Mandibles of rhizodontids: anatomy, function and evolution within the tetrapod stem-group

Jonathan E. Jeffery

ABSTRACT: The Rhizodontida (Pisces: Sarcopterygii) is a clade of predatory fishes from the Upper Devonian (*Aztecia*; ?Givetian of Antarctica) through to the Upper Carboniferous (*Strepsodus*; Moscovian of northern Europe and North America). They form the most basal plesion within the tetrapod stem-lineage. The mandibles were dominated by large symphysial tusks on the dentary. Not much else is known of the mandibles in primitive rhizodontids. However, later forms show several derived characters: the mandible is very deep dorsoventrally and narrow linguolabially; the coronoid fangs bear only a single fang and no other dentition; the Meckelian element was unossified, leaving the adductor fossa unfloored by bone; the prearticular produced a large dorsal process lingual to the adductor fossa, presumably for muscle attachment. These and other characters are discussed in the context of the evolution of the tetrapod stem-group.

The mandible appears to have been split into two functional units, one comprising the firmly sutured prearticular, coronoids and dentary, the other comprising the firmly sutured infradentaries. The connection between the two units was weak, suggesting a longitudinal intramandibular hinge. The possibility that this acted as a 'torsion grip' during feeding is discussed.

KEY WORDS: dentition, evolution, functional morphology, Rhizodontida, *Rhizodus*, *Screbinodus*, stem-tetrapod, *Strepsodus*, tetrapodomorph.

Rhizodontids are predatory fishes ranging from the Upper Devonian to the Upper Carboniferous. In the majority of cases, they are found in sediments formed in shallow, freshwater environments (Jeffery 1999, 2001). However, many of these beds show evidence of occasional brackish or saltwater incursions (e.g. Whyte 1994), and some disarticulated remains have been found in shallow (near-shore) marine deposits (Janvier *et al.* 1984). Derived members of the group reached very large sizes (*Rhizodus* may have reached 7 m in length: Andrews & Westoll 1970; Jeffery 1999). Their jaws bear large, deeply rooted teeth (hence the ordinal name; Fig. 6c, d). Interest in the group was initially stimulated by the teeth (e.g. Hibbert 1833), as they were thought to belong to saurians (see Andrews 1982, 1985 for a review). Traquair (1877a) used the type species *Rhizodus hibberti* in some of the earliest comparative studies of fossil sarcopterygian jaws. He was the first to recognise that there are two rows of teeth, borne on separate bones (on the dentary and on the coronoid series). He was also the first to note the series of bones ventral to the dentary, coining the term 'infradentaries' and proposing their homologies with similar bones in actinopterygians (Traquair 1877a). More recently, interest has been revived by a series of new discoveries (e.g. Andrews 1985; Long 1989; Young *et al.* 1992; Johanson & Ahlberg 1998; Davis *et al.* 2001), and cladistic studies suggesting that rhizodontids belong to the tetrapod stem-group (e.g. Ahlberg 1991; Young *et al.* 1992; Cloutier & Ahlberg 1996; Ahlberg & Johanson 1998; Jeffery 1999).

1. Methods and materials

1.1. Specimens and preparation
Specimens were prepared under a stereomicroscope using a Chicago Pneumatic Airscribe CP9361, a Techdent dental mallet and a mounted tungsten carbide needle. Where needed, specimens were consolidated using a solution of Paraloid B72 in acetone. Some specimens of *Barameda* were negatively-prepared with acid in a previous study (Long 1989). One specimen of *Strepsodus* (NEWHM 19.18) was negatively-prepared by the late Dr S. M. Andrews, but never described by her. Silicone rubber peels made of NEWHM 19.18 during this study have been deposited at the Hancock Museum, Newcastle.

1.2. Taxonomy and terminology
Taxonomy. Two poorly known species of *Strepsodus* (*S. portlocki* Portlock 1843 and *S. sulcidens* Hancock & Atthey 1870) were once considered to form their own genus, *Archichthys* Hancock & Atthey 1870. They were transferred to *Strepsodus* by Woodward & Sherborn (1890) without clear justification. Since the tooth morphology of these two species is quite different from other species of *Strepsodus*, Andrews (1985) suggested that *Archichthys* might be a valid genus (however, Andrews herself seems to have become confused; see below). A detailed discussion of the taxonomy of *Strepsodus* is beyond the scope of this paper. However, for the sake of clarity, I will exclude *S. portlocki* and *S. sulcidens* from my description of *Strepsodus* material. They will be discussed in a review of *Strepsodus* and *Archichthys* currently in preparation.

Terminology. There are no universally accepted terms to describe the relative position of bones along the mandibular ramus. The terms 'anterior' and 'posterior' fail to take into account the curvature of the mandible towards the symphysis. I have therefore adopted the terms recommended by the Federative Committee on Anatomical Terminology (F.C.A.T. 1998) for describing teeth. Here the terms 'mesial' and 'distal' mean, respectively, towards and away from the mandibular

symphysis. Thus 'anterior' and 'posterior' are used only when the curvature of the mandible is not relevant (see Fig. 1).

In each species of rhizodontid, the dentition of the mandible falls into four non-overlapping size categories. These will be referred to as, from largest to smallest, the tusks (symphysis of dentary), fangs (coronoids), teeth (dentary, parasymphysial) and denticles (in fields on various bones). This does not necessarily imply differences in morphology or ontogeny (particularly between the tusks, fangs and teeth) but conveniently distinguishes the size ranges. 'Teeth' is also used as a general term for dentition.

The four categories of dentine-folding established by Schultze (1969)—polyplocodont, labyrinthodont, eusthenodont, dendrodont—are phenetic, in that they are defined on overall form and not on inferred autapomorphies. Dendrodont folding is clearly defined, and appears to be restricted to a monophyletic clade (the porolepiforms). However, polyplocodont, labyrinthodont and eusthenodont folding are less clearly distinguished, and are best regarded as organisational 'grades'.

1.3. Abbreviations of institutions
AMNH—American Museum of Natural History, New York; AMF—Australian Museum, Sydney; BGS—British Geological Survey, Keyworth, Notts.; GLAHM—Glasgow Hunterian Museum; MM—Manchester Museum; NEWHM—Newcastle Hancock Museum; NHM—Natural History Museum; NMS G/HM—National Museums of Scotland, Edinburgh; NMV—National Museum of Victoria, Australia; SME—Sedgwick Museum of Geology, Cambridge; UN-DG—Departamiento de Geociencias, Universidad Nacional de Colombia, Bogotá.

2. Mandibular morphology

2.1. Gross morphology
The mandible is best known in three derived genera: *Rhizodus*, *Screbinodus* and *Strepsodus*. The pattern of bones is primitive for the sarcopterygian crown group—the labial face is formed from four infradentaries ventral to a tooth-bearing dentary. The principal bone of the lingual face is the prearticular. Between the prearticular and dentary there is a series of tooth-bearing coronoids. The jaws of *Rhizodus*, *Screbinodus* and
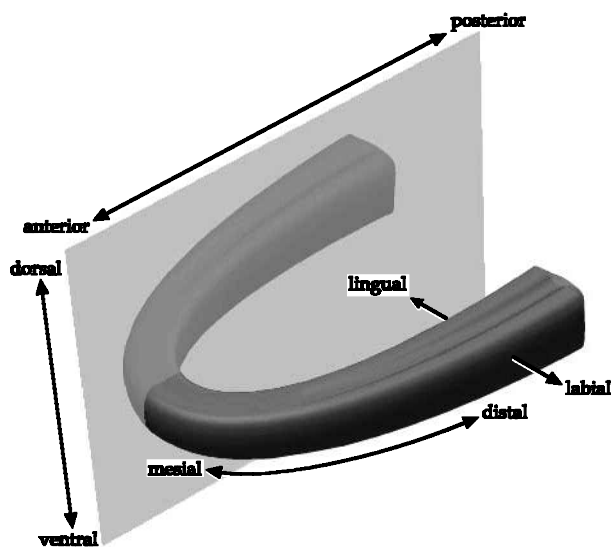

Figure 1 Anatomical terminology. Stylised mandible showing the directional terms used in this paper. Note the use of mesial (towards symphysis) and distal (away from symphysis).

Strepsodus are dominated by a series of large tusks and fangs. The endoskeletal component (the Meckelian element including the articular bone) appears not to have ossified. Cosmine is not known in any rhizodontid.

2.2. *Rhizodus hibberti*
The best-preserved material of the mandible belongs to *Rhizodus* (Figs 2, 4–7). The mandible is deep dorsoventrally at its mesial tip, in comparison to other rhipidistians (*sensu* Cloutier & Ahlberg 1996). It is also extremely narrow linguolabially. At the level of the first coronoid fang, the thickness of the dentary makes up about one third of the total thickness of the mandible (compared with about 10% in the rhipidistian *Eusthenopteron* (Jarvik 1980; Fig. 3). Most of the known material has been flattened during fossilisation, but NMS G 1950.38.68 shows that the infradentaries contributed little to the width (Figs 1, 2).

Labial face. This is best seen in NHM P3317, SME 4702 and GLAHM V3069 (Fig. 4). The exposed surface of the mandible is covered with fine vermicular ornament. It is formed by a tooth-bearing dentary dorsally and a series of infradentaries ventrally. The dentary overlaps the infradentaries labially, except the first infradentary. This fits into a ventral groove in the dentary, formed between the main ornamented lamina and the thickening for the symphysial tusk (Fig. 2e, f).

The dentary bears a row of around 20 marginal teeth, with a deeply rooted tusk near the symphysis. There is a slight lip on the dentary labial to the tooth row (the 'labial lip'; Fig. 2c, d), so that the bases of the crowns of the teeth are not visible in labial view.

The first infradentary is a small bone. Beyond the anterior limit of the dermal ornament is a mesial, ridged surface (anteromes. rug. infradent. 1; Fig. 2). This may be an overlap surface for the right first infradentary, or it may have contacted one or more anamestic median bones. Dorsal to this, the dentary bears a rugose surface (antermes. rug. dentary; Fig. 2), clearly separate from the symphysial surface mesially and from the ornamented surface labially. It has a number of deep pits, similar to those of the symphysial surface, suggesting that it anchored connective tissues.

The second and third infradentaries are poorly preserved in all specimens showing the labial face of the mandible. The suture between the first and second infradentaries describes a semicircle. On NMS G 1950.38.68 (Fig. 2) it forms a double overlap, the second infradentary overlapping the first infradentary ventrally, but the first infradentary overlapping the second infradentary dorsally. The third infradentary overlaps the fourth infradentary labially. The overlap surface is complex, with ridges and 'terracing' running horizontally (i.e. oblique to the direction of the suture).

The fourth infradentary forms the entire labial face and dorsal margin of the posterior 25–40% of the mandible. It overlaps the shallow distal tip of the dentary. The overlap surface is visible on GLAHM V3069 (Fig. 4g). The rhomboid shape of the bone means that the labial rim of the adductor fossa is angled distally, and the jaw articulation is ventral to the tooth rows. The distal tip of the fourth infradentary is only preserved on GLAHM V3069 (dist. tip infradent. 4; Fig. 4g) where it is fairly blunt, curving mesoventrally onto the ventral margin. It may have formed a retroarticular process.

Lingual face. The lingual face of the mandible is best seen on NMS G 1950.38.67 (Fig. 2) and 1950.36.68 (Fig. 5a, b; see Traquair 1877b, c) and GLAHM V3065 (Fig. 5c, d). As with the labial face, it may be divided dorsoventrally into two halves of approximately equal depth. The dorsal half consists of the lingual face of the dentary mesially and the coronoids
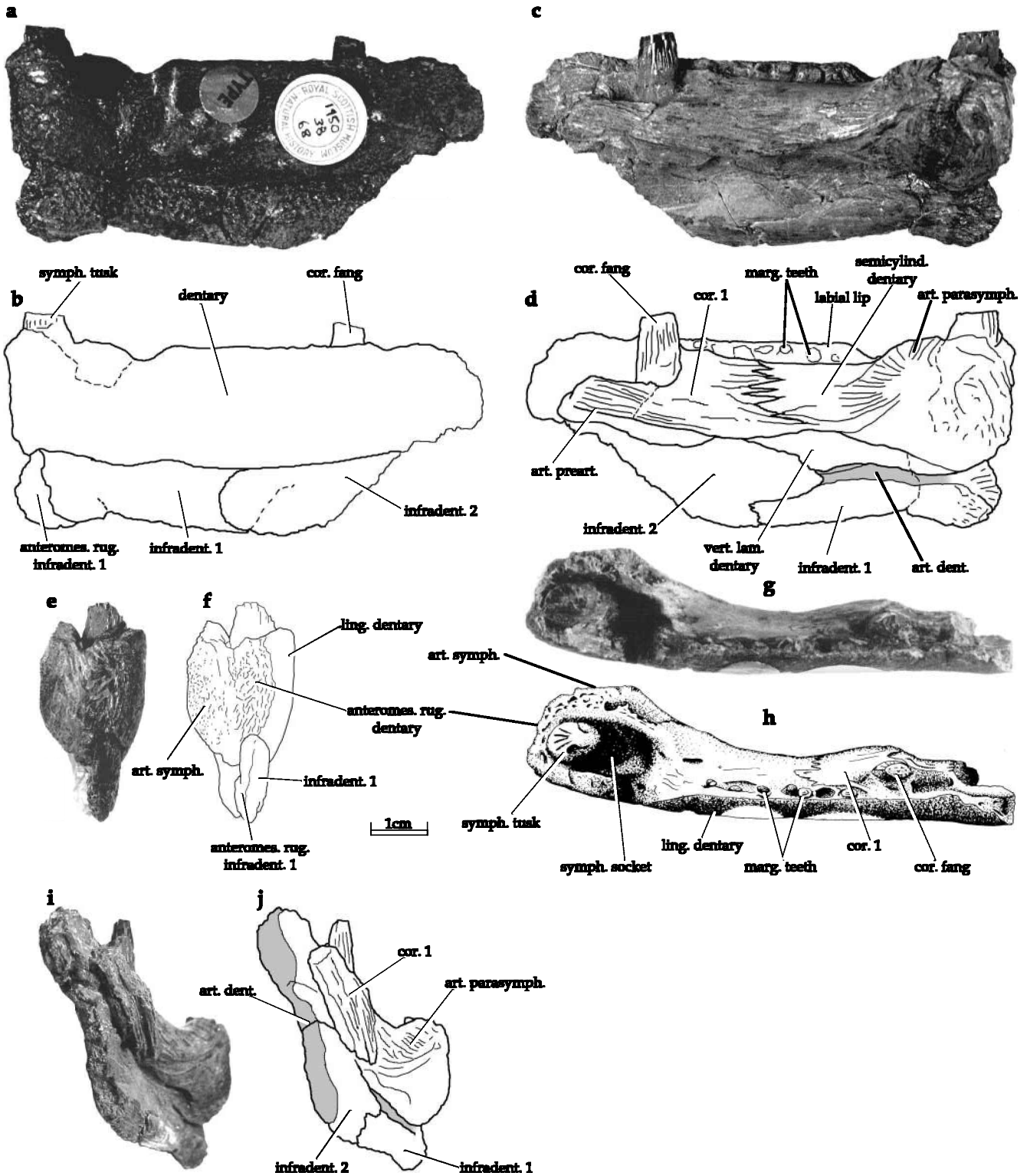
Figure 2 *Rhizodus hibberti*. Photographs and interpretative sketches of a mesial section of left mandible NMS G 1950.38.68 (*cf.* Traquair 1877a,b):
(a), (b) labial view; (c), (d) lingual view. Smooth area on first infradentary articulating with the distal tip of dentary coloured grey; (e), (f) anterior view; (g), (h) dorsal view; (i), (j) proximolingual view. Broken distal tip of the specimen and area on first infradentary articulating with the distal tip of dentary coloured grey. Note the shallow overlap of the dentary and second infradentary. Note the narrow aspect of the mandible.

and prearticular distally. The ventral half consists of the lingual faces of the infradentaries.

On the dentary, the thickening for the root of the symphysial tusk carries the symphysial articulation surface (art. symph.; Figs 2, 5). This surface is complex, with many small processes on its dorsal part, loosely interdigitating with similar processes on its antimere. The parasymphysial bone sat

on a ridged area on the distal part of the root thickening (art. parasymph.; Figs 2, 5). There is no depression or trough for that bone; it formed a distinctly raised surface above the dentary. It must have been weakly attached, as it is known in articulation only on the left mandible on NMS G 1950.38.67 (parasymph.; Fig. 5b) where it is a triangular bone, thick dorsoventrally. Its mesial face bears an articular surface for its
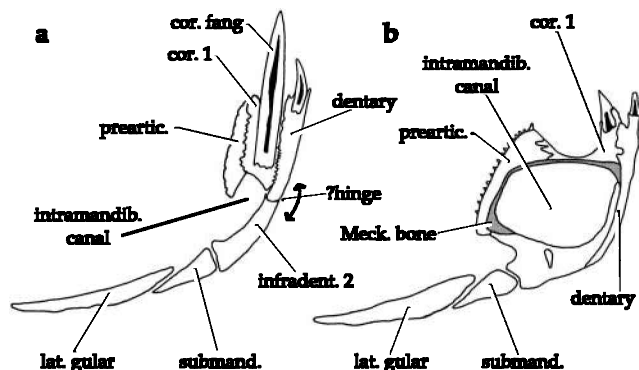
Figure 3 *Rhizodus hibberti* and *Eusthenopteron foordi*. Schematic transverse cross-sections of the mandible at the level of the first coronoid fang.
(a) *Rhizodus hibberti*. Note the narrow aspect of the jaw, the open intramandibular canal, lack of endochondral Meckelian bone, and the possible hinge-joint running longitudinally between the dentary and infradentaries. At the level of this section, the socket for the coronoid fang is open labially (see Fig. 5). However, the coronoid is strongly sutured to the dentary mesially and distally.
(b) *Eusthenopteron foordi*. Note the lingual lamina of the coronoid, the large overlap between the dentary and infradentary, and the 'box-girder' construction. This morphology, stiff in torsion, is primitive for osteichthyians (see discussion).
(a) based on NMS G 1950.38.68 (see Fig. 2); (b) based on Jarvik (1980).

antimere. The dorsal surface of the bone is damaged on NMS G 1950.38.67.

There are three coronoids (approximately equally spaced from one another), each bearing a single fang and no other dentition (cor. fangs; Fig. 5b). There are no intercoronoid fossae. The coronoids are extremely narrow labiolingually (Fig. 7), being not much wider than the base of the fang, and they lack any dorsolingual lamina (see Fig. 2). They are also very deep dorsoventrally, each matching the corresponding depth of the dentary (e.g. NMS G 1950.38.68, GLAHM V3066 and V3065). The root of the fang extends for the entire depth of the coronoid. The pit for the fang is only walled on its lingual face; the labial margin is 'open' (i.e. walled only by the adjacent dentary—e.g. NMS G 1950.38.66; Fig. 7). The first coronoid articulates with the dentary a short way distal to the parasymphysial bone (which it does not contact; Fig. 2g, h). There is no precoronoid fossa. The lingual face of the dentary is semicylindrical at this point (semicylind. dentary; Figs 2d, 4g) and the first coronoid simply wraps around it, the suture strengthened by longitudinal interdigitating ridges (art. dent.; Figs 7d, 6b). The semicylindrical ridge of the dentary tapers away distal to the articulation with the first coronoid, becoming a thickened, dorsal lingual ridge, approximately square in cross-section (square dentary; Fig. 4g). This bears the marginal teeth, and its lingual face bears longitudinal ridges for articulation with the distal coronoids. The lingual face of the first coronoid bears longitudinal ridges for articulation with the prearticular (art. preart.; Fig. 7b). The second and third coronoids are similar to the first, but well-preserved examples are not known (e.g. ?cor. 2; Fig. 6b).

The prearticular bone runs the length of the lingual face of the mandible from the level of the first coronoid fang. The prearticular is very shallow dorsoventrally at its mesial tip, apparently not covering the ventral-most parts of the first coronoid. There was no contact between the prearticular and first infradentary. The dorsal margin runs more or less parallel to the dorsal margins of the coronoids until just distal to the

third coronoid fang, where it forms part of the adductor fossa (see below). The ventral margin of the prearticular runs in a gentle, convex curve, so that the bone doubles its depth distally (e.g. NMS G 1950.38.67; Fig. 5a, b). No specimen shows the distal tip of the prearticular. There are no obvious denticle fields on the prearticular of NMS G 1950.38.67 or GLAHM V3069, although this may be due to damage during preparation prior to the current study.

The coronoids and prearticular do not contact the lingual faces of the infradentaries. The prearticular on NMS G 1950.38.67 has been flattened (Fig. 5), but the ventral margin appears to have hung free, ventral to the coronoids. There is no trace of the Meckelian ossification, meaning that the intramandibular canal was open (or at least closed only with unossified cartilage) along its entire ventral length (cf. Fig. 3a).

The overlap surfaces between the infradentaries bear longitudinal ridges (e.g. ridged art. infradent. 4; Fig. 5b). The ventral third of the lingual faces of the infradentaries are thickened into a smooth ridge, presumably for articulation with the submandibular series (overlap. submandib.; Fig 5b). Only the fourth infradentary has a robust overlap with the dentary. The first infradentary fits in a shallow, smooth groove in the dentary (Fig. 2f), and the second and third infradentaries have only a slight overlap, with no interdigitating ridges (Fig. 2i, j). For example, the second infradentary overlaps the dentary for a maximum of 10–15% of its total dorsoventral depth (cf. 50–60% in *Eusthenopteron*; Fig. 3).

Distal to the symphysial surface of the dentary, a short section of the main vertical lamina of the dentary is exposed (vert. lam. dentary; Figs 2d, 5b). It is bounded ventrally by the first infradentary and part of the second infradentary. At the mesial end of this lamina is a deep dorsolabial pit. It is smooth and featureless, and probably marks the mesial extent of the unossified Meckelian element.

Adductor fossa. The distal end of the mandible, including the adductor fossa, is a complex arrangement of the prearticular, dentary and the fourth infradentary. It is not easily visible on any one specimen, but NMS G 1950.38.67 (Fig. 5a, b) and SME 4702 (Fig. 4a–e) show the lingual and labial aspects, respectively. Additional specimens (GLAHM V3065, NMS HM 345, NMS HM 374) add some detail.

Just distal to the third coronoid, the dorsal margin of the prearticular curves sharply dorsally. It produces a vertical, labially directed flange which contacts the dentary and marks the mesial rim of the adductor fossa. Distal to this, the dorsal margin of the prearticular (forming the lingual rim of the adductor fossa) is horizontal. However, it soon ends in a ragged, convex distal margin. For most of its length, the lingual rim of the adductor fossa (formed by the prearticular) is considerably dorsal to the labial rim (formed by the dentary and fourth infradentary). This raised lingual rim will be referred to as the 'prearticular process' (preart. proc.; Figs 4d, 5b). There is a distinct overhanging ridge on the labial face of the prearticular process, running the length of the adductor fossa (ridge preart. proc.; Fig. 4e). Dorsal to this ridge the prearticular has a very fine, shallow vermicular texture. Ventral to the ridge, and running parallel to it, is a series of shallow ridges which resemble an articulation surface. On the labial face of the adductor fossa, the labial lip continues from the dentary onto the fourth infradentary. Both the dentary and the fourth infradentary produce a lingual shelf, which partially occludes the adductor fossa (see Figs 4d, e, 12c). Crushing during fossilisation has closed the adductor fossa entirely in both SME 4702 and NMS G 1950.38.67, but the shelf probably would have covered half the linguolabial width of the adductor fossa mesially, and possibly less distally. The
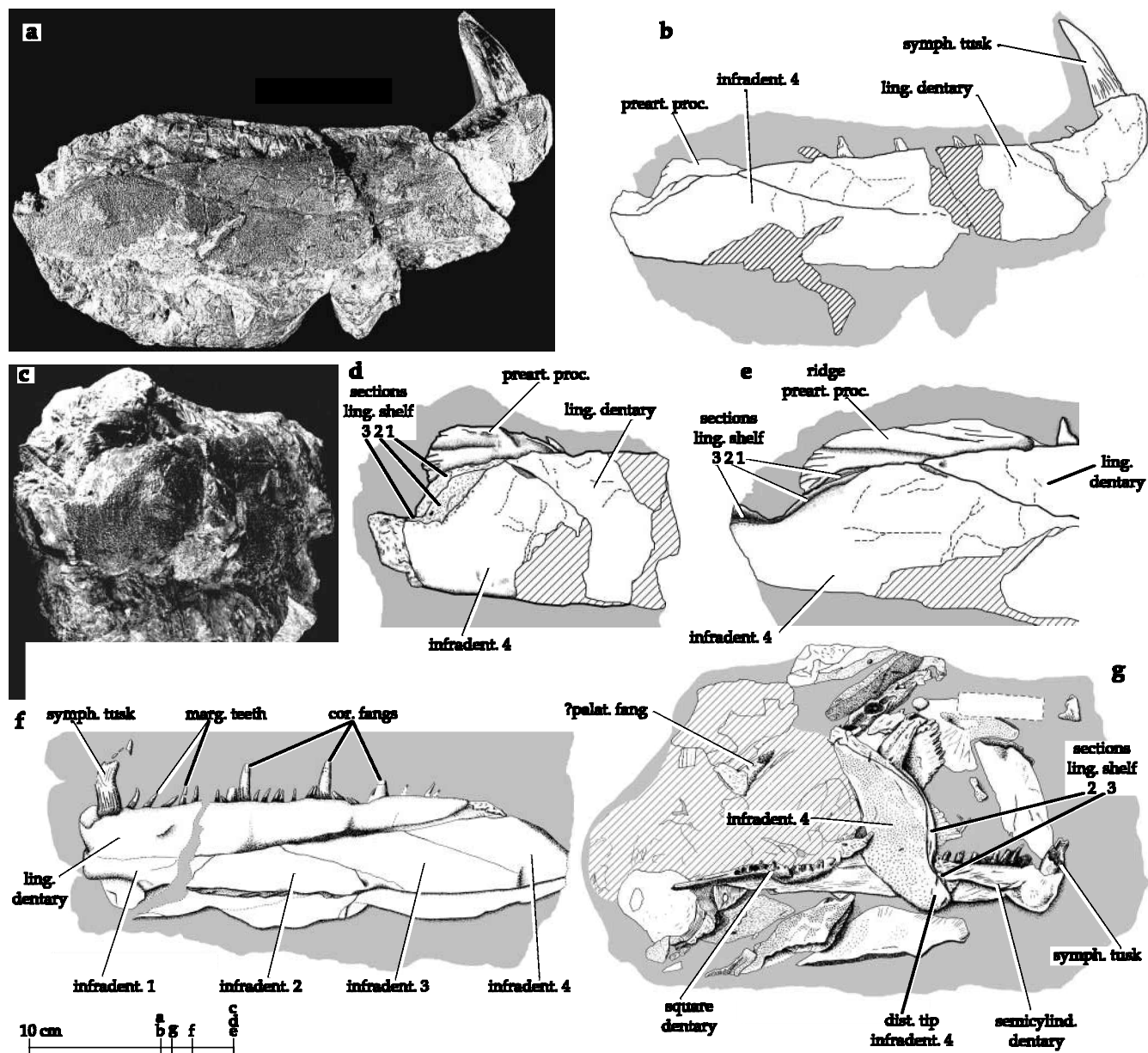
Figure 4 *Rhizodus hibberti.* Specimens showing the labial and distal morphology of the mandible.
(a)–(e) Photographs and interpretative sketches of SME 4702: (a), (b) whole mandible in labial view; (c), (d) detail of distal part of mandible in posterolateral view; (e) detail of distal part of mandible in lateral view. Note the prearticular process, and the three sections of the lingual shelf, which in life would have partly occluded the adductor fossa.
(f) NHM P3317 showing the relative size and shape of the dentary and infradentaries. The prearticular process is either lost, or still buried in the matrix
(g) GLAHM V3069 showing the morphology of the fourth infradentary, including the overlap surface for the dentary, and the lingual shelf.
Grey ⊃ matrix; diagonal hatching ⊃ areas of heavily damaged bone; dashed lines ⊃ cracks, or uncertain margins.

surface of the shelf is slightly textured with a similar ornament to the dorsal part of the prearticular process. Distally, on the fourth infradentary, the shelf differentiates into two sections (sections ling. shelf 1 and 2; Fig. 4d, e): a lingual section (1) resembling the mesial part of the shelf, and a slightly raised labial section (2), greater in width, which bears a more distinct ornament.

The lingual section of the shelf tapers away distally. The labial section of the shelf also starts to taper away, but then gives rise to a third shelf surface (sections ling. shelf 3; Fig. 4d, e, g). This expands sharply, to form the dorsal surface of the distal 20% of the fourth infradentary. This shelf surface is smooth, concave and angled at about 45° dorsolingually. Its

lingual margin is ragged and poorly formed. The broken distal tip of SME 4702 shows that the shelf is very deep dorsoventrally, but there is no sign of any Meckelian ossification in this area (specifically the articular).

Lateral-line canals. The lateral-line system is highly elaborated, and there is often a wide, irregular field of pores (*cf.* Andrews 1985). On one fourth infradentary (GLAHM V3069) lateral-line pores cover almost the entire ventral and distal portions—there are about 25–30 pits/cm^2 on a bone with dimensions of 140 mm by 55 mm. NMS G 1950.38.68 has lateral-line pores on the second and first infradentaries, arranged in a more obvious band than on the fourth infradentary (Fig. 2; pores not shown). They run along the
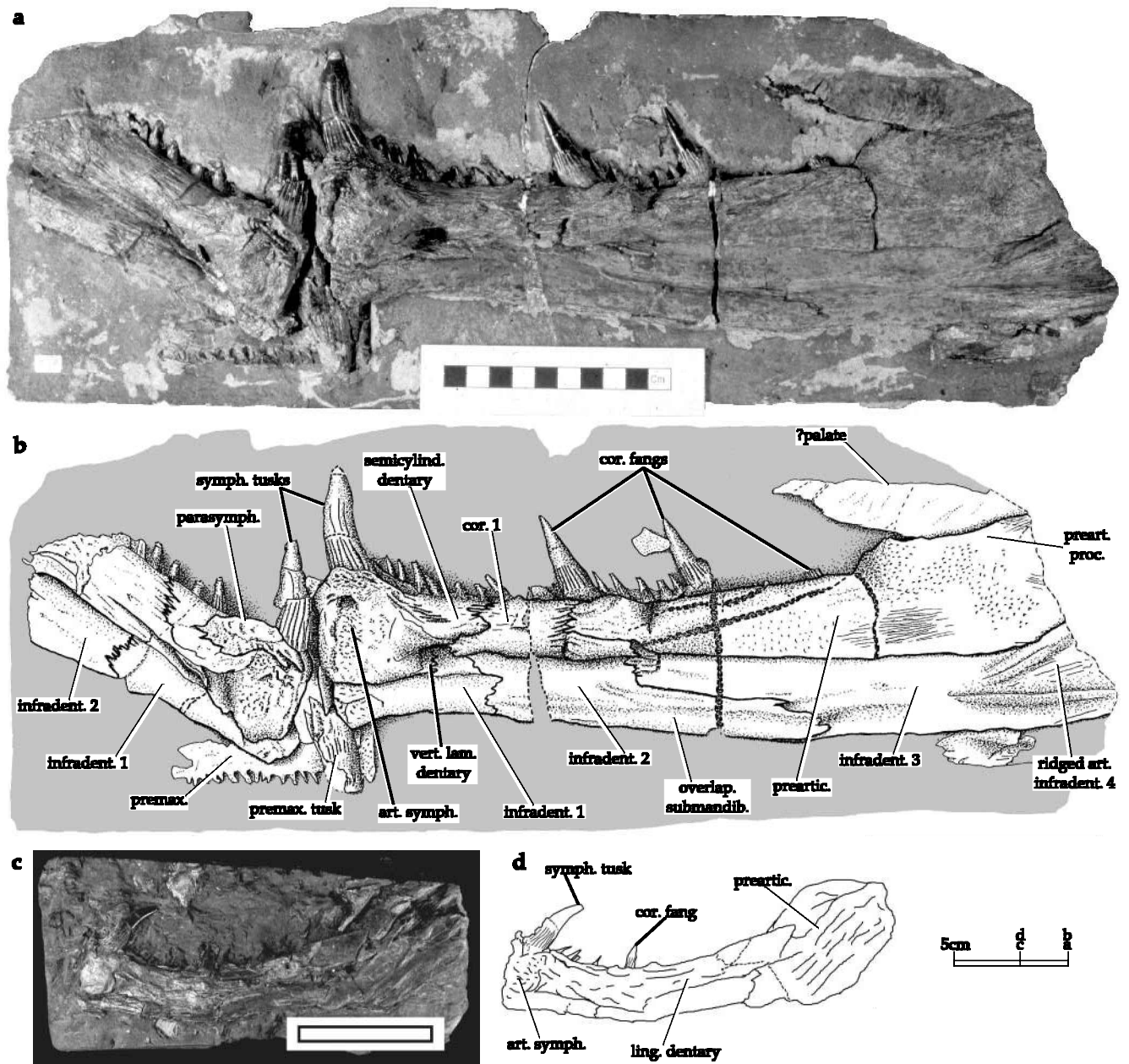
Figure 5 *Rhizodus hibberti*. Specimens showing the lingual face of the mandible: (a), (b) photograph and interpretative sketch of NMS G 1950.38.67, showing the mesial parts of the left and right mandibles. The symphysial region is lying on top of a left premaxilla. Note the articulated parasymphysial bone.
(c), (d) Photograph and interpretative sketch of GLAHM V3069. This specimen is badly crushed, but confirms some of the details of NMS G 1950.38.67.
Grey ⊃ matrix; dashed lines ⊃ cracks, or uncertain margins.

middle third of the bones dorsoventrally. No specimen shows any sign of superficial pit-lines on the second and fourth infradentaries (*cf. Eusthenopteron*, Jarvik 1980).

2.3. *Screbinodus ornatus*

Very few specimens of its mandible are known. It is best seen in SME 4714 (Fig. 8c, d), although they are damaged and partial overlain by cheek bones. The distal tip of the mandible is exposed in both lingual and labial view on NMS G 1874.6 (Fig. 8a, b).

The dentary appears to be similar to that of *Rhizodus hibberti*. Where visible, the articulations between the infradentaries are similar to those of *Rhizodus*, although the fourth infradentary is proportionally smaller, forming only the distal 15% of the ventral margin of the mandible.

NMS G 1874.6 shows the adductor fossa in dorsal view. It is similar to that of *Rhizodus*. A lingual shelf is produced by the dentary and fourth infradentary sections (ling. shelf; Fig. 8b). Unlike *Rhizodus*, it does not differentiate into two distinct regions distally, although there is an area on the labial face of the fourth infradentary which has a similar texture to the labial section of the shelf in Rhizodus. The shelf tapers away about two-thirds of the way along the distodorsal margin of the fourth infradentary. Here a third surface arises, similar to that in *Rhizodus*, very deep dorsoventrally, although it is partially obscured by a dermal cheek (derm. cheek; Fig. 8) bone at this point.

The prearticular forms a similar 'prearticular process', with a distinct horizontal ridge, similar to that in *Rhizodus* (ling. preart.; Fig 8b). The distal extent of the bone is unknown, as it is overlain by the same dermal cheek bone obscuring the end of the fourth infradentary.
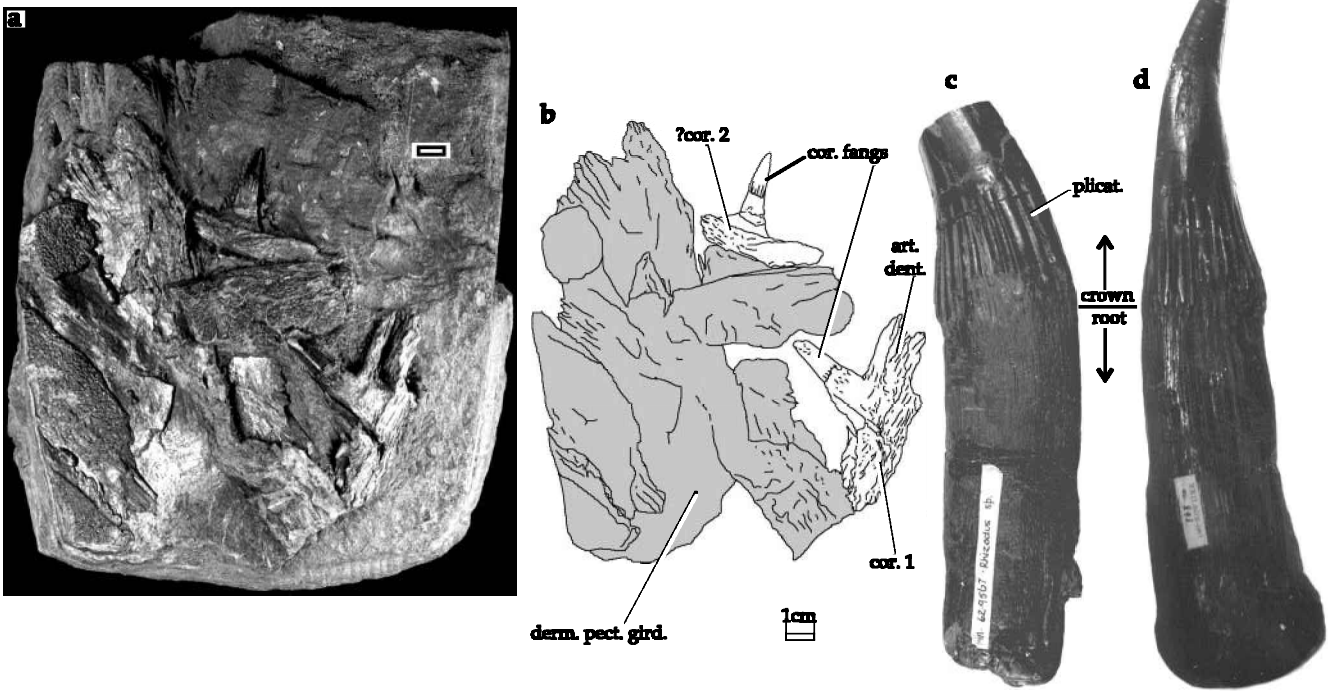
Figure 6 *Rhizodus hibberti*. Other specimens.
(a), (b) Photograph and interpretative sketch of GLAHM V3066, showing a first coronoid and probable second coronoid.
(c), (d) Symphysial tusks: (c) NMS G 1911.62.9567; (d) NMS G 1911.62.893. Note the plications around the base of the crown, and the robust roots.
Grey ⊃ crushed dermal pectoral girdle.

Part of the lateral-line system is visible on the infradentaries on SME 4714. There are fewer pores than in *Rhizodus* (this could be related to the much coarser nature of the dermal ornament).
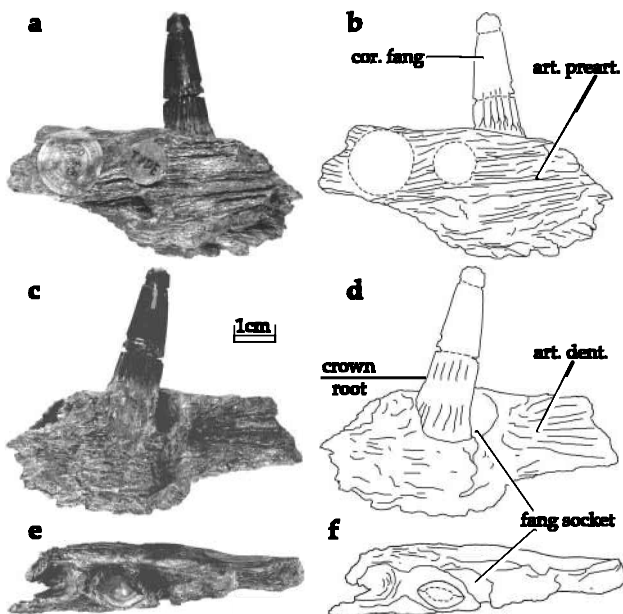

Figure 7 *Rhizodus hibberti*. Photographs and interpretative sketches of first coronoid NMS G 1950.38.66 (*cf*. Traquair 1877a,b):
(a), (b) lingual view; (c), (d) labial view; (e), (f) dorsal view. Note the single, oversized socket for the function fang and its replacement twin. This socket is 'open' on its lingual face. Note also the lack of additional, marginal teeth.

2.4. *Strepsodus* species and referred material

S. sauroides. The dentary, seen in labial view in NMS G 1957.1.5721 (Fig. 9a, b), is generally similar to that of *Rhizodus hibberti* and *Screbinodus ornatus*, although there are fewer marginal teeth which are relatively taller and narrower (see below).

The lingual face of the mandible of *Strepsodus* is partly preserved on NEWHM G19.18 (Fig. 9 e–h). The dentary, three coronoids and mesial part of the prearticular are visible, and are remarkably similar to those seen in *Rhizodus* NMS G 1950.38.67 and 68 (Figs 2, 5a, b). The parasymphysial bone is missing, but judging from the articulation surface on the dentary (art. parasymph.; Fig. 9f), it appears to have been more vertically orientated than in *Rhizodus*, following closely the dorsal and lingual edges of the symphysial surface (art. symph.; Fig. 9f). The prearticular (dentic. preart.; Fig. 9f) has a denticle field clearly visible along the central third of the bone level with the second coronoid fang. A number of short horizontal ridges and possible isolated denticles are visible mesially.

The three coronoids are narrow linguolabially and deep dorsoventrally, each bearing a fang and no other dentition (cor. fangs.; Fig. 9f).

The first and second infradentaries are detached from the rest of the mandible, but lie nearby in close association. The articulation between them is strengthened by interdigitating horizontal ridges (art. infradent. 1 and 2; Fig. 9h), and complex double overlap similar to that of *Rhizodus*. The second infradentary has a smooth overlap surface for the dentary running along its dorsal margin (art. dent.; Fig. 9h). Distally, the overlap surface for the third infradentary is oblique, with some horizontal ridges on the articulation surface (art. infradent. 3; Fig. 9h).
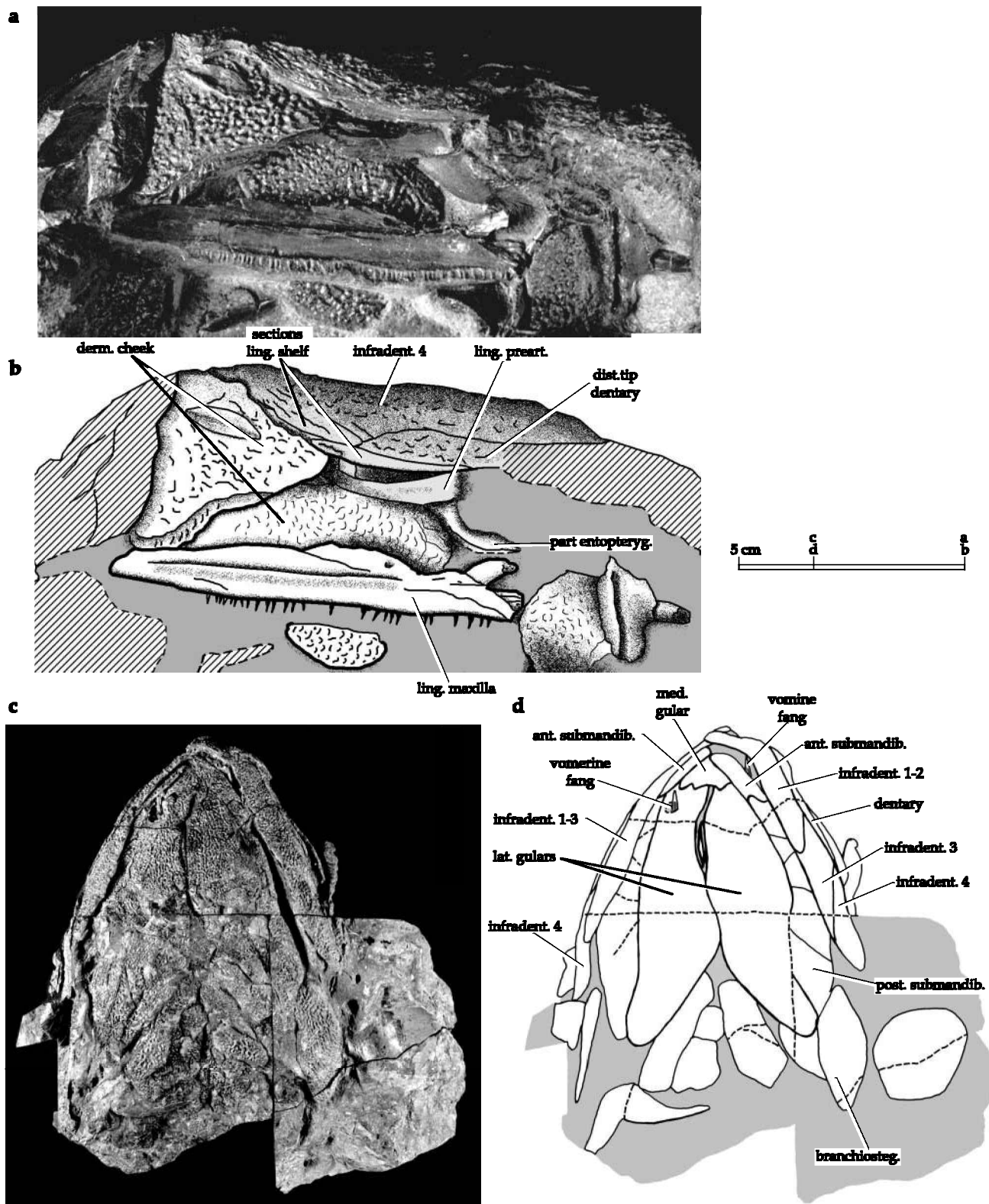
Figure 8 *Screbinodus ornatus.* Photograph and interpretative sketches of the best material of the mandible. (a), (b) NMS G 1874.6. Distal part of mandible in dorsal view, partly obscured by dermal cheek bones. Note the sections of the lingual shelf. Dark grey ⊃ matrix; pale grey ⊃ mandible. (c), (d) SME 4714. Articulated skull in ventral view, showing some details of mandibular morphology. Grey ⊃ matrix.

Cowdenbeath material. Material collected from Cowdenbeath, Fife (Andrews *et al.* 1977) includes an isolated mesial tip of a dentary (NMS G 1975.48.31; Fig. 9c, d). It has been prepared in three dimensions and is almost uncrushed. This is probably part of the material Andrews (1985, p.80) referred to as 'material under preparation, which is apparently of *S.*

sauroides...'. The symphysial surface is not fully prepared, but appears to be similar to that in *S. sauroides*. There is also a rugose surface between the symphysial surface and the dermal ornament (anteromes. rug.; Fig. 9d), as in *Rhizodus hibberti*.

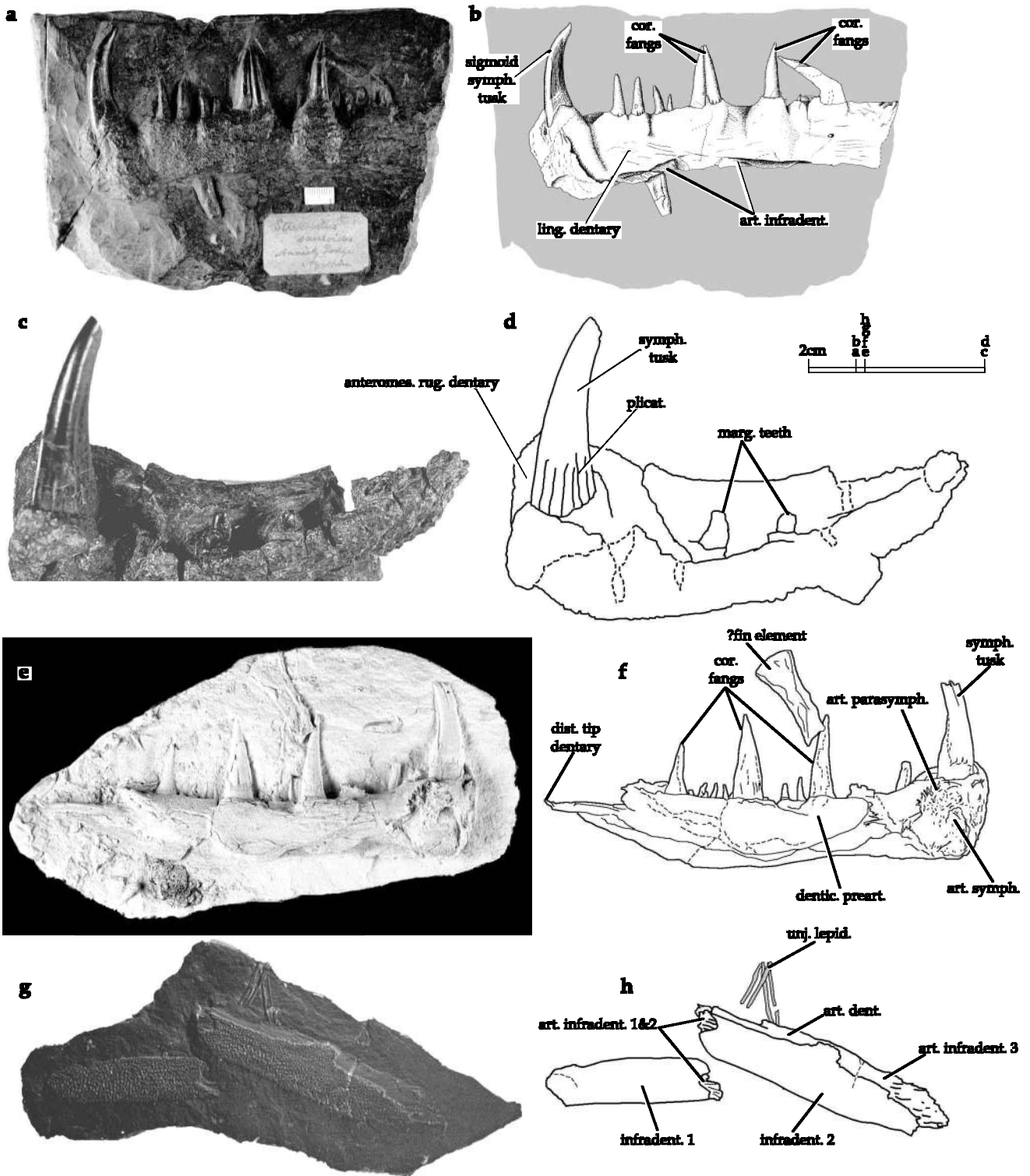*S. anculonamensis.* The dentary of *Strepsodus anculonamensis* (NMS G 1993.56.4) was described and figured by Andrews

Figure 9 *Strepsodus sauroides.* Photograph and interpretative sketches of the best material of the mandible. (a), (b) NMS G 1957.1.5721. Note the tall, narrow form of all the teeth, and the sigmoid shape of the symphysial tusk.
(c), (d) NMS G 1975.48.31 (*cf.* Andrews 1985, p.80) Material from Fife currently under preparation).
(e)–(h) NEWHM G19.18. Silicone rubber peels of material negatively prepared by the late Dr S.M. Andrews. The two peels were taken a few centimetres apart on a single block of coalshale. (g) reproduced in negative for better contrast.

(1985). It compares well with the dentaries of adult *Strepsodus sauroides.* The symphysial surface is badly damaged and comparisons with Andrews' (1985) figure are no longer possible. However, a complex surface similar to that in *S. sauroides* (and *Rhizodus*) does seem to have been present. The dorsal ridge does not bear any longitudinal articulation ridges for the coronoids, although this may be a function of the small size of the bone.

'Foulden Large Form'. Besides *S. anculonamensis*, Andrews (1985) described much larger remains from Foulden, which she

did not name. A single mesial tip of a dentary exists (NMS G 1980.40.46) with dermal ornament similar to that of *Strepsodus*. There is also an isolated right parasymphysial bone, NMS G 1984.67.111 (Fig. 10), originally identified by Andrews (1985, p83) as a possible incomplete vomer. Its true identity was realised by Dr P.E. Ahlberg (pers. comm.). It is very similar in size and shape to the bone seen on *Rhizodus hibberti* NMS G 1958.38.67 (Fig. 5a, b), but preserves the dorsal surface. This surface is smooth, except for a small area at the mesial tip of the bone; this area is approximately triangular and covered in many small denticles (dentic. field; Fig. 10b) which increase in size lingually. Along the lingual edge of the area there was a row of small teeth (11 tooth-bases or sockets are visible, but all the crowns are missing). These teeth increase in size distally, but even the largest would probably have been very much smaller than the marginal teeth of the dentary.

Devonian *Strepsodus* material. Material has been tentatively assigned to *Strepsodus* sp. from two Devonian deposits: the Strunian ('TN1a') Köprülü shales of Turkey (Janvier *et al.* 1984) and the Frasnian Cuche Formation of Colombia (Janvier & Villarroel 2000). Whilst both sets of material are certainly rhizodontid, the Turkish material shows no *Strepsodus* autapomorphies. The Colombian material includes the impression of part of a small dentary (UN-DG-PALV45; Fig. 11a), bearing a tall, sigmoid symphysial tusk. However, it is morphologically different from true *Strepsodus* tusks (see 3).
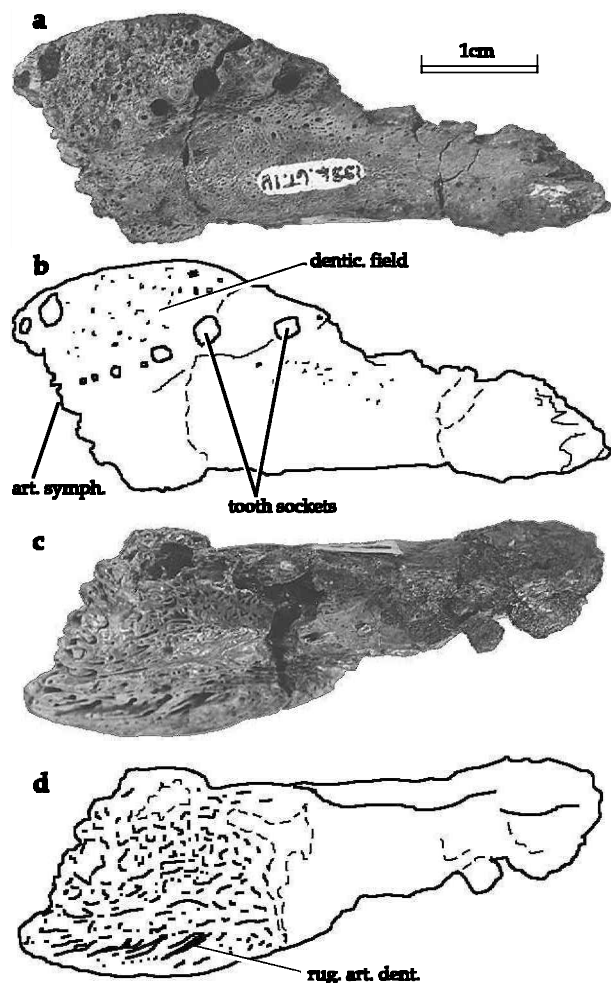
2.5. *Barameda decipiens*

Mandibular material of *Barameda decipiens* was figured and briefly described by Woodward (1906) when founding the species. Long (1989) figured a juvenile specimen (NMV P160 881). Here the mesial tip of a left mandible in lingual view approximates to that of *Rhizodus hibberti*. Long (1989) stated that 'the bones of the coronoids each bore 2 large fangs', possibly meaning that each had a functional fang and a replacement twin, as the photographs and illustrations of NMV P160 880 (Long 1989, Figs 1, 2) show what appear to be single first and second coronoid fangs, spaced widely apart. A denticulate prearticular is partly visible. On NMV P160 880 the first infradentary appears to articulate with a small symphysial bone ('?Sy' of Long 1989, Fig. 2) similar to that
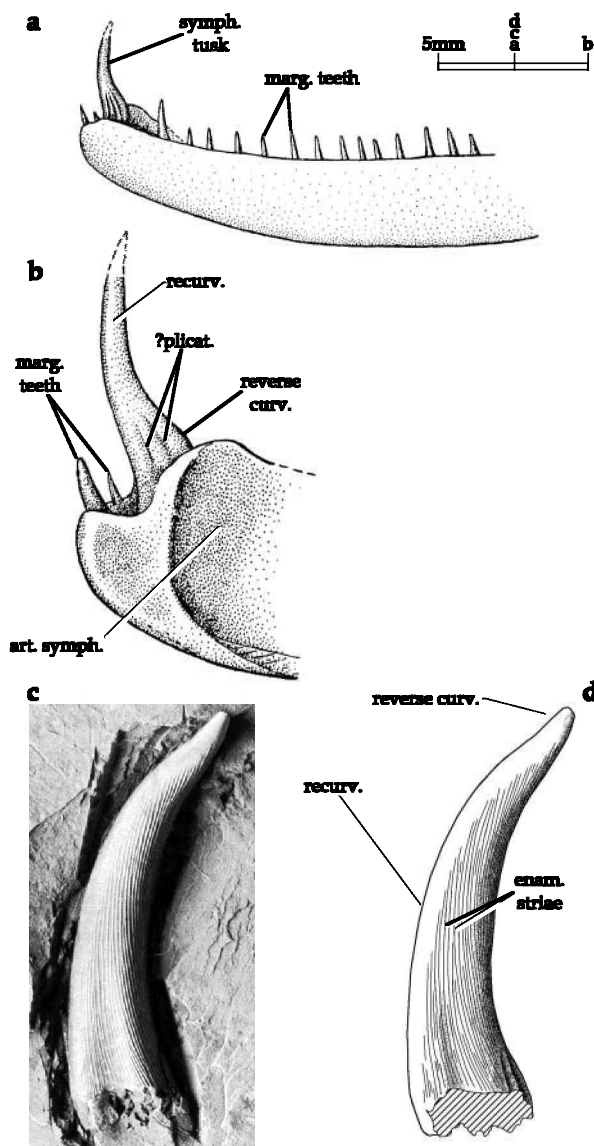

Figure 11 Colombian rhizodontid and *Strepsodus*. Sketches showing the morphology of the symphysial tusk.
(a), (b) UN-DG-PALV45, from the Upper Devonian of Colombia, attributed to *Strepsodus* (Janvier & Villarroel 2000; but see main text). Note that the sigmoid crown shows slight reverse-curvature at the base, but the majority of the tusk is recurved. See main text for discussion.
(c), (d) One of the 12 tusks accession as NHM P11542, under the name *Strepsodus striatulus*, a junior synonym of *S. sauroides* (see main text and Traquair 1882). Note that the sigmoid crown is mostly recurved, with a slight reverse-curvature at the apex. The base of the crown is damaged, and so plications cannot be seen (cf. Fig 9c, d).
(a), (b) reproduced from Janvier & Villarroel (2000, text-Fig. 15), with the kind permission of the Palaeontological Association.

Figure 10 ?*Strepsodus sauroides*. Photograph and interpretative sketches of the parasymphysial bone NMS G 1980.40.46:
(a), (b) dorsal view; (c), (d) ventral view

implied by the articulation surface seen in *Rhizodus hibberti*. Johanson & Ahlberg (2001) noted that the parasymphysial bone of *Barameda* was elongated and extended distally to contact the first coronoid.

2.6. *Gooloogongia loomesi*

The mandible is preserved in articulation in the two main specimens of *Gooloogongia loomesi* (AMF 96860 and 100073; Johanson & Ahlberg 1998, 2001), although only parts of the dentary and first and second coronoids are visible. The dentary bears small marginal teeth and a symphysial tusk. Both the first and second coronoids bear fangs, and the presence of other dentition cannot be ruled out. The lightly denticulated parasymphysial bone is elongated, and appears to run distally to the level of the first coronoid (Johanson & Ahlberg 2001). The tusks and fangs are recumbent, and both specimens are preserved with a considerable under-bite, which Johanson & Ahlberg (1998, 2001) suggested is natural, and not a preservational artefact. There is a small dermal symphysial bone, as in *Barameda*. Nothing is known of the infradentaries or prearticular.

2.7. *Notorhizodon mackelveyi*

Young *et al.* (1992) described and figured the mandible of *Notorhizodon mackelveyi*. This species was identified as a rhizodontid on the basis of pectoral girdle material associated with the mandible. However, the morphology of the mandible is very different from *Rhizodus, Screbinodus, Strepsodus* and *Barameda*. Johanson & Ahlberg (2001) separated the pectoral material as a new rhizodontid species, *Aztecia mahalae*, and identified the remaining material of *Notorhizodon* (including the mandible) as a tristichopterid.

2.8. *Sauripterus species*

S. taylori. This is the type species of the genus (*cf.* Jeffery *et al.* 2002). There is some jaw material on the reverse of the block bearing the lectotype pectoral girdle (AMNH 3341). This is currently under study by Marcus Davis, University of Chicago. The assigning of any tooth material in museum collections to *S. taylori* must be considered dubious. Similarly, any species of *Sauripterus* (or the variant spelling *Sauripteris*) founded on the basis of isolated teeth (e.g. *S. favosus* (Agassiz 1833–1844); *S. crassidens* Traquair 1897) must be considered to be *nomina dubia* (*cf.* Andrews 1985).

3. Dental morphology

3.1. Gross morphology

The dental morphology of rhizodontids is best known in *Rhizodus, Screbinodus* and *Strepsodus*, but the preserved tooth material of *Barameda* and *Gooloogongia* appears to be similar. The dentition (particularly the symphysial tusks and coronoid fangs) is deeply rooted (Figs 6c, d, 7c, d). In *Rhizodus, Screbinodus* and *Strepsodus* many hundreds of isolated crowns are known, suggesting that the root was completely resorbed prior to shedding. *In situ*, the sockets are not grouped in pairs (i.e. a functional tooth and its replacement 'twin'). Rather, the socket of the functional crown is oversized, and shared with its replacement (Figs 2h, 7f; *cf.* Cruickshank 1968). A few specimens show a replacement tusk abutting the functional tusk (e.g. *Rhizodus* SME 4703, *Strepsodus* NMS G 1957.1.5721). The symphysial tusks are about twice the size of the coronoid fangs, which are in turn about twice the size of the marginal teeth. The condition is apparently similar in *Barameda* (Long 1989), but the condition of *Gooloogongia* is

uncertain. All five genera show plications of the base of the teeth (e.g. Figs 6c, d, 9c). In all the genera except *Gooloogongia* this is known to reflect the internal folding of the dentine ('plicidentine'; e.g. Cruickshank 1968; Smith 1989; Long 1989). Plicidentine is also likely to have been present in *Gooloogongia*, but this genus is known only from endocasts, where the internal structure of the teeth cannot be investigated.

3.2. *Rhizodus hibberti*

Symphysial tusks. The crowns of the tusks are lenticulate in cross-section due to mesial and distal thickenings. They are recurved, although the degree of recurvature is variable; a few tusks appear almost straight. There are 20–22 plications (plicat.; Fig. 6c, d) around the base of the crown of the tusk—the number appears to be consistent regardless of the size of the tusk. The surface of the crown is otherwise smooth, although it may be covered with a pattern of very fine, irregular vertical lines (probably reflecting the crystalline structure of the enamel; see below).

Other dentition. The morphology of the other teeth and fangs is similar to that of the symphysial tusks. However, the coronoid fangs never show any recurvature (Fig. 7b). The marginal teeth of the dentary are recurved, but are round in cross-section. There are 7–10 marginal teeth between the symphysial tusk and the first coronoid fang, and 5–10 marginal teeth between the first and second coronoid fangs (e.g. Fig. 5b).

Internal structure. The internal structure of the tusk was first described by Owen (1840) and Barkas (1876). More recently, it has been studied by Cruickshank (1968), Schultze (1969, 1970) and Smith (1989), and several sectioned tusks exist (e.g. NHM P11524–7). Smith (1989) showed that the enamel of *Rhizodus* is about 40–60μm thick (and thicker along the mesial and distal edges) and is formed from columns of branching crystals. The dentine is folded into 20–22 main folds (corresponding to the external plications), each with a narrow ramus of the pulp cavity. Each main fold produces a number of smaller villi, usually in bilateral pairs. There are around 7–10 villi on each side of a fold at the level of the base of the crown in NHM P11524–7. The largest of the villi may contain pulp cavities continuous with that of the main fold, although most of the smaller villi show no pulp cavities at all.

The main, central, oval pulp cavity occupies approximately the central one-fifth of the tusk. The junctions between the folds and the central cavity are narrow slits, intermediate in width between the open junctions of *Eusthenopteron* and the occluded junctions of *Panderichthys* (Schultze 1969). The complexity of the dentine folding at the level of the base of the crown of both *Eusthenopteron, Panderichthys* and *Rhizodus* have been specifically referred to as 'polyplocodont' by Schultze (1969, 1970).

Towards the tip of the crown, the folding becomes progressively simpler. In the apical two-thirds of the crown the dentine is unfolded, with a simple pulp cavity occupying up to one-fifth of the tusk's diameter, oval in shape with its long axis aligned with the mesial and distal thickenings (Cruickshank 1968). In the root the folding of the plications becomes extremely complex, so that the course of the main fold cannot be traced. Spongy 'bone of attachment' fills the gap between the folds, and also forms a distinct ring around the outside of the tusk, filling the socket (*cf.* Schultze 1969, plate XI, Figs 1–4).

3.3. *Screbinodus ornatus*

The fangs and tusks are extremely similar to their equivalents in *Rhizodus hibberti*—in isolation they are indistinguishable (except by the larger size of adult *Rhizodus hibberti*). This led

to *Screbinodus ornatus* originally being described as a species of *Rhizodus* (*Rhizodus ornatus* Traquair 1878). An isolated fragment of dentary, NHM P363, shows that the marginal teeth are recurved and rounded in cross-section (i.e. with no thickened mesial and distal edges), similar to *Rhizodus hibberti*.

3.4. *Strepsodus* species and referred material

S. sauroides. The teeth of *S. sauroides* are tall, and strongly recurved lingually (e.g. Fig. 9). They are oval in cross-section, with the long axis parallel to the plane of recurvature. There are plications around the base of the crown (Fig. 9c, d) similar to those of *Rhizodus* and *Screbinodus*. However, they are often not clearly visible, either because the labial lip of the dentary overlies them (e.g. Fig. 9a, b), or because the base of the crown is missing (in isolated teeth; e.g. Fig. 11c, d). Thickened mesial and distal edges are never present. In some teeth the recurvature is reversed on the most dorsal 10% of the crown, producing a sigmoid aspect to the whole tooth (reverse. curv.; Figs 9, 11d). However, 'reverse curvature' is not seen in all the teeth. It may be restricted to the symphysial tusks, but the small sample of well-preserved mandibles with all their teeth *in situ* makes this uncertain. Because the recurvature is always directed lingually, in laterally compressed specimens the symphysial tusk can appear to be recurved *distally*, whilst the marginal teeth and coronoid fangs can appear straight because the recurvature is obscured by matrix (e.g. Fig. 9b). Uncrushed jaws show that all teeth were recurved (e.g. NMS G 1993.56.4), although the degree of recurvature of the coronoid fangs remains uncertain. Andrews (1985, p. 80) seems to have confused the distinctive tooth morphology associated with specimens of *Archichthys* (see 1.2, above) with *Strepsodus* teeth lacking the 'reverse curvature'.

All well-preserved teeth show fine, regularly spaced, raised striae on the lingual (concave) face of the tooth (enam. striae; Fig. 11d). They may also cover the more lingual areas of the mesial and distal walls of the teeth. The striae remain vertical regardless of the recurvature of the tooth. Thus a lingual striation can wrap onto the mesial or distal wall as it runs towards the tip. However, the striae all taper away before apex, and are never seen on the reverse-curved region (if present). Also, striae are never seen on the labial (convex) wall of the tooth. Smith (1989, p.107, Fig. 11) showed that the striae are produced by sharply defined branching outgrowths of the 'protoprisms' of the unusually thin ($15–20\mu$m) enamel layer. They are not followed in any way by the underlying dentine and it is not clear what their structural or functional purpose was. The striae do not appear to branch or converge at all, but individual lines may taper away quite sharply and a new striation begin adjacent to it. It is often difficult to study the entire length of an individual striation as the matrix (usually coalshale) is difficult to remove completely without damaging the tooth. There are anything from 6–12 striae per millimetre; the exact number of striae per millimetre seems to be constant on an individual tooth, but this figure is not related to the size of the tooth. However, the width of individual striae remains constant at $40–50\mu$m regardless of the number of striae per millimetre (probably reflecting the consistent width of the underlying protoprisms). Thus some teeth appear to have much coarser striae relative to their size. As most teeth known are isolated crowns, it has not been possible to study the variation of width, length or density of the striae on the teeth within a single jaw.

Schultze (1969) described secondary deposits of dentine in *Strepsodus* as similar to the 'dark dentine' seen in some digited stem-tetrapods (*Ichthyostega* (Schultze 1969, Abb. 13); *Crassigyrinus* and anthracosaurs (Panchen 1985)). In the digited stem-tetrapod taxa, dark dentine is found at the external apex

of each fold. It has tubules arranged radially, unconformable with the tubule arrangement in the surrounding dentine. In *Ichthyostega* it appears to have been deposited within the cavity of the fold, whereas in *Crassigyrinus* and the anthracosaurs it appears to have been deposited with the walls of the folds, and approaches the enamel layer (Panchen 1985, Figs 13–15). I have not had the opportunity to examine thin sections of *Strepsodus* teeth, but a photograph in Schultze (1969, plate 12, Fig. 4) does seem to show some dark deposits at the apex of the fold. It appears to be restricted to the wall of the fold, rather than to the cavity, but it does not reach the enamel layer. However, a detailed histological survey would have to be carried out before anything could be said about the homologies of this tissue.

Schultze (1993) suggested that isolated teeth identified by von Huene (1943) and Schultze (1973) as representing the youngest occurrence of an onychodontid species (*Onychodus* cf. *ostrovensis*), in fact belong to *Strepsodus*. Certainly the tooth figured by von Huene (1943) and at least one of the teeth figured by Schultze (1973, plate 33, Fig. 4) show the morphology described above for *S. sauroides*.

Cowdenbeath material. NMS G 1975.48.31 (Fig. 9c, d) bears a large symphysial tusk and fragments of three marginal teeth. All are damaged and it cannot be determined if they were sigmoid or simply recurved. However, they all show *S. sauroides*-type striae on the lingual surface.

S. striatulus. This species was established by Traquair (1882) from isolated teeth collected in Borough Lee, Scotland. They are similar to those of *S. sauroides*, but Traquair (1882, p.545) considered that they were not as recurved. Although the holotype specimen (NMS G 1950.38.73) is lost, one tooth in the Sedgwick Museum of Geology, Cambridge (SME 4740) was collected from Borough Lee and identified by Traquair himself, and thus may well be a paratype. There also exists a set of 12 teeth (all NHM P11542) and four partial dentaries (all NHM P11544) from Niddrie and Loanhead respectively, received posthumously from Traquair's collection. None of this material is distinguishable from *S. sauroides*, if some degree of variation in tooth recurvature is accepted.

S. minor. Little material attributed to *S. minor* exists, but the type material (Traquair 1890) includes a single tooth about 8 mm long (NMS G 1881.43.42) which is indistinguishable from the more densely striated of the teeth of *S. sauroides*.

S. anculonamensis. The teeth of *S. anculonamensis* appear to be mostly sigmoid with some simply recurved marginal teeth (e.g. NMS G 1980.40.36 and NMS G 1993.56.4). Andrews (1985, Fig. 9a, b, c) over-emphasised the straight aspect of the marginal teeth as they are figured in lingual view with the axis of recurvature towards the viewer. The teeth of NMS G 1993.56.4 and 1980.40.36 appear to be striated in a manner identical to *S. sauroides*, although there are comparatively few striae. This may be due to the exceptionally small size of the teeth—the symphysial tusk in NMS G 1993.56.4 is only 3 mm tall.

'Foulden Large Form'. Partial dentary NMS G 1980.40.46 bears a symphysial tusk and the eight marginal teeth, all broken off at the base. They are plicated around the base. The base of the symphysial tusk and an associated tip of a coronoid fang show *Strepsodus*-type striae. Andrews (1985, p.84 and Fig. 9e) stated that the fang was simply recurved, but further preparation shows the tip to have been snapped off before fossilisation, so it may have been sigmoid.

Besides the material listed above (all collected during a concerted excavation of the Foulden site in the early 1980s), three isolated teeth are known (NHM P13124, 13127 and 13128). These were discovered early in the twentieth century by

an amateur collector, and eventually passed to the Natural History Museum (White 1927). Whilst one (NHM P13124) is indistinguishable from *S. sauroides*, the other two are quite different. White (1927) correctly noted the similarity of these teeth to those of *S. sulcidens* (i.e. *Archichthys*; see 1.2, above). The holotype material of *S. sulcidens* comes from Newsham, Northumberland, and is associated with many specimens of *S. sauroides*. It is interesting that a similar association appears to occur at the much older Foulden site, although not enough stratigraphic information is recorded for NHM P13127 and 13128 to establish their position within the complex stratigraphy of Foulden (described by Wood & Rolfe 1985). Too little is known about the location of the *Archichthys* fossils in either site to establish their relations to the more common *Strepsodus* fossils. Foulden was a semi-permanent floodplain lake a few kilometres across (Anderton 1985) and Newsham was an oxbow lake a few kilometres in length (Boyd 1984), and so both could have offered separate niches for the two species. Also, both lakes had a very dynamic palaeoenvironment, with possible seasonal cycles of flooding and evaporation as well as longer-term trends of water-depth change (e.g. by silting-up). It is therefore possible that the two species were never truly sympatric, but occupied different (even alternating) time periods across the history of the lakes.

Devonian ?*Strepsodus* material. Janvier & Villarroel (2000) described an isolated small dentary (40 mm as preserved) from the Frasnian Cuche Formation in Colombia (UN-DG-PALV45; Fig. 11a). This is obviously very much earlier than any previously attributed material, over 60 My earlier than the abundant Newsham material. The symphysial tusk is small, and preserved as a natural mould (Fig. 11b). It bears some ridges, but these appear to be plications resulting from plicidentine, rather than raised striae. Further, although the tusk is sigmoid, it shows reverse curvature basally and recurvature in the apical 80% (a 'reverse–recurve' morphology). This is clearly unlike *S. sauroides* (a 'recurve–reverse' morphology). Thus it is unlikely that the Colombian dentary belongs to *Strepsodus*; it probably belongs to a new species, but a formal description must await more material.

3.5. *Gooloogongia loomesi*

The following is based on the description of Johanson & Ahlberg (1998, 2001). Each ramus of the dentary bears a slender, symphysial tusk, which is extremely recurved. This correlates with the under-bite of the jaw. AMF 100073 shows two tall, slender coronoid fangs, also very recurved. The marginal teeth are more gently recurved. Johanson & Ahlberg (2001) stated that there are some 'light striations' around the base of the symphysial tusks, but as the material consists of natural moulds, the internal structure of the teeth cannot be investigated.

4. Phylogenetic patterns

4.1. *Strepsodus* species

A formal review of the genus *Strepsodus* is currently in preparation. As described above (see also Jeffery 1999), for the purposes of this study it has not proven possible to distinguish between the following 'species': *S. sauroides* (Binney 1841; the genotype); *S. anculonamensis* Andrews 1985; *S. striatulus* Traquair 1882; *S. minor* Traquair 1890; the 'Cowdenbeath material' (Andrews *et al.* 1977; Andrews 1985) and the 'Foulden large form' (Andrews 1985; with the exception of the two *Archichthys* teeth noted above). They will therefore be treated as a single taxonomic unit, under the name *Strepsodus*.

4.2. Rhizodontida

The Rhizodontida are widely recognised to be a monophyletic group, but there have been few attempts to elucidate their interrelationships (e.g. Young *et al.* 1992; Johanson & Ahlberg 1998, 2001; Jeffery 1999). Jeffery (1999) recovered a single most parsimonious tree for the five taxa analysed (*Gooloogongia*, *Barameda*, *Strepsodus*, *Rhizodus* and *Screbinodus*) but with weak support. Another recent analysis (Johanson & Ahlberg 2001) examined the relationships of the same five taxa plus *Aztecia* and *Sauripterus*. The published tree was a strict consensus of four most parsimonious trees, one of which was congruous with that of Jeffery (1999). As nothing is known of the mandible of either *Aztecia* or *Sauripterus*, the tree topology of Jeffery (1999) will be used to analyse the patterns of evolution within the Rhizodontida (see Fig. 14). Unfortunately, very little is known of the mandible of the two most basal taxa on this tree, *Gooloogongia* and *Barameda*. This creates difficulties in determining the nodes at which changes occur.

Jaw length. The mandible clearly protrudes in the well-preserved material of *Gooloogongia*. This correlates with the recumbent form of the symphysial tusks. However, the jaw does not seem to have protruded in the more derived rhizodontids—in *Screbinodus* direct measurements of the upper and lower jaws can be taken from SME 4714 (Fig. 8c, d), and in *Screbinodus*, *Rhizodus* and *Strepsodus* the large, upright symphysial tusks would have had a restricted function if they were in front of the snout. Also, in *Screbinodus* and *Rhizodus* there is a clearly defined 'prenasal pit' between the tusk-bearing premaxillae and vomers, which could have received the symphysial tusk (Jeffery 1999). If the condition in *Gooloogongia* is primitive for rhizodontids, then *Screbinodus*, *Rhizodus* and *Strepsodus* represent a secondary reversal to the condition primitive for crown group gnathostomes.

Recently, Long & Ahlberg (1999) have reinterpreted the mandible of *Barameda* as jutting out beyond the snout. This interpretation is certainly plausible, based on the skull NMV P160 880 (Long 1989). The small size of the skull ($\sim$ 8 cm long) and some morphological features (e.g. large orbits) led Long (1989) to suggest that the specimen was juvenile. Furthermore, both Woodward (1906) and Long (1989) figured much larger material, including fragments of mandible over 30 cm long. One, NMV P160 881 (Long 1989, Fig. 7b), bears what appears to be a tall symphysial tusk, similar to that of *Rhizodus*. If Long & Ahlberg's (1999) interpretation is correct, then the jaw and tooth morphology changed with growth in *Barameda*, or the larger jaw may belong to a second, larger taxon in Mansfield formation (much like *Screbinodus* and *Rhizodus* in the UK).

Dentition. All rhizodontids for which data are available (including the Devonian material from Colombia) show enlarged symphysial tusks. This is likely to be primitive for the group. *Barameda*, *Screbinodus*, *Rhizodus* and *Strepsodus* all possess plicidentine, with a similar folding pattern. The condition is unknown in *Gooloogongia*, but Dr P.E. Ahlberg (pers. comm.) suggests that the 'striations' (Johanson & Ahlberg 2001) could reasonably be interpreted as the outward expression of plicidentine. Thus, it is likely that plicidentine is primitive for the group.

The morphology of the symphysial tusks and coronoid fangs is extremely varied. The symphysial tusks (and probably coronoid fangs) of *Gooloogongia* are tall, thin and recumbent. Those of *Barameda* are recurved, but apparently more robust. The Colombian specimen (Fig. 11b; Janvier & Villarroel 2000) shows plications around the base (a possible indication of plicidentine), and a 'reverse–recurve' sigmoid shape. This is
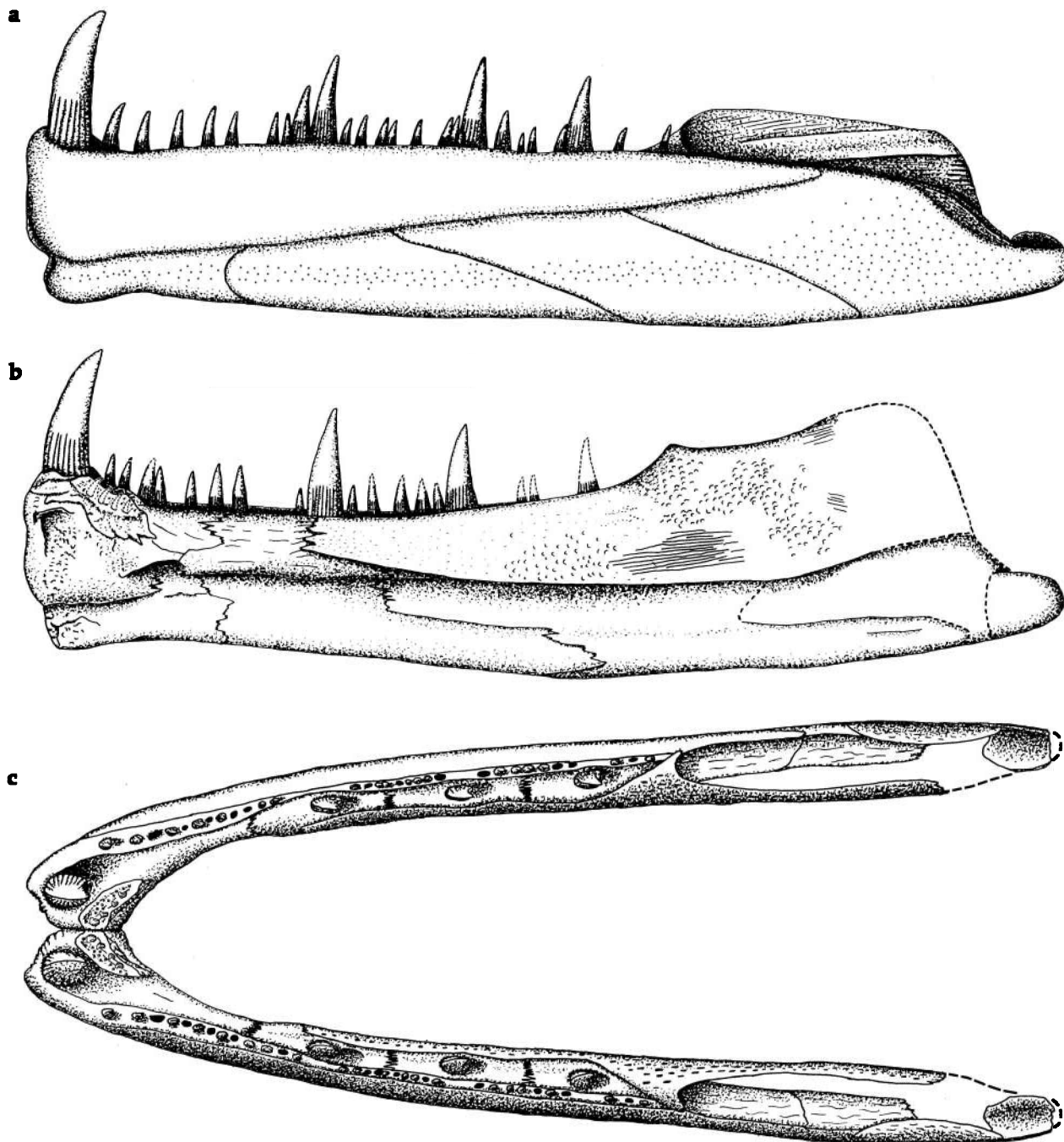
Figure 12 *Rhizodus hibberti.* Reconstruction of the mandible.
(a) Labial view, principally based on SME 4702, NHM P3317, GLAHM V3069 and NMS G 1950.38.68.
(b) Linguoventral view, principally based on NMS G 1950.38.67 and NMS G 1950.38.68.
(c) Dorsal view, principally based on NMS G 1950.38.68, NMS G 1950.38.67 and SME 4702.
Note the dorsoventral depth and linguolabial narrowness of the mandible. No bone is preserved on the floor of the adductor fossa.

probably convergent with the teeth of *Strepsodus*, which have a 'recurve–reverse' sigmoid shape (or may be simply recurved). Raised striae in the enamel is autapomorphic for *Strepsodus* within the Rhizodontida (striae have evolved convergently in some other fishes and tetrapods, including the onychodontid *Onychodus*, Jessen 1967). Only *Rhizodus* and *Screbinodus* show shared tooth morphology—robust, recurved symphysial tusks, and non-recurved coronoid fangs, both with thickened mesial and distal edges.

Lateral-line canals and dermal ornament. *Gooloogongia* has no dermal ornament on the skull, and shows an elaboration of the lateral line system (Johanson & Ahlberg 2001). The

infradentaries are not clearly preserved, but lateral-line pores cover all but the most dorsal parts of the dentary. In *Barameda* the dentary bears dermal ornament, but lateral-line pores have not been reported. Amongst the derived rhizodonts (*Rhizodus*, *Screbinodus* and *Strepsodus*), each genus has its own distinctive dermal ornament on the mandible. In *Rhizodus*, the fourth infradentary has a wide field of pores, with a more ordered band of pores on the first and second infradentaries (presumably following an underlying canal). There are no pores on the dentary. *Screbinodus* appears to have only a few pores on the infradentaries, nestled amongst its robust ornament in a linear arrangement. Again, there are no pores

on the dentary. The distribution of lateral-line pores is unknown in *Strepsodus*. However, rhizodontids share an elaboration of the lateral-line system over the head and trunk (Andrews 1985; Long 1989; Johanson & Ahlberg 1998; Jeffery 1999). *Gooloogongia* (Johanson & Ahlberg 1998, 2001), *Rhizodus* and *Strepsodus* (Jeffery 2001) all show lateral-line pores on the pectoral girdle, whilst *Screbinodus* bears a pit-line (Jeffery 2001; the condition is unknown in *Barameda*). Thus it is conceivable that an elaboration of the mandibular lateral-line canal in *Gooloogongia* represents the primitive condition, with an elaboration on the infradentaries retained in *Rhizodus*.

4.3. Tetrapod stem-group

All recent studies using cladistic methodology have placed the rhizodontids near the base of the tetrapod stem-group (*sensu* Patterson 1993). More derived members of this group include the 'osteolepiform' (*sensu lato*) and elpistostegid fishes, and digited stem-tetrapods such as *Acanthostega* and *Ichthyostega* (Ahlberg 1991; Young *et al.* 1992; Cloutier & Ahlberg 1996; Zhu & Schultze 1997; Forey 1998; Johanson & Ahlberg 1998; Jeffery 1999; Zhu *et al.* 1999). Membership of the clade is significant, as the conditions in rhizodontids can help elucidate the transformational sequences and homoplasies leading to the tetrapod crown-group (*sensu* Patterson 1993). The most detailed analysis to date of the tetrapod stem-group is Ahlberg & Johanson (1998; Fig. 14). This study found one genus (*Kenichthys*) to be the most primitive member of the tetrapod stem-group. The rhizodontid clade was the next most primitive member. The osteolepiforms, a traditionally recognised group of more-derived, non-digited stem tetrapods, was found to be paraphyletic with respect to the tetrapod crown-group. However, a number of sub-divisions of the osteolepiforms (*sensu lato*) were found to represent increasingly crown tetrapod-like clades. These included the megalichthyids (*Ectosteorhachis*, *Megalichthys* and *Cladarosymblema*), the canowindrids (*Canowindra*, *Beelarongia* and *Koharalepis*) and the tristichopterids (*Tristichopterus*, *Eusthenopteron*, *Jarvikina*, *Platycephalichthys*, *Cabonnichthys*, *Mandageria*, *Eusthenodon*, also *Notorhizodon* (Johanson & Ahlberg 2001)).

Amongst stem-tetrapods, detailed data on jaw morphology have been published on the tristichopterid *Eusthenopteron* (Jarvik 1980), the elpistostegid *Panderichthys* and a range of digited stem-tetrapods (Gross 1941; Ahlberg & Clack 1998). Less detailed data are available for several genera lying between rhizodontids and digited stem-tetrapods, e.g. *Medoevia* (Lebedev 1995; Fig. 13a, b), *Gogonasus* (Long *et al.* 1997), *Megalichthys* (Watson 1926), *Ectosteorhachis* and *Cladarosymblema* (Fox *et al.* 1995), *Cabonnichthys* (Ahlberg & Johanson 1997) and *Notorhizodon* (Young *et al.* 1992; Johanson & Ahlberg 2001). Almost nothing is known of the mandible in canowindrids (Thomson 1973; Long 1985, 1987; Young *et al.* 1992).

There is not yet a consensus over which of the living groups of sarcopterygians forms the sister-group of the tetrapods. Recent analyses have arrived at two alternative topologies: the first topology has lungfish as the living sister-group of tetrapods, with porolepiform fishes forming part of the lungfish stem-group (e.g. Ahlberg 1991; Cloutier & Ahlberg 1996; Ahlberg & Johanson 1998; Forey 1998; Jeffery 1999; Zhu *et al.* 1999; Zhu *et al.* 2001). The second topology has the coelacanth as the living sister-group, onychodontid fishes forming part of the coelacanth stem-group, and the porolepiforms as the sister-group of the coelacanth tetrapod clade (e.g. Schultze 1987; Zhu & Schultze 1997; Zhu *et al.* 1999). Despite this controversy, it is still possible to estimate some of the character states primitive for the tetrapod total-group. Under both topologies, porolepiforms are informative, sug-

gesting primitive conditions for either the lungfish total-group, or for the coelacanth tetrapod clade. In either case, where stem-tetrapods share character-states with porolepiforms, they are most parsimoniously interpreted as stem-tetrapod plesiomorphies. Detailed data on the structure of the mandible are available for the porolepiform genera *Glyptolepis* and *Holoptychius* (Gross 1941; Jarvik 1972; Ahlberg 1991), and less detailed data for *Porolepis* (Gross 1941; Jarvik 1972) and *Duffichthys* (Ahlberg 1992).

Cosmine. Cosmine is found primitively in porolepiforms (Gross 1941; Ahlberg 1991; Cloutier & Ahlberg 1996) and is thus likely to be primitive for stem-tetrapods. It is found in *Kenichthys* (Chang & Min 1993) and a number of more derived stem-tetrapod taxa (e.g. *Gogonasus* (Long *et al.* 1997), *Megalichthys* (Watson 1926), *Cladarosymblema* (Fox *et al.* 1995) and *Medoevia* (Lebedev 1995)). Cosmine is not known in any rhizodontid, which is most parsimoniously interpreted as a loss at the base of the clade. A convergent loss of cosmine is seen in the [tristichopterids [Panderichthys digited tetrapods]] clade, and in one canowindrid genus (*Canowindra*; Long 1985).

Pre- and intercoronoid fossae. In the mandibles of many stem-tetrapods there is a deep fossa mesial to the first coronoid, and at the sutures between the coronoids. These are referred to as the precoronoid fossa and the intercoronoid fossae, respectively (precoro. & intercoro. fossa; Fig. 13a, b). They may have served to accommodate palatal tusks when the jaws were closed (e.g. *Gogonasus*; Long *et al.* 1997). Precoronoid fossa are known in *Kenichthys* (Chang & Min 1993), the megalichthyids *Cladarosymblema* (Fox *et al.* 1995) and *Megalichthys* (Watson 1926; the condition is unclear in *Ectosteorhachis*), in *Medoevia* (Lebedev 1995), the tristichopterids (Jarvik 1972; Young *et al.* 1992; Ahlberg & Johanson 1997; Johanson & Ahlberg 1997) and *Panderichthys* (Ahlberg & Clack 1998). The fossa is weakly developed in *Gogonasus* (Long *et al.* 1997).

Intercoronoid fossae have a similar phylogenetic distribution, although they are normally developed in *Gogonasus* (Long *et al.* 1997), and are absent in *Kenichthys* (Chang & Min 1993). Amongst rhizodontids, *Rhizodus* lacks both pre and intercoronoid fossae. *Strepsodus* lacks a precoronoid fossa, but it is not known if intercoronoid fossae are present or not. No data are available for other rhizodontids.

Ahlberg (1992) stated that pre-coronoid fossae are found in all porolepiforms, with the exception of *Duffichthys* (which was interpreted as an autapomorphy of that genus, not the primitive condition). He also described intercoronoid fossae in holoptychiid porolepiforms (*cf.* Gross 1941), including *Duffichthys*. This makes it likely that the presence of both pre- and intercoronoid fossae is primitive for stem-tetrapods. Thus the absence of intercoronoid fossae in *Kenichthys* is a derived feature. Similarly, pre- and intercoronoid fossae were lost at some undetermined point within the rhizodontid clade, below *Rhizodus*. A convergent loss of these fossa is seen in the digited stem-tetrapods (Ahlberg & Clack 1998).

Symphysial region. Dentary symphysial tusks are not present in porolepiforms (Gross 1941; Jarvik 1972, 1980; Ahlberg 1992) and this is probably the primitive condition for stem-tetrapods (Ahlberg & Johanson 1998; Chang & Min 1993). However, the presence of dentary symphysial tusks is homoplastic within more derived stem-tetrapods. They are not present in *Kenichthys* (Chang & Min 1993), *Gogonasus* (Long *et al.* 1997), *Osteolepis* (Ahlberg & Johanson 1998), *Medoevia* (Lebedev 1995) and *Gyroptychius* (Ahlberg & Johanson 1998). Dentary tusks appear to have evolved independently in the rhizodontids, the megalichthyids, and within 'higher' tristi-
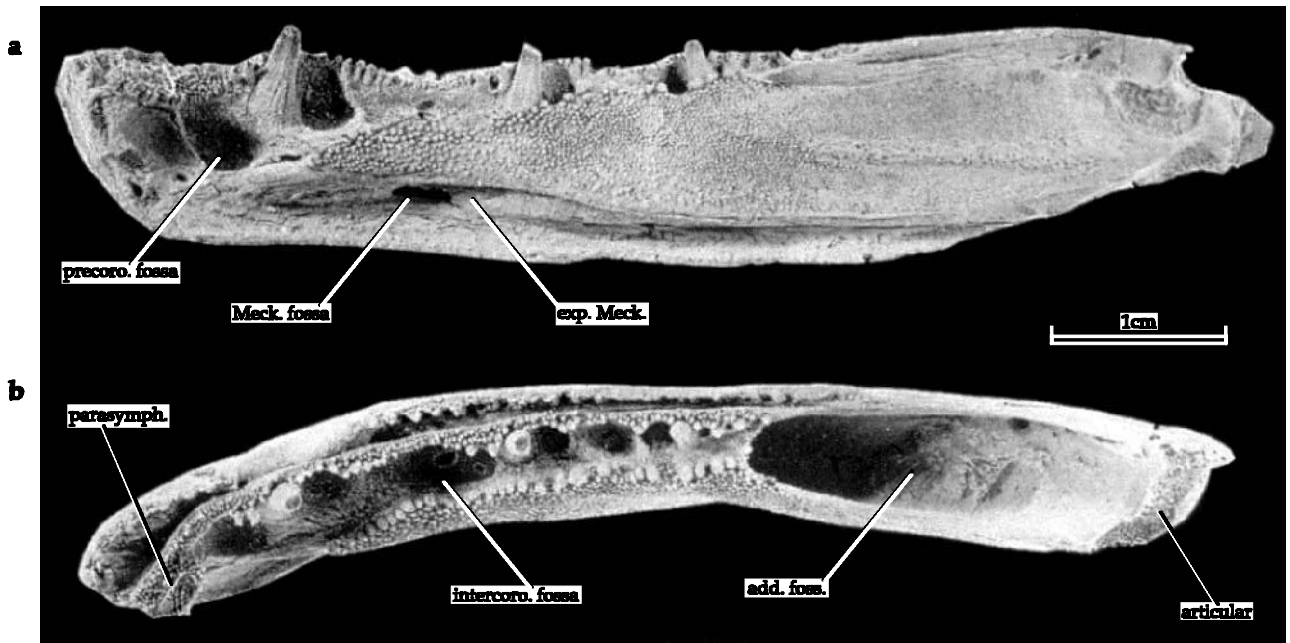
Figure 13 *Medoevia lata*: mandible in (a) lateral and (b) dorsal view, showing some primitive and derived stem-tetrapod characters. For discussion see main text.
(a), (b) © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris, reproduced from Lebedev (1995, Fig. 11), with the kind permission of the author and the Muséum national d'Histoire naturelle, Paris.

chopterids (*Platycephalichthys*, *Cabonnichthys*, *Mandageria*, *Eusthenodon* and *Notorhizodon*; Ahlberg & Johanson 1997; Johanson & Ahlberg 2001). *Panderichthys* bears dentary tusks, and they are widespread amongst digited stem-tetrapods (Ahlberg & Clack 1998). In rhizodontids, the megalichthyids *Cladarosymblema* and *Ectosteorhachis* (Fox *et al.* 1995), and the derived tristichopterids (Ahlberg & Johanson 1997; Johanson & Ahlberg 1997), the presence of a tusk more-or-less excludes the marginal dentary dentition from reaching the symphysis. In the [*Panderichthys*　tetrapod] clade, the tusks are accompanied by marginal dentary dentition at the symphysis (Ahlberg & Clack 1998; Ahlberg *et al.* 2000). A convergent condition is seen in *Megalichthys* (Watson 1926).

In the porolepiforms *Porolepis*, *Glyptolepis* and *Holoptychius* (Gross 1941; Jarvik 1972; Ahlberg 1992) there are paired parasymphysial bones. Each bears a linguolabial 'whorl' of fangs, with a number of accessory tooth rows. They do not contact the coronoid series. In *Duffichthys* the parasymphysial bone is large. It bears a single large fang and a few marginal teeth, and contacts the first coronoid (Ahlberg 1992). Ahlberg (1992) interpreted this condition as an autapomorphy of *Duffichthys*. In all porolepiforms, however, the parasymphysial bones bear the only dentition in the symphysial region (i.e. the dentary bears no teeth in this region). Several other groups of sarcopterygians possessed large parasymphysial tooth whorls (e.g. the onychodontids *Strunius* and *Onychodus* (Jessen 1966, 1967; Long 2001), the stem-dipnoan *Youngolepis* (Chang 1991)). In the probable stem-sarcopterygian *Psarolepis*, the mandible bears an articulation surface for a large parasymphysial bone (Yu 1998). Thus, under both hypotheses of sarcopterygian interrelationships described above, paired parasymphysial bones bearing large tooth whorls would be the primitive condition for stem-tetrapods.

However, in *Kenichthys* the parasymphysial bone bears only small teeth, continuous with similar tooth-fields on the first coronoid (Chang & Min 1993). In rhizodontids the tusks of the dentary form the main dentition at the symphysis. In *Gooloogongia* the morphology of the parasymphysial bone is poorly known, but it is 'lightly denticulated' and appears to contact the first coronoid (Johanson & Ahlberg 2001). The

morphology of the parasymphysial bone is unknown in *Screbinodus*, and incompletely known in *Barameda* and *Rhizodus*. However, in *Strepsodus* there is a row of small teeth and a denticle field. Johanson & Ahlberg (2001) stated that the parasymphysial bone of *Barameda* contacted the first coronoid. In *Rhizodus* the prearticular was well separated from the first coronoid, and the well-preserved articular surfaces of *Strepsodus* suggest a similar condition.

In *Gogonasus* the parasymphysial bone bears only a denticle field. It is elongated and contacts the first coronoid, a morphology comparable to that of *Kenichthys* (Chang & Min 1993; Long *et al.* 1997). A similar condition is seen in *Medoevia* (Lebedev 1995; Fig. 13b) and the megalichthyids *Cladarosymblema* and *Ectosteorhachis* (Fox *et al.* 1995), although in these taxa there is a precoronoid fossa. The parasymphysial bone runs around the labial side of the fossa. Jarvik (1972) noted that the parasymphysial bone is very small in the tristichopterid *Eusthenopteron*. As with more basal stem-tetrapods, it bears only denticles. The first coronoid extends labial to the precoronoid fossa and closely approaches the parasymphysial bone, but they do not contact (Jarvik 1972, 1980). The morphology is less well known in the other tristichopterids, but the condition appears similar in *Mandageria* (Johanson & Ahlberg 1997), *Cabonnichthys* (Ahlberg & Johanson 1997), *Notorhizodon* (Young *et al.* 1992) and *Eusthenodon* (Jarvik 1972). In *Panderichthys* the parasymphysial bone bears 'small teeth arranged in somewhat irregular rows' (Ahlberg & Clack 1998, p.14). As with tristichopterids, it is a small bone, but it contacts part of the first coronoid running labial to the precoronoid fossa. Within the digited stem-tetrapods the parasymphysial bone becomes firmly sutured to the first coronoid, dentary and prearticular. It bears a more defined tooth row, although denticles may still be present (Ahlberg & Clack 1998).

Meckelian ossification. Detailed data based on thin-sectioned material are available for the porolepiforms *Glyptolepis* and *Holoptychius*, and the tristichopterid *Eusthenopteron* (Jarvik 1972, 1980). In these species, between the first coronoid and the adductor fossa, the dermal bones form a box in transverse cross-

section (*cf.* Fig. 3b). The dentary forms much of the labial side, the infradentaries form part of the labial and all of the ventral side. The prearticular forms the lingual side, and a lingual lamina of the coronoids forms the dorsal side. The space thus enclosed is the intramandibular canal. The canal is partly lined by endochondral Meckelian bone. Distal to the third coronoid the canal opens dorsally to form the adductor fossa (see Fig. 13b, add. foss.). Comparison with the living coelacanth *Latimeria* (Millot & Anthony 1958) and living actinopterygians (e.g. *Amia*; Jarvik 1980) suggests that the adductor fossa and intramandibular canal of stem-tetrapods contained the adductor musculature and associated connective tissue of the mandible. Distal to the adductor fossa the jaw articulation is formed by the endochondral articular bone, another Meckelian ossification (see Fig. 13b). At the mesial tip of the mandible, the intramandibular canal is more-or-less filled by Meckelian bone, sometimes referred to as the mentomeckelian ossification. This may contribute material (along with the dentary) to the symphysial surface, although the extent of this contribution can be difficult to determine (Ahlberg & Clack 1998). For most of its length, the prearticular does not contact the infradentaries, exposing a band of the Meckelian lining of the intramandibular canal (exp. Meck., Fig. 13a). Towards the mesial tip of the jaw, however, the prearticular contacts the first infradentary.

Although less detailed information is available, as far as can be determined, a similar morphology is seen in *Psarolepis* (Yu 1998), *Youngolepis* (Chang 1991), *Kenichthys* (Chang & Min 1993), all the 'osteolepiform' stem-tetrapods (*sensu lato*; Watson 1926; Ahlberg 1989; Fox *et al.* 1995; Lebedev 1995; Ahlberg & Johanson 1997; Johanson & Ahlberg 1997; Ahlberg & Clack 1998; Long *et al.* 1997) and *Panderichthys* (Ahlberg & Clack 1998).

In *Rhizodus* and *Strepsodus* (and what is known of *Screbinodus*) there is no trace of Meckelian bone—it appears to have remained cartilaginous, and was not fossilised. Specimens preserve the intramandibular canal open between the prearticular and the infradentaries (see Fig. 3a), and there is no floor to the adductor fossa (Fig. 12c). Besides this, the prearticular tapers towards the mesial tip of the jaw, and is widely separated from the first infradentary (Figs 5a, b, 12c). The coronoids lack a lingual lamina, and each bears a single, deeply rooted fang and no other dentition (see Figs 3a, 7). This makes them extremely deep dorsoventrally. They are strongly sutured to each other, and to the dentary and prearticular. The firm integration of the dentary, coronoids and prearticular, coupled with a shallow dentary–infradentary overlap, has profound implications for the function of the jaw (discussed below). However, a lack of data for basal rhizodontids makes it impossible to analyse the evolution of this highly apomorphic jaw morphology within the rhizodontids. In *Rhizodus* and *Strepsodus* the robust symphysis is formed entirely by the dentary, and there are no gaps indicating a contribution from an unossified Meckelian element. This is clearly a derived condition within rhizodontids, but again, without data for *Gooloogongia*, *Barameda* or *Screbinodus* nothing can be said about its evolution.

Basal tetrapods reduced Meckelian ossification, convergently with rhizodontids. In *Acanthostega*, *Ichthyostega* and *Ventastega* there is a gap between the prearticular and infradentaries, instead of an exposure of Meckelian bone (Ahlberg & Clack 1998). However, the articular bone and at least part of the mentomeckelian ossification remains. The first infradentary (known as the splenial) produces a significant mesial lamina, becoming U-shaped in cross-section. The parasymphysial bone becomes a more integral structural part of the jaw, firmly sutured to the dentary, splenial and first coronoid (Ahlberg & Clack 1998).

5. Functional morphology

5.1. Tooth strength and attachment

Tooth sockets. Where known (*Rhizodus*, *Screbinodus* and *Strepsodus*) the tooth sockets for the symphysial tusks and the coronoid fangs are in 'oversized' sockets, which is shared by the functional crown and its replacement twin. This is probably an adaptation for the growth of such extremely large, deeply rooted dentition where there is little room for separate pits. The complexity of the dentine folding gradually increases towards the base of the root. 'Bone of attachment' penetrates between the folds, and firmly anchors the root in the socket.

Strength. The morphology of a tooth affects its strength under various loads. This will in turn affect its optimum function. The large conical teeth seen in *Gooloogongia*, *Barameda*, *Rhizodus*, *Screbinodus* and *Strepsodus* were probably best suited to piercing and holding prey (Alexander 1967).

The symphysial tusks of *Gooloogongia*, *Barameda*, *Rhizodus* and *Screbinodus* are recurved; in those of *Strepsodus* and the Colombian jaw recurvature is predominant. Recurvature acts to increase the strength of a tooth under loadings opposing the direction of recurvature. It is also a means of increasing the effective depth of prey penetration without increasing the absolute length of the tooth (Rieppel 1979). However, the maximum bite pressure may be exerted when the tooth tip is normal to the surface of the prey, presenting the smallest tooth area for the bite force to be transmitted through (Rieppel 1979). This is more difficult to achieve with posteriorly recurved teeth. *Gooloogongia* (and perhaps *Barameda*) seems to have overcome this by a protrusion of the mandible. *Rhizodus*, *Screbinodus* and *Strepsodus* did not protrude their mandibles, and so probably had to employ an extremely wide gape.

In *Rhizodus* and *Screbinodus* the teeth bear thickened mesial and distal edges. These are not sharp, and are unlikely to have had a significant cutting effect. Rather, they probably represent strengthening of the tooth in the direction of maximum load—in this case mesial–distal loads, rather than lateral. This could be to compensate for the recurvature, which is markedly reduced in *Rhizodus* and *Screbinodus* when compared to *Gooloogongia* and *Strepsodus*.

The action of sigmoid teeth has been studied in booid snakes (Cundall & Deufel 1999; Deufel & Cundall 1999). Here the shape serves two main functions. Firstly, it can be used to increase the distance between the tip of one tooth and the shaft of the next. Increased spacing of tooth tips affects the pressure exerted by each individual tooth and therefore the likelihood of it penetrating the prey. However, in *Strepsodus* jaws there are no teeth directly posterior to the sigmoid symphysial tusks, and thus it is unlikely that the need to increase tooth-spacing was a factor in the evolution of the sigmoid teeth. The other main function of sigmoid teeth is to increase piercing of the prey surface when used in a 'lunging' attack, by angling the tip of the tooth towards the prey during a forward lunge. It is possible that this was the function of the sigmoid tusks in *Strepsodus* (*cf.* Andrews 1985)—as the prey recoiled, the benefits of ordinary recurvature would be gained from the shaft of the tusks.

The symphysial tusks of *Rhizodus*, *Screbinodus* and *Strepsodus* are much larger than the coronoid fangs. They were also opposed by similarly sized tusks on the premaxillae and vomers (Jeffery 1999). This, and their distance from the coronoid fangs, suggests that the prey was initially held in a 'pinch' at the tip of the jaws. It is possible that prey was
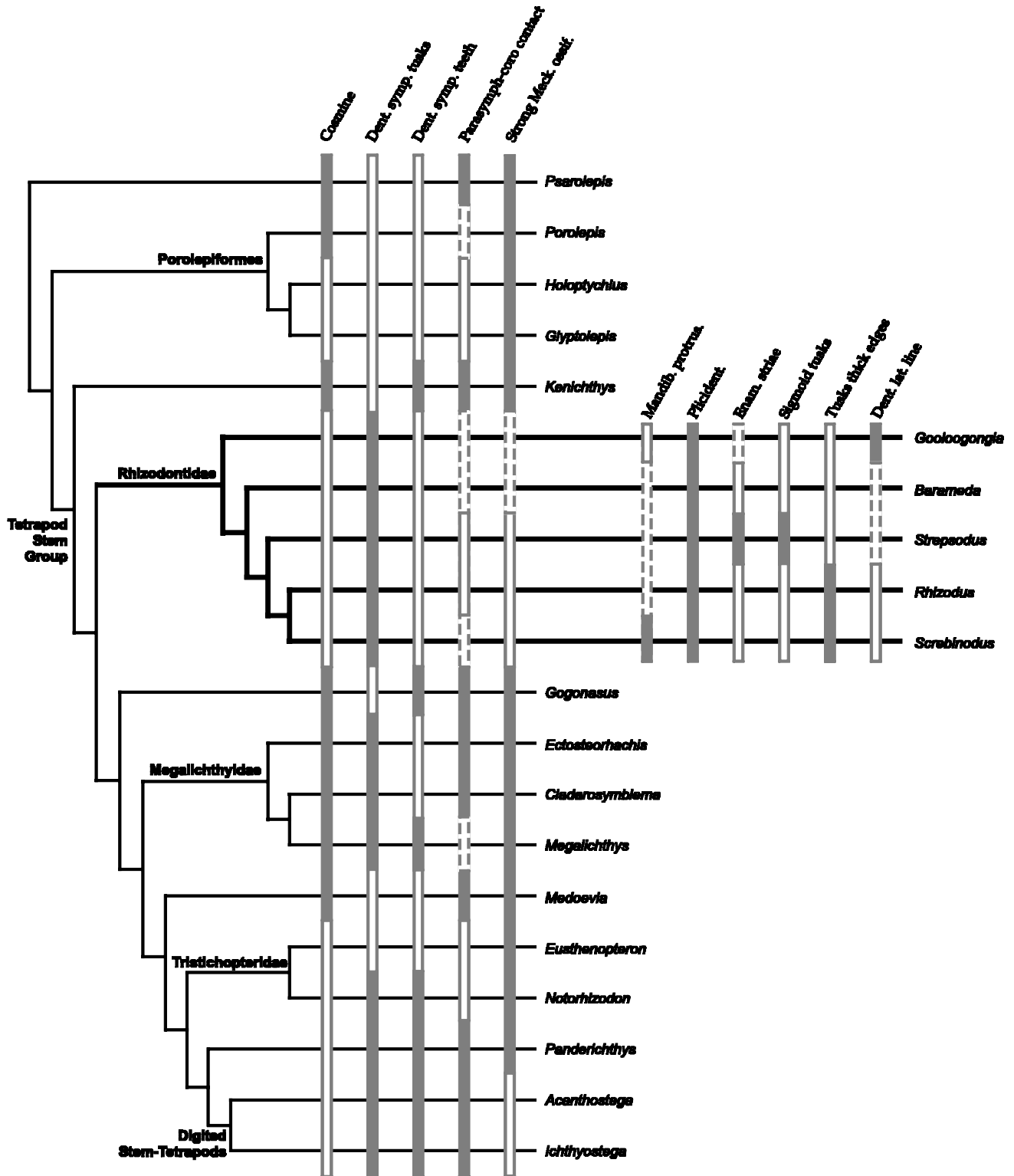
Figure 14 Stem-tetrapod jaw evolution. Cladogram showing the interrelations of selected stem-tetrapods. Main phylogeny after Ahlberg & Johanson (1998), rhizodontid phylogeny after Jeffery (1999). Morphological characters are mapped on to the phylogeny to show their distribution (for discussion see main text). Character abbreviations: Cosmine—cosmine on mandible; Dent. symp. tusks—symphysial tusks on dentary; Dent. symp. teeth—marginal teeth on dentary at symphysis; Strong Meck. ossif.—strong Meckelian ossification along intramandibular canal; Parasymph-coro contact—contact between parasymphysial bone and first coronoid; Mandib. protrus. — protrusion of mandible; Plicident.—plicidentine; Enam. striae—raised striae on enamel; Tusks thick edges—tusks and fangs with thickened mesial and distal edges; Dent. lat. line—lateral-line pores on dentary.
Grey fill ⊃ present; white fill ⊃ absent; dashed line ⊃ uncertain.

thrashed prior to swallowing, either to kill it or to break off manageable chunks (*cf*. Taylor 1987, Table 1). Prey may also

have been manipulated into the optimum position for swallowing (usually head first). Finally, it is possible that

some prey items were dragged to locations more favourable for the rhizodontid (for example, dragging large semi-aquatic tetrapods into deeper waters). The robust pectoral fin and girdle would have been well suited to providing the power for such behaviours (Jeffery 2001).

5.2. A kinetic mandible?

The unusual construction of the mandible known in *Rhizodus*, *Screbinodus* and *Strepsodus* suggests a unique function. When a prey item is bitten, the jaw transmits the force from the adductor muscles to the prey. The resistance of the prey to this force puts a load on the jaw, acting through the teeth. Because of the shape of the mouth, the size and positioning of teeth, and the position of the prey item, the mandible experiences both bending moments (mostly dorsoventral) and torsional moments. The 'box' structure described above as primitive for rhipidistians (see Fig. 3b) would be reasonably stiff both in bending and in torsion (Alexander 1968). The condition in *Rhizodus*, *Screbinodus* and *Strepsodus* is clearly derived with respect to other rhipidistians, and is unlikely to have been as stiff (see Figs 2i, j, 3a). It is therefore possible that, rather than resisting torsional forces, these species were utilising them in some way.

The mandibles of *Rhizodus*, *Screbinodus* and *Strepsodus* appear to be divided into two functional units. The pre-articular, coronoids and dentary constitute an upper unit—they are tightly integrated, and would probably have deformed in unison. The infradentary series forms a lower unit—they are also tightly integrated and would have deformed in unison. This lower unit probably supported the cartilaginous articulation of the mandible with the rest of the skull, in the region of the fourth infradentary. The upper units of the left and right jaw rami appear to have had only ligamentous connections to each other, at the dentary symphysis and the mesial rugose surface. This would have allowed some 'give' between the upper units of each ramus, depending on the stiffness of the ligaments. The lower units may have been more firmly connected, with either left and right first infradentaries overlapping, or a median anamestic bone overlapping both (*cf. Barameda* and *Gooloogongia*). For most of its length, the connection between the upper and lower units (the overlap surfaces of the dentary and the infradentaries) was shallow and smooth (see Figs 2i, j, 3a). Only the fourth infradentary has a more robust overlap, but even this was with the shallow distal tip of the dentary. The nature of the overlap makes it unlikely that the connection between the two units was rigid. Rather, it seems possible that the line of contact formed a longitudinal intramandibular hinge, allowing some degree of movement of the units relative to each other (?hinge, Fig. 3a). When biting, the large symphysial tusks would probably be the first point of contact with the prey, followed by the coronoid fangs. Under this sort of loading, the jaw is likely to have 'buckled' longitudinally, with the upper unit rotating lingually relative to the lower unit.

Along the relatively straight 'shaft' of the jaw (see Fig. 12c), movements between the two units would be fairly simple. However, at the mesial tip of the jaw, where it curves towards the symphysis, the relative movements would become more complex. The curvature itself would act to restrict buckling of the jaw, unless one or other of the units was able to 'warp', or some degree of disarticulation of the two units was possible. This is difficult to model, as the exact curvature of the jaw and the stiffness of any ligaments is unknown. However, the degree of distortion or disarticulation could have been reduced by the upper unit sliding posteriorly relative to the lower unit. The contact between the two units in this region correlates with

this—the first infradentary sits in a groove on the ventral side of the dentary (Fig. 2e, f) which might have formed a sliding joint. At the symphysis, the ligamentous connections would have to allow the left and right upper units to roll lingually towards each other. Although such movement would ultimately bring the tips of the left and right symphysial tusks into contact, a large degree of movement would be possible before this occurred.

In *Rhizodus* and *Screbinodus*, the coronoid tusks are not recurved at all, but the marginal teeth on the dentary are recurved lingually. Thus the buckling would act to roll the marginal teeth lingually (digging into any prey item held by the jaws), whilst the lower unit maintained the stiffness of the jaw under vertical bending forces. To prevent the jaw from collapsing completely, the buckling would have to have been constrained by connective tissues between the two units. Such tissues may also have acted to return the jaw to its resting position after the biting load was removed.

It is not clear if a similar 'torsion grip' could have operated in *Strepsodus*, as the exact morphology of the coronoid fangs is uncertain. An extreme recurvature could act against a lingual twisting, but it would raise questions about how the fangs were rotated labially to bring their tips normal to the prey surface. Without knowledge of the unusual jaw structure, Andrews (1985) suggested that the mandibles were rotated labially on opening, to bring the tooth tips into an optimal position (*cf.* Rieppel 1979). In any case, the similarities of the jaw morphology of *Strepsodus* to that of *Rhizodus* and *Screbinodus*, means that torsional forces would have to have played a significant role in jaw action.

The rest of the skull (especially the braincase) is too poorly known to attempt to reconstruct any potential kinesis (Jeffery 1999). However, in *Gooloogongia*, *Barameda*, *Screbinodus* and probably *Strepsodus* the dermocranial joint was widely open (Andrews 1985; Long 1989; Johanson & Ahlberg 1998; Jeffery 1999). *Screbinodus* had a poorly ossified braincase and surprisingly small overlaps between many of the cheek bones (Jeffery 1999). This suggests that rhizodontids had a degree of kinesis in their skulls also.

Ahlberg & Clack (1998) note that in two digited stem-tetrapods (*Acanthostega* and *Ventastega*) and several temnospondyls (putative stem lissamphibians; Coates *et al.* 2000) the dentary is also weakly connected to the infradentaries. Unlike rhizodontids, in these taxa the strongest suture is with the first infradentary (in digited tetrapods called the splenial), not the fourth (the surangular). However, it is not clear if this weak attachment could have formed a longitudinal intramandibular joint, nor how any such joint might have functioned.

6. Acknowledgements

thanks must go to Dr J.A. Long, who generously donated a cast of NMV P160 880 to the University Museum of Zoology, Cambridge; to Dr. Ph. Janvier, who loaned me the rhizodontid material from Colombia before it was formally described; and to Dr O. Lebedev for permission to reproduce figures of *Medoevia lata*. Finally, I gratefully acknowledge the help of Kate Brunskill and Jan den Blaauwen in transporting specimens.

7. Abbreviations used in figures

add. foss.—adductor fossa
ant. submandib.—anterior submandibular
anteromes. rug. dentary—rugose anteromesial area on dentary
anteromes. rug. infradent. 1—rugose anteromesial area on first infradentary
art. dent.—articular area for dentary
art. infradent.—articular area for infradentaries
art. parasymph.—articular area for parasymphysial bone
art. preart.—articular area for prearticular bone
art. symph.—symphysial articular area
branchiosteg.—branchiostegal bone
cor. 1—first coronoid
cor. 2—second coronoid
cor. 3—third coronoid
cor. fang(s)—coronoid fang(s)
dentic. field—denticle field
dentic. preart.—denticulated prearticular bone
derm. cheek—dermal cheek bones
derm. pect. gird.—dermal pectoral girdle
dist. tip dentary—distal tip of dentary
dist. tip infradent. 4—distal tip of fourth infradentary
enam. striae—raised striae in the enamel of the crown
exp. Meck.—exposed Meckelian bone
?hinge—possible hinge-point between dentary and infradentary
infradent. 1—first infradentary
infradent. 2—second infradentary
infradent. 3—third infradentary
infradent. 4—fourth infradentary
intercoro. fossa—intercoronoid fossa
intramandib. canal—intramandibular canal
lat. gular—lateral gular
ling. preart.—lingual face of prearticular
ling. dentary—lingual face of dentary
ling. maxilla—lingual face of maxilla
marg. teeth—marginal teeth of dentary
Meck. bone—Meckelian bone
Meck. fossa—Meckelian fossa
med. gular—median gular plate
overlap. submandib.—overlap surface for submandibulars
?palat. fang—probable palatine fang
parasymph.—parasymphysial bone
part entopteryg.—part of entopterygoid
plicat.—plications around base of crown, reflecting internal morphology of plicidentine
post. submandib.—posterior submandibular
preart. proc.—process of prearticular
preartic.—prearticular bone
precoro. fossa—precoronoid fossa
premax.—premaxillary bone
premax. tusk—premaxillary tusk
recurv.—recurved section of crown of tusk
reverse curv.—section of crown of tusk with reversed (forward) curvature
ridged art. infradent. 4—ridged articular area for fourth infradentary
rug. art. dent.—rugose articular area for dentary
sections ling. shelf—sections of distal lingual shelf
semicylind. dentary —ridge on dentary semicylindrica in cross-section
square dentary—ridge on dentary square in cross-section
submand.—submandibular bone
symph. tusk—symphysial tusk of dentary
symph. socket—socket for symphysial tusk

unj. lepid.—unjointed lepidotrichial segments
vert. lam. dentary—vertical lamina of dentary

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JONATHAN E. JEFFERY, University Museum of Zoology, Downing Street, Cambridge, CB2 3EJ, UK.
Current address: Instituut Biologie Leiden, Universiteit Leiden, Postbus 9516, 2300 RA Leiden, The Nethelands.
E-mail: jeffery@rulsfb.leidenuniv.nl