

Cranial structure in the Devonian lungfish *Soederberghia groenlandica* and its implications for the interrelationships of ‘rhyngodipterids’

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ABSTRACT: New cranial material of the ‘rhyngodipterid’ lungfish *Soederberghia groenlandica* from Upper Devonian (Famennian) strata in East Greenland is described. Previously unknown structures identified here include components of the hyoid arch (ceratohyal, hypohyal) and the lower jaw (prearticular, dentary). Earlier interpretations of the cheek and mandible of *Soederberghia* are reconsidered in the light of new fossil specimens. Some of the difficulties in assessing the homologies between cheek bones in *Soederberghia* and those of other lungfishes stem from confusion over the arrangement in *Rhyngodipterus*, and a revised interpretation of this genus is proposed. The single infraorbital bar found in *Soederberghia* probably originates, in part, from an expanded bone 10 (quadratojugal) of the kind found in *Griphognathus*. Hypotheses that posit ‘rhyngodipterid’ polyphyly seem unlikely in light of a set of derived cranial characters that define a coherent radiation of long-snouted, denticle-bearing lungfishes known from the Late Devonian. The hypothesis presented here places ‘rhyngodipterids’ as a paraphyletic grade with respect to fleurantiids. *Rhyngodipterus*, *Soederberghia*, and fleurantiids form a clade to the exclusion of the species of *Griphognathus*. *G. minutidens* is the sister taxon to this apical group, while *G. sculpta* and *G. whitei* are more remote from it.



KEY WORDS: Aina Dal Formation, Dipnoi, East Greenland, Famennian, Fleurantiidae, *Griphognathus*, Rhyngodipteridae

Soederberghia groenlandica is a large lungfish first described from the Upper Devonian (Famennian) Aina Dal Formation of East Greenland (Säve-Söderbergh 1934, 1937; Lehman 1955, 1959). Subsequent finds of remains attributed to this genus in roughly contemporaneous deposits in North America (Ahlberg *et al.* 2001), Australia (Campbell & Bell 1982; Ahlberg *et al.* 2001), and Europe (Clément & Boisvert 2006) suggest that it was a cosmopolitan member of continental ichthyofaunas near the close of the Devonian. *Soederberghia* is distinguished by an elongated, flattened rostrum and, instead of the tooth plates typical of most other lungfishes, is equipped with a dentition consisting primarily of denticles. A similar morphology characterises four additional Late Devonian lungfish genera: *Griphognathus*, *Rhyngodipterus*, *Jarvikia*, and *Fleurantia*. While these last two taxa are widely held to be closely related to each other (Vorobyeva & Obruchev 1964; Miles 1977; Campbell & Barwick 1990; Cloutier 1996; Cloutier & Ahlberg 1996), there is some controversy concerning the relative phylogenetic positions of *Soederberghia*, *Rhyngodipterus*, and *Griphognathus*. Together, these three genera comprise the nominal family Rhyngodipteridae (Moy-Thomas & Miles 1971; Miles 1977), the coherence of which as either a clade or a grade has been challenged on the basis of apparent discrepancies between *Rhyngodipterus*/*Soederberghia* and *Griphognathus*, as well as similarities between the latter genus and ‘holodontids’ (Ahlberg *et al.* 2001, 2006). Unfortunately, inadequate documentation of many aspects of morphology in *Soederberghia* makes it difficult to select between competing hypotheses of ‘rhyngodipterid’ relationships (Ahlberg *et al.* 2001, 2006; Schultze 2001).

Many outstanding uncertainties concerning the anatomy of *Soederberghia* relate to the skull. This contribution is a complement to recent studies that have focused on the neurocranium (Friedman 2007) and postcranium (Friedman *in press*) of *Soederberghia*, and examines aspects of the dermal cheek, hyoid arch, and mandible. In many cases, these new morphological details have an important bearing on the status of ‘rhyngodipterid’ lungfishes (Ahlberg *et al.* 2001, 2006; Schultze 2001; Friedman 2003, 2005, 2007, *in press*; Long 2005), a subject that is explored in the second half of this study.

1. Materials and methods

1.1. Materials examined

The membership of family-level lungfish taxa follows that used in Friedman (2007, *in press*). As in those contributions, the content of these groups is defined to reflect common usage, with the acknowledgement that many of these groups are probably para- or polyphyletic. In cases where monophyly is uncertain or unlikely, these group names are enclosed in inverted commas. Content of groups is as follows: ‘Chirodiptera’: *Chirodipterus* (which is polyphyletic; Friedman 2007), *Gogodipterus*, *Pillararhynchus* and *Sorbitorhynchus*; ‘Dipnorhynchidae’: *Dipnorhynchus*, *Eriki*, *Speonesdyrion*, and *Westollrhynchus*; ‘Dipteridae’: *Dipterus*, *Orlovichthys*, *Rhinodipterus*; Fleurantiidae: *Jarvikia* and *Fleurantia* (the nominal fleurantiids *Andreyevichthys* and *Barwickia* are not included in this group following the discussion given in section 4.2.4); ‘Holodontidae’: *Holodipterus* (which itself is

probably paraphyletic; Friedman 2007) and *Holodus*; 'Phaneropleuridae': *Andreyevichthys*, *Barwickia*, *Howidipterus*, *Oervigia*, *Pentlandia*, *Phaneropleuron*, *Scaumenacia*; 'Rhynchodipteridae': *Griphognathus*, *Rhynchodipterus* and *Soederberghia*.

Fleurantiidae. *Fleurantia denticulata*, Escuminac Formation (Frasnian), Miguasha, Québec, Canada: BMNH P 6785, P 24745.

Jarvikia arctica, ?Aina Dal Formation, 'Remigolepis Series' (Famennian), Stensiö Bjerg, East Greenland: MGUH VP 3072+3073, 28401, 28402.

'Rhynchodipteridae.' *Griphognathus minutidens*, Snetnaya Group (Frasnian), Koknese, Latvia: MBf.576, 9228, UU 1022.

Griphognathus sculpta, Oberer Plattenkalk (latest Givetian-earliest Frasnian), Bergisch-Gladbach, Germany: MBf 5541, NRM P 5777, 6851.

Rhynchodipterus elginensis, Rosebrae Beds (Famennian), Elgin, Scotland: E 1898.2 A+B.

Soederberghia groenlandica, Aina Dal Formation (Famennian), East Greenland: MGUH VP 3035+3036, 3043+3044, 3051, 3055, 3088, 3098, 3106, 6206, 28393, 28395, 28397, 28411, 28412, 28413, 28414.

Soederberghia simpsoni, Mandagery Sandstone (Frasnian), Canowindra, New South Wales, Australia: AMF102819.

1.2. Methods

1.2.1. Anatomical and nomenclatural conventions. Many aspects of lungfish cranial anatomy are highly derived with respect to other sarcopterygian fishes, and the homologies of bones between these groups are not always clear. Forster-Cooper's (1937) alphabetic-numeric scheme is applied to the dermal skull, with additional considerations drawn from White (1965) and Thomson & Campbell (1971). Where possible, sarcopterygian homologies as inferred by Ahlberg (1991) follow in parentheses. It should be noted that although Forster-Cooper's (1937) system is used here, these names are essentially shorthand and should not necessarily be taken to indicate homology with similarly named bones in other lungfish taxa. Instances where uncritical application of these conventions can yield misleading interpretations are highlighted below (see section 4.1). For a valuable review of the problems related to dermal bone nomenclature in dipnoan skulls, see Miles (1977, pp. 220–6).

1.2.2. Fossil preparation. Most *Soederberghia* material in this present contribution was either prepared conventionally or acid-etched. This latter approach was reserved for badly eroded fossils for which mechanical preparation was unfeasible. Negative preparations were accomplished by immersing specimens in a bath of 10% hydrochloric acid (HCl) solution. Following dissolution of eroded bone, specimens were rinsed in water to remove acid residues. The resulting moulds were then cast in black-tinted latex backed with cotton gauze. Most specimens were dusted with a sublimate of ammonium chloride (NH₄Cl) prior to being photographed.

Details of the internal cranial anatomy of *Rhynchodipterus* have been revealed by computed tomography (CT) scanning of the type and only specimen of this genus. This is part of an ongoing study in collaboration with N. Clark (Hunterian Museum, Glasgow, Scotland) and C. Adams (Royal Alexandra Hospital, Paisley, Scotland), and full results of this research will be published at a later date.

2. Systematic palaeontology

Osteichthyes Huxley, 1880
Sarcopterygii Romer, 1955

Dipnomorpha Ahlberg, 1991

Dipnoi Müller, 1845

Rhynchodipteridae Moy-Thomas, 1939

Soederberghia Lehman, 1959

Soederberghia groenlandica Lehman, 1959

(Figs 1–10, 12)

For synonymy, see Schultze (1992b)

Holotype. MGUH VP 3036, complete dermal skull roof. The counterpart to this specimen is catalogued as MGUH VP 3035.

Locality and age. The holotype of *Soederberghia groenlandica* was collected from the Upper Devonian (middle [latest Fa2a to Fa2b] to early late [Fa2d] Famennian; Marshall *et al.* 1999) Aina Dal Formation (Celsius Bjerg Group) of Nathorst Bjerg (372 m elevation), Gauss Halvø, East Greenland.

Diagnosis. From Friedman (2007): long-snouted, denticle-bearing lungfish differing from other 'rhynchodipterids' in the following combination of characters: bones 4 and 5 excluded from the orbit; width of dermal cheek exceeds the maximum diameter of the orbit.

3. Description

3.1. Dermal skull

3.1.1. Cheek. The precise arrangement of the bones contributing to the dermal cheek and circumorbital region of *Soederberghia groenlandica* has been the source of considerable uncertainty. Only three individuals (MGUH VP 3035+3036, 3043+3044, 3051) described by Lehman (1959) preserve this region, and his figures (Lehman 1959, figs 2–6) disagree over the number and arrangement of bones. One major difference concerns the number of bones of the cheek that bear the infraorbital canal but do not contribute to the orbital margin, with two shown for one specimen (Lehman 1959, fig. 5) and three reconstructed in the others (Lehman 1959, figs 2–3, 6). The structure of the infraorbital bar in *Soederberghia* is also unclear in published accounts. All of Lehman's (1959) figures show a vertical suture running through this bar at or anterior to mid-orbit, but this interpretation has been challenged by Campbell & Bell (1982) for the individual MGUH VP 3043+3044 (Lehman 1959, fig. 5). While these authors agreed with the arrangement of the bones in the postorbital region posited by Lehman, they concluded that the sutures he indicated in the infraorbital bar are not genuine. Instead, Campbell & Bell (1982) reconstructed a large bone extending from the ventral margins of 3 and 5 to far beyond the anterior margin of the orbit, comprising the entire infraorbital bar plus much of the ventral cheek (Campbell & Bell 1982, fig. 4). A new specimen of *Soederberghia groenlandica* (MGUH VP 28393; Fig. 1), coupled with re-examination of Lehman's (1959) original material, provides a critical test of previous interpretations.

Sensory canal patterns were noted as the weathered specimen was being acid etched. Canal-bearing bones of the cheek (Fig. 1) are immediately distinguished by large pores and pustules that are clearly visible on their external surfaces. Bone 3 (3, Fig. 1) in the new specimen is expansive, framing the entire dorsal margin of the orbit. There is no indication of a branch of the infraorbital canal entering this bone. Directly posterior to bone 3 is a large bone 4 (postorbital; 4, Fig. 1), which carries the continuation of the infraorbital canal from KX (KX, Fig. 1) and makes a considerable contribution to the posterior margin of the cheek. The next bone of the infraorbital series is identified as bone 5 (jugal; 5, Fig. 1), as the sensory canal within this ossification gives off a posterior

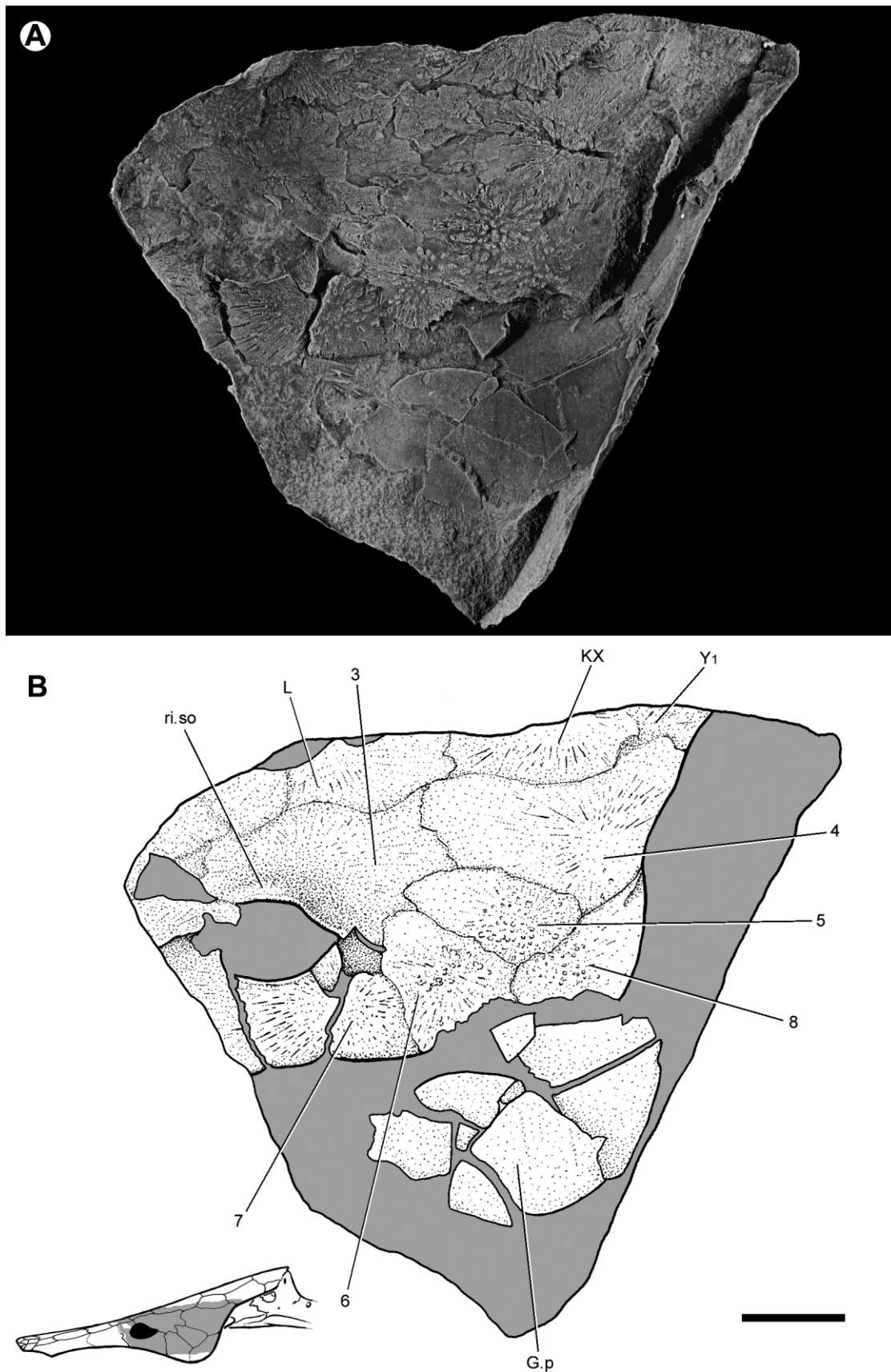


Figure 1 *Soederberghia groenlandica*, MGUH VP 28393, left dermal cheek in lateral view. Latex cast of a negative preparation. Anterior is to right: (A) specimen photograph; (B) interpretive drawing. Dark grey shading represents matrix. Shaded regions in inset drawing represent regions preserved in (A) and (B). Scale bar = 20 mm.

branch – the preopercular canal – that extends posteriorly into a semilunate bone 8 (squamosal; 8, Fig. 1). Bone 8 makes a considerable contribution to the posteroventral margin of the dermal cheek, and the preopercular canal exits from it

posteriorly. Bone 8 contacts bone 4 dorsally, while anteriorly it contacts bone 5 and the next ossification that carries the infraorbital canal. This latter bone is identified as '6' ('6', Fig. 1) by convention, but it might not be the homologue of the

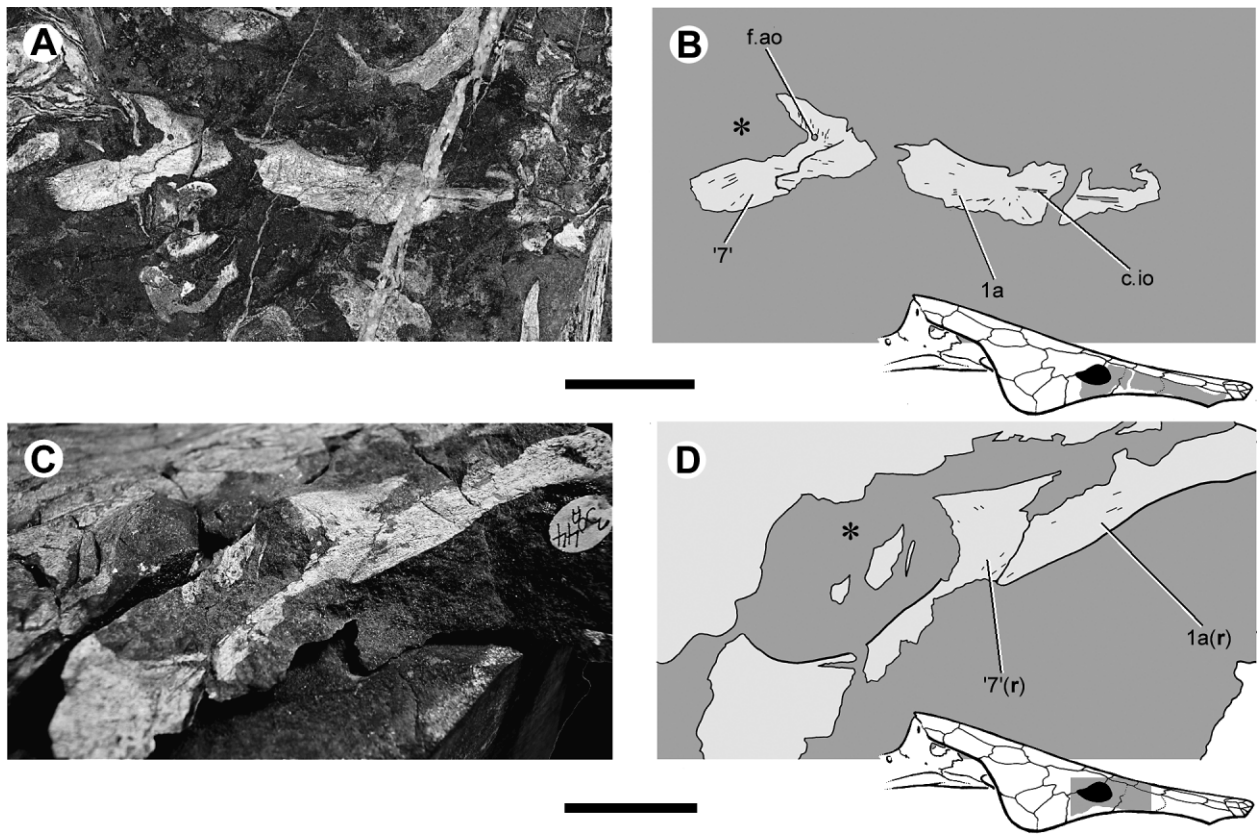


Figure 2 *Soederberghia groenlandica*, antorbital region of dermal skull: (A) specimen photograph, MGUH VP 28412; (B) interpretive drawing; (C) specimen photograph, MUGH VP 3044; (D) interpretive drawing. Dark grey shading represents matrix, light grey shading indicates damaged bone surface. Asterisks mark position of the orbit. Preserved regions marked by shaded areas in inset drawings. Scale bars=20 mm.

bone of the same name in *Dipterus* so it is enclosed in inverted commas here (see section 4.1). Anterior to '6' is a bone that forms the entire infraorbital bar and is provisionally identified as '7' ('7', Fig. 1) by strict application of Forster-Cooper's (1937) nomenclatural scheme. Here too, homology with the homonym in *Dipterus* is unlikely.

The arrangement of bones in this new specimen of *Soederberghia groenlandica* agrees with the pattern described for the Australian *S. simpsoni* (Ahlberg *et al.* 2001). In both specimens, there are three bones that bear the infraorbital canal between KX and the infraorbital bar. This is also the case in the best preserved of Lehman's material of *S. groenlandica* (pers. obs. MGUH VP 3051; Lehman 1959, fig. 6, pl. 12). The region occupied by bones '6' and '7' in other *Soederberghia* specimens is indeed occupied by a single ossification in the individual MGUH VP 3043+3044, consistent with the interpretations of Lehman (1959) and Campbell & Bell (1982). This probably represents individual variation.

The new cheek specimen terminates just anterior to the orbit, making it difficult to determine whether the infraorbital bar is part of a large bone that extends far anterior to the orbit, as suggested by Campbell & Bell (1982), or if it instead terminates near the anterior margin of the orbit and is preceded by one or more bones bearing the infraorbital canal (1 bone[s]), consistent with Lehman's (1959) interpretations and the condition found in other early lungfishes, including *S. simpsoni* (Ahlberg *et al.* 2001). In three specimens that clearly preserve this region (MGUH VP 3043+3044, 28398, 28412), there is no obvious sutural division that separates bone '7' from the ossification forming the anterior margin of the orbit. However, an inclined suture separates bone '7' from the more anterior bones that carry the infraorbital canal and form the margin of the upper jaw (Fig. 2). This suture is visible in

the specimen used by Campbell & Bell (1982) for their revised reconstruction (Fig. 2C–D), which did not show this division. Lehman (1959) was therefore correct in indicating a suture that delimits the infraorbital bar anteriorly, but his placement of it at the level of mid-orbit was not accurate. The anterior position of the suture in *S. groenlandica* agrees with the condition in *S. simpsoni*, in which this division lies immediately anterior to the orbit (Ahlberg *et al.* 2001, figs 2A–B, 3A).

3.1.2. Dermal jaw.

External dermal series. The external dermal bones of the lower jaw of *Soederberghia groenlandica* have been described briefly by Lehman (1959) and Schultze (1969). Consistent with the criticism of Miles (1977), there is no evidence for the separate ossifications identified by Schultze (1969) as 'Infracentrale' and 'hinteres Dentale' in the area posterior to the glenoid. This interpretation seems to have been influenced by the erroneous identification of topologically similar elements ('unteres Infracentrale' and 'oberes Infracentrale') in the mandible of *Griphognathus minutidens* (Gross 1956, fig. 25). The sharp intersection between the ascending lamina and the lateral face of the jaw in this species probably contributed to the original misinterpretation (Miles 1977).

The external dermal series of *S. groenlandica* is dominated by a large bone that extends from the rear of the jaw to near the symphysis (Id2, Figs 3–6). This is consistent with the single ossification centre identified for this region by Lehman (1959, fig. 19), which he termed the 'supraanguloangularie'. A small, anteroventrally located infradentary identified in *G. whitei* on the basis of radiographs (Miles 1977) has a direct equivalent in *Soederberghia* (Id1, Fig. 3). This bone was noted by Lehman (1959, p. 31), but he did not indicate its presence on either his text-figures or plates. It is, however, clear in a plate that shows

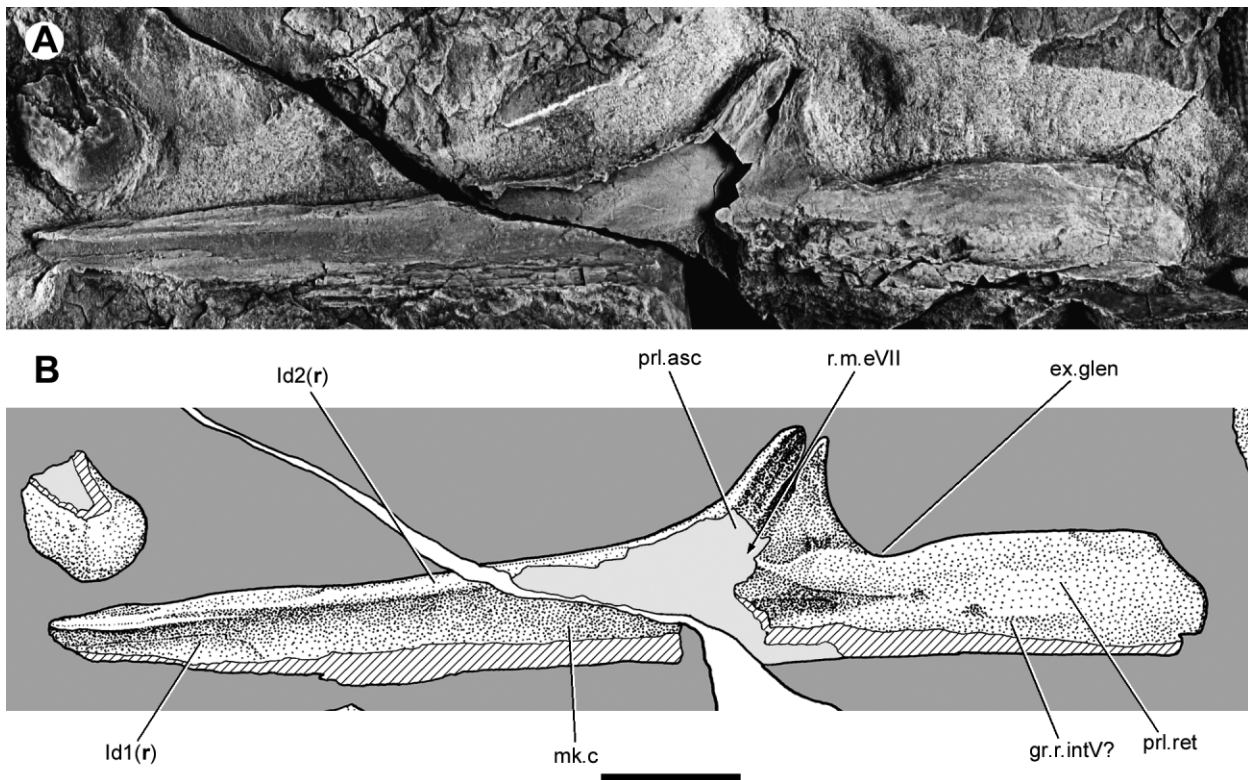


Figure 3 *Soederberghia groenlandica*, right mandibular ramus in lingual view, MGUH VP 28414: (A) specimen photograph; (B) interpretive drawing. Dark grey shading represents matrix, light grey shading indicates bone impression. Damaged bone indicated by diagonal hatching. Scale bar=20 mm.

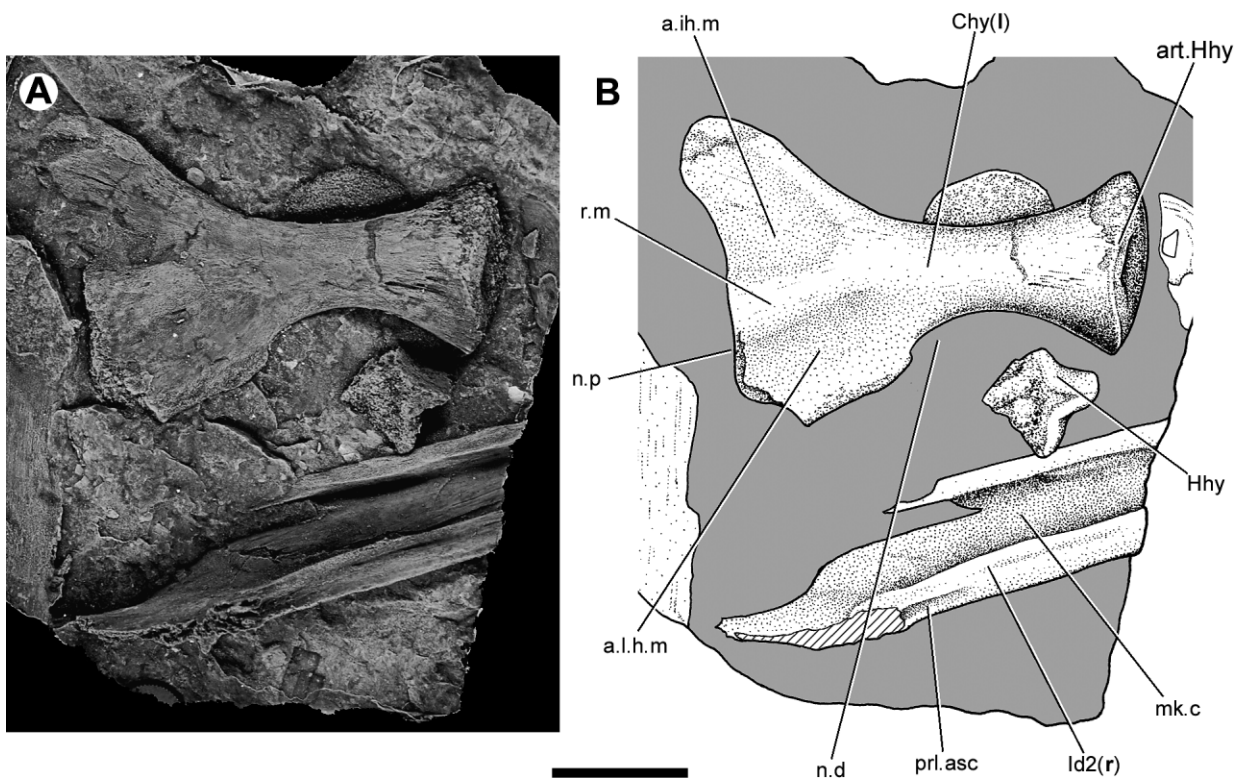


Figure 4 *Soederberghia groenlandica*, MGUH VP 28411, right mandibular ramus in dorsal view and left ceratohyal (depicted with ventral margin facing dorsally) in lateral view. Latex cast of a negative preparation: (A) specimen photograph; (B) interpretive drawing. Dark grey shading represents matrix, diagonal hatching indicates damaged bone surface. Scale bar=20 mm.

an eroded mandible in external view (Lehman 1959, p. 31, pl. 8).

A prominent feature of the mandible of *Soederberghia* is the long lateral retroarticular process (prl.ret, Figs 3, 5, 6), which is

composed entirely of the second infradentary. The lateral retroarticular process of *S. groenlandica* is relatively longer than that in the species of *Griphognathus* (Gross 1956; Schultze 1969; Miles 1977) as well as the jaw attributed to *S. cf.*

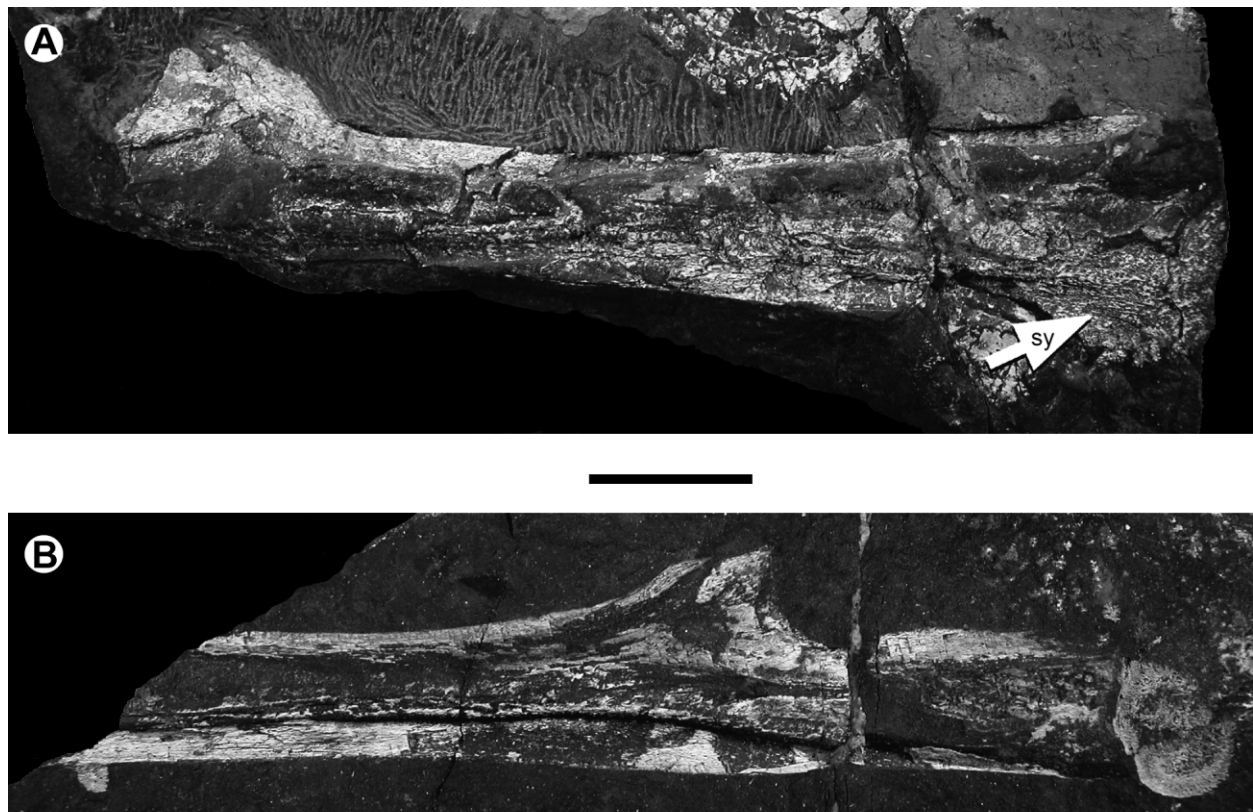


Figure 5 *Soederberghia groenlandica*, mandibular rami: (A) specimen photograph of impression of lingual surface of right mandibular ramus, MGUH VP 3098; (B) specimen photograph of lingual surface of left mandibular ramus, MGUH VP 3106. Scale bars=20 mm.

groenlandica by Clément & Boisvert (2006). The exceptionally long retroarticular process of *S. groenlandica* is mirrored by the exceptionally broad dermal cheek in this species (Fig. 1).

The dorsal margin of the dermal retroarticular process is continuous with the shallow excavation for the glenoid (ex.glen, Figs 3–6). This embayment is bounded anteriorly by a large, hook-shaped lateral ascending process (prl.asc, Figs 3–6) that, along with a complementary process on the prearticular and the unossified Meckelian element, contributes to the falcate preglenoid process of *Soederberghia*. The posterior margin of the process is gently concave, continuous with the glenoid. The anterior border of the ascending process curves smoothly into the dorsal margin of the elongated mandibular ramus. Anteriorly, the dorsal margin of the mandibular ramus flattens and flares laterally. In this region, the dorsal surface of the jaw is roughened by a series of striations that probably represents the attachment area for the dentary.

Only the posterior portion of the dentary of *Soederberghia* is known. It is sutured with the prearticular mesially, and has a non-denticulated strip along its dorsal margin that appears to bear a weakly developed ‘tooth ridge’ (Fig. 7A) of the sort found in *Griphognathus* (Fig. 8B). While details of the symphysis, such as the possible presence of an adsymphyseal plate or foramen, remain unknown for *Soederberghia*, the gross form of this region is clearly shown in multiple specimens. The symphysis of this genus is relatively short (Figs 5A, 7, 8D), consistent with Schultze’s (1969, 1992a) placement of *Soederberghia* in the group of long-snouted dipnoans that have elongated their jaws by extending the mandibular rami. This arrangement, which is also found in *Rhynchodipterus*, *Griphognathus*, and fleurantiids, stands in contrast to that of *Rhinodipterus*, which has arrived at elongated jaws primarily through lengthening the symphysis (Jarvik 1967, fig. 4B).

Soederberghia shows no noticeable embayment for the adductor fossa in the dermal bones of the mandible (Figs 3–5). This suggests that the adductor musculature inserted largely on dermal bone, and that the mandibularis externus V entered dorsally through a small gap between the prearticular and posterior infradentary.

The sensory line canals of the lower jaw of *S. groenlandica* have been described by Lehman (1959) and Schultze (1969), while Clément and Boisvert (2006) have described the pores marking the entrance of the sensory canals in a Belgian *Soederberghia* jaw. A weathered mandible shows sediment infilling of the sensory canals, and confirms most aspects of these descriptions. The mandibular (c.md, Fig. 6) and oral canals (c.o, Fig. 6) are buried within the second infradentary, and are closely spaced over much of their length (cf. Schultze 1969, fig. 39). The mandibular canal is posteriorly extensive, surpassing the level of the glenoid fossa.

The outer surface of the mandible is not well known in *Soederberghia* material from East Greenland, but the inner face can be described in detail. The mesial surface of the dermal retroarticular process is smooth, with the exception of a broad, shallow groove (gr.r.intV?, Fig. 3) that originates on its posterior margin and extends to the level of the lateral ascending process. This depression is subtle posteriorly, but becomes more pronounced anteriorly. The location of this groove is consistent with the canal in other Devonian dipnoans that enters the posterior end of the jaw between the last infradentary and the articular. Several authors have proposed that this groove transmitted the ramus intermandibularis V (Thompson & Campbell 1971; Miles 1977), although there is no clear evidence in support of this assertion. The intermandibularis V exits the jaw ventrally in *Neoceratodus* (Jarvik 1980), and at no point during development does it show the

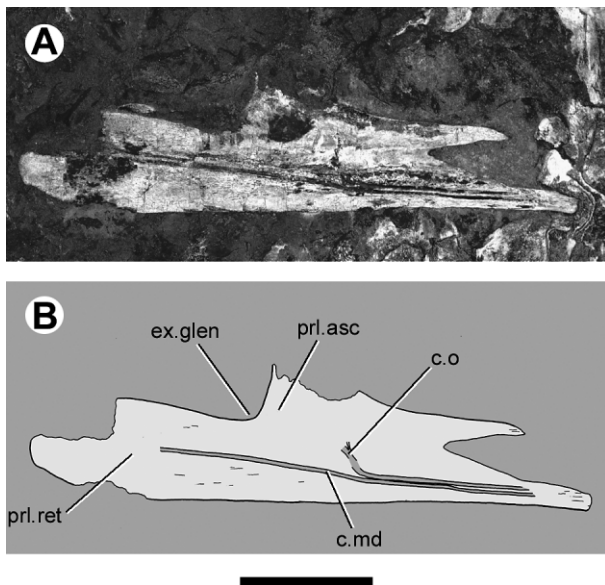


Figure 6 *Soederberghia groenlandica*, MGUH VP 28412, eroded left mandibular ramus. Anterior is to the left: (A) specimen photograph; (B) interpretive drawing. Light grey shading represents damaged bone surface, while dark grey shading indicates matrix or sediment infill of sensory canals. Scale bar = 20 mm.

radical posterior extension required by this interpretation (Fox 1965). Campbell & Barwick (1982b, p. 313) suggested that the equivalent canal in *Chirodipterus australis* might have transmitted the mentalis internus VII, while Thompson & Campbell (1971, p. 55) interpreted it as a conduit for the exit of the facialis mandibularis vein in *Dipnorhynchus*. Regardless of its biological significance, the posterior foramen for this canal is consistently identifiable in Devonian lungfishes.

A well-developed notch marks the apex of the ascending process of the second infradentary (r.m.e VII, Figs 3, 5, 8D). Lehman (1959, p. 31) noted this feature, but did not indicate its presence on any of his plates or text-figures. He suggested that it accommodated a branch of the trigeminal nerve (V), while Schultze (1969) interpreted it as giving passage to branches of both the trigeminal and facial (VII) nerves. Neither of these interpretations agree with the condition in the Recent *Neoceratodus* (Fox 1965; Jarvik 1967, 1980), in which the ramus mentalis externus VII inserts into the lower jaw in the region of the preglenoid process and the ramus mandibularis V enters the lower jaw more anteriorly, via a separate foramen which pierces the external dermal bone of the mandible. The arrangement in *Neoceratodus* is consistent with the general osteichthyan condition, in which the ramus mandibularis externus V enters the lower jaw via the adductor fossa while ramus mentalis VII enters more posteriorly (Allis 1897; Millot & Anthony 1958; Jarvik 1980; Forey 1998). In *Neoceratodus*, the condition is specialised due to closure of the adductor fossa, but the plesiomorphic positional relationship between the insertions of the nerves is nevertheless preserved. Miles' (1977, p. 193) conclusion that the mandibularis externus V entered the lower jaw between the prearticular and external dermal bones anterior to the insertion of the mentalis externus VII in the Gogo dipnoans is therefore in full accord with the generalised arrangement, and is preferable to the interpretations of Lehman (1959) and Schultze (1969). Thus the notch in *Soederberghia* is identified as bearing the ramus mentalis externus VII.

The trough-like Meckelian canal (mk.c, Figs 3–5, 8D) becomes well-defined at the level of the glenoid, and is bounded by the inturned dorsal and ventral margins of the mandible. The thickening of the ventral margin begins behind posterior

limit of the glenoid, and is particularly well-developed immediately below the ascending process (Figs 5B, 8D).

Internal dermal series. Of the internal dermal bones of the mandible, only the prearticular (Figs 7A, 8D; Prart, Figs 9–10) has been recovered. This bone lies in a vertical plane posteriorly (Fig. 9), but twists outwardly at midlength such that it is nearly horizontal at the symphysis (Figs 7A, 8D).

The shape of the prearticular mirrors that of the external dermal bones of the lower jaw, complete with well-developed retroarticular (Fig. 8D; prm.ret, Fig. 9) and ascending processes (Fig. 8D; prm.asc, Fig. 9). The ventral margin of the prearticular is strongly arched beginning near the level of the ascending process (v.con, Figs 8D, 9–10). The same condition characterises *G. minutidens* (Fig. 8C) and *Rhynchodipterus* (pers. obs. E 1898.2). The prearticular of *G. whitei* is strongly arched in this region, but it also bears a depressed ventral lamina that gives the bone a straight ventral margin (dep.l, Fig. 8B). While such a lamina is absent in *G. minutidens* or *Soederberghia*, one is present in *Holodipterus longi* (Fig. 8A).

An extensive denticle field (Figs 7A, 8D; d.f.Prart, Fig. 9) covers much of the mesial surface of the prearticular anterior to the glenoid. The dorsal margin of the prearticular bears a tooth ridge in *Soederberghia* (Fig. 8D; t.r, Fig. 10) composed of small, evenly spaced, subtriangular teeth. These structures are quite different from the large, irregular excrescences that form the tooth ridge in *G. whitei* (Fig. 8B), but are similar to the fine marginal dentition of *G. minutidens* (Fig. 8C; Gross 1956, fig. 27). An anteriorly tapering band of smooth bone lies ventral to the raised denticle field of the prearticular, and bears a shallow gutter near the posterior margin of the denticle field.

The lateral surface of the prearticular is only known from a small section (Prart, Fig. 10) whose precise position along the bone is difficult to determine. Dorsally, it bears a groove, located just below the tooth ridge, that presumably formed the contact with the dorsal margin of the second infradentary.

Although fragmentary, this prearticular has implications for the overall morphology of the bone, as well as its relationship the rest of the jaw. First, it indicates that this bone is shallow in the region above the ventral concavity. This is consistent with the state in *G. minutidens* (Fig. 8C), although the condition in *Soederberghia* might have been even more exaggerated (Fig. 8D). Second, it suggests that the prearticular did not extend far above the dorsal margin of the second infradentary. Only a slight thickening is present ventral to the tooth ridge on the dorsal margin of the prearticular of *Soederberghia*, and it is probable that this was the only portion of this bone exposed laterally. This differs from the arrangement in *G. whitei*, in which a broad band of the prearticular is exposed on the lateral surface of the jaw, dorsal to the second infradentary (Miles 1977, fig. 100B). However, this interpretation for *Soederberghia* agrees with the condition seen in *G. minutidens*, in which only the thin dorsal strip of the prearticular that bears the tooth ridge is exposed in lateral view (Gross 1956, figs 25C, F; Schultze 1969, fig. 3).

Mandible: Meckelian ossification. Lehman (1959) correctly asserted that the Meckelian element in *Soederberghia* is unossified. Several mandibles preserve the extensive and deeply concave Meckelian canal (mk.c, Figs 3–5, 8D), but none show any trace of endoskeletal ossification. This differs from the condition in *G. whitei*, where the Meckelian element is extensively ossified (Fig. 8B; Miles 1977), and in *G. sculpta* and *G. minutidens* (Fig. 8C) in which it is clear that at least the articular region is ossified.

3.2. Hyoid arch

3.2.1. Ceratohyal. Lehman (1959, fig. 30, pl. 16A) identified a bone that he considered to be a ceratohyal, and

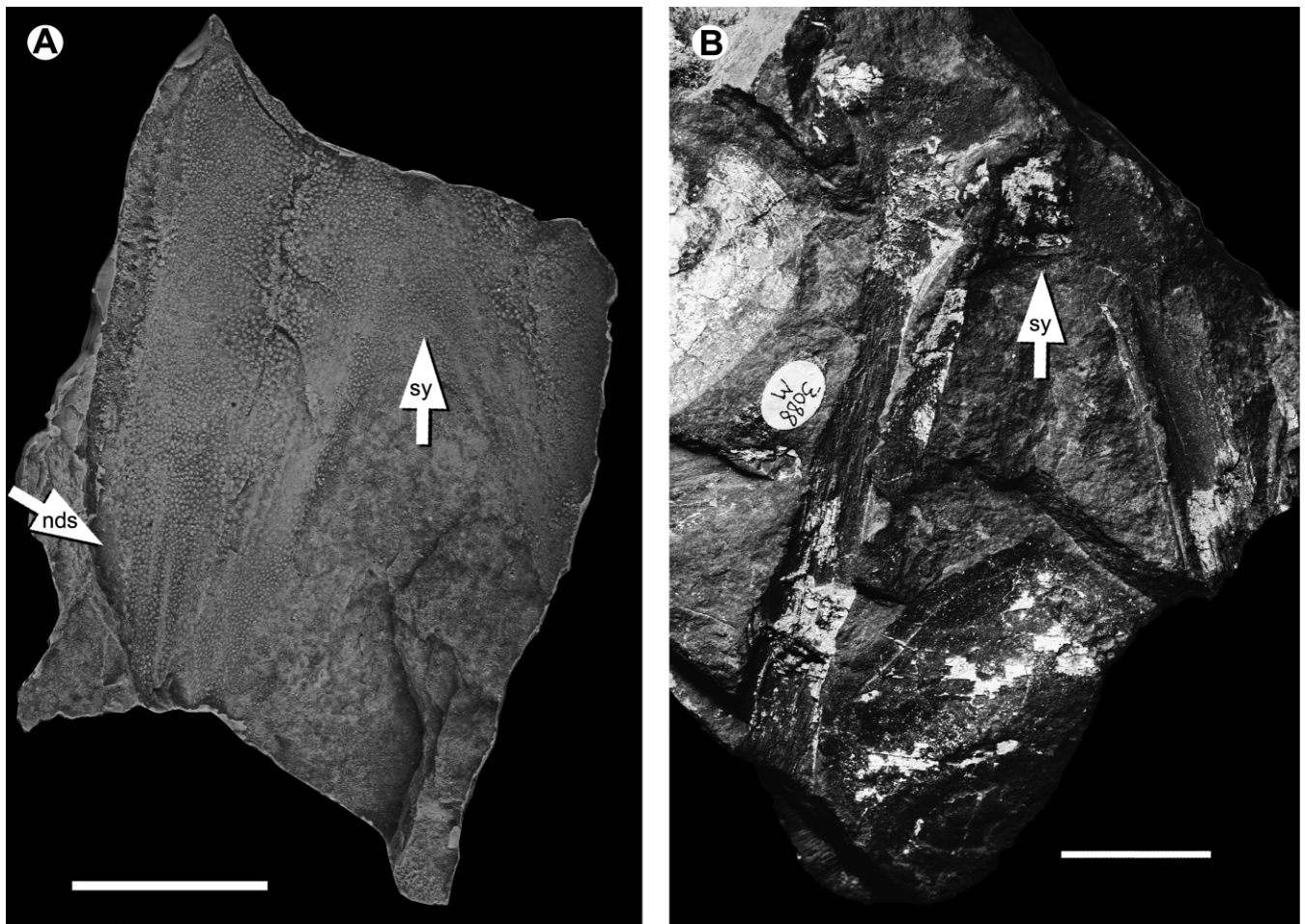


Figure 7 *Soederberghia groenlandica*, symphyseal region of the lower jaw: (A) Latex cast of a negative preparation of the dorsal surface of MGUH VP 28413 showing denticulated field. Longitudinal sutures on either side of the symphysis mark the division between the dentaries and the prearticulars; (B) Eroded impression of ventral surface of mandibular symphysis and lower jaw rami, MGUH VP 3088. Anterior is to the top in both figures. Scale bars = 20 mm.

tentatively referred it to *Soederberghia*. It is clear that this bone does belong to *Soederberghia*; it is in association with one of the dermal skull roofs figured by Lehman (1959, fig. 8, pl. 14A; MGUH VP 3055) as well as other remains attributable to this taxon. The interpretation of this bone as a ceratohyal is more in doubt. This bone is roughly similar in shape to the ceratohyal of the extant *Neoceratodus* (Günther 1871; Ridewood 1894), but it is a better match to the basal plate of the second dorsal fin of *Soederberghia* (MGUH VP 28395; Friedman in press) and is probably an internal fin support. Endoskeletal bones that correspond more closely to the ceratohyals of other early lungfishes have been found in association with the cranial remains of several specimens of *Soederberghia* (Chy, Figs 4, 10). This morphological correspondence, coupled with the close association of these bones with the gular region, allows them to be identified confidently as ceratohyals.

The most complete ceratohyal of *Soederberghia* is preserved in association with an incomplete mandible (Chy, Fig. 4). Comparison with an *in situ* bone visible in CT renderings of *Rhynchodipterus* indicates that this is a left ceratohyal exposed in lateral view.

The ceratohyal of *Soederberghia* is only slightly expanded anteriorly but is conspicuously enlarged posteriorly. The ventral margin of this bone defines a smooth concavity, while the dorsal margin of some specimens bears a distinct notch (n.d, Fig. 4). An identical notch is present in *Rhynchodipterus* (pers. obs. E 1898.2 A). The ceratohyal of *Soederberghia* shows exaggerated 'waisting' of the sort seen in *Rhynchodipterus*

(pers. obs. E 1898.2 A), *Jarvikia* (Fig. 11E; Lehman 1959, fig. 25, pl. 19C) and *Fleurantia* (Graham-Smith & Westoll 1937, fig. 5). The anterior face of the ceratohyal is marked by an unfinished depression that indicates the area of articulation with the hypohyal (art.Hhy, Figs 4, 10). Much of the posterior surface of this bone also lacks a perichondral coat, resulting in a more extensive unfinished surface in this region compared to most other Devonian lungfishes (Miles 1977). The posterodorsal margin of the ceratohyal is excavated (n.p, Fig. 4), similar to the arrangement found in *Rhynchodipterus* (pers. obs. E 1898.2 A) and *Jarvikia* (Fig. 11E).

The lateral surface of the ceratohyal is marked by two depressions (a.l.h.m, a.i.h.m, Fig. 4) that are separated by a broad ridge (r.m, Fig. 4). In the Gogo dipnoans (Fig. 11B, D), Miles (1977) identified the most dorsal of these as the site of insertion of the levator hyoideus muscle and its larger, ventral complement as the insertion site of the interhyoideus muscle. This interpretation has been applied subsequently to a range of early lungfishes (Fig. 11A, C). In *Neoceratodus*, a retractor mandibulae also inserts in the region that corresponds to the dorsal depression of *Soederberghia* (Fox 1965, fig. 7), suggesting that Miles' (1977) interpretation might be oversimplified. There is no indication of a deep groove for the efferent hyoid artery in *Soederberghia* of the kind described for *Sorbitorhynchus* (Wang *et al.* 1993, fig. 3) or *Chirodipterus australis* (gr.e.h.a, Fig. 11B), nor are there foramina that indicate that this vessel pierced the bone as in *Pillararhynchus* (Barwick & Campbell 1996, fig. 12A, B).

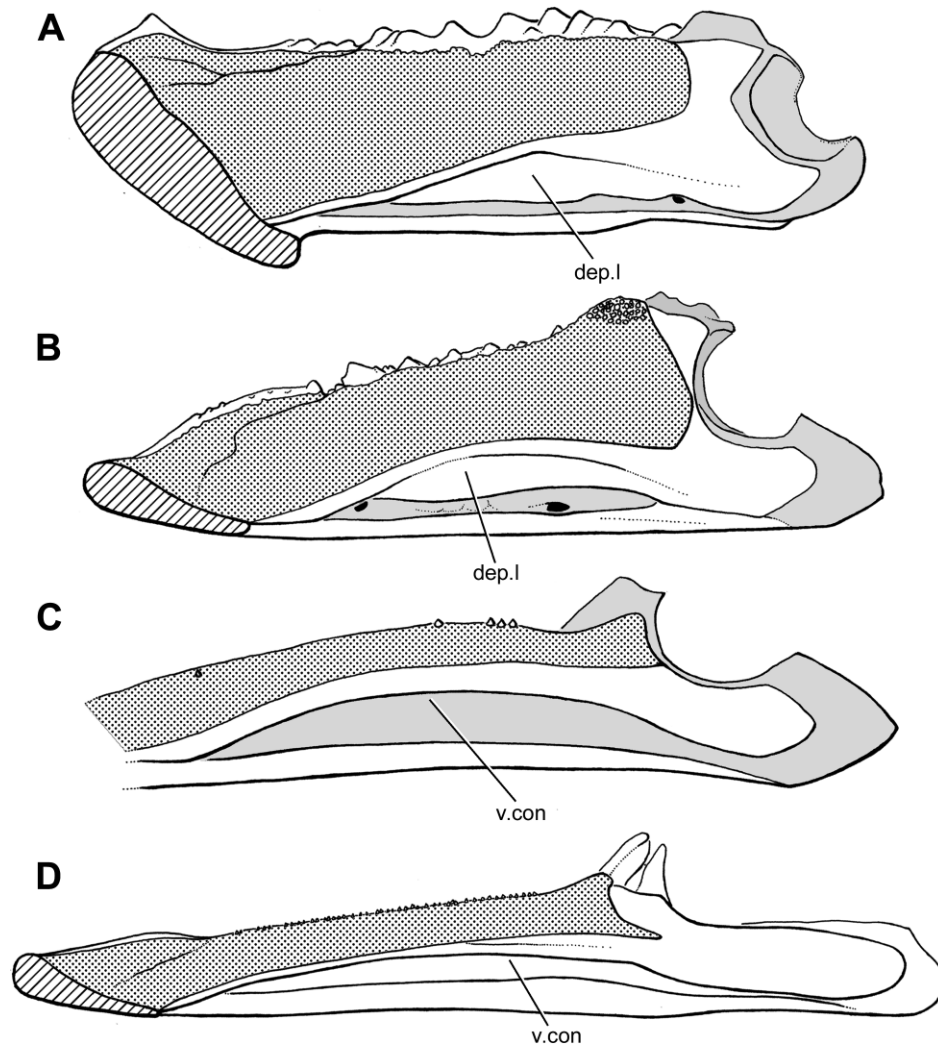


Figure 8 Comparison of the inner surface of the lower jaws of ‘holodontid’ and ‘rhynchodipterid’ lungfishes: (A) *Holodipterus longi* (modified from Campbell & Barwick 1991 and Pridmore *et al.* 1994); (B) *Griphognathus whitei* (modified from Miles 1977); (C) *G. minutidens* (modified from Gross 1956); (D) *Soederberghia groenlandica*. Light grey shading represents endoskeletal ossification (Meckelian element unossified in *Soederberghia*), while mechanical stipple indicates the extent of the prearticular denticle field. Note the absence of a depressed lamina of the prearticular in *G. minutidens* and *Soederberghia*. Images not to scale.

The mesial surface of the ceratohyal is incompletely known, but the portions that are preserved show no conspicuous features (Fig. 10). The surface is slightly depressed posteriorly, while the anterior margin of the articular surface bears a slight embayment.

3.2.2. Hypohyal. A small, irregularly-shaped endoskeletal ossification found associated with the anterior end of one of the ceratohyals is interpreted as a hypohyal (Hhy, Fig. 4). Most of the preserved surface of this bone is convex and lacks a perichondral coat, indicating that it represents the articular surface for the ceratohyal.

4. Discussion

4.1. Homologies of the bones of the dermal cheek in *Soederberghia* and ‘rhynchodipterids’

The arrangement and homologies of the dermal cheek bones in ‘rhynchodipterid’ lungfishes are uncertain. While *Griphognathus whitei* and *G. sculpta* have dermal cheeks that are readily compared with other lungfishes, those of *Soederberghia* and *Rhynchodipterus* have proven less tractable. Miles (1977, pp. 246–7) considered that ‘the pattern has not been worked out accurately in either *Rhynchodipterus* or *Soederberghia*’, and

that ‘more convincing accounts’ were necessary to assess bone homologies. Re-examination of material of both genera confirms Miles’ (1977) assessment of previous descriptions. Bone patterns in *S. groenlandica* have already been reviewed (section 3.1.1), but the arrangement in *Rhynchodipterus* must be revisited. Previous interpretations of *Rhynchodipterus* have been based, in part, upon a series of lines painted by G. Save-Söderbergh on the skull of the only specimen. These mark features that he believed to be sutures (Save-Söderbergh 1937, fig. 1A; Westoll 1949, p. 149), but many are not, and the paint now serves only to obscure already faint details.

The only previous consideration of the homologies of the dermal cheek bones in *Rhynchodipterus* was offered by Schultze (1969), and this was subsequently utilised by Ahlberg *et al.* (2001) as a comparative model in their description of *S. simpsoni*. However, several aspects of Schultze’s (1969) interpretive drawing are in error. This is due to Save-Söderbergh’s painted ‘sutures’ and, perhaps more importantly, few available comparators; at the time when Schultze’s (1969) study was executed, dermal cheeks were only known for a handful of Devonian lungfishes.

One problematic feature of earlier accounts of *Rhynchodipterus* concerns the identification of a small bone located at the posteroventral corner of the cheek (Fig. 12). Schultze

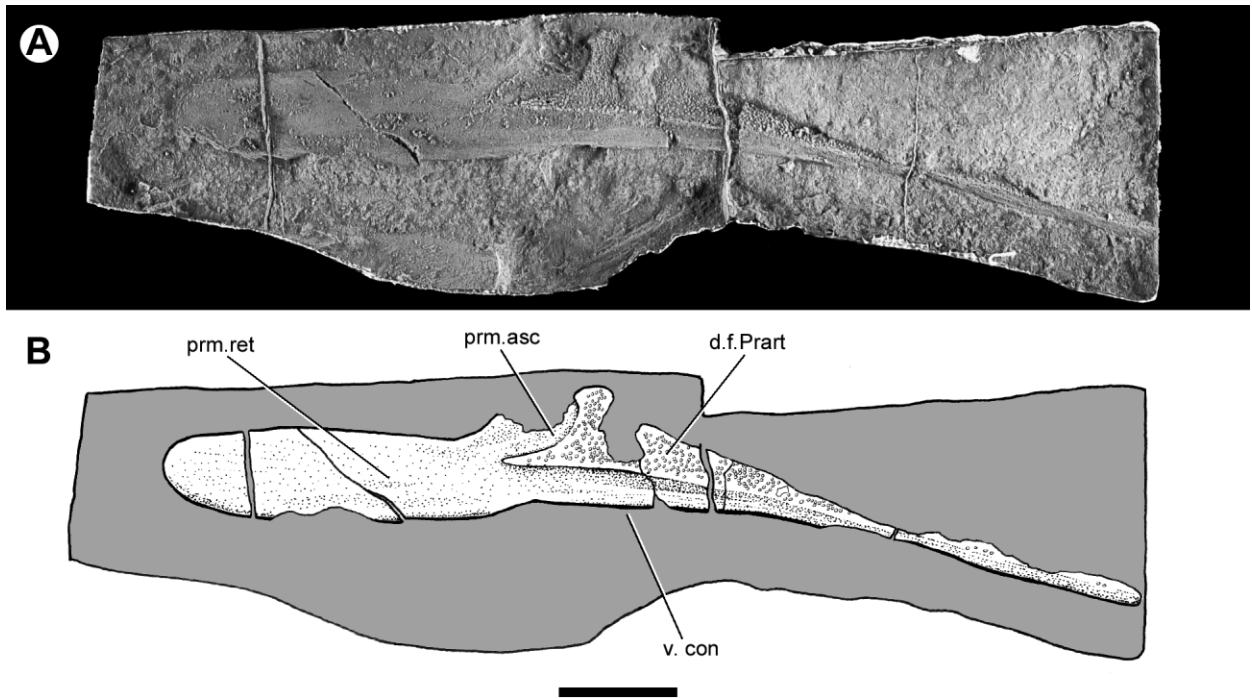


Figure 9 *Soederberghia groenlandica*, MGUH VP 6206, left prearticular in lingual view. Latex cast of negative preparation: (A) specimen photograph; (B) interpretive drawing. Dark grey shading indicates matrix. Scale bar=20 mm.

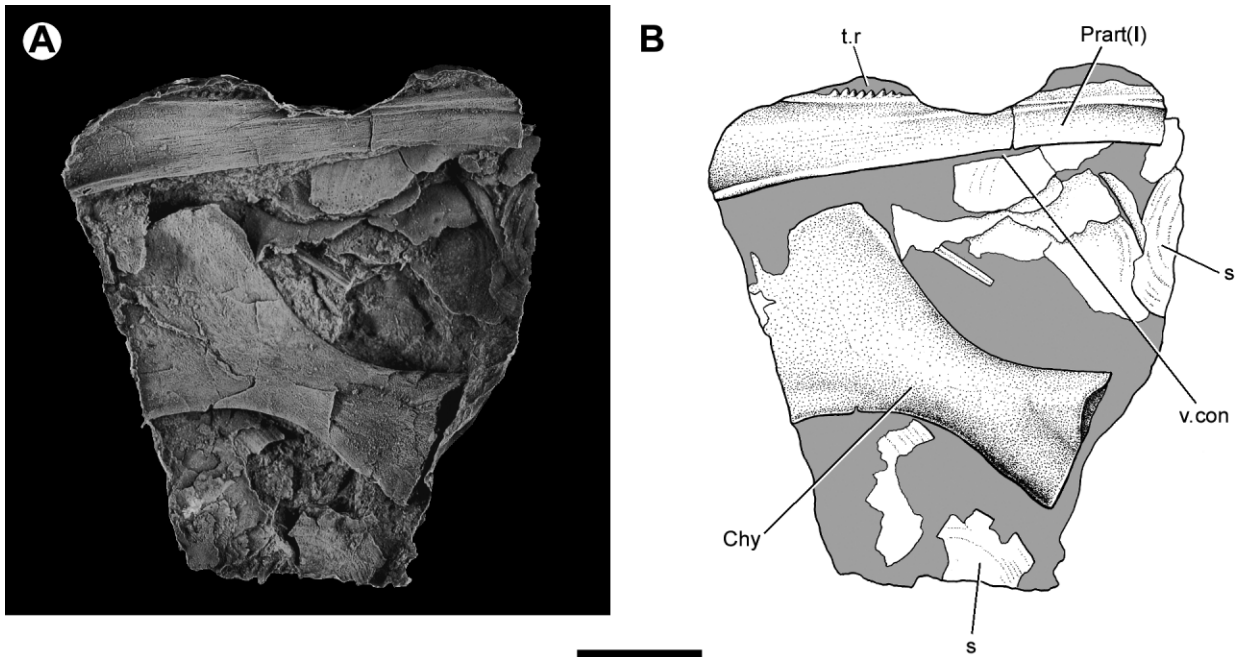


Figure 10 *Soederberghia groenlandica*, MGUH VP 28397, left prearticular in labial view and ceratohyal in internal view. Latex cast of negative preparation: (A) specimen photograph; (B) interpretive drawing. Dark grey shading indicates matrix. Scale bar=20 mm.

(1969) identified this as bone 10 (quadratojugal), apparently on the basis of positional correspondence to that bone in *Dipterus* (White 1965), and Ahlberg *et al.* (2001) used this conclusion in their interpretation of *Soederberghia*. However, the relationships of this bone in *Rhynchodipterus* to other features of the cheek are inconsistent with those of bone 10 in other early dipnoans. In Schultze's (1969) figure of *Rhynchodipterus*, the putative bone 10 blocks the entire posteroventral margin of the bone identified as 5+8. This is an unusual interpretation, as bone 10 does not border bone 8 (squamosal) posteriorly in any of the dipnoan taxa for which both bones have been

convincingly identified (White 1965; Schultze 1969; Miles 1977; Schultze 1982; Pridmore *et al.* 1994). This proposed arrangement would require redirection of the course of the preopercular canal, which exits the cheek of other dipnoans from the posterior border of bone 8 – the same border obstructed by the bone identified as bone 10.

Examination of the cheek of *Rhynchodipterus* shows that that the 'suture' between Schultze's (1969) '5+8' and '6' is an infilling of the preopercular canal and not the division between separate ossifications (Figs 12, 13). Furthermore, the putative bone 10 in *Rhynchodipterus* corresponds closely in position

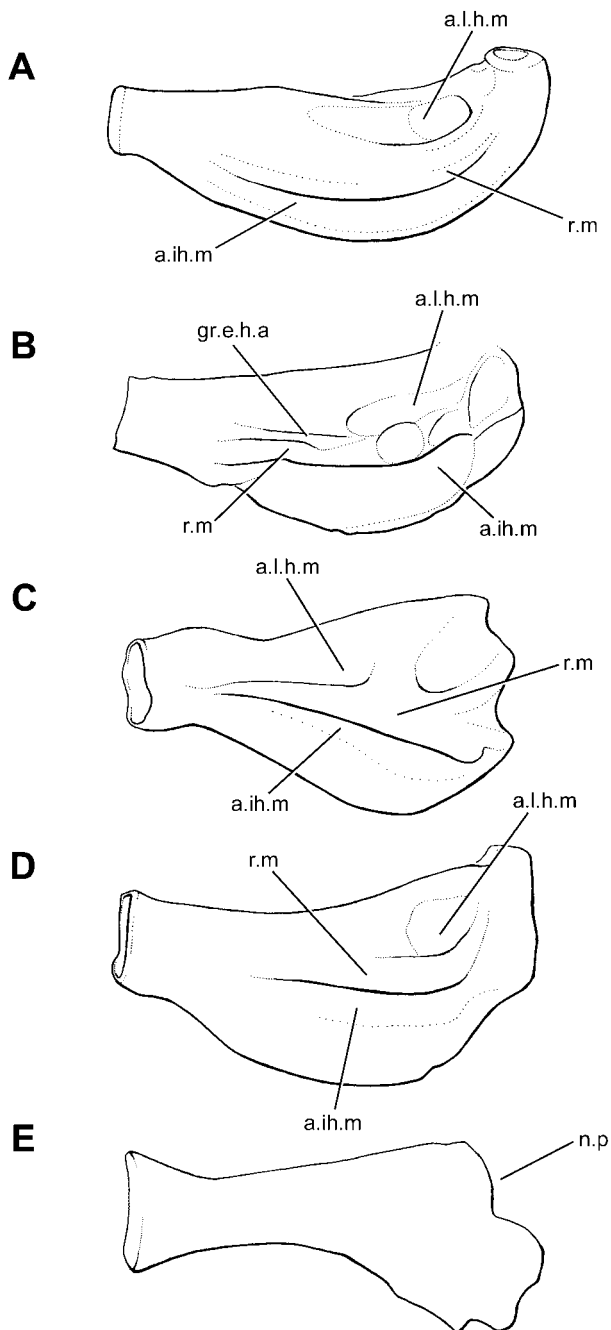


Figure 11 Comparison of early lungfish ceratohyals in left lateral view: (A) *Uranolophus wyomingensis* (modified from Campbell & Barwick 1988); (B) *Chirodipterus australis* (modified from Miles 1977); (C) *Barwickia downunda* (modified from Long 1992); (D) *Griphognathus whitei* (modified from Campbell & Barwick 1988); (E), *Jarvikia arctica* (modified from Lehman 1959). External features not shown in *Jarvikia* because they have been obliterated by mechanical preparation. Note that *Jarvikia* shares a posterodorsal notch of the ceratohyal with *Soederberghia* (Fig. 4). Of the remaining examples, this condition is most closely approached by *Barwickia*. Images not to scale.

(posteroventral corner of the cheek) and shape (crescentic) to the bone unambiguously identified as bone 8 in both species of *Soederberghia*. It is also noteworthy that the incomplete infilling of the preopercular canal extends toward the putative bone 10 in *Rhynchodipterus*. This arrangement provides further evidence that this bone is actually bone 8; the preopercular canal typically branches from the infraorbital canal within the body of bone 5 (jugal), extending posteriorly through bone 8 and exiting the cheek via a series of small ossifications termed 9 bones.

A new picture of the cheek of *Rhynchodipterus* emerges from these observations. Like *Soederberghia*, this genus is characterised by a bone 8 placed at the posteroventral corner of the cheek. This differs from the more dorsal position found in *Griphognathus*, which retains the primitive lungfish condition, based on outgroup comparison with 'chirodipterygians' (Miles 1977), 'dipterygians' (White 1965) and 'dipnoans' (Thomson & Campbell 1971). In addition, there is no evidence that *Rhynchodipterus* had anything but a conventional bone 5 (*contra* Schultze 1969), but the sutures that might delimit this bone from the infraorbital bar cannot be traced (Figs 12, 13).

These new conclusions concerning *Rhynchodipterus* have considerable implications for the most recent interpretation of cheek bone patterns in *Soederberghia*. Ahlberg *et al.* (2001) identified a small, posteroventrally located cheek bone as bone 10 in *S. simpsoni*, an interpretation possibly influenced by Schultze's (1969) problematic figure of *Rhynchodipterus*. These authors then argued that this arrangement showed that *Rhynchodipterus* and *Soederberghia* are not closely related to *Griphognathus*, in which bone 10 is large and extends below the orbit.

It is now clear that the bone in *Rhynchodipterus* previously interpreted as bone 10 is bone 8, but the identity of the small object identified as bone 10 in *S. simpsoni* remains unclear. Examination of *S. simpsoni* has led to two interrelated questions concerning the putative bone 10 of this species: is the structure in question a bone at all, and, if so, what is its probable homologue among other dipnoans? The first question is not trivial because two aspects of the putative bone 10 (Fig. 14) suggests that it might not be an ossification: (1) its surface texture is similar to that of the matrix and differs markedly from that of surrounding bones; and (2) the 'bone' itself is raised above the rest of the cheek. *S. simpsoni*, like all fossil fishes from Canowindra, is preserved as a natural mould that has been cast for study. It is possible that this 'bone' represents an area of damage to the surface of original fossil that has been translated into a feature with positive relief upon casting, accounting for both the unusual surface texture and position of this structure. This interpretation draws additional support from the fact that 'bone 10' aligns with an area of surficial damage that traverses the cheek of *S. simpsoni* (sd, Fig. 14). Although this same region of the cheek is incomplete in the new *S. groenlandica* specimen described here (Fig. 1), there is no evidence for an equivalent bone in another skull of this species that preserves this area (MGUH VP 3043+3044), further suggesting that the feature in *S. simpsoni* is an artefact.

If the structure in *S. simpsoni* is interpreted as a bone of the dermal cheek (Ahlberg *et al.* 2001), then it is difficult to reconcile its position with bone 10 in other dipnoans. Bone 10, as the homologue of the quadratojugal of other sarcopterygians (Ahlberg 1991), shows a tight positional linkage with the articular head of the quadrate in early lungfishes (Fig. 15). In plesiomorphic dipnoans such as *Dipterus* and 'chirodipterygians' (White 1965; Miles 1977), bone 10 occupies a position at the posteroventral margin of the cheek, mirroring the primitive position of the quadrate at the posterior corner of the cheek (Fig. 15A). The position of bone 10 in *Soederberghia* as interpreted by Ahlberg *et al.* (2001) is consistent with these primitive examples, but this comparison is not appropriate because it is clear that the quadrate occupied a derived infraorbital position in *Soederberghia* (Fig. 12). This is similar to the condition in *Griphognathus*, in which an anteriorly shifted quadrate is accompanied by an anteriorly displaced bone 10 (Figs 12, 15C). If the feature identified as bone 10 in *S. simpsoni* is in fact a bone, its position and morphology seem more consistent with one of the 9 bones, a series of small

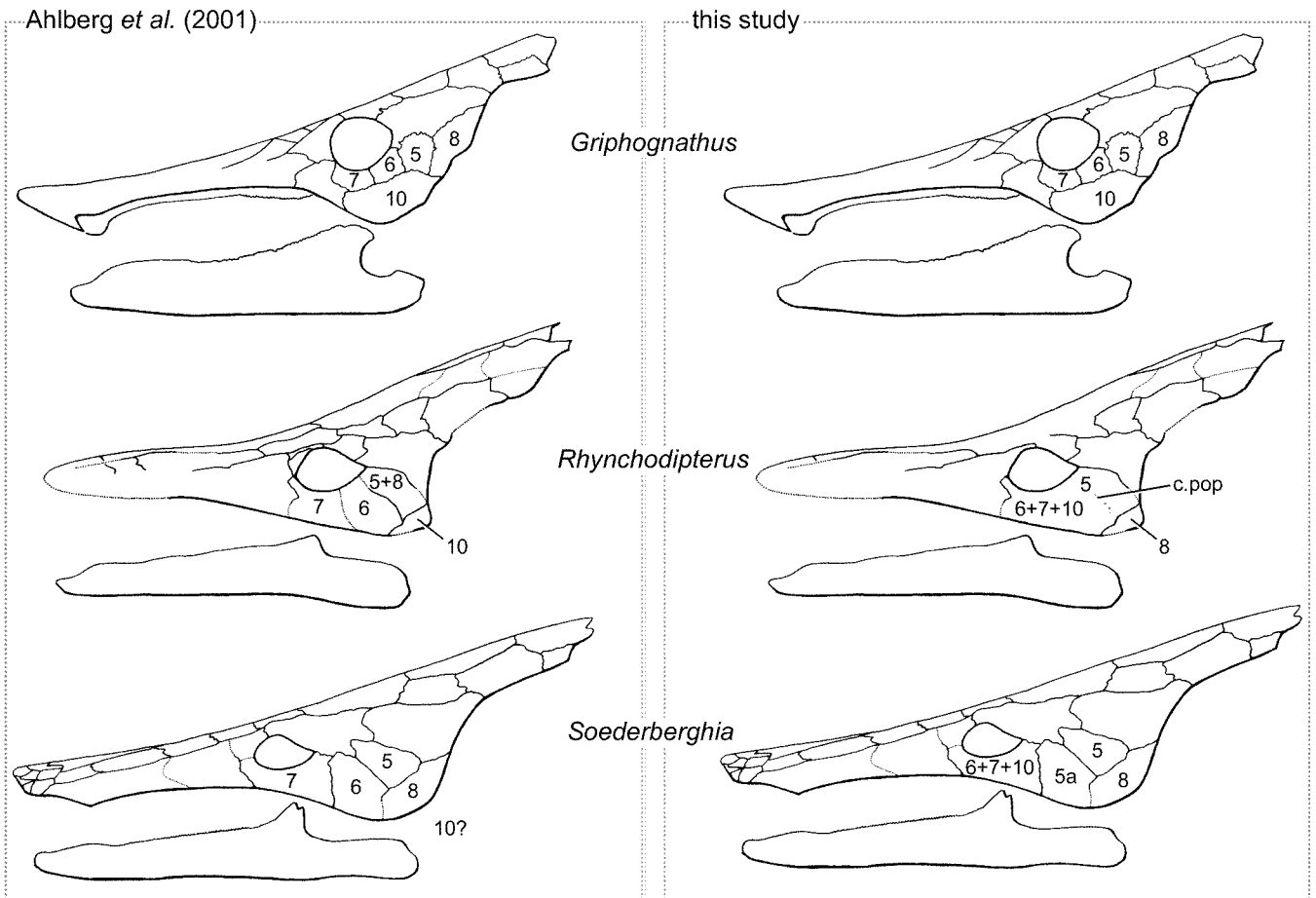


Figure 12 Hypothesised homologies of dermal cheek bones in 'rhynchodipterid' lungfishes. Left column shows homology scheme suggested by Ahlberg *et al.* (2001), applied to *Griphognathus whitei* (top; modified from Miles 1977), *Rhynchodipterus elginensis* (middle, modified from Schultze 1969, with details of jaw based on CT study of E 1892.2 A) and *Soederberghia groenlandica* (bottom; original). Right column indicates homologies proposed by the current study. The jaws associated with each skull clearly show that quadrate occupied an advanced infraorbital position in each of these three taxa. Images not to scale.

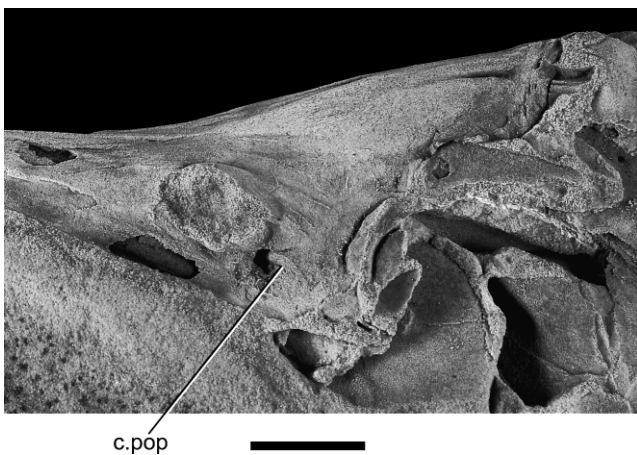


Figure 13 *Rhynchodipterus elginensis*, E 1898.2 A, left dermal cheek in lateral view. Label marks the feature interpreted as a suture by Schultze (1969), but which represents an infilled sensory canal.

ossifications that bear the preopercular canal between the cheek and the mandible.

Although it seems clear that the features previously interpreted as bone 10 in *Rhynchodipterus* and *Soederberghia* are in fact not that bone, this ossification has yet to be convincingly identified in either genus. A solution to this problem might lie in the unusual infraorbital regions of these taxa. Both species of *Soederberghia* have an infraorbital bar that consists of a

single ossification. Schultze (1969) split the infraorbital bar of *Rhynchodipterus* into two bones (bones 6 and 7), but this suture was indicated only with a dashed line, which appears to be an inference derived from using an archetypal Devonian lungfish, such as *Dipterus*, as an interpretive model. There is no evidence of sutures on the infraorbital bar, and it was probably undivided (Figs 12, 13). While the infraorbital bar of *Soederberghia* and *Rhynchodipterus* comprises a single ossification, that of *Griphognathus* is composed of three separate bones: 6, 7, and 10. Bones 6 and 7, which form the ventral margin of the orbit, are much reduced, while the infraorbital bar is dominated by an enlarged bone 10. This expanded bone 10 might give clues to the homologies of the single infraorbital ossification of *Rhynchodipterus* and *Soederberghia*. The close spatial relationship between the quadratojugal and the quadrate found in lungfishes (and sarcopterygians in general) is preserved even in *Griphognathus*, where the anteriorly extensive bone 10 reflects an anteriorly shifted quadrate. There is clear evidence for a similarly displaced quadrate in both *Rhynchodipterus* and *Soederberghia*. CT scan data showing details of the palate unambiguously demonstrate that the quadrate must have occupied an infraorbital position in *Rhynchodipterus*, while comparing the proportions of the mandible and dermal skull in *S. groenlandica* point to a similar arrangement in this species (Lehman 1959, fig. 3; Fig. 12). The anteriorly displaced quadrate in both *Rhynchodipterus* and *Soederberghia* is flanked by the infraorbital bar, which suggests that this bone might be related to the quadratojugal of other lungfishes. The expansion

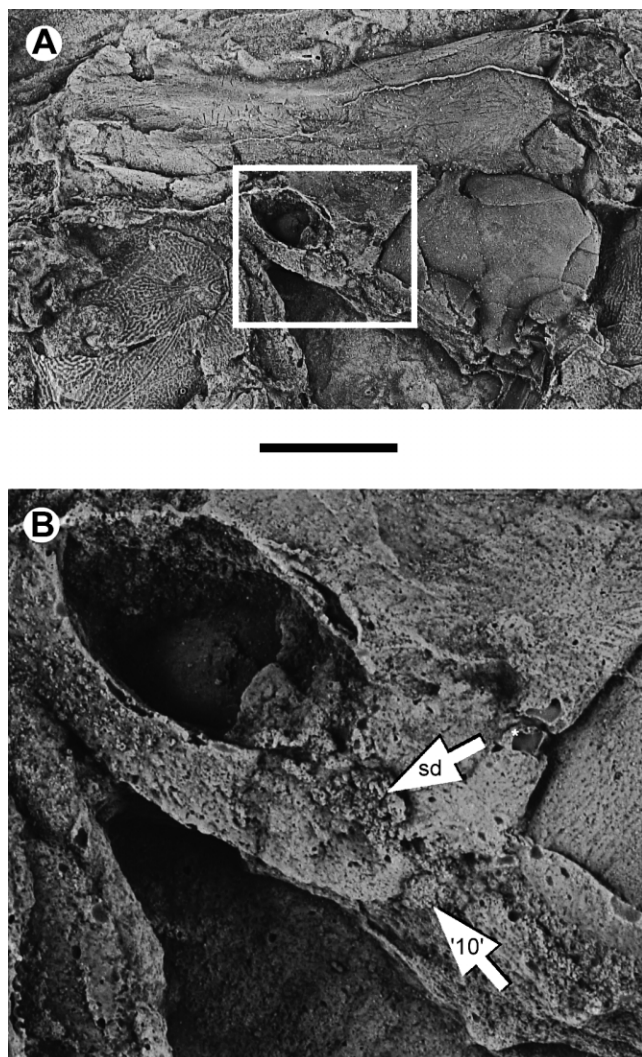


Figure 14 *Soederberghia simpsoni*, AMF102820, dermal skull in left lateral view. Positive plaster cast of specimen preserved in negative: (A) specimen photograph; (B) close-up of region indicated by box in (A). Arrow in (B) marked as '10' indicates feature identified by Ahlberg *et al.* (2001) as bone 10, while that marked as 'sd' highlights an area of surficial damage (an excavation on the mould that has translated to a positive feature upon casting) that is coincident with this putative ossification. Scale bar=20 mm.

of bone 10 seen in *Griphognathus*, coupled with the concomitant reduction of bones 6 and 7, could be interpreted as intermediate between the generalised dipnoan arrangement and the consolidated infraorbital bar of *Rhynchodipterus* and *Soederberghia*, with the latter arrangement being derived through bone fusion or loss. It is noteworthy in this context that bones 6 and 7 of *G. sculpta* appear to be highly unstable, frequently appearing to 'fuse' either with each other or surrounding bones (Schultze 1969, figs 7, 13, 16). In such an interpretation, the infraorbital bar of *Soederberghia* and *Rhynchodipterus* is descended from the quadratojugal, thus preserving the tight positional association between this bone and the quadrate. It seems likely that the anteriorly shifted quadrate in 'rhynchodipterids' has resulted in complementary remodelling of the overlying dermal cheek relative to other lungfishes, placing the primitive posterior margin of the cheek in an infraorbital position.

The hypothesis presented here accounts for the identity of the infraorbital bar in *Soederberghia* and *Rhynchodipterus* as '6+7 +10', but it fails to explain the origin of the bone between

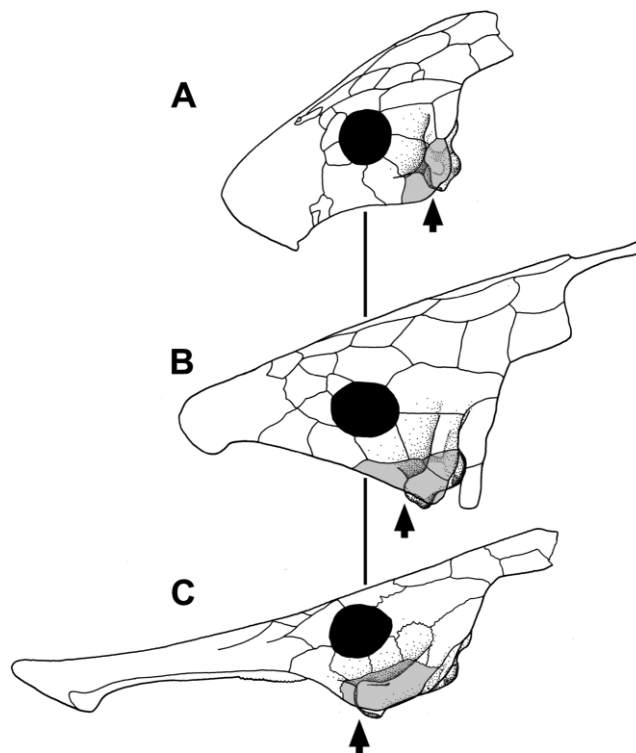


Figure 15 Diagram showing the consistent association between bone 10 (quadratojugal) and the articular surface of the quadrate in lungfishes. All skulls are aligned at mid-orbit, while the quadratojugal is shaded in grey and the position of the quadrate is marked with an arrow. (A) *Chirodipterus australis*; (B) *Holodipterus* (composite of *H. gogoensis* and *H. meemannae*, modified from Miles 1977 and Pridmore *et al.* 1994); (C) *Griphognathus whitei* (modified from Miles 1977). Note that anterior extension of the quadrate is mirrored by the quadratojugal. The progression of taxa shown here is not intended to be interpreted as an evolutionary sequence. Images not to scale.

the infraorbital bar and bone 5 seen in some specimens of *Soederberghia*, identified previously as '6' under Forster-Cooper's (1937) naming scheme (section 3.1.1). This bone is renamed 5a here (Fig. 12), but this is not meant to carry with it an implication of homology. Either subdivision of pre-existing bones or the development of a neomorph ossification in the lineage leading to *Soederberghia* could reasonably account for the pattern seen in this genus. A similar abnormality, in which two bones are located in the area typically occupied by bone 5, has been described for a specimen of *Chirodipterus australis* (Campbell & Barwick 1982a: fig. 5C).

4.2. The interrelationships of long-snouted, denticle-bearing lungfishes

The following discussion is arranged as a series of sections, each of which details characters supporting the monophyly of successively less inclusive groups of long-snouted, denticle-bearing lungfishes. Each section reviews characters previously advanced in support of the proposed clade, and outlines a new set of cranial apomorphies illuminated by the current study. Only the distribution of these novel characters is given in Figure 16. As most analyses of lungfish interrelationships indicate that 'rhynchodipterids' and fleurantiids are more closely related to each other than either is to cosmine-bearing lungfishes (Campbell & Barwick 1990; Krupina & Reis 2000; Schultze 2001; Ahlberg *et al.* 2006), the polarity of the characters discussed here has been determined through out-group comparison to 'dipnorhynchids', 'chirodipterids', and 'dipterids'.

Two qualifications must precede this discussion. First, these new character lists are not comprehensive, and, with the single

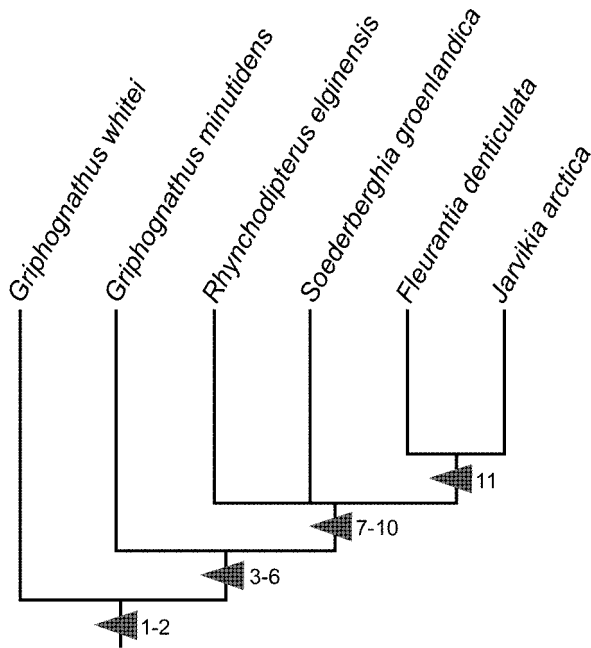


Figure 16 Cladogram showing the distribution of characters supporting the monophyly of a clade comprising 'rhynchodipterids' and fleurantiids, as well as those that support successively less inclusive groups within this radiation. The characters shown here are keyed to those in the text, which are limited to features of the dermal skull roof and cheek, hyoid arch, and mandible (those anatomical components of *Soederberghia* reviewed in this contribution) with the exception of character 11.

exception of a character supporting the monophyly of [*Jarvikia*+*Fleurantia*], they are limited to features that can be determined on the basis of the *Soederberghia* material discussed earlier in this contribution. Secondly, these putative synapomorphies have not been tested using a more comprehensive analysis, as this is beyond the scope of the current study.

4.2.1. 'Rhynchodipterids' plus fleurantiids. 'Rhynchodipterids', when defined in the 'classical' sense as including *Griphognathus*, *Rhynchodipterus*, and *Soederberghia* (cf. Moy-Thomas & Miles 1971), are probably non-monophyletic. They can only be differentiated from another set of long-snouted, denticle-bearing Devonian lungfishes (the fleurantiids) on the basis of retained primitive characters: a short-based second dorsal fin and paired E-bones. Multiple cladistic analyses suggest that *Rhynchodipterus* and *Soederberghia* are more closely related to fleurantiids than either is to *Griphognathus* (Krupina and Reisz 2000; Friedman 2005; Ahlberg *et al.* 2006).

Despite the strong evidence against 'rhynchodipterid' monophyly, there appears to be little support for claims of 'rhynchodipterid' polyphyly (Schultze 2001; Friedman 2007; *contra* Ahlberg *et al.* 2001, 2006). Ahlberg *et al.* (2006) have recently conducted a cladistic analysis with a novel data set incorporating a series of detailed dental characters. Consistent with the conclusions of Ahlberg *et al.* (2001), the published cladogram arising from their most comprehensive analysis (Ahlberg *et al.* 2006, fig. 6A) indicates that 'rhynchodipterids' are polyphyletic, with *Griphognathus* falling as the sister taxon of *Holodipterus*, and *Soederberghia* lying further crownward along the dipnoan stem as the unexpected sister taxon of the Permo-Carboniferous genus *Conchopoma*. This cladogram represents a strict consensus of the three shortest cladograms (of unspecified length) recovered by maximum parsimony analysis of their total data set, but re-analysis of their published matrix using the analytical methods they specified fails to deliver the same solution. Instead, this yields 153 trees of

228 steps (consistency index=0.456; retention index=0.707; rescaled consistency index=0.322), and places *Griphognathus* and *Soederberghia* as successive plesions along the dipnoan stem.

P. Ahlberg (UU) has kindly provided a copy of the correct data matrix for Ahlberg *et al.* (2006), which permits an examination of the morphological evidence for the cladograms given by that study, which did not present a synapomorphy scheme underlying its preferred solution. Analysis of this matrix shows that the monophyly of [*Griphognathus*+*Holodipterus*] is supported by eight unambiguous character changes, but none of these are unique to this clade. They include (character numbers and states from the correct matrix of Ahlberg *et al.* 2006 are given in parentheses; instances where these differ from those in the published account are noted): diffuse dentine deposition across the palate (10[0]; identical condition in *Soederberghia*); extensive resorption of dentition along plate origin (13[1]); 'additive' mesial and posterior edges on tooth plates absent (15[0]; identical condition in *Soederberghia*); parasphenoid fused to entopterygoids (26[0]; this appears as 29 in the published character list); short adductor fossa (37[1]; this multistate character appears as 40 in the published list and is inconsistently coded for *Griphognathus* in the two matrices [published matrix: state 2; correct matrix: state 1], with the coding in the published matrix being the appropriate one; in any case, it is clear that *Soederberghia* shares with *Griphognathus* an adductor fossa more reduced than that found in any 'holodontid'); persistent otoccipital fissure (58[0]; this appears as character 61 in the published list); bone 6 excluded from margin of cheek by 10 (64[1]; this appears as character 67 in the published list, and might show the identical condition in *Soederberghia* if the argument given in section 4.1 is accepted); a strongly arched palate (78[1]; this appears as character 25 in the published list, but is character 24 in the matrix; the same condition is present in *Soederberghia*). Few of these characters provide convincing support for a clade comprising *Griphognathus* and *Holodipterus* to the exclusion of *Soederberghia* because so many of them also appear in that last genus.

Five unambiguous character changes support placement of *Soederberghia* crownward of [*Griphognathus*+*Holodipterus*] in the preferred solution of Ahlberg *et al.* (2006): sectorial teeth (5[1]; coded as '?' for *Soederberghia*); no addition of marginal blisters to the entopterygoid or prearticular (6[0]; coded as '?' for *Soederberghia*); an elaborated parasphenoid stalk that can be divided into two regions (23[2]; this appears as character 26 in the published list); unossified Meckelian element (46[1]; this appears as character 49 in the published list); absence of cosmine (69[2]; this appears as character 72 in the published list). Just as with those underpinning [*Griphognathus*+*Holodipterus*], each of these characters is homoplastic.

The failure of the present study to find any unique, unambiguous synapomorphies that support either [*Griphognathus*+*Holodipterus*] or the placement of *Soederberghia* crownward of this clade raise questions about the reliability of this particular phylogenetic arrangement. Generally speaking, most nodes in Ahlberg *et al.* (2006) are poorly supported. With the exception of two clades ([*Griphognathus*+*Holodipterus*]; [*Scaumenacia* [*Fleurantia* [*Barwickia*+*Howidipterus*]]]), all lungfishes crownward of *Gogodipterus*, including *Soederberghia*, collapse into a polytomy in a strict consensus of trees one step longer (230 steps) than the shortest solution (229 steps). A strict consensus of trees at 231 steps leaves [*Holodipterus gogoensis*+*H. meemannae*] and [*Fleurantia*+*Barwickia*+*Howidipterus*] as the only clades resolved in a polytomy above *Diabolepis*. Ahlberg *et al.* (2006) concede that many aspects of early lungfish phylogeny remain uncertain in

the face of their results, and ‘do not claim that they represent the final word on Paleozoic lungfish phylogeny’ (p. 342).

Set against the weak evidence for this alternative arrangement is the extensive set of potential synapomorphies underpinning a ‘rhynchodipterid’/fleurantiid clade. These include: elongated snout; long mandibular rami with a short symphysis; reduction or loss of the adductor fossa; dentition consisting largely of denticles; vertebral column composed of well-ossified disc centra (absent in *Fleurantia*); retroarticular process; infradentary count reduced to two, with the posterior member of the series contributing to a majority of the jaw; external laminae of cleithrum and clavicle overlap postbranchial laminae, with no outturned ridge (Campbell & Barwick 1990; Krupina & Reisz 2000; Schultze 2001; Friedman 2007, in press). Many derived neurocranial characters appear to link *Griphognathus* and *Soederberghia* (presence of a cranial centrum; nasal capsules set far back from the oral margin; course of the lateral dorsal aortae over the parasphenoid stalk; Friedman 2007), but most of these characters cannot be assessed for fleurantiids. In addition, ‘rhynchodipterids’ and fleurantiids appear to share a series of derived characters with some or all ‘holodontids,’ including a skull with a concave dorsal margin in lateral view and deeply interdigitated transverse sutures between bones of the dermal skull roof (Pridmore *et al.* 1994). Another derived character shared by some of these taxa is a rasp-like basihyal that bears denticulated toothplates. This highly specialised arrangement was previously known to be present in some ‘holodontids’ (Pridmore *et al.* 1994), *G. sculpta*, and *G. whitei*, but CT scan data show an identical structure in *Rhynchodipterus*. Unfortunately, the condition in other putative members of this clade is unclear. No ossified basihyal has been reported for *Soederberghia* or *Fleurantia*, while only the posterior tip of this bone is preserved in *Jarvikia* (pers. obs. MUGH VP 3072+3073).

A weakness of the putative synapomorphies reviewed above is that many have not been documented for key taxa, most notably *Rhynchodipterus* and *Jarvikia*. With the exception of a reduced infradentary count, which cannot be established owing to the coarse resolution of the CT scans, it is now clear that *Rhynchodipterus* shares all of the derived mandibular features cited as possible synapomorphies of the ‘rhynchodipterid’+fleurantiid clade. Furthermore, an exposed region of the entopterygoid shows that the dentition of *Rhynchodipterus* consists of a fine denticle shagreen, and there is no indication of organised tooth plates in any CT renderings. Many uncertainties remain for *Jarvikia*, but a mandible found with a new specimen of this genus bears similarities to those of other long-snouted, denticle-bearing lungfishes (pers. obs. MUGH VP 28401+28402). The jaw of *Jarvikia* has a well-developed retroarticular process and narrow, elongated rami. Although the symphysis is not preserved, it seems probable that it was short based on the geometry of the intact portions of the mandible.

In addition to this series of previously proposed synapomorphies, the current study has highlighted the following cranial characters that support the clade containing ‘rhynchodipterids’ and fleurantiids:

1. **Falcate preglenoid process of the posterior infradentary (lateral ascending process), bearing an apical notch for the ramus mentalis externus N.VII.** In the most plesiomorphic lungfishes, there is no well-developed dermal ascending process, and the ramus mentalis externus N.VII fails to notch the infradentaries (Thomson & Campbell 1971; Miles 1977; Campbell & Barwick 1988). However, in *Soederberghia groenlandica*, and *Fleurantia* (BMNH P 24745), and *Griphognathus*, there is a well-developed, hook-shaped dermal preglenoid process that is notched at its apex; this undoubtedly represents a derived arrangement. *Rhynchodipterus* and *Jarvikia* also have falcate preglenoid processes; CT scan data are too coarse to determine whether this process was intersected by N.VII in *Rhynchodipterus*, while the same feature appears to have been pierced by a canal for this nerve in *Jarvikia* (pers. obs. MUGH VP 28401+28402). Dermal preglenoid processes are present in many other early lungfishes (Wang *et al.* 1993, fig. 14; Barwick & Campbell 1996, fig. 6) but they rarely assume the hook-like morphology common to ‘rhynchodipterids’ and fleurantiids, and the notch for N.VII, if present, is located on the posterior margin of this feature (Jarvik 1967, fig. 7; Thomson & Campbell 1971, fig. 24).
2. **Quadrate occupies an infraorbital position.** Primitively in lungfishes, the articular head of the quadrate is located far posterior to the orbit (Fig. 15A, B), as in other early sarcopterygian fishes. However, ‘rhynchodipterids’ and fleurantiids have radically remodeled palates with quadrates that occupy an infraorbital or preorbital position. This is most clearly documented for *Griphognathus whitei* (Miles 1977; Figs 12, 15C) and *G. sculpta* (Schultze 1969, pl. 3, fig. 4), but can also be shown for *Soederberghia groenlandica* (Lehman 1959, fig. 3; Fig. 12), *Rhynchodipterus* (Fig. 12), and *Fleurantia* (Cloutier 1996, fig. 12; pers. obs. BMNH P 6785). The anterior position of the quadrate ramus in *G. minutidens* (Schultze 1969, fig. 10) and *Jarvikia* (pers. obs. MUGH VP 3072+3073) relative to the orbit is clear evidence that they also shared the derived condition.

4.2.2. *Griphognathus minutidens* plus *Rhynchodipterus* plus *Soederberghia* plus fleurantiids. Most studies of lungfish interrelationships have not tested the monophyly of *Griphognathus*, and have instead used *G. whitei* as an exemplar for this genus. Those few studies that have included multiple species of *Griphognathus* appear to support its monophyly (Krupina & Reisz 2000; Schultze 2001), but Friedman (2007) presented neurocranial evidence that *G. minutidens* is more closely related to *Soederberghia* than to *G. whitei*, rendering the genus *Griphognathus* paraphyletic. In that study, Friedman (2007) also discussed a series of non-neurocranial apomorphies found in *G. minutidens* and *Soederberghia* but not *G. whitei*. Some of these possible synapomorphies are discussed in greater detail here.

While it is clear that *G. minutidens* and *G. whitei* do not form a natural group, it is uncertain how *G. sculpta* relates to these two taxa. This species combines some mandibular features suggesting a close relationship with *G. minutidens* and other derived ‘rhynchodipterids’ (arrangement of the sensory canals, large dermal retroarticular process), with some unusual and possibly derived features found in *G. whitei* (a dorsal fin basal plate comprising multiple, closely appressed endoskeletal ossifications; Friedman in press).

Cranial characters supporting the monophyly of a group including *Rhynchodipterus*, *Soederberghia*, fleurantiids, and *G. minutidens* to the exclusion of *G. whitei* include:

3. **External dermal retroarticular process.** While a retroarticular process appears to be characteristic of ‘rhynchodipterids’ and fleurantiids, it shows different degrees of development in members of these groups. In *Griphognathus whitei*, the retroarticular process is short and is composed almost exclusively of the endoskeletal articular; both the prearticular and posterior infradentary in this species appear to terminate at approximately the level of

the posterior margin of the glenoid (Fig. 8B). The confinement of these dermal bones at or anterior to the level of the glenoid is primitive, as demonstrated by outgroup comparison (Thomson & Campbell 1971; Miles 1977; Campbell & Barwick 1988). In contrast, *Soederberghia*, *Rhynchodipterus*, *Fleurantia*, *Jarvikia*, *Griphognathus minutidens*, and *G. sculpta* have large retroarticular processes with a major dermal component: in each of these taxa, the posterior infradentary bears a posterior extension that terminates posterior to the level of the jaw joint.

4. **Posterodorsal displacement of the posterior pore for the mandibular canal.** In *G. whitei*, the mandibular canal enters the jaw near the ventral margin of the infradentaries, well anterior to the glenoid (Miles 1977, fig. 99; Campbell & Barwick 1986, fig. 14B). This arrangement appears to be primitive for dipnoans, based on comparison with cosmine-bearing 'chirodipterids' (Miles 1977) and the Early Devonian genera *Dipnorhynchus* and *Uranolophus* (Thomson & Campbell, 1971; Campbell & Barwick 1988).

G. minutidens, *G. sculpta* (Schultze 1969; Miles 1977), *Soederberghia groenlandica*, the Belgian *Soederberghia* (Clément & Boisvert 2006), and *Fleurantia* (Cloutier 1996, fig. 12) display a derived condition in which the posterior pore for the mandibular canal is posteriorly displaced, located at or behind the level of the glenoid. In addition, the entrance for the mandibular canal in *Soederberghia groenlandica*, *Griphognathus minutidens* (Schultze 1969, fig. 3), and *Fleurantia* (Cloutier 1996, fig. 12) occupies a position on the lateral face of the posterior infradentary, well above the generalised position on the ventral margin of the external dermal bones of the jaw. Interestingly, *G. sculpta* (Schultze 1969, fig. 13) seems intermediate in condition between the derived state of these taxa and the primitive condition found in *G. whitei*. This character is probably related to the extension of the dermal retroarticular process in these taxa (character 3 above).

5. **Arched ventral margin of the prearticular.** The ventral margin of the prearticular in *Griphognathus whitei* is straight (Fig. 8B), corresponding to the generalised dipnoan arrangement (Fig. 8A). However, in *Rhynchodipterus* (pers. obs. E 1898.2 A), *Soederberghia groenlandica* (Fig. 8D), *G. minutidens* (Gross 1956, pl. 7; Fig. 8C), the ventral margin of the prearticular is conspicuously arched. This derived arrangement appears to have arisen from the loss of the depressed lamina located ventral to the denticulated field, which is found in taxa such as *Holodipterus longi* and *G. whitei* (Fig. 8A, B).
6. **Dorsal prearticular dentition comprised of small, triangular 'teeth.'** Excepting *Orlovichthys* (Krupina *et al.* 2001) and the species of *Rhynchodipterus* (Ørvig 1961), which bear tooth plates, all long-snouted dipnoans have dentitions that consist primarily of denticles. There is some diversity in these denticulate dentitions, with apparent tooth rows in *Soederberghia* (Friedman 2007) and *Fleurantia* (Graham-Smith & Westoll 1937; Cloutier 1996), large palatal caluses in *Griphognathus whitei* (Campbell & Barwick 1999, figs 3D, 11), and remodelled vermiform ridges in *Jarvikia* (Clément & Boisvert 2006; Friedman 2007).

In addition to specialisations of the palatal denticle fields, many 'rhynchodipterids' and fleurantiids have a pseudomarginal dentition found on the dorsal margin of the prearticular. In *Griphognathus whitei* (Fig. 8B), these assume the form of irregular excrescences that resemble those in *Holodipterus longi* (Fig. 8A), suggesting this is the primitive arrangement. The derived dorsal prearticular dentition of *Soederberghia* (Figs 8D, 10), *G. minutidens* (Gross 1956; Schultze 1969; Fig. 8C), and *Fleurantia*

(Graham-Smith & Westoll 1937; Cloutier 1996) is developed as a series of small, regularly-spaced triangular cusps.

4.2.3. *Rhynchodipterus plus Soederberghia plus fleurantiids.*

At least three cranial characters have been noted that might link these taxa: posterior extensions of the entopterygoids ('posterior prong of the entopterygoid'; Friedman 2007), extended L-bones that contact the E-bones, and reduction or loss of the D-bone (Krupina & Reisz 2000). However, the reliability of these final two must be viewed with some skepticism. Apart from *Soederberghia*, *Rhynchodipterus* (Schultze's 1969 figure incorrectly shows divided L-bones; pers. obs. E 1898.2 A, B), and fleurantiids, anteriorly extensive L-bones are also found in *Oervigia* (Lehman 1959), *Phaneropleuron* (Westoll 1949), and *Andreyevichthys* (Krupina 1987). Cloutier (1996) associated the latter taxon with fleurantiids, but there are few compelling characters that would appear to link this genus to either *Fleurantia*, *Jarvikia* or the more extensive radiation of long-snouted, denticle-bearing lungfishes hypothesised here (see section 4.2.4). Reduction or loss of the D-bone is similarly problematic. It is difficult to objectively establish when a D-bone is 'reduced,' while D-bone loss is highly homoplastic in most estimates of dipnoan phylogeny (Campbell & Barwick 1990; Schultze & Marshall 1993; Schultze 2001).

While it seems that fleurantiids likely form a clade within this radiation, the relative positions of *Soederberghia* and *Rhynchodipterus* remain uncertain. *Rhynchodipterus* has a very narrow snout reminiscent of *Fleurantia* and *Jarvikia*, while it also shares derived, teardrop-shaped orbits with *Soederberghia* (Figs 12, 13).

Four additional characters highlighted by the current study appear to support a clade comprising *Rhynchodipterus*, *Soederberghia*, and fleurantiids:

7. **Loss of Meckelian ossification.** Ossification of the Meckelian element is primitive for lungfishes, and is found in all nominal species of *Griphognathus* (Schultze 1969; Miles 1977). However, *Soederberghia*, *Rhynchodipterus*, and fleurantiids show no evidence of Meckelian ossification. However, the reliability of this character is questionable, as Meckelian ossification is also absent in many other lungfishes, including *Adololopas* (Campbell & Barwick 1998), *Holodipterus meemannae* (Pridmore *et al.* 1994), and all post-Devonian lungfishes (e.g. Schultze & Chorn 1997).
8. **Posterior embayment of the ceratohyal.** In most Devonian lungfishes, the posterior margin of the ceratohyal is straight or convex. This arrangement characterises a wide range of early dipnoans, including *Uranolophus* (Fig. 11A), 'chirodipterids' (Fig. 11B), and *Griphognathus*. A similar geometry is found in porolepiform sarcopterygians (Jarvik 1972), suggesting that this is the plesiomorphic dipnoan, and dipnomorph, condition. A different, and presumably derived, arrangement is found in 'rhynchodipterids' and fleurantiids, in which the posterodorsal margin of the ceratohyal is conspicuously excavated. Such a posterior concavity, which appears to arise from incomplete ossification of the ceratohyal posterodorsally, is present in *Soederberghia groenlandica* (Fig. 4), *Jarvikia arctica* (Fig. 11E; pers. obs. MGUH VP 3072+3073), and *Rhynchodipterus* (pers. obs. E 1898.2). Although the ceratohyals of *Fleurantia* are known (Graham-Smith & Westoll 1937; *contra* Cloutier 1996), they are too poorly preserved to reliably determine the state of this character. This condition is most closely approximated outside this clade by the 'phaneropleurid' *Barwickia* (Fig. 11C), but the embayment in this genus does not closely resemble that of

Jarvikia, *Rhynchodipterus*, and *Soederberghia*, and is less well developed than in any of these long-snouted genera.

9. **Infraorbital bar comprises a single ossification.** In plesiomorphic, cosmine-bearing lungfishes, the infraorbital bar is constructed of multiple ossifications, most typically bones 5 and 6. However, *Fleurantia* (Cloutier 1996), *Rhynchodipterus* (Fig. 12), and the species of *Soederberghia* (Ahlberg *et al.* 2001; Figs 1–2, 12) have an undivided infraorbital bar. This region of the skull is incompletely known in *Jarvikia*, although one specimen of *J. arctica* (MGUH VP 3072+3073) preserves a badly weathered infraorbital bar that appears to only have one centre of ossification. No cheek material is known for *J. lebedevi* (Krupina 1999).

A consolidated infraorbital bar is also present in the Givetian *Barwickia*, which Long (1992) believed to be a fleurantiid. However, this taxon lacks numerous derived features common to both fleurantiids and derived ‘rhynchodipterids’. A notable example concerns the position of the quadrate. Long’s (1992) reconstruction, as well as his specimen photographs and interpretive drawings, leave little doubt that the quadrate in *Barwickia* occupied a position at the posteroventral corner of the dermal cheek, consistent with the generalised dipnoan, and osteichthyan, arrangement. The lower jaw in this genus, which lacks a long retroarticular process, appears to corroborate this inference. This primitive arrangement suggests that the consolidated infraorbital bar of *Barwickia* might simply correspond to the ‘fusion’ of bones 5 and 6, while it is probable that the infraorbital bar of ‘rhynchodipterids’ and fleurantiids can trace its ancestry to bone 10 (quadrate-jugal; see section 4.1). In many respects, the anatomy of *Barwickia* corresponds closely to that of ‘phaneropleurid’-grade taxa such as *Pentlandia* and *Howidipterus*, and its true affinities might lie with these lungfishes and not fleurantiids.

10. **E-bone(s) anteriorly trifurcate.** The E-bone(s) of *Rhynchodipterus* (pers. obs. E 1898.2), *Soederberghia* (Lehman 1959; Campbell & Bell 1982; Ahlberg *et al.* 2001), and fleurantiids (Lehman 1959; Krupina 1999) has a distinctive anterior margin, with a single midline projection flanked by two lateral projections. The median E-bone of *Andreievichthys* bears an anterior midline projection, but lacks the lateral extensions found in ‘rhynchodipterids’ and fleurantiids (Krupina 1987, fig. 1).

4.2.4. Fleurantiids. Here, Fleurantiidae contains two genera: *Fleurantia* and *Jarvikia*. While these two taxa are considered to be fleurantiids by most authors (Vorobyeva & Obruchev 1964; Miles 1977; Campbell & Barwick 1990), some have suggested that the membership of this group is more extensive. Long (1992) described *Barwickia* as a fleurantiid, an interpretation subsequently adopted by Cloutier (1996), who also placed *Andreievichthys* in this group. The cladistic solution presented by Krupina & Reisz (2000) also indicated a large fleurantiid radiation, placing *Fleurantia* and *Jarvikia* closer to the tooth plate bearing taxa *Oervigia* and *Andreievichthys* than to other long-snouted, denticle-bearing lungfishes. While a close relationship between *Jarvikia* and *Fleurantia* seems clear, relationships between these taxa and *Andreievichthys*, *Barwickia*, and *Oervigia* are less convincing because these putative fleurantiids lack many of the derived characters discussed in previous sections. Most striking among these are denticulate dentition (absent in *Andreievichthys* and *Oervigia*); disc centra (absent in *Andreievichthys*, *Barwickia* and *Oervigia*); elongated rostra (absent in *Andreievichthys* and *Barwickia*, unknown in *Oervigia*); deeply interdigitated trans-

verse sutures of the skull roof (absent in *Andreievichthys*, *Barwickia* and *Oervigia*); extensive retroarticular process (absent in *Andreievichthys* and *Barwickia*, unknown in *Oervigia*); prong-shaped preglenoid process (absent in *Andreievichthys* and *Barwickia*, unknown in *Oervigia*); anteriorly displaced quadrate (absent in *Barwickia*, unknown in *Andreievichthys* and *Oervigia*); an infraorbital bar comprising a single ossification (present in *Barwickia*, absent in *Andreievichthys*, unknown in *Oervigia*); and an anteriorly trifurcate E-bone (absent in *Andreievichthys*, *Barwickia*, and *Oervigia*). However, both *Andreievichthys* and *Oervigia* share with *Jarvikia* and *Fleurantia* anteriorly extensive L-bones (which also characterise *Soederberghia* and *Rhynchodipterus*), while *Andreievichthys* also shares a single median E-bone with these ‘core’ fleurantiids (present in all specimens of *Jarvikia* and most specimens of *Fleurantia*; Lehman 1959; Cloutier 1996; Krupina 1999). Notably, expanded L-bones are found elsewhere in *Phaneropleuron* (Westoll 1949), and *Oervigia* and *Andreievichthys* appear to correspond more closely to this genus than they do to either *Fleurantia* or *Jarvikia*. It is probable that these three Late Devonian tooth plate-bearing forms are closely related, and that the superficial similarities they share with fleurantiids are homoplastic.

Andreievichthys, *Barwickia*, and *Oervigia* lack not only the extensive series of characters that underpin various levels of the putative ‘rhynchodipterid’+fleurantiid radiation, but also the following derived character that appears to unite *Fleurantia* and *Jarvikia*:

11. **Anteriorly extensive parasphenoid.** While the most phylogenetically primitive lungfishes possess parasphenoids that extend far anteriorly and divide the entopterygoids over much of their length (Schultze 1992a; Otto & Bardenheuer 1996), all phylogenetic hypotheses nest *Jarvikia* and *Fleurantia* within a clade of lungfishes that lack such projections (Miles 1977; Campbell & Barwick 1990; Schultze & Marshall 1993; Schultze 2001; Ahlberg *et al.* 2006). However, both of these genera appear to show a reversal to the primitive dipnoan condition, in which the parasphenoid is produced anteriorly (Lehman 1959, fig. 24; Cloutier 1996, fig. 10A; Clément & Boisvert 2006). This is particularly pronounced in *Jarvikia*, where the parasphenoid extends along nearly the entire length of the entopterygoids.

5. Conclusions

New fossil material, combined with renewed study of old specimens, has clarified many aspects of cranial structure in *Soederberghia*. This, coupled with recently described aspects of neurocranial and postcranial anatomy (Friedman 2007, in press), make this genus one of the more completely understood Late Devonian lungfishes. Despite assertions to the contrary (Ahlberg *et al.* 2001, 2006), there is considerable morphological evidence for the close relationship between (but not monophyly of) ‘rhynchodipterid’ lungfishes.

The intractability of Devonian lungfish systematics is a common lament, but much of the confusion surrounding the interrelationships of early lungfishes is artefactual. Considerable inconsistency has arisen from the radically divergent approaches to phylogenetic reconstruction applied by different researchers, but an equal, or perhaps greater, contributor to current uncertainty lies with the inadequate description of many fossil lungfishes. This has led directly to impoverished data sets that are forced to employ features known to be highly variable within taxa and proportional characters that lack any clear biological justification. As a consequence, most analyses

have treated well-known taxa like their less complete contemporaries, neglecting potentially character-rich aspects of morphology while focusing almost exclusively upon the dermal skull and superficial aspects of dentition. New, detailed character sets concerning dentitions (Ahlberg *et al.* 2006), neurocranial structure (Friedman 2007), and postcranial anatomy (Friedman in press) provide welcome additions to existing matrices, but much work remains to be done on inadequately documented lungfish taxa. Basic morphological descriptions of these poorly known dipnoans will provide the solid empirical foundation necessary for future phylogenetic analyses.

6. Acknowledgments

Much of the work contained in this contribution was submitted in partial requirements for the degree of MPhil at the University of Cambridge under the supervision of J. Clack. My examiners, P. Janvier and S. Conway-Morris, provided constructive comments on my thesis, which also benefited from discussion with my colleagues at Cambridge: M. Allinson, H. Blom, E. Sharp and R. Wade. M. Coates (University of Chicago) read and commented on drafts of this contribution. P. Ahlberg, P. Forey and M. Richter (NHM), G. Cuny (MGUH), J. Kriwet (MB), T. Mörs (NRM), D. Addison (E) and S. Stuenes (UU) kindly permitted access to specimens in their care. Special thanks are due to P. Ahlberg (now at UU), who lent casts of *S. simpsoni* and the prearticular of *S. goenlandica*, and sent a copy of the correct data matrix for Ahlberg *et al.* (2006). J. A. Long and Z. Johanson provided helpful reviews of this manuscript. This work was funded by a National Science Foundation Predoctoral Fellowship, award number DGE-0228235, the Lerner-Grey Fellowship for Marine Research from the American Museum of Natural History, and Hinds Fund Grant from the University of Chicago.

7. Abbreviations

7.1. Anatomical

1a—bone 1a
3—bone 3
4—bone 4
5—bone 5
6—bone 6
7—bone 7
8—bone 8
10—bone 10

a.ih.m—insertion area for the interhyoideus muscle
a.l.h.m—insertion area for the levator hyoideus muscle
art.Hhy—articular surface for the hypohyal
c.io—infraorbital canal
c.md—mandibular canal
c.o—oral canal
c.pop—preopercular canal
Chy—ceratohyal
d.f.Prart—denticle field of the prearticular
dep.l—depressed lamina of the prearticular
ex.glen—excavation for the glenoid
f.ao—antorbital foramen
G.p—gular plate
gr.e.h.a—groove for the efferent hyoid artery
gr.r.intV?—possible groove for the ramus intermandibularis N.V

Hhy—hypohyal
Id1—first infradentary
Id2—second infradentary
KX—bone KX
L—bone L
mk.c—Meckelian canal
Prart—prearticular
prl.asc—lateral ascending process of preglenoid process
prl.ret—lateral retroarticular process
prm.asc—mesial ascending process of the preglenoid process
prm.ret—mesial retroarticular process
n.p—posterior notch of the ceratohyal
n.d—dorsal notch of the ceratohyal
nds—non-denticulated strip on dorsal surface of dentary
r.m—median ridge of the ceratohyal
r.m.eVII—ramus mentalis externus N.VII
ri.so—supraorbital ridge
s—scale
sd—surficial damage
sy—symphyseal region
t.r—tooth ridge of the prearticular
v.con—ventral concavity of the prearticular
Y₁—bone Y₁

7.2. Institutional

AMF—Australian Museum, Sydney, Australia
BMNH—The Natural History Museum, London, England
E—Elgin Museum, Elgin, Scotland
MB—Museum für Naturkunde, Berlin, Germany
MGUH—Geological Institute, Copenhagen, Denmark
NRM—Department of Palaeozoology, Naturhistoriska Riksmuseet, Stockholm, Sweden
UU—University of Uppsala, Uppsala, Sweden

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MS received 22 May 2006. Accepted for publication 5 July 2007.