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The cranial skeleton of the Early Permian aquatic reptile *Mesosaurus tenuidens*: implications for relationships and palaeobiology

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The cranial osteology of the aquatic reptile *Mesosaurus tenuidens* is redescribed on the basis of new and previously examined materials from the Lower Permian of both southern Africa and South America. *Mesosaurus* is distinguished from other mesosaurs in exhibiting an absolutely larger skull and possessing relatively longer marginal teeth. The teeth gradually angle outwards as one progresses anteriorly in the tooth row and become conspicuously procumbent at the tip of the snout. The suggestion that mesosaurs used their conspicuous dental apparatus as a straining device for filter feeding is based upon erroneous reconstruction of a high number of teeth in this mesosaur. Reinterpretation of the morphology and the organization of the marginal teeth of *Mesosaurus* suggests that they were used to capture individually small, nektonic prey. General morphological aspects of the skull support the idea that *Mesosaurus* was an aquatic predator and that the skull was well adapted for feeding in an aqueous environment. The anatomical review permits critical reappraisal of several cranial characters that have appeared in recent phylogenetic analyses of early amniotes. Emendation of problematic characters and reanalysis of amniote phylogeny using a slightly modified data matrix from the literature strengthens the hypothesis that mesosaurs form a clade with millerettids, procolophonoids and pareiasaurs within Reptilia. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, **146**, 345–368.

ADDITIONAL KEYWORDS: aquatic adaptation – evolution – Gondwana – Reptilia.

INTRODUCTION

Several amniote lineages invaded aquatic environments during the Palaeozoic, but the most enigmatic are the mesosaurs. Known only from Lower Permian sediments in southern Africa and eastern South America, these early reptiles are characterized by their elongate skulls, numerous long and slender teeth, paddle-like limbs and greatly thickened trunk ribs (Gervais, 1865; MacGregor, 1908; Oelofsen & Araújo, 1987). Mesosaurs are distinguished from other Palaeozoic amniotes not only by their distinctive anatomy, but also by their geographical distribution: they are the oldest amniotes known from the southern palaeolatitudes, pre-dating by several million years the diverse synapsid and reptilian faunas of Late Permian Gondwana. The presence of mesosaurs in Permian deposits on both sides of the Atlantic Ocean was adduced as compelling palaeobiological evidence in one of the earliest arguments for continental drift (Du Toit, 1927).

The anatomy of mesosaurs has puzzled palaeontologists since the descriptions of *Mesosaurus tenuidens* by Gervais (1865, 1864–66). The type and the early referred specimens, collected from the white-weathering black shales of South Africa, could be studied only once the bones were removed mechanically from the encasing matrix. Given the fragility of the black shales, this procedure resulted almost invariably in the collection of partial skeletons. The resultant negative moulds were then cast in material such as gutta percha in order to produce positive casts. However, such casting compounds revealed only the most

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salient anatomical relief and precluded detailed observations of skull morphology. Attention therefore was focused on the postcrania in early studies. During this period the hypothesis that mesosaurs were ancestral to sauropterygians was advanced by Seeley (1892), who compared the postcrania extensively with that of nothosaurs.

The need for well-preserved cranial materials became pronounced following the publication of studies that emphasized temporal fenestration as an important diagnostic tool for the classification of amniotes (Osborn, 1903; Williston, 1917). Several specimens collected from the black shales of the Irati Formation of Brazil and described by MacGregor (1908) had complete skulls, yet the casting technologies of the time did not permit a confident interpretation of skull-roof morphology. Thus, MacGregor's (1908) tentative restoration of the skull of *Mesosaurus* with two pairs of temporal openings appears to have been influenced by Osborn (1903), who favoured a diapsid identity for mesosaurs.

The uncertain morphology of the skull roof and the strong appeal of fenestration-based classifications defined how mesosaurs were considered in the scope of reptile phylogeny. Although von Huene (1922) proposed that mesosaurs were ancestral to ichthyosaurs, he (von Huene, 1941) later abandoned that postulate in favour of one that posited synapsid affinities for mesosaurs. The latter hypothesis was based upon the presence of what was considered to be a lower temporal opening in one specimen. Although von Huene's (1941) interpretation of the mesosaurid skull roof appears to have been accepted provisionally by subsequent workers (Romer, 1966; Araújo, 1976; Hamley & Thulborn, 1993), the hypothesis of a synapsid origin for mesosaurs did not receive wide support. Romer (1966) considered mesosaurs to have originated independently from 'stem reptiles', which were identified by Carroll (1969) as members of the Permo-Carboniferous group Protorothyrididae (his 'Protorothyridae', formerly 'Romeriidae'). The idea that protorothyridids were ancestral to all other amniotes was promoted in a series of papers (Carroll & Baird, 1972; Clark & Carroll, 1973; Carroll, 1982), but later succumbed to cladistic hypotheses which identified the protorothyridid *Paleothyris* as a close relative of diapsid reptiles (Reisz, 1981; Heaton & Reisz, 1986).

The first cladistic analysis to consider the phylogenetic position of mesosaurs within Amniota was conducted by Gauthier, Kluge & Rowe (1988), who identified them as basal members of a clade whose members were referred to informally as 'parareptiles'. Gauthier *et al*. (1988) did not have much confidence in their parareptile grouping, and, citing the relatively low consistency indices for each of the synapomorphies identified for the clade, predicted that it would not withstand detailed analysis. Indeed, Laurin & Reisz (1995) discovered in their analysis of early amniote phylogeny that mesosaurs formed a sister-group relationship with the crown clade of reptiles; the rarely used name 'Sauropsida' was applied to the resultant grouping (Gauthier, 1994; Laurin & Reisz, 1995). The remaining parareptile taxa of Gauthier *et al*. (1988) formed a monophyletic group that included turtles. Laurin & Reisz (1995) attached Olson's (1947) taxon name 'Parareptilia' to this clade and defined it as a stem-based name, but their phylogenetic definition was equivalent to that made by Gauthier *et al*. (1988) for 'Anapsida'. The latter name was accepted by Modesto (1999b) for the clade of millerettids, pareiasaurs and procolophonids. Notably, Laurin & Reisz (1995) cautioned that the addition of a single step to their most parsimonious tree resulted in mesosaurs forming a sister-group relationship with anapsids (parareptiles *sensu* Laurin & Reisz, 1995), thereby resurrecting the content of Gauthier *et al*.'s (1988) 'parareptiles'. Such uncertainty in the relationships of mesosaurs highlights the need for a much better understanding of these aquatic reptiles.

New information on the mesosaur *Stereosternum tumidum*, together with phylogenetic data gleaned from recent studies on other early reptiles (Lee, 1995; Modesto, 1998), prompted a reanalysis of basal amniote phylogeny using a modified version of the data matrix of Laurin & Reisz (1995) with the addition of two new phylogenetic characters (Modesto, 1999b). The resultant phylogeny (Modesto, 1999b) suggested that mesosaurs were the closest relatives of parareptiles (*sensu* deBraga & Reisz, 1996). Again, however, only a single additional step was required to dislodge mesosaurs, but this time with the result that mesosaurs became basal eureptiles. This continuing lack of phylogenetic resolution with regard to the position of mesosaurs is symptomatic of the paucity of descriptions of mesosaur anatomy.

With this in mind, the skull of *Mesosaurus tenuidens*, the best represented mesosaur species, is redescribed here in detail. A description of the postcrania of this mesosaur will be the subject of a forthcoming paper. Finally, mesosaurs have long been regarded as aquatic forms (MacGregor, 1908; Romer, 1966; Carroll, 1982), yet only superficial aspects of their anatomy have been attributed to their aquatic habitus. Accordingly, the cranial description is followed by a discussion of the implications for the phylogenetic position of mesosaurs among basal amniotes, and a reappraisal of the aquatic adaptations that are manifest in the skull of *Mesosaurus tenuidens*.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; GPIT, Institüt

und Museum für Geologie und Paläontologie der Universität Tübingen; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; SAM, Iziko: South African Museum of Cape Town; SMNH, Swedish Museum of Natural History, Uppsala.

Anatomical abbreviations used in Figures 3–12: an, angular; ar, articular; at ic, atlantal intercentrum; at na, atlantal neural arch; at pc, atlantal pleurocentrum; ax, axis; ax ic, axial intercentrum; bo, basioccipital; bs, basisphenoid; cop, hyoid copula; cv, caudal vertebra; d, dentary; eo, exoccipital; ep, epipterygoid; f, frontal; ha, haemal spine; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sa, surangular; sm, septomaxilla; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer.

MATERIAL AND METHODS

All specimens of *Mesosaurus tenuidens* examined here are preserved as natural moulds in black shale. These were cast in latex rubber and drawn from photographs or by use of a camera lucida. The list of examined specimens includes: GPIT 1757-1, partial skull of a juvenile individual; MCZ 3373, partial skull, mandibles and articulated presacral column; MCZ 4028a, partial skull and cervical series of a large subadult, counterpart to MCZ 4028b, skull in left lateral view; MCZ 4030h, skull, anterior thorax and caudal series; MCZ 4031a, partial skull and anterior thorax; SMNH R202, nearly complete mandible of a large adult; SMNH R207a, skull of a large individual in right lateral view and counterpart to SMNH R208, skull of a large individual in left lateral view; SMNH R207c, skull of a large adult exposed in dorsal view; SMNH R212, partial skull of an adult exposed in ventral view; SAM PK-K8381, part and counterpart of partial skull with mandible and anteriormost cervical vertebrae. This list is not exhaustive and serves only to identify specimens that were examined for this study. The SAM specimen is from the Whitehill Formation, Ecca Group of South Africa, whereas the remaining specimens are from the Irati Formation, Passa Dois Group of Brazil. These two formations are considered coeval by Oelofsen & Araújo (1987) and are thought by those authors to be latest Sakmarian in age.

The three mesosaur genera *Mesosaurus*, *Stereosternum* and *Brazilosaurus* are monotypic; for the sake of convenience, these names are used in preference to their respective specific binomens in the description and discussion sections.

DESCRIPTION

A thorough understanding of the skull has proved to be most problematical aspect of mesosaurid anatomy. This can be attributed to the small size and exquisite thinness of many of the roofing bones. These elements are usually distorted or crushed in most specimens. In combination with the limited detail afforded by gutta percha, gelatine and plaster, the poor preservation of the cranial materials that were available to earlier workers precluded them from reporting anything but the most superficial aspects from their study of casts. Recent advances in latex casting technology (Baird, 1955; Heaton, 1982) permit a comprehensive understanding of the cranial anatomy of *Mesosaurus*, and it is now possible to draft a composite skull reconstruction (Fig. 1). Information was derived largely from latex casts of the SMNH specimens described originally by Wiman (1925) and von Huene (1941). Additional anatomical information is provided by casts of heretofore undescribed materials collected by Friedrich von Huene and reposited in the GPIT, and more recently collected specimens reposited in the MCZ. The SAM specimen that served as the basis of Oelofsen's (1981) unsatisfactory reconstruction (reproduced in part by Lee, 1995: figs 12, 13) was the source of additional information.

The reconstruction of the skull of *Mesosaurus* illustrates the remarkably long rostrum (Fig. 1), which is formed by the premaxillae and the maxillae. The nasal clearly does not extend anteriorly beyond the external naris. The latter is anteroposteriorly elongate, formed almost entirely by the nasal and the septomaxilla, and lies directly dorsal to the internal naris. A small accessory opening, the foramen nariale obturatum, pierces the suture between the nasal and the lacrimal just posterior to the external naris. The posterior region of the skull is low and broad. No temporal openings are present. Postparietals are absent, and the supraoccipital may have contacted the skull table via cartilage (Fig. 2). The post-temporal openings are relatively large due to the narrow breadth of the supraoccipital and the small size of the tabulars. The great length of the mandible is formed mainly by the dentary. The posterior end of the dentary is overlain laterally by the surangular, and together these two elements form a low coronoid eminence. The coronoid is not visible in lateral aspect. The surangular and the angular are relatively long, extending anteriorly as far as the level of the external naris. The marginal teeth of both upper and lower jaws are conspicuously procumbent anteriorly. As one proceeds posteriorly along the tooth row, the teeth gradually become more vertically orientated. No reconstruction of the mandible in lingual view is offered because the available specimens do not permit a confident

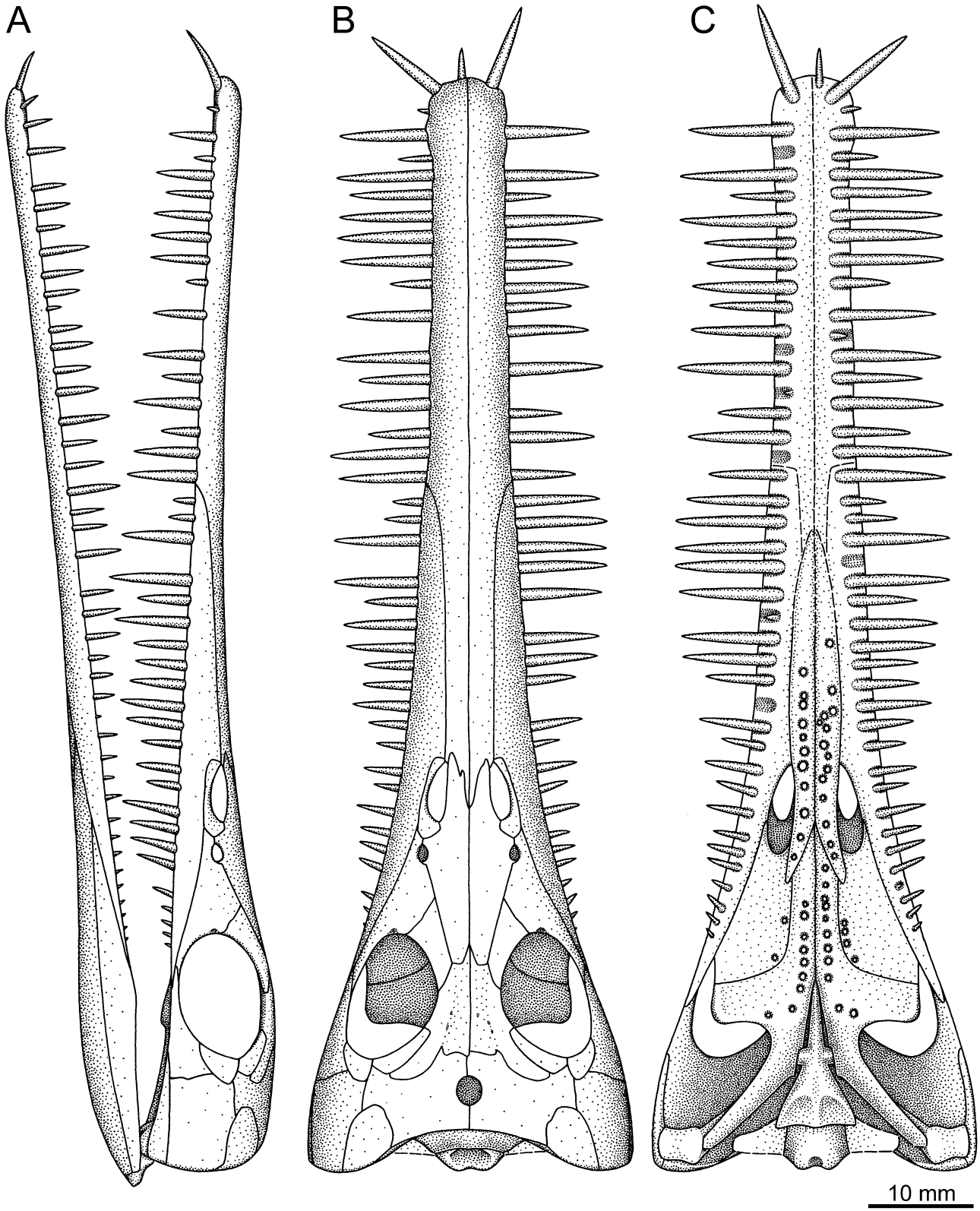

Figure 1. Reconstruction of the skull and the mandible of *Mesosaurus tenuidens* in (A) left lateral, (B) dorsal and (C) palatal views.

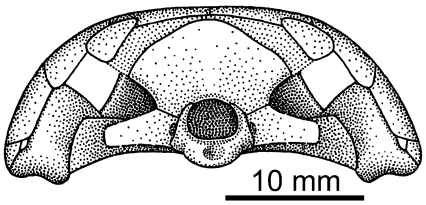

Figure 2. Reconstruction of the skull of *Mesosaurus tenuidens* in occipital view. The regular stipple pattern represents a hypothetical cartilaginous bridge between the skull roof and the braincase.

restoration of the relative proportions of the medial postdentary bones or of the adductor fossa.

In the following description, specimen illustrations are intended to serve in lieu of an exhaustive description, and emphasis is placed on autapomorphies and apomorphies that are shared with other basal amniotes. Plesiomorphies and suture patterns are described only where they serve as morphological landmarks, or when relevant to the subsequent phylogenetic and functional discussions.

Skull roof

The premaxilla (Figs 3, 4) is the largest skull element. It consists of a ventral tooth-bearing portion and a slightly curved dorsal sheet. In contrast to earlier interpretations, the premaxilla contacts the nasal via an oblique, overlapping suture at the level of the external naris. The premaxilla accommodates about 20 teeth with no discernible pattern of long and short (replacement?) teeth (Fig. 3). This contrasts sharply with the condition in *Stereosternum* where there is a distinct pattern of alternating long and short teeth that number no more than 15 (Modesto, 1999b). Tooth morphology is described below in a separate section. The anteriormost premaxillary teeth were highly procumbent (Fig. 4). However, none of the tooth sockets is exposed well enough for description. Judging from alveoli in the opposing portion of the dentary, the premaxillary teeth would have changed gradually from an anteroventral angulation to one approximating 45° more posteriorly.

Despite the greater anteroposterior length of the premaxilla, the maxilla remains the predominant tooth-bearing bone of the upper jaw (Figs 3–6). The anterior end of the maxilla extends well forward of the external naris and so is reminiscent of the condition seen in ichthyosaurs (Massare & Callaway, 1990). There are 24–25 tooth positions in the maxilla, almost all of which are occupied in well-preserved specimens. The tooth row ends below (the level of) the anterior margin of the orbit, and the edentulous posterior tip

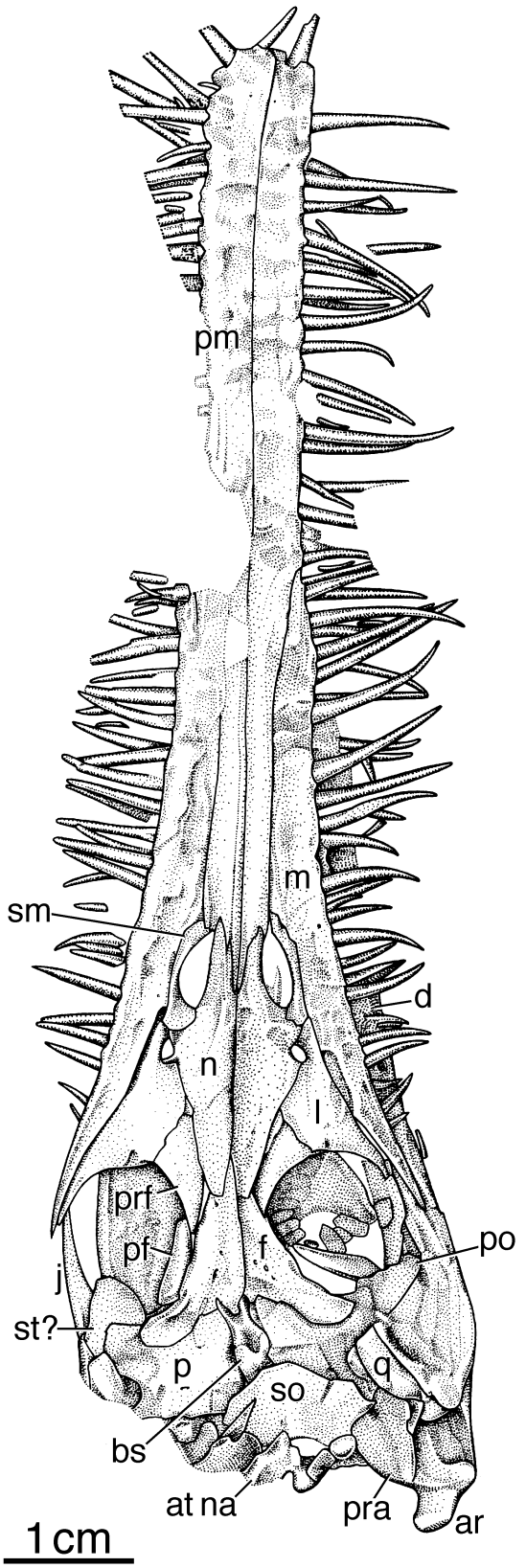

Figure 3. *Mesosaurus tenuidens*, SMNH R207c. Skull in dorsal view.

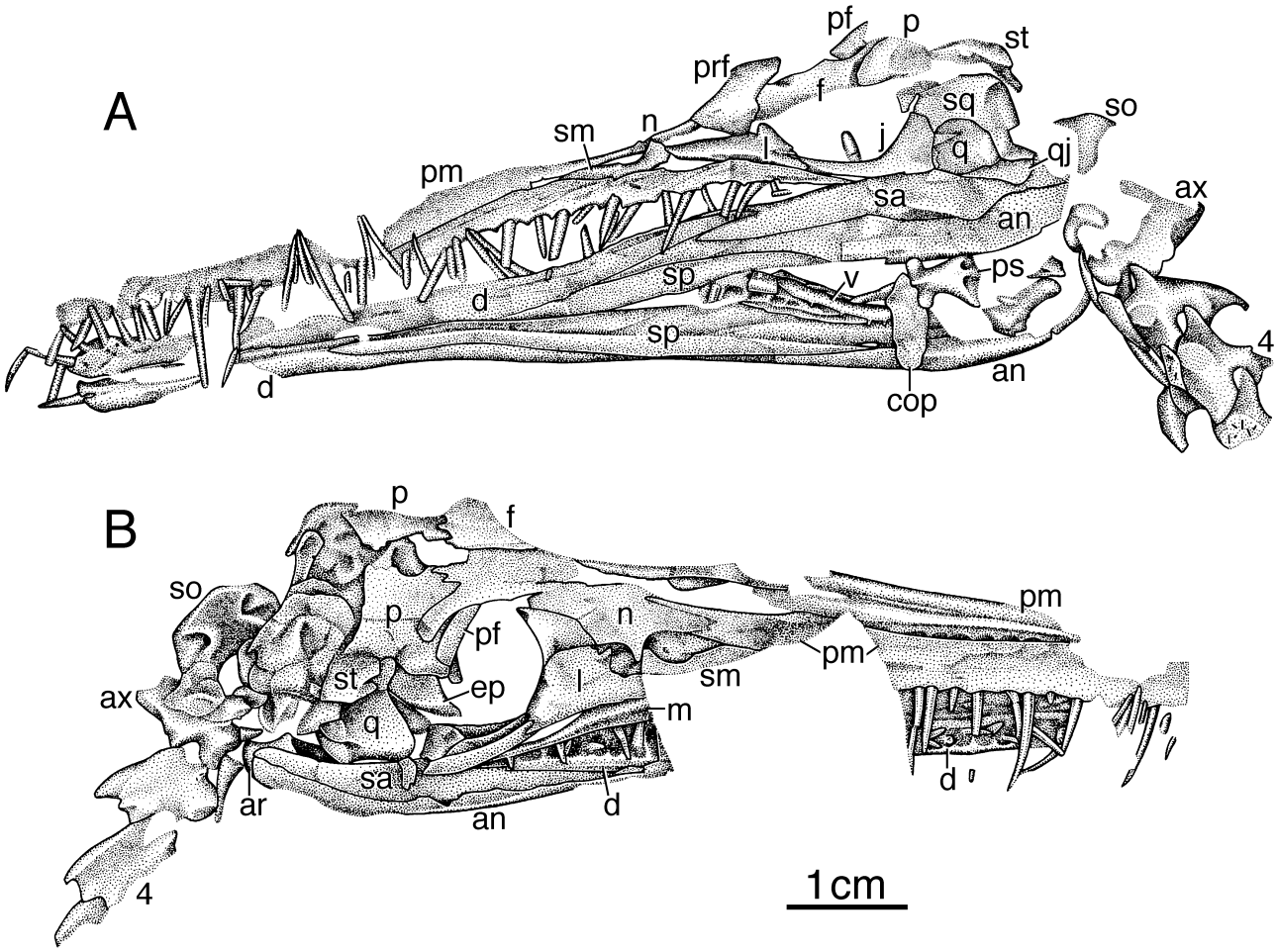

Figure 4. *Mesosaurus tenuidens*, part and counterpart. A, SMNH R208. Skull, mandible and anterior cervical vertebrae in left lateral view. B, SMNH R207a. Skull, mandible and anterior cervical vertebrae in right lateral view. Arabic numerals denote presacral vertebrae in this and subsequent figures.

continues caudally to terminate below the midpoint of the orbit. There does not appear to be a scar or bevelled area on the posteriormost tip that could indicate contact with the quadratojugal. The teeth are anchored in U-shaped excavations (Fig. 5). Whereas the anterior tooth sockets are directed slightly laterally, succeeding sockets become more vertically aligned posteriorly.

The septomaxilla is a transversely compressed element, and its lateral surface is confluent with those of the surrounding roofing bones (Figs 3–6). An elongate anterior process forms the ventral edge of the external naris. The anterior end of this process is expanded slightly and has a small contact with the premaxilla.

The nasal resembles those of other early amniotes in its basic structure. Despite its slightly more elongate appearance, its external midline length is only marginally greater than that of the frontal (Figs 3–5). The highly acuminate anterior end of the nasal underlies the premaxilla, and posteriorly it overlies the frontal. Ventrolaterally, the nasal forms the dorsal border of a subcircular opening unique to mesosaurs that von Huene (1941) called the 'foramen nariale obturatum'. It is a small opening with a diameter approximately one-fifth the long diameter of the external naris.

The lacrimal is characterized by an acuminate anterior end and a long posteroventral process, which extends almost as far posteriorly as the maxilla (Figs 3–6). A rounded notch posterodorsal to the anterior tip forms the ventral margin of the foramen nariale obturatum. The lacrimal duct, its former course indicated by a prominent fault in the lateral surface of the bone in one specimen (Fig. 7), appears to have emptied into the foramen nariale obturatum.

Although the prefrontal appears externally as a simple triangular wedge (Figs 3–6), its ventral process

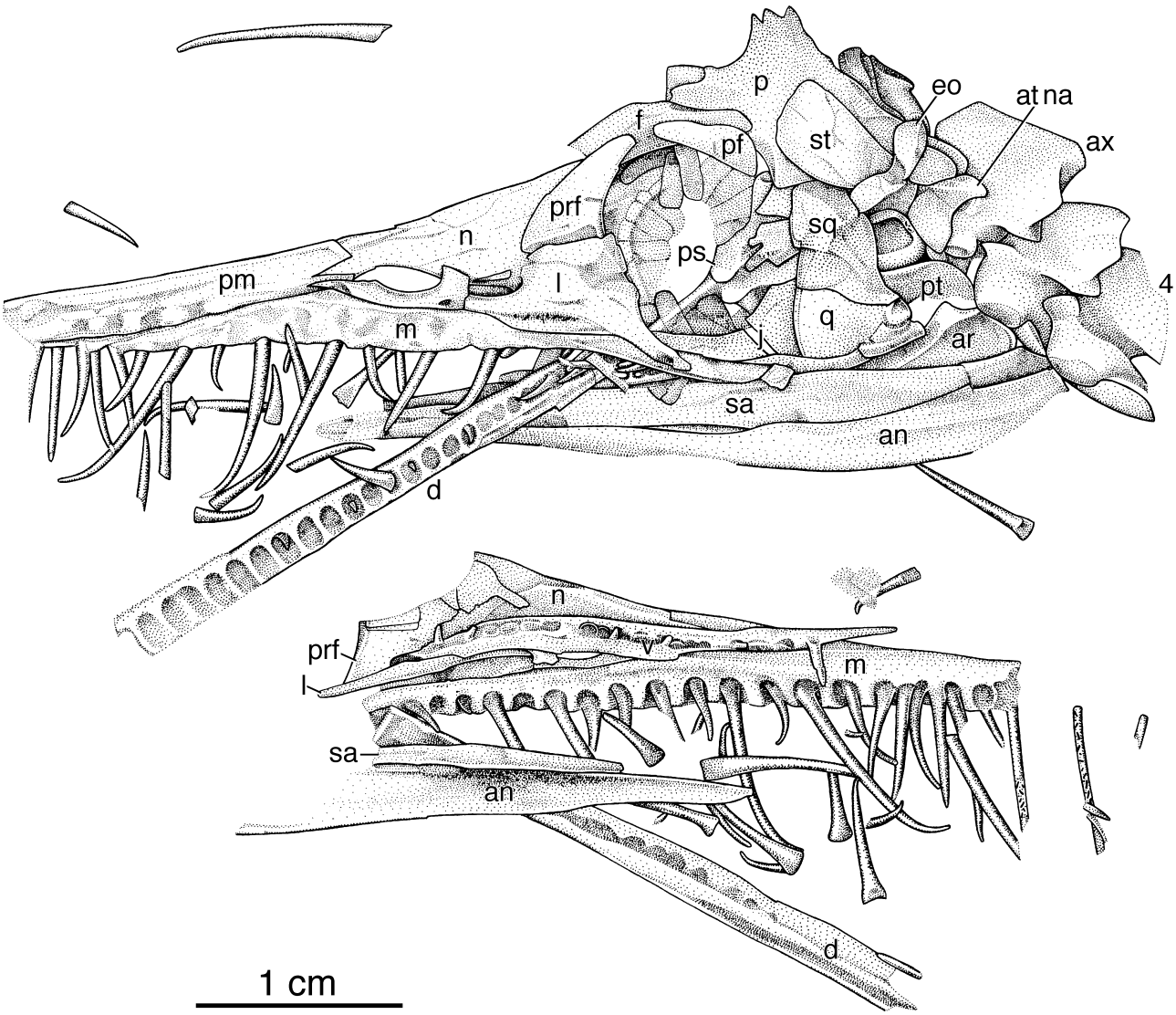

Figure 5. *Mesosaurus tenuidens*, MCZ 4028, part and counterpart. Left lateral view of skull, mandible and anteriormost cervical vertebrae (MCZ 4028b) above, with counterpart of snout and partial mandible in medial view, with associated vomer (MCZ 4028a) below.

is tall and is deeply overlain by the posterodorsal corner of the lacrimal, an arrangement that doubtlessly strengthened the antorbital region (Fig. 5). However, the ventral process is exceedingly thin transversely, and it is unlikely that it contacted the palatine ventrally.

The frontal is transversely broad posteriorly, with a breadth just under one-half its midline length (Fig. 3). Half of its width consists of an extensive, tongue-like posterolateral process that extends between the postfrontal and the parietal. The anterolateral edge of this lappet bears a shallow flange for the reception of the posterior edge of the postfrontal. Both the lappet and the posteromedial portion of the frontal overlie the anterior edge of the parietal. The free edge of the frontal bordering the orbit is raised slightly above the remainder of the bone, resulting in a slight longitudinal depression of the skull roof between the orbits.

The postfrontal is a small crescentic bone that borders the posterodorsal corner of the orbit (Figs 3–6). The bone is widest at its posteroventral end. Despite the interposition of the frontal posterolateral lappet, the postfrontal retains a strong contact with the parietal via an extensive overlapping suture.

The parietal is the most prominent element of the skull table (Figs 3–6). Broader transversely than anteroposteriorly, the parietal extends anterolaterally to underlie the postfrontal and nearly reaches the

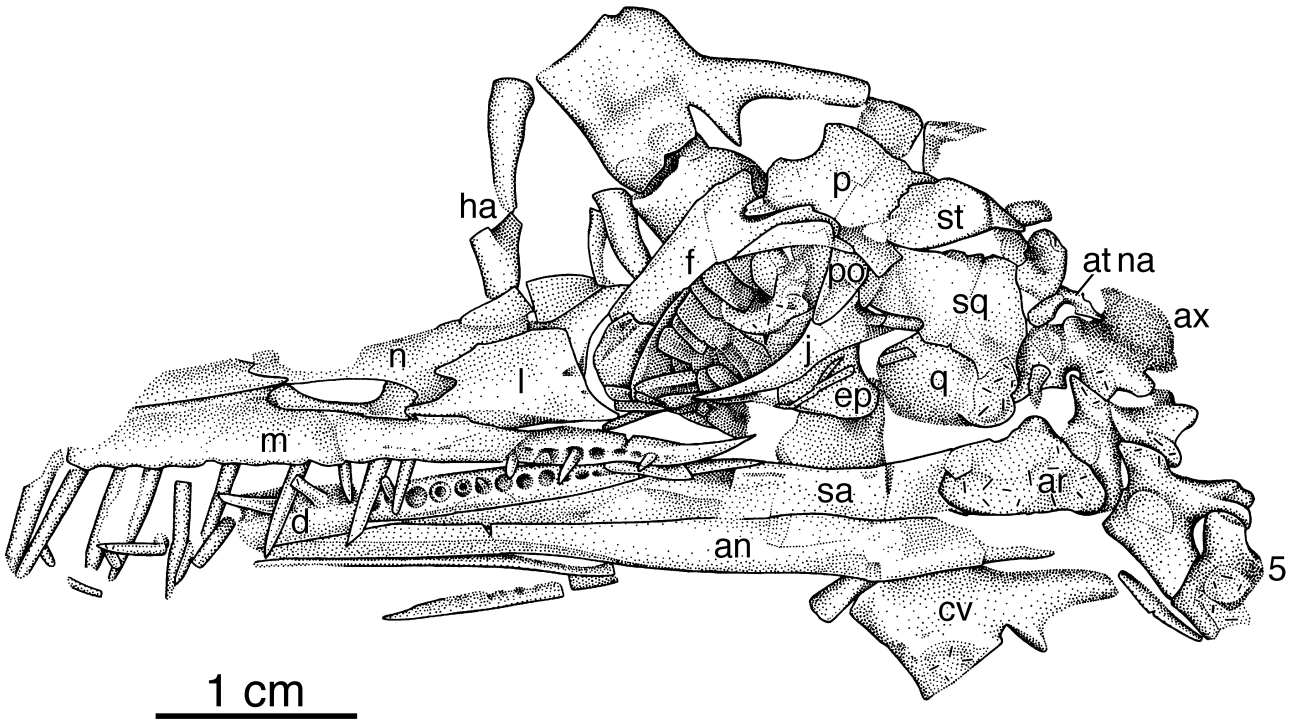

Figure 6. *Mesosaurus tenuidens*. MCZ 4030h. Skull, mandible, cervical vertebrae and caudal vertebrae in left lateral view.

orbital margin. Posterolaterally the parietal is deeply embayed for the reception of the supratemporal (Figs 3, 6). The lateral margin of the bone forms a short but distinct suture with the squamosal, effectively separating the postorbital from the supratemporal. The posterior margin of the parietal is roughly straight and there are no scars preserved which might indicate attachment of postparietals. The parietal foramen is positioned on the approximate midpoint of the interparietal suture. It is slightly elliptical in outline, with the long diameter aligned sagittally.

In strong contrast with von Huene's (1941) description of the jugal as deeply bifurcate posteriorly (thereby suggestive of the presence of a lower temporal opening), examination of his specimens and of more recently collected material reveals that the temporal portion of most mesosaurid jugals is spatulate (Fig. 4). However, the jugal of MCZ 4030 does indeed appear to be slightly concave posteriorly (Fig. 6). Close inspection of this area, however, reveals a shallow shelf on the jugal that would have received the complementary-shaped anterior margin of the squamosal. Aside from its notable thinness, the jugal differs little in shape and relationships from those of captorhinids and protorothyridids. The suborbital process of the jugal tapers anteriorly to an acuminate point.

The postorbital is roughly triangular in outline (Figs 3, 6). It differs from those of other amniotes in that the free margin forming part of the orbit is not markedly thickened and that there is no distinct posterodorsal process. Accordingly, the anteroposterior length of the postorbital is about two-thirds its dorsoventral height. The postorbital is separated posteriorly by the squamosal and the parietal from the supratemporal.

The squamosal, like neighbouring temporal elements, is relatively thin and is usually distorted by the underlying quadrate. However, some squamosals are reasonably well preserved and demonstrate that this bone differs little from those of other amniotes that lack lower temporal fenestrae (Fig. 6). Anteriorly it shared a shallow, overlapping suture with the jugal. The ventral margin was bordered entirely by the quadratojugal. The occipital flange curves gently posteromedially from the temporal portion to contact the dorsal lamella of the quadrate. The medial margin of the flange is free and forms the lateral margin of the post-temporal opening.

The quadratojugal is an elongate bone that forms the ventral margin of the temporal region (Fig. 4). There is no direct evidence regarding whether the quadratojugal contacts the maxilla in specimens of *Mesosaurus*, although in juvenile specimens of *Stereosternum* the former element approaches the posterior tip of the latter but does not make contact with it (my pers. observ.). The available cranial materials suggest that this bone did not extend anteriorly beyond the posteriormost point of the orbit, and reconstruction of

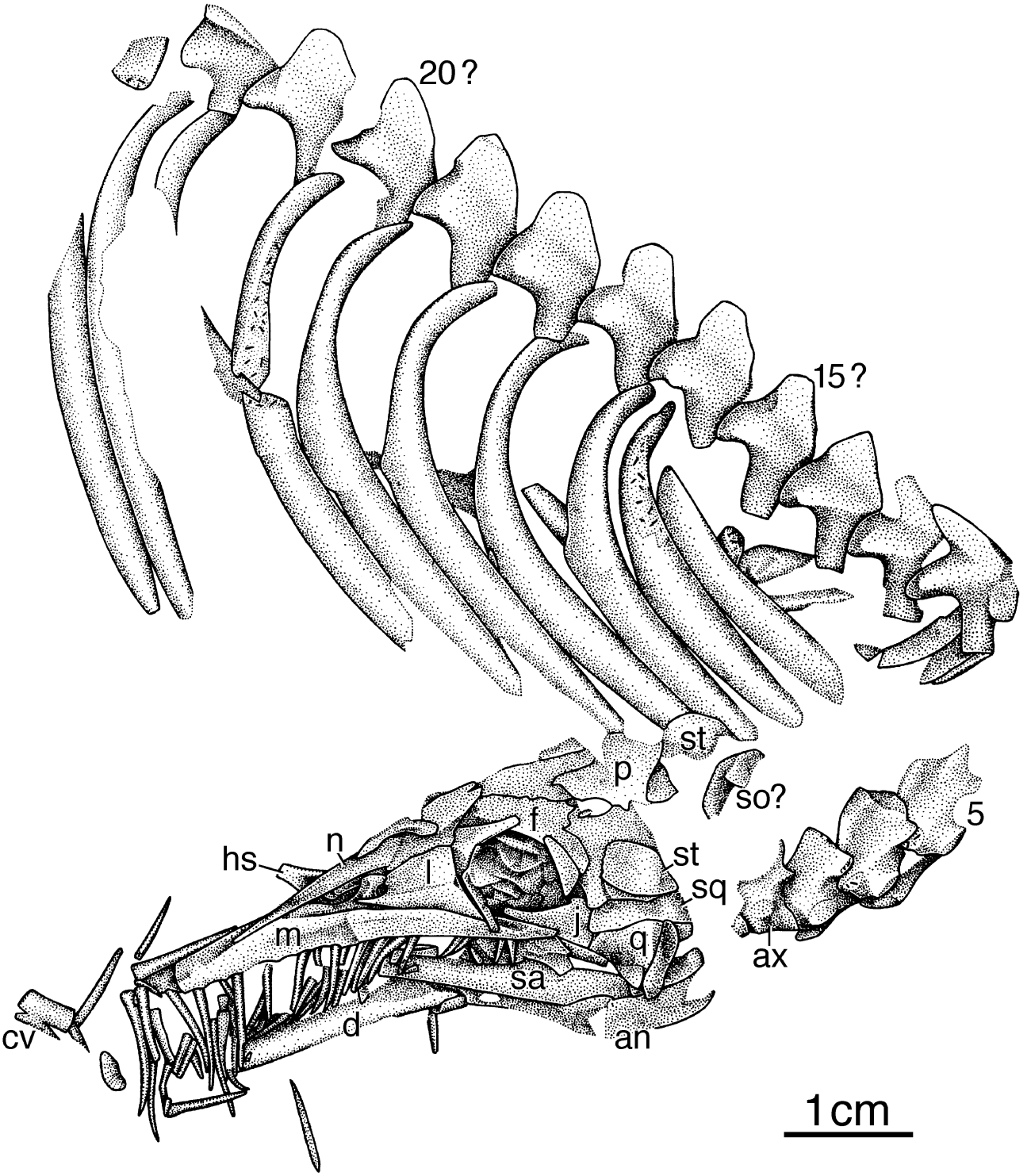

Figure 7. *Mesosaurus tenuidens*, MCZ 4031a. Skull, mandible, and cervical vertebrae in left lateral view, and dorsal vertebrae and ribs in right lateral view.

ventral margin of the cheek suggests strongly that the quadratojugal would have to be extended greatly in order to contact the maxilla.

The supratemporal is an ovoid or rounded quadrangular bone that fits into a deep notch formed by the parietal (Figs 4–6) and in its natural position the long axis of the bone is aligned anteromedially (Fig. 4). The dorsal surface is slightly domed. In immature individuals the supratemporal appears to be an element of substantial size compared with the neighbouring parietal (Fig. 5) but it is relatively smaller in adult specimens (Fig. 4). The supratemporal has a dorsoventrally short occipital flange that contacts the same of the squamosal ventrally and the tabular medially, and contributes to the dorsal and lateral margins of the post-temporal opening.

Surprisingly, the tabular is not preserved in any of the adult skulls. There is a small, teardrop-shaped bone present in GPIT 1757-1, the skull of a juvenile (Fig. 8), and it is in the position the tabular occupies in basal parareptiles and romeriids (*sensu* Gauthier *et al*., 1988). Because this element appears undisturbed and is appressed to the occipital flange of the parietal, it is identified here as the tabular. It is a fully occipital element and makes direct contact only with the supratemporal and the parietal, although it might have made contact with a cartilaginous dorsal extension of the supraoccipital. The tabular does not extend ventrally further than halfway down the occipital flange of the supratemporal. Reconstruction of the occiput suggests that the tabular formed most of the dorsal margin of the post-temporal opening (Fig. 2).

Dermal palate and palatoquadrate ossifications

The ventral surface of the palate is characterized by the absence of the ectopterygoid and by the presence of prominent teeth on the remaining palatal bones. The organization of palatal dentition departs dramatically from that seen in other amniotes, which are characterized by the presence of three denticulate patches on the palatine and the pterygoid. These two bones bear parasagittal lines of socketed, homodont teeth in *Mesosaurus*. There are no teeth on the transverse flange, although the posterior end of the tooth row which borders the interpterygoid vacuity appears to encroach upon the medial base of the flange.

The vomer is elongate and extends posteriorly beyond the choana (Figs 4, 5, 9). It is also remarkably slender, being apparently no wider than is necessary to accommodate an irregular row of up to 20 teeth. They project vertically out of what appear to be shallow, circular sockets. These teeth may be quite long, with a total length up to four and five times the basal diameter, although the length of these teeth exceeds that of only the smallest posterior teeth in the marginal series. The vomers abut one other for most of their length, but posteriorly each vomer curves laterally and comes to overlie the anterior processes of the palatine and the pterygoid in ventral aspect. The dorsal surface of the bone is flat and featureless.

The palatine is a broad, rectilinear bone that lies between the maxilla laterally and an embayment of

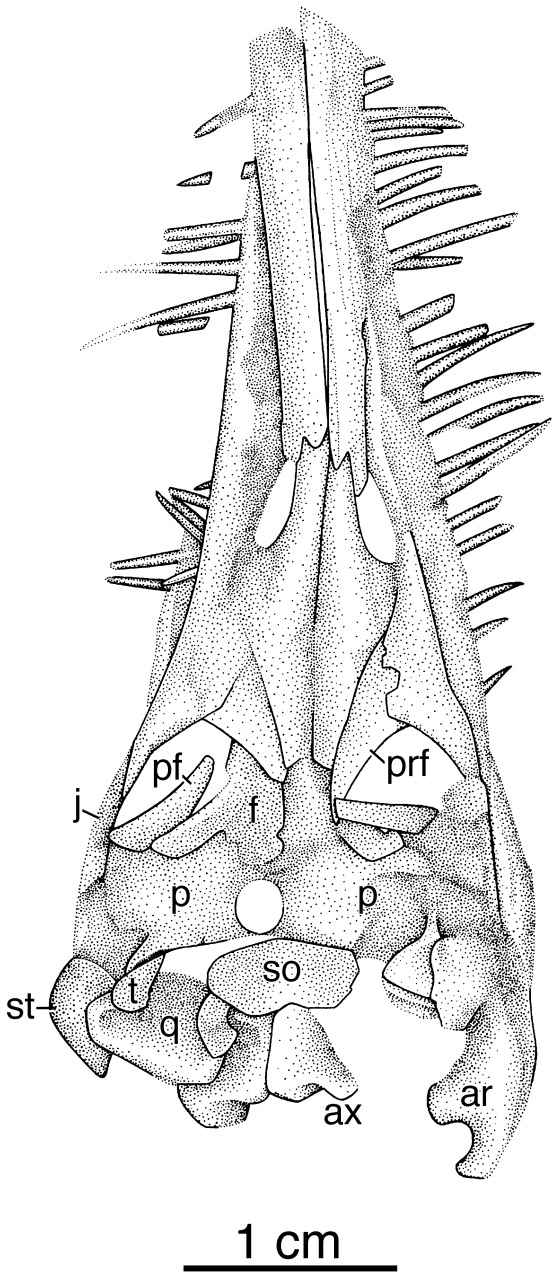

Figure 8. *Mesosaurus tenuidens*, GPIT 1757-1. Skull of immature individual in dorsal view.

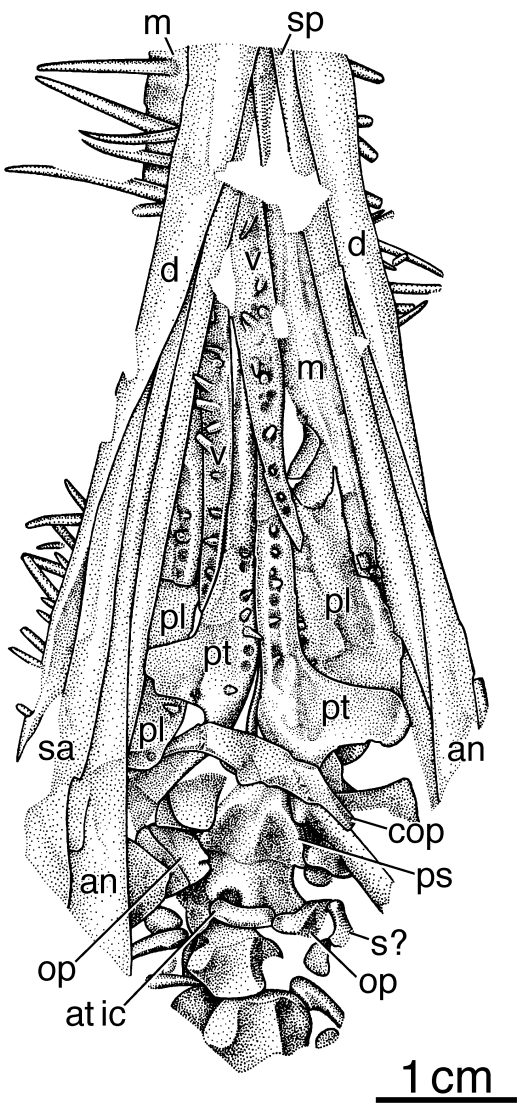

Figure 9. *Mesosaurus tenuidens*, SMNH R212. Palate, braincase, hyoid element, mandible and anteriormost cervicals in ventral view.

the pterygoid medially (Figs 9, 10). It is roughly symmetrical in ventral aspect, and its posterior end is slightly wider transversely than its anterior end. The palatine is deeply bifurcate anteriorly where it forms the posterior half of the internal naris; the medial fork is largely overlapped by the vomer. Except for the presence of up to eight teeth along the medial edge, the ventral surface of the bone is unremarkable. The dorsal surface is similarly devoid of features, except for a rugose thickening of the bone directly above the tooth positions, and a slight transverse thickening, which runs transversely across the dorsal surface just posterior to the internal naris and presumably represents the orbitonasal ridge. The presence of a suborbital foramen cannot be determined with the available material. The lateral margin of the palatine is extremely thin and invariably crushed or distorted in all specimens and the exact nature of the contact with the cheek is uncertain.

The pterygoid differs remarkably from those of other reptiles in terms of the organization of the palatal, the transverse and the quadrate rami, and in the arrangement of the palatal teeth (Figs 9, 10). The anterior, palatal ramus is relatively narrow and, like the vomer, consists mainly of an alveolar strip of bone that appears only wide enough to accommodate one or two rows of teeth. It abuts the palatine laterally for most of its length. A narrow triangle of edentulous bone separates the alveolar ridge from the palatine posteriorly and is continuous with that forming the ventral surface of the transverse flange. The tooth row extends far posteriorly and curves laterally to terminate onto the base of the transverse flange. The teeth are identical in size, shape and spacing to those described for the vomer and the palatine. The transverse flange extends almost directly laterally as a blade-like flange of bone, and clearly does not display the strong posteroventral angulation typical of other basal amniotes where the flange projects well below the ventral rim of the cheek. Teeth are absent from the area on the transverse flange, which typically bears a denticulate patch or distinct row of teeth in terrestrial amniotes. The posterior margin is slightly concave and forms a square angle with the lateral margin. The posterior half of the latter edge is slightly thickened and, judging from its rounded surface, probably did not contact the cheek. The same cannot be said with certainty for the pterygoid anterior to this thickened, rounded portion, as the edge here appears to be confluent with the lateral margin of the palatine, and the bone here is the same thickness as the neighbouring area of the palatine. The quadrate flange of the pterygoid is angled about 35° from the palatal ramus, and it is inclined approximately 50° from vertical (Fig. 10). It is relatively thick proximally, with a convex dorsal surface and a flat medioventral surface. The pterygoid forms the basipterygoid recess. Proximally, there is a separate, elongate tear-shaped scar on the dorsolateral surface of the flange for the epipterygoid, directly above the basipterygoid recess (Fig. 10). A prominent medial projection, termed the postbasal process by Berman *et al*. (1995), marks the area bordering the posterior margin of the recess, and appears to have buttressed the basipterygoid joint. The medial surface of the quadrate flange is smoothly finished, with no development of a tympanic (arcuate) shelf. Posterior to the basipterygoid recess, the quadrate flange becomes blade-like and increases slightly in dorsoventral height.

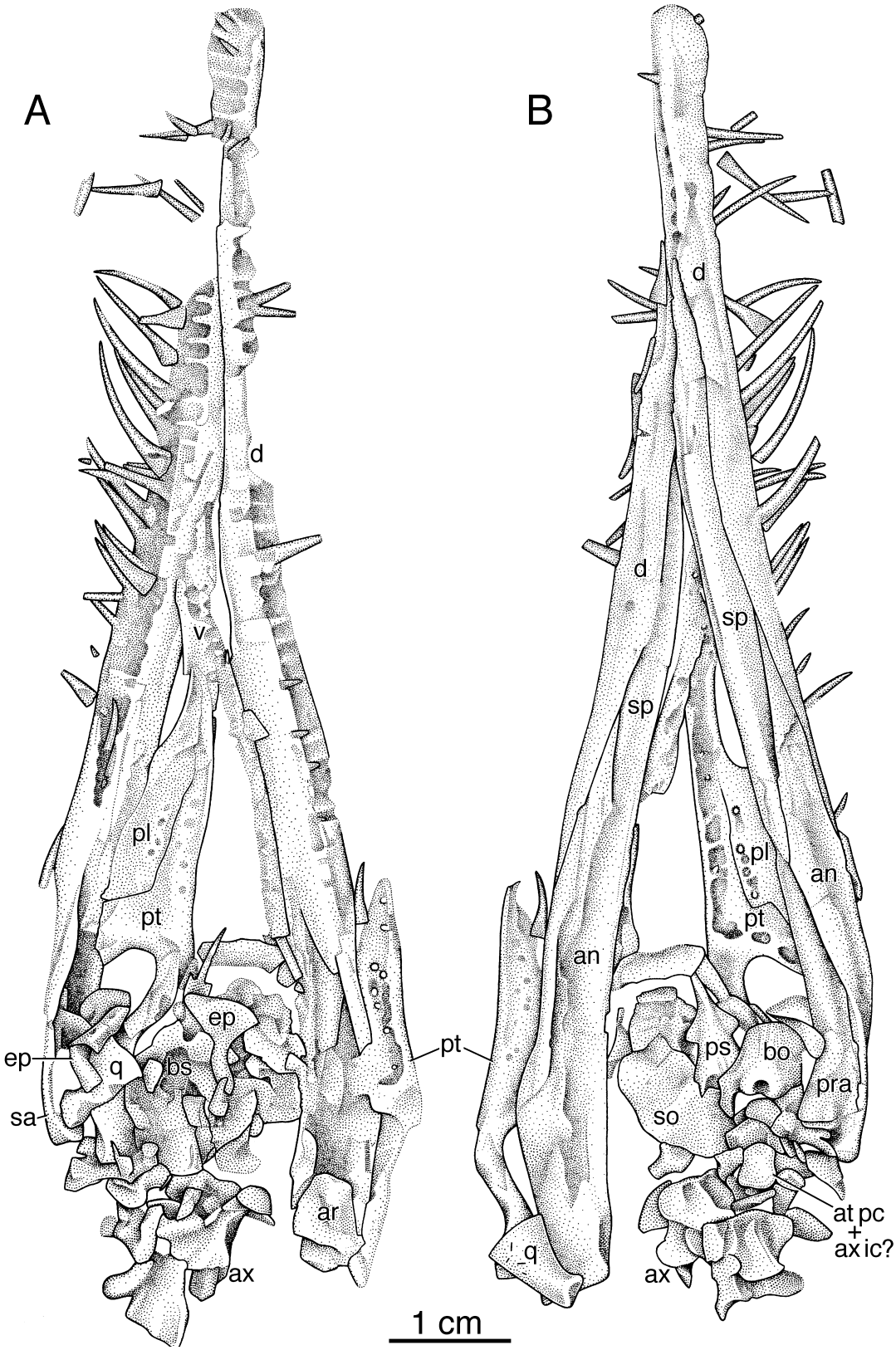

Figure 10. *Mesosaurus tenuidens*, SAM PK-K8381 (part and counterpart). Palate, braincase, mandible and anteriormost cervical vertebrae in (A) dorsal and (B) ventral views.

The epipterygoid is present in several specimens, but is seen in its entirety only in SAM PK-K8381 (Fig. 10). This bone resembles closely those of other basal amniotes in possessing a triangular base and a posteriorly curving dorsal process. The anterior end of the base is the thickest part of the bone, but it does not contribute to the basipterygoid recess. Smoothly surfaced on both sides, the triangular base of the epipterygoid is roughly 60% longer than it is high. The dorsal process is subcircular in cross-section and forms approximately half the total height of the bone.

Braincase

As in many other early amniotes, the braincase of *Mesosaurus* is marked by fusion among its constituent elements. The basisphenoid and the parasphenoid are always fused together indistinguishably, as are the basioccipital and the exoccipitals. Neither the prootic nor the sphenethmoid is recognizable in any of the available specimens. The absence of the postparietal appears to be genuine because there are no sutural markings on the posterodorsal surface of the supraoccipital that would suggest the presence of that dermal bone.

The cultriform process of the parasphenoid is slightly longer than the post-cultriform length of the bone (Figs 4, 10). The latter displays a progressive increase in transverse breadth posteriorly, and has the outline of an isosceles triangle in ventral view. Just posterior to the base of the cultriform process the basipterygoid processes project directly laterally. In ventral view these processes are nipple-shaped (Fig. 4), but the dorsal surface of each is slightly flattened and presumably represents the articulating facet. Apart from having a slightly constricted neck region, each basipterygoid process is also distinguished from the main body of the bone by a narrow groove, the vidian sulcus (Heaton, 1979). There is no evidence of foramina for the internal carotid arteries on the ventral surface of the parasphenoid, suggesting that these vessels entered the bone further dorsally, possibly via vidian (parabasal) canals, as described for millerettid and procolophonid parareptiles (Gow, 1972; Kemp, 1974; Spencer, 2000). However, the available materials do not allow for the determination of the presence of such canals in mesosaurs. In dorsal view, the cristae trabeculares, located above and dorsal to the basipterygoid processes, extend dorsolaterally as stout, shallow flanges (Fig. 10A). The retractor pit is relatively small, and its diameter is exceeded by that of the basipterygoid process. The clinoideus processes to either side of the retractor pit give rise to poorly ossified processi sellares, which are separated by a prominent notch. Only the base of the dorsum sellae appears to have been ossified in the largest specimen in which it is visible (SAM PK-K8381, Fig. 10A). Ventrally, the region leading from the base of the cultriform process posteriorly to the bases of the cristae ventrolaterales is strongly convex transversely, and as such represents the most ventral region of the parasphenoid. The cristae ventrolaterales extend posterolaterally from the convexity as sharp ridges and define the lateral limits of the bone posteriorly. A low rounded ridge runs sagittally along the ventral surface to the posterior margin of the bone; anteriorly, the base of this ridge is continuous with that of the convex, anterior portion of the bone. A narrow groove in turn runs atop the median ridge along the ventral midline. Paired fossae, acutely parabolic in outline, lie between the angles formed by this median ridge and the two cristae (Figs 4, 9). In the organization of these ventral ridges and the presence of paired fossae, the parasphenoid of *Mesosaurus* resembles closely that illustrated for the holotype of the Carboniferous reptile *Paleothyris acadiana*, MCZ 3481 (Carroll, 1969: fig. 1). Parenthetically, MCZ 3484, a paratype of *P. acadiana*, preserves a parasphenoid with a single, median furrow that extends from the base of the cultriform process to the suture with the basioccipital (Carroll, 1969: fig. 5). This is the condition seen in most Palaeozoic amniotes, and its presence in MCZ 3484 suggests that this specimen is not referrable to *P. acadiana*. MCZ 3484 might be attributable to *Archaeothyris florensis*, a synapsid present at the same locality, and the only other contemporaneous amniote known from adequate materials (Reisz, 1972).

The opisthotic is a robust, irregularly shaped bone which resembles that of a small captorhinid illustrated by Heaton (1979: fig. 28). The medial portion abutting the other braincase elements is clearly the largest region of the bone, and a notch for the vagus nerve is present on the ventromedial margin of the bone (Fig. 9). There is no identifiable otic flange. The bone appears to decrease gradually in cross-sectional thickness towards its distal tip. The paroccipital process appears to have made contact with neither the quadrate nor the skull roof.

The basioccipital and the exoccipitals are fused indistinguishably together. The basioccipital portion is a shield-like plate forming the floor of the cavum cranii posteriorly (Fig. 10) but it is unclear if contact was made with the basisphenoid. Low, parallel median ridges extend anteriorly from the condyle along the ventral surface of the bone. The ventral surface is otherwise smooth and featureless, with not even the slightest indication of the anterolateral tubera seen in other amniotes (e.g. *Captorhinus*; Modesto, 1998: fig. 6). The hemispherical condyle is pierced deeply by the notochordal pit, which appears to encroach upon

the dorsal margin of the condyle in the form of a notch that is visible in ventral view (Fig. 10). The exoccipitals extend dorsally from the condyle as slender crescents of bone. The thick medial edge of each is slightly rounded where it forms the lateral margin of the foramen magnum, but thins laterally where contact is made with the supraoccipital dorsolaterally and the opisthotic ventrolaterally. A slight concavity on the lateral edge marks the exoccipital contribution to the vagus foramen.

The supraoccipital is invariably the best preserved and most easily identifiable occipital element (Figs 3, 4, 8, 10). It has been described as broad and plate-like (Laurin & Reisz, 1995), but in truth it is a relatively narrow element as in other basal reptiles because its transverse breadth is less than that of the parietal. As in *Captorhinus* (Modesto, 1998), the main body of the bone is slightly arched posteriorly in horizontal section, but not as dramatically. The thick dorsal margin is slightly bevelled and may have abutted the posterior margins of the parietals either directly or via a cartilaginous cap. The lateral edges are slightly concave in the largest specimens (Fig. 3) and clearly mark the medial borders of the post-temporal openings. The ventral border is dominated by the notch forming the dorsal margin of the foramen magnum. The anterior surface of the supraoccipital can be divided into a median, hourglass-shaped depression and paired, lateral rugosities (Fig. 4B). The depression is dorsoventrally symmetrical, and the two halves are almost separated from one another by median extensions of the lateral rugosities, again as in *Captorhinus*. The lateral rugosities are well developed, but are deeply incised by chevron-shaped channels that formed part of the membranous labyrinth of the inner ear. The channels appear to end blindly at the dorsal edge of the bone, but ventrally they open onto the lateral margin and presumably continued into the opisthotic. The posterior surface of the supraoccipital is smooth and devoid of any scars or rugosities.

Well-preserved stapes are not identifiable in most skulls. Much of the stapes is present in SMNH R212 (Fig. 9). By comparison with the stapes of AMNH 23799, a small juvenile of *Stereosternum* (my pers. observ.), the larger of the two flanges in SMNH R212 appears to be the dorsal process. The quadrate process of the latter specimen is quadrangular in outline and approximately as tall as the dorsal process is wide, which suggests that the quadrate process did not undergo dramatic increase in size during ontogeny, assuming there are no major differences in the growth of the braincases of *Mesosaurus* and *Stereosternum*. The stapes of AMNH 23799 possesses a well-formed footplate and stapedial foramen, features that cannot be determined in the available material of *Mesosaurus*.

Mandible

Most mandibular elements are elongate, as is the jaw symphysis, which accounts for approximately 40% of the total length of the jaw. The anterior end of the mandible is slightly spatulate in ventral aspect. Teeth are present only on the dentary. There are no meckelian openings, and the lingual surface of the mandible posterior to the symphysis was sheathed mostly by the splenial.

The dentary is extremely slender and elongate Figs 4, 6, 10–12). The largest known dentary (Fig. 11) accommodates approximately 54 teeth. As inferred for the upper marginal series, the orientation of the dentary teeth can be seen to change gradually from a procumbent stance anteriorly to a more vertical orientation posteriorly. The two dentaries share an extensive sagittal suture that accounts for most of the jaw symphysis (Fig. 11). The postdental region of the dentary forms the coronoid eminence and is overlapped ventrolaterally by the surangular.

The splenial is an elongate bone that is appressed to the medial surface of the dentary for most of its length (Figs 9, 11). It is predominantly a lingual element and has only a slight lateral exposure along the ventral margin of the jaw. It extends anteriorly halfway to the midpoint of the jaw symphysis, and posteriorly it extends to the adductor fossa (Fig. 10). The lingual surface of the bone is smoothly finished and convex lingually in transverse section.

As in other reptiles, there is a single coronoid. Although it is the least exposed mandibular element of the available specimens, it is seen almost in its entirety in MCZ 3373 (Fig. 12). What can be noted here is that the coronoid has a short, sharply pointed anterior end, an even shorter acuminate posterodorsal process and a posteroventral process that contributes to the medial wall of the adductor fossa.

The prearticular (Fig. 10) largely resembles that of other reptiles in its basic relationships to neighbouring elements. It appears to be only slightly longer than the adductor fossa and ends just a couple of millimetres short of the last tooth position. The posterior end is broader and more rounded in medial aspect than the anterior end, and it covers the ventromedial surface of the articular (Figs 3, 10).

The surangular is a long, simple sheet of bone (Figs 4–6, 9, 10). Although it is clearly not as long as the dentary or the splenial, its elongate nature is apparent when compared with the skull: the rostral tip of the surangular extends anteriorly past the level of orbit to that of the external naris (Fig. 1C). Anterodorsally, the surangular overlies much of the lateral surface of the posterodorsal tip of the dentary. Interestingly, its suture with the dentary is longer than the suture between that bone and the angular; the reverse

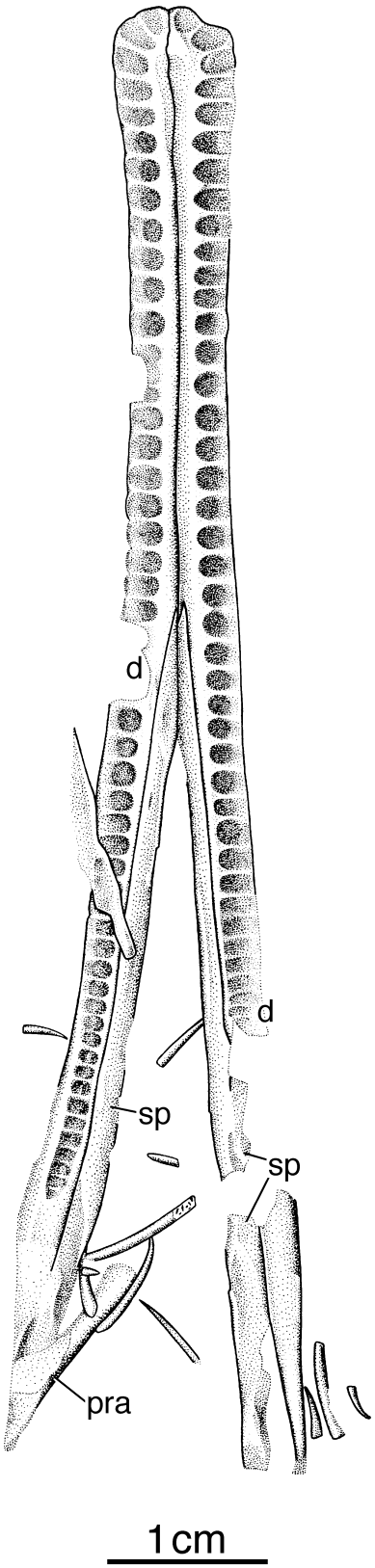

Figure 11. *Mesosaurus tenuidens*, SMNH R202. Mandible in dorsal view.

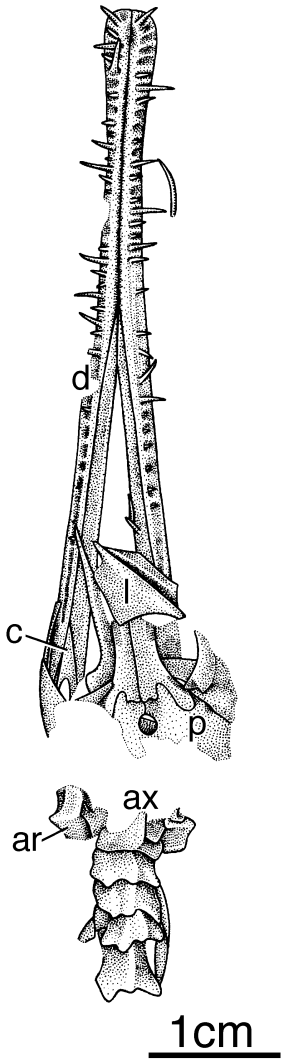

Figure 12. *Mesosaurus tenuidens*, MCZ 3373 (in part). Skull roof, mandible, and cervical vertebrae 2–6 in dorsal view.

is usually the case for amniotes. Posteriorly it overlies the dorsal half of the lateral surface of the articular; the posteriormost tip contributes to the basal, lateral portion of the retroarticular process of the articular. In contrast to the markedly convex dorsal margins in other reptiles, the dorsal margin of the surangular is slightly concave in lateral aspect.

Except for its great length, the angular is little modified over the plesiomorphic form of a large, ventrolaterally convex bone spanning the posteroventral portion of the mandible (Figs 4–6, 9, 10). It is largely an external jaw element in mesosaurs; its lingual exposure is probably limited to a narrow strip along the ventral margin of the mandibular ramus. The depth of the bone is greatest posteriorly; it decreases

gradually in height anteriorly to a sharp tip. The most notable feature, aside from its elongation, is its broadly convex ventral margin in lateral aspect. Posteriorly, the angular sheathes the ventrolateral base of the retroarticular process.

The articular, distinguished in lateral view by a large retroarticular process and a prominent post-condylar process, is the most robust mandibular element Figs 3–6, 10). Most of the lateral surface of the articular is flat and is covered by the posterior processes of the surangular and the angular. The lateral surface of the retroarticular process is confluent with that of the mandible proper. It is compressed obliquely and in life would have leaned laterally in posterior view. Its posteromedial margin is slightly swollen, which gives the process its concave dorsal border when viewed in lateral aspect. The post-condylar process projects dorsally from the base of the retroarticular process. In lateral view the post-condylar process cups the posteroventral surface of the quadrate's condyles and may have served to prevent hyperabduction of the lower jaw. A well-developed pterygoideus process projects medially from the main body of the bone; as in other amniotes, the ventral surface of this process was sheathed by the prearticular. The articulating surfaces receiving the condylar portion of the quadrate are simple, anteroposteriorly orientated concavities separated slightly by a parasagittal ridge. The articular is truncated immediately anterior to the articulating surfaces, but in life presumably continued forwards as cartilage.

Dentition

The marginal teeth are long, slender and sharply pointed. The length of the largest teeth exceeds the length of five tooth positions (Fig. 5); in comparison, the longest teeth in *Stereosternum* are approximately three tooth positions in length (Modesto, 1999b). Expressed in other relative terms, the longest teeth in *Mesosaurus* are just over 10% the length of the skull, whereas those of *Stereosternum* are no more than 7% skull length. The teeth of *Mesosaurus* are absolutely longer than those of *Stereosternum*; even those of immature *Mesosaurus* exceed those of mature *Stereosternum* specimens of the same skull length by several millimetres (Rossmann, 2002). Relative to their basal diameters, the longest teeth in *Mesosaurus* are very slender, with a basal diameter approximately 11% the length of the tooth from base to tip. The gradual change in the orientation of the teeth along the tooth row is described above for the premaxilla, the maxilla and the dentary.

Teeth are basically homodont with circular cross-sections. The surfaces of well-preserved teeth do not exhibit wear, and very fine fluting is visible on the tips of the teeth under light microscopy. The teeth display a gradual decrease in diameter distally (Figs 3–6), and in life the tips appear to have curved lingually (i.e. downwards for premaxillary and maxillary teeth and upwards for dentary teeth). This inward curvature is not immediately apparent in specimens with a full complement of teeth, but is suggested strongly by the observation that teeth with tips curving anteriorly and those curving posteriorly are preserved in roughly equal proportions. The lingual curvature of the tips may have served to counteract the canting of the teeth, as suggested for the posterior teeth of the plesiosaur *Cryptoclidus eurymerus* (Brown, 1981). No single tooth in either the premaxillary or the maxillary series can be described as caniniform, nor is there evidence of a caniniform region in the upper dentition. Except for the reduction in length and diameter at the posterior end of the series, there does not appear to be any organization of the teeth with respect to size in *Mesosaurus*. Presumably the randomly positioned smaller teeth seen in relatively complete dentitions are replacement teeth that had not reached their full length at the time of death.

The marginal teeth are implanted in protothecodont fashion in shallow, regularly spaced pits (Fig. 5). All but the most posterior pits occur in U-shaped excavations that are set apart from neighbouring tooth positions by low walls (Fig. 11). Ankylosis of the teeth to the jaw does not appear to have been strengthened by the extensive bone of attachment seen in some early amniotes (de Ricqlès & Bolt, 1983). The reduction or absence of such anchoring bone, combined with the thin construction of the tooth bases (Fig. 6), probably accounts for the commonly seen displacement of mesosaur teeth and their complete loss from many disarticulated tooth-bearing elements. Resorption pits are never present on the lingual surface of the alveolar ridges of the tooth-bearing bones, and when present the tips of replacement teeth are seen in the exact centre of the alveoli; the marginal teeth can be considered to be 'alveolarized' *sensu* Rieppel (2001). Together, these observations suggest strongly that the manner of tooth replacement in *Mesosaurus* is derived with respect to that described for other Permo-Carboniferous amniotes, in which replacing teeth appear in lingually positioned resorption pits in the bone that supports soon-to-be-shed teeth (Bolt & DeMar, 1974; de Ricqlès & Bolt, 1983).

Palatal teeth are present on the vomers, the palatines and the pterygoids. The palatal teeth are homodont and subcircular in cross-section, but unlike those of the marginal series, they are straight and vertically orientated (Figs 5, 9). Most palatal teeth are much smaller than the shortest marginal teeth, but the attached remains of others (Fig. 5) indicate that some equalled at least average-sized marginal teeth in

basal diameter. The palatal teeth were set in shallow sockets, although crushing in some specimens has obscured the boundaries of several pits. Replacement scars are visible in a few specimens, indicating that the alveolar regions were reworked during successive episodes of replacement and that the palatal teeth were not alveolarized.

Hyoid apparatus

The hyoid is present in several specimens as a single median body, the copula (Figs 4, 9). This element appears to be at least as thick dorsoventrally as the tooth-bearing portions of the palatal bones. The copula is distinguished from those of other basal amniotes in being a transversely broad element. The slightly irregular outline of the copula of SMNH R208 (Fig. 4) suggests that it was not fully ossified even in this large, presumably mature individual. The lateral ends of the well-ossified copula of SMNH R212 (Fig. 9) terminate with short, tapering processes. These 'cornua' are directed slightly posteriorly and add greatly to the transverse breadth of the copula; the fully formed element in this individual is almost twice the width of the parasphenoid. It is uncertain if the cornua represent co-ossified ceratohyoids. The latter are present in many basal amniotes as paired, rod-like bones (Gow, 1972; Heaton, 1979; Carroll & Lindsay, 1985; Reisz, Dilkes & Berman, 1998) that are never seen in mesosaurid specimens.

PHYLOGENETIC ANALYSIS

Mesosaurs formed a sister-group relationship with a clade comprising all other non-synapsid amniotes in a phylogenetic analysis by Laurin & Reisz (1995), who attached the name 'Sauropsida' to the clade of non-synapsid amniotes and the name 'Reptilia' to the mesosaurid sister group. Reptilia, as defined phylogenetically by Laurin & Reisz (1995), was a crown clade, and as a result mesosaurs were the only stem sauropsids in their tree. Following an analysis that used an augmented version of the data matrix of Laurin & Reisz (1995), Modesto (1999b) suggested that mesosaurs formed a clade with millerettids, pareiasaurs, procolophonoids and turtles. This topology resurrected Gauthier *et al.*'s (1988) 'parareptiles' clade, but Modesto attached the name 'Anapsida' to the clade of mesosaurs, millerettids, pareiasaurs, procolophonoids and turtles because Gauthier's (1994: 138) stem-based definition ('chelonians and all other amniotes more closely related to them than they are to saurians') for Anapsida preceded Laurin & Reisz's (1995: 186) stem-based definition for Parareptilia ('testudines and all amniotes more closely related to them than to diapsids'). The name 'Parareptilia' (*sensu* deBraga & Reisz, 1996) was retained by Modesto (1999b) for the clade of millerettids, pareiasaurs, procolophonoids and turtles.

Mesosaurs were excluded from Reptilia by Laurin & Reisz (1995) because the former were regarded as possessing the plesiomorphic condition for five of seven characters (the remaining two being indeterminate). Because all these characters concern morphology of the skull, it is desirable to re-examine each in detail here in light of the new information on mesosaurid cranial anatomy. In the following paragraphs, each reptilian apomorphy of Laurin & Reisz (1995) is discussed; character numbering, enclosed in parentheses, follows those authors.

Tabular small or absent (17)

According to Laurin & Reisz (1995), mesosaurs share the presence of a large tabular with synapsids, diadectomorphs and the basal batrachosaur genus *Seymouria*. However, if the tabular was a large bone in mesosaurs, one would expect it to be preserved in many skulls. Only a single specimen of *Mesosaurus* studied here can be described as preserving a tabular (Fig. 7), where it is a relatively small bone resembling those of reptiles such as *Protorothyris acadiana* and *Milleretta rubidgei*. This apomorphy either diagnoses a more inclusive clade of amniotes (i.e. 'Sauropsida') or it diagnoses a Reptilia that includes mesosaurs.

Suborbital foramen present (49)

The presence or absence of this opening could not be confirmed in mesosaurs by Laurin & Reisz (1995). Because they used delayed-transformation optimization, this character was recognized as an ambiguous synapomorphy of reptiles in their analysis. The available specimens of *Mesosaurus* are unhelpful concerning the presence or absence of a suborbital foramen.

Parasphenoidal recess for cervical musculature (50)

Mesosaurs were described as having the plesiomorphic state of this apomorphy, the presence of paired excavations on the ventral surface of the parasphenoid. This condition was ascribed also to some early synapsids and limnoscelid diadectomorphs (Laurin & Reisz, 1995). Paired excavations are indeed present in *Mesosaurus*, the only mesosaur in which the ventral surface of the parasphenoid can be examined. However, virtually identical excavations are present in the holotype of the basal eureptile *Paleothyris* (Carroll, 1969). Somewhat similar excavations are present on the parasphenoid of the basal synapsid *Basicranodon fortsillensis* (Vaughn, 1958; synony-

mized with *Mycterosaurus longiceps* by Reisz, Wilson & Scott, 1997). The condition seen in limnoscelids (e.g. *Limnoscelis paludis*: Fracasso, 1987; *L. dynatis*: Berman & Sumida, 1990) is similar to that seen in *Mesosaurus* and *Paleothyris*, but differs in that anteriorly the midline ridge is distinct from the midline confluence of the basitubera. Accordingly, the limnoscelid condition might not be strictly homologous with that exhibited by the amniotes mentioned here, and perhaps it should have been coded as a separate state by Laurin & Reisz (1995). The absence of paired recesses was regarded as apomorphic by Laurin & Reisz (1995), although this condition was present in their ultimate outgroup *Seymouria*. Lee (1995), by contrast, regarded the absence of paired excavations as plesiomorphic for amniotes. The evolution of this character appears to be more complex than outlined by Laurin & Reisz (1995).

Parasphenoid wings absent (51)

This apomorphy is somewhat problematic in that the term 'parasphenoid wing', which Laurin & Reisz (1995) use to refer to posterolateral extensions of the parasphenoid, differs from its long established use by workers such as Olson (1947), who used it to describe either of the parasphenoid tubera. Laurin & Reisz (1995) regard the presence of 'broad parasphenoid wings' in mesosaurs, basal synapsids, diadectomorphs and *Seymouria* as the plesiomorphic state, and the absence of such wings, which they ascribe to all their reptilian taxa, as the apomorphic condition. However, there is no posterolateral process of the parasphenoid in mesosaurs: in ventral view the crista ventrolaterales is narrow and the lateral surface drops precipitously to the lateral margin of the bone. If Laurin & Reisz (1995) are referring to the breadth of either basitubera, then they have coded mesosaurs incorrectly, but if they are referring merely to the transverse breadth of the parasphenoid, then there is a problem because Laurin & Reisz (1995) did not quantify what they regarded as 'broad' and 'narrow'. Modesto (1998) reinterpreted this character by measuring the maximum breadth across the basitubera against the minimum width of the body of the parasphenoid (immediately posterior to the basipterygoid processes). In this manner it was demonstrated that the parasphenoids of mesosaurs, basal synapsids and captorhinid reptiles were of similar dimensions. The presence of 'broad' parasphenoid wings in captorhinids alone would render the evolution of 'narrow' wings in other reptile groups uncertain in the Laurin & Reisz (1995) tree. Clearly, the evolution of this character is much more complicated than reconstructed by those authors.

Supraoccipital anterior cristae present (54)

Heaton (1979) was the first worker to describe anterior cristae in the supraoccipital of a Palaeozoic reptile. The presence of supraoccipital anterior cristae has since been regarded as a reptilian synapomorphy (Heaton & Reisz, 1986; Gauthier *et al.*, 1988; Laurin & Reisz, 1995). Among extant reptiles this feature is documented in lizards (e.g. Oelrich, 1959), where it arises from an alar process that is formed with the prootic (Modesto, 1998: fig. 8e, f). Re-examination of Heaton's (1979) materials failed to confirm the presence of either an anterior crista or an alar process in captorhinids (Modesto, 1998). Similarly, Evans (1986, 1987) did not report anterior cristae in the early diapsids *Youngina capensis* and *Prolacerta broomi*. Modesto (1998) concluded that the presence of anterior cristae probably diagnoses a less inclusive clade of reptiles.

Supraoccipital plate narrow (55)

Mesosaurs were described as possessing relatively broad supraoccipitals, a condition ascribed also to both synapsids and diadectomorphs and interpreted as plesiomorphic by Laurin & Reisz (1995). Those authors regarded a supraoccipital as 'broad' if it extended laterally further than the postparietal (Laurin & Reisz, 1995), a definition that is problematic for mesosaurs because they lack a postparietal. For the matter, this definition is also problematical for captorhinids, which have a postparietal that occupies the former area of the absent tabular and extends far laterally to contact the supratemporal (Modesto, 1998). The supraoccipital of *Mesosaurus* resembles that of *Captorhinus*, except that it lacks the median dorsal and dorsolateral processes characteristic of captorhinids (Heaton, 1979; Modesto, 1998). The mesosaurid supraoccipital might then be considered 'narrow', based on its similarity to those of captorhinid reptiles. Furthermore, the supraoccipital of *Mesosaurus* forms only the median border of the post-temporal opening, as in *Protorothyris* and *Petrolacosaurus*. In contrast, the greater breadth of the synapsid supraoccipital appears to be accomplished by dorsolateral processes that project over and form the dorsal margins of the post-temporal openings. Accordingly, the condition seen in mesosaurs could be intepreted as 'narrow' using this last criterion. In any case, it appears that the morphology and the relative dimensions of the supraoccipital of *Mesosaurus* resemble more those known for reptiles than those that are known for synapsids and diadectomorphs.

Post-temporal fenestra large (60)

This was an ambiguous synapomorphy for reptiles in Laurin & Reisz (1995) because they were unable to

determine the condition in mesosaurs. A large post-temporal opening in reptiles appears primarily to be the result of modifications of the two primary elements that define its shape and its size: the tabular and the supraoccipital. For example, the tabular extends ventrally to contact the lateral tip of the opisthotic and thus forms the lateral margin of the post-temporal opening in synapsids and diadectomorphs (where such an opening is present), whereas the dorsal and medial margins of the opening are formed by the supraoccipital (as described in the preceeding paragraph). Accordingly, the organization of the post-temporal opening in *Mesosaurus* can be equated with that of reptiles because the tabular is a small element that contributes little to the opening and because the supraoccipital, which lacks a dorsolateral process, is a relatively narrow bone that forms the entire medial margin of the opening. Using these criteria, *Mesosaurus* could be considered to possess the apomorphic condition. However, character 60 is considered redundant here as all these criteria were used as separate characters (16, 17 and 55) in Laurin & Reisz's (1995) analysis.

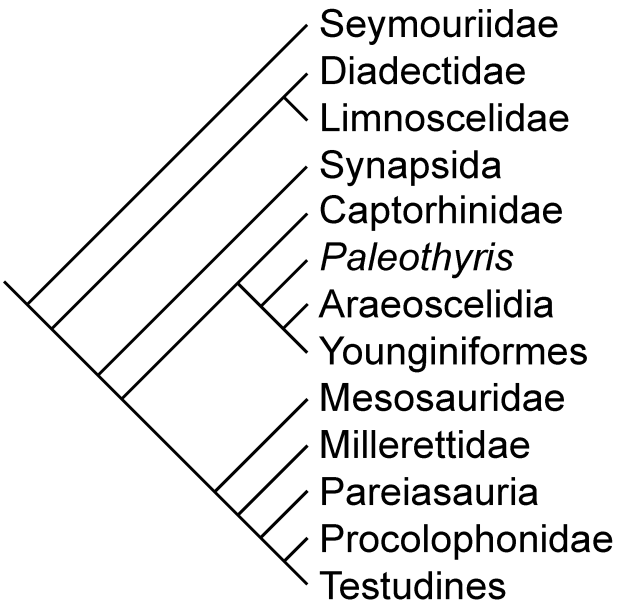

Figure 13. Cladogram illustrating relationships of mesosaurs based on a PAUP analysis of a modified version of the data matrix in Laurin & Reisz (1995), with additional characters from Modesto (1999b). See text for discussion. Tree length = 328, consistency index (excluding uninformative characters) = 0.66, rescaled consistency index = 0.41.

Analysis and results

It is beyond the scope of the present study to conduct a full reappraisal of the phylogenetic relationships of mesosaurs. That is the subject for future work. Instead, the relationships of mesosaurs are evaluated here by using a modified version of the data matrix in Laurin & Reisz (1995). The details of the modifications are as follows, with character numbers from Laurin & Reisz (1995): Mesosauridae was recoded as '1' for character 17 and '2' for character 55. *Paleothyris* was recoded as '0' for 50 and Captorhinidae was rescored as '0' for 51. Characters 54 and 60 were deleted. The former character does not apply to the Palaeozoic taxa under consideration (see above), whereas the latter is redundant as discussed in the previous paragraph (character 60). The modified data matrix was subjected to the branch-and-bound search algorithm of PAUP 4.0*b*10, following the options listed by Laurin & Reisz (1995), except that all characters remained unordered. Parsimony was the optimality criterion.

Mesosaurs form a clade with millerettids, pareiasaurs, procolophonoids and turtles in the single, optimal tree found by PAUP (Fig. 13). This clade ('Anapsida' *sensu* Gauthier, 1994; 'Parareptilia' *sensu* Laurin & Reisz, 1995; 'Proganosauria' *sensu* Modesto, 1999b) is diagnosed by the following synapomorphies (numbering follows Laurin & Reisz, 1995): (24) caniniform region absent; (91) caudal haemal arches attached to preceding centrum; (97) supraglenoid foramen absent; and (113) femoral shaft long and slender; the last apomorphy is ambiguous and as such may diagnose Amniota under the accelerated transformation option. The clade of mesosaurs, millerettids, pareiasaurs, procolophonoids and turtles is not particularly robust because only a single step beyond the most parsimonious resolution results in mesosaurs becoming basal eureptiles (*sensu* Laurin & Reisz, 1995), and three extra steps are required to position mesosaurs as stem sauropsids (*sensu* Laurin & Reisz, 1995). If the two additional characters utilized by Modesto (1999b) are added to the analysis, two extra steps are needed to position mesosaurs as basal eureptiles, and four extra steps are required to position mesosaurs as stem sauropsids (i.e. reiterate the results of Laurin & Reisz, 1995). In this second analysis, the clade of mesosaurs, millerettids, pareiasaurs, procolophonoids and turtles is diagnosed by the above synapomorphies plus: (125) posterior margin of skull table with single median embayment (from Modesto, 1999b). Although these analyses are not comprehensive treatments of mesosaurid relationships (because there are numerous postcranial characters that remain to be evaluated), the available phylogenetic evidence suggests strongly that mesosaurs are not 'stem sauropsids', but instead are nested within Reptilia. Unfortunately, the nomenclature of the eureptile sister group is problematic because of the phylogenetic

lability of turtles and because of the phylogenetic reconception of the long established name Anapsida (Modesto & Anderson, 2004). Accordingly, the clade of mesosaurs, millerettids, pareiasaurs, procolophonoids (and which may or may not include turtles; see Modesto & Anderson, 2004) is not named here in order to avoid further conflation of the nomenclature of this group of reptiles.

Functional anatomy of the skull

Mesosaurs have long been regarded as aquatic forms, but only their most conspicuous skeletal features have been considered as adaptations to an aquatic lifestyle (Gervais, 1865; Seeley, 1892; Osborn, 1903; Carroll, 1982). Furthermore, the degree to which mesosaurs may have been adapted to life in the water has not been explored fully, although many opinions have been ventured in the literature (Bakker, 1975; Carroll, 1982; Oelofsen & Araújo, 1983, 1987). A reappraisal of the aquatic adaptations of mesosaurs is of interest because many of their apomorphies were acquired convergently by aquatic diapsids, and a detailed understanding of their biology should advance palaeobiological studies of amniote adaptations to aquatic environments.

Given the high number of apomorphies that are present in *Mesosaurus* and other mesosaurs (Modesto, 1999b; my pers. observ.), it almost seems as though no portion of their skeleton had escaped modification for an aquatic existence. This statement applies especially to the skull, although most previous workers limited their observations to the long, slender snout, the posteriorly positioned external nares and the numerous teeth. The preceding description of the cranial morphology and the elucidation of dental organization in *Mesosaurus* reveal a host of new features that are undoubtedly related to living and feeding in the water.

The skull of *Mesosaurus* is strongly characterized by an elongate, gavial-like snout which supports numerous long, slender teeth. The whole of the skull, from the tip of the snout to the occiput, is compressed in the dorso-ventral plane: the height of the snout through the premaxillae is less than one-third its transverse breadth, whereas the height of the skull through the posterior cheeks is, as restored, roughly two-thirds maximum skull width. In this respect the mesosaurid skull is similar to those of eusauropterygians (nothosaurs and plesiosaurs), in which a flattened skull is thought to have minimized drag and facilitated lateral movements of the head underwater (Taylor, 1987; Taylor & Cruickshank, 1993). Not surprisingly, both mesosaurs and eusauropterygians have a long neck which could have executed wide lateral excursions of the skull.

Whereas the head is dominated by the elongate rostrum, the skull proper is actually greatly reduced in size: the skull of the basal mesosaur *Brazilosaurus* is equal in length to six dorsal centra (my pers. observ.), a figure comparable with that of terrestrial basal reptiles; the skull of *Stereosternum* is slightly longer (eight dorsal centra: my pers. observ.), which is, in turn, exceeded in relative length by that of *Mesosaurus* (11 dorsals). These figures suggest an increase in skull length within the group. Considering that the relative length of the skull of *Brazilosaurus* is not significantly different than those of terrestrial forms, and that most of the skull's length (at least 75%) consists of the snout, the mesosaurid skull is probably interpreted better as having undergone a reduction in general size. A similar decrease in skull size was interpreted for plesiosaurs by Taylor (1992) as an adaptation for reducing downward pitching movements caused by the placement of the head on the end a long neck. That hypothesis is supported further in mesosaurs by the very thin construction of most dermal roofing bones, which would reduce the mass of the skull and serve further to minimize pitch. The large relative size of the orbits probably reflects the small size of the skull, rather than implying any enhancement of vision, and at the same time suggests that the eyes of mesosaurs continued to serve as important sensory organs.

As noted in most previous descriptions, the external nares are located far posteriorly on the rostrum in all mesosaurs including *Mesosaurus*. The nares are also positioned further dorsally on the side of the face than in basal terrestrial amniotes. Plesiosaurs also have dorsally located nares, a placement thought to reflect the presence of deeply rooted teeth in these reptiles (Taylor & Cruickshank, 1993). Although the teeth of mesosaurs are not deeply rooted, the combination of diminutive skull size and streamlined build of the skull roof presumably placed a premium on snout height (especially with regards to the depth of the alveolar portion of the maxilla), thereby resulting in the dorsal position of the nares in mesosaurs. Interestingly, two studies have suggested that plesiosaurs did not use their nares for respiration, but instead employed them in underwater olfaction, a hypothesis based mainly on the ram scoop-like morphology of the internal nares, but also on the argument that extant aquatic amniotes that use a narial system for respiration and olfaction also possess secondary palates (Cruickshank, Small & Taylor, 1991; Taylor & Cruickshank, 1993). Considering that the nostrils in *Mesosaurus* are almost half the size of the internal nares, which are positioned directly ventral to the nostrils, it is difficult to believe that air did not pass through these openings.

The function of the foramen nariale obturatum, the small opening just posterior to the external naris, is less clear. The foramen could be homologous with the anterior maxillary foramen of parareptiles. The latter opening was postulated to be the egress of a duct from a salt gland that may have been housed in the nasal cavity in those reptiles (Modesto, 1999a). Mesosaurs are commonly thought to have lived under marine conditions (Oelofsen, 1981; Oelofsen & Araújo, 1987; Pickford, 1995) and, if so, mesosaurs might be expected to have had some means to eliminate excess salts, and the foramen nariale obturatum might then represent an osteological manifestation of a salt gland. However, recent stable isotope analysis suggests that the Whitehill and Irati sediments were deposited in fresh to brackish waters (Faure & Cole, 1998). In addition, the salt glands of Galapagos marine iguanas have been described as hyper-developed with respect to those of terrestrial iguanids (Dawson, Barthlomew & Bennett, 1977), yet augmentation of these glands has left no mark on the marine iguanid skull. Fortuitous crushing in one mesosaur specimen (MCZ 4031a, Fig. 7) suggests that the lacrimal duct emptied directly into the foramen nariale obturatum. In contrast, the groove for the lacrimal duct in *Colobomycter pholeter* (Modesto, 1999a: fig. 2) indicates that the duct emptied into the external naris in parareptiles, an observation that is consonant with the idea that the foramen nariale obturatum is not homologous with the anterior maxillary foramen of parareptiles.

The palate appears to share many modifications with other aquatic reptiles. However, these are difficult to evaluate in an adaptive context, considering the lack of attention given to this region of the skull in other aquatic reptiles and the dearth of suitable modern analogues. The interpterygoid vacuity of *Mesosaurus* is quite narrow and teeth are absent from the transverse flange of the pterygoid, which itself is aligned roughly in the horizontal plane. These modifications doubtless reflect a vastly altered role for the palate in the manipulation of food underwater. Similar modifications of the palate are variously developed in aquatic diapsids, including the Upper Permian reptile *Claudiosaurus germaini* (Carroll, 1981), basal sauropterygians (Carroll & Gaskill, 1985) and Triassic ichthyosaurs (Massare & Callaway, 1990). Notably, the vomer extends posteriorly beyond the internal naris, between the anterior ends of the palatine and the pterygoid. This sutural pattern is seen also in ichthyosaurs (Massare & Callaway, 1990) although the exact configuration of these bones differs conspicuously from the pattern seen in mesosaurs. The ectopterygoid is absent in both mesosaurs and ichthyosaurs, but its absence in turtles and captorhinid reptiles, and its retention by mosasaurs and sauropterygians, suggests that the loss of this bone can hardly be considered an aquatic adaptation.

Reduction in the ossification of the braincase is commonly cited as a characteristic of aquatic reptiles (Romer, 1946), and this is true of *Mesosaurus* to some degree. The supraoccipital and opisthotic are never co-ossified as they are in most adult terrestrial basal amniotes (e.g. Reisz, 1981). In the absence of the postparietal (which, along with the tabular, bridges the gap between the skull table and braincase in basal cotylosaurs), the supraoccipital of *Mesosaurus* may have made contact with the parietal via a cartilaginous extension of its dorsal margin.

The ventral surface of the parasphenoid is characterized by paired, parabolic excavations that have been interpreted as pockets for the insertion of cervical muscles (Laurin & Reisz, 1995). Although the absence of such ventral pockets was interpreted as a reptilian synapomorphy by Laurin & Reisz (1995), they are present in at least two other Palaeozoic reptiles. One is the aquatic eosuchian *Claudiosaurus germaini*, which, like mesosaurs, is characterized by a relatively small head mounted on a long neck (Carroll, 1981). Accordingly, the elaboration of the ventral surface of the parasphenoid for attachment of the neck musculature might be associated with reduced skull size and a long neck, at least among basal reptiles. On the other hand, parasphenoidal pockets are present also in the small, Westphalian-age reptile *Paleothyris acadiana*, which does not share these proportions of the axial skeleton (Carroll, 1969). These excavations are also seen in the larger but similarly built varanopid synapsid *Basicranodon fortsillensis* (Vaughn, 1958); somewhat similar proportions of the skull and neck are seen in species of the diadectomorph genus *Limnoscelis* (Fracasso, 1987; Berman & Sumida, 1990). Accordingly, it is difficult to link parasphenoidal excavations with a particular skeletal design.

Although the diet of mesosaurs, particularly *Mesosaurus*, has been the subject of much speculation, it has not been considered in association with a detailed appraisal of the dentition. *Mesosaurus* has been portrayed as a fish eater by some workers (MacGregor, 1908; Bakker, 1975), but the long, slender teeth appear to be ill-suited for piscivory. Instead, *Mesosaurus* is widely regarded as a suspension feeder (Romer, 1966; Carroll, 1982; Chiappe & Chinsamy, 1996), presumably having used its pectinate dentition to strain crustaceans common to the same deposits. Unfortunately, the hypothesis of filter-feeding is based on the fallacy that the marginal teeth were tightly packed and numerous enough to form a straining device, an idea derived from von Huene's (1941) flawed reconstruction of the skull of *Mesosaurus*. He misidentified the dentary teeth in one of his specimens (SMNH R207c) as smaller members of the upper dentition,

and restored them as such, interspersed between the longer teeth of the premaxilla and the maxilla (von Huene, 1941: figs 17–19). Accordingly, von Huene's (1941) reconstruction of the skull of *Mesosaurus* features almost twice the number of teeth in dorsal and ventral views that each jaw should accommodate. Furthermore, the hypothesized food of the mesosaurs, notocaridid crustaceans, were not so diminutive that their capture would have required a sieving mechanism: these krill-like crustaceans reached a length of 3 cm (Brito & de Quadros, 1978; Pinto & Adami-Rodrigues, 1996).

As restored here (Figs 1, 2), the skull of *Mesosaurus* appears well suited for capturing small, nektonic prey. Although gut contents have yet to be described for any mesosaur, several features of the dentition and the skull suggest that *Mesosaurus* preyed upon notocaridids. The snouts of all mesosaurs are very gavial-like and would have served very well for capturing, with quick snapping movements, small prey that required little force to subdue (Taylor, 1987). Unlike gavials, however, the teeth of *Mesosaurus* are unusually long and slender. The longest teeth of *Mesosaurus* have a crown height/gullet width ratio of 0.55, and so greatly exceed those of modern aquatic predators (where crown height/gullet width ratios range from 0.14 to 0.30 according to Massare, 1987, who regarded 'gullet width' as the width between the jaw articulations). This ratio alone would identify *Mesosaurus* as a very specialized aquatic predator using Massare's (1987) criteria. Intriguingly, members of her 'Pierce I' marine reptile guild are characterized by the complete absence of gut contents and unworn teeth, as are mesosaurs. Massare (1987) hypothesized a diet of relatively small, soft-bodied prey (such as small fish and soft cephalopods) for this guild. Despite meeting Massare's (1987) criteria for the Pierce I guild, it is highly unlikely that the teeth of *Mesosaurus* were used to impale prey, given that the orientation of the teeth of *Mesosaurus* changes across the series. The procumbent and slender build of the teeth, together with their shallow implantation in the alveoli, indicates that they were wholly unsuited for piercing and disabling prey, and instead the marginal teeth probably functioned strictly to entrap and to restrain prey. The remarkable organization of the dentition appears to have provided *Mesosaurus* with an effective 'bite width' that was marginally greater than gullet width.

The skull of *Mesosaurus* thus appears to be well suited for feeding in an aqueous environment, and the morphology and the organization of the dentition strongly suggests a specialization for small, relatively soft prey that were easily subdued upon capture. As prey items for mesosaurs, the most likely candidates appear to be the free-swimming, shrimp-like notocaridids. Given the size of these crustaceans, mesosaurs probably preyed upon individual notocaridids, much as crab-eater seals are believed to attack individual krill (Sanderson & Wassersug, 1993). The shrimp-like aspect of notocaridids and their endemic distribution in the '*Mesosaurus* Sea' (term following Pickford, 1995) suggests that they were a Palaeozoic analogue of krill. Recent krill support a great number of marine vertebrates, ranging from teleosts to seabirds and mysticete cetaceans. The krill-based Antarctic ecosystem is thought widely to be less complex than other marine systems (Nicol & de la Mare, 1993), an idea consistent with the interpretation that the ancient sea occupied by mesosaurs was essentially depauperate in terms of both vertebrate and arthropod diversity (Oelofsen, 1981; Pickford, 1995). Compared with marine deposits of the Palaeozoic tropics, the striking paucity of animal taxa in the Irati and the Whitehill formations (Oelofsen, 1981; Oelofsen & Araújo, 1983) suggests that the '*Mesosaurus* Sea' may have been an equally 'simple' marine system, with notocaridids the primary food resource of *Mesosaurus*, other mesosaurs and the palaeoniscoid fish found in the same deposits.

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