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Cranial morphology of the Carboniferous rhizodontid *Screbinodus ornatus* (Osteichthyes: Sarcopterygii)

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Well-preserved material is described of several specimens of *Screbinodus ornatus*, a small (approximately 1.5 metres long) rhizodontid sarcopterygian, from the Visean (Mississippian, Carboniferous) of Scotland. This species shows numerous 'typical' rhizodontid characteristics, such as post-parietals with a median 'tail', pectoral lepidotrichia with elongated basal segments, large symphysial tusks on the dentary and a 'reverse' overlap relationship between the cleithrum and clavicle. It also shows several characters unknown in other rhizodontids, such as the loss of the extratemporal and subopercular, and the probable exclusion of the postorbital from the orbital margin. A phylogenetic analysis finds that rhizodontids are the sister group to all other members of the tetrapod total group (with the exception of *Kenichthys*). This confirms that resemblances between derived rhizodontids and digited stem-tetrapods such as *Acanthostega* (noted by several previous authors) are due to convergence. A second analysis finds that *Screbinodus* is a derived rhizodontid, and part of a monophyletic Carboniferous radiation.

Keywords: Rhizodontida; Rhizodontidae; *Rhizodus*; *Strepsodus*; stem-tetrapod; phylogeny

Introduction

Screbinodus ornatus (Traquair 1878) is a Carboniferous freshwater predatory fish, a member of the Rhizodontida (Sarcopterygii). The best material was discovered in the 19th century at a quarry in Gilmerton, on the outskirts of Edinburgh, UK, although its remains have been reported from a number of sites around the Midland Valley of Scotland. These deposits were formed in the Visean, in the system of shallow rivers and lakes associated with the 'coastal alluvial plain' (Anderton 1985) that existed in this area for much of the Carboniferous.

The study of *Screbinodus* dates back to the work of Louis Agassiz (e.g. Agassiz 1835, 1843, p. 68), Samuel Hibbert (Hibbert 1835) and Sir Richard Owen (Owen 1840), although it was not distinguished from the rhizodontid *Rhizodus hibberti* until Traquair (1875, 1878) partly prepared and described a skull and pectoral fin (now NMS GY 1874.6) and used it to establish the species *Rhizodus ornatus*. Miall (1875) figured and briefly described a specimen which showed the ventral surface of *R. ornatus* (now SME 4714), although he misinterpreted it as the dorsal surface (Fig. 1G). Andrews (1973) published a reconstruction of a postparietal shield (based on NMS GY 1963.16.18; Fig. 2A, B), and later established the genus *Screbinodus* Andrews, 1985, to emphasize the differences between *Rhizodus ornatus* and the type species of *Rhizodus*,

R. hibberti (Owen 1840). A wider interest in rhizodontids as a whole was revived in the 1980s by the discovery of the first specimen to show the overall shape of the body (of *Strepsodus*; Andrews 1985) and the first detailed description of an articulated skull (of *Barameda*; Long 1989). Over the last 10 years, interest has centred around the discovery of new rhizodontid material in North America (*Sauripterus* and *Letognathus*; Daeschler & Shubin 1998; Davis *et al.* 2001, 2004; Brazeau 2005) and Australia (*Gooloogongia* and *Strepsodus*; Johanson & Ahlberg 1998, 2001; Johanson *et al.* 2000; Garvey *et al.* 2005; Parker *et al.* 2005; Holland *et al.* 2007), and from several phylogenetic studies which suggest that they are the sister group to all other members of the tetrapod total group (*sensu* Patterson 1993) with the exception of *Kenichthys* (e.g. Cloutier & Ahlberg 1996; Zhu & Schultze 1997; Johanson & Ahlberg 1998, 2001; Jeffery 1999; Zhu & Ahlberg 2004; Long *et al.* 2006).

Despite the revived interest in rhizodontids, the morphology of *Screbinodus* has not been described, except for the brief reports of Miall (1875), Traquair (1875, 1878) and Andrews (1973, 1985). This paper therefore describes all the material known from the UK (including several articulated or associated specimens), followed by sections reviewing comparative material of other British and Australian species. The skull material of *Screbinodus* is among the most extensive and best preserved for any rhizodontid and most bones are represented by more than
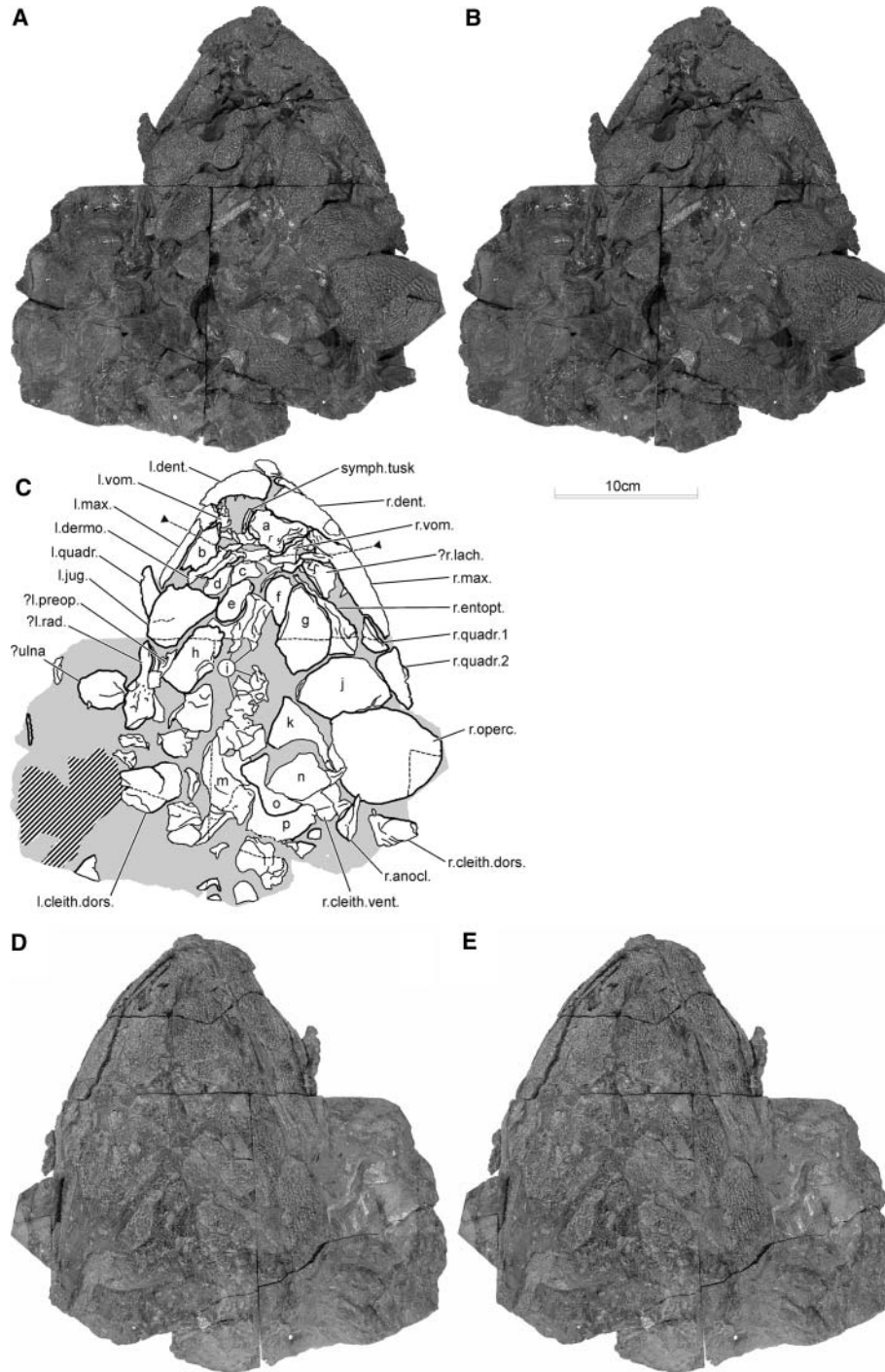
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Figure 1. *Screbinodus ornatus*, general views of complete skull SME 4714. **A, B,** stereopair in dorsal view; **C,** interpretive sketch of A and B; **D, E,** stereopair in ventral view; **F,** interpretive sketch of E and F; G, sketch of SME 4714 in ventral view, reproduced from Miall (1875). Note that Miall confused the ventral for the dorsal surface. In Miall's interpretation: Orb = orbit (in fact a damaged area of right principal gular); Ne = nasal foramen (a space between the median gular and the mandible); Eth = ethmoid (median gular); Mx = maxilla (infradentary 1 and 2); Fr = frontal (the anterior part of the left principal gular); Pa = parietal (left principal gular). **H, I,** stereopair of snout in oblique ventral view; **J,** interpretive sketch of H and I. The ventral half of this specimen is articulated, but it sustained damage during the original preparation and subsequent storage. The dorsal half is mostly disarticulated and scattered in three dimensions, although it retains some of the natural relationships between the bones. In A–F and H–J, thick outline = natural margin; thin outline = broken edges; grey = matrix; hatching = areas of badly damaged bone; dashed line = cracks in specimen. Abbreviations: a, premaxilla; b, left lachrymal; c, indeterminate bone from the parietal shield or snout; d, left entopterygoid; e, left parietal; f, right parietal; g, right jugal; h, left postorbital; i, braincase fragments; j, right squamosal; k, right tabular; m, ventral part of left cleithrum; n, median extrascapular; o, right lateral extrascapular; p, ?left lateral extrascapular; q, right principal gular; r, left principal gular; s–w, left submandibular series; x, left third infradentary.
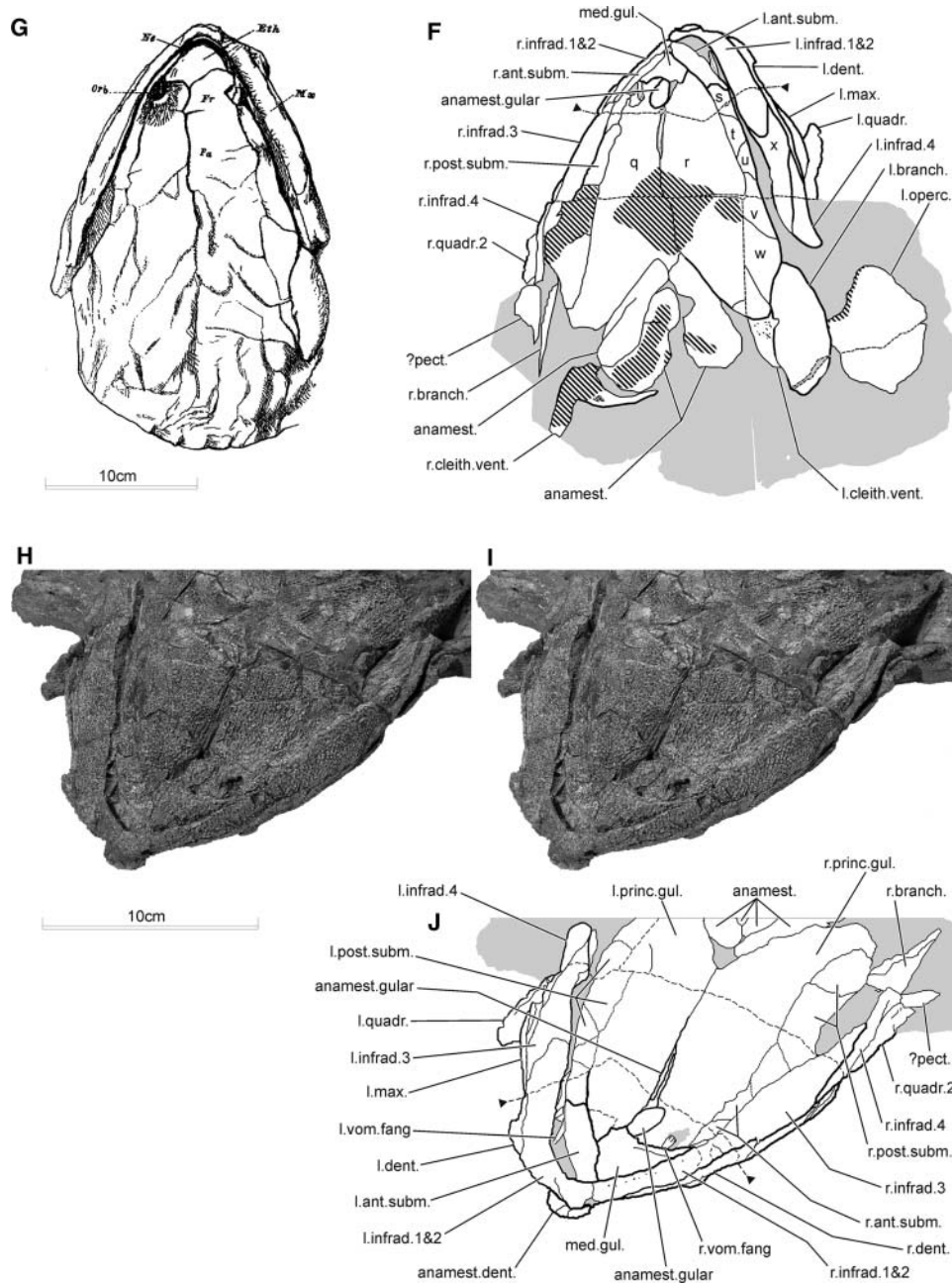
Figure 1. Continued.

one example (often revealing both internal and external surfaces). By contrast, the bones in material of the other rhizodontid species for which well-preserved skulls are known (*Gooloogongia* and *Barameda*, from the Upper Devonian and Mississippian of Australia respectively) can generally only be viewed from one perspective (indeed, much of the material is in the form of natural moulds).

Material and methods

Material
Screbinodus ornatus. The four most-complete specimens of *Screbinodus* were recovered in the mid-19th century from the Venturefair Pit near Gilmerton, Edinburgh (the pit has long since closed, but was situated at approximately 55° 49′ 44″ N, 3° 7′ 49″ W, OS Landranger co-ordinates NT293601; pers. comm. J. Schlesinger, City of Edinburgh Council). These are SME 4714 (left and right cheeks posterior to the orbits, palate and complete operculogular system; Fig. 1), NMS GY 1963.16.18 and 1998.28.1 (both showing post-parietal shields, extrascapulars and isolated cheek bones; Fig. 2), and NMS GY 1874.6 (the holotype specimen, with various scattered skull bones; Fig. 12A–C). No stratigraphical information is available for these specimens, but there are differences in their preservation. SME 4714 and NMS GY 1874.6 are both preserved as nut-brown
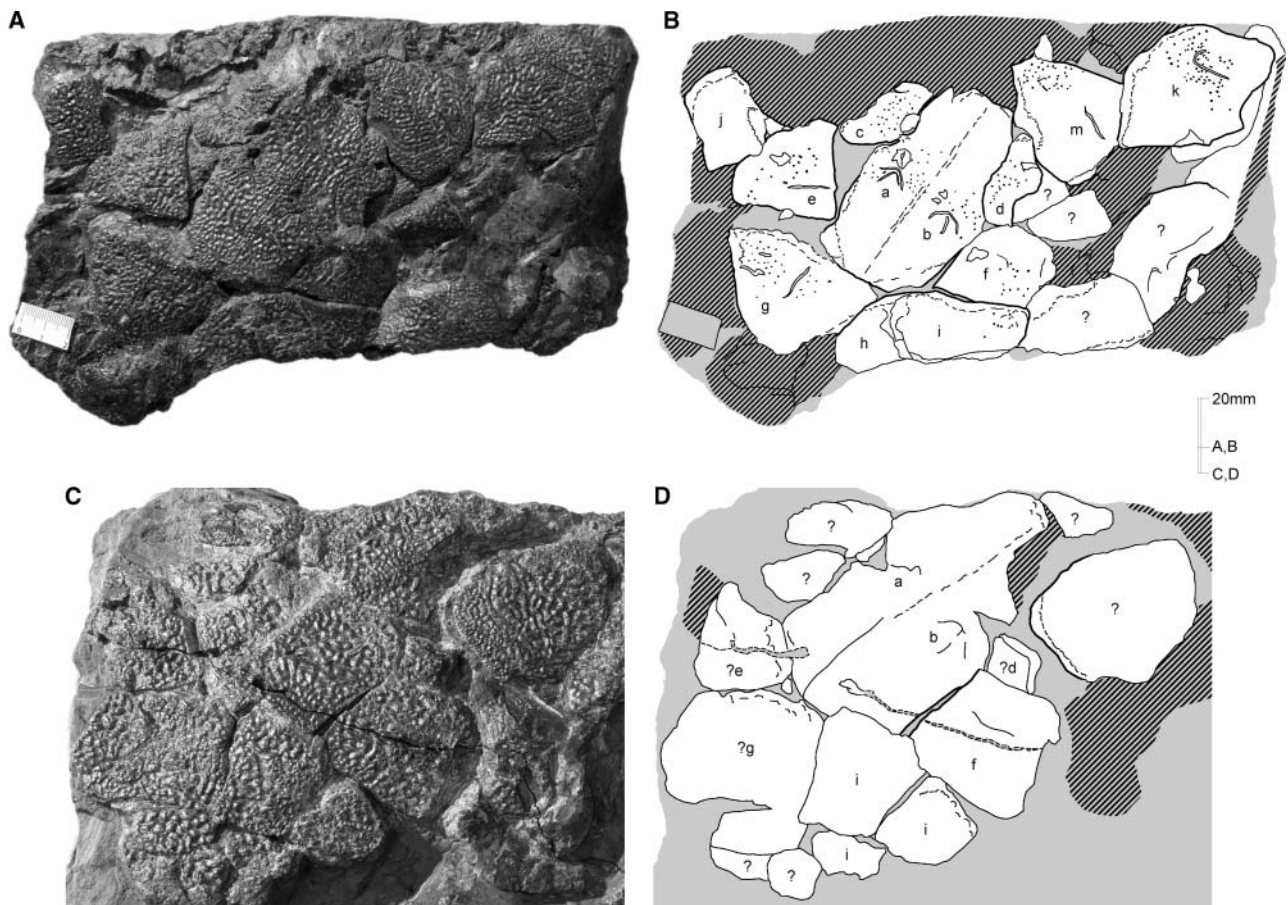
Figure 2. *Screbinodus ornatus*, specimens showing the skull roof. **A, B,** photograph and interpretive sketch of NMS GY 1963.16.18; **C, D,** photograph and interpretive sketch of NMS GY 1998.28.1. Both specimens are flattened into a single plane (anterior is roughly to the top right). NMS GY 1998.28.1 has been badly damaged at some time in the past. Shading conventions are the same as in Fig. 1; dots mark the position of sensory pits. Abbreviations: a, left postparietal (including pitlines); b, right postparietal (including pitlines); c, left supratemporal; d, right supratemporal; e, left tabular (including pitline); f, right tabular (including pitline); g, left lateral extrascapular (including pitline); h, median extrascapular; j, left squamosal; i, right lateral extrascapular; k, right squamosal (including pitline); m, right postorbital (including pitline).

bones, slightly scattered in three dimensions (with bones overlying each other) in Gilmerton Ironstone, a matrix of fine-grained, light-grey siliceous limestone, with many narrow seams of coal (1–2 mm thick), calcite intrusions, hard nodules of orange oxides and extremely hard dark grey to black nodules. NMS GY 1963.16.18 and G 1998.28.1 are both preserved as dark grey bones, flattened into a single plane in a much more homogenous, dark grey limestone matrix.

Cross-scaling various bones suggest that all four individuals were within 7% of each other in size. A very small number of isolated bones (e.g. isolated median extrascapular NHM P36912 (Fig. 10G, H) and right postparietal NMS GY 1972.28.1 (Fig. 8A–D)) show that some individuals grew up to 20% larger.

Further preparation was carried out on these and other specimens for this study. In particular, the dorsal side of SME 4714 was prepared for the first time. To facilitate the preparation of SME 4714, a diamond wire saw (0.1 mm diameter) was used to divide the specimen into three pieces (anterior, and left- and right-posterior).

Other British rhizodontids. Collections of the Carboniferous rhizodontids *Rhizodus* and *Strepsodus* from several museums were studied. Most specimens are isolated bones or completely disarticulated assortments of bone, but a few preserve articulated sections, or close natural associations. Several specimens were prepared in the 19th century, although in most cases further preparation was carried out.

Australian rhizodontids. Specimens of *Gooloogongia* and *Barameda* have been described in detail by previous authors (Long 1989; Johanson & Ahlberg 1998, 2001; Long & Ahlberg 1999). Recently Holland *et al.* (2007) published a description of a new specimen of *Barameda* (NMV P212715) along with a reassessment of the

taxonomy of that genus. The authors noted that *Barameda* material is found in two distinct size-ranges which also show some differences in morphology of the jaw and pectoral fin (see also Jeffery 2003, p. 267). They therefore established a second species, *B. mitchelli*, for the smaller size range, and *B. decipiens* was restricted to the larger size-range, including the original type series (Woodward 1906) and NMV P212715. A detailed cast of *B. mitchelli* (NMV P160 880) was donated to the Cambridge University Museum of Zoology by Dr John Long (Natural History Museum of Los Angeles County, USA) to aid comparisons during this study.

Preparation

The preparation was conducted under a stereomicroscope, using a Chicago Pneumatics Airscribe CP9361, a Techdent dental mallet, and a mounted needle. Exposed bone was consolidated with a solution of Paraloid B72 in acetone.

Terminology

Teeth in *Screbinodus*, *Rhizodus* and *Strepsodus* fall into four non-overlapping size categories. This paper follows Jeffery (2003) in referring to these (from largest to smallest) as tusks, fangs, teeth and denticles, while noting that "this does not necessarily imply differences in morphology or ontogeny (particularly between the tusks, fangs and teeth) but conveniently distinguishes the size ranges" (Jeffery 2003, p. 356).

Institutional abbreviations

AMF: Australian Museum, Sydney, Australia; **IGS**: British Geological Survey, Murchison House, Edinburgh; **NEWHM**: Hancock Museum, Newcastle-upon-Tyne, UK; **NHM**: Natural History Museum, London, UK; **NMS GY**: National Museums of Scotland, Edinburgh, UK; **NMV**: National Museum of Victoria, Melbourne, Australia; **PMG**: Paisley Museum Geological Collection, Paisley, UK; **SME**: Sedgwick Museum of Geology, Cambridge, UK.

Figure abbreviations

add. foss. mand.: adductor fossa of the mandible; **anamest.**: anamestic bone; **anamest. dent.**: anamestic bone separating dentaries; **anamest. gular**: anamestic bone separating the principal gulars; **ant. lam. r. vom.**: anterior lamina of the right vomer; **ant. lat. proc.**: anterolateral process of vomer; **ant. pal. foss.**: margin of the anterior palatal fossa; **art. ant. sup.**: articular facet for the anterior supraorbital; **art. ant. tec.**: articular facet for the anterior tectal; **art. antim.**: articular facet for antimere; **art. branch.**: articular facet for the branchiostegal; **art. cheek**: articular facet for cheek bones; **art. entopt.**: articular facet for the entopterygoid; **art. intert.**: articular facet for the intertemporal; **art. jug.**: articular facet for the jugal; **art. lach.**: articular facet for the lachrymal; **art. lat. extra.**: articular facet for the lateral extrascapular; **art. lat. rost.**: articular facet for the lateral rostral; **art. lat. rost./ant. tec.**: articular facet for the lateral rostral and anterior tectal; **art. max.**: articular facet for the maxilla; **art. med. extra.**: articular facet for the median extrascapular; **art. med. gul.**: articular facet for the median gular; **art. med. rost.**: articular facet for the median rostral; **art. nasal/supraorb.**: articular facet for the nasal or supraorbital; **art. operc.**: articular facet for the opercular; **art. par.**: articular facet for the parietal; **art. pit**: pit for articular ligament; **art. post. sup.**: articular facet for the posterior supraorbital; **art. postorb.**: articular facet for the postorbital; **art. postp.**: articular facet for the postparietal; **art. premax.**: articular facet for the premaxilla; **art. preop.**: articular facet for the preopercular; **art. quadr.**: articular facet for the quadratojugal; **art. quadr.2.**: articular facet for the secondary quadratojugal; **art. squam.**: articular facet for the squamosal; **art. suprat.**: articular facet for the supratemporal; **art. tab.**: articular facet for the tabular; **asc. proc. l. max.**: ascending process of the left maxilla; **asc. proc. r. max.**: ascending process of the right maxilla; **attach.**: area for ligament attachment; **brain**: fragment of braincase; **canal**: entrance to canal for lateral line; **cheek**: dermal cheek bones; **choan. foss.**: choanal fossa; **choan. foss. l. vom.**: choanal fossa on the left vomer; **choan. foss. max.**: choanal fossa on the left maxilla; **choan. foss. r. vom.**: choanal fossa on the right vomer; **coro. fang**: coronoid fang; **dent. tusk**: dentary tusk; **divert.**: diverticulum of lateral line canal; **dors. art. jug.**: dorsal articular facet for the jugal; **dors. art. lach.**: dorsal articular facet for the lachrymal; **ectopt. fang**: ectopterygoid fang; **foss. coro.**: fossa to receive coronoid fang; **foss. lat.**: fossa carrying ramus of lateral line; **indet.**: indeterminate bone from the parietal shield or snout; **l. ant. pal. foss.**: margin of anterior palatal fossa on left vomer; **l. ant. subm.**: left anterior submandibular; **lat.**: fossae associated with lateral line canals; **l. branch.**: left branchiostegal; **l. cleith. dors.**: dorsal part of left cleithrum; **l. cleith. vent.**: ventral part of left cleithrum; **l. dent.**: left dentary; **l. dermo.**: left dermopalatine; **l. entopt.**: left entopterygoid; **l. infrad. 1 and 2**: left first and second infradentary; **l. infrad. 3**: left third infradentary; **l. infrad. 4**: left fourth infradentary; **l. jug.**: left jugal; **l. lach.**: left lachrymal; **l. max.**: left maxilla; **l. operc.**: left opercular; **l. par.**: left parietal; **l. post. subm.**: left posterior submandibular; **l. postorb.**: left postorbital; **l. preart.**: left prearticular; **l. preop.**: left preopercular; **l. princ. gul.**: left principal gular; **l. quadr.**: left quadratojugal; **l. rad.**: left radial; **l. tab.**: left tabular; **l. vom.**: left vomer; **l. vom. fang**: left vomerine fang; **marg. add. foss.**: margin of the adductor fossa; **med. extra.**: median extrascapular; **med. flange**: median flange of the dermopalatine; **med. gul.**: median gular; **med. rost.**: median rostral; **orb. marg.**: orbital margin; **overlap antim.**: overlap flange for the antimere; **pal.**: dorsolingual part of the entopterygoid; **pal. fang**: palatal fang; **pect.**: pectoral endoskeletal fin bone; **pin.**: depressed area surrounding the pineal foramen; **post. lam. l. vom.**: posterior laminar of the

left vomer; **post. lam. r. vom.**: posterior lamina of the right vomer; **premax. tusk**: premaxillary tusk; **preop.**: preopercular; **r. anocl.**: right anocleithrum; **r. ant. pal. foss.**: margin of anterior palatal fossa on right vomer; **r. ant. subm.**: right anterior submandibular; **r. branch.**: right branchiostegal; **r. cleith. dors.**: dorsal part of right cleithrum; **r. cleith. vent.**: ventral part of right cleithrum; **r. dent.**: right dentary; **r. ectopt.**: right ectopterygoid; **r. entopt.**: right entopterygoid; **r. front.**: right frontal; **ridge. art. palate**: ridge for articulation with the palate; **r. infrad. 1 and 2**: right first and second infradentary; **r. infrad. 3**: right third infradentary; **r. infrad. 4**: right fourth infradentary; **r. jug.**: right jugal; **r. lach.**: right lachrymal; **r. lat. extra.**: right lateral extrascapular; **r. max.**: right maxilla; **r. operc.**: right opercular; **r. par.**: right parietal; **r. post. subm.**: right posterior submandibular; **r. premax.**: right premaxilla; **r. preop.**: right preopercular; **r. princ. gul.**: right principal gular; **r. quadr. 1**: right quadratojugal; **r. quadr. 2**: right secondary quadratojugal; **r. squam.**: right squamosal; **r. tab.**: right tabular; **r. vom. fang**: right vomerine fang; **r. vom.**: right vomer; **symph. tusk**: symphysial tusk; **vent. art. jug.**: ventral articular facet for the jugal; **vent. art. lach.**: ventral articular facet for the lachrymal; **vent. marg. branch.**: ventral margin of the branchiostegal; **vent. premax.**: ventral margin of the premaxilla.

Systematic palaeontology

Sarcopterygii Romer 1955
Rhizodontida Andrews & Westoll 1970, p. 463
Rhizodontidae Traquair 1881a, p. 16

Remarks. Traquair originally intended to establish Family Rhizodontidae in an article (Traquair 1881b, p. 179) based on a paper read before the Royal Society of Edinburgh in May 1877. However, it was published after another article (based on a paper read in July 1880) in which he used the name Rhizodontidae in a table of fossil genera (Traquair 1881a, p. 16). The Rhizodontidae as defined by Traquair included several taxa now recognized as rhizodontids (*Strepsodus*, *Archichthys* and *Rhizodus*, which at the time included *Screbinodus*), as well as two other stem-tetrapods (*Tristichopterus* and *Rhizodopsis*). Andrews and Westoll (1970) restricted the family to *Strepsodus* (now including *Archichthys*), *Rhizodus* (including *Screbinodus*) and *Sauripterus* based on shared characteristics of the pectoral girdle and fin, and established Order Rhizodontida, co-extensive with the Rhizodontidae. This definition of Rhizodontida and Rhizodontidae has been widely accepted in the subsequent literature, modified only by the inclusion of newly defined genera.

Genus *Screbinodus* Andrews 1985, p. 93
Type and only species. *Screbinodus ornatus* (Traquair, 1878).

Screbinodus ornatus (Traquair, 1878)

1875 *Rhizodus hiberti* (Owen); Traquair: 266.
1875 *Rhizodus* (Owen); Miall: 624.
1878 *Rhizodus ornatus* Traquair: 659.
1970 *Rhizodus ornatus* Traquair; Andrews & Westoll: 432.

Holotype. NMS 1874.6, articulated skull and pectoral fin, Visean (P2), Gilmerton Ironstone (Lower Limestone Group), Gilmerton, Edinburgh, UK.

Best skull material. NHM P11540 (opercular from Traquair's collection), NHM P29286 (left squamosal), NHM P3322 (median extrascapular and opercular), NHM P3322a (median extrascapular and opercular), NHM P3322b (tip of left principal gular), NHM P36911 (opercular), NHM P36912 (median extrascapular), NHM P47718 (left principal gular, part and counterpart), NMS GY 1876.20.2 (median extrascapular labelled as a *Rhizodus* scale), NMS GY 1890.104.8 (left clavicle), NMS GY 1963.16.18 (articulated skull roof), NMS GY 1972.28.1 (left post parietal), NMS GY 1998.28.1 (articulated skull roof), SME 4714 (articulated skull).

Diagnosis. A medium-sized rhizodontid. The dermal skull bones have a robust ornament of humps and ridges. The extratemporal is absent or fused with a large tabular. The tusks on the dentaries and the fangs on the coronoids, premaxillaries and vomers, have a lenticular cross-section (see Jeffery 2003). Sensory pitlines are present on cleithrum (see Jeffery 2001).

Occurrence. Principal and type locality: Venturefair Pit near Gilmerton, Edinburgh, UK (Carboniferous, Visean). Isolated remains from many other UK sites.

Genus *Strepsodus* Huxley in Huxley & Etheridge, 1865, p. 145
Type and only species. *Strepsodus sauroides* (Binney, 1841, p. 165).
Strepsodus sauroides (Binney, 1841)

Holotype. An isolated tooth, now lost, from the Pendleton coalfield near Manchester, UK. Neotype is an isolated tooth, SME 4721, from Longton, Staffordshire, UK (Jeffery 2006), probably from the Moscovian Pottery Coalshales.

Best skull material. NEWHM G17.46 (tip of left maxilla), NEWHM G18.03 (postparietal), NEWHM G18.62 (right postparietal), NEWHM G18.77 (left postparietal), NEWHM G18.78 (left postparietal), NEWHM G18.93 (left postparietal), NEWHM G183.01 (?vomer), NEWHM G22.34 (left premaxilla), NEWHM G59.65 (parts of mandible and maxilla), NEWHM G59.66 (right mandible), NEWHM G7.17 (parts of mandible), NHM P364 (2) (cast of right premaxilla), NMS GY

1898.83.9 (right maxilla), NMS GY 1975.48.30 (left squamosal), NMS GY 1977.46.14 (operculum), NMS GY 1978.4.10 (dermopalatine), NMS GY 1978.4.16 (left post-parietal), NMS GY 1978.4.17 (right postparietal), NMS GY 1980.40.36 (complete juvenile specimen), NMS GY 1980.40.43 (opercular), NMS GY 1977.46.14 (lateral extrascapular), NMS GY 1980.40.44 (?lateral extrascapular), PMG 1329 (?vomer).

Diagnosis. Large rhizodontid with sigmoid tusks (a complete diagnosis and synonymy is given in Jeffery (2006)).

Occurrence. Abundant isolated remains are known from many localities in the UK and northern Europe. They are usually found in sediments formed in shallow freshwater environments, such as coalshales and freshwater limestones. Some material is also known from North America (e.g. Godfrey 1989) and Australia (e.g. Johanson *et al*. 2000; Parker *et al.* 2005). Specimens are known from the Ivorian stage of the Mississippian (Foulden; Andrews 1985) to the Kashirskian stage of the Pennsylvanian (e.g. Newsham; Boyd 1984).

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Genus **Rhizodus** Owen, 1840, p. 75
Type and only species. *Rhizodus hibberti* Owen, 1840.
Rhizodus hibberti Owen, 1840

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1835 *Megalichthys hibberti* Hibbert: 33 (parts only; see
    Andrews 1985).
1843 *Rhizodus ferox* Morris: 343.
1854 *Rhizodus gracilis* McCoy in Sedgwick & McCoy: 17.
1856 *Rhizodus angustus* Newberry: 99.
1856 *Rhizodus incurvus* Newberry: 99.
1888 *Rhizodus anceps* Newberry: 191.

Holotype. NMS GY 1950.38.63, an isolated dentary tusk from the Asbian Burdiehouse Limestone, Edinburgh, UK (see Thomson 1966; White & Baird 1967; Melville & China 1970).

Best skull material. NMS GY 1950.38.67 (mandibles and premaxilla), NMS GY 1894.183.30 (tip of left maxilla; but see below), PMG 140, 142 and 145 (part of a postparietal), NMS GY 1885.58.4 (principal gular), NHM P3321 (opercular).

Diagnosis. A large rhizodontid with dermal ornament comprising fine, vermiculating ridges. The tusks are lenticular in cross-section. The cleithrum bears a robust depressed posterior flange which rises to meet the post-branchial lamina dorsally (see Andrews 1985; Jeffery 1999, 2001).

Occurrence. Isolated remains (mostly teeth and scales) are known from many localities in the UK, usually from coal-shales or freshwater limestones. The material dates from the Holkerian stage (S2) of the Visean (e.g. Wardie Shales; Jeffery 2001) to the Brigantian stage (P2) of the Visean (e.g. Gilmerton Ironstone; see below). Specimens which may belong to *Rhizodus* have been recovered from the Pendleian (E1) Niddrie South Parrot Coalshale (but see below).

Some material is known from North America (e.g. Newberry 1888; Storrs & Holland 2009); the material described by Storrs & Holland (2009) is from the Chesterian of the Serpukhovian.

Descriptions

Screbinodus ornatus

Snout and cheek. The premaxilla is preserved on the right side of SME 4714 (Figs 1A, B (bone 'a'), 3A, B), although it has been flattened during fossilization. The bone is 'L' shaped and bears a row of small teeth. There is a larger tusk mesially, set slightly lingual to the tooth row ('premax. tusk', Fig. 3B). It has been only partially exposed, but appears to be of a similar size to the opposing symphysial tusk on the dentary. The mesial margin is relatively straight and vertical, and is deep linguolabially to accommodate the root of the tusk. It bears no obvious overlap or articulation surfaces for its antimere. Dorsally, a deep notch and terraced articulation surface provided firm attachment to a median rostral or rostral series (?art. med. rost, Fig. 3B; rostrals are not preserved in any specimen). A similar terraced articulation surface distally would articulate with the lateral rostral and anterior tectal (also not preserved in any specimen). There are surprisingly few lateral-line pores visible on the premaxilla; they are mostly clustered close to the ventral margin, but a few are visible near the dorsalmost tip. It is possible that the distortion of the bone has squashed many pores closed.

The left and right maxillae are visible in external view on SME 4714 (Fig. 4A, B) and the right maxilla is visible in internal view on NMS GY 1874.6 (Fig. 4C–E). It is a long bone, approximately triangular in shape, reaching its maximum dorsoventral depth at about halfway along its length, adjacent to the lachrymal–jugal suture. The ventral margin appears to bear the gentle undulations seen in many sarcopterygians. All but the posterior 10% of the bone bears a row of small teeth (NMS GY 1874.6 bears 48 teeth, the majority fully erupted). The dorsal surface is divided anteroposteriorly into four regions, representing articular edges with the lateral rostral (unknown in any specimen), the lachrymal, the jugal and the anterior portion of the quadratojugal (art. lat. rost., art. lach., art. jug. and art. quadr., respectively; Fig. 4B, D, I). The posterior three regions show little or no overlap surface, but anteriorly the articular region for the lateral rostral bears a large terraced articulation surface, matching similar surfaces on the premaxilla and lachrymal (see below). This implies
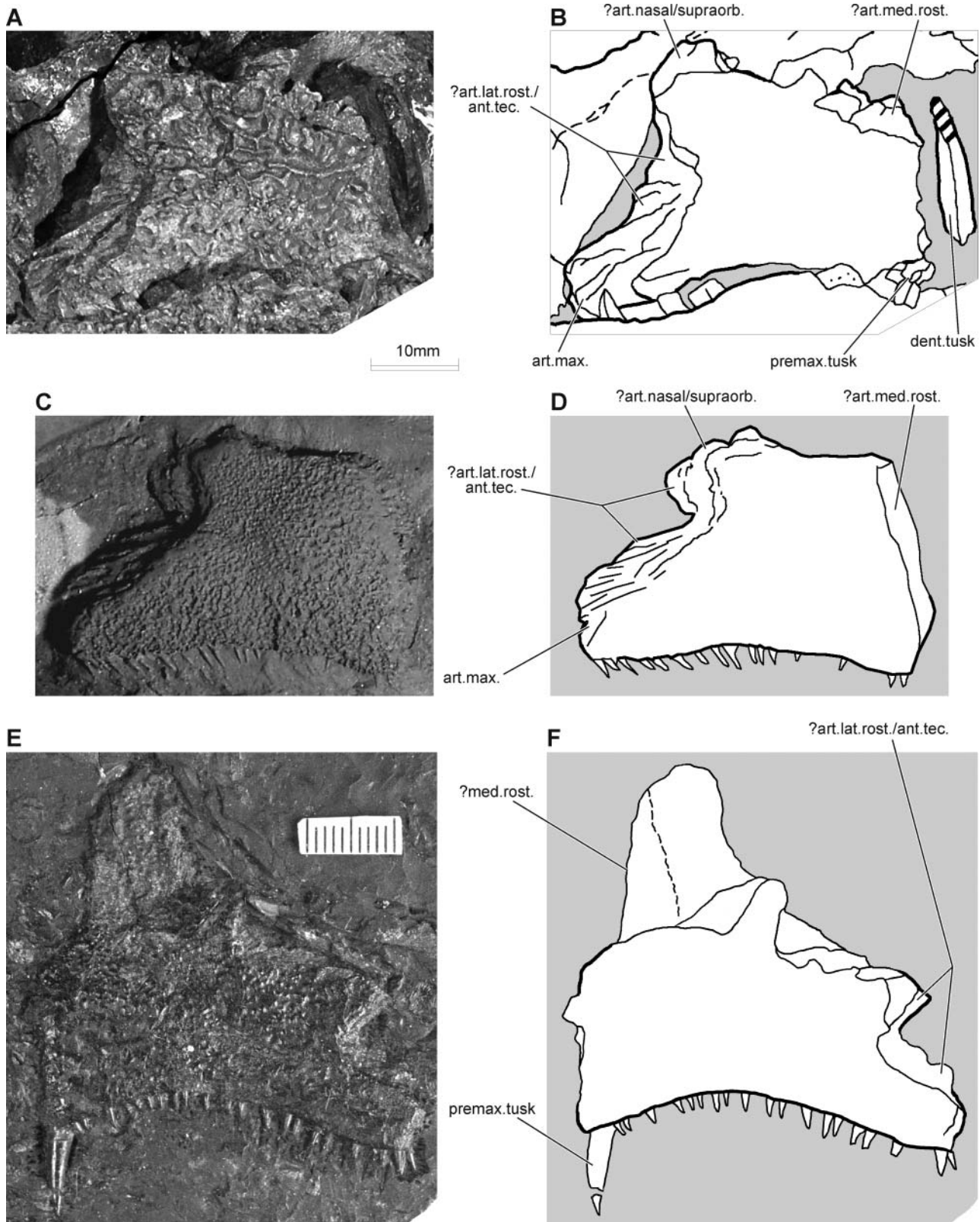
Figure 3. Premaxilla. **A, B,** right premaxilla of *Screbinodus ornatus*, SME 4714; photograph and interpretive sketch; **C, D,** right premaxilla of *Strepsodus sauroides*, NMS GY P364-2 (silicone cast of natural mould); photograph and interpretive sketch; **E, F,** left premaxilla of *Strepsodus sauroides*, NEWHM G22.34; photograph and interpretive sketch. Shading conventions as in Fig. 1.

an unusual degree of integration of the snout and cheek regions, although it is difficult to reconstruct this area precisely. The articular edge for the lachrymal also gives rise to a large dorsomedial process. The internal surface articulates with the posterolateral wall of the vomer, to form part of the fenestra exochoanalis (see below). The anterior tip of the maxilla bears a cluster of longitudinal ridges representing the articular surface with the premaxilla (art. premax; Fig. 4B, D, G, I). The internal face of the maxilla is divided longitudinally by a ridge for the articulation with the dermopalatine and ectopterygoid (ridge. art. palate; Fig. 4B). This groove becomes much more pronounced anteriorly, forming a horizontal ledge. Near the anterior tip of the maxilla it rises to join the dorsomedial process. The base of the process bears an extremely rugose articulation surface for the vomer. On both SME 4714 and NMS GY 1874.6 the anterior face of the process has a shallow fossa (choan. foss. max; Fig. 4D). This would probably align with a fossa on the vomer to form an enclosed choanal channel connecting the fenestra exochoanalis to the olfactory bulbs (see below).

The lachrymal is only clearly visible on the left side of SME 4714 (Fig. 5A–C). A cross-section (visible along a break in the specimen) confirms that the lachrymal and maxilla abutted without overlap. However, anteriorly there is a robust overlap surface with longitudinal ridges for the lateral rostral (art. lat. rost.; Fig. 5C), diverging slightly from a matching surface on the maxilla. The anterodorsal margin shows no overlap surfaces, but is slightly bevelled on its internal face, so it may have been overlapped internally by the anterior tectal (unknown in any specimen). Part of the anterodorsal margin represents the ventral margin of the orbit (orb. marg.; Fig. 5C). It contacts the jugal portion of the orbital margin at an acute angle, giving the orbit a distinct posteroventral 'corner'. The articulation (visible on the left side) includes interlocking embayments, but very little overlap (dors. art. jug and vent. art. jug; Fig. 5C). The lachrymal bears a few lateral line pores (from the infraorbital canal) running anteroposteriorly from the ventral lobe of the articulation with the jugal (and adjacent to the pores on the jugal) up towards the anterodorsal margin; these are only clearly visible under a microscope. Nothing is known of the anterior tectal or lateral rostral, although a small ornamented dermal bone is visible in section in a break in the specimen, which may represent one of these bones.

The jugal is preserved on both sides of SME 4714 (Fig. 5D–G); it is a subrectangular bone, about twice as long anteroposteriorly as dorsoventrally. It appears to have simply abutted the quadratojugal, with little or no overlap. Part of its anteroventral margin is slightly concave and bevelled internally, making the bone very thin at its edge. This represents the posterior margin of the orbit (orb. marg.; Fig. 5E, G). The majority of the dorsal margin of the jugal is sharply bevelled to produce a narrow overlap surface for the postorbital (art. postorb.). However, anteriorly the

margin dips to meet the orbital. The apparent lack of a corresponding dip in the ventral margin of the postorbital (see below) suggests that this part of the jugal articulated with an additional bone (presumably the posterior supraorbital; art. post. sup.; Fig. 5E, G). Posteriorly the articulation with the squamosal (art. squam.; Fig. 5E, G) involved little or no overlap. A number of lateral line pores can be seen on the jugal on both sides of SME 4714 (as with the lachrymal, they are only clearly visible under a microscope). A field of pores runs anteroventrally from the margin adjacent to the squamosal to the articular margin for the lachrymal. A few pores are visible more dorsally, near the articular margin for the postorbital.

The postorbital is a roughly triangular bone, approximately equal in area to the jugal. A right postorbital is preserved on NMS GY 1963.16.18 (bone m; Fig. 2B) and a left postorbital is preserved on SME 4714 (l. postorb.; Fig. 5H–J). The overall proportions of the postorbital appear to be slightly different between SME 4714 and NMS GY 1963.16.18. The anterodorsal margin is divided into two roughly equal embayments, each with a large, dished overlap surface. These are likely to be for the supratemporal and intertemporal (art. suprat. and art. intert.; Fig. 5J). The ventral margin is obscured in both specimens but it appears to be fairly straight, matching the main dorsal margin of the jugal. However, as noted above, the anterior part of the dorsal margin of the jugal dips towards the orbit and there does not appear to be a corresponding dip on the ventral margin of the postorbital. This would imply that the postorbital did not form part of the margin of the orbit. Unfortunately, the preservation of the two postorbitals (and their slightly differing proportions) makes it difficult to establish the precise relationship between the jugal, postorbital and posterior supraorbital in this region. There are a number of lateral line pores visible on the postorbital on both specimens. In NMS GY 1963.16.18 they form a dense field on the anterior section of the bone.

The quadratojugal is a large trapezoidal bone (l. quadr. and r. quadr.; Figs 4D, 5J, M, P). It is preserved in association with the maxilla on both sides of SME 4714 (Fig. 1). On the right side the quadratojugal has ossified in two sections (r. quadr. 1 and 2; Fig. 5M, P), the two parts together making a unit of approximately the same shape as the single quadratojugal on the left. The anterior part has the articular surface with the maxilla (art. max.; Fig. 5P); the two bones appear to have simply abutted one another, with only a slight overlap. The articular surface for the jugal, visible on the right quadratojugal, is similarly slight (art. jug.; Fig. 5J). Although it is partly obscured by other bones, the posterior margin of the quadratojugal shows some bevelling, and a reduction of the dermal ornament, presumably for contact with the preopercular.

The right squamosal is preserved in natural association with the other cheek bones on SME 4714 (Fig. 6A, B) and NMS GY1963.16.18 (Figs 2B, 6E, F) and in isolation in
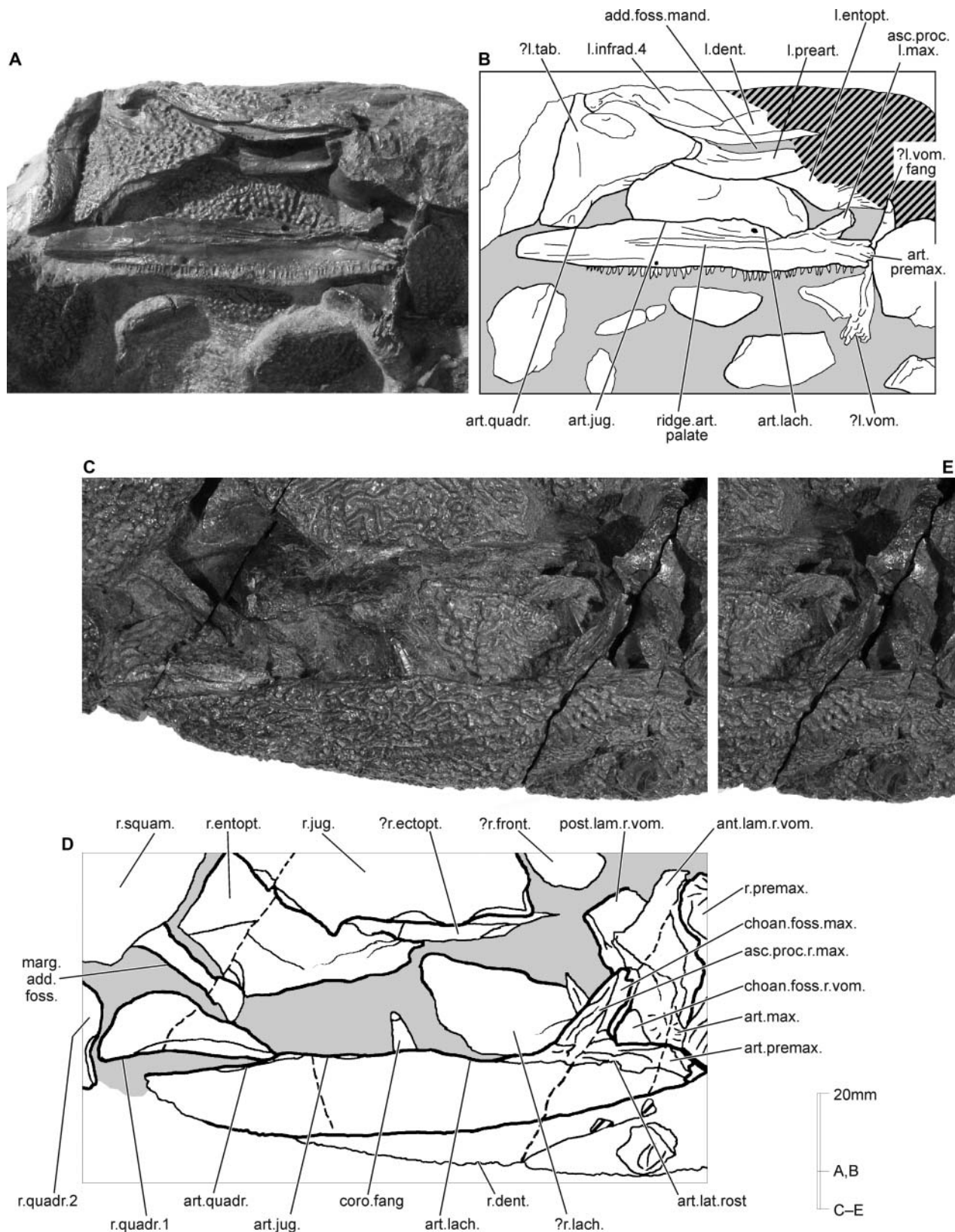
Figure 4. Maxilla. **A, B,** right maxilla, parts of the cheek and vomer of *Screbinodus ornatus*, SME 4714; photograph and interpretive sketch; **C, D,** left maxilla and scattered skull bones of *Screbinodus ornatus*, NMS GY 1874.6; photograph and interpretive sketch (anterior is to the right); **E,** tip of right maxilla and vomer of *Screbinodus ornatus*, NMS GY 1874.6; stereopair matching part of C, showing details of ascending process of the maxilla and the vomer; **F, G,** tip of right maxilla of ?*Rhizodus hibberti*, NMS GY 1894.183.30; photograph and interpretive sketch. **H, I,** right maxilla of ?*Strepsodus sauroides*, NMS GY 1898.83.9; photograph and interpretive sketch. Shading conventions as in Fig. 1.
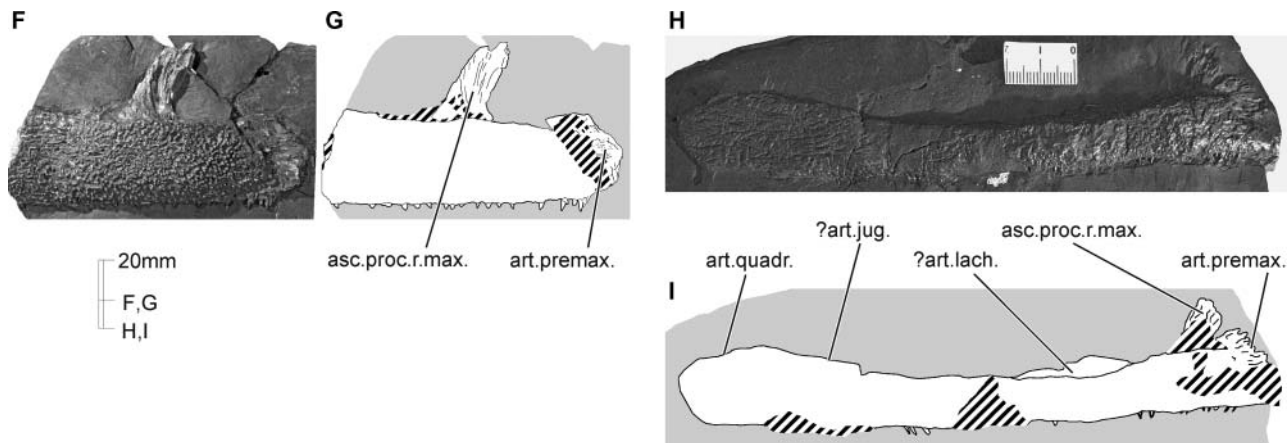
Figure 4. Continued.

NHM P29286 (Fig. 6C, D; note that most of the margins of this bone are damaged, making interpretation difficult). The squamosal is a trapezoidal bone, about twice as tall dorsoventrally as anteroposteriorly. The ventral margin is fairly straight, to articulate with the dorsal margin of the quadratojugal. There is no evidence of any overlap; they appear to abut squarely. The squamosal bears a distinct, depressed overlap surface anterodorsally, probably for the postorbital. There is a deep embayment posteroventrally, bevelled internally, probably the articular surface for the preopercular (poorly known in most rhizodontids). A possible preopercular is visible on SME 4714, but it is almost entirely overlain by the squamosal and quadratojugal. As in most sarcopterygians, the squamosal carries part of the preopercular lateral line canal, running nearly horizontally in a broad swathe from the anteroventral margin to the embayment for the preopercular. A pitline crosses this swathe on NHM P29286 and NMS GY 1963.16.18.

Parietal shield. A pair of bones on SME 4714, which may be the left and right parietals (?l. par. and ?r. par.; Fig. 7C), lie on either side of the midline of the specimen, separated by fragments of the braincase (see below). They are anterior and medial to the jugals and postorbitals. The identification of these bones is largely based on their size; they are too large to be nasals, intertemporals or rostrals, and the presence of lateral line pores make them unlikely to be supraorbitals. They are also similar in size and shape to the parietals of *Barameda michelli* and *Gooloogongia* (though slightly more rounded). However, the identification remains tentative, because no pit-lines are visible (cf. *Barameda michelli*, Long 1989; and *Gooloogongia*, Johanson & Ahlberg 2001), and there is no clear pineal foramen. However, a shallow depressed area by the mesial margin of both bones (?pin.; Fig. 7C) may represent the region surrounding a pineal foramen, similar to that seen in *Barameda michelli* (Fig. 16C). As preserved, the left

parietal is overlain by another dermal bone anteriorly (see below), and by a braincase ossification anterolaterally, although enough of it is clearly visible to reconstruct the course of the obscured margins. The right parietal is overlain posterolaterally by the right jugal. There are no overlap surfaces apparent and the bone appears to be quite thick. If these bones are parietals they could not have articulated closely with the postparietals; the dermal intracranial joint would have been widely open (i.e. closed only by connective tissue), suggesting a degree of skull kinesis.

A third bone lies anterior to (and partly covers) the possible left parital (indet.; Fig. 7C). It is rounded, with its long axis being nearly twice as long as its short axis. The lateral margin is bevelled into a slightly rugose overlap surface, but the other margins show no sign of overlap. A lateral line canal runs between the anterior and posterior margins. Only a few pores are visible, but a break in the specimen reveals a canal just before the anterior margin. The presence of pores makes it unlikely to be a supraorbital or tectal. It is too small to be an intertemporal (based on the size of bone suggested by the relationship between the postorbital and supratemporal) and its shape makes it unlikely to be a nasal. It is, perhaps, one part of a compound intertemporal, or an irregular bone from the snout.

Postparietal shield. The postparietal shield of *Screbinodus* is best seen in NMS GY 1963.16.18 (Fig. 2A, B). Andrews (1973) produced a reconstruction using this specimen but did not figure the original material, nor give a detailed description of it. A second specimen, NMS GY 1998.28.1, previously undescribed but rather similar, confirms much of the detail of NMS GY 1963.16.18 (Fig. 2C, D). The shield is similar to those of other stem-tetrapods. The postparietals are flanked by the supratemporal and the tabular. On NMS GY 1963.16.18 these bones are articulated on the right side of the specimen, and lying in close association on the left side. There is no extratemporal in *Screbinodus*.
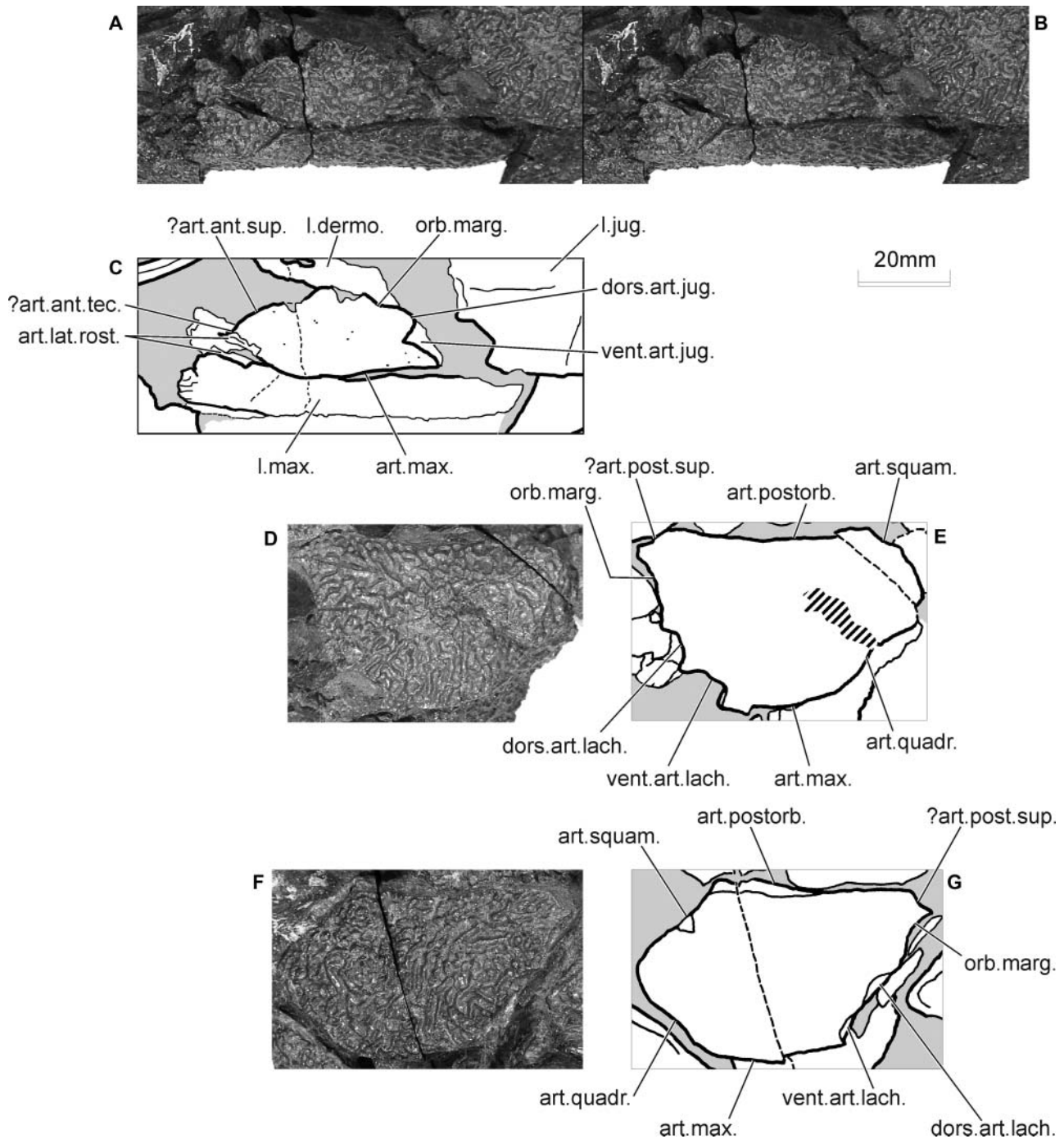
Figure 5. *Screbinodus ornatus*, cheek bones of SME 4714. The bones are disarticulated, but preserve their natural relationships. **A, B,** stereopair of the left lachrymal (anterior is to the left); **C,** interpretive sketch of A and B (dots mark the position of sensory pits); **D, E,** photograph and interpretive sketch of the left jugal (anterior is to the left); **F, G,** photograph and interpretive sketch of the right jugal (anterior is to the right); **H, I,** stereopair of posterior part of left cheek in lateral view (anterior is to the left); **J,** interpretive sketch of H and I; **K, L,** stereopair of posterior part of right cheek in lateral view (anterior is to the right); **M,** interpretive sketch of K and L; **N, O,** stereopair of the right anterior quadratojugal and parts of the palate in median view. This shows the same region to K and L, but from median view (anterior is to the left). **P,** interpretive sketch of N and O. Shading conventions are the same as in Fig. 1; dots mark the position of sensory pits.
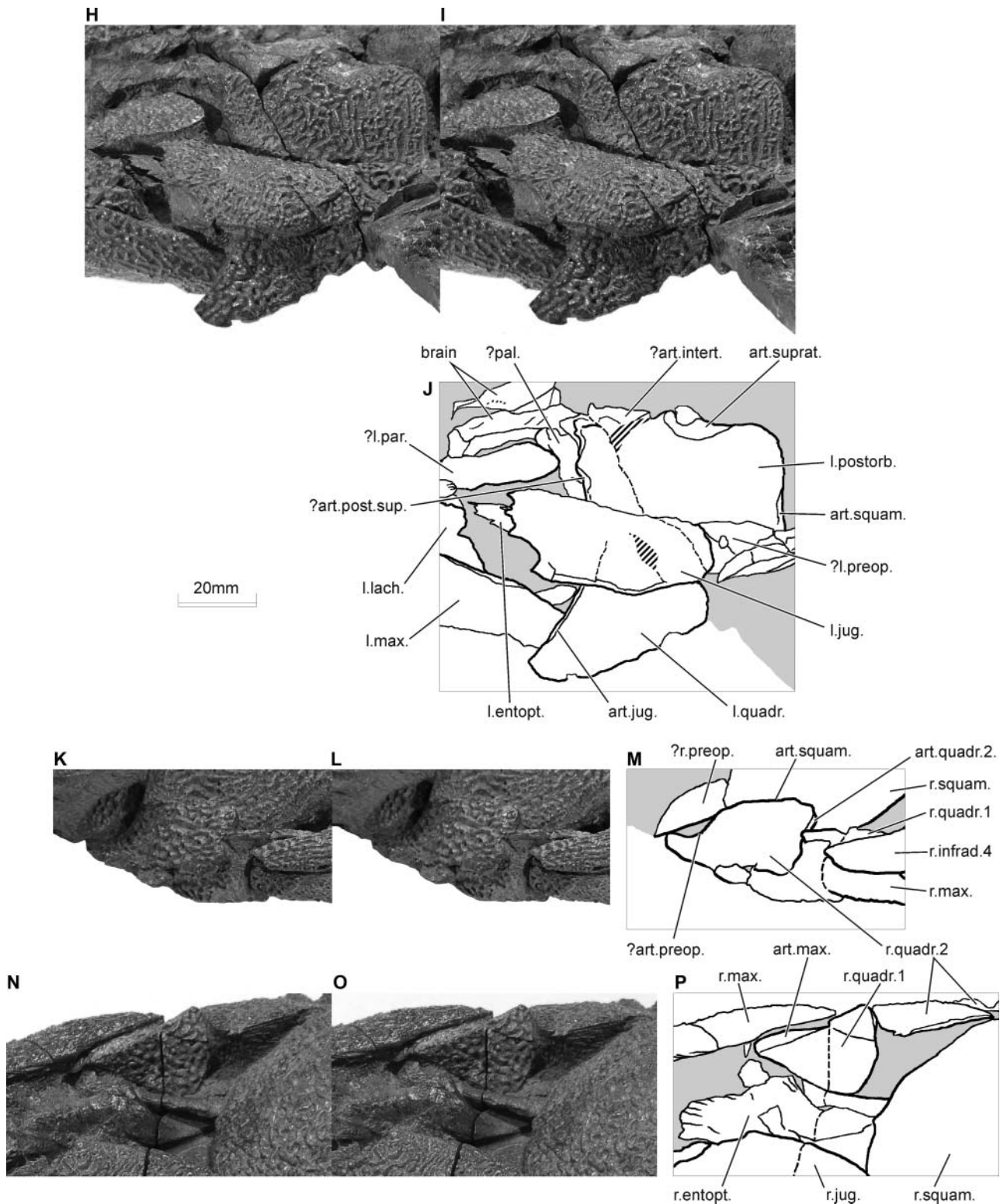
Figure 5. Continued.

The median articulation between the postparietals is very straight, with no bevelling or reduction of the ornament, so that it is difficult to follow its course in articulated specimens. Isolated right postparietal NMS GY 1972.28.1 shows

a small overlap surface posteriorly for its antimere (overlap antim.; Fig. 8B). It lies internal to (and is sharply differentiated from) the median edge of the bone. At the lateral margin there is an overlap surface for the tabular, but the
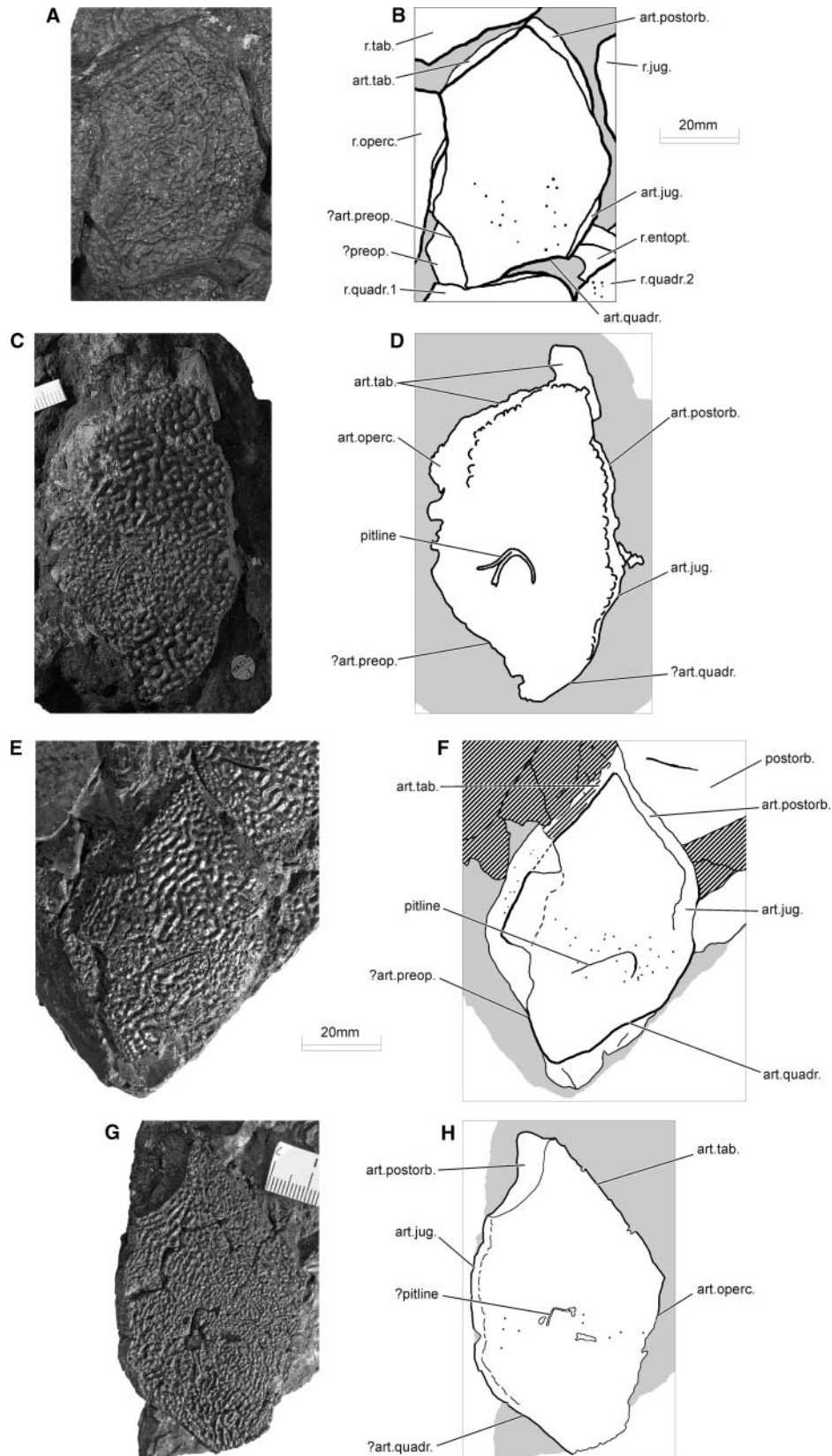
Figure 6. *Screbinodus* squamosals. **A, B,** right squamosal of *S. ornatus*, SME 4714; photograph and interpretive sketch; **C, D,** right squamosal of *S. ornatus*, NHM P29286; photograph and interpretive sketch; **E, F,** right squamosal of *S. ornatus*, NMS GY 1963.16.18; photograph and interpretive sketch; **G, H,** left squamosal of *S. sauroides*, NMS GY 1975.48.30; photograph and interpretive sketch. Shading conventions as in Fig. 1; dots mark the position of sensory pits.
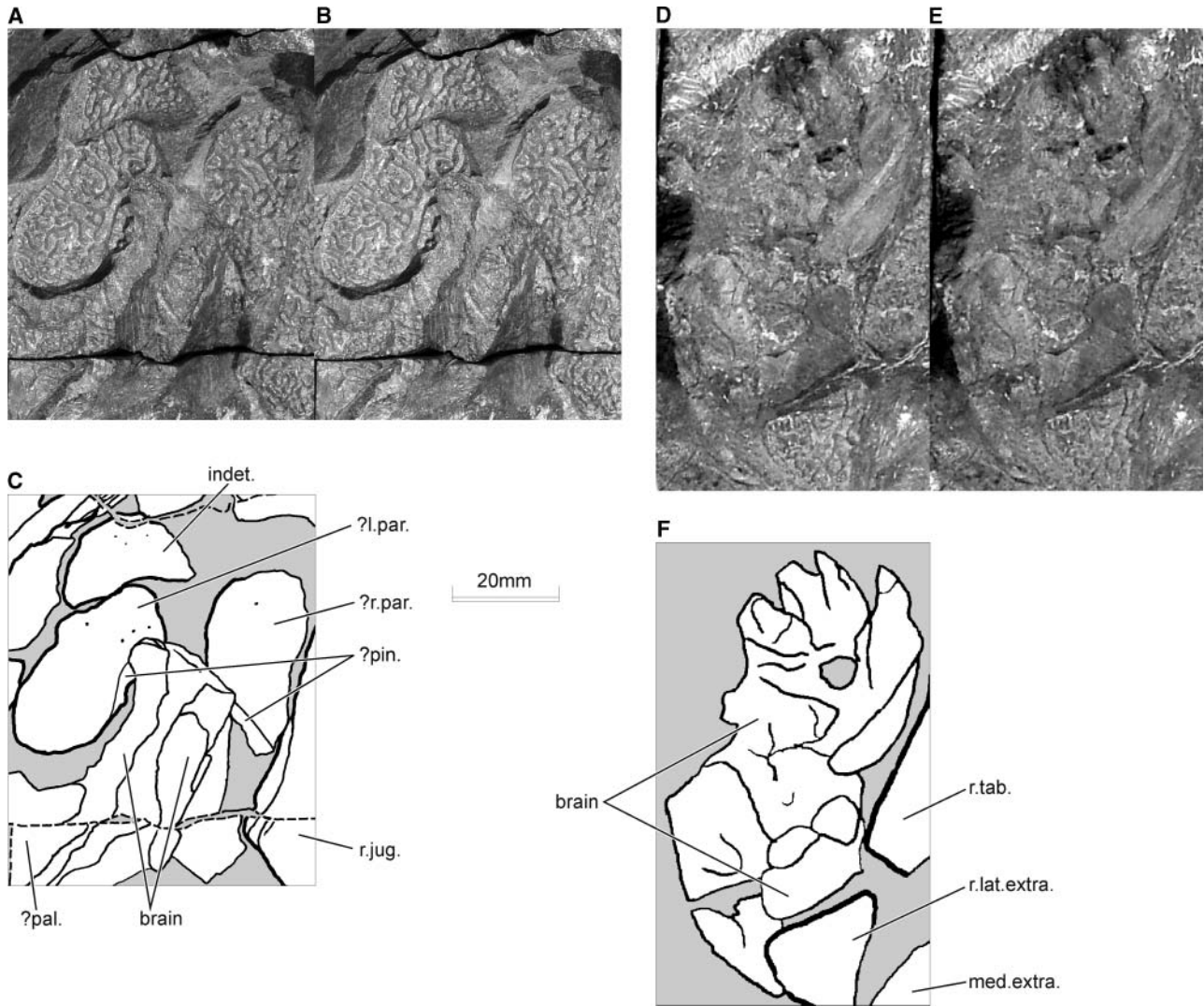
Figure 7. Possible parietal shield and braincase fragments of *Screbinodus ornatus*, SME 4714. **A, B,** stereopair of possible parietals and parts of the ethmosphenoid unit; **C,** interpretive sketch of A and B; **D, E,** stereopair of possible parts of otoccipital unit. **F,** interpretive sketch of D and E. Shading conventions as in Fig. 1.

supratemporal abuts without overlap. Posteriorly, the angled articulation with the lateral extrascapulars and the short articular edge for the median extrascapular (see Figs 2A, B, 8A, B) gives the postparietal a distinctive 'tail', seen in other rhizodontids: *Gooloogongia* (Johanson & Ahlberg 2001; Fig. 16B), *Barameda mitchelli* (Long 1989; Fig. 16D) and *Strepsodus* (Jeffery 2006).

The supratemporal has a complex shape. The lateral margin is concavely curved, to articulate with (and overlap) parts of the anterodorsal margin of the postorbital (bones c and d; Fig. 2B, D). The probable orientation of the postorbital and supratemporal (see Fig. 21) suggests that the intertemporal may have had a curved, oblique articulation with the supratemporal, similar to that seen in *Barameda* (Fig. 16C).

The tabular is a large, quarter-circular bone (bones e and f; Figs 2B, D, 9). On the left tabular of NMS GY 1963.16.18 and the right tabular on NMS GY 1998.28.1, the anterolateral margin follows a smooth arc; on the right tabular of NMS GY 1963.16.18 it seems to be less smoothly curved. There are no clear overlap surfaces laterally, although a slight bevelling of the margin may be to allow the squamosal to overlap it. There is no evidence of a suture across the lateral section of the left tabular of NMS GY 1963.16.18 as suggested by Andrews (1973); she appears to have been misled by a cluster of lateral line pores. There is no extratemporal in *Screbinodus* although the tabular is similar in size to the combined area of the tabular and extratemporal in *Gooloogongia* and *Barameda* (see Fig. 16).
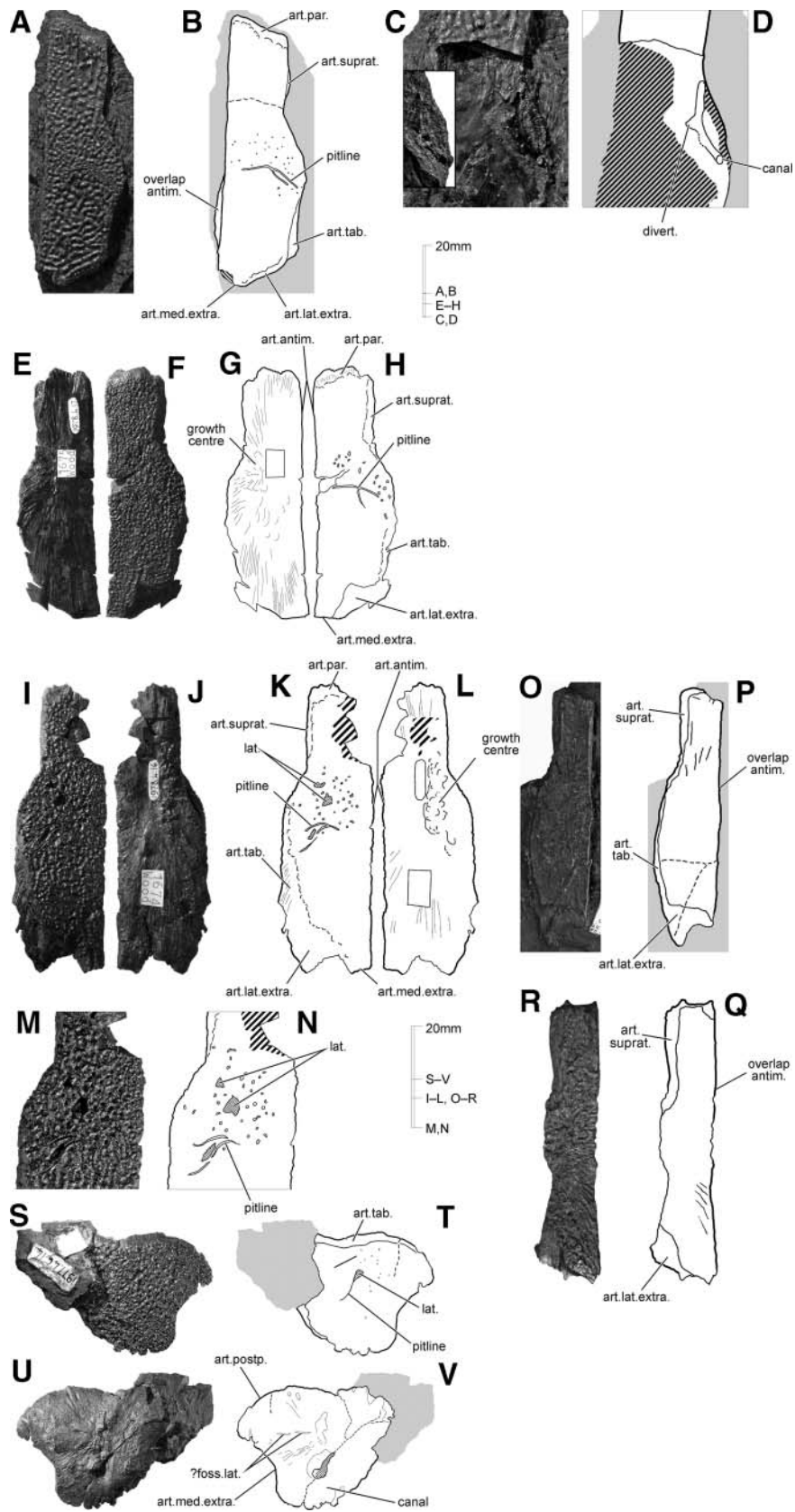
Extrascapular series. The median and lateral extrascapulars form a smoothly curved posterior margin to the skull (Fig. 21). The median extrascapular is poorly preserved in NMS GY 1963.16.18 (bone h; Fig. 2B) and SME 4714 (Figs 10I, J); in both it is overlain by the lateral extrascapulars. However, it is preserved in isolation in several specimens (Fig. 10A–H). It is a roughly quarter-circular bone, becoming very thin along the curved posterior margin.

The lateral extrascapulars are best visible on NMS GY 1963.16.18 (bones g and i; Fig. 2B), although they are also present on NMS GY 1998.28.1 (bones g and i; Fig. 2B) and SME 4714 (bones o and p; Fig. 1C). They are quite large triangular bones and have a long, straight anterior margin which is slightly bevelled for the overlap of the tabular. More medially, there is a short anteromedial margin, not well preserved on any specimen. However, on NMS GY 1963.16.18 it does not appear to be bevelled, suggesting that it simply abutted the posterior margin of the postparietal. The overlap relationships of the extrascapulars (laterals overlapping median) are of the pattern seen in actinistians and onychodonts, as well as other stem-tetrapods.

There are many pit-lines and lateral line pores over the postparietal shield and extrascapular series (Figs 2, 21). The lateral line canals broadly correspond to the 'H' pattern thought to be primitive for osteichthyans (e.g. Forey 1998, p. 91 and references therein). However, in *Screbinodus* the exact course of the underlying canals is rarely obvious as the surface pores are widely spread, presumably reflecting a complex branching pattern of canaliculae. In several areas the pores are associated with deep fossae in the bone. These fossae show no pores on their base, but are always associated with one or two foramina running laterally into the surrounding bone (lat.; Fig. 8K, N). They do not appear to be caused by post-mortem decay or damage to the bone as they are always lined with smooth bone (e.g. NHM P36912; Fig. 10G, H; and NMS GY 1963.16.18; Fig. 2A, B); they are possibly the result of periodic bone resorption. Pores of the otic lateral line canal run anteriorly from the lateral extrascapular onto the tabular. A wide swathe of pores runs across the tabular from its posterolateral corner diagonally to the anterior section of the medial margin. The canal enters the postparietal just posterior to the point of its greatest mediolateral width, although the kinked course of the otic canal through the postparietal is not as clear as suggested by Andrews (1973, Fig. 2d). Postparietal NMS GY 1972.28.1
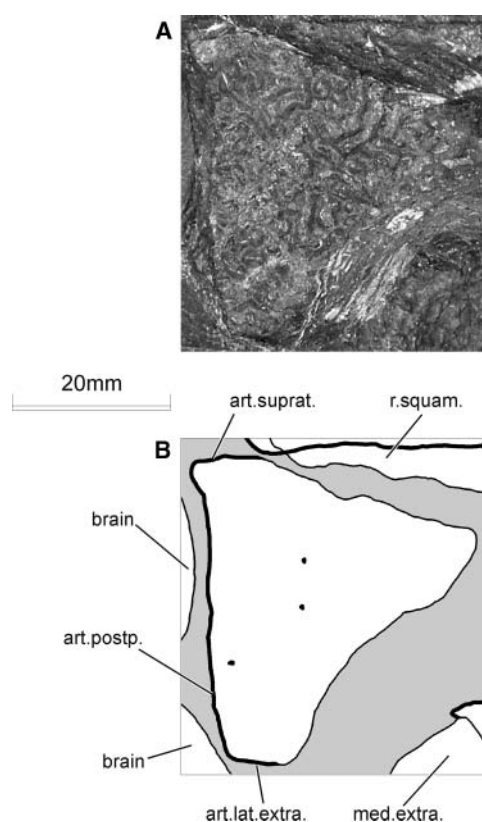

Figure 9. *Screbinodus ornatus*, right tabular of SME 4714; **A,** photograph; **B,** interpretive sketch.

shows part of the actual canal across a break in the specimen (Fig. 8C, D). It appears to take quite a short loop from the tabular to the supratemporal; more medial pores are connected to a medial diverticulum (divert.; Fig. 8C, D).

Palate. SME 4714 shows all the dermal bones of the palate (vomers, dermopalatines, entopterygoids and ectopterygoids) in internal view (Figs 1A–C, 12D–I). Unfortunately, almost all the bones are covered to some degree by cheek or jaw bones. NMS GY 1874.6 (Fig. 12A–C) shows parts of both vomers, a single ectopterygoid and a fragment of the left entopterygoid. No endoskeletal bone is visible, suggesting that bones such as the pterygoquadrate and autopalatine were not ossified (a similar situation is seen with the Meckelian cartilage on the mandible of *Screbinodus* and *Rhizodus*; see Jeffery 2003).

Figure 8. Postparietals and lateral extrascapular of *Screbinodus*. **A, B,** right postparietal of *S. ornatus*, NMS GY 1972.28.1; photograph and interpretive sketch; **C,** detail of NMS GY 1972.28.1 with part of bone removed to show the course of the lateral line canal (inset shows counterpart in mirror image for comparison); **D,** interpretive sketch of C; **E, F,** right postparietal of *S. sauroides*, NMS GY 1978.4.17 in internal and external views; **G, H,** interpretive sketches of E and F; **I, J,** left postparietal of *S. sauroides*, NMS GY 1978.4.16 in internal and external views; **K, L,** interpretive sketches of I and J; **M,** detail of NMS GY 1978.4.16 to show lateral line canals and pit-lines; **N,** interpretive sketch of M; **O, P,** left postparietal of *S. sauroides*, NEWHM G18.78; photograph and interpretive sketch; **Q, R,** left postparietal of *S. sauroides*, NEWHM G18.93; photograph and interpretive sketch; **S–V,** left lateral extrascapular of *S. sauroides*, NHM GY 1977.46.14; photograph and interpretive sketch of the external surface (S, T); photograph and interpretive sketch of the internal surface (U, V). Shading conventions as in Fig. 1, plus stippled area = areas of deep shadow.

The vomers on SME 4714 (Fig. 12D–I) are both overlain by a number of bones. Those of NMS GY 1874.6 (the holotype; Fig. 12A–C) are still deeply embedded in matrix. What is visible is very similar to a well-preserved vomer of uncertain affinities from Cowdenbeath (NMS GY 1975.5.9; Fig. 11; described in detail below). The tusks (protruding between the gulars and submandibulars on the ventral side of SME 4714; r. and l. vom. fang; Fig. 1J) are roughly equal in size to the coronoid and dermopalatine fangs. They are straight (i.e. not recurved) and bear two carinae. The right vomer appears to have a single small marginal tooth on its lateral margin (clearly visible only under a microscope), although the extent of any tooth row, if present, is obscured by an overlying gular. The dorsal surface is strongly concave, so that its anterior edge takes the form of a raised dorsal lip (ant. lam. r. vom.; Figs 4D, 12D). A semicircular embayment forming the dorsal tip of the choanal fossa is clearly visible dorsally (choan. foss. l. vom. and choan. foss. r. vom.; Figs 4D, 13C, I). Along the posterior edge of the dorsal surface there is a large vertical lamina, almost as tall as the rest of the vomer (excluding the fang; post. lam. l. vom. and post. lam. r. vom.; Figs 4D, 12C, F). This probably strengthened the postnasal wall of the braincase (apparently not ossified in *Screbinodus*), helping to support the anterior end of the palate. This lamina is clearly visible on both sides of SME 4714, and on one of the vomers on NMS GY 1874.6.

The dermopalatine is best seen on the left side of SME 4714 (l. dermo.; Fig. 12F). It is approximately twice as long anteroposteriorly as mediolaterally. Its lateral margin is fairly straight, although the left lachrymal covers the most posterior sections. There is a mesial flange anteriorly, making the bone 'L' shaped overall. The posterior and mesial margins bear large, terraced surfaces for the overlap of the entopterygoid (which lies nearby; l. entopt.; Fig. 12F), and anteriorly the medial lamina overlapped the most anterior parts of the entopterygoid. This complex overlap relationship between the two bones must have given a very firm connection in life. The anterior margin of the dermopalatine is quite ragged, with no clear articulation surface for the vomer. A slight notch where the anterior and lateral margins meet presumably marks the posterior margin of the fenestra exochoanalis. The internal face is quite smooth, with a large foramen to receive one of the coronoid fangs from the mandible (foss. coro.; Fig. 12F). The bone bevelled to become very thin anteriorly, at the margin of the fenestra exochoanalis. On SME 4714 a break in the specimen reveals a section through the dermopalatine and exposes a small section of the buccal face. This face is smooth, with little marginal dentition laterally, except for a large fang (equivalent in size to the coronoid fangs, with similar carinae) and possibly its replacement twin.

Both ectopterygoids are visible on SME 4714, but are almost entirely overlain by other bones (e.g. ?r. ectopt.; Fig. 4D). However, a single ectopterygoid is visible in lateral view on NMS GY 1874.6 (Fig. 12A–C). It is not possible to say which side it belongs to as this bone is fairly symmetrical and the specimen is completely disarticulated. It is about half the anteroposterior length of the dermopalatine. A deep horizontal groove runs along the lateral face of the bone, which would articulate well with the horizontal ridge on the medial face of the maxilla, to secure the palate against the cheek (art. max; Fig. 12C). The dorsal part of the lateral face is rugose. The ventral part is smooth, presumably representing the part of the lateral face exposed in the buccal cavity. It bears a single fang, similar in size to that of the dermopalatine and bearing two carinae, in an oversized socket shared with its replacement twin. There does not appear to be any other dentition. The small part of the dorsal surface of the ectopterygoid visible on the right side of SME 4714 does not appear to be any wider mediolaterally than the width of the fang socket. It is also very tapered anteriorly, and could not have met the dermopalatine with a broad transverse articulation as is primitive for osteichthyans (e.g. Gardiner 1984, p. 306). It may even have sat lateral to both the entopterygoid and the posterior parts of the dermopalatine (an unusual arrangement in sarcopterygians). The medial margin is curved slightly, which may be part of a foramen to receive a coronoid fang, as in some porolepiforms (e.g. Glyptolepis groenlandica; Jarvik 1980, fig. 189). However, the lack of any clear continuation of this curvature onto the dermopalatine makes this unlikely.

The entopterygoid is by far the largest bone of the palate, and is best visible on SME 4714 (bone d and r. entopt.; Fig. 1C; r. entopt.; Fig. 4C–E; l. entopt.; Fig. 12D). However, even on this specimen most of the posterior and medial parts of the bone are overlain by the cheek bones. The anterior margin has a complex shape, closely matching the posterior margin of the dermopalatine (art. entopt.; Fig. 12F). The lateral margin cannot be completely traced, but it appears to be quite ragged and slightly curved (to match the curvature of the cheek). Its relationship with the ectopterygoid is not clear, as the medial face of the ectopterygoid is unknown. For the most part, the dorsolateral (visceral) face of the entopterygoid is smooth and flat, but posteriorly it twists to form the vault of the buccal cavity. The right entopterygoid of SME 4714 (marg. add. foss.; Fig. 4D) and the left entopterygoid of NMS GY 1874.6 (l. entopt.; Fig. 4B) show a lateral embayment, edged with thickened bone, marking the anterior part of the subtemporal fossa. A small amount of preparation of the buccal face on SME 4714 was possible near the posterior margin of the bone, along one of the diamond-wire cuts in the specimen. It appears to be covered in many small denticles. Part of the left entopterygoid on SME 4714 is closely associated with part of the braincase (see below). It is presumably a dermal process associated with the (?unossified) processus ascendens. Unfortunately, the bones are crushed together and

partly obscured by the postorbital, so it is hard to distinguish the division between the entopterygoid and the braincase.

Operculogular series. The operculogular series is best seen in *Screbinodus* in SME 4714 (Figs 1D–F, H–J, 14G–K, 15A–E), in which the ventral surface is more or less undisturbed. The submandibulars, gulars, opercular and branchiostegals are visible, although the gulars and submandibulars were originally prepared with a hammer and chisel sometime before 1875 (cf. Miall 1875; Fig. 1G), and have been damaged in the process and by subsequent storage. Some other isolated operculars and gulars are also known (Figs 14, 15).

There are two large principal gulars covering most of the space between the mandibles (bones q and r; Fig. 1F; l.; r. princ. gul.; Fig. 1J), and a single, smaller median gular anteriorly (med. gul.; Fig. 1F, J). Between these and the mandibular rami is a row of submandibular bones. The opercular on each side is linked to the ventral sections of the operculogular series by a large branchiostegal bone (l. and r. branch; Figs 1F, 14G–J). Anteriorly, the median margins of the principal gulars are separated by an anamestic bone, roughly oval in shape, which overlaps them both externally (anamest. gular; Fig. 1F, J). Another narrow anamestic bone bearing a thin line of dermal ornament separates the two principal gulars further posteriorly. However, NHM P47718, an isolated *Screbinodus* right principal gular partly exposed in internal view, bears a convexly curved medial margin, implying uninterrupted overlap with its antimere (Fig. 14C–F). A shallow, straight ridge a short distance lateral to the medial edge appears to mark the true midline of the body and the extent of the overlap (art. antim.; Fig. 14E). The exact course of the lateral margin of both principal gulars of SME 4714 is indistinct posteriorly due to damage and some overlying submandibulars. However, anteriorly it follows a shallow convex curve, matching that of the mandibles.

The median gular slightly overlaps the anterior tips of the principal gulars. Part of the articulation surface is visible on the right principal gular on SME 4714 and on isolated gular tip NMS P3322b (Fig. 14A–C). It bears a very fine ornament. The broad submandibular series is best visible on the left side of SME 4714 (Fig. 1D–F, G–J), overlapping the gulars externally. It cannot be ascertained if the median
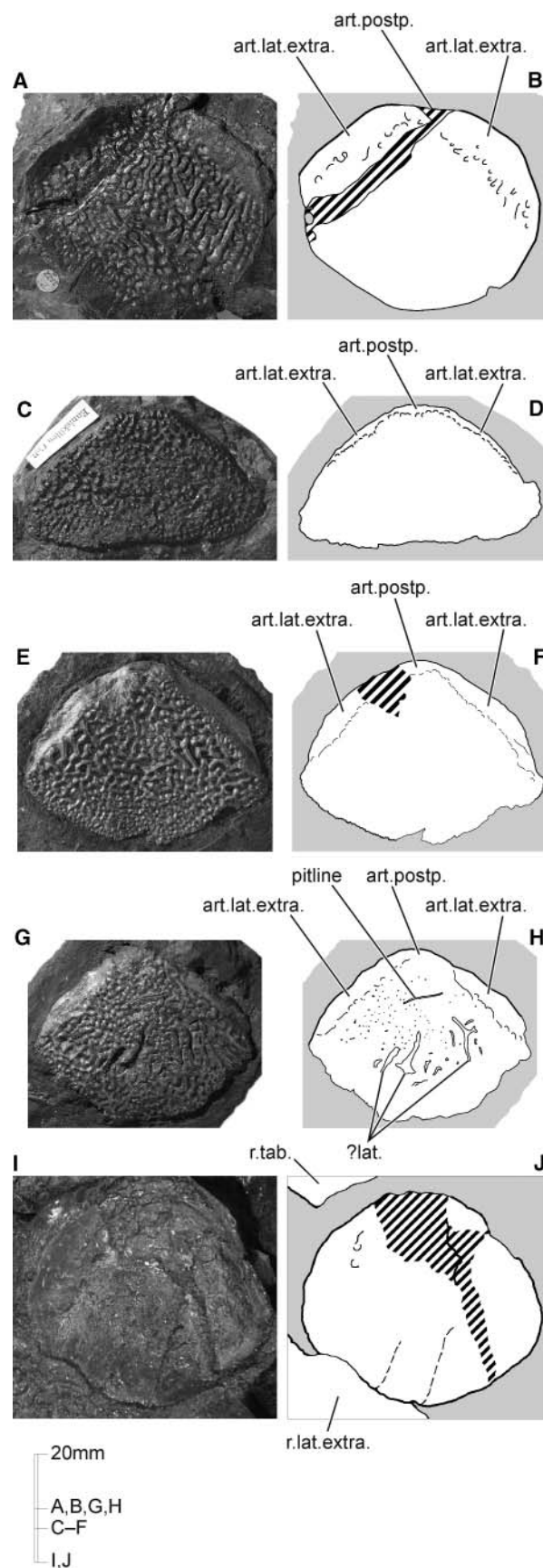

Figure 10. *Screbinodus ornatus*, median extrascapular. **A, B,** median extrascapular of NHM P3322a; photograph and interpretive sketch; **C, D,** median extrascapular of NHM P3322; photograph and interpretive sketch; **E, F,** median extrascapular of NMS GY 1876.20.2; photograph and interpretive sketch; **G, H,** median extrascapular of NHM P36912; photograph and interpretive sketch; **I, J,** median extrascapular of SME 4714; photograph and interpretive sketch in internal view. Shading conventions same as in Fig. 1; dots mark the position of sensory pits.

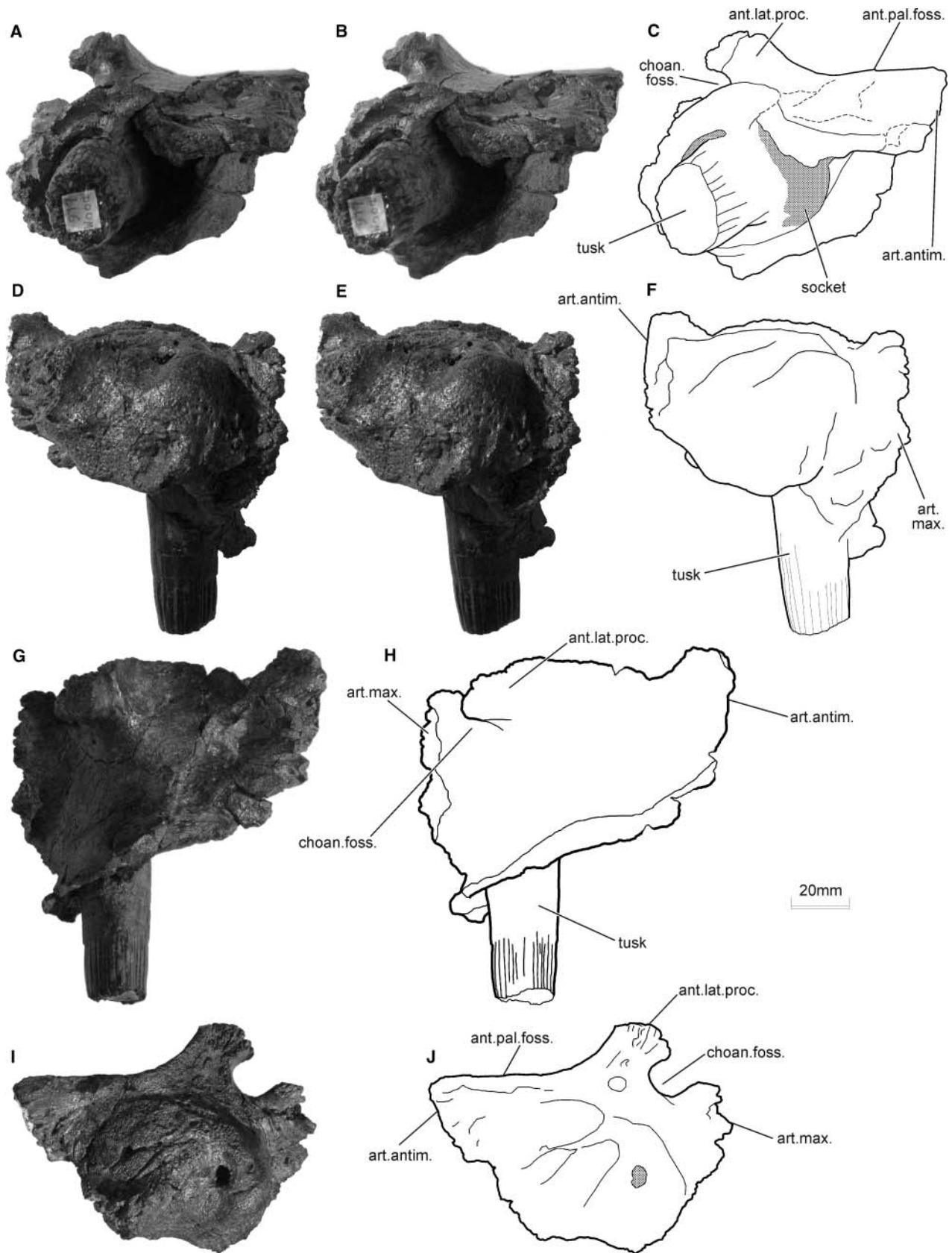**Figure 11.** Rhizodontid indet., very large right vomer, NMS GY 1975.5.9. **A, B,** stereopair in ventral view; **C,** interpretive sketch of A and B; **D, E,** stereopair in posterolateral view; **F,** interpretive sketch of D and E; **G, H,** photograph and interpretive sketch in anterior view; **I, J,** photograph and interpretive sketch in dorsal view. Shading conventions same as in Fig. 8.

gular contacted the mandibles anteriorly, or whether the relatively large first submandibulars met at the midline (as in porolepiforms; Jarvik 1972). The principal gulars bear a smooth, bevelled overlap surface for them along their lateral margins. There are probably seven submandibulars on each side, although this is uncertain due to damage to the specimen. The ?sixth and ?seventh submandibulars are markedly wider mediolateral than the anterior submandibulars, and have a deeper overlap with the principal gulars.

The opercular is preserved on both sides of SME 4714 (Figs 1A–F, 15A–E), and several isolated examples are known (e.g. NHM P3322, P3322a, P36911 and P11540; Fig. 15F–M). It is oval in shape, with an aspect ratio of approximately 1 to 1.28, and its long axis is oriented vertically. The anteroventral margin is very slightly concave, producing an anteroventral 'notch'. The ornament is similar to that on other dermal bones, with tubercles and connecting ridges. However, the ridges are relatively longer and more
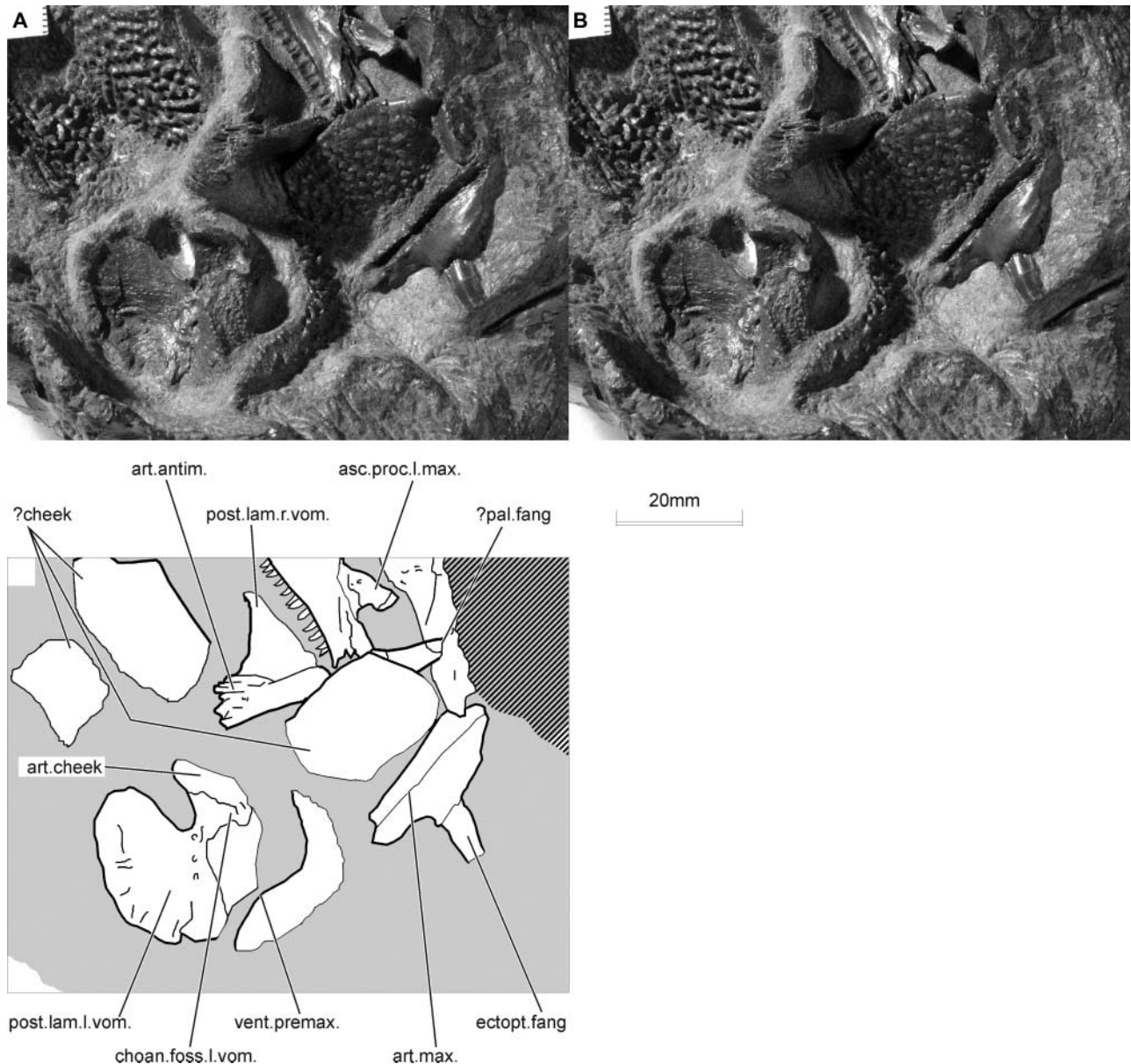

Figure 12. *Screbinodus ornatus*, bones of the palate. **A, B,** stereopair of vomers and ectopterygoid of NMS GY 1876.4; **C,** interpretive sketch of A and B; **D, E,** stereopair of vomers and ectopterygoid of SME 4714; anterior is to the top; the specimen is disarticulated but most bones are in dorsal/internal view; **F,** interpretive sketch of D and E; **G, H,** stereopair of vomers of SME 4714; view is similar to D and E but includes only anterior block of the specimen (separated along the crack marked ▶——◀ in Fig. 1); **I,** interpretive sketch of G and H. Shading conventions as in Fig. 1.
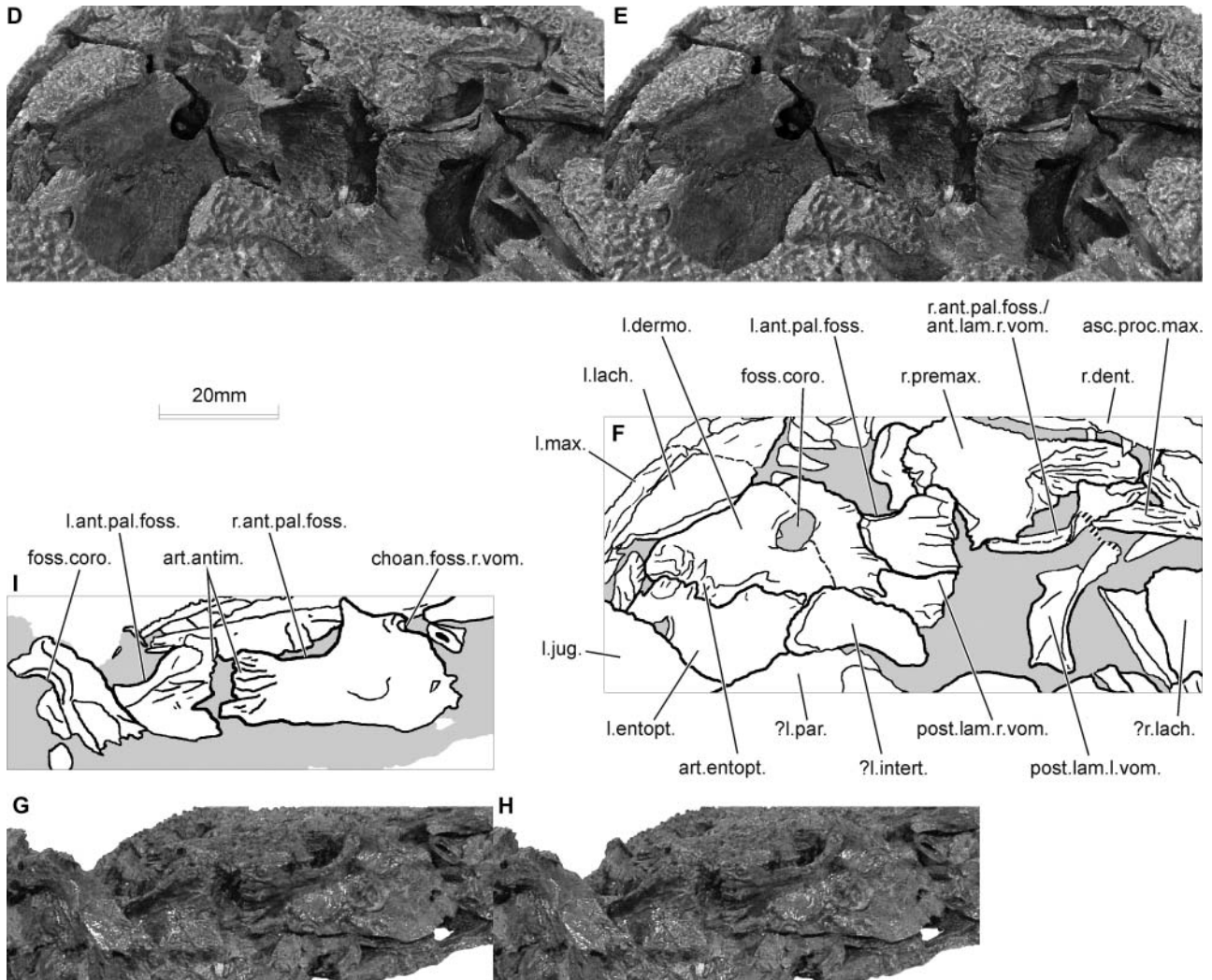
Figure 12. Continued.
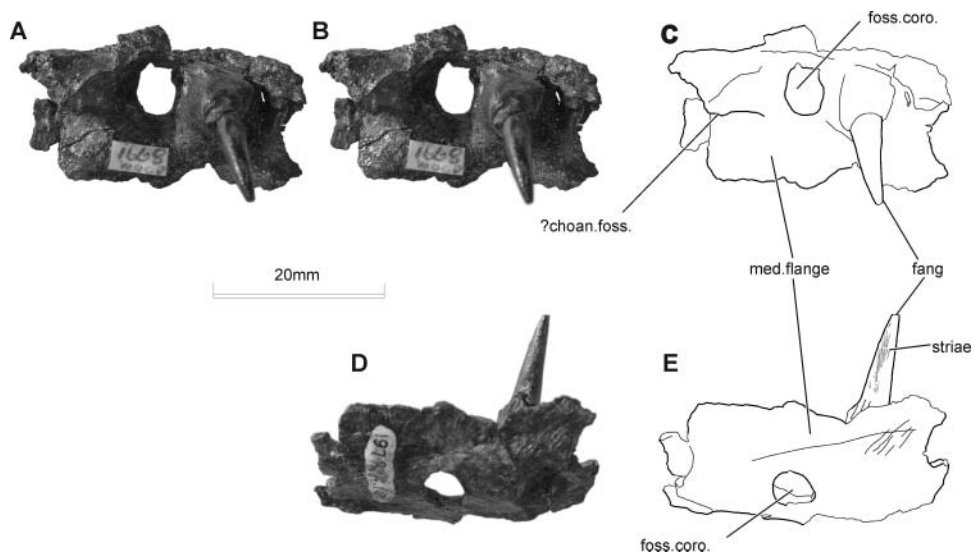
Figure 13. *Strepsodus sauroides*, dermopalatine of NMS GY 1978.4.10. **A, B,** stereopair in dorsal view; anterior is to the left; **C,** interpretive sketch of A and B; **D, E,** ventromesial view; photograph and interpretive sketch. Shading conventions as in Fig. 1.
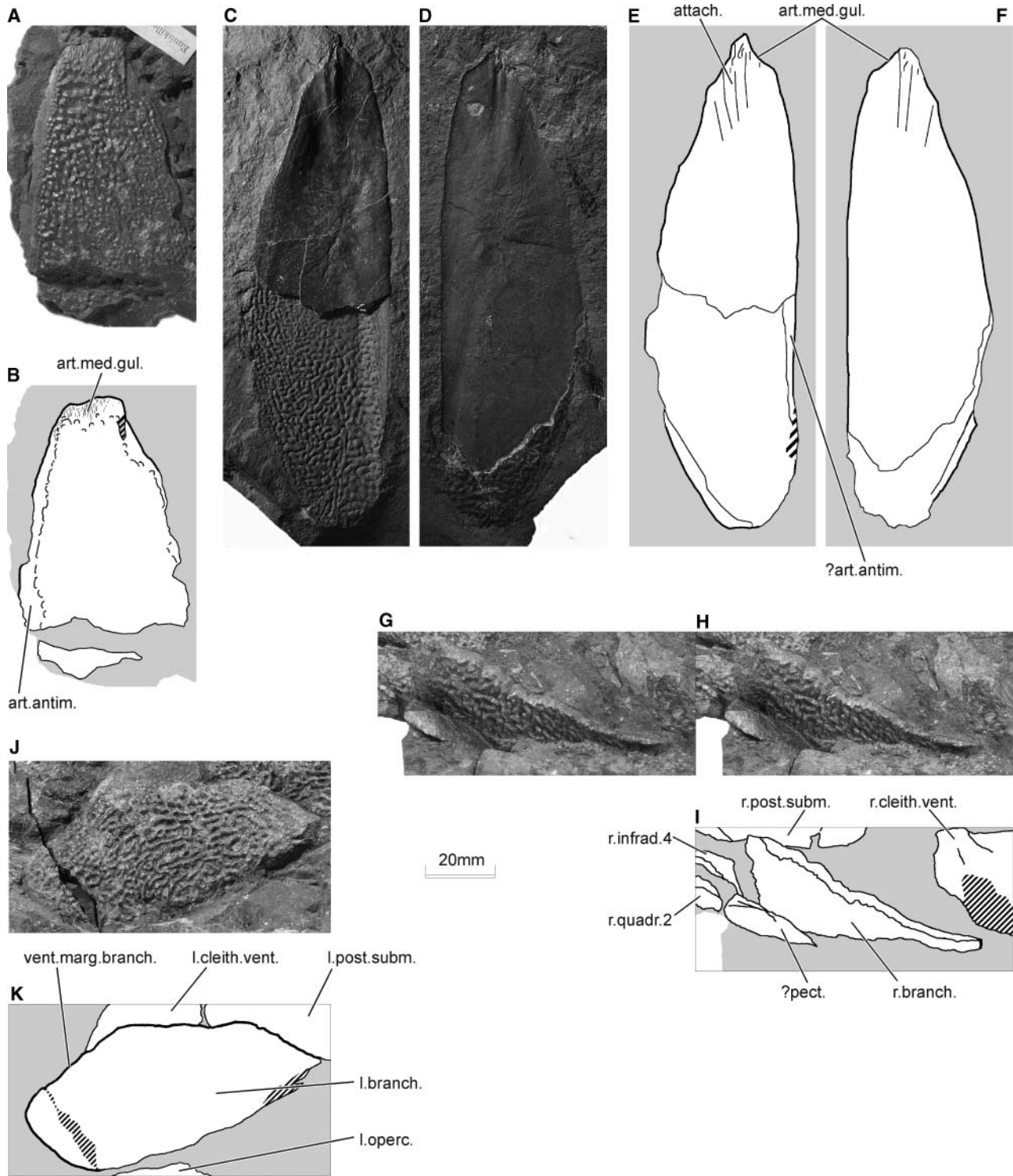
Figure 14. *Screbinodus ornatus*, gulars and branchiostegals. **A, B,** tip of left median gular, NHM P3322b; photograph and interpretive sketch; **C, D,** left median gular, NHM P47718; part and counterpart showing internal and external structure; **E, F,** interpretive sketches of C and D; **G, H,** stereopair of the right branchiostegal of SME 4714, still partly buried in the matrix; **I,** interpretive sketch of G and H; **J, K,** left branchiostegal of SME 4714; photograph and interpretive sketch. Shading conventions as in Fig. 1.

A, B, D, F, H, J, K, L, N, P, R: photographs; C, E, G, I, M, O, Q, S: interpretive drawings.

Labels: l.operc., l.branch., l.infrad.4, l.princ.gul., l.cleith.vent.; r.anocl., art.lat.extra., r.squam., r.cleith.dors., art.branch., r.quadr.2; art.lat.extra.; art.lat.extra., art.branch.; art.lat.extra.; art.lat.extra., art.pit; art.pit, art.branch.; ?art.branch.

Scale: 20mm — R,S; A–O; P,Q
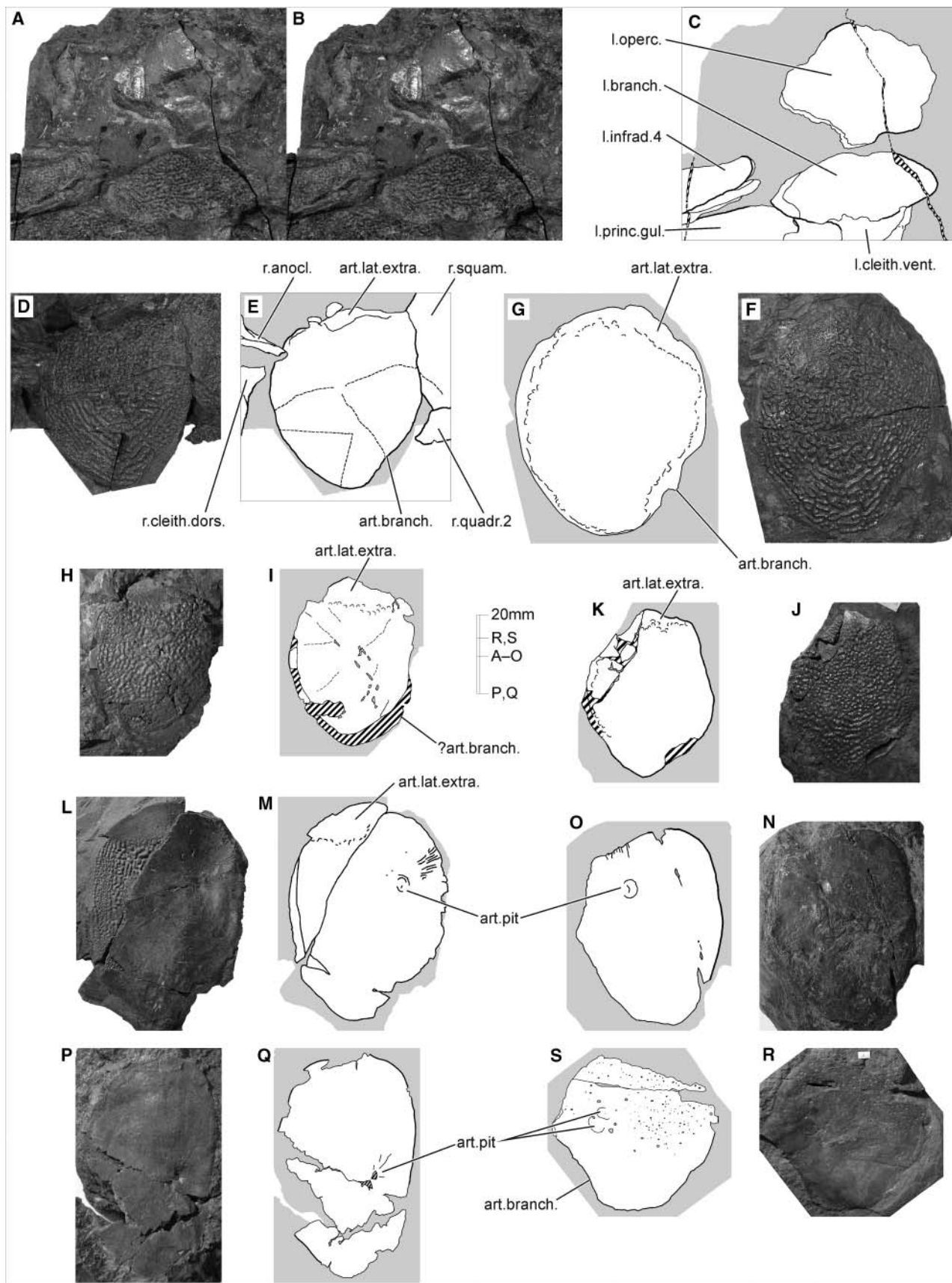
abundant, and are arranged in loosely defined concentric rings. There are no clear overlap surfaces for the preopercular or squamosal, although dorsally the ornament fades to a smooth surface, for the overlap of the median extrascapular. In *Strepsodus* NMS GY 1980.40.36, the lack of overlap surfaces on the opercular for the posterior cheek bones, coupled with its rounded margins, led Andrews (1985, p. 81) to suggest that it may not have articulated directly with the cheek, but rather formed the solid centre to a larger, leathery opercular flap (as it does in the living coelacanth *Latimeria*; Forey 1998, p. 15). This seems a reasonable conclusion for *Screbinodus* also. The internal surface of the opercular, best seen in the isolated specimen NHM P11540 (Fig. 15L, M), is largely smooth, with a rugose area (for muscle or ligament attachment) near the anterodorsal margin. Just posterodorsal to this is a distinct pit, perhaps for articulation with the hyomandibular. The opercular is very large relative to the skull compared to other rhipidistians (*sensu* Cloutier & Ahlberg 1996). Also, its shape and proportions (taller dorsoventrally than anteroposteriorly) are unusual; it covers an area similar to the opercular plus subopercular in the tristichopterid *Eusthenopteron*, osteolepids *Osteolepis*, *Gyroptychius* and *Cabonnichthys*, and porolepiforms *Porolepis* and *Holoptychius* (Ahlberg 1989; Ahlberg & Johanson 1997; Jarvik 1980). Between the opercular and the submandibulars on SME 4714 there is an oval bone, over twice as long as broad, oriented with its long axis pointing anteroposteriorly (best preserved on the left side, but also visible on the right side; l. and r. branch; Figs 1F, 14G–K). The anteroventral margin bears a smooth overlap surface for the seventh submandibular, with which it remains closely associated on both sides. Its relative size and position resembles that of the branchiostegal of *Eusthenopteron* (= 'submandibulo-branchiostegal' of Jarvik 1980) and *Cladarosymblema* (= 'subopercular 2' of Fox *et al.* 1995). Regardless of the precise homology of the two bones described above (notoriously difficult to establish where elements may have been lost or fused during evolution), the salient point is that *Screbinodus* has fewer, larger bones in this region than either porolepiforms or more derived stem-tetrapods such as tristichopterids or osteolepids.

There is a further mass of ornamented dermal bone lying medially, posterior to the principal gulars (anamest.; Fig. 1F). This has been disrupted during fossilization and further damaged during 19th century preparation, but it appears to have consisted of a mosaic of irregular, anamestic bones.

Visceral skeleton and braincase. Little is preserved of the visceral skeleton of the skull of *Screbinodus*. This correlates with the lack of Meckelian ossification in the mandible of *Rhizodus* and *Screbinodus*. However, some fragments are visible on SME 4714 (Fig. 7).

Braincase material is present on *Screbinodus* SME 4714 in the form of two plates of bone anteriorly (tentatively interpreted as the posterior end of the ethmosphenoid unit; Fig. 7A–C), and a crumpled mass of bone posteriorly (?part of the otoccipital unit; Fig. 7D–F). Of the two plates, the left one is in contact with the entopterygoid and is partly obscured by the left postorbital and parietal. It is much thicker than the dermal bones of the cheek, and is covered. It is covered in periosteal bone except for the anterior and posterior margins, which are unfinished (and quite hard to distinguish from the surrounding matrix). The right plate is not overlain by any bones; its lateral face is smooth and covered in periosteal bone, and becomes concave posteriorly. A few small foramina pierce the plate anteriorly. Both plates are transected by one of the diamond wire cuts in the specimen; they join ventrally (i.e. forming a floor to the braincase), but this region decayed before fossilization and merges imperceptibly with the adjacent matrix. The posterior mass of perichondral bone is so distorted as to make any interpretation impossible; however, based almost entirely on its relative position, it is possibly part of the left otic region.

There are two thick rod-like endochondral elements, one on each side of the specimen, visible in section along a break in *Screbinodus* specimen SME 4714. They are surrounded on all sides by cheek and palatal bones, so nothing can be said about their morphology, other than that they are approximately oval in cross-section, with their long axis roughly horizontal. From their size and position, they may be extremely robust ceratohyals.

Strepsodus sauroides sensu Jeffery (2006)
Snout and cheek. Andrews (1985) described the skull of a (probably juvenile) *Strepsodus* specimen NMS GY 1980.40.36 (Andrews used the name *S. anculonamensis*, but see Jeffery 2006). Unfortunately, the skull of this specimen is completely disarticulated and scattered between the part and counterpart. The bones do not appear to be fully formed, and most lack any overlap surfaces. This, coupled with the extremely small size of the bones, makes interpretation very difficult. Thus, the identification of individual bones and the total skull reconstruction must be treated

Figure 15. Operculars. **A–O,** *Screbinodus ornatus*. **A, B,** stereopair of the left opercular of SME 4714 in internal view; **C,** interpretive sketch of A and B; **D, E,** right opercular of SME 4714; photograph and interpretive sketch; **F, G,** right opercular of NHM P36911; photograph and interpretive sketch; **H, I,** right opercular of NHM P3322; photograph and interpretive sketch; **J, K,** ?right opercular of NHM P3322a; photograph and interpretive sketch; **L, M,** left opercular of NHM P11540; photograph and interpretive sketch; **N, O,** right opercular of NHM P41124 in internal view; photograph and interpretive sketch; **P, Q,** ?left opercular of *Strepsodus sauroides*, NMS GY 1980.20.24 in internal view; photograph and interpretive sketch; **R, S,** right opercular of *Rhizodus hibberti* in internal view, NHM P3321; photograph and interpretive sketch. Shading conventions as in Fig. 1.

with caution (as noted by Andrews 1985, pp. 77–79). Most notably, Andrews' identification of a posterior exonaris (and thus a probable lack of choanae) has been questioned (Jeffery 2006; Long & Ahlberg 1999), as it contradicts what is clearly seen in *Gooloogongia* (Johanson & Ahlberg 1998, 2001) and *Screbinodus*.

Very little can be said about the cheek bones of any adult specimens of *Strepsodus*. A number of isolated bones are preserved, notably premaxillae and postparietals, but often the material has been damaged by earlier preparation attempts. Also, although rare, material of the probable rhizodontid *Archichthys* is found alongside *Strepsodus* at several sites. Dental morphology is currently the only way to distinguish these species (Jeffery 2006), and in the absence of well-preserved teeth, attribution to *Strepsodus* must remain provisional.

The premaxilla is preserved in a few specimens, for example natural mould NHM P364 (2) (Fig. 3C, D; Long & Ahlberg 1999), NEWHM G22.34 (Fig. 3E, F) and IGS J518514 (Andrews 1985, fig. 9g). There are also four poorly preserved specimens from Newsham (NEWHM G7.17, G17.46, G59.65 and G59.66), previously attributed to *Archichthys*, in which tooth morphology demonstrates their identity as *Strepsodus* (cf. Jeffery 2006). NHM P364(2) does not have a prominent mesial embayment for a median postrostral bone; other than this, shape of the premaxilla is generally similar among *Screbinodus*, *Strepsodus* and *Archichthys* (known from a single specimen, NEWHM G7.17). It has not proved possible to identify lateral line pores on any of these premaxillae.

A poorly preserved, isolated right maxilla preserved in external view from the South Parrot Coal Seam shale at Niddrie (NMS GY 1898.83.9; Fig. 4H, I) has been attributed to *Strepsodus* (although it may belong to *Archichthys*). It is comparable in shape to that of *Screbinodus*, although the posterior end does not taper away where it would articulate with the quadratojugal. Instead, it ends quite abruptly just posterior to the point of greatest dorsoventral depth (although this may be due to post-mortem breakage). It is quite large compared to other *Strepsodus* remains; an estimate using *Screbinodus* suggests that this individual is at least twice the size of the other examples of *Strepsodus* known from skull bones. NEWHM G17.46 shows the anterior tip of a left maxilla (including a dorsomedial process) which, although crushed, appears to be similar to that seen in *Screbinodus*.

Postparietal shield. Four isolated postparietals from Newsham have been attributed to *Strepsodus*. However, as noted above, there is a possibility that one or more of them may belong to smaller individuals of *Archichthys*. Two specimens show a little of the internal surface (NEWHM G18.62 and G18.77) but they are still partly coated in a layer of coalshale which is difficult to remove without damaging the underlying bone. NEWHM G18.78 (Fig. 8O, P) is preserved in external view and NEWHM G18.93

(Fig. 8Q, R) is prepared on both sides. All four specimens are of a similar size and morphology, and resemble the postparietal of *Screbinodus* in general shape and proportions. The size and number of overlap surfaces does differ slightly from *Screbinodus*; the section articulating with the supratemporal is bevelled into a large overlap surface textured with shallow longitudinal ridges. The margin that articulates with the lateral extrascapular is not straight but 'notched', with a smooth, dished overlap surface. An isolated lateral extrascapular, NMS GY 1977.46.14 (Fig. 8S–V), has a corresponding lobe for overlapping the postparietal. This would have given the postparietals a more pronounced 'tail' and the median extrascapular is likely to have been offset with respect to the lateral extrascapular, much like the condition seen in *Gooloogongia* (Johanson & Ahlberg 2001; Fig. 16B). The only other lateral extrascapular known, NMS GY 1980.40.44, was figured by Andrews (1985, Fig. 7b) as a belonging to the 'Foulden large form' rhizodontid (but probably *Strepsodus*; Jeffery 2006). Its margins are incomplete and little can be said about its overall shape.

Postparietals NEWHM G18.03 and G18.78 both show a cluster of lateral line pores approximately half-way along the bone anteroposteriorly (visible only under a microscope), but the preservation is not clear enough to distinguish the path of any underlying canals. No pit-lines are visible, nor are there are any clear growth lines radiating from a 'growth centre' associated with the lateral line pores (*contra* Andrews 1973, p. 145, 1985, p. 77; Fig. 7). Lateral extrascapular NMS GY 1977.46.14 has several pores arranged in an anteroposterior line. There is no indication of a mesial commissural canal, although two shallow fossae on the internal surface (?foss. lat.; Fig. 8V) may indicate that this nerve ramus was not embedded in the bone. There is also a prominent pit-line, which ends in a fossa similar to those seen in *Screbinodus*.

Three isolated skull bones are known from Cowdenbeath, Fifeshire, which were mentioned by Andrews (1985, p. 80: "Material from Fife currently under preparation, which is apparently *S*[*trepsodus*] *sauroides*...") but not described by her. Mandibular material recovered nearby certainly belongs to *Strepsodus* (Jeffery 2003, 2006) and it is likely that these three skull bones do too, although there is always the possibility of *Archichthys* being present. Two of the bones are isolated postparietals, extremely similar to those described above (NMS GY 1978.4.16 and NMS GY 1978.4.17; Fig. 8E–N). They also show a large number of lateral line pores and there are two pit-lines running across the pore field (Fig. 8M, N).

The third bone is a left squamosal preserved in external view, NMS GY 1975.48.30 (Fig. 6G, H), from a similarly sized individual to those represented by the postparietals. It is very similar to the squamosal of *Screbinodus*, although its dermal ornament matches that of the two postparietals. Its exact proportions cannot be measured as the posteroventral section has broken away; also nothing can be said about
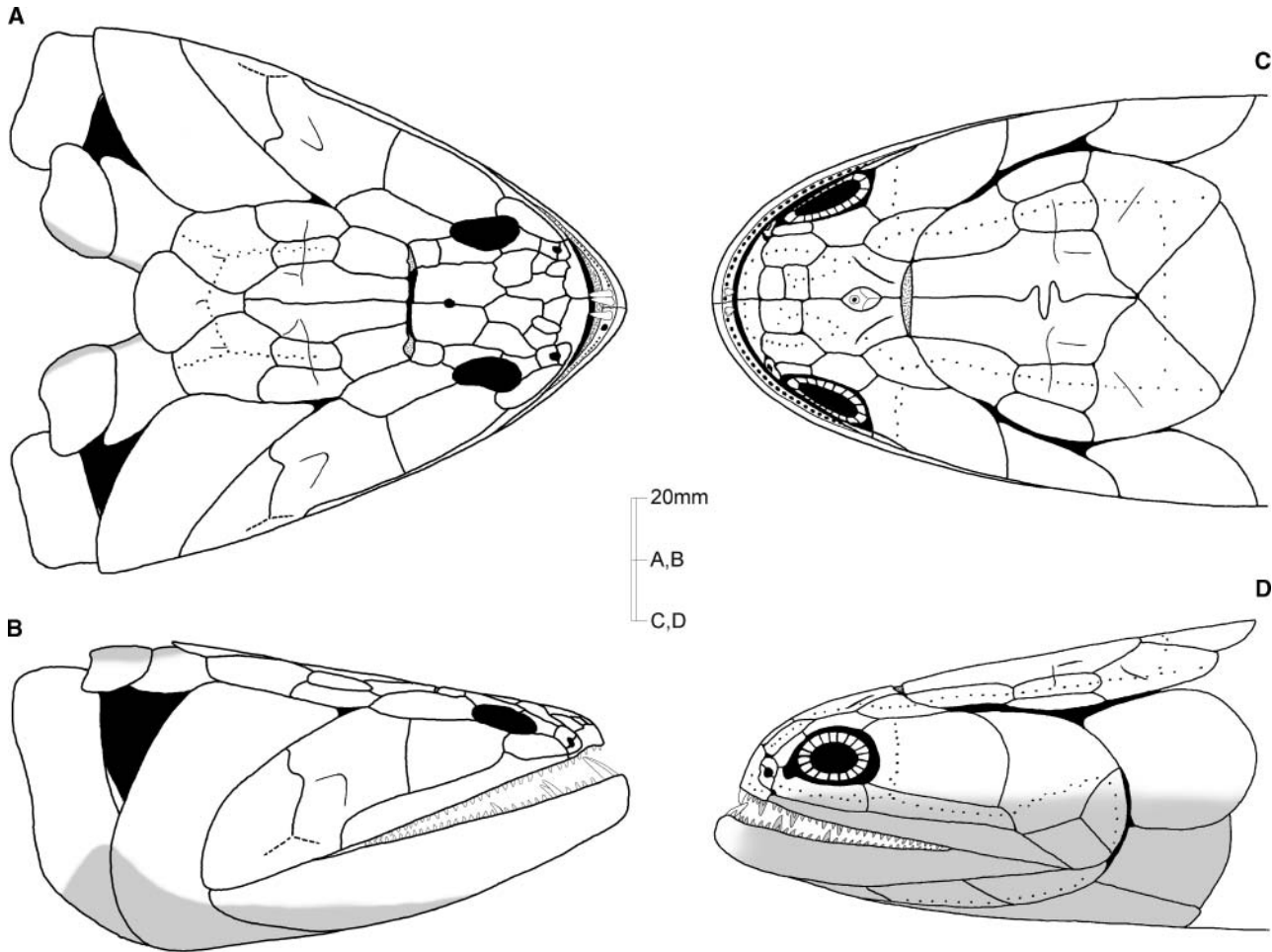
Figure 16. Skull reconstructions of two Australian species of rhizodontid. **A, B,** *Gooloogongia loomesi* in right lateral and dorsal view, redrawn after Johanson & Ahlberg (2001, figs 17, 18); **C, D,** *Barameda mitchelli* in left lateral and dorsal view, redrawn from Long (1989, Fig. 5) and Long & Ahlberg (1999, fig. 4). Bones shaded in grey are poorly known or unknown and are speculatively reconstructed based on other stem-tetrapods.

the presence or absence of an embayment for the preopercular (cf. *Screbinodus*, above). However, the articulation surfaces for the jugal and postorbital are similar to those in *Screbinodus*. There is a band of lateral line pores running posterodorsally across the bone, as in *Screbinodus*, including two small fossae. No pit-line is visible, although a crack in the specimen may run along the course of the pit-line.

Palate. Three probable vomers with fangs bearing *Strepsodus*-type striae (cf. Jeffery 2006) are known; PMG 1329 (from Annick Lodge, Ayrshire), NEWHM G183.01 (probably from Newsham) and NEWHM G7.17 (from Newsham; originally attributed to *Archichthys sulcidens*). PMG 1329 and NEWHM G183.01 bear sigmoid fangs. All three vomers have been damaged by their original, partial, preparation and do not yield much information.

An isolated dermopalatine NMS GY 1978.4.10 is known from Cowdenbeath (Fig. 13). Bearing a recurved (not

sigmoid) fang, it has been cracked and repaired during its original preparation and is missing most of its margins. However, the bone is similar to that of *Screbinodus*, with a single fang and a foramen to receive a coronoid fang (foss. coro.; Fig. 13C–E). The buccal face is smooth, producing a ridge on the anterior part of its lateral margin. This ridge ends in a rugose surface, possibly for articulation with the vomer, and on its lingual face there is a broad fossa (?choan. foss.; Fig. 13C), possibly related to the fenestra exochoanalis.

Operculogular series. Andrews (1985, fig. 9a) reconstructed the principal gulars of the probably juvenile *Strepsodus* NMS GY 1980.40.36. They are similar to those of *Screbinodus*, although the posterior parts were missing on the specimen and so it cannot be said if there were wide posterior submandibulars similar to those of *Screbinodus* SME 4714. The right principal gular apparently overlaps the left, but the margins are unclear. Andrews (1985, p. 80)

described anterior growth centres, as the left principal gular bears 'an internal thickening near the midline' at this point.

The opercular of *Strepsodus* NMS GY 1980.40.36 (Andrews 1985, fig. 9d) and NMS GY 1980.40.43 (Fig. 15P, Q) shows a similar shape, relative size and orientation to that of *Screbinodus* SME 4714. The internal surface includes a single large pit anteroventral to the bone's centre. The bone on NMS GY 1980.40.36, which Andrews identified as a 'suboperculum' (Andrews 1985, fig. 5a), is probably the homologue of the bone here identified in *Screbinodus* as a branchiostegal.

Very little else is known of the operculogular series of *Strepsodus*, as almost nothing can be certainly assigned to either *Strepsodus* or *Archichthys* (cf. Jeffery 2006).

Rhizodus hibberti

Very little is known of the skull of *Rhizodus*. Of the little material that is known, much has been badly damaged by the original preparation or by the subsequent years of storage. Also, isolated material can be difficult to distinguish from that of *Screbinodus* if it is preserved in internal view, other than by the extremely large size of some *Rhizodus* remains.

Snout and cheek. On NMS GY 1950.38.67 a damaged left premaxilla is partly visible in internal view beneath the mandibles (Jeffery 2003, fig. 4a, b). It bears a mesial tusk of a similar size to that of the dentary along with a number of marginal teeth.

NMS GY 1894.183.30 is the anterior portion of a large left maxilla preserved in external view, attributed to *Rhizodus*, from the South Parrot Coal shale of Niddrie (Fig. 4F, G). It is similar to those described for *Screbinodus* and *Strepsodus*, although it preserves nothing which can indisputably identify it as belonging to *Rhizodus*. The marginal teeth have a varying morphology; the most anterior tooth appears to have carinae typical of *Rhizodus* dentary teeth, but the most posterior tooth preserved appears to have no carinae, and bear striae something like those of *Archichthys* (see Jeffery 2006; note that some variation of tooth morphology is known in *Archichthys*). This, and the fact that *Strepsodus* teeth have also been found at Niddrie (e.g. NMS GY 1898.83.9), means that the attribution to *Rhizodus* must remain tentative (see Henricksen 1970, 1972; Paton 1976; Smithson 1985 for details of the complex stratigraphy of Niddrie).

Postparietal shield. The only other skull remains attributed to *Rhizodus* come from Dalry, Ayrshire. There are four large bone fragments, possibly from a single individual, registered as PMG 140, 142 and 145 (the accession numbers are poorly linked to the specimens, and there are no further collection details). Andrews (1985, fig. 7d) figured one of the fragments as the posterior section of a postparietal of *Rhizodus*, giving the accession number PMG 142. Her figure suggested that the postparietal was complete with

a growth centre, pit-line and lateral line pores. However, although the 'growth centre' is easily distinguished on the internal face (the point of convergence of numerous ridges), there is no sign of the lateral line canal figured by Andrews, and the 'pit-line' is an artefact of preparation. It may well be a rhizodontid postparietal (a humerus attributed to *Rhizodus* is known from the same site, and possibly from the same individual; Andrews & Westoll 1970, pl. 9; Jeffery 2001, fig. 4), although every margin is damaged, and thus few comparisons can be made with other rhizodontids.

Operculogular series. NMS GY 1885.58.4 from Gilmerton is a principal gular, whose size suggests that it belongs to *Rhizodus* (it has an anteroposterior length of ∼60 cm). Unfortunately, it is not very well preserved, although the curving medial margin implies a reasonable degree of antimere overlap. It is preserved in internal view, and is of the same approximate shape as those of *Screbinodus* and *Strepsodus*. However, the posteromedial margin appears to have a more 'squared-off' appearance than in *Screbinodus*.

An isolated opercular (NHM P3321 from Burdiehouse; Fig. 15R, S) probably belongs to *Rhizodus*; its size (14.6 × 12.6 cm as preserved) makes it too large to belong to *Screbinodus* (also found at Burdiehouse). Although much of the posterior margin is broken away, traces in the matrix suggest that it would have been less oval-shaped than the opercular of *Screbinodus* and *Strepsodus*. Much of the dorsal half of the internal surface is covered in small pits, but anteroventral to the centre of the bone are two larger pits, in a similar position to the single pit of *Screbinodus* and *Strepsodus*.

Rhizodontid indet

Vomer. NMS GY 1975.5.9 (Fig. 11) is a large, isolated vomer (approximately 107 mm mediolaterally). Its similarity to the vomers of *Screbinodus* allows a confident attribution to the Rhizodontida, and its size suggests that it belongs to *Rhizodus* (although a large individual of *Strepsodus* or the rare *Archichthys* cannot be ruled out). The bone has several cracks running through it, and is missing some parts, but it is generally complete and uncrushed. As preserved, it is about 1.5 times wider mediolaterally than anteroposteriorly (slightly narrower mediolaterally than those of *Screbinodus*; Fig. 12). Its medial margin is a ragged, interdigitating surface for articulation with its antimere (art. antim.; Fig. 11C, J). The anterior face is very slightly crushed, but in life was flat, with an extremely fine vermicular texture. The lateral and anterior faces form a lip surrounding the base of the crown of a single, large tusk. Where the anterior and lateral faces meet dorsally there is a robust anterolateral process (ant. lat. proc.; Fig. 11C), defining the lateral margin of the anterior palatal fossa (ant. pal. foss.; Fig. 11C, H, J) and the anterior margin of the choanal fossa (choan. foss.; Fig. 11C, H, J). This fossa runs posteroventrally across the lateral face of the vomer to its posteriormost corner. A gutter on the

dorsomedial process of the maxilla would align with the fossa on the vomer to form an enclosed choanal channel (perhaps necessary because of the great dorsoventral depth of the vomer). The posterior face of the vomer forms a rounded mass of unfinished bone, with numerous foramina, fossae, sulci and rugosities, which merges smoothly with the similar dorsal face of the bone (Fig. 11D–F, I, J). The dorsal surface does not bear a vertical lamina as seen in *Screbinodus*. The medial face is slightly crushed and broken, but appears to bear a rugose surface for articulation with the parasphenoid. Both the medial and posterior faces are much shallower dorsoventrally than the anterior and lateral faces, meaning that the socket of the tusk is relatively open on these sides. The socket itself is much larger than the root of the tusk (socket; Fig. 11C), implying that, as elsewhere, the tusk and its replacement twin share a communal socket (as seen in the mandible of *Screbinodus*, *Rhizodus* and *Strepsodus*; Jeffery 2003). There is no other dentition, and neither a horizontal anterior lamina (forming part of the roof of the anterior palatal fossa) nor a 'posterior process' (extending the contact with the parasphenoid), as is seen in some other stem-tetrapods.

Notes on Australian rhizodontids

Of the other rhizodontid species described, only *Gooloogongia* (Fig. 16A, B) and *Barameda* (Fig. 16C, D) have significant cranial material. Both have been described by previous authors (Johanson & Ahlberg 1998, 2001 for *Gooloogongia*; Long 1989; Long & Ahlberg 1999; and Holland *et al.* 2007 for *Barameda*), and so only a brief summary will be given below for comparative purposes.

Gooloogongia loomesi
The premaxilla is 'L' shaped, but the distal ramus (separating the lateral rostral from the jaw margin) is very narrow, in contrast to the robust distal ramus seen in *Screbinodus* or *Strepsodus*. As with *Screbinodus*, the maxilla reaches its maximum dorsoventral depth at the level of the lachrymal–jugal suture, although this is positioned more anteriorly than in *Screbinodus* (ventral, rather than posterior to the orbit). The squamosal is very large. It contacts the posterior part of the maxilla and, more posteriorly, may form part of the ventral margin of the cheek; the quadratojugal is poorly known, but does not seem to have contacted the maxilla. The preopercular is also very large (about two-thirds the size of the squamosal). As in *Screbinodus*, the jugal is much larger than the lachrymal, and it forms a large part of the posterior orbital margin. However, the postorbital forms part of the orbital margin, and is closer in shape to the postorbitals of other, non-rhizodontid stem-tetrapods than it is to that of *Screbinodus*.

The parietals bear a pit line, and enclose a pineal foramen. The postparietals have an even more pronounced dorsal

'tail' between the lateral extrascapulars than *Screbinodus* and the extrascapular series do not make a rounded posterior margin to the skull; instead, the median extrascapular protrudes somewhat.

The opercular is a more angular bone than those of Carboniferous rhizodontids although it is similar in being much taller than wide. It is not clear if a subopercular is present, but if so it would have to be very much smaller than the opercular.

Parts of the ethmosphenoid unit are known. The sphenoid region is broad, resembling that of porolepiforms (Ahlberg 1989; Jarvik 1972) and the stem-tetrapods *Kenichthys* (Zhu & Ahlberg 2004) and *Gogonasus* (Long *et al.* 1997). Johanson & Ahlberg (2001, p. 53) stated that the basipterygoid articulation is "in a substantially more anterior and somewhat more dorsal position than is usual among sarcopterygians". However, Holland *et al.* (2007) reinterpreted the specimen, based on the new *Barameda decipiens* material, and suggested that the basipterygoid articulation is in fact in a similar position to that of *Eusthenopteron*.

Barameda mitchelli
The snout contains very few bones, with a single large nasal bone on each side and no tectal series. Little is known of the cheek bones, although the postorbital does appear to form part of the orbital margin.

The parietals bear a pit-line and enclose the pineal foramen. The otic lateral line canal does not enter the postparietal but runs in a fairly straight line through the centre of the tabular. There is a single transverse pit-line running across the tabular (transecting the otic canal) and onto the postparietal, in contrast to the separate tabular and postparietal pit-lines seen in *Screbinodus*. The extrascapular series resembles that of *Screbinodus*, forming a rounded posterior margin to the skull.

Two specimens show the anterior palate of *Barameda mitchelli*; NMV P160 880 shows a small section of right ectopterygoid and entopterygoid, while NMV P160 882 shows the vomers, entopterygoids and dermopalatines. Long (1989, p. 9) stated "the palate is not unlike that of osteolepiforms". The vomer bears a single large fang along with some marginal dentition anteromedially (unlike *Screbinodus*) and a well-developed anterior face ("descending laminae from the anterior margins"; Long 1989). The entopterygoid is denticulate and quite broad mediolaterally right up to its anterior tip. The dermopalatine is correspondingly narrow and thus unlike the wide bone in *Screbinodus* (but more like other stem-tetrapods). It bears at least three fangs and apparently some marginal dentition. The ectopterygoid articulates with the dermopalatine and bears a series of small teeth or fangs, again quite unlike the single large fang of *Screbinodus*.

Barameda mitchelli specimen NMV P160 880 includes an articulated opercular, but much of the anterior and ventral parts of the opercular are obscured and thus the relative size

and orientation cannot be determined. Long (1989, p. 8, fig. 4e, f) used an isolated opercular (NMV P160 884) to suggest that it differed from that of *Strepsodus* as figured by Andrews (1985). In fact, the shape of this opercular does resemble those of *Screbinodus* and *Strepsodus*, but rotated and in mirror image (i.e. it is right opercular with its long axis vertical rather than a left opercular with its long axis horizontal).

The parasphenoid of NMV P160 880 is mostly overlain by the entopterygoids, but the anterior portion appears to be narrow and tristichopterid-like, articulating with the vomers posteromedially (Long 1989). Two fragments of ?otoccipital unit were reported by Long (1989, fig. 6c) on NMV P160 882; these may be the anterior parts of a larger unit, although they may be isolated ossifications, similar to those described above on *Screbinodus*.

Barameda decipiens

This species contains the larger size-range of *Barameda* material (see Holland *et al.* 2007), including the material originally described by Woodward (1906). A new specimen described by Holland *et al.* (2007), NMV P212 715, shows a few details of the skull roof, premaxilla, maxilla, palate and the principal gular. The premaxilla and maxilla are generally similar to those of other rhizodontids. However, the distal ramus of the premaxilla is noticeably longer and narrower than in *Screbinodus* and *Strepsodus*, and the posterior end of the maxilla is apparently quite blunt, without the distinctive slope on the dorsal margin seen in *Screbinodus* (where the quadratojugal articulated). A single left vomer appears to be extremely similar to the vomers of *Screbinodus* and NMS GY 1975.5.9. The principal gular has a concave lateral margin, unlike the convex lateral margin of *Screbinodus* and *Strepsodus*.

Parts of the ethmosphenoid region of the braincase are preserved. This resembles the same region as preserved in *Gooloogongia* specimen AMF 100073A, showing a characteristically elongated optic nerve foramen and well-developed suprapterygoid process.

Phylogenetic analysis

Introduction

Analyses of the phylogenetic relationships of the Rhizodontida, both within the group and to other sarcopterygians, have always been hampered by a lack of data: most of the taxa are known from incomplete remains. Also, until the description of *Gooloogongia* (Johanson & Ahlberg 1998, 2001), all the well-preserved material was from relatively derived Carboniferous taxa (e.g. *Rhizodus*, *Screbinodus*, *Strepsodus* and *Barameda*), offering few insights into primitive conditions. Finally, comparisons within the group are complicated because much of what is known of each species

does not overlap (see Table 1). For example, *Rhizodus* is known mostly from pectoral fin and lower jaw material; the best-known material of *Screbinodus* is the cheek and skull roof. Despite this, the monophyly of the Rhizodontidahas been accepted by all authors since Andrews & Westoll (1970) formalized its taxonomic status. This is based on a number of shared characteristics (e.g. elongated basal lepidotrichial segments in the pectoral fin; expanded ventral lamina of the cleithrum, with 'reverse overlap' relationship to the clavicle; a posteromedial 'tail' on postparietals; dentaries bearing large, deeply rooted symphysial tusks).

The description of more Devonian rhizodontid material (Daeschler & Shubin 1998; Johanson & Ahlberg 1998, 2001; Davis *et al.* 2001, 2004) has helped resolve some of the primitive conditions within the Rhizodontida, but overall the lack of comparative data is still a serious obstacle, and recent phylogenies of the clade are poorly resolved or poorly supported (Johanson & Ahlberg 1998, 2001; Jeffery 1999; Brazeau 2005; Holland *et al.* 2007; see below). However, several of the studies have recovered a clade of Carboniferous rhizodontids consisting of (at least) *Rhizodus*, *Screbinodus* and *Strepsodus*.

Position within the Sarcopterygii

All recent analyses of the position of the rhizodontids within the Sarcopterygii have identified them as stem-tetrapods (e.g. Cloutier & Ahlberg 1996; Zhu & Schultze 1997; Ahlberg & Johanson 1998; Forey 1998; Jeffery 1999; Johanson & Ahlberg 2001; Zhu & Ahlberg 2004; Long *et al.* 2006; Friedman 2007; Friedman *et al.* 2007). All apart from Forey (1998) placed rhizodontids as the basal-most clade within the stem-tetrapod lineage; Forey was unable to resolve stem-tetrapod relationships to any degree.

Friedman *et al.* (2007) used 216 characters and 37 operational taxonomic units (OTUs), including three rhizodontids (*Barameda*, *Gooloogongia* and *Sauripterus*). The dataset was a development of the dataset in Friedman (2007), which in turn was a development of the dataset of Zhu & Yu (2002). As noted above, the analysis found rhizodontids to be the clade at the base of the tetrapod stem-group, with only the plesion *Kenichthys* being more basal. They recovered 162 most parsimonious trees (MPTs) of 510 steps (CI 0.478, RI 0.735, RC 0.352; Fig. 17A). A strict component consensus (SCC) retained a monophyletic coelacanth clade, a dipnoan clade (including the porolepiforms as part of the stem-group), and a tetrapod clade (including *Kenichthys* as the sister group to all the other tetrapods, and the rhizodontids as the sister group to all the other tetrapods except *Kenichthys*).

In this study, in order to test the position of the rhizodontids further, the matrix of Friedman *et al.* (2007) was expanded to include three more rhizodontid OTUs (*Rhizodus*, *Screbinodus* and *Strepsodus*), and the existing scores for the *Barameda*, *Gooloogongia* and *Sauripterus* were modified where necessary. Introducing the three additional

Table 1. Species of rhizodontids referred to in this paper. The right hand columns indicates what is known of each species ($\sqrt{}$ = well known; — = partly known; × = poorly known or unknown).

| Species	Age and location	Skull roof	Cheek	Palate	Operculogular	Lower jaw	Pectoral girdle	Pectoral fin	Body shape
Archichthus portlocki (Portlock, 1843)	Moscovian, most remains from northern England and southern Scotland.	×	×	×	×	×	×	×	×
Aztecia mahalae Johanson & Ahlberg, 2001	?Upper Givetian Aztec Siltstone, southern Victoria Land, Antarctica.	×	×	×	×	×	—	—	×
Gooloogongia loomesi Johanson & Ahlberg, 1998	Famennian Mandagery Sandstone of Canowindra, New South Wales, Australia.	$\sqrt{}$	$\sqrt{}$	×	—	—	—	—	$\sqrt{}$
Sauripterus taylori Hall, 1843	Famennian Catskill Formation, Pennsylvania, USA.	×	×	×	×	—	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$
Strepsodus sauroides (Binney, 1841)	Mississippian to Pennsylvanian, most remains from NE England and southern Scotland, but specimens found across Europe, North America and Australia (see Jeffery 2005).	—	—	—	—	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$
Letognathus hardingi (Brazeau, 2005)	Tournaisian of Horton Bluff, Nova Scotia, Canada	×	×	×	×	$\sqrt{}$	—	×	×
Barameda decipiens (Woodward, 1906)	Tournaisian Mansfield Group of Victoria, Australia.	$\sqrt{}$	—	—	—	—	$\sqrt{}$	$\sqrt{}$	×
Barameda mitchelli Holland *et al.*, 2007	Tournaisian Mansfield Group of Victoria, Australia.	—	—	—	—	—	$\sqrt{}$	$\sqrt{}$	×
Screbinodus ornatus (Traquair 1878)	Viséan, most remains from southern Scotland.	$\sqrt{}$	×	×	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$	—	×
Rhizodus hibberti Owen, 1840	Viséan, most remains from southern Scotland.	×	×	×	×	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$	×
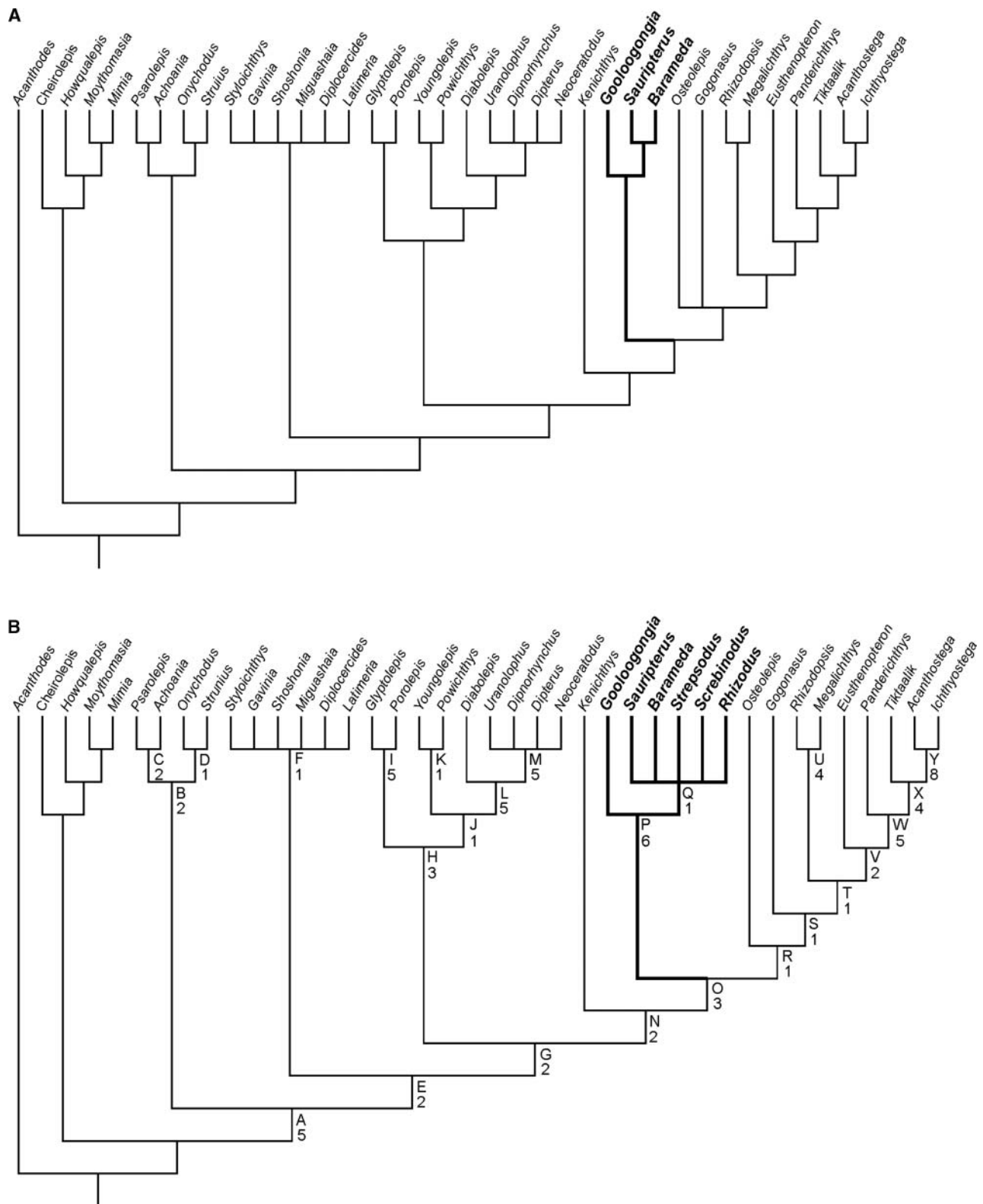
Figure 17. Phylogenetic trees of stem-tetrapods including rhizodontids. **A,** Strict component consensus (SCC) of 162 most parsimonious trees (MPTs) of 510 steps (CI 0.478, RI 0.735, RC 0.352) recovered by Friedman *et al.* (2007) using 216 characters and 37 OTUs, including three rhizodontids (*Barameda*, *Gooloogongia* and *Sauripterus*); **B,** SCC of 594 trees of 523 steps (CI 0.470, RI 0.739, RC 0.348) recovered in this study, using a dataset expanded and modified from Friedman *et al.* (2007), including six rhizodontids (*Rhizodus*, *Screbinodus*, *Strepsodus*, *Barameda*, *Gooloogongia* and *Sauripterus*). The letter at each node relates to the list of unambiguous apomorphies available in the supplementary data; the numbers at each node are Bremer support values. Rhizodontid OTUs are indicated with bold lines and typeface.

OTUs provided more information on the skull, palate and lower jaw than was available for the three rhizodontids originally included (see Online Supplementary Material for character definitions and notes on individual scores). One character was uninformative (character 106, 'Paired pectoral spines'), although this was retained to aid comparisons with the original dataset.

The modified dataset was checked for taxonomic equivalence (*sensu* Wilkinson 1995a, b) and all OTUs were found to contribute unique character combinations. The dataset was then analysed using a heuristic search strategy in PAUP* v. 4.10b (Swofford 2002), and 594 MPTs of 525 steps were recovered (CI 0.469, RI 0.738, RC 0.346). An SCC of these trees was very similar to the SCC of the original analysis (except that *Osteolepis* and *Gogonasus* no longer form a polytomy with 'higher' tetrapods; Fig. 17B). The nodes present in the SCC were well supported (Bremer support values are given for each node in Fig. 17B). The Online Supplementary Data includes a full list of the 'unequivocal' apomorphies of each node (i.e. the changes common to that node on all trees under all most parsimonious character reconstructions), generated using MacClade v. 4.08 (Maddison & Maddison 1999). The following discussion will concentrate of the position of the rhizodontid clade.

The total-group Rhipidistia (i.e. Dipnoi + Tetrapoda; Fig. 17B, node G) is supported by eight unequivocal synapomorphies (character 15, extratemporal present; character 56, tusks of coronoids present; character 72, median gular present; character 77, vomerine tusks present; character 105, dorsal end of cleithrum broad and rounded; character 130, cosmine with large pore ornamentation absent; character 161, number of dermopalatines one; character 183, complete resorption and redeposition of odontotes and enamel). Of these, six can be scored in one or more of the rhizodontid OTUs (characters 56, 72, 77, 105, 130 and 161) and, where data were available, all rhizodontids retained the apomorphic condition. Only character 183 could not be scored, because insufficient histological data are available.

The tetrapod total group (Fig. 17B, node N) was supported by four unequivocal synapomorphies (character 8, number of tectals one; character 20, median extrascapular overlapped by lateral extrascapulars; character 51, parasymphysial tooth whorl absent; character 91, vomeral area with grooves and raised areas). Three of these can be scored in one or more of the rhizodontid OTUs (characters 8, 20 and 51) and, where data were available, all rhizodontids retained the apomorphic condition.

The node crownward of *Kenichthys* (i.e. rhizodontids + 'higher' tetrapods; Fig. 17B, node O) was supported by six unequivocal synapomorphies (character 25, lacrimal posteriorly enclosing posterior nostril absent; character 28, course of ethmoid commissure through centre of premaxilla; character 43, preopercular–maxillary contact: absent; character 57, dentition on coronoids narrow marginal tooth row; character 74, palatal opening surrounded by premaxilla, maxilla, dermopalatine, and vomer (choana): present; character 89, anterior palatal fenestra present. All six can be scored in one or more of the rhizodontid OTUs and, where data were available, all rhizodontids show the apomorphic condition for this node (except for character 57 in *Rhizodus*, which shows an autapomorphic condition of bearing only a tusk and no marginal dentition).

The monophyly of the rhizodontids (Fig. 17B, node P) was supported by seven unequivocal synapomorphies (character 129, pore canal absent; character 188, extratemporal/supratemporal contact present; character 189, dentary fang present; character 195, scapulocoracoid on cleithrum dorsally positioned; character 201, pectoral radials: bifurcate; character 212, distal fin or limb domain expanded across A–P axis; character 216, lateral line multiple). Five of the characters (129, 189, 195, 201 and 212) can be scored for all the rhizodontid OTUs, and the scores are invariant. The other two synapomorphies can be scored for two or more rhizodontids, although the available scores are invariant. Only a single clade was recovered within the rhizodontids; the rhizodontids above *Gooloogongia* (Fig. 17B, node Q), supported by a single unequivocal synapomorphy (194, 'Cleithrum waisted'), scored for all rhizodontids OTUs.

The OTUs crownward of the rhizodontid clade form a Hennigian comb (with the exception of a clade comprising *Rhizodopsis* and *Megalichthys*; Fig. 17B, node U). The node adjacent to the rhizodontid clade (Fig. 17B, node R) is supported by a single unequivocal synapomorphy (character 193, anocleithrum exposed). This character can be scored for four of the rhizodontid OTUs (*Gooloogongia*, *Sauripterus*, *Screbinodus* and *Strepsodus*), and these all possess a subdermal anocleithrum. The next node (Fig. 17B, node S) includes *Gogonasus*, *Rhizodopsis*, *Megalichthys*, *Eusthenopteron*, *Panderichthys*, *Tiktaalik*, *Acanthostega* and *Ichthyostega*. It is supported by a single unequivocal synapomorphy (character 57, dentition on coronoids single tooth row). Three of the rhizodontid OTUs possess a narrow marginal tooth row (*Gooloogongia*, *Barameda* and *Strepsodus*), *Rhizodus* possesses an autapomorphic state (no tooth row), and *Sauripterus* and *Screbinodus* cannot be scored. The node crownward of *Gogonasus* (Fig. 17B, node T) is supported by two unequivocal synapomorphies: character 75, posterior process of vomer present; and character 190, anterior infradentary sutured to prearticular. Vomers are known in *Barameda*, *Rhizodus* (assuming this is the correct designation of the large vomer NMS GY 1975.5.9) and *Screbinodus*. All lack the posterior process. The condition of the anterior infradentary is known in *Barameda*, *Rhizodus* and *Strepsodus*, where it remains unfused to the prearticular.

The node including *Eusthenopteron*, *Panderichthys*, *Tiktaalik*, *Acanthostega* and *Ichthyostega* (Fig. 17B, node V) is supported by five unambiguous synapomorphies;

character 124, well-ossified ribs present; character 129, pore-canal network absent; character 160, entopterygoid proportions – anterior end considerably anterior to processus ascendens; character 184, ethmosphenoid region significantly longer than otoccipital region; character 191, posterior coronoid much longer than penultimate coronoid. Character 124 can only be scored for *Barameda*, *Screbinodus* and *Sauripteris*, but these OTUs show a character state convergent with the group defined by node V. Similarly, all the rhizodontid OTUs lack a pore-canal network (this is clearly a function of the convergent loss of cosmine in rhizodontids and the group defined by node V). Characters 184 and 191 can only be scored for some rhizodontid OTUs but, where known, they show the primitive state. There are no data on the relationship of the entopterogoid to the processus ascendens for any rhizodontid OTU.

In summary, the position of rhizodontids as the sister group of the all other tetrapods (except *Kenichthys*) is well supported by the evidence, with the condition in rhizodontids congruent with the gradual acquisition of character states across the sarcopterygian tree. A notable exception is node V (*Eusthenopteron* and the 'higher' stem-tetrapods), where two of the unequivocal synapomorphies supporting the node show convergence with some or all of the rhizodontids. A similarity between many character states of rhizodontids and 'higher' stem-tetrapods, particularly in the lower jaw and pectoral fin, has been noted by several previous authors (Andrews & Westoll 1970; Andrews 1972; Daeschler & Shubin 1998; Coates *et al.* 2002; Brazeau 2005). However, on detailed examination, many of the similarities are superficial and differences can be highlighted by the use of more precisely defined character states. Furthermore, this study has recovered four unequivocal synapomorphies on the nodes between rhizodontids and node V where there is no convergence with rhizodontids. Therefore, it must be concluded that rhizodontids are basal stem-tetrapods, with some of the members of the clade showing some convergent features with tristichopterid and digited stem-tetrapods.

Rhizodontid interrelationships; review of previous studies

There have been seven attempts to elucidate the interrelationships of the Rhizodontida: Young *et al.* (1992), Johanson & Ahlberg (1998), Jeffery (1999), Johanson & Ahlberg (2001), Johanson (2004), Brazeau (2005), Parker *et al*. (2005) and Holland *et al*. (2007). Many of these analyses used similar characters, either explicitly following the definitions of previous authors, or arriving independently at similar definitions. This section will review these analyses and then undertake a new analysis.

The earliest analysis by Young *et al.* (1992) involved a simple dataset analysed by hand, i.e. without the help of computer algorithms, and favoured the topology [*Notorhi-*

zodon [*Barameda* [*Screbinodus* [*Rhizodus* [*Strepsodus*]]]]]. It should be noted that Young *et al.* (1992) described the remains of the rhizodontid now known as *Aztecia mahalae* Johanson & Ahlberg, 2001 along with some tristichopterid remains, under the name *Notorhizodon mackelveyi*. A thorough search of the dataset undertaken for this study using PAUP* v. 4.0b10 (Swofford 2002) resulted in 100,886 MPTs, an SCC of which was completely unresolved (pers. obs). However, the dataset and selected characters were thoroughly reviewed by Jeffery (1999), and so will not be considered further here; the following section will review the remaining six analyses, all of which used modern computer methods to search for the MPTs. Reviewing these previous analyses also assisted in the selection and definition the characters used the new analysis performed for this study.

Johanson & Ahlberg (1998). This study was part of the preliminary report of *Gooloogongia*. It analysed 10 OTUs (including five rhizodontids) with 29 characters. Only six of the characters (1, 3, 7, 12, 24 and 29) showed informative variation across the rhizodontids, i.e. constituted parsimony-informative characters with two different, parsimony-informative states scored within the rhizodontids, and thus had the potential to affect ingroup topology. The remaining characters showed no informative variation, although many indicated the monophyly of the group. Two of the characters (11 and 27) were parsimony-uninformative. The analysis recovered 135 MPTs, an SCC of which (Fig. 18A) left rhizodontid interrelationships unresolved. A second analysis removed the Devonian rhizodontid *Sauripterus* (of which only the pectoral girdle and fin are well-known), and recovered 15 MPTs, an SCC of which showed a limited resolution of within the rhizodontids; [*Gooloogongia* [*Strepsodus*, *Barameda*, *Rhizodus*, *Screbinodus*]] (Fig. 18B).

Five of the six characters that have informative variation within the rhizodontids have been included in the new analysis (see below; some characters were modified). The sixth (character 24; long unjointed basal lepidotrichial segments in posterior fins) could only be scored for three rhizodont taxa, and would not be parsimony-informative given the outgroups selected for the new dataset.

Jeffery (1999). This study analysed 10 OTUs (including five rhizodontids) with 79 characters. Twelve characters showed informative variation within the rhizodontids (2, 9, 12, 16, 18, 19, 21, 22, 36, 56, 57 and 64), 24 characters were parsimony-uninformative (8, 10, 13, 14, 17, 25, 27, 28, 30–33, 35, 39, 43, 52, 55, 58, 59, 65, 67 and 72–75); character 38 (cycloid scales thick, or thin and sometimes subrectangular) would also have been uninformative but for an apparent miscoding of *Moythomasia*. Many of the remaining characters indicated rhizodontid monophyly. The analysis recovered two trees, reported as 109 steps, although

re-running the analysis during this current study found the same two trees with a length of 111 steps. An SCC of the two trees had the ingroup topology [*Gooloogongia* [*Barameda* [*Strepsodus* spp. [*Rhizodus*, *Screbinodus*]]]] (Fig. 18C).

All except for three of the characters with informative variation within rhizodontids are included in the new analysis. The three which were not used are: character 12 (tabular narrower mediolaterally than postparietal, or wider mediolaterally), omitted because it would be uninformative given the outgroups selected for the new dataset, and is closely related to the presence or absence of an extratemporal (known to be absent only in *Screbinodus*); character 22 (postparietal suture superficially straight, or interdigitated), omitted because it is was autapomorphic for *Barameda* (in fact it was only observable in NMV P160 880) and would be uninformative given the outgroups selected for the new dataset; furthermore, the megalichthyid *Cladarosymblema narrienense* is known to be polymorphic for this character (Fox *et al.* 1995, figs 5, 9), raising the possibility that it might be developmentally plastic within stem-tetrapods; and character 36 (mediolateral widths of dermopalatine and ectopterygoid similar, or dermopalatine much broader mediolaterally than ectopterygoid), omitted because the character can only be observed in *Barameda* and *Screbinodus*, and would not be informative given the outgroups selected for the new dataset.

Johanson & Ahlberg (2001). This study analysed 10 OTUs (including seven rhizodontids) with 27 characters. The matrix was modified from Johanson & Ahlberg (1998), sharing many character definitions. Eleven characters showed informative variation with the rhizodontids (1–3, 5, 6, 9, 10, 15, 16, 22 and 23), while six characters (8, 17, 20, 21, 26 and 27) were parsimony-uninformative. The analysis recovered four trees, reported as 40 steps, although re-running the analysis during this current study found the same four trees with a length of 39 steps. An SCC of the four trees resulted in the ingroup topology [*Gooloogongia* [[*Aztecia*, *Sauripterus*], [*Barameda*, *Rhizodus*, *Screbinodus*, *Strepsodus*]]] (Fig. 18D).

All except for two of the characters with informative variation within rhizodontids are included in the new analysis. These characters are: character 16 (large preaxial flange on humerus), referring to the pectoralis process, omitted because the definition of 'large' is not clear (e.g. *Sauripterus* is scored as present, but *Rhizodus* and *Strepsodus* are scored as absent); and character 23 (braincase unossified or ossified), omitted because reliable data are not available for enough species, especially to distinguish between lack of ossification and simple lack of preservation in the fossil record.

Davis *et al.* (2004) described new material of the pectoral fin of *Sauripterus*, and gave modified scores for

the *Sauripterus* for seven characters (9, 13, 14, 20–22, 24) although they did not reanalyse the dataset.

Johanson (2004). This study analysed 10 OTUs (including seven rhizodontids) with 32 characters. The matrix was a slightly expanded version of the preceding matrices of Johanson & Ahlberg (1998) and Johanson & Ahlberg (2001). Fifteen characters showed informative variation with the rhizodontids (1, 2, 4, 5, 8, 9, 18, 19, 21, 22, 27, 28, 30–32), while four characters (4, 25, 26 and 29) were parsimony-uninformative. Johanson (2004) did not publish her dataset, but reported six trees of 43 steps. However, a reanalysis using a dataset provided by Z. Johanson (pers. comm.) resulted in three trees of 44 steps, with a slightly more resolved SCC. The ingroup topology reported was [*Gooloogongia* [*Sauripterus*, *Aztecia* [*Barameda* [*Rhizodus*, *Screbinodus*, *Strepsodus*]]]], but the reanalysis recovered [*Gooloogongia* [*Sauripterus* [*Aztecia* [*Barameda* [*Rhizodus*, *Screbinodus*, *Strepsodus*]]]]] (Fig. 18E).

Nine of the characters with informative variation within the rhizodontids were included in the new analysis (1, 2, 4, 5, 8, 9, 21, 31 and 32). Of the remainder, character 18 (long basal lepidotrichial segments in other fins) and character 19 (jointed segments in other fins) were not defined clearly enough to be scored; character 22 (braincase ossified or unossified) could not be reliably scored (cf. Johanson & Ahlberg 2001, character 23, above); character 27 (position of condyles for distal mesomeres on humerus; on distal surface of humerus; also present on dorsoanterior surface of humerus) and character 28 (separation of ulnal and radial condyles may be distinct or largely continuous) are not clearly enough defined; character 30 was similar to character 16 of Johanson & Ahlberg (2001; see above) and was rejected for similar reasons.

Brazeau (2005). This study analysed 15 OTUs with 24 characters. Seven of the OTUs were rhizodontids, including the newly recognized *Letognathus hardingi* (Dawson, 1868) and two species of *Strepsodus* (*S. sauroides* and *S. anculonamensis*). Because *Letognathus* is mostly known from jaw material, 22 of the 24 characters addressed features of the mandible. This might be expected to limit the ability of the dataset to resolve the interrelationships of the rhizodontids, although it does serve to highlight the morphological variation of the mandible within the group. In fact, 10 of the characters showed informative variation with the rhizodontids (1, 4, 6–9, 11, 15, 17 and 23), and two were parsimony uninformative (14 and 20).

Brazeau (2005) ran two versions of the dataset, one using *Glyptolepis* as the outgroup, the other excluding *Glyptolepis* from the dataset and using *Kenichthys* as the outgroup. The first analysis recovered three MPTs and the second analysis recovered six MPTs, although in both cases the topology of the rhizodontids in an SCC was the same:
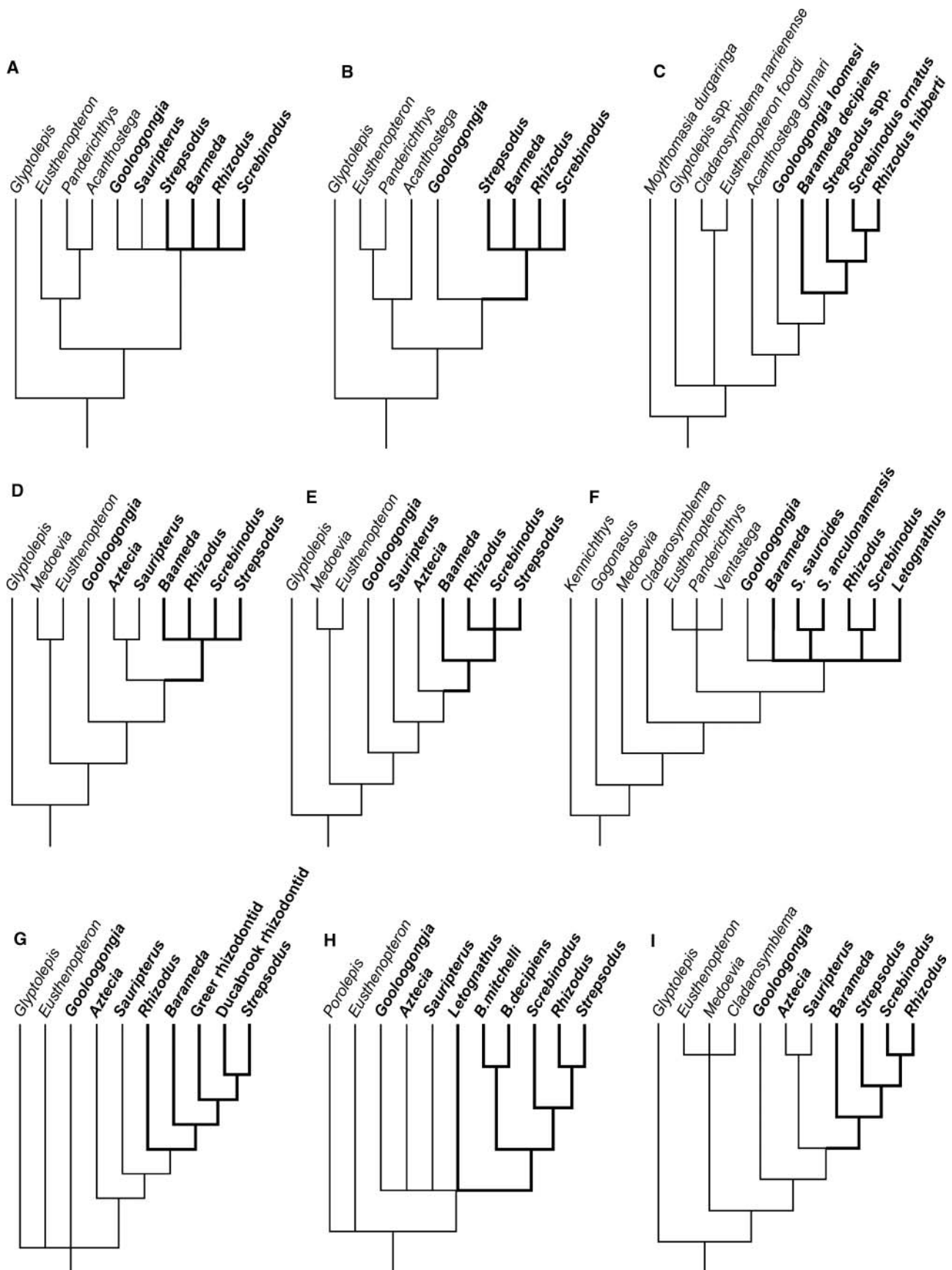
[*Gooloogongia*, *Barameda*, *Letognathus* [[*Rhizodus*, *Screbinodus*], [*S. anculonamensis*, *S. sauroides*]]] (Fig. 18F).

Four of the characters with informative variation within the rhizodontids were included in the new analysis (4, 8, 15 and 17). The characters omitted are: character 1 (parasymphysial dentition a tooth whorl, or a denticle field continuous with coronoid, or a denticle field not continuous with coronoid, or an ordered tooth row), omitted because it is similar to (and shares a character state distribution with) character 15 in the new analysis; character 6 (raised, longitudinal enamel striations of teeth absent, or fine, closely spaced and irregular, or long, smoothly curving and separated by broad bands of enamel and tooth polished labially) and character 7 (sigmoid tusks), omitted because they are only informative if *S. sauroides* and *S. anculonamensis* are included as separate OTUs (*contra* Jeffery 2006); character 9 (sensory canal openings on dentary) would not be informative in the absence of *Letognathus* (see below); character 11 (anterior projection of the dentary forming a dorsal border for the anteromesial rugosity and symphysial plate), omitted because further examination of this characteristic (the equivalent of the anteromesial rugose area of the first infradentaries described by Jeffery 2003, p. 256) suggests that it is a synapomorphy of the rhizodontids (pers. obs.), without informative variation within the group; character 23 (coronoid tooth row interrupted by fangs) would be uninformative within the new dataset.

Parker *et al*. (2005). These authors published a data matrix of 18 characters (exclusively concerned with the pectoral fin and girdle) and 11 OTUs. Seven of the OTUs were rhizodontid genera, and a further two comprised rhizodontid material from Ducabrook, Queensland, Australia (Johanson *et al.* 2000; Parker *et al.* 2005) and Greer, West Virginia, USA (Godfrey 1989), both of which have been provisionally assigned to *Strepsodus*. Unusually, the authors did not report on any analysis of the dataset. Twelve of the characters (1, 2, 7–15 and 17) showed potentially informative variation within the rhizodontids, and two characters (4, 16) were parsimony-uninformative. An analysis of the data undertaken during the current study recovered 18 MPTs of 28 steps (CI 0.821, RI 0.815, RC 0.669), an SCC of which gave the ingroup topology [*Aztecia*

[*Sauripterus* [*Barameda*, *Rhizodus*, *Screbinodus*, *Strepsodus*, Ducabrook rhizodontid, Greer rhizodontid]]]. In half the MPTs *Gooloogongia* was recovered as the sister taxon to the other rhizodontids, but in the other half it formed a clade with the outgroup taxon *Eusthenopteron*.

Screening the original data for taxonomic equivalents revealed that *Screbinodus* was the one-way asymmetric potential equivalent of *Strepsodus* (i.e. where data were present for *Screbinodus* the character states were identical to those for *Strepsodus*) and the two-way asymmetric potential equivalent of *Aztecia*, *Barameda*, *Rhizodus* and the Ducabrook and Greer material (i.e. where data were present for *Screbinodus* the character states were either identical to those of the other OTUs, or the other OTUs had missing data). This shows that *Screbinodus* introduces no unique character-state combinations to the dataset, and cannot therefore affect the most parsimonious interpretation of any of the other OTUs. Worse, because it is similar to a number of the other OTUs, it can be placed equally parsimoniously at several different positions within the ingroup; the resulting set of MPTs reflects this ambiguity, and thus an SCC is poorly resolved.

Re-running the analysis excluding *Screbinodus* resulted in just two MPTs which, as might be expected, were the same as the two non-redundant trees remaining when *Screbinodus* was pruned from the original 18 MPTs. The ingroup topology was [*Aztecia* [*Sauripterus* [*Rhizodus* [*Barameda* [Greer rhizodontid [*Strepsodus*, Ducabrook rhizodontid]]]]]] (Fig. 18G). Again, in one MPT *Gooloogongia* was recovered as the sister taxon to the other rhizodontids, in the other it formed a clade with *Eusthenopteron*.

The ambiguous position of *Gooloogongia* and *Screbinodus* simply reflect a paucity of data on their endochondral fin skeletons. In particular, it does not raise serious doubts about the membership of *Gooloogongia* to the Rhizodontida; the broader character choice of the three previous analyses demonstrated the presence of a number of rhizodontid synapomorphies.

Seven of the 12 characters to show potentially informative variation within the rhizodontids were included in the new analysis (1, 2, 7, 8, 12, 13, 17; some characters were modified). Of the remaining five, two (character 11, ulnar and radial condyles offset from each other; and

Figure 18. Cladistic analyses of rhizodontid interrelationships. **A,** Johanson & Ahlberg (1998), using 29 characters, a strict component consensus (SCC) of 135 most parsimonious trees (MPTs); **B,** Johanson & Ahlberg (1998), a second analysis of the same dataset, excluding *Sauripterus*; SCC of 15 MPTs; **C,** Jeffery (1999), using 79 characters, SCC of two trees; **D,** Johanson & Ahlberg (2001), using 27 characters, SCC of four trees; **E,** Johanson (2004), using 32 characters, SCC of three trees; **F,** Brazeau (2005), using 24 characters, SCC of six trees; **G,** Parker *et al*. (2005), using 18 characters; although no analysis of the dataset was reported in the original publication, this is an SCC of two MPTs recovered in an analysis undertaken in this study (see main text for details); **H,** Holland *et al*. (2007), using 30 characters, SCC of five trees; note that the lack of resolution is, in part, caused by a lack of data for *Screbinodus*; if the data is reanalysed with *Screbinodus* excluded, the ingroup is fully resolved (see main text for details); **I,** analysis of the 35 character dataset shown in the Online Supplementary Material, SCC of two MPTs. In all trees the rhizodontid OTUs are marked by bold typeface, and the position of Carboniferous OTUs are noted by bold lines.

character 14, relationship between pectoral process and dorsal ridge continuous, separated by low rugose area/pectoral ridge, or separated by enlarged ridge and foramina set in deep groove) were only informative because the Ducabrook material was treated as a separate OTU; I accept its assignment to *Strepsodus* and have treated it accordingly. In character 9 (humeral ridge between pectoral process and entepicondyle confluently straight, shallowly notched, or deeply notched) the last state (deeply notched) is only informative because of the treatment of the Greer and Ducabrook material as separate OTUs, and the first state (confluently straight) is informative because of a score for *Aztecia*, *Eusthenopteron* and *Glyptolepis*. However, it is difficult to compare the morphological landmarks of the humerus in these three taxa, and on balance it was decided to reject this character until more data were available. Character 10 (pectoral process enlarged) was similar to character 16 of Johanson & Ahlberg (2001; see above) and was rejected for similar reasons. The final character (15, entepicondyle long and gracile) is not clearly defined; the authors score the published entepicondyles of *Rhizodus* and *Barameda* as missing data, so the operational definition is unclear.

Holland *et al*. (2007). This study analysed 11 OTUs (including nine rhizodontids) with 30 characters. Nineteen characters showed informative variation within the rhizodontids (1, 3–5, 8, 13, 15–21, 24–29), and one character (30) was parsimony-uninformative. The authors reported finding 12 MPTs of 50 steps, although re-running the analysis during the current study found only five trees (also of 50 steps). An SCC of the five trees resulted in the ingroup topology [*Gooloogongia*, *Aztecia*, *Sauripterus*, *Letognathus* [[*B. mitchelli*, *B. decipiens*], [*Screbinodus* [*Rhizodus*, *Strepsodus*]]]] (Fig. 18H).

This lack of ingroup resolution is caused in part by the coding for *Screbinodus* which has a high proportion of missing entries (19 out of 30), second only to *Aztecia* (23 out of 30), but more significantly it is the two-way asymmetric potential equivalent of *Aztecia*. Thus, while *Screbinodus* does bring some unique character-state combinations to the dataset (and therefore cannot be removed without losing information), its inclusion is unlikely to yield a well-resolved SCC. This was confirmed by re-running the analysis with *Screbinodus* deleted, resulting in only three MPTs and a highly resolved SCC with the ingroup topology [*Gooloogongia* [*Sauripterus* [*Aztecia* [*Letognathus* [[*B. mitchelli*, *B. decipiens*], [*Rhizodus*, *Strepsodus*]]]]]].

Of the 19 characters that have informative variation within the rhizodontids, ten have been included in the new analysis (1, 2, 5, 8, 17, 20, 21, 24–26). The remaining nine are: character 4 (anterior projection of the dentary forming a dorsal border for the anteromesial rugosity and symphysial plate), omitted for the same reasons as character 11 of Brazeau (2005; see above); character 13 (tusk size in relation to fangs: larger, or the same size or smaller), 19 (raised longitudinal enamel striae on teeth: absent, or fine, closely spaced and irregular, or long, smoothly curving and separated by broad bands of enamel, or fine, closely spaced and regular) and 28 (humerus containing columnar area with distinct grooves), omitted because they are only informative if two species of *Barameda* are included; character 15 (parasymphysial dentition is a denticle field, or an ordered tooth row with or without denticles), omitted because it would not be informative given the outgroup taxa selected in the new dataset; character 16 (coronoid tooth row and fangs; tooth row only, or tooth row and fangs, or fangs only) has apparently erroneous scores (see below) and correcting these scores means that the character would be uninformative given the taxon selection in the new dataset; character 18 (teeth polished labially, adapted from character 6 of Brazeau (2005)), omitted because of the difficulties in using tooth characters unless a broad sample of *in situ* teeth is available (see Jeffery (2006); character 27, which is based on Parker *et al.* (2005) character 9, and rejected for the same reasons; character 29 (ectepicondylar depression, a groove of the humerus separating the dorsal ridge from the distal condyles), omitted because it would not be informative if the scores are modified according to published data (see below).

Characters 15, 16 and 29 contain erroneous scores. In character 15 *Porolepis* is scored as possessing only a denticle field (cf. Jarvik 1972, pl. 26.6), *Screbinodus* is scored as possessing denticles and *Rhizodus* is scored as possessing a tooth row although the exact condition is unknown in both rhizodontids. In character 16 *Gooloogongia*, *Barameda mitchelli* and *Letognathus* are scored as lacking fangs, although these have been described: Johanson & Ahlberg (2001, p. 53) for *Gooloogongia*, Long (1989, p. 8) for *B. mitchelli* and Brazeau (2005, p. 1485) for *Letognathus*. Also *Rhizodus* is scored as possessing marginal dentition on the coronoid (*contra* Jeffery 2003, figs 2, 7). In character 29 the ectepicondylar depression is scored as absent in *Sauripterus*, although both Davis *et al.* (2004, p. 31) and Garvey *et al.* (2005, p. 11) both noted its presence in that taxon. Similarly, Parker *et al.* (2005, fig. 10) showed the groove to be present in at least some *Strepsodus* specimens. In *Aztecia* the condition is scored as unknown, although the authors use the respective presence and absence of the ridge to distinguish *Aztecia* from *Barameda* (Holland *et al.* 2007, p. 298).

New analysis
A phylogenetic analysis was performed using a new dataset, based in part on the previous datasets reviewed above. This dataset consists of 11 OTUs (including seven rhizodontids; *Aztecia*, *Barameda*, *Gooloogongia*, *Rhizodus*, *Sauripterus*, *Screbinodus* and *Strepsodus*) and 35 characters. The individual characters and scores are discussed in detail in the Online Supplementary Material.
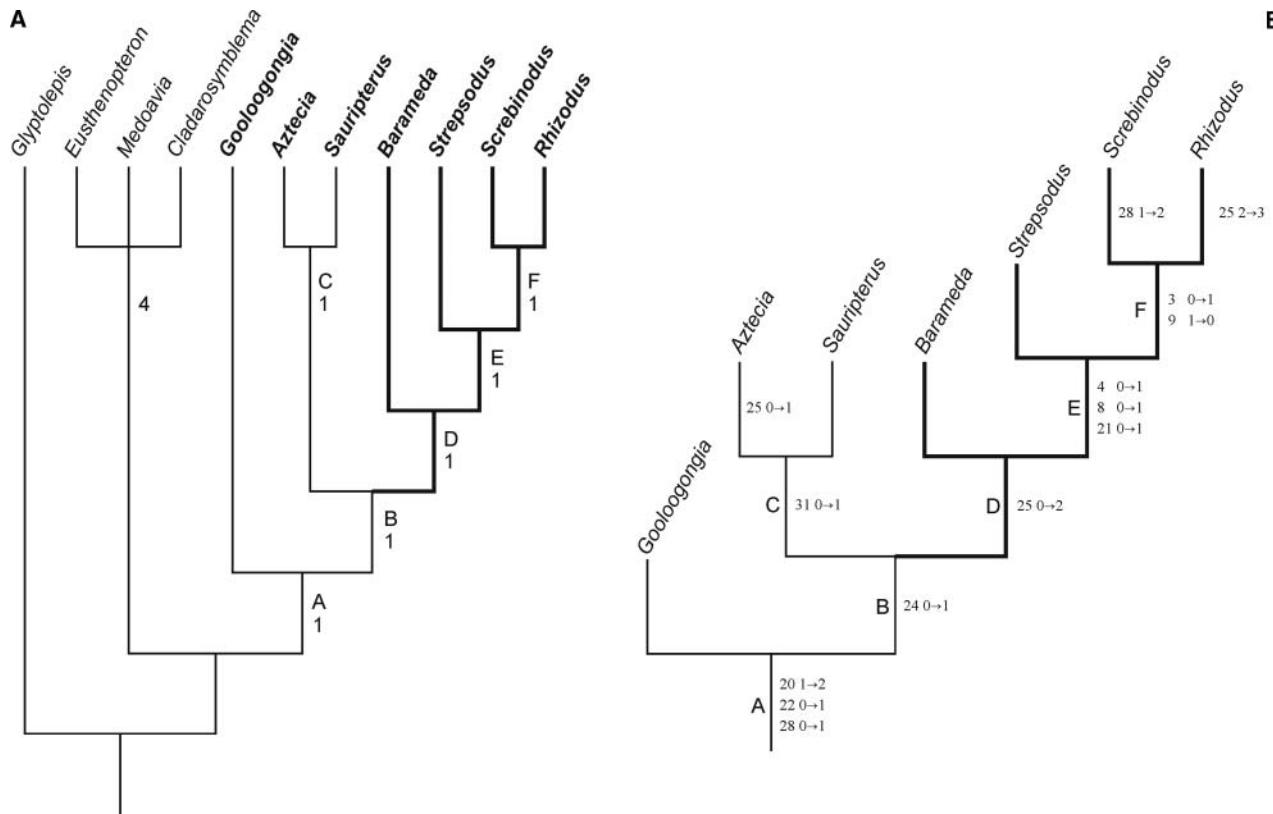
Figure 19. Cladistic analysis of the Rhizodontida using the dataset described in the Online Supplementary Material. **A,** strict component consensus (SCC) of two most parsimonious trees (MPTs) of 56 steps (CI 0.750, RI 0.778, RC 0.583). Rhizodontid OTUs are marked by bold typeface. The letter at each node relates to the list of apomorphies given in the Online Supplementary Material; the numbers at each node are Bremer support values. **B,** unequivocal character-state changes along each branch of the ingroup (the changes are also tabulated in the Online Supplementary Material). The positions of Carboniferous OTUs are indicated by bold lines.

The dataset was checked for taxonomic equivalence and all OTUs were found to contribute unique character combinations. The dataset was then analysed using a branch-and-bound search strategy in PAUP* v. 4.10b (Swofford 2002). Two trees of 56 steps were recovered (CI 0.750, RI 0.778, RC 0.583), differing only in outgroup relationships: [*Cladarosymblema* [*Medoevia* [*Eusthenopteron*]]] versus [*Eusthenopteron* [*Medoevia*, *Cladarosymblema*]] (Figs 18I, 19, 20). Rhizodontid monophyly was supported, with *Gooloogongia* as the most primitive member of the group. *Aztecia* and *Sauripterus* were resolved as the sister group to a Carboniferous clade with the hierarchy [*Barameda* [*Strepsodus* [*Screbinodus*, *Rhizodus*]]].

Bremer support is weak, with no ingroup node sustained in an SCC of trees even a single step longer (Fig. 19A); this is not surprising for a small dataset with a high proportion of missing data (e.g. *Aztecia* has an ambiguity score for 25 of the 35 characters, *Sauripterus* for 21 of the 35 characters). However, a double decay analysis (Wilkinson *et al.* 2000; fig. 20) shows that there is greater support for various ingroup nodes if *Aztecia* is excluded, or both *Aztecia* and *Sauripterus* are excluded.

MacClade v. 4.08 (Maddison & Maddison 1999) was used to plot the unequivocal changes in both trees (summarized in Fig. 19B). Rhizodontid monophyly was supported by three unequivocal synapomorphies (character 20, extratemporal present and in contact with the supratemporal; character 22, postparietal shield with posterior tail; character 28, lateral line pores on cleithrum).

A clade of Carboniferous OTUs is supported by a single unequivocal synapomorphy (character 25, posterior flange of the cleithrum well developed, and tapers away dorsally), although this lack of unequivocal support is a consequence of the large amount of missing data concentrated at the base of the rhizodontid clade (*Gooloogongia*, *Aztecia* and *Sauripterus* share 59 of the 100 missing entries for the whole rhizodontid clade). Five further characters show an unequivocal, derived character state within the Carboniferous clade, but missing data in either *Gooloogongia* or *Aztecia* and *Sauripterus* prevented them from being considered as synapomorphies (character 1, premaxillary tusk present; character 5, diastema of marginal tooth row at symphysis or symphysial tusks; character 6, parasymphysial denticle field does not reach the posterior margin of
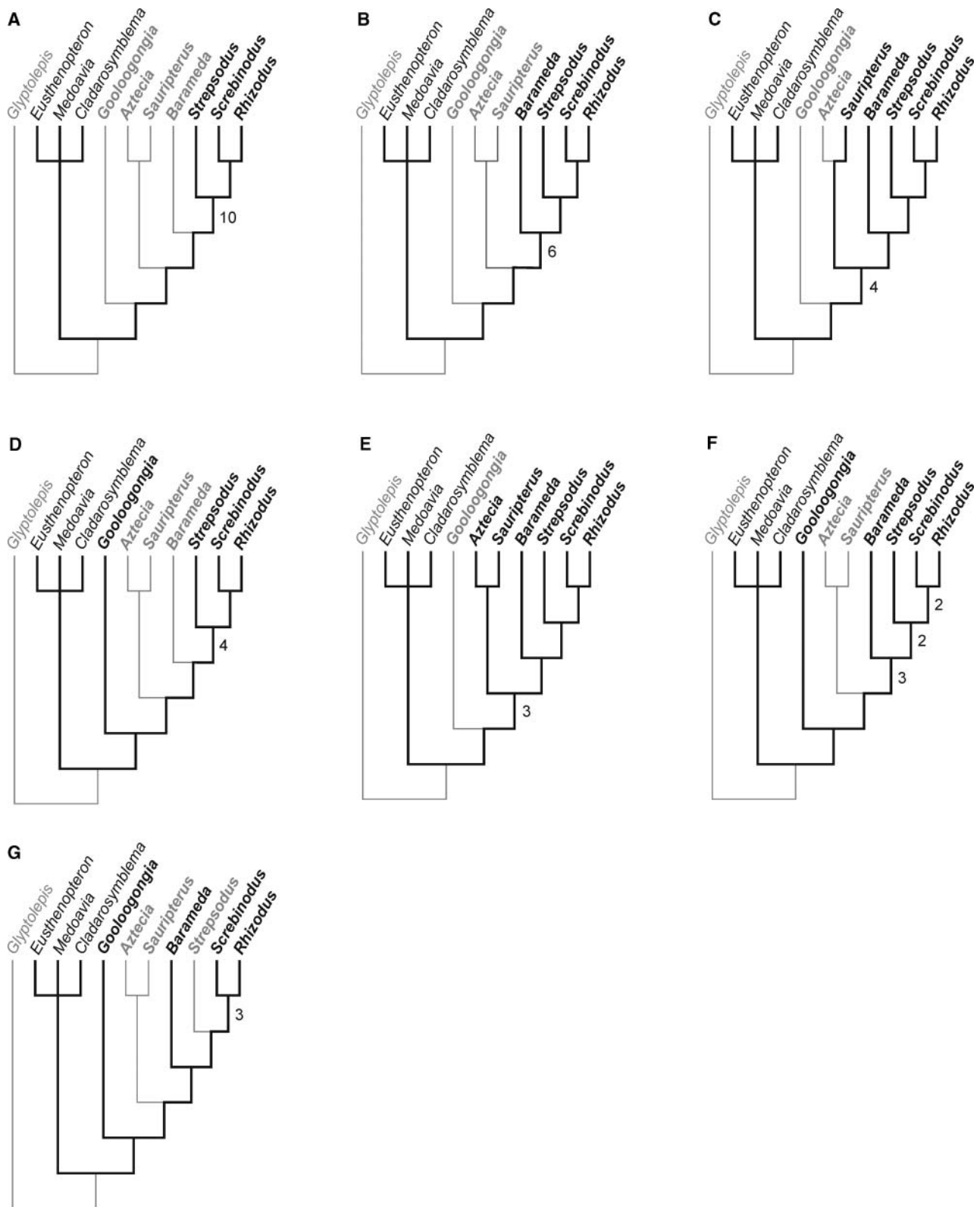
Figure 20. Cladistic analysis of the Rhizodontida using the dataset described in the Online Supplementary Material. **A–G,** results of a double decay analysis (Wilkinson *et al*. 2000) showing the Bremer support of various 'splits' of the tree. Grey typeface and lines indicate OTUs excluded from the split; black typeface and lines indicate included OTUs; bold typeface indicates rhizodontids. The numbers are Bremer support values for the relevant nodes.
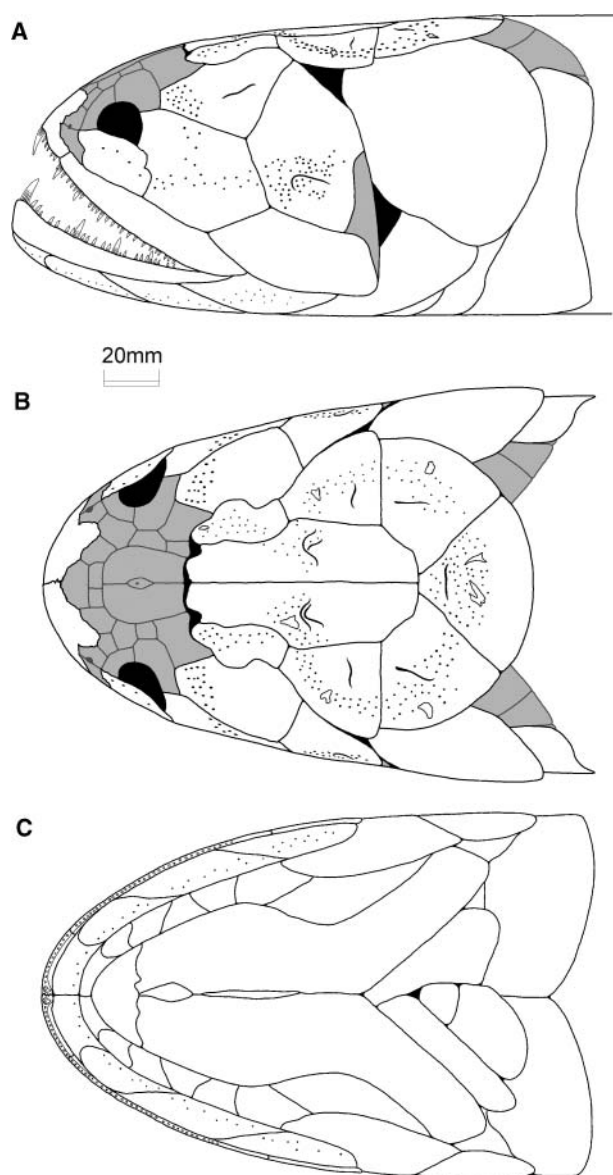
Figure 21. Reconstructions of the skull of *Screbinodus ornatus*, based on all available material. **A,** dorsal view; **B,** lateral view; **C,** ventral view, jaws closed. Plasticine templates were cut for each bone, rescaled where necessary to a match the size of the most complete specimen (SME 4714), and then mounted around a modelling-clay core. The resulting rough model formed the basis of these reconstructions. SME 4714 provided much of the data for the skull in ventral view, including the overall profile of the skull. As the lower jaw is not easily studied on any specimen, the lateral view is based on additional information from *Rhizodus hibberti* (Jeffery 2003). The cheek is largely based on evidence from SME 4714 and NMS GY 1963.16.18 (bones from the left and right sides), and the pectoral girdle is largely based on NMS GY 1874.6 (Jeffery 2001). The skull roof was largely based on NMS GY 1963.16.18. These reconstructions can only be approximate (particularly in the cheek region), as the bones on SME 4714 and NMS GY 1963.16.18 have slightly different proportions (indeed, there is asymmetry between the left and right quadratojugals of SME 4714). Bones shaded in grey are poorly known or unknown, and are speculatively reconstructed based on *Gooloogongia* and *Barameda*.

parasymphysial; character 18, dermocranial joint is loosely fitting; character 30, caput humeri is a ball separated from body of humerus by a neck).

A clade of *Strepsodus*, *Screbinodus* and *Rhizodus* is supported by three synapomorphies (character 4, replacement pair of the fangs in the palate and mandible: both share a single, oversized socket; character 8, parasymphysial does not contact coronoid; character 21, otic lateral line canal runs through postparietals).

Discussion

Our understanding of rhizodontid anatomy and evolution has increased greatly over the last 20 years, with many new specimens described, and existing material reanalysed. Unfortunately, despite this, no rhizodontid is well known in all respects and no part of the anatomy is well known in all (or most) of the species (see Table 1). *Screbinodus* is the first rhizodontid for which a reasonable amount of morphology is known for most parts of the skull, internal and external. It complements data from other taxa (notably *Gooloogongia* and *Barameda*) and gives insights into the anatomy of an advanced member of the group.

Radiation of the Rhizodontidae

Within the Rhizodontida, the Carboniferous OTUs (*Rhizodus*, *Screbinodus*, *Strepsodus* and *Barameda*) form a clade. Although missing data hampered analysis of character evolution within the Rhizodontida, this clade is supported by a single unequivocal synapomorphy and five other characters with less certain state distributions. Furthermore, where comparisons can be made, there is a noticeable similarity between the cheek and skull roof bones of the Carboniferous *Screbinodus* and *Strepsodus*, far more than between *Screbinodus* and the Devonian *Gooloogongia*. Similarly, although the lower jaw is only partially known in *Screbinodus*, it appears to be similar to the highly derived morphology seen in *Rhizodus*, *Strepsodus* and *Letognathus*. This supports the idea that these species represent a distinct radiation rather than separate lines of evolution from Devonian ancestors.

In six of the previous analyses discussed above, a similar clade of Carboniferous OTUs was recovered in all the MPTs (Johanson & Ahlberg 1998, 2001; Jeffery 1999; Johanson 2004; also Parker *et al*. 2005 and Holland *et al.* 2007, when analysed without *Screbionodus*). I therefore propose that the Family Rhizodontidae be restricted to the following taxa: *Archichthys*, *Barameda*, *Letognathus*, *Rhizodus*, *Screbinodus* and *Strepsodus* (thus excluding *Aztecia*, *Gooloogongia* and *Sauripterus*). As discussed above, there is no aspect of the anatomy of this revised family that is well known for all members of the group. However, based on what is known, a provisional list of characters can be drawn up: (1) the cleithrum bears a well-developed

posterior flange; (2) the caput humeri is a ball separated from body of humerus by a neck; (3) the premaxilla bears a tusk; (4) the dermocranial joint is loosely fitting; and (5) the lower jaw morphology shows the suite of derived characters described by Jeffery (2003), including an intramandibular canal open along its ventral edge.

Extremely large body size is only seen in members of the Carboniferous radiation; possibly 3 to 5 metres for *Strepsodus* and 5 to 7 metres for *Rhizodus* (based on a mandibular length of 15.8% of total body length; Jeffery 1999, cf. Schultze 1984). This compares with 0.9 metres for *Gooloogongia* and perhaps 1.5 metres for *Sauripterus* (based on the size of the pectoral girdle and fin reported by Davis *et al.* 2004). *Aztecia* appears to have been somewhat smaller than *Gooloogongia*, but this estimate is based on a single specimen (AMF 113914). *Screbinodus* was about 1.5 metres in length and therefore one of the smaller members of the Carboniferous radiation, along with *Barameda decipiens* (Woodward 1906; Long 1989; Garvey *et al.* 2005), which may have been about 2 metres in length. The lower jaws of *Letognathus* suggest an animal of a similar size, but (as with *Aztecia*) the limited range of material makes it impossible to be confident of this. By far the smallest Carboniferous species is *Barameda mitchelli* (e.g. NMV P160880), which would have had a body length of about 0.35 metres.

Strepsodus may be the earliest member of the clade; material is known from the upper part of the Tournaisian (∼350 Ma) from Foulden, Berwickshire, UK (Andrews 1985). *Barameda* and *Letognathus* come from the Tournaisian of Australia and Canada, respectively (Brazeau 2005; Holland et al. 2007), although more precise dating is not available. The wide distribution of the group by the end of the Tournaisian, at the latest, makes it likely that it emerged some time close to the Devonian–Carboniferous boundary, although it also makes it impossible to construct any hypothesis on the palaeogeographical origin of the clade.

Morphology

This study revealed a number of unusual characteristics in *Screbinodus* which could not be used in the phylogenetic analysis because of a lack of data in other taxa. These are documented below in the hope that they may be useful when more comparative data are available.

Firstly, *Screbinodus* shows several derived characteristics with respect to *Gooloogongia* and *Barameda*, but the lack of information for *Strepsodus* and *Rhizodus* made it unclear if they are autapomorphic or not. For example, the postorbital may be excluded from the orbital margin (a trait also seen in advanced tristichopterids; Johanson & Ahlberg 1997, p. 49; Johanson & Ahlberg 1997, appendix 1, character 3), and the extratemporal is lost or fused with the tabular.

Secondly, *Screbinodus* shows some characteristics which are derived with respect to non-rhizodontids, but for which there is no data for other rhizodontids. For example, the quadratojugal is a very long bone (over half the length of the maxilla), the ectopterygoid is a short bone (less than half the anteroposterior length of dermopalatine), and there are only two bones in the opercular region (a large opercular, and a long branchiostegal connecting with the submandibular series). This last character may be related to a reliance on suction feeding: the subopercular is lost or reduced in many actinistians, including the extant *Latimeria* (known to be a powerful suction feeder; Cloutier 1991a, b; Forey 1998).

Thirdly, *Screbinodus* shares some characteristics with *Barameda mitchelli*, but the condition in other Carboniferous rhizodontids is unknown; for example the extrascapular series forms a smooth quarter-circular arc to the end of the skull roof.

Finally, there is the question of the degree of endochondral ossification in the skull. The braincase of *Gooloogongia* appears to have been fully ossified (Johanson & Ahlberg 2001), but the only Carboniferous rhizodontid that is known to have significant braincase ossification is *Barameda*; *B. mitchelli* specimen NMV P160 882 shows small braincase fragments (Long 1989, fig. 6C) and *B. decipiens* specimen NMV P212 715 shows the posterior part of the ethmosphenoid. Only small fragments of braincase are known for *Screbinodus* and none at all for *Strepsodus*, *Letognathus* and *Rhizodus*. This is only negative evidence for the reduced ossification of the braincase, but the absence of significant material from two largely complete, adult *Screbinodus* skulls (NMS GY 1874.6 and SME 4714) strongly implies that it did not ossify. This correlates with poor endochondral ossification in the mandible of *Rhizodus*, *Strepsodus* and *Letognathus* (Brazeau 2005; Jeffery 2003) and could also account for the complete disarticulation commonly seen in specimens of these species.

during my stay. Finally, Jeff Liston and Alison Brown played host to an impromptu fossil fish meeting in Glasgow in November 2005; I greatly appreciated this opportunity to discuss my ideas with them and with Martin Brazeau and Jan den Blaauwen (who also took the photographs of all the Edinburgh specimens).

Supplementary material

Supplementary material can be viewed online. 10.1080/14772019.2011.595961

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