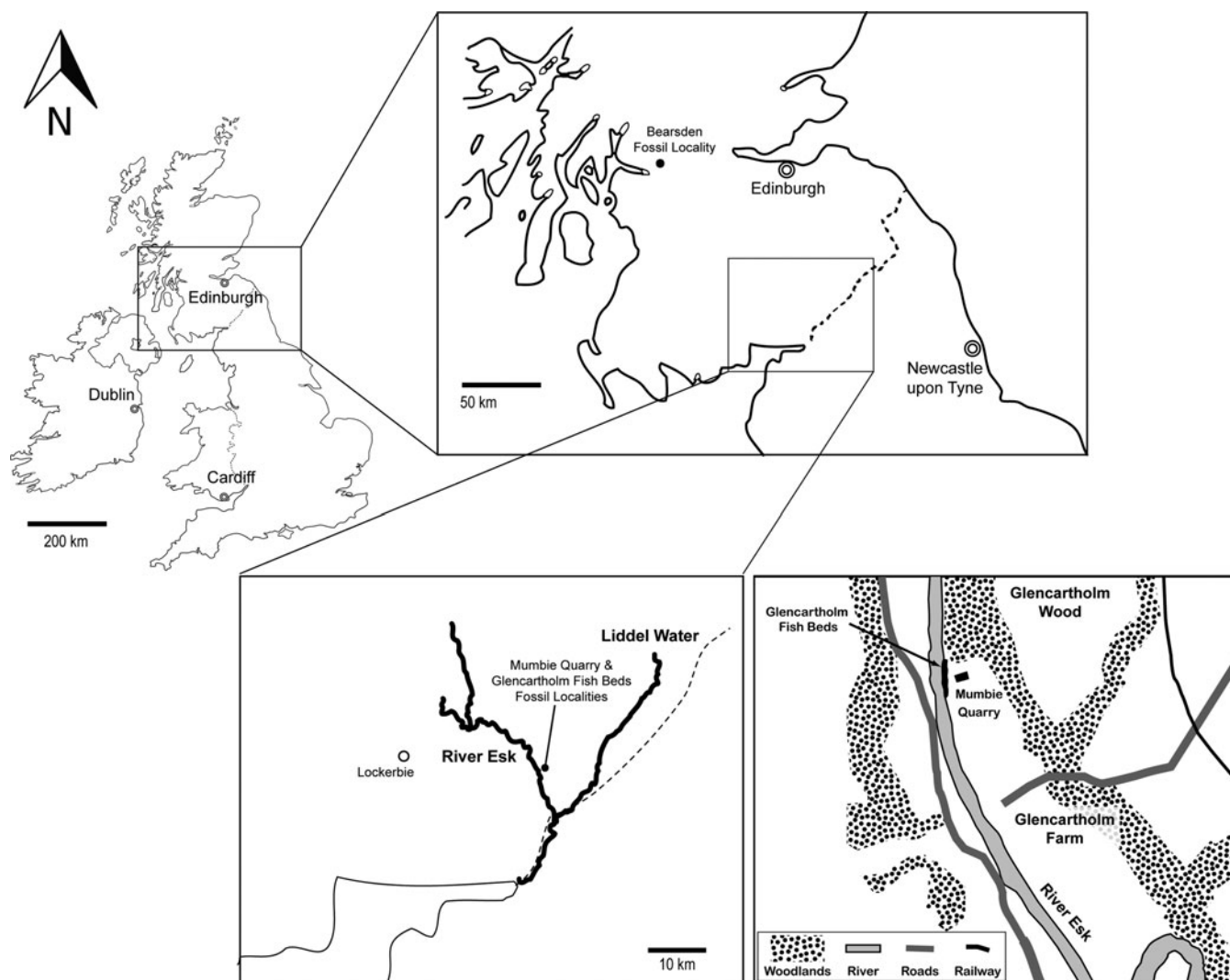


Figure 2 Map of southern Scotland detailing several important early vertebrate localities, including the Glencartholm Fish Beds, from which the original *Chondrenchelys* material described by Moy-Thomas (1935) is derived, and the Mumbie Quarry locality, opened by S. P. Wood, from which the new specimens, NMS 1998.35.1 and NMS 2002.68.1 are derived. Base maps of the Republic of Ireland and the United Kingdom from Geomapapp: <http://www.geomapapp.org>. Inset map of the Glencartholm area redrawn from fig. 9.16, in Dineley & Metcalf (1999). Glencartholm Fish Beds from Ordnance Survey Grid reference [NY 376795].

(Fig. 2), a site opened and developed by the distinguished Scottish fossil collector S. P. Wood (Coates & Gess 2007; Finarelli & Coates 2012). Mumbie Quarry is adjacent to exposures of the Glencartholm Volcanic Beds (GVB), and is laterally equivalent to the Glencartholm Fish Bed (GFB) (Dineley & Metcalf 1999) that produced the classic *Chondrenchelys* material (Traquair 1888b; Moy-Thomas 1935): Glencartholm, Dumfries District, Dumfries and Galloway Region, Scotland, Ordnance Survey grid reference [NY 376 795]. The GFB comprises a thin unit within the GVB, which is in turn part of the larger Upper Border Group of the Calciferous Sandstone (Lumsden *et al.* 1967). This unit was deposited in a near-shore marine environment (Schram 1983). The GVB span the Holkerian/Asbian regional substage boundary (Livian/Warnantian) of the early Viséan Stage, Mississippian Subsystem, Early Carboniferous (George *et al.* 1976; Cossey *et al.* 2004), approximately 336.5 Ma (Gradstein *et al.* 2012).

2. Materials

2.1. Image preparation

Photographs of fossils were prepared using a Leica DFC490 camera attached to a Zeiss Stemi SV6 microscope. Line draw-

ings were prepared using a camera lucida attachment installed for this microscope. Digital image processing was performed in Image-Pro Plus 6.2. We created multiple z-stacks of digital images, which were aligned and processed using the enhanced depth of field function. We note in the figure captions when specimens were whitened with ammonium chloride to enhance depiction of surface profile detail. Figure 6e was produced by means of reflectance transformation imaging (RTI); for technical details, see: <http://culturalheritageimaging.org/Technologies/RTI/>. Details on the settings used within the GNU-licensed RTI software application (RTIViewer) are provided in the figure caption.

2.2. Abbreviations

Explanations of anatomical abbreviations are provided in figure captions. Terminology follows Patterson (1965) and Didier (1995; Didier *et al.* 2012).

Institutional abbreviations. NMS, National Museum of Scotland, Edinburgh, Scotland, UK; RSM, Royal Scottish Museum, Edinburgh, Scotland, UK (now the NMS); BGS-GSE, British Geological Survey, Edinburgh, Scotland, UK; HM, Hunterian Museum, University of Glasgow, Glasgow, Scotland, UK; NHMUK, Natural History Museum, London,

UK; CMNH, Carnegie Museum of Natural History, Pittsburgh, PA, USA.

2.3. Additional fossil chondrichthyan taxa

To facilitate our re-description of *Chondrenchelys*, we studied additional early chondrichthyan taxa. These include Carboniferous chondrichthyans from the Serpukhovian Bear Gulch Limestone of Montana, USA, in the collections of the Carnegie Museum of Natural History, Pittsburgh, PA, USA, including, *Harpagofututor volsellorhinus* (Lund 1982). In addition, we examined specimens of *Helodus* (Agassiz 1838) in the collections of the Natural History Museum, London, UK.

2.4. Systematic palaeontology

Class Chondrichthyes (Huxley 1880)
Subclass Holocephali (Bonaparte 1832)
Family Chondrenchelyidae (Berg 1940)

Emended diagnosis. Holostylic chondrichthyans distinguished from other holocephalans by their anguilliform body, spineless, elongate dorsal fin, and dentition consisting of large, posterior tooth plates, preceded by smaller subtriangular anterior tooth plates in the upper and lower jaws. Axial skeleton composed of dorsal and ventral couplets of wedge-shaped (in lateral view) chordacentra consisting of non-tessellate calcified cartilage, supporting slender neural and haemal arches, and neural spines with long spines in the caudal region, which occasionally bifurcate. Pre-caudal axial skeleton varies from monospondylous to diplospondylous; ratio of vertebral arches to chordacentra becomes irregular within the caudal region. No synarcual is present. Pectoral fins with well-developed central axis and pre- and post-axial radials branching from close to fin base. Male pelvic fins bear a spatulate myxopterygial cartilage flanked proximally by a large, subtriangular distal radial cartilage.

Genus *Chondrenchelys* (Traquair 1888b)

Emended diagnosis. Chondrenchelyids distinguished by possession of a single pair of upper and a single pair of lower anterior tooth plates with high ridges, and an extramandibular arcade of small, low-crowned teeth. Cranium with elongated rostral region bearing a distinct trough along the dorsal midline, and widely separated orbits with subtriangular, highly mineralised antorbital crests. Postorbital rim broad and flanks, laterally, the anterior part of the otic capsule. Dorsal fin supported by two (proximal and distal) radial series. Anteriorly, the fin originates with a non-mineralised keel supporting paired denticles along the leading edge. The fin terminates posteriorly, short of the caudal extremity, with the axial skeleton terminating in a slender whip or rat-tail. Pectoral fins are sexually dimorphic. In both sexes, the fins are paddle-like; female pectoral fins are poorly preserved and distinctly smaller than male examples. The larger male pectoral fins have a dibasal articulation with the girdle, hypertrophied radials, claw-like denticles at the fin perimeter, and supported a distal fringe of short ceratotrichia.

Species *Chondrenchelys problematica* (Traquair 1888b)

Syntypes. GSE 2601 and counterpart GSE 2602, RSM 1885.54.5A and B (part and counterpart), RSM 1886.31.24 and counterpart NHMUK P.4085 (after Lund 1982).

Referred specimens. NMS 1998.35.1 (Fig. 3) is a single slab with an individual (female) approximately 185 mm in length. The body is lying on its right side, with the cranium rotated and visible in dorsolateral aspect. The dentition of this specimen was figured by Finarelli and Coates (2012, fig. 2). The axial skeleton is exceptionally complete, and a faint, organic stain

is visible for much of the body length, suggesting the outline of soft tissues at deposition. The cranium is approximately 18 mm in rostrocaudal length.

NMS 2002.68.1 (Fig. 4) preserves an individual (male) approximately 140 mm in length in part and counterpart. The anterior portion (pectoral girdle and forward) of NMS 2002.68.1 is preserved in dorsal (part) and ventral (counterpart) views. Caudal to the pectoral girdle, the axial skeleton twists to preserve the body in lateral view. The counterpart, NMS 2002.68.1-cp (Fig. 4a) preserves, uniquely, the upper dentition in oral view, the neurocranium base in ventral view, and portions of the axial skeleton, right scapulocoracoid and distal parts of the left pectoral fin. The part, NMS 2002.68.1-p (Fig. 4b), preserves the mandible and dentition in oral view (figured in part by Finarelli & Coates 2012, figs. 1B, 3A; Ginter & Sun 2007, fig. 8A), portions of the axial skeleton, the majority of the pectoral fins and parts of the pectoral girdle, the pelvic girdle and part of the pelvic fins.

HM V.7173 (Fig. 5), previously identified as the actinopterygian *Phanerosteon mirabilie*, was referred to *Chondrenchelys problematica* by Finarelli & Coates (2012). This specimen consists of a single, small slab containing the anterior trunk, pectoral and cranial skeleton. Precise locality information is not available (see: Finarelli & Coates 2012), although ostracods in the attached matrix suggest it originated from the Calciferous Sandstone: Lower Limestone Group, and probably from the Glencartholm Fish Bed. HM V.7173 also includes phosphatic concretions suggestive of gut contents.

RSM 1885.54.5A (part), figured by Traquair (1888a, b), Moy-Thomas (1935), Frickhinger (1991) and Stahl (1999), and B (counterpart), presents an individual with a crushed and coarsely prepared cranium (on the part, 54.5A) and axial skeleton. The dentition is mostly intact, preserving at least three anterior tooth plates (Moy-Thomas 1935, text-fig. 1).

RMS 1886.31.24, figured by Traquair (Traquair 1888a, b), displays the cranium figured by Moy-Thomas (1935, text-fig. 4). Although in generally poor condition, the counterpart, NHMUK P.4085, includes well-preserved sections of the caudal skeleton.

RMS 1891.53.33, referred to *Chondrenchelys* and figured by Lund (1982), preserves several identifiable tooth plates, portions of the cranium and anteriormost axial skeleton, including a three-dimensionally intact series of centra, and a moderately complete pectoral fin.

NHMUK P.18054, figured by Moy-Thomas (1935, plate II, fig. 2; text-figs. 2, 11; Field number J.A.M.T.2.1933) includes the mandible and dentition in oral view, and parts of the axial skeleton.

NHMUK P.18055 and counterpart NHMUK P.22967, figured by Moy-Thomas (1935, plate II, fig. 1; text-fig. 6; Field number J.A.M.T.2.1934) includes well-preserved anterior axial skeleton, cranial outline, pectoral and pelvic skeletons.

NHMUK P.18056 and counterpart NHMUK P.18057, figured by Moy-Thomas (1935) includes well-preserved pectoral and pelvic skeletons.

GSE 13328, figured by Lund (1982, fig. 5F), Ginter & Sun (2007, fig. 8B) and Finarelli & Coates (2012, fig. 3B) is notable for well-preserved palatal tooth plates.

Diagnosis. As for genus: monotypic.

3. Description of *Chondrenchelys problematica*

3.1. Skull

We augment the comparative anatomical content of the following description by including images of the cleared and stained braincase and palate of a pre-hatchling elephant shark, *Callorhynchus milii*, juxtaposed with images of the cranium of *Chondrenchelys problematica* (Fig. 6). Further sources of chimaeroid

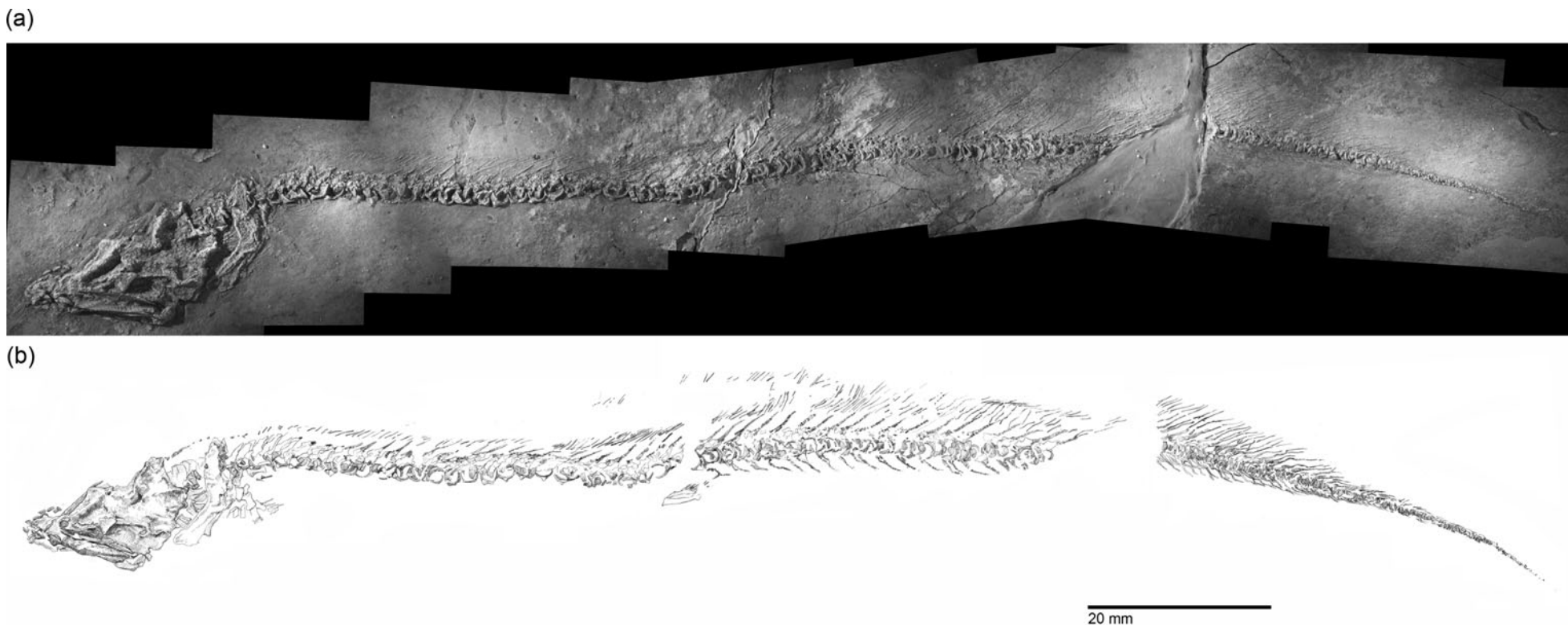


Figure 3 *Chondrenchelys problematica*, female, NMS 1998.35.1: (a) compound photograph and (b) camera lucida drawing of entire specimen. In the photograph in part (a), the specimen has been whitened with ammonium chloride. In parts (a) and (b), anterior is to the left, with dorsal to the top of the image.



Figure 4 *Chondrenchelys problematica*, male, NMS 2002.68.1, compound photographs of entire specimen: (a) counterpart, anterior to right; (b) part, anterior to left. Specimen has been whitened with ammonium chloride; in both images, the postcranial skeleton is shown with the dorsal surface towards the top of the figure.

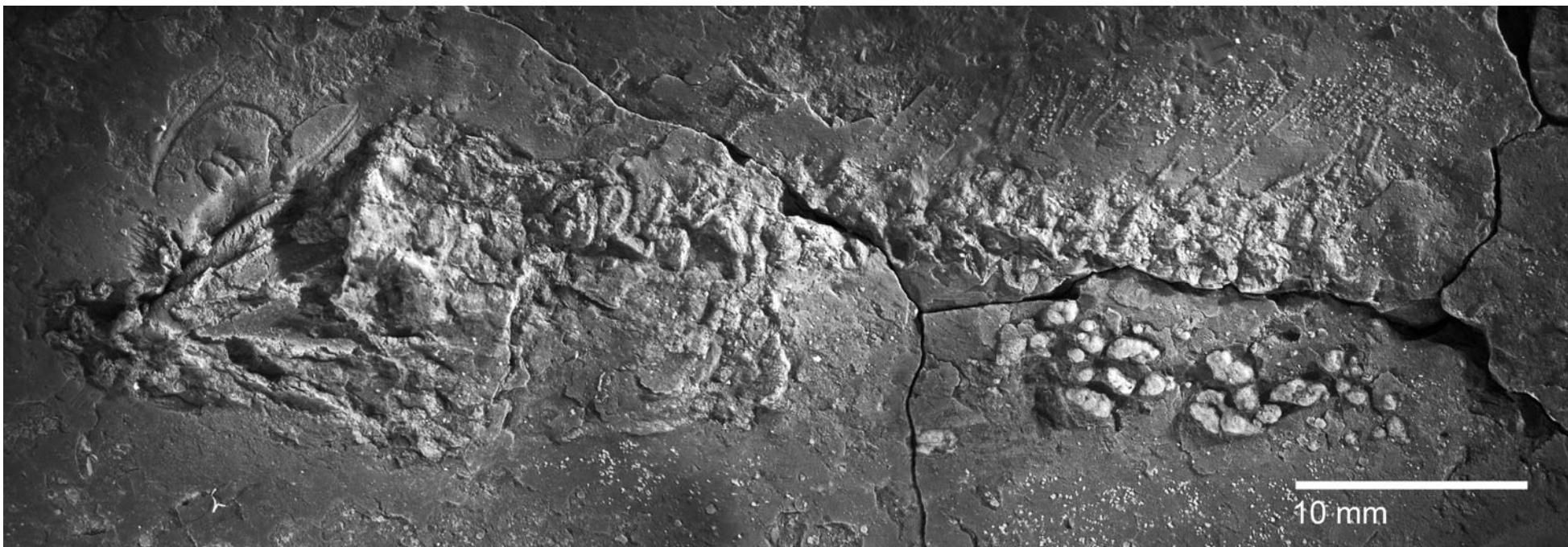


Figure 5 *Chondrenchelys problematica*, HM V.7173: photograph of entire specimen. Postcranium revealed in left lateral view; cranium broken to reveal upper dentition in dorsal view; specimen whitened with ammonium chloride. Anterior is to the left, with dorsal to the top of the image.

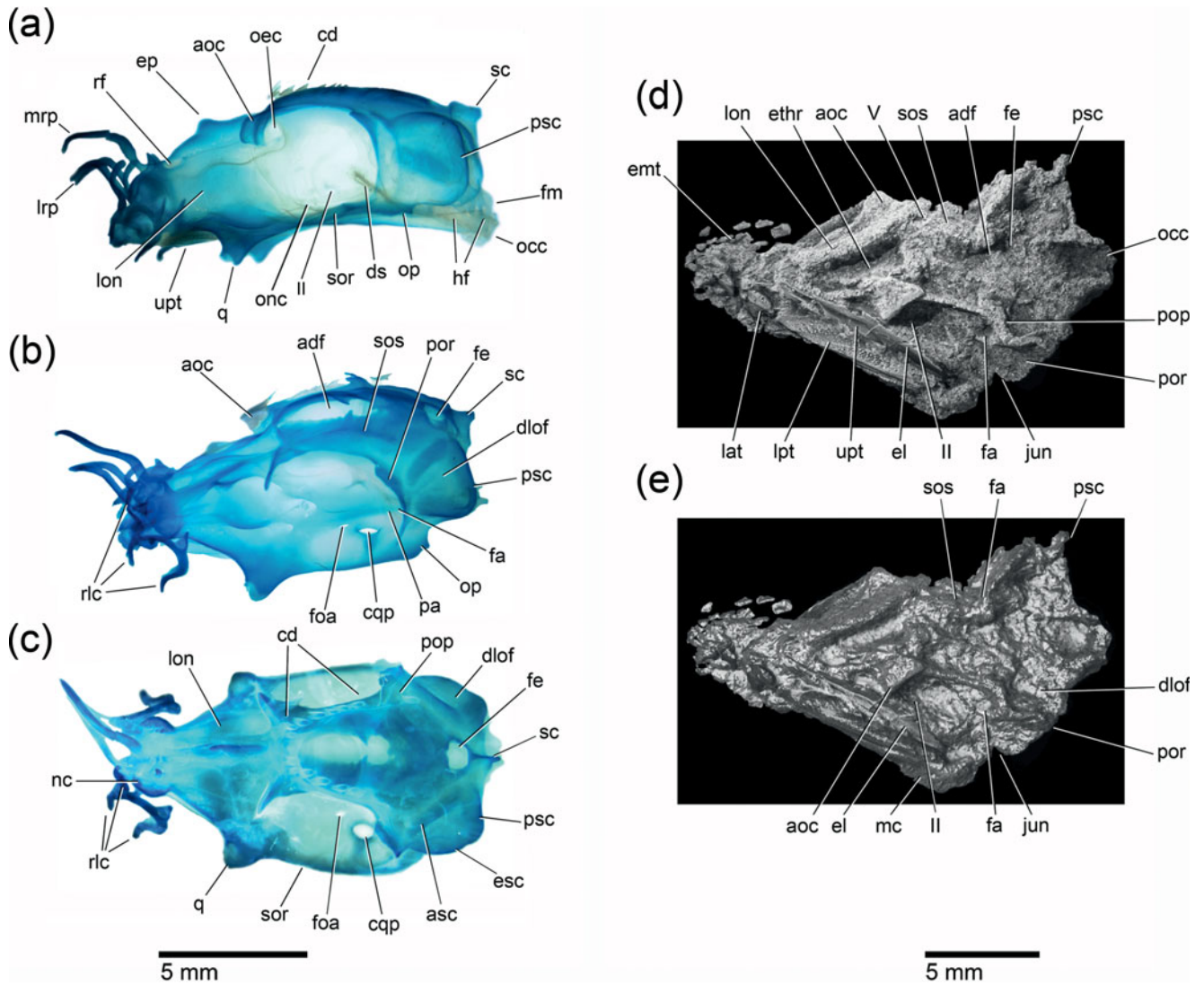


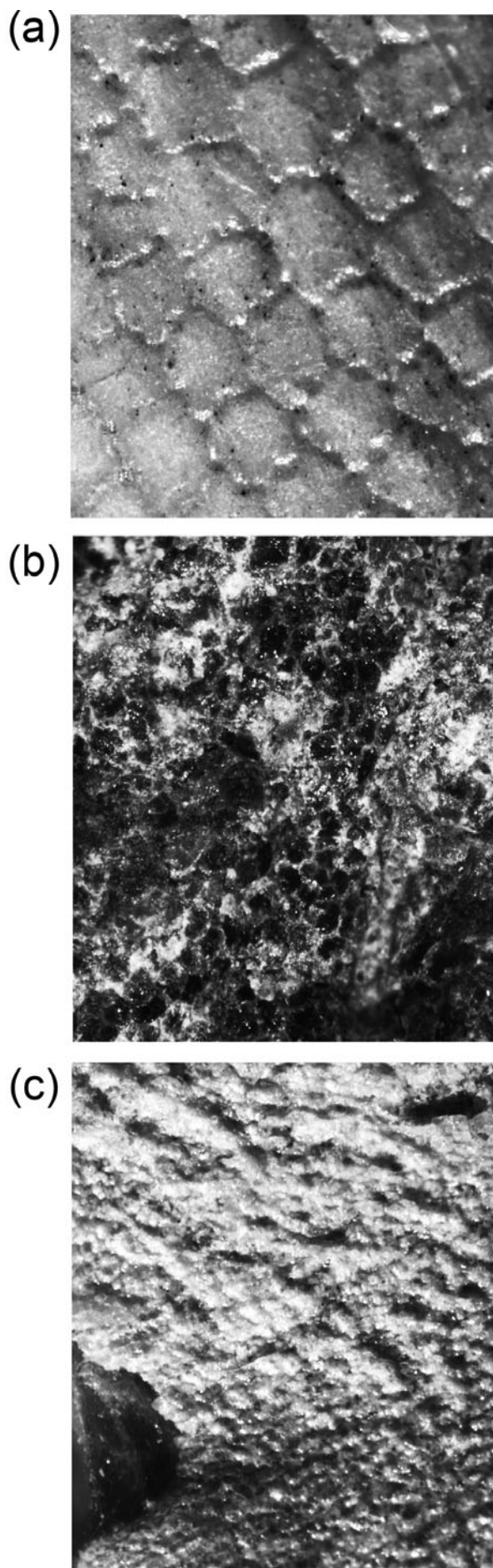
Figure 6 Comparison of holocephalan crania: extant *Callorhynchus millii* and the Lower Carboniferous *Chondrenchelys problematica* (specimen NMS 1998.35.1). *Callorhynchus millii*, embryonic neurocranium and palate (stage 36, Didier *et al.* 1998), cleared and stained (cartilage with methyl blue) shown in (a) lateral, (b) dorsolateral and (c) dorsal aspect; images illuminated via combination of transmitted and reflected light. (d) *Chondrenchelys problematica* NMS 1998.35.1, specimen whitened with light coating of ammonium chloride; (e) photographic rendering processed via RTI Viewer using specular enhancement option. In parts (d) and (e), the view is of the dorsal skull surface, with anterior is to the left. Abbreviations: adf = dorsal fontanelle; aoc = antorbital crest; asc = anterior semicircular canal; cd = cranial denticles; cqp = cranioquadrate passage; dlof = dorsolateral otic fossa; ds = dorsum sellae; el = external lamina; emt = extramandibular teeth; ep = ethmoid process; esc = external semicircular canal; ethr = ethmoid roof; fa = antotic foramen; fe = endolymphatic foramen; foa = foramen for orbital artery; fm = foramen magnum; hf = hypoglossal foramina; jun = jugal notch; lat = lower posterior tooth plate; lon = lamina orbitonasalis; lpt = lower posterior tooth plate; lrp = lateral rostral process; mc = Meckel's cartilage; mrrp = medial rostral process; nc = nasal cartilage; occ = occipital cotylus; oec = opening (posterior) of ethmoid canal; onc = orbitonasal canal; op = otic process; pa = pila antotica; pop = postorbital process; por = postorbital rim; psc = posterior semicircular canal; q = quadrate; rf = rostral foramen of the ethmoid canal; rlc = rostral labial cartilages; sc = sagittal crest; sor = suborbital ridge; sos = supraorbital shelf; upt = upper posterior tooth plate; II = optic nerve foramen; V = foramen for anterior branch of superficial ophthalmic nerve. *Callorhynchus* specimen prepared and supplied by Dr Andrew Gillis. Note that rostral processes (mrrp, lrp) of *C. millii* are broken and bent toward the specimen's right side. Cranial cap denticles (cd) are a transitory feature of embryonic chimaeroids, generally shed at or shortly after hatching (Didier *et al.* 2012).

cranial morphology are summarised in the introduction to the discussion section.

The *Chondrenchelys* cranium and mandible are composed of tessellate calcified cartilage. Although the absolute size of the tesserae varies considerably, the patterns of close-packed polygonal mineralisations at cartilage surfaces are indistinguishable from other Palaeozoic chondrichthyans and Recent elasmobranchs (Fig. 7a, b). In modern chimaeroids, tesserae are not obvious at the cartilage surface. Cartilage mineralisation is superficially smooth, although closer inspection reveals a micro-

spherulitic, granular texture (Fig. 7c). Histological studies show that subsurface tesserae are indeed present in chimaeroids (A. Plamen, pers. comm. to MIC, 2012).

Rostrocaudal length of the cranium in both NMS 1998.35.1 (Figs 6a, b, 8d) and NMS 2002.68.1p (Fig. 8a–c) is approximately 18 mm, the otic roof is approximately 10 mm wide, and the inter-quadrate distance is approximately 17 mm. Moy-Thomas (1935) reconstructed a wedge-shaped cranium, with subequal rostral, orbital and postorbital proportions. However, in NMS 1998.35.1 and RSM 1885.54.5, the rostral and orbital



1 mm

regions each occupy approximately 40% of total skull length, with the post-orbital region being correspondingly short. Unlike modern chimaeroids (Fig. 6a–c), where the jaw articulation with the quadrate (q) is positioned at, or anterior to, the level of the antorbital crest (aoc), in *Chondrenchelys* (Fig. 6d, e), the articulation is just anterior to the level of the postorbital rim (por).

Jaw suspension in *Chondrenchelys* is holostylic, like modern chimaeroids, with the palatoquadrate completely fused to the ventral surface of the neurocranium (Moy-Thomas 1935; Lund 1982). In modern adult chimaeroids, large orbits are separated by a narrow septum of connective tissue, and are displaced dorsally relative to the cranial space housing the forebrain. The orbits are similarly large in *Chondrenchelys*, but widely separated, with substantially mineralised medial walls, such that there is no interorbital septum. In addition, there is no dorsal displacement, with the forebrain lying between the orbits, as in modern elasmobranchs.

The space occupied by the otic labyrinth in *Chondrenchelys* is substantially smaller than the orbit. There is no indication of “wedging” of the occipital arch between otic capsules (Fig. 6d, e) (Maisey 1983). The otico-occipital roof is subrectangular, with a posterolateral prominence formed by the outermost rim of the posterior semicircular canal (psc). The relation of this prominence to the lateral occipital process of other chondrichthyans (Schaeffer 1981) is uncertain. In NMS 1998.35.1, a concavity lies anterior to the ridge overlying the posterior semicircular canal: the dorsolateral otic fossa (dlof; Fig. 6). The anterior boundary of this fossa probably marks the location of the anterior semicircular canal (cf. asc; Fig. 6c). The otic roof bears no trace of a midline sagittal crest (sc) or metotic fissure. The occipital wall, cotylus and arch are well-mineralised and stand in high relief relative to surrounding cartilages and matrix. In contrast, the lateral wall of the otic region is poorly preserved in all specimens. The occipital arch and cotylus complex (occ) encompassing the foramen magnum is posteriorly prominent in all three specimens, also apparent in *Harpagofututor* (Lund 1982, figs 2A, 3A).

The braincase roof between the orbits in NMS 1998.35.1 has collapsed to form a shallow trough, indicative of a broad, underlying, interorbital space. Two midline foramina are present, the margins of which are distinct and show no signs of being the result of breakage due to the collapse of the cranial roof. The elongate (approximately 0.7 mm), anterior foramen is identified as an anterior dorsal fontanelle (adf), and is positioned just anterior to the level of the postorbital process (pop), similar to the dorsal midline opening in the chondrocranial roof of *Cladodoides wildungensis* (“ms” in Maisey 2005, fig. 4). The small, foramen-like recess immediately posterior to the anterior dorsal fontanelle, might represent the exit of the endolymphatic ducts (fe), although it is substantially smaller than the endolymphatic opening in the similarly sized chondrocranium of *Callorhynchus* (compare Figs 6c and d).

A large, subtriangular antorbital crest (aoc) forms the anterior boundary of the orbit roof. More substantially calcified than other parts of the braincase, this crest persists as a prominent feature, and serves as a convenient landmark, even in severely-crushed specimens (e.g., RMS 1888.54.5). The absence of such a crest in *Harpagofututor* (Lund 1982, text-fig. 2 and elsewhere) presents a distinctive difference between these otherwise similar genera. Posteriorly, the antorbital crest is continuous with the supraorbital shelf (sos), a concave lateral rim that

Figure 7 Calcified cartilage from three chondrichthyans, showing clearly defined tesserae in (a) the lateral surface of *Squalus acanthias* Meckel’s cartilage and (b) the roof of *Chondrenchelys problematica* chondrocranium; (c) granular mineralisation forms the lateral surface of *Hydrolagus collei* Meckel’s cartilage. All images are to same scale.

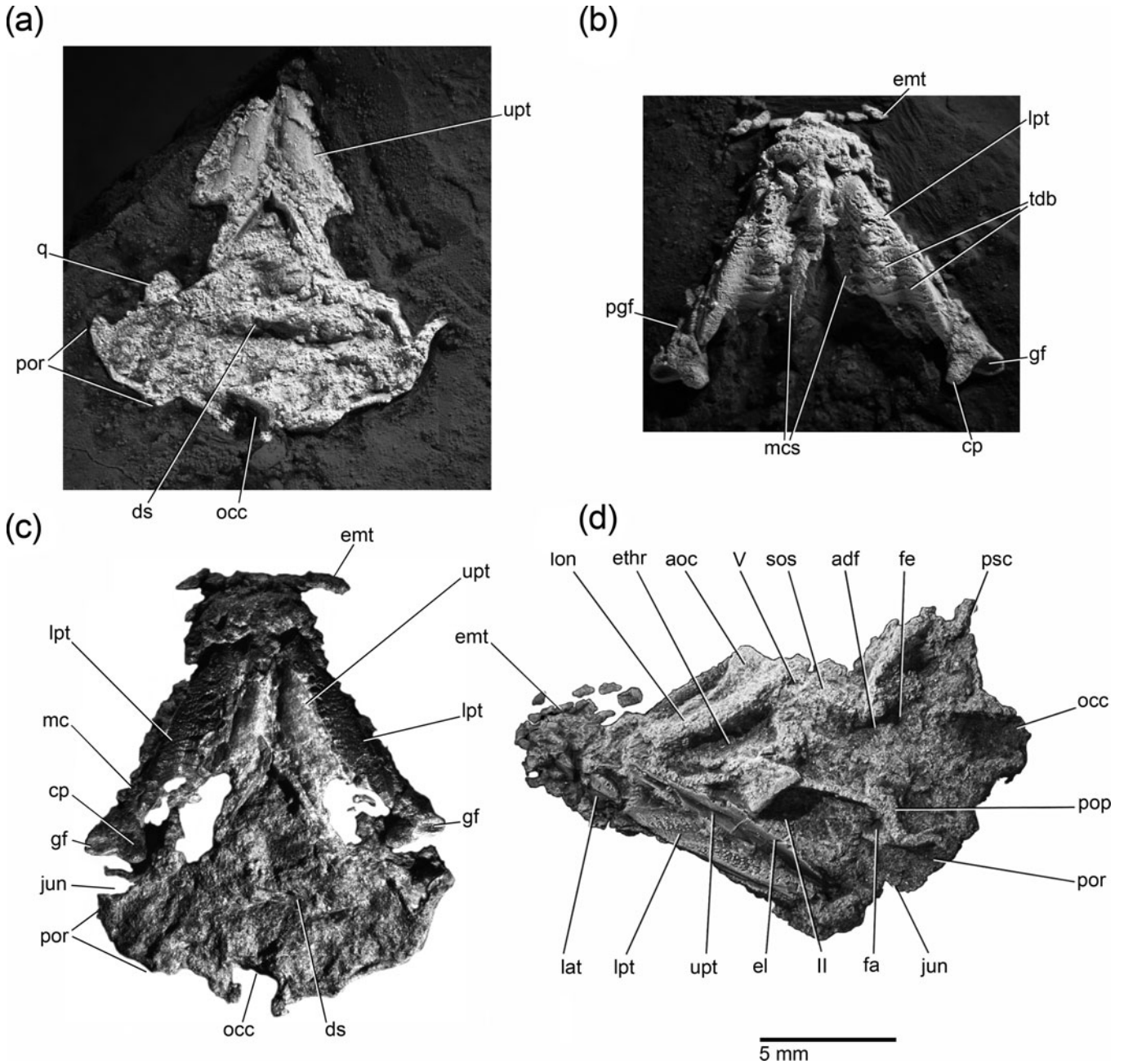


Figure 8 *Chondrenchelys problematica*: (a) NMS 2002.68.1, cp, showing base of neurocranium in ventral view; (b) NMS 2002.68.1, p, showing the mandible and associated dentition in dorsal (oral) view; (c) part and counterpart mapped on onto each other, showing the degree of overlap; (d) NMS 1998.35.1, neurocranium exposed in dorsolateral aspect. Specimens shown in (a), (b) and (d) whitened with ammonium chloride. Part (d) in this figure is repeated from Figure 6d to provide a complete reference to the *Chondrenchelys* chondrocranium. Abbreviations: adf = dorsal fontanelle; aoc = antorbital crest; cp = condylar (mandibular) process; ds = dorsum sellae; el = external lamina; emt = extramandibular teeth; ethr = ethmoid roof; fa = antotic foramen; fe = endolymphatic foramen; gf = glenoid fossa; jun = jugal notch; lat = lower anterior tooth plate; lon = lamina orbitonasalis; lpt = lower posterior tooth plate; mc = Meckel's cartilage; mcs = mandibular cartilage shelf; occ = occipital cotylus; pgf = preglenoid lateral flange; pop = postorbital process; por = postorbital rim; psc = posterior semicircular canal; q = quadrate; sos = supraorbital shelf; tdb = transverse dentine bands; upt = upper posterior tooth plate; II = optic nerve foramen; V = foramen for anterior branch of superficial ophthalmic nerve. All images are to same scale.

is also robustly mineralised, and persists in otherwise crushed specimens (e.g., HM V.7173; RSM 1888.54.5).

The roof of the pre-orbital region (ethr) is concave, forming in a midline trough flanked, laterally, by high walls, presumably formed by the lamina orbitonasalis cartilage (lon) (de Beer 1937). In NMS 1998.35.1, the walls of the lamina orbitonasalis remain in position, with the cartilage of the roof of the ethmoid region visible along the midline between them. The position of this trough roughly corresponds to the ethmoid canal of extant chimaeroids, which is an enclosed extracranial space, into

which the superficial and deep ophthalmic nerves pass upon exiting the orbit (oec). The ophthalmic nerves pass anteriorly through the canal to the nasal capsule, exiting via the rostral foramen (rf) (de Beer 1937; Didier 1995). A large foramen is visible just caudal to the antorbital crest on each side of the neurocranial roof of NMS 1998.35.1. We interpret these as the exit for part of the superficial ophthalmic nerve (V) from onto the dorsal surface of the skull, as in modern elasmobranchs (Goodrich 1930; Marinelli & Strenger 1959). We argue that there is no ethmoid canal in *Chondrenchelys*, and that the

nerve supply to the rostral sensory array was on the dorsal, external aspect of the chondrocranium, and that the pre-orbital endocranial space in NMS 1998.35.1 enclosed only the olfactory tracts. Moreover, it is also important to note that the roof of the ethmoid region was closed and that there is no evidence of a precerebral fontanelle in *Chondrenchelys*.

The orbits of *Chondrenchelys* are substantially larger than previous reconstructions (Moy-Thomas 1935). The caudal border of the exposed left orbit of RSM 1888.54.5 (Traquair 1888b; Moy-Thomas 1935) is highly damaged, which lead to their underestimation of the orbit's size and overestimation of post-orbital length. In NMS 1998.35.1, the left orbit postorbital rim is nearly complete and remarkably well-developed. Importantly, the rim extends laterally and posteriorly to form the anterior part of the otic wall, as in modern chimaeroids (Fig. 6d, e, por). We interpret the deep notch near the caudoventral orbit border as a recess for passage of the jugular vein (jun).

Within the orbit, there is a large foramen in the posterior wall, which we interpret as the foramen antoticum (fa) (Fig. 6d, e), observed in similarly sized embryos of *Chimaera* (de Beer & Moy-Thomas 1935) and *Callorhynchus* (Fig. 6b, c). The foramen antoticum transmits much of the trigeminofacial nerve complex (nerves V and VII) to the orbit. Close to the anterior base of the orbit in NMS 1998.35.1 there is a large foramen, the size and position of which match the entry of the optic nerve (II) into the orbit (Kesteven 1932; de Beer & Moy-Thomas 1935). The orbit wall shows no evidence for an optic pedicel. Other openings likely to have been present (e.g. foramina for the pituitary vein, and nerves III, IV and VI) are unknown, and probably obscured through postmortem compression.

The orbit is floored by a cartilage shelf, which likely supported the dental epithelium of the upper posterior tooth plates (upt). This shelf was probably reinforced by the underlying tooth plates (Fig. 9) (Finarelli & Coates 2012). In modern chimaeroids, this floor is formed by the palatoquadrate cartilage, and extends posteriorly beyond the level of the postorbital rim (por), meeting the lateral extension of the otic wall to form the otic process (Fig. 6a, b: op) (Grogan *et al.* 1999). Whether this process is present in *Chondrenchelys* remains uncertain, as all specimens are damaged in this region. The orbit floor is visible in both NMS 1998.35.1 (Figs 6d, e, 8e) and RMS 1885.54.5. Unlike extant chimaeroids, there is no sub-orbital ridge (sor) forming a distinct lateral boundary to the orbit along its ventral and posterior margin. Rather, in *Chondrenchelys*, the lateral margin is reinforced by the external lamina (el) (= "descending lamina" of Patterson 1992) of the upper posterior tooth plate (upt) (Finarelli & Coates 2012).

Extant chimaeroids lack an anterior skeletal wall to the orbit (Fig. 6c, d); the anterior orbit boundary is formed by a preorbital fascia, which is reinforced by the anterior belly of the *M. adductor mandibularis* (Anderson 2008). In *Chondrenchelys*, the orbit is deeply recessed relative to the preorbital cranial wall, with a marked anterior skeletal border. However, this anterior skeletal wall is not like those observed in other early chondrichthyans, such as *Xenacanthus* (Schaeffer 1981) or *Cobelodus* (Maisey 2005), in which a skeletal anterior orbit margin is formed by the posterior face of the nasal capsule (which is derived from the lamina orbitonasalis) (de Beer 1937). In modern chimaeroids and *Chondrenchelys*, the nasal capsule is separated from the orbit by an extended ethmoid region, and the resultant preorbital wall (itself formed by the lamina orbitonasalis) is occupied by *M. adductor mandibularis*. Due to the configuration of the lamina orbitonasalis cartilage and the median trough of the ethmoid region, we conjecture that the nasal capsules, although not preserved in *Chondrenchelys*, were well-separated from the orbits.

NMS 2002.68.1cp (Fig. 8a, c) preserves the basicranium in ventral view. A deep, transverse trough separates the orbital and otic regions, in the same position as the osteichthyan ventral otic fissure. We suggest that it reflects retention of a fragile region of cartilage in the adult (Janvier 1996). Immediately anterior to this trough, the basicranial floor collapsed to the interior of the braincase, over a robust ridge of cartilage, highlighting an internal feature that likely marks the location of the dorsum sellae (ds; see also Fig. 6a) (de Beer 1937). Although the cranial floor anterior to the dorsum sellae is indented and fractured, we find no convincing evidence for a hypophyseal opening (Goodrich 1930); absence of a hypophyseal opening is shared with chimaeroids and iniopterygians (Khonsari *et al.* 2013), and contrasts with other early chondrichthyans (Coates & Sequeira 1998; Maisey 2005, 2007). The broken rim of the upper posterior tooth plate is visible on the left and right sides of the palate (Fig. 8a), and much of the area covered by this tooth plate is shown in Figure 9a and c.

The ventral surface of the occipital region is incompletely known. Although much of the basicranial surface is preserved in NMS 2002.68.1cp, mapping the part onto the counterpart reveals a rim of poorly preserved cartilage embedded within the matrix behind this lower jaw, suggesting that the complete ventral extent of the occipital region in NMS 2002.68.1p remains concealed in the matrix. It is not possible to determine whether this cartilage includes a canal for the dorsal aorta. No such canal is present in modern chimaeroids, yet an antero-posteriorly short and ventrally prominent aortic canal is present in *Helodus* (Patterson 1965; pers. obs. JAF & MIC: NHMUK P.8212). Other basicranial openings in *Chondrenchelys* are difficult to identify because of the likely size similarity with the calcified tesseræ and post mortem compression. However, there is no evidence for a cranioquadrate passage in NMS 2002.68.1, consistent with NMS 1998.35.1.

The lateral surface of Meckel's cartilage is most visible in NMS 1998.35.1, although the lateral profile of the mandible is best observed in NHMUK P.18055. In NMS 1998.35.1, the articular portion has been deformed nearly 90 degrees relative to the corpus of the jaw, such that the articular surfaces are directed medially and obscured. NMS 2002.68.1p provides the first undistorted view of these surfaces (Fig. 8b). As in extant chondrichthyans, the mandible of *Chondrenchelys* possesses a two-part jaw articulation, with a well-formed lateral glenoid fossa (gf) flanking a medial condylar process (cp) couplet. This contrasts with much less distinct fossa-condyle couplets observed in iniopterygians (Pradel 2010) and in *Helodus* (pers. obs. JAF & MIC: NHMUK P.8212). As in extant chimaeroids, the articular surface of *Chondrenchelys* is located on the rearmost extremity of Meckel's cartilage (mc), oriented in a principally anteroposterior direction. There is no retroarticular process or flange on the mandible, and no offset between the two articular surfaces: the glenoid is situated immediately lateral to the condyle. In contrast, we note that in *Hydrolagus*, the glenoid is displaced anteriorly relative to the condyle. In addition, the two halves of the lower jaw are united firmly (presumably fused) across the symphysis. No otherwise compressed, distorted or broken examples of *Chondrenchelys* show isolated halves of the complete mandible.

Much of Meckel's cartilage is concealed beneath the prominent lower posterior tooth plate (lpt) (Finarelli & Coates 2012). However, NMS 2002.68.1 shows that the ventral-most part of the jaw is curved medially, to form an incomplete shelf or floor to the intermandibular area (Fig. 8b). In dorsal view, this shelf (mcs) bears a series of laterally-oriented, elliptical depressions arranged in an anteriorposterior series. These depressions coincide with the major transverse dentine bands (tdb) of the tooth plate, and this registration between tooth

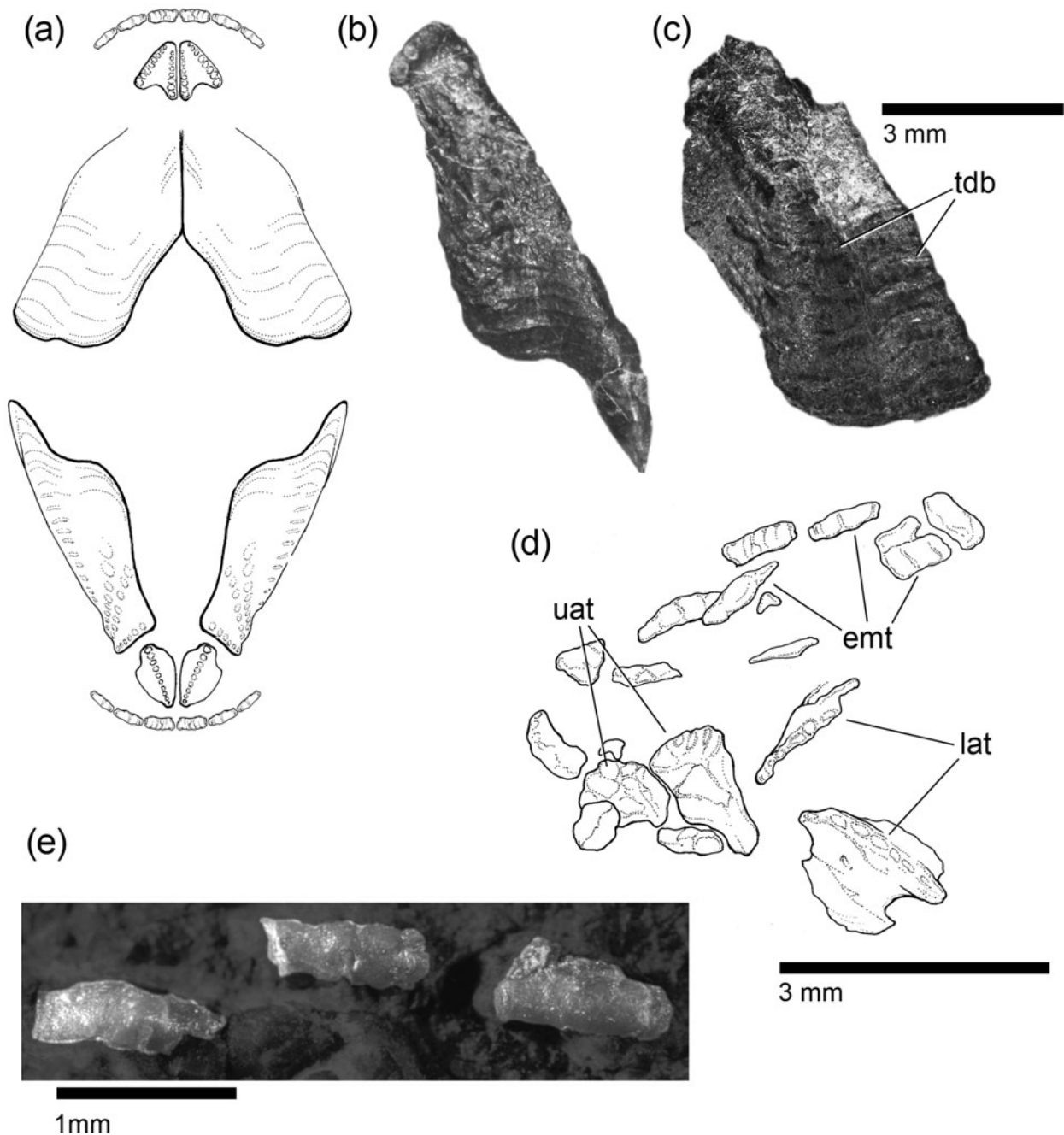


Figure 9 *Chondrenchelys problematica*, the complete dentition: (a) reconstructed as if looking into the open mouth, number of extramandibular teeth estimated; (b) NMS 2002.68.1p, right lower posterior tooth plate, oral surface; (c) BGS-GSE 13328, left upper posterior tooth plate, oral surface; (d) NMS 1998.35.1, anterior dentition, camera lucida drawing; (e) NMS 1998.35.1, extramandibular teeth, coronal view. Abbreviations: emt = extramandibular teeth; lat = lower anterior tooth plate; tdb = transverse dentine bands; uat = upper anterior tooth plate. Tooth plates in (b) and (c) to same scale.

plate banding and skeletal features in the jaw suggests coordinated, episodic dentine accretion and cartilage growth (see: Finarelli & Coates 2012). A flange (pgf) projects from the lateral face of Meckel's cartilage below the posteriormost third of the external lamina (el) of the lower posterior tooth plate. This feature is visible in NMS 1998.35.1 and NMS 2002.68.1, and might be equivalent to a pre-glenoid lateral flange in *Hydrolagus* (pers. obs. JAF & MIC). A similarly-positioned ventrolateral flange is clearly present in *Helodus* (pers. obs. JAF & MIC: NHMUK P.8212), and is possibly also present in *Iniopera* (Pradel 2010).

The dentition of *Chondrenchelys* is described in detail by Finarelli & Coates (2012). Here (Fig. 9a), we figure the complete dentition, reconstructed as if looking into the open mouth (following the convention employed by Patterson 1965; Stahl

1999; Stahl & Hansen 2000; Stahl & Parris 2004). Each quadrant of the jaws bears a large posterior tooth plate (Fig. 9a–c) and a smaller anterior tooth plate (Fig. 9a, d). *Chondrenchelys* is further distinguished by possessing an extramandibular dentition (emt), consisting of small teeth arranged around the anterior of the gape that bear striking resemblances to isolated teeth referred to petalodonts (Fig. 9a, d, e). The skeletal support of these extramandibular teeth remains uncertain, although it is possible that rostral cartilages (rlc) were involved (c.f. *Callorhynchus*, Fig. 6b, c).

3.2. Branchial arches

The branchial cartilages (bc) of NMS 1998.35.1 (Fig. 10a–c) are preserved in a restricted space between the rear of the skull

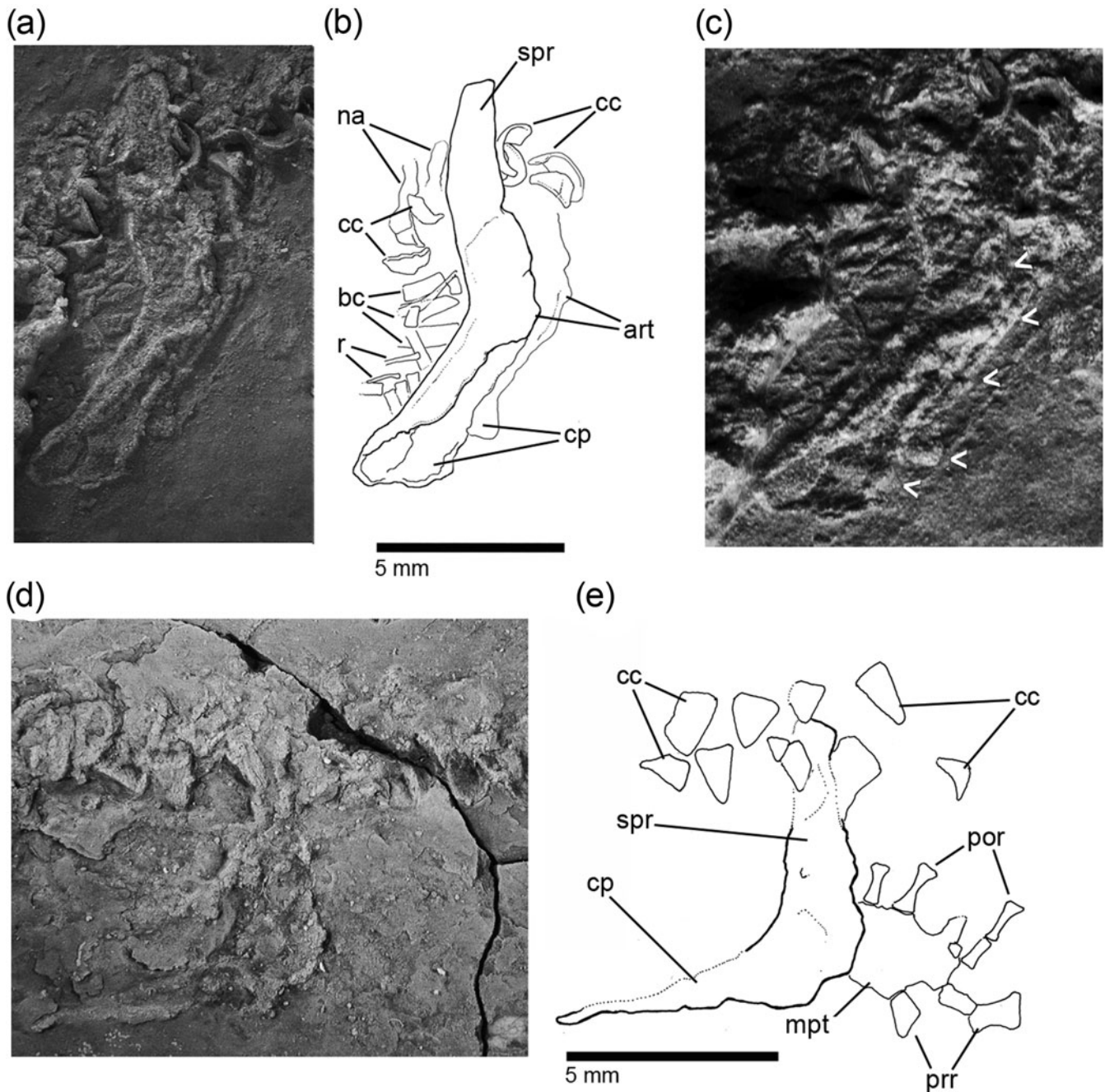


Figure 10 *Chondrenchelys problematica*, branchial skeleton and pectoral girdle: (a) NMS 1998.35.1; (b) camera lucida drawing showing branchial skeleton visible between the occiput and pectoral girdle; (c) NMS 1998.35.1 with low angle illumination, white chevrons indicating radiating cartilage ridges; (d) HM V.7173, showing scapulocoracoid in lateral view; (e) camera lucida drawing, with female-pattern pectoral fin outline included, although the fin is barely visible in specimen photograph. Specimens in (a) and (d) whitened with ammonium chloride. Abbreviations: art = articular area for pectoral fin; bc = branchial arch cartilage; cc = chordacentrum; cp = coracoid plate; mpt = metapterygium; na = neural arch; por = postaxial radial; prr = preaxial radial; r = cartilage ray; spr = scapular process.

and the scapulocoracoid. The identity of individual arch components in NMS 1998.35.1 is unclear, as they are disarticulated. HM V.7173 also preserves traces of arches, but these remain mostly covered in matrix. Given the proximity of the scapulocoracoid to the caudal margin of the skull, the branchial basket almost assuredly contacted the pectoral girdle, although it is significant that in both specimens the branchial arches are positioned, at least in part, behind the caudal skull margin, and are not completely “subterbranchialian,” like extant chimaeroids (Zangerl 1973, 1997; Didier 1995).

The most robust of the branchial cartilages are subrectangular and overlain by gracile rods composed of bead-like tes-

serae, which are similar in form to the dorsal fin radials (see below). These cartilaginous rays (r) are variably-oriented, and in some cases are curved, which suggests that they were flexible (Fig. 10a–c). In NMS 1998.35.1, several rays cross the anterior margin of the scapulocoracoid, and low-angle illumination highlights a series of ridges and rays extending posteriorly from the rear of the gill chamber. The structures might represent either continuation of the gill skeleton, branchial rays, or cartilaginous supports for an opercular flap. Branchial rays are absent in modern adult chimaeroids, but are clearly present in juveniles (Gillis *et al.* 2011).

3.3. Pectoral girdle and fins

Most of the information on the pectoral girdle is obtained from NMS 1998.35.1 (Fig. 10a–c) and HM V.7173 (Fig. 10d, e). The girdle in NMS 2002.68.1 is incomplete and compressed dorsoventrally, and the specimens used in Moy-Thomas's (1935) description are, as he acknowledged, in generally poor condition.

NMS 1998.35.1 and HM V.7173 preserve the girdle in lateral view, with the left scapulocoracoid overlying the right. Three or four vertebral segments are visible between the occiput and the anterior edge of the scapular process. Previous reconstructions proposed a short coracoid plate relative to the length of the scapular process (Moy-Thomas 1935; Patterson 1965). However, in NMS 1998.35.1 and HM V.7173, the coracoid plate (cp) and scapular process (spr) are subequal in length. The scapular process is oriented nearly orthogonal to the axial skeleton until the level of the fin articulation (art), below which the coracoid plate is directed anteriorly, forming a near right angle in lateral view (most clearly visible in HM V.7173, Fig. 10d, e).

The lateral face of the scapular process in *Chondrenchelys* is mostly smooth (Fig. 10a, b). Significantly, there is no trace of the dorsoventrally oriented ridge that is present in modern chimaeroids, providing insertion sites for a suite of muscles, including the *cuticularis superficialis* and the *retractor mesoventralis pectoralis*. The fin articulation faces posteriorly and is positioned low on the flank, *contra* previous reconstructions (Moy-Thomas 1935; Patterson 1965). Although we find no evidence for a distinct 'backwardly-directed knob' on the shoulder girdle (Moy-Thomas 1935), the articular region is thicker and more prominent than adjacent areas of cartilage.

In NMS 1998.35.1, the preservation of the pectoral girdle gives the appearance of a forward projection under the occipital region, resembling modern and fossil chimaeroids (Patterson 1965; Didier 1995) and iniopterygians (Zangerl 1973, 1997; Pradel *et al.* 2010). However, post-mortem deformation has translated the cranium in NMS 1998.35.1 such that it now lies caudally and ventrally to its in-life position. HM V.7173 (Figs 5, 10d, e) more accurately preserves the relative in-life positions of the cranium and pectoral girdle. In this specimen, the pectoral girdle does not contact the occipital region, and the branchial region is more substantially posterior to the skull (as in elasmobranchs, but unlike chimaeroids). A small portion of the forward-projecting coracoid plate is also preserved in NMS 2002.68.1p, and is visible anterior to the large dislocated occipital cartilage (see above). As such, the coracoid does reach the occiput and projects slightly forward of the caudal margin of the cranium; however, not to the extent observed in iniopterygians (Zangerl 1973, 1997). In life, the left and right coracoids formed a broad, flat, near-horizontal plate, flooring the branchial chamber.

Specimens of *Harpagofututor* (e.g., CMNH 27326) confirm Lund's (1982) reconstruction of a scapulocoracoid with near-equal proportions of the scapular and coracoid processes in that taxon as well. Additionally, the coracoid plate probably projected anteriorly under the gill basket, as in *Chondrenchelys*. We also note a general similarity to the scapulocoracoid of the enigmatic Bear Gulch chondrichthyan *Squatinactis caudispinatis* (Lund & Zangerl 1974), which displays the sharp anterior redirection of the coracoid under the gill basket. Comparisons with other early chondrichthyans (Stahl 1999; Coates & Gess 2007; Lane & Maisey 2009) suggest that the shape of pectoral girdle in *Chondrenchelys* and *Harpagofututor* represents a shared character. Like other early holocephalans, the chondrenchelyid coracoid region lacks a pronounced anterior shoulder, there is no diazonal foramen in lateral view, and the apex of the scapular process has no more than a weakly developed post-

erolateral angle. It should be noted that these features are also observed in iniopterygians (Pradel *et al.* 2010)

In NMS 1998.35.1 (Fig. 3) and HM V.7173 (Fig. 10e), the pectoral fins are poorly preserved. In NMS 1998.35.1, remains of left and right pectoral fins are superposed, and include a few stout, axial cartilages and narrower radials along the dorsal and perhaps the postaxial side, with pre-axial radials appearing broader. This pattern is also observed in the slightly better preserved left pectoral fin of HMV.7173 (Fig. 10e), in which a broad central axial cartilage supports thin radials. Notably, these fins are similar to the pectorals of *Harpagofututor*. Lund (1982) first observed that although this morphotype is present in both males and females of *Harpagofututor*, in *Chondrenchelys* it is restricted to females (as determined by the dimorphic pelvic fins). The Mumbie Quarry specimens support Lund's argument: we observe the hypertrophied, paddle-like pectoral fin morphology described by Moy-Thomas (1935) only in male *Chondrenchelys* specimens.

The classic restoration of the male pectoral fin (Moy-Thomas 1935; reproduced repeatedly: e.g., Patterson 1965; Stahl 1999) was compiled from specimens NHMUK P.18056 and NHMUK P.18057 (part and counterpart of the same fin, from the same individual) and NHMUK P.18055. We complement these data with male-pattern left (Fig. 11a–c) and right (Fig. 11a, d, e) pectoral fins from NMS 2002.68.1, and an incomplete left fin from NMS 1891.35.33. Combining data from the left and right fins from NMS 2002.68.1 permits reconstruction of a near-complete articulated fin skeleton (Fig. 11f). This new reconstruction closely resembles Moy-Thomas's (1935) estimate, but several substantial differences deserve attention.

Most importantly, we find that the pectoral fin in *Chondrenchelys* is dibasal, resembling other holocephalans (see: Stahl 1999), not monobasal as in previous reconstructions (Moy-Thomas 1935; Lund 1982). The combined part and counterpart of NMS 2002.68.1 (Fig. 11a) clearly shows two cartilages articulating with the scapulocoracoid, in both the left and right fins. For the sake of convention, we refer to the leading-edge articulating cartilage as the propterygium (prpt) and the posterior cartilage as the metapterygium (mpt). The metapterygium corresponds to the most proximal cartilage in the monobasal axis of Moy-Thomas's (1935) reconstruction. The propterygium occurs in conjunction with the metapterygium in the left fin of NMS 2002.68.1 (Fig. 11b, c), but it is more completely preserved in the right fin (Fig. 11d, e) in which the metapterygium is incomplete. The propterygium is L-shaped (inset box in Fig. 11a), bearing a process that forms the most proximal part of the fin's leading edge (Fig. 11f, g). At least two radials articulate within the notch of this 'L', although when camera lucida copies from all fins are superimposed (Fig. 11f) there appears to be room for three. Thus far, there is no evidence of a propterygium in the female pectoral fin skeleton of *Chondrenchelys*, in agreement with Lund (1982).

The main axis of the pectoral fin is formed by three robust cartilages. The metapterygium is the most proximal of these, and is about half the proximodistal length of the second segment. The third, distalmost segment is the smallest and is variable in shape; it is squat in NMS 2002.68 but elongate in NHMUK P.18056. The arrangement of radials extending outward from this axis, toward the leading fin edge is conserved in all examples, and is more regular than previously reconstructed. Pre-axial radials consist of a short, subcylindrical, proximal segment, a longer and spatulate mid segment with a proximal, mineralised shaft flattening distally to a truncated, lozenge-shaped profile, and finally a short distal radial terminating the series. The pre-axial series includes approximately nine radials in total (Fig. 11f, g).

The distal portion of the fin is supported by three or four radials extending from the third axial segment. Each radial is composed of simple, subcylindrical segments. The total number and pattern of post-axial radials is less certain (Fig. 11a–c, f). They are generally larger and more irregularly shaped than their pre-axial counterparts, and form a cartilage pavement much as in the pectoral post-axial fin skeleton in modern *Chimaera* (Stahl 1999).

Claw-like denticles are arrayed along the leading edge of the male-pattern fin (Figs 11, 12). As far as we can determine, denticles are not present on the female-pattern fin. Moy-Thomas (1935) described these denticles as attached to distal cartilages, tipping the pectoral fin rays and embedded within the fin edge. Lund (1982) reinterpreted these denticles as scales associated with the lateral line. Lund is mistaken, as these denticles are distinct, in both position and morphology, from the lateral line in NMS 2002.68.1. Individual denticles bear a single, pointed crown on a subcircular and proximally concave base (Fig. 12). Denticle crowns are slightly curved, so that the convex surface seems to face the distal part of the fin. Most examples are buried in matrix, but a single denticle presents its concave surface, showing the span of the crown with an almost fingernail-like morphology above a slightly constricted waist (Fig. 12). These fin denticles form a paired series, with one set along the dorsal surface of the leading edge, and a matching series along its ventral surface. Denticle bases are positioned proximal to the fin rim, close to the distal extremity of the endoskeletal radials. Unusually, for fossil material, the full extent of the fin beyond the endoskeleton can be inferred from traces of ceratotrichia (Fig. 11e, f). These are preserved mostly on the right pectoral fin of NMS 2002.68.1p, with traces overlapping the terminal radial cartilages and indicating that the fin is markedly plesodic.

Finally, we note that the male pectoral fin in *Chondrenchelys* is proportionately larger than estimated by Moy-Thomas (1935) and the pectoral fins in *Harpagofututor*. The maximum length of the endoskeleton, measured from the proximal articulation to distal tip is almost 25% longer than the mandible, implying that the pectoral fin area is approximately the size of the entire head in lateral view. In comparison, the pectoral fin of a male *Harpagofututor* is approximately 20% shorter than the lower jaw.

3.4. Pelvic girdle and fins

The most complete male pelvic skeletons are those of NHMUK P.18055 and NHMUK P.18057 (Fig. 13a), with additional data from NMS 2002.68.1 (Fig. 13b). Our restoration of the male girdle and fin is in broad agreement with Moy-Thomas (1935, text-fig. 9) and comments by Lund (1982). The well-preserved pelvic girdle (pg) in NMS 2002.68.1 is simple, as in *Harpagofututor*, narrow anteriorly and broad posteriorly, with two articulation surfaces for a dibasal fin. Thus, the pelvic fin in *Chondrenchelys* is not polybasal, as Lund (1982) suggested for *Harpagofututor*. The anterior, propterygial pelvic radial (prpt) is small, supporting a single distal radial. The posterior proximal radial is a large basiptyerygium (bpt), with a stepped or faceted ventral/lateral edge supporting six or seven distal radials. About five shorter and broad intermediate cartilages (intc) articulate in line between the caudal or distal end of the basiptyerygium and the proximal end of the long myxopterygial cartilage (mxpt), and further distal radials (dra) articulate with these intermediate cartilages. These are more distinctive, morphologically, than anterior pelvic radials, possibly contributing to Moy-Thomas's disputed restoration of a pelvic fin with twin axes (see: Lund 1982). The proximal part of the myxopterygium is flanked posteriorly by a narrow, triangular, cartilage

that appears to be the most posterior member of the distal radial series, a feature that is also observed in *Harpagofututor* (Lund 1982, text-fig. 3).

The full complexity of the pelvic claspers remains unclear. There is no evidence for a pre-pelvic tenaculum in any of the new *Chondrenchelys* specimens. Pelvic fin cartilages in NMS 2002.68.1 are more poorly preserved than in NHMUK P.18057; however, they do preserve a series of large denticles (Fig. 13b, dnt) arrayed at the tips of the distal radials (Fig. 13c) and at the distal end of the myxopterygium, similar to male specimens of *Harpagofututor* (Lund 1982). NHMUK P.18057 shows a further series of small objects associated with the intermediate cartilages (shaded grey in Fig. 13a), whose exposed surfaces suggest a different histology, and which might be the bases of additional denticles aligned with the main axis of the male pelvic fin. A restoration of the pelvic skeleton, without denticles, is shown in Figure 13d.

Lund (1982) identified the first specimen of a female pelvic skeleton in NMS 1885.54.5, describing it as tiny and splint-like, with about seven fine radials. A second example of a female pelvic skeleton is observed in NMS 1998.35.1 (Fig. 3), although the remains of this fin are limited to a small cartilage, approximately 5 mm in length, ventral to the vertebral column and just anterior to the haemal arch series. The anterior end of the cartilage is incomplete, but the posterior portion bears a series of fine radials composed of small bead-like cartilages, again similar in composition to the midline fin radials (see below). These extend along the medial edge of the primary cartilage, and the relative size of these elements agrees with the description of female pelvic fins in *Harpagofututor* (Lund 1982).

3.5. Vertebral column

The axial skeletons of *Chondrenchelys* and *Harpagofututor* are remarkably similar (Fig. 14a, b). Both taxa possess neural arches (na) and spines (nsp), haemal arches (ha) and spines (hsp), and mineralised central elements that enclose the notochordal space. In agreement with Patterson (1965; see also: Didier 1995; Stahl 1999) we regard these mineralisations as chordacentra (chc) (*contra* Lund 1982, who interpreted these as arcualia). Each chordacentrum appears to be composed of calcified cartilage (c.f. Moy-Thomas 1935). In living chimaeroids, chordacentra form complete mineralised rings within the notochordal sheath, are closely packed, and are anteroposteriorly short (Goodrich 1930; Patterson 1965; Didier 1995; Stahl 1999). In contrast, the chordacentra of *Chondrenchelys* and *Harpagofututor* are much longer, anteroposteriorly. Most of the chordacentra are broken and/or displaced, but short coherent sequences are preserved in place. For *Chondrenchelys*, examples include specimens NMS 1891.53.33 (Fig. 14c) and NMS 1998.35 (Fig. 3b); and for *Harpagofututor*, specimens CM 272326 (Fig. 14b) and CM 41073. These show that each chordocentral segment is composed of distinct dorsal and ventral, thin walled half-rings (hemicentra), at least within the trunk region. Each hemicentrum is wedge-shaped in lateral aspect (Fig. 14c), although there is regional differentiation in form. The thin walled profile of these units is shown well in a series of collapsed centra facing laterally within the trunk region of NMS 1998.35 (Fig. 14d). Each centrum bears a small, sub-triangular boss (sb) in the mid-ventral region, the significance of which is unknown. Within the caudal series, these hemicentra are more irregularly shaped (see also: Moy-Thomas 1935). NMS 1891.53.33 preserves lozenge-shaped gaps between adjacent chordocentra pairs (Fig. 14c, icg), visible in lateral view. In *Chondrenchelys*, the chordacentra are not tightly packed as in extant chimaeroids. Lund's (1982) reconstruction

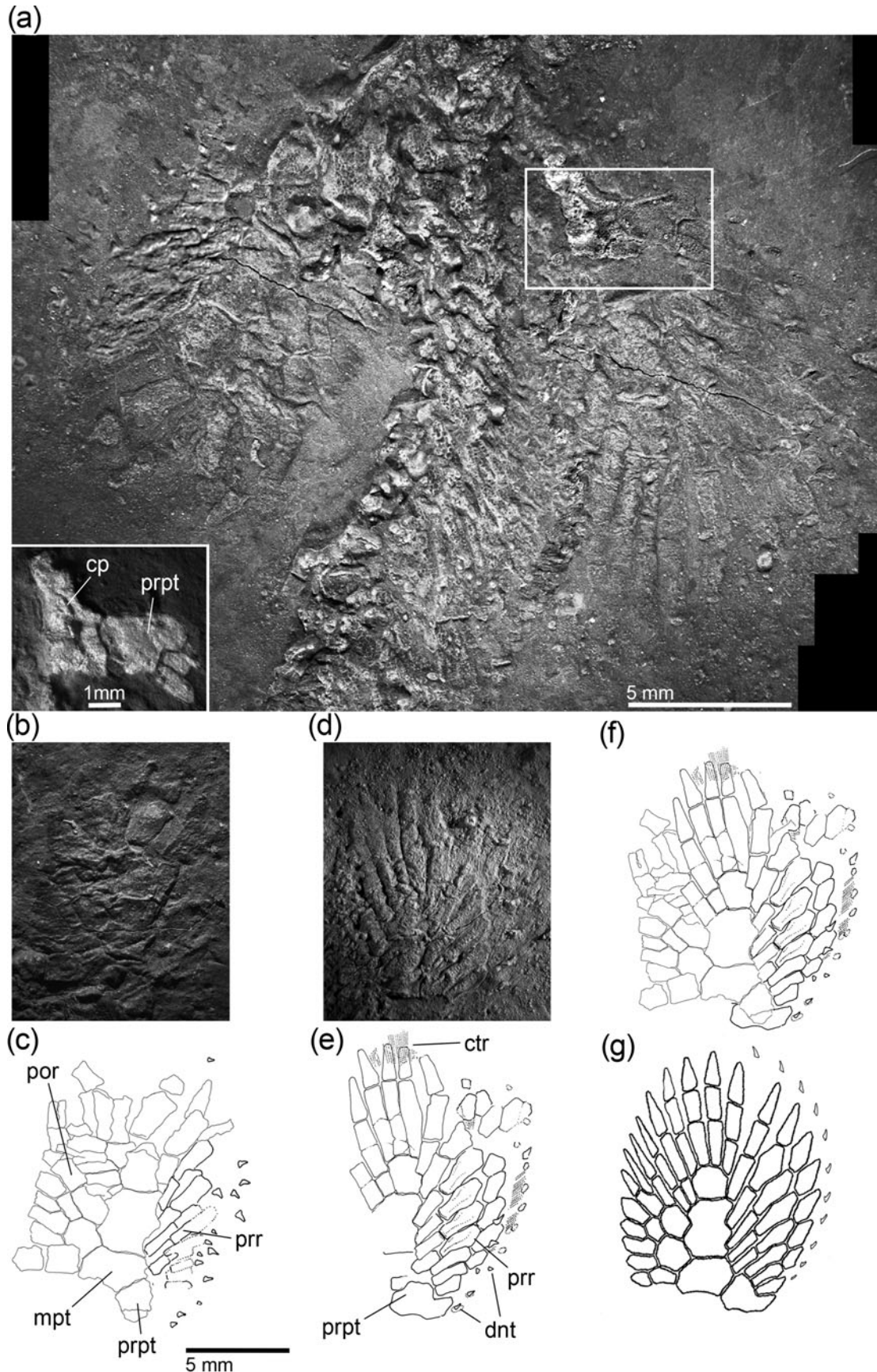


Figure 11 *Chondrenchelys problematica*, male-pattern pectoral fins from NMS 2002.68.1: (a) NMS 2002.68.1p, with parts of NMS 2002.68.1cp superposed to create a composite image of the pectoral skeleton in dorsal view; anterior at top of page. Boxed area of right pectoral fin encloses propterygium; inset image shows higher magnification image of propterygium and adjoining coracoid region (matrix masked to highlight fin and girdle cartilage); (b) left pectoral fin from NMS 2002.68.1p, distal at upper margin, leading edge at right margin; (c) drawings of left pectoral fin skeleton from part and counterpart; (d) Right pectoral fin from NMS 2002.68.1p, distal at upper margin, reversed to show leading edge at right margin; (e) drawings of right pectoral fin skeleton from part and counterpart; (f) combined fin skeletons of left and right pectoral fins; (g) restoration of complete pectoral fin skeleton. All specimens whitened with ammonium chloride except for inset image of propterygium. Abbreviations: cp = coracoid plate; ctr = ceratotrichia; dnt = denticles; mpt = metapterygium; por = postaxial radials; prpt = propterygium; prr = preaxial radials.

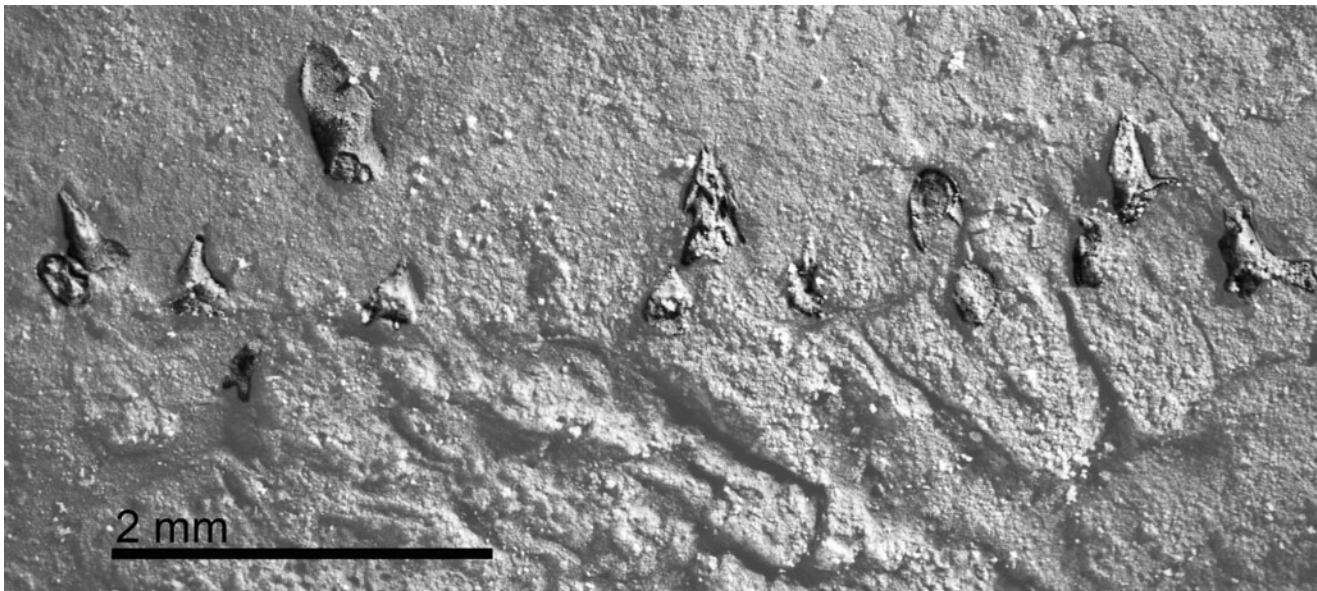


Figure 12 *Chondrenchelys problematica*, male pectoral fin denticles from left side, NMS 2002.68.1p. Image masked to highlight denticles against surrounding matrix and adjacent cartilages. Anterior (proximal) to right; leading edge towards upper margin.

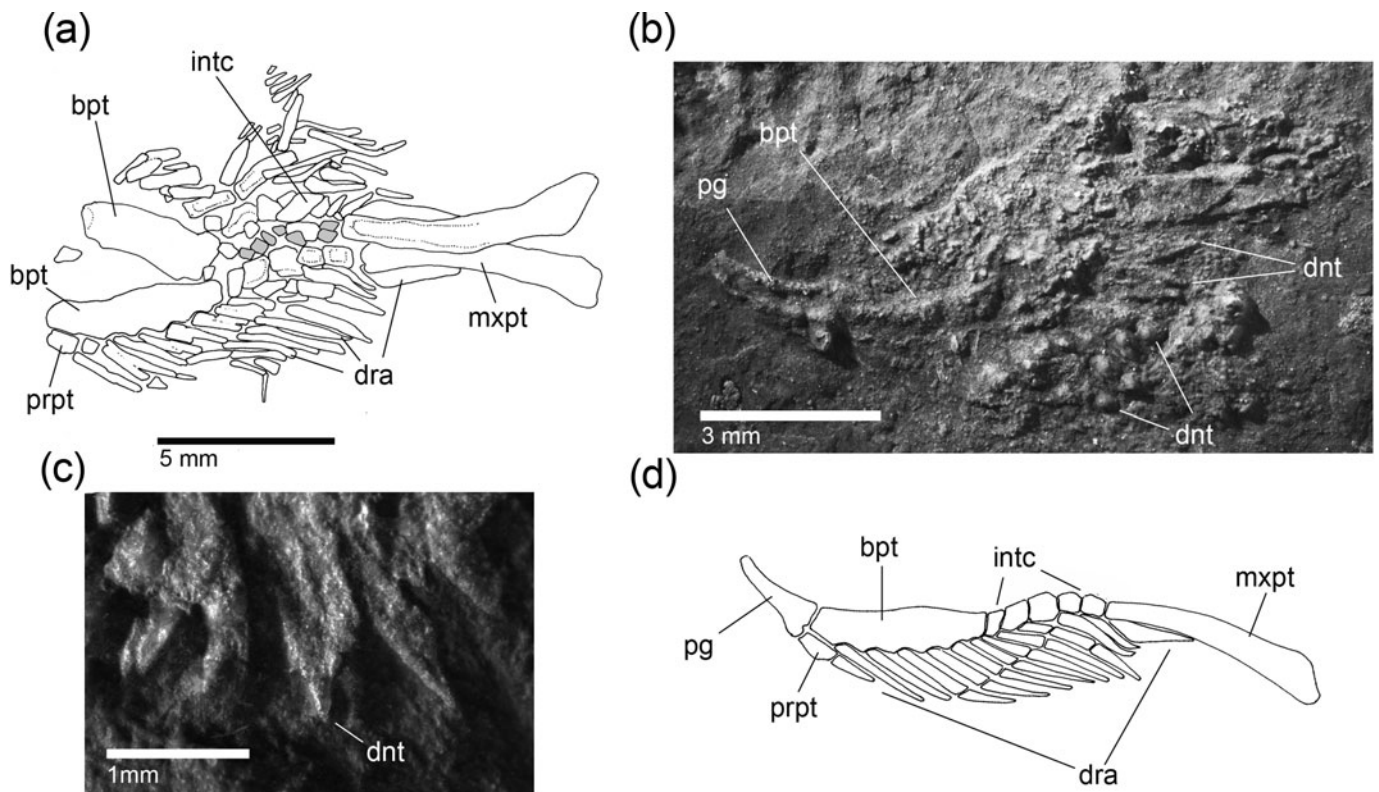


Figure 13 *Chondrenchelys problematica*, male pelvic fin: (a) NMHUK P.18057, camera lucida drawing from original specimen, showing left and right fins in ventral view with anterior to the left. Gray shaded areas probably represent denticle bases; (b) NMS 2002.68.1p, girdle and fin, with many of the cartilaginous radials obscured by large denticles (specimen coated with ammonium chloride). Specimen is in latero-ventral view with anterior to the left; (c) NMS 2002.68.1p, detail of radial tips with terminal denticles (matrix masked to highlight skeletal material). Distal is to the bottom of the image; (d) reconstruction of pelvic girdle and fin skeleton. Abbreviations: bpt = basipterygium; dra = distal radials; dnt = denticles; intc = intermediate cartilages; mxpt = myxopterygium; pg = pelvic girdle; prpt = pelvic propterygium.

of *Harpagofututor* shows very widely-spaced centra. This differs from our observations of CMNH 27326 (Fig. 14b), which more closely resemble *Chondrenchelys*.

The register of centra (each consisting of a chordacentral pair) to the neural, and posteriorly haemal, arches varies

throughout the axial skeleton of *Chondrenchelys*. A simple segmental arrangement of complete vertebral units (one centrum to one arch and spine) appears to be present in the pectoral region, and possibly persists through the entire pre-pelvic region (Fig. 3), but it is difficult to find any region of the axial skeleton

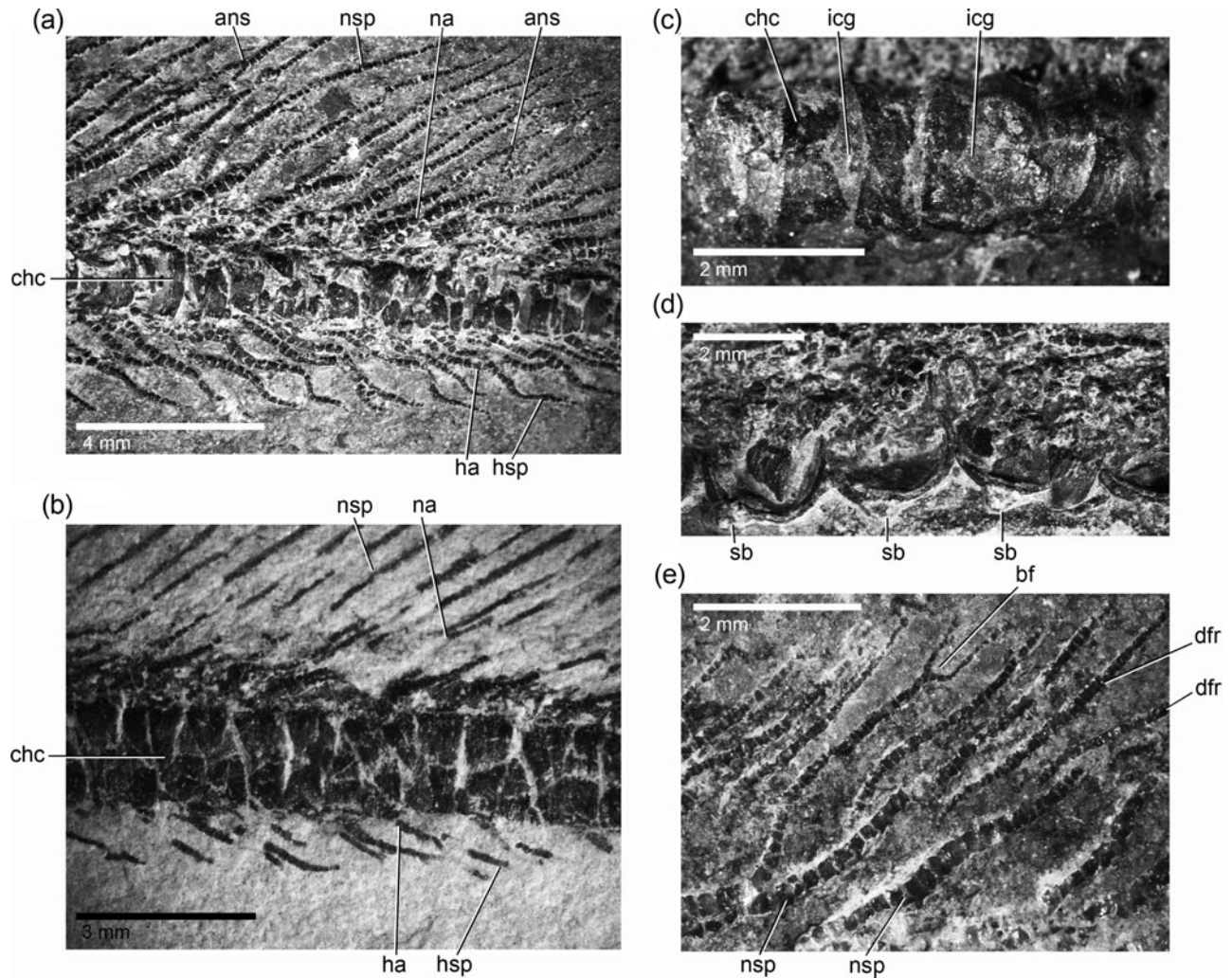


Figure 14 Chondrenchelyid axial skeletons: (a) *Chondrenchelys problematica* NMS 1998.35, detail of anterior caudal region showing extremities of neural and heamal spines, and anastomosing neural spines; (b) *Harpagofututor volsellorhinus* CM 27326, detail of anterior caudal region; (c) *Chondrenchelys problematica* NMS 1891.53.33, intact series of chordacentra forming a cylindrical axial column; (d) *Chondrenchelys problematica* NMS 1998.35 detail of trunk chordacentra; (e) *Chondrenchelys problematica* NMS 1885.54.5A, detail of caudal skeleton showing bifurcating neural spine and dorsal fin radials. Anterior to left of page; images in (b) and (e) reversed. Abbreviations: ans = anastomosed neural spines; bf = bifurcated neural spine; chc = chordacentrum; dfr = dorsal fin radial; ha = haemal arch; hsp = haemal spine; icg = inter-central gap; na = neural arch; nsp = neural spine; sb = subtriangular boss;

that is consistently mono- or diplospondylous. It is noteworthy that in living chimaeroids, the ratio of arches to centra is fundamentally irregular throughout the vertebral column (Didier 1995).

The axial skeleton is substantially longer than previously appreciated (compare Figs 1, 3 and 4). Moy Thomas's (1935) reconstruction produced a pectoral–pelvic length relative to total axial column length ratio of 1:2.5 (using specimens now known to be males). Here, NMS 1998.35.1 (female) has ratio of 1:3, and NMS 2002.68.1 (male) is proportionally (though not absolutely) longer, at 1:3.25. Characterising the axial skeleton in terms of vertebral counts is difficult. Both Moy-Thomas (1935) and Patterson (1965) estimated approximately one hundred vertebrae in *Chondrenchelys*. Lund (1982) was more cautious, noting that in *Harpagofututor* it is “impossible to obtain accurate counts past the midcaudal part of the tail.” We counted precaudal neural arches, using each arch as a proxy for a “vertebral segment.” Defining the start of the caudal region at the first haemal arch (Sallan 2012), in NMS 1998.35 (large female: Fig. 3), there are at least 36 pre-caudal vertebral segments. In NMS 1885.54.5A (small female) and NMS 2002.68.1 (large male: Fig. 4), the counts are around 35 segments. These counts

are substantially larger than Moy-Thomas's (1935) reconstruction (26 segments), and are more compatible with Lund's (1982) restoration of *Harpagofututor* (32 pre-caudal vertebrae) and modern *Rhinochimaera* (34 pre-caudal segments) (Patterson 1965, fig. 1).

Neural and haemal arch morphology conforms to previous descriptions (Moy-Thomas 1935; Patterson 1965). In contrast to the chordacentra, to which their bases are firmly attached, the arches consist of what might be described as tessellate calcified cartilage, at least proximally. The anteriormost cervical series, including those overlapped by the scapular process, consists of about five segments. These cervical arches in addition to the following five or six arches are anteroposteriorly broad (Moy-Thomas 1935). Caudal to these, neural arches and spines narrow rapidly and are preserved as delicate chains of bead-like calcifications (Moy-Thomas 1935; Stahl 1999). In NMS 1998.35, these beads are slightly spool-shaped, so that the spines are, in effect, segmented (Fig. 14a, d).

As preserved, many of these arches and spines exhibit a sinuous curvature (Fig. 14a) reminiscent of fossil crinoid appendages, suggesting a high degree of flexibility in life. Functionally, this would be highly unusual for a vertebrate; the

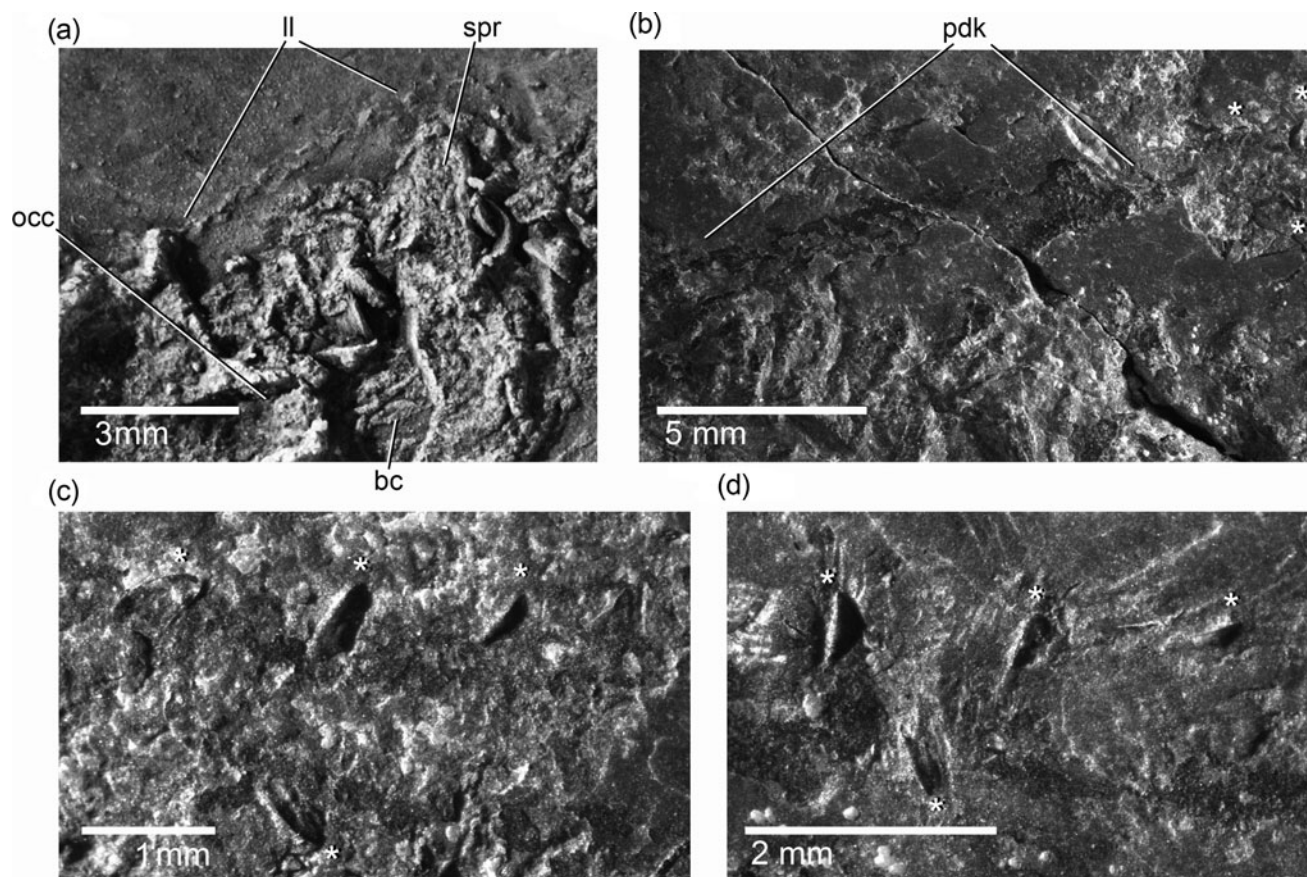


Figure 15 *Chondrenchelys problematica*, scales: (a) NMS 1998.35.1, area between occipital region and pectoral girdle, showing lateral line scales; (b) HM V.7173, showing pre-dorsal fin keel; (c) and (d) dark stain flanked by simple scale. Anterior to left of page; specimen in (a) coated with ammonium chloride and contrast enhanced to highlight lateral line scales. Abbreviations: bc = branchial cartilages; ll = lateral line scales; occ = occipital cotylus; pdk = pre-dorsal fin keel; spr = scapular process of pectoral girdle; asterisks mark scales aligned with perimeter of dorsal fin.

straighter vertebral arches and spines of *Harpagofututor* (Fig. 14b) are far more conventional in this respect. A further unusual feature of the axial skeleton, first noted in *Chondrenchelys* by Moy-Thomas (1935) and subsequently reported in *Harpagofututor* (Lund 1982), is that some of the neural spines bifurcate distally. We confirm this, and also note bifurcations in caudal neural spines as well, e.g. NMS 1885.54.5a (Fig. 14e, b, f), although the occurrence of these bifurcations is rare along the axial skeleton. Finally, *Chondrenchelys* specimens NHMUK P.4085 and NMS 1998.35.1 display a further apomorphic characteristic: irregularly spaced anastomoses between distal parts of adjacent members of the neural spine series and haemal spine series, (Fig. 14a, ans).

3.6. The midline fin

The dorsal fin is most completely preserved in NMS 1998.35.1 (Fig. 3). Gracile radials extend from a level above the neural spines, starting at approximately the scapulocoracoid and continuing caudally. However, they do not reach the posterior distal extremity (see below). These radials are well preserved in NMS 1998.35.1 (Fig. 3) and HM V.7173 (Fig. 5). In NMS 2002.68.1 (Fig. 4), the midline fin radials are only preserved in the more caudal portion of the body. Radials (dfr) consist of a single column of bead-like or spool-shaped calcifications, which resemble the adjacent distal extremities of the neural spines. Throughout most of the fin, such radials are arranged in proximal and distal rows, and several fin radials correspond to each neural arch/spine segment. In the anterior part of the fin, around four radials intercalate between each neural spine

(c.f. Moy-Thomas 1935), whereas in the posterior trunk and caudal region this ratio decreases (Fig. 14e). Moy-Thomas illustrated a series of robust, anteroposteriorly broad radials of the dorsal fin of male specimens, forming a robust fan in the cervical and pectoral region of the axial column (Moy-Thomas 1935, plate 2, fig. 1; easily confused with the broad, anterior-most neural spines). Re-examination of NMS 1891.53.33 reveals this is actually a preservational artifact and that that these radials are actually the hypertrophied radials of a subjacent male pectoral fin.

Importantly, in all examined specimens, there is no evidence for a series of radials beyond the haemal spines. As such, and in agreement with Lund (1982), we note that *Chondrenchelys*, like *Harpagofututor*, lacks a hypocaudal fin. Previous reconstructions (Moy-Thomas 1935, reproduced in both Patterson (1965) and Stahl (1999)) show arches/spines and a series of radials supporting both the dorsal and ventral body walls, with a separate dorsal and ventral midline fins reconstructed externally to all of these skeletal structures (see Fig. 1). In fact, the dorsal body wall is supported by the neural arches/spines, with the midline fin supported by the radials and, in the more posterior parts of the fin, by the distal extremities of the neural spines that extend outwards as far as the tips of the radials. In addition, the dorsal fin, as indicated by the caudalmost extent of the neural radials and spines (NMS 1998.35.1, NMS 2002.68.1), terminates short of the distalmost extremity of the axial skeleton by 25–30% of the post-pelvic axial column length, giving *Chondrenchelys* a distinctive “rat tail”. This is only evident only in better-preserved and prepared specimens

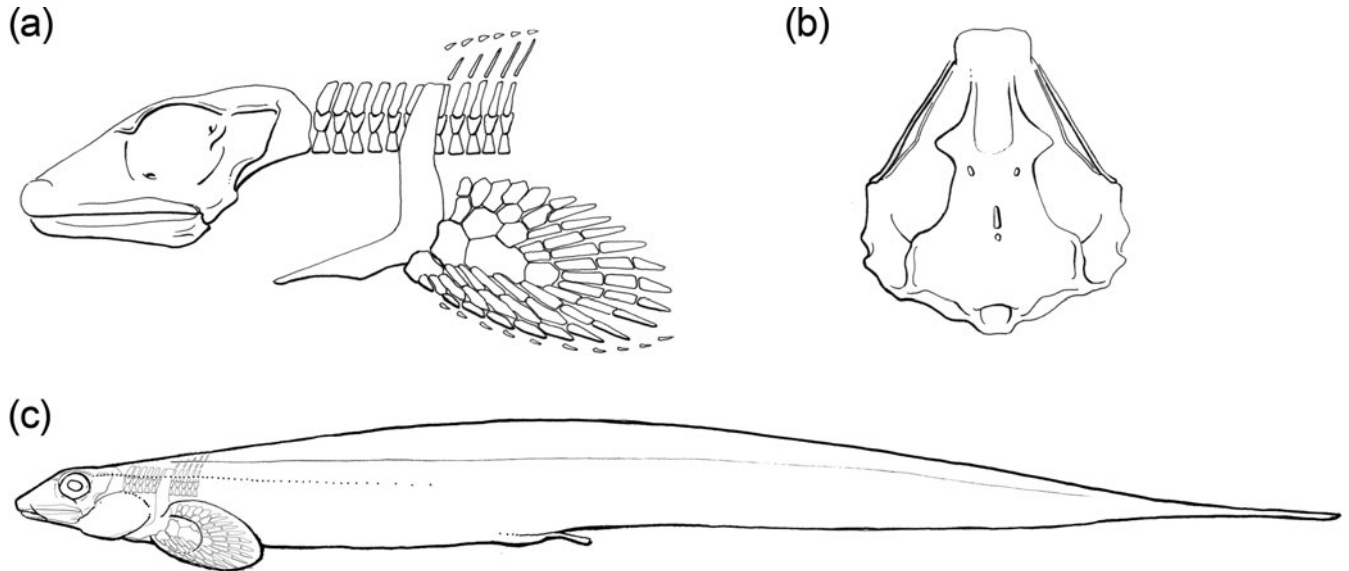


Figure 16 New reconstruction of *Chondrenchelys problematica*: (a) cranium, pectoral girdle and fin, and anterior section of axial skeleton in lateral view; (b) cranium in dorsal view; (c) complete body outline in lateral view. Compare (c) with Figure 1.

(Figs 3, 4, 16). The unusual extent of the dorsal fin, in conjunction with no ventral midline fin, is reminiscent of the extant *aba aba*, *Gymnarchus niloticus*.

3.7. Squamation

Modern adult chimaeroids lack scales covering the body, and, in adults the squamation is mostly restricted to areas of the clasping organs in males, and a series of specialised, crescent-shaped denticles supporting the lateral line canals in both sexes (Didier 1995). Previous descriptions, as well as the current work, highlight similarly minimal scale coverage for *Chondrenchelys* (Moy-Thomas 1935; Lund 1982). Those scales that are present are restricted to specific structures, such as the extremities of the paired fins in males (Figs 11–13).

The paths of sensory canals are not well preserved in *Chondrenchelys*, but a short series of anteriormost main lateral line scales is preserved on the right side of the pre-pectoral area in NMS 1998.35.1 (Fig. 15a, ll), a female. These scales run from the posterolateral prominence of the neurocranial roof to the area dorsal to the scapular process. Lateral line scales are also visible, but very poorly preserved in NMS 2002.68.1, a male. All are broken and preserved as fragments overlying the chordacentra. The shape of these lateral line scales is difficult to determine, but each example appears to be antero-posteriorly elongate, forming a short gutter.

A further and previously unreported series of scales is associated with the dorsal fin. Thus far, these are exposed uniquely on HM V.7173 (Fig. 15b–d). In this female *Chondrenchelys* specimen, a keel-like area of dark material slopes dorsally and posteriorly from the occipital region. Note that in Figure 5, this dark film of material is mostly obscured by ammonium chloride sublimate. In Figure 15b, the leading edge of this pre-dorsal keel (pdk) is gently convex, the trailing edge is distinctly concave and slightly mineralised, and the apex continues posteriorly as a narrow, dark belt, dorsal to the neural spines and radials. Simple, flattened scales flank this dark strip. Each scale (examples marked by an asterisk in Fig. 15b–d) is about twice as long as wide, with a pointed, spearhead shape; these are morphologically distinct from lateral line scales. These scales are broadly similar to those associated with the male tenaculum preserved in *Harpagofututor* (e.g., CMNH 27326), but they do not appear to be recurved in *Chondrenchelys*.

Ornamentation, in the form of specialised scales and other tenaculum-like structures on the head, appears to be common a feature among stem holocephalans: *Harpagofututor* (Lund 1982), *Harpacanthus*, (Lund & Grogan 2004), and among chondrichthyans more generally, including *Falcatus* (Lund 1985), *Damocles* (Lund 1986) and *Akmonistion* (Coates & Sequeira 2001). Notably, embryonic and hatchling chimaeroids possess scales on the dorsal surface of the head and trunk (Didier *et al.* 2012), seen here in *Callorhinchus* (Fig. 6a, c). Such specialised and regionally-restricted squamation might represent a plesiomorphic condition for the Holocephali.

4. Discussion

Extant elasmobranchs and holocephalans are morphologically distinct and disjunct clades, and this marked dissimilarity in the Recent has contributed to a growing debate over the nature of ancestral chondrichthyan conditions and membership along the stem elasmobranch, holocephalan and chondrichthyan lineages. Effectively, the central question concerns the phylogenetic depth of the node defining the crown-clade of Chondrichthyes, and it is worth noting that this issue bears further on estimates of plesiomorphic gnathostome conditions (Maisey 1984, 2012; Janvier 1996; Coates & Sequeira 2001; Brazeau 2009; Anderson *et al.* 2011; Gillis *et al.* 2011, 2013; Davis *et al.* 2012; Finarelli & Coates 2012; Pradel *et al.* 2013; Zhu *et al.* 2013). Relating the morphological disparity of living chondrichthyans to the increasingly detailed range of Palaeozoic forms presents a growing challenge; hence the significance of the new Mumbie Quarry specimens, which offer a more detailed and effective comparison between ancient and modern holocephalans.

The following discussion attempts to compare and contrast what we now know of the skeletal anatomy of *Chondrenchelys* to character states used in several recent phylogenetic analyses, highlighting likely new characterisations of morphology that may then be incorporated into future analyses. We do not undertake a phylogenetic reconstruction here; a comprehensive analysis will be undertaken in a related study (currently in preparation) on undescribed specimens from Bearsden, Scotland (Dick 1978; Wood 1982; Stahl 1999). Character states discussed below are drawn principally from Pradel *et al.*'s (2011) analysis

of early chondrichthyans, Stahl's (1999) summary cladogram of holocephalan interrelationships, and Patterson's (1965) seminal list of "major characters peculiar to the living chimaeroids".

Few detailed illustrations of the modern chimaeroid chondrocranium are available, in contrast to the numerous photographs, line drawings and, increasingly, rendered CT scans of modern and fossil elasmobranchs. The recently published CT scan of an embryonic *Callorhincus milii* (Khonsari *et al.* 2013; Pradel *et al.* 2013) represents a notable addition to this still limited data set. Most depictions of chimaeroid anatomy are recycled from Dean (1906) and de Beer & Moy-Thomas (1935), although several others are available (e.g., Kesteven 1932; Ribbnik 1971; Didier 1995). This has prompted the preparation of new photographs of a cleared and stained braincase and palate of a pre-hatchling elephant shark, *Callorhincus milii* (Fig. 6a–c). This specimen is at a slightly younger stage than the example depicted in newly available CT scans (Khonsari *et al.* 2013; Pradel *et al.* 2013). Importantly, these examples of pre-hatchling *Callorhincus* display little of the dorsoventral offset between the levels of the basicranium and quadrate observed in adults (Kesteven 1932, figs 3, 4; Didier 1995, fig. 18A), permitting a remarkably straightforward comparison with many of the morphological features observed in *Chondrenchelys*.

4.1. Skeletal tissues, dentition and scales

Multilayered tesseræ of calcified cartilage in the outer neurocranial wall was suggested by Schaeffer (1981) and used by Pradel *et al.* (2011) to unite a subgroup of early chondrichthyans exclusive of holocephalans. Although *Chondrenchelys* shows no evidence of the multilayered condition, multilayered tesseræ are evident in the laterally compressed and fractured preorbital region of *Harpagofututor* (CMNH 27326). The visibility of such tesseræ (Fig. 7b) in *Chondrenchelys* and several other early holocephalan genera, contrasts markedly with the absence of superficially visible tesseræ in extant chimaeroids. Consequently, we suggest that visible tesseræ at the cartilage surface is plesiomorphic relative to crown clade holocephalans.

Chondrenchelys is united with the holocephalans on the basis of a reduced number of tooth families and the presence of tooth crowns reinforced with hypermineralised tissue (Stahl 1999). Finarelli & Coates (2012) noted that the gross morphology of the large posterior tooth plates in *Chondrenchelys* closely resembles Mesozoic and Cenozoic holocephalans. Moreover, growth of the posterior tooth plates in *Chondrenchelys* and these more recent holocephalans is achieved via accretion along the caudal boundary. These similarities are consistent with our observation that *Chondrenchelys* and *Harpagofututor* share very similar tooth plate histologies (e.g., CM 27326A, CM 41091, CM 37521), and Lund's (1982, p. 944) observation that tooth plate histology in *Harpagofututor* is "virtually indistinguishable" from the Triassic and Jurassic genus *Myriacanthus*. However, while the crowns of these tooth plates contain tubular dentine (Patterson 1965), in *Chondrenchelys*, it is not clear that this distinctive histology is restricted to the tritons (Stahl 1999).

Chondrenchelys does not possess a sparse scattering of simple conical scales, *contra* Stahl (1999). Scale covering is greatly reduced (e.g., Patterson 1965), but we note distinct scale morphologies specific to different body regions, with the pectoral fin extremity being the most notable example. Differing from *Harpagofututor* (Lund 1982), in *Chondrenchelys*, scales are monocuspid, non-growing (synchronomerial) and placoid, and therefore structurally similar to modern elasmobranchs (Patterson 1965).

4.2. Cranial morphology

The continuous orbit floor in *Chondrenchelys* (Figs 6, 8) suggests that substantial development of a basitrabecular process (de Beer 1937; see also Pradel *et al.* 2011) contributes to the holostylic cranium. It is also apparent that the skull is not trochibasic (Pradel *et al.* 2011), and the orbits are neither elevated nor continuous across the midline dorsal to the space for the forebrain (Patterson 1965). The roof of the ethmoid region is closed in *Chondrenchelys*, with no precerebral fontanelle (Pradel *et al.* 2011) (Fig. 6), a condition that is widespread among fossil holocephalans and iniopterygians (Pradel 2010). However, in *Chondrenchelys*, the ethmoid roof is depressed centrally, deflected upward on either side forming a ridge along a vertical cartilage (likely the orbitonasal lamina, Fig. 6d, e). In this respect, *Chondrenchelys* resembles *Helodus* (Patterson 1965; pers. obs. JAF & MIC: NHMUK P.8212), which also exhibits a troughed roof of the ethmoid region, flanked by upgrowths of the lamina orbitonasalis without a precerebral fontanelle (Moy-Thomas 1936; Patterson 1965). In *Helodus*, foramina for the superficial ophthalmic nerves are anteriorly-directed (Patterson 1965, fig. 39) suggesting that the steeply-downturned ethmoid roof reflects in-life morphology, not post-mortem collapse. The presence of a trough in the ethmoid region of *Helodus* has been proposed as an incipient ethmoid canal (de Beer & Moy-Thomas 1935; Didier 1995). However, Patterson (1965) doubted this interpretation, hypothesising that the ethmoid canal appeared late in holocephalan phylogeny, due to lateral compression of an originally broad cranium. From our observations of these new specimens (which are manifestly uncompressed laterally), it is clear that there is no ethmoid canal in *Chondrenchelys* and that this trough is not homologous to the ethmoid canal. We suggest that this trough constitutes a potential early holocephalan synapomorphy, but the relationship to conditions in crown group holocephalans and other, putative members of the total group (e.g. sibirhynchid iniopterygians (Pradel *et al.* 2009a; Pradel 2010) remains unclear.

The presence of efferent superficial ophthalmic foramina opening below and anterior to the origin of the antorbital crest constitutes a further, as yet unexploited, morphological character visible in a subgroup of those holocephalan taxa that lack an ethmoid canal (e.g., *Squaloraja*, *Helodus*). In contrast, *Chondrenchelys* exhibits a condition similar to elasmobranchs (possibly plesiomorphic for chondrichthyans, although this remains to be tested) where the largest and most anterior superficial ophthalmic foramen perforates the cranial roof postero-medial to the antorbital crest.

As in living chimaeroids, the ethmoid region of *Chondrenchelys* is elongate, with separation of the anterior boundary of the orbit from the posterior margin of the nasal capsules presenting a broad pre-orbital surface in lateral view. This arrangement is strikingly different from that of iniopterygians (Pradel 2010). In living chimaeroids, the antorbital crest anchors substantial parts of the *adductor mandibularis anterior* and *levator anguli oris* muscles (Edgeworth 1935; Anderson 2008; MIC pers. obs.). The abbreviated postorbital region and proportionally large orbit imply that posteriorly oriented jaw adductors would impinge on the eye during contraction, whereas the combination of a pre-orbital cartilage wall (orbitonasal lamina) and well-formed antorbital crest in *Chondrenchelys* suggests that the bulk of the jaw adductor muscle inserted anterior to the eye, as in extant chimaeroids (Kesteven 1932; Ribbnik 1971; Didier 1995; Anderson 2008). The absence of a suborbital ridge in *Chondrenchelys* (present in modern chimaeroids: Fig. 6a, c) argues against any substantial muscle attachment below the eye. Re-positioning of the jaw adductor muscles to insert on the

rostral wall has been repeatedly linked (Patterson 1965; Didier 1995; Janvier 1996) to: (1) an anteriorly displaced jaw joint; (2) an anteriorly positioned gill basket; and (3) dorsally located orbits. Notably, all three of these characters are absent in *Chondrenchelys*.

Early chondrichthyans tend to exhibit a generalised crown gnathostome condition in which the postorbital arcade encloses the jugular canal (Pradel *et al.* 2011), and the posteriorly continued route of the jugular vein is nested close to the otic capsule wall. Extant chimaeroids (Patterson 1965; Didier 1995) and several fossil holocephalans (e.g., *Helodus*; Moy-Thomas 1936; Patterson 1965) are characterised by an alternative, specialised condition, in which the jugular vein passes through the subocular shelf via an opening known as the cranioquadrate passage (cqp) (Fig. 6b, c). In this configuration, the pathway of this major vein is remote from the otic region. Neither of these conditions is apparent in *Chondrenchelys*, with no evidence for either an enclosed passage or a jugular route close to the otic wall (Figs 6a, b, 8a, c). Rather, there is a laterally-positioned jugular notch (Fig. 6d, e), which is similar to the notch visible in the comparably sized six-month embryo of *Hydrolagus colliciei* (see: Dean 1906, fig. 84b). Later in ontogeny, this notch closes around the jugular vein with the expansion of the palatoquadrate cartilage to form the cranio-quadrate passage (see Fig. 6b, c). Significantly, a jugular canal is now known to be present in iniopterygians (Pradel 2010). Therefore, *Chondrenchelys* appears to show an alternative condition, a jugular notch in the ventral part of the lateral margin of the postorbital arcade or rim, much like pre-hatchling chimaeroids prior to full enclosure of the jugular vein (Dean 1906; de Beer & Moy-Thomas 1935; de Beer 1937).

The otico-occipital region is chimaeroid-like in several respects, including its diminutive proportions relative to the orbital and ethmoid regions, the absence of persistent cranial fissures and the absence of a dorsal otic ridge bordering part of the endolymphatic fossa (Schaeffer 1981; Coates & Sequeira 1998; Pradel *et al.* 2011; Davis *et al.* 2012). The postorbital arcade requires additional mention here, as it flanks the anterior portion of the otic capsule, and therefore the inferred location of the anterior ampulla. However, with the exception of otico-occipital proportions, Pradel *et al.* (2011) note that these characteristics are also present, to varying degrees, in crown-clade elasmobranchs, making their status as holocephalan synapomorphies uncertain.

In placoderms, osteichthyans, *Acanthodes* and many early chondrichthyans, the occipital block is positioned posterior to the otic capsules, in contrast to extant and fossil elasmobranchs, where the occipital block is “wedged” between the otic capsules (Maisey 2005). There is no evidence in *Chondrenchelys* for any such “wedging” of the occipital unit and, in *Callorhynchus*, occipital arch intrusion between the otic capsules is minimal: note the anterior-posterior level of the posterior rim of the endolymphatic fossa (Fig. 6a–c, fe). Indeed, the condition in *Chondrenchelys* is similar to what is observed in *Acanthodes* (Davis *et al.* 2012, supplementary figs 15a, c–e, End, Pdf) and *Cladodoidea* (Maisey 2005, fig. 4). Thus, if slight intrusion of the occipital arch between the otic capsules represents a diagnostic character state, it must represent a synapomorphy for a much deeper node in gnathostome phylogeny.

Few chimaeroid synapomorphies have been identified in the lower jaw. Stahl (1999) comments on symphyseal fusion, now known to be present in *Chondrenchelys*. The terminal posterior articulation of the mandible is also characteristic of chimaeroids and some broader set of fossil holocephalans, notably including *Chondrenchelys*.

4.3. Postcranial morphology

Like modern chimaeroids, the vertebral column of *Chondrenchelys* is polyspondylous with variable registration between arch and chordacentra elements. Yet, in other respects the axial skeleton of *Chondrenchelys* is not representative of extant holocephalan conditions. The anguilliform body shape is a morphotype confined to only a handful of Palaeozoic members of the clade. The absence of a synarcual and dorsal fin spine is also unusual, but it is unclear if this represents apomorphic or symplesiomorphic conditions. Among holocephalans, a synarcual cartilage seems to be functionally linked to muscular support for the dorsal fin spine (Didier 1995), thus absence in *Chondrenchelys* might be secondarily derived. *Harpacanthus* (Lund & Grogan 2004), a non-holostylic cartilaginous fish, but likely close relative of the Holocephali from Bear Gulch, provides an intriguing comparison, as it also lacks a fin spine/synarcual, and possesses a sub-anguilliform postcranium with a single, extended dorsal fin. The posterior off-set of the gill skeleton and pectoral girdle relative to the position normally observed in holocephalans might also be linked to the anguilliform postcranial proportions in *Chondrenchelys*, rather than representing plesiomorphic chondrichthyan conditions. Mehta *et al.* (2010), following Nelson (1966), found a consistent relationship between “branchial-arch displacement” (rostral–pectoral length/cranial length) and degree of body elongation (total length/maximum body diameter). This suggests that longer eels have progressively more posteriorly displaced branchial arches, which implies that the relative positions of the gill skeleton and pectoral girdle in *Chondrenchelys* might be secondarily derived.

The pectoral girdle of *Chondrenchelys* is itself unremarkable, displaying no clear synapomorphies with the highly sculpted surfaces of extant chimaeroid examples. However, the pectoral fin of male examples (at least) is now known to be dibasal, as in other holocephalans. The monobasal condition of pelvic fins in chimaeroids is manifestly absent in *Chondrenchelys*, in which is also dibasal (in males at least).

The dorsal fin is highly specialised. The occasionally branched and reticulated network of axial endoskeletal in chondrenchelyids supports is unusual. The underlying network of cartilage and connective tissue in the dorsal fin was likely more extensive than the mineralised component that is preserved, which raises questions about the biomechanical consequences of this arrangement. A comparison may be made with the endoskeletal supports found in batoid wings, which also exhibit cross-bracing between radial elements that, occasionally, branch distally. Functionally, such cross-bracing is associated with oscillatory swimming requiring large amplitude deformations of the fin (Schaefer & Summers 2005). In conjunction with the gross similarity in body plan and dorsal fin morphology to *Gymnarchus niloticus*, this could potentially offer insight into the functional nature of the midline fin and locomotion in *Chondrenchelys*.

4.4. General comments on the age, morphology and significance of *Chondrenchelys*

Perhaps the most cogent point to emphasise is that *Chondrenchelys*, which is the earliest holocephalan that is known from substantial skeletal remains (Moy-Thomas 1935; Patterson 1965), is much closer to conditions observed in crown-clade chimaeroids than previously appreciated (Lund 1982; Stahl 1999). This parallels previous observations that its dentition is similarly more derived than previously thought (Finarelli & Coates 2012). Moreover, some of the apparent symplesiomorphies in chondrenchelyids might actually be secondary reversals associated with a highly specialised body plan. Until we have a

more secure phylogenetic hypothesis for early chondrichthyans, conventionally shark-like Palaeozoic fishes must remain less securely attached to either the elasmobranch or chondrichthyan stems (Maisey 2012). It is, however, difficult to conceive of a credible phylogeny that would place *Chondrenchelys* anywhere other than the Holocephali. It follows that *Chondrenchelys* constitutes a secure calibration marker, providing a hard minimum age for the last common ancestor of elasmobranchs and chimaeroids.

If *Chondrenchelys* is to be used as a hard minimum for the divergence age estimate, we note that this age (336.5 Ma) is approximately 50 million years younger than the oldest tooth plate fragment that has been attributed to the Holocephali, from the Middle Devonian (Givetian) of France (Darras *et al.* 2008). However, rounded and low-crowned teeth or tooth plates with osteodentine or similar histologies evolved independently among several early gnathostome lineages. Examples include the varied shapes of lungfish tooth plates (Smith *et al.* 1987; Smith & Chang 1990), the specialised dentitions of hybodontid and orodontid sharks (Maisey *et al.* 2004; Ginter *et al.* 2010) and the bulbous surfaces of tooth plates in amphicentrid actinopterygians (Traquair 1879; Bradley Dyne 1939). The Darras *et al.* (2008) datum is plausible, but alone it is insufficiently resolved to meet the criteria of a secure fossil marker (Parham *et al.* 2012).

By the time body fossils are observed in the fossil record, holocephalans look decidedly modern, and the stratigraphic incongruence with their outgroups implies a considerable quantity of missing data, even if a Middle to Upper Devonian date for the chondrichthyan crown radiation is postulated (consistent with the isolated tooth plate record: Stahl 1999; Darras *et al.* 2008). Importantly, *Chondrenchelys* also demonstrates that the suite of cranial apomorphies characterising extant chimaeroids does not constitute a single morphological complex, despite several compelling ontogenetic arguments (Goodrich 1930; de Beer & Moy-Thomas 1935; de Beer 1937). Rather, there is a decoupling of the specialised forward-rotated jaw musculature, inserting on an extended rostral region, from other distinctly holocephalan features (e.g.: anteriorly-displaced jaw articulation; dorsally-displaced orbits with an inter-orbital septum; ethmoid canal housing the ophthalmic nerves).

Combined with observations of a decidedly modern dental morphology (Finarelli & Coates 2012), *Chondrenchelys* expands the diversity and range of chondrichthyan ecomorphospace following the Hangenberg extinction events (Sallan & Coates 2010; Smithson *et al.* 2012). The full impact of *Chondrenchelys* on early chondrichthyan phylogeny remains unclear, as many of the cranial features addressed in our descriptions (including Finarelli & Coates 2012) are not yet adequately integrated into the context of existing phylogenetic datasets (Stahl 1999; Coates & Sequeira 2001; Pradel *et al.* 2011; Grogan *et al.* 2012). In closing, we note that body elongation and an anquiliform body plan may be linked to particular ecological niches and complex feeding behaviours (Mehta *et al.* 2010) which appear to be consistent with many of the extraordinary dental and skeletal characters of this early holocephalan.

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