

# B R E V I O R A

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### THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA VII. THE POSTCRANIAL SKELETON OF THE TRAVERSO- DONTID *MASSETOGNATHUS PASCUALI* (THERAPSIDA, CYNODONTIA)

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**ABSTRACT.** The postcranial skeleton of *Massetognathus pascuali* is described from a single nearly complete individual and four disarticulated specimens; manus, pes and pubis could not be described from the available material. *M. pascuali* has a postcranial skeleton morphologically similar to that in *Pascualgnathus polanskii* (an earlier traversodontid) and in African Triassic cynodonts. The basic skeletal pattern of all these forms differs from that in *Exaeretodon* sp., an advanced traversodontid. The specialized, imbricating ribs of *M. pascuali* are intermediate in form between those of *P. polanskii* (which are diademodontid in form) and those of *Exaeretodon* sp. (which essentially have lost the cynodont specialization).

Although Richard Owen made the first study of a cynodont more than a century ago, a detailed knowledge of cynodonts has accumulated only recently. First known only from Africa, representatives of this advanced group of mammallike reptiles have now been recovered from Asia and North and South America. The most specialized and, during the early and middle Triassic, the most abundant cynodonts were the herbivorous gomphodonts. Transversely broad, multicuspid postcanine molars with heavy occlusal wear (often to the point of effacing the original crown pattern) are characteristic of the group. Romer (1967) recognized three gomphodont families: Diademodontidae, Traversodontidae, and Trirhachodontidae. *Massetognathus pascuali* is a traversodontid and is one of two species described by Romer (1967) from the

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Chañares Formation of Argentina. Other undoubted traversodontid genera include *Traversodon* from the Santa María Formation of Brasil, *Exaeretodon*, *Proexaeretodon* and *Ischignathus* from the Ischigualasto Formation of Argentina, and *Scalenodon* and *Scalenodontoides* from the Manda and Molteno beds, respectively, of Africa. *Pascualgnathus polanskii* from the Puesto Viejo Formation of Argentina, originally classified as a diademodontid (Bonaparte, 1966a; 1966b), is now interpreted as a primitive traversodontid on the basis of tooth morphology (Bonaparte, 1967, and personal communication).

The present account of the *Massetognathus pascuali* postcranial skeleton is based upon the disarticulated remains of at least four individuals and an almost completely articulated skeleton of a fifth individual, all about the same size and preserved in a nodule several inches thick and two and one-half feet in diameter. The 1964-65 expedition of the Museo de la Plata and Museum of Comparative Zoology collected the nodule from the Chañares Formation in the Chañares-Gualo region of western Argentina. All the skeletal material is catalogued as No. 3691 in the Museum of Comparative Zoology.

Although the available postcranial material of *Massetognathus pascuali* is incomplete, there are two reasons why even a partial account is important. First, some workers regard cynodonts as ancestral to mammals (Crompton and Jenkins, 1968; Hopson and Crompton, 1969). Gomphodont cynodonts are certainly not directly related to mammals, but they undoubtedly possessed a degree of biological organization that at least approximated that of their carnivorous-insectivorous relatives (from some form of which mammals were derived). Thus all cynodonts are relevant to evaluating the reptile-mammal transition. Second, most published investigations of cynodonts have been restricted to cranial anatomy. Well-preserved, generically determinate postcranial skeletons are rare. Of South American genera, only *Belesodon* (von Huene, 1935-1942), *Exaeretodon* (Bonaparte, 1963a) and *Pascualgnathus* are known from relatively complete skeletons; the preservation of known *Belesodon* material is poor, however, and *Exaeretodon* appears to be morphologically aberrant in comparison to the general pattern known from other cynodonts. Postcranial material associated with *Traversodon* and *Chiniquodon* (von Huene, 1935-1942) is only fragmentary, although Romer (1969) has recently described more complete limb bones of *Chiniquodon*. I have reviewed the postcranial skeletons of African cynodonts (Jenkins, in

press). Of the Russian forms very little is known; some data is available for *Permocynodon* (Konjukova, 1946).

### Vertebral column and ribs

The number of presacral vertebrae in *Massetognathus pascuali* is at least 23 and is here interpreted to be about 26. A hiatus in the lumbar series of the one nearly complete, articulated vertebral column is responsible for this uncertainty. Present are 7 cervicals, 16+? dorsals, and 6 sacrals. Judging from the length of several articulated but incomplete caudal series, tail vertebrae numbered at least 17 and probably as many as 25. A count of 26 presacral vertebrae in *M. pascuali* compares with 26 in *Leavachia duvenhagei* (Broom, 1948), 27 in *Thrinaxodon liorhinus* (Jenkins, in press), 28 in *Exaeretodon* sp. (Bonaparte, 1963a), 29 in *Cynognathus crateronotus* (Seeley, 1895) and at least 30 in a large cynodont identified tentatively as *Diademodon* sp. (Brink, 1955; Jenkins, in press).

Two separately articulating atlas arches appear to conform to the general pattern known from African Triassic cynodonts (Jenkins, in press), but their preservation is too poor to allow specific description or comparison. The atlas intercentrum, transversely elongate and ventrally convex, bears a posteriorly directed process or lip (1, Fig. 1B). A concave articular facet on the dorsal surface of this lip contacts a median convex facet on the anterior aspect of the atlas centrum (f a i, Fig. 6B). The lateral extremities of the intercentrum each bear, on their dorsal surfaces, a concave facet that articulates with the ventral aspect of one of the two occipital condyles. The atlas centrum (6 mm long) is synostosed

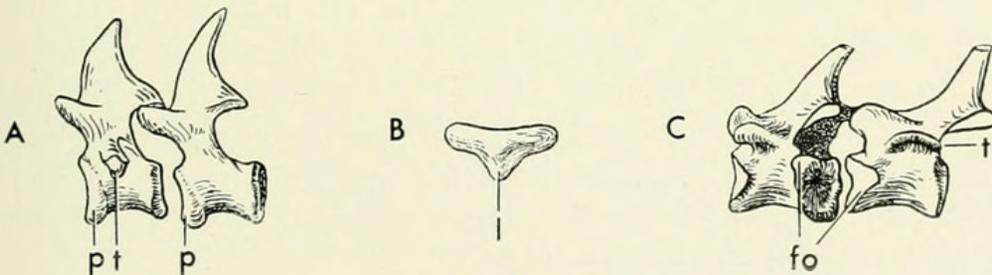


Figure 1. Vertebral elements in *Massetognathus pascuali*. A, Cervical vertebrae, probably the third and fourth, in lateral view. B, First or atlantal intercentrum in ventral view with anterior margin toward the top of the page. C, Anterior dorsal ("thoracic") vertebrae; vertebra on the right is in lateral view, on the left posterolateral view. All  $\times 1$ . Abbreviations: fo, costal fovea for rib head; 1, posterior lip of the intercentrum; p, parapophysis; t, transverse process.

to the axis centrum (8.5 mm long), forming a conspicuously large vertebra. On the dorso-lateral aspects of the atlas centrum are two facets, one for each atlas arch half (f a a, Fig. 6B). Protruding from the median aspect of the centrum between these facets is a small process (d, Fig. 6B) homologous with the dens or odontoid process of mammals. Elsewhere (Jenkins, 1969; in press) I have proposed that the mammalian dens originated as a neomorphic process from the atlas centrum of cynodonts. The occurrence of a dens in *Massetognathus pascuali* is unequivocal and supports the theory that both a dens and an atlas centrum (of which the dens was formerly thought to be a vestige) occur together among cynodonts.

The axis centrum of the one articulated cervical series is about 9 mm long, 1 mm longer than the centra of the following cervicals. The axial prezygapophyses have been broken off on all specimens, but from the appearance of their narrow bases—no thicker than the laminae from which they protrude—they are vestigial. Axial postzygapophyses of normal size bear articular facets at an angle estimated to be  $25^\circ$  to the horizontal. The axial spine, a flat blade with a distinctly mammalian shape, exhibits a straight dorsal margin that was probably slightly convex during life. The robust transverse processes are directed posterolaterally.

Cervical centra are amphicoelous, as are all other centra in *Massetognathus pascuali*, with the exception of the atlas (only the posterior aspect bears a notochordal concavity) and possibly some of the smaller caudal vertebrae. In cervical vertebrae, the rim surrounding the notochordal concavity on each end is swollen, and this increases the concave curvature of the sides and ventral aspect of each centrum. A bulbous parapophysis is to be found on the ventrolateral aspect of each anterior rim (p, Fig. 1A). If the rib head articulated on the apex of the parapophysis, as seems most likely on the basis of the large size of the process, then this condition differs from that in species of *Thrinaxodon* and *Cynognathus*, in which cervical rib heads are situated intervertebrally. A median ventral keel, similar to that in other cynodont cervicals, traverses the length of each cervical centrum.

Cervical pedicles are narrow anteroposteriorly and bear short, stout transverse processes (t, Fig. 1A). Cervical spines, broken off on all but two disarticulated cervicals (Fig. 1A), are transversely slender and recurved, and taper abruptly toward the apex. Of particular interest are the zygapophyses, which provide a basis for distinction between cervical and dorsal (anterior thoracic) vertebrae. As noted above, the axial postzygapophyseal facets are

oriented at an angle of about  $25^\circ$  to the horizontal; the orientation of posterior facets on the third through sixth cervical are more than  $25^\circ$ —probably about  $35^\circ$ . The distance between their lateral margins is approximately 7 mm. The anterior articular facets of the seventh cervical of course conform in orientation and spacing to those of the foregoing series. The posterior articular facets, however, appear to be oriented at about  $45^\circ$ . Those on the succeeding (eighth) vertebra are nearly parasagittal—i.e., within a few degrees of vertical—and are only 3.5 mm apart. The articular facet characteristics of the eighth vertebra, continued (with gradual modification) through the dorsal series, definitely establish a different pattern. Although transitional, the seventh vertebra most closely resembles other neck vertebrae and thus may be regarded as the last cervical. Similar changes in facet orientation and spacing, together with other morphological changes, occur between the seventh and eighth vertebrae of *Thrinaxodon liorhinus* and *Cynognathus crateronotus* (Jenkins, in press). The condition in *Massetognathus pascuali* reaffirms the fact that the “mammalian” number of seven cervical vertebrae was already established in cynodonts.

With the exception of the atlas intercentrum, no other cervical intercentra have been identified. The broad grooves formed by the rims of adjacent centra are evidence that intercentra were present—as in *Thrinaxodon liorhinus*, for example—and the state of disarticulation accounts for their postmortem loss.

The dorsal vertebral column in cynodonts is either a relatively undifferentiated dorsal series (as in most reptiles) or two series—“thoracic” and “lumbar” (as in mammals). In certain African Triassic cynodonts, separation of thoracic and lumbar regions may be made on the basis of distinct morphological specializations of the posterior dorsal (= lumbar) ribs (Jenkins, in press). In other cynodonts (e.g., *Exaeretodon* sp.; Bonaparte, 1963a) the trunk cannot be divided into thoracic and lumbar regions because the posterior ribs are not specialized. *Massetognathus pascuali* has specialized “lumbar” ribs and clearly belongs to the first category. The exact number of thoracic and lumbar vertebrae is unknown because a complete vertebral column with ribs is not yet available. Therefore, thoracic and lumbar vertebrae will be given only a general description as anterior and posterior dorsals, respectively, although the ribs (to be discussed below) clearly give evidence of a differentiated series.

The centra of anterior dorsal vertebrae are approximately 8.5 mm long; those of posterior dorsals are about 11 mm long (10 mm

in the one articulated specimen). The costal foveae (fo, Fig. 1C) of anterior dorsal vertebrae form a cleft for reception of the rib head, which is therefore intervertebral in position. On posterior dorsals the rib head articulates with a parapophysis (p, Fig. 2B) and is not intervertebral. Transverse processes are laminar and bowed dorsally on anterior dorsal vertebrae (t, Fig. 1C) but are rodlike and round in cross-section on posterior dorsals (t, Fig. 2B). The posterior intervertebral notch is deep throughout the dorsal series, the anterior notch negligible or absent. In contrast to many cynodonts, anapophyses are lacking. Dorsal prezygapophyses are robust, extending to or slightly beyond the level of the anterior aspect of the centrum. Articular facets on the first dorsal vertebra are about 3.5 mm apart and on the ninth are 4.0 mm; an abrupt widening takes place at some point in the middle or posterior dorsal series, for the articular facets of the penultimate dorsal vertebra are about 7 mm apart. The narrowly-spaced facets of anterior dorsals are nearly vertical, whereas those wider apart on the posterior dorsals are oriented at angles of as much as  $45^\circ$ . Neural spines on anterior dorsals are narrow, but unlike cervical spines, do not taper significantly at the apex; they incline caudad at angles of about  $30^\circ$ . Spines on posterior dorsal vertebrae are broad anteroposteriorly, leaving only a narrow gap between vertebrae; their inclination is only a few degrees caudad.

Sacral vertebrae successively decrease in size posteriorly. The centrum of the first sacral is approximately as long as those of the posterior dorsals (about 10 mm), while the sixth and last sacral centrum is some 2 mm shorter. Massive synapophyses—representing fused parapophyses and transverse processes—arise from the pedicles and from the anterior half of the side of the centrum. The zygapophyses, proportionately less robust than in the dorsal series, diminish in size on successively more posterior sacrals. In contrast to the orientation and spacing in the posterior dorsals, sacral articular facets incline nearly parasagittally and are narrowly spaced. At the last dorsal-first sacral articulation, the facets are 5.5 mm apart, but between the third and fourth and fourth and fifth sacrals they are only about 2 mm apart. At the fifth-sixth sacral articulation the trend is reversed; the facets are spaced 3.5 mm apart and appear to be inclined at  $10^\circ$  from the vertical. The trend toward less verticality of facets is continued into the caudal series. Sacral spines successively diminish in height and anteroposterior breadth. The spine on the first sacral is approximately 8 mm in height and 7 mm in breadth (*versus* 8.5 mm height and 8 mm breadth for the last dorsal spine). On the fifth sacral

the same measurements are 5.5 mm and 4.2 mm respectively. This trend is continued into the caudal series. The apices of sacral spines tend to be oval in contrast to those of the posterior dorsals which are elongate and attenuated at each end.

Caudal centra decrease in length from 6.5 mm at the first caudal to about 5 mm at the fifth. More posterior caudals preserved with MCZ 3691 are disarticulated, and their position cannot be positively assigned. However, one isolated series of eleven caudals shows a decrease in centrum length from 5 mm (which is evidence that it is approximately the fifth caudal) at the first to 4 mm at the last (? fifteenth caudal). Other specimens show that at least the first five caudals bear synapophyses. Articular facets are inclined at approximately  $45^\circ$ , at least through the first five caudals. The width between the lateral edges of these facets decreases from 6 mm (between the last sacral and first caudal) to 4.5 mm (between the fourth and fifth caudals). The terminal caudal is unknown.

*Massetognathus pascuali* probably possessed ribs on all presacral vertebrae, as in other cynodonts for which adequate material is known. Ribs were not found in association with the first six cervical vertebrae, although the morphology of the transverse processes and parapophyses on the axis through sixth cervical is clear evidence of their existence. These features cannot be verified at present on the atlas. The ribs of the seventh cervical appear to have been shorter than, but otherwise similar to, those of the anterior dorsal series.

Dorsal ribs in *Massetognathus pascuali* are of basically two types: in the anterior and middle dorsal series, a freely articulating rib of normal costal form and proportions, and in the posterior dorsal series, a fused rib with a Y-shaped distal end. Unfortunately, the transitional ribs between the two types are as yet unknown.

The proximal ends of anterior and middle dorsal ribs are basically triangular. The tuberculum and capitulum form two corners of the triangle; the shaft arises from the third (Fig. 3A). On the anterior aspect of this triangular surface is a slight crest (c, Fig. 3A) comparable to a similar feature on the anterior dorsal ribs of *Cynognathus* sp. (c, Fig. 3B, C). There is no other apparent feature that makes this type of rib distinctive. The maximum widths of the shafts near their proximal ends are between 2.5 and 3 mm. The distal ends, as preserved, are approximately 1.5 mm thick. Ribs of this basic morphology (as opposed to the specialized posterior

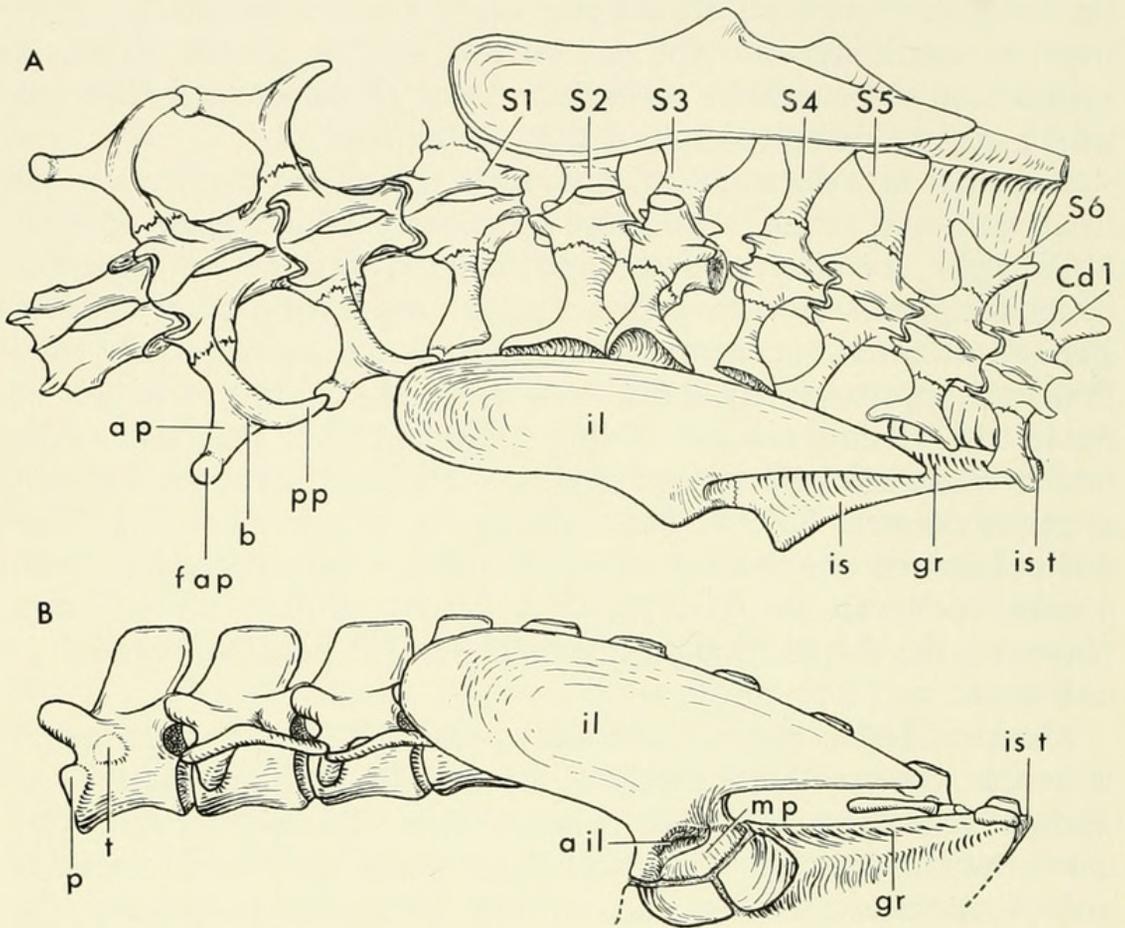


Figure 2. The posterior dorsal and sacral region in *Massetognathus pascuali* in A, dorsal and B, lateral views.  $\times 1$ . Abbreviations: a il, acetabular facet of the ilium; a p, anterior process of rib shaft; b, ridge on dorsal aspect of rib shaft; f a p, articular facet on anterior process of rib shaft; gr, groove on dorsal margin of ischium; il, ilium; is, ischium; is t, ischial tuberosity; m p, medial process on base of ilium for articulation with ischium and pubis; p, parapophysis; p p, posterior process of rib shaft; t, transverse process.

dorsal ribs to be described next) are associated with at least the first thirteen dorsal vertebrae.

The following description of the specialized posterior dorsal ribs is based on the penultimate and last dorsal ribs preserved in articulation (Fig. 2) and in addition, a few disarticulated pieces of similar morphology. These ribs have a short shaft that bifurcates into a Y-shaped terminus with two processes (ap, pp, Figs. 2, 4B). The anterior process is broader than the posterior and bears, on the dorsal surface of its tip, a rather flat, round facet (f a p, Figs. 2A, 4B). Articulating with this facet is the end of the posterior process of the preceding rib. Presumably, the underside of the

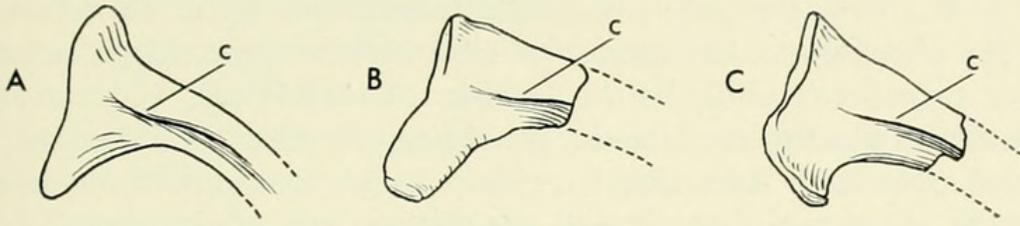


Figure 3. Proximal ends of dorsal ribs of *A*, *Massetognathus pascuali* ( $\times 2$ ), and of *B* and *C*, *Cynognathus* sp. ( $\times \frac{1}{2}$ ) in anterior view. Abbreviations: c, crest on anterior aspect of shaft (see text for details).

posterior process also bears a facet. The rib as a whole projects laterad from the vertebral column and appears not to have had any ventral curvature. In lateral view (Fig. 2B) the shaft and point of bifurcation are at approximately the same level, but the anterior and posterior processes incline somewhat ventrally. A low, bony ridge (b, Figs. 2A, 4B) runs obliquely onto the posterior process from the point of bifurcation where it is most prominent. This feature is comparable to a similar ridge on the ribs of *Cynognathus* sp. (b, Fig. 4A) and other cynodonts; in the fourteenth thoracic

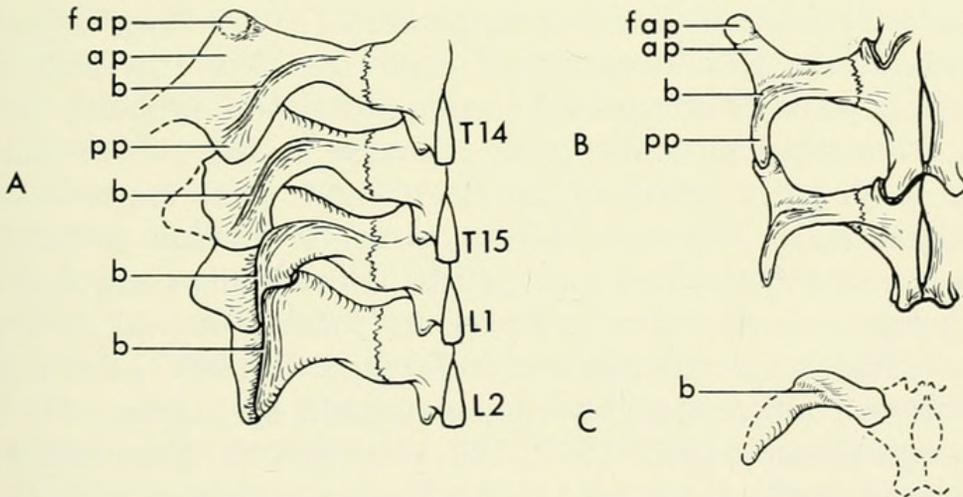


Figure 4. Specialized posterior dorsal ("lumbar") ribs of various cynodonts. *A*, *Cynognathus crateronotus* (British Museum of Natural History no. R. 2571),  $\times \frac{1}{4}$ . *B*, *Massetognathus pascuali*,  $\times 1$ . *C*, *Leavachia duvenhagei* (Rubidge Collection, Graaf Reinet, South Africa, no. 92),  $\times \frac{1}{2}$ . All dorsal views. Abbreviations: a p, anterior process of rib; b, ridge on dorsal aspect of rib shaft (of unknown function but probably homologous in the forms shown here); f a p, articular facet on anterior process of rib shaft; L1, L2, first and second lumbar vertebrae; p p, posterior process of rib shaft; T14, T15, fourteenth and fifteenth thoracic vertebrae.

rib of *C* (T14, Fig. 4A), the ridge is merely a linear elevation on the flat costal plate. On successive ribs, however, the ridge becomes more prominent until, in the lumbar ribs (L1, L2, Fig. 4A), it reflects forward to contact the preceding rib plate (see Jenkins, in press). No such reflection is evident in *Massetognathus pascuali*, but the ridge morphology and general pattern of the process are nevertheless similar to that of the fourteenth and fifteenth thoracic rib plates of *C*.

Specialized, imbricating ribs are common but not universal among cynodonts. Known members of the earliest cynodont family, the procynosuchids, apparently did not possess this specialization (see discussion below, however, for a possible exception). Galesaurids, typified by the well known *Thrinaxodon liorhinus* (Jenkins, in press), developed costal expansions on all presacral ribs. Members of three other families, e.g., *Cynognathus crateronotus* (Cynognathidae; Seeley, 1895), *Diademodon* sp. (Diademodontidae; Jenkins, in press) and *Cricodon metabolus* (Trirachodontidae; Crompton, 1955), possessed imbricating ribs only in the posterior dorsal region. The ribs in chiniquodontids (von Huene, 1935-1942) are as yet unknown. There remains only the Traversodontidae, which Bonaparte (1963b) characterized, on the basis of species of *Exaeretodon* and supposedly *Traversodon*, as lacking synostosed ribs with overlapping processes. For this and other reasons, Bonaparte interpreted traversodontids as probably having arisen from procynosuchids along a lineage separate from that ancestral to all other cynodont families (whose members possess rib specializations). However, *Massetognathus pascuali* unquestionably possesses synostosed lumbar ribs with details comparable to the *Cynognathus-Diademodon* pattern. *Pascualgnathus polanskii*, now classified as a traversodontid (Bonaparte, 1967), has lumbar ribs that are unquestionably diademodontid in pattern. Furthermore, von Huene (1935-1942; 137-140) described expanded ribs ("Fächerrippen") synostosed to the lumbar vertebrae in *Traversodon stahleckeri*. Crompton (1955) presented circumstantial evidence that the traversodont *Scalenodon* from the African Manda beds also possessed the expanded rib specialization. Yet Bonaparte (1963a) amply demonstrated that at least one traversodont, *Exaeretodon* sp., did not possess such specialization. Presacral ribs in *Exaeretodon* sp. are morphologically uniform and are more or less freely articulating (although the more "solid" attachment of the last three dorsal ribs, as described by Bonaparte, possibly represents a vestige of a less mobile articulation typical of expanded ribs). In view of this unexpected association at the family level of

forms possessing and forms lacking rib specializations, the taxonomic significance of this character should be reassessed. Further comment is reserved for the discussion below.

Sacral ribs in *Massetognathus pascuali* have an essentially confluent capitulum and tuberculum, a short shaft and an expanded distal end for articulation with the iliac blade. Proximally each rib is synostosed to its corresponding vertebra. If I may judge from the disarticulated condition of every known sacroiliac joint, ligaments and cartilage must have been chiefly responsible for binding the ilium and sacral ribs. The concave distal ends of the sacral ribs conform to the gently convex internal surface of the ilium, but they do not appear to form any osseous interdigitation by which sacroiliac joints are commonly reinforced. Viewed from above, the distal end of the first sacral rib (S1, left side, Fig. 2A) is Y-shaped with processes directed anterolaterad and posterolaterad. Articulating with the dorsal surface of the anterolateral process is the posterior process of the last dorsal (lumbar) rib. The second sacral rib has the largest distal expansion; irregularly shaped and widest anteriorly, the expansion is 7 mm long in one well preserved specimen. The third, fourth and fifth ribs bear more or less symmetrical distal expansions that are successively smaller caudally. The first four sacral rib shafts are oriented more or less laterally, the fifth slightly anterolaterally. The sixth and last sacral rib bears a shaft that is directed posterolaterally and a bifurcated, Y-shaped terminus resembling that of posterior dorsal ribs. Its iliac articular surface is narrow and strap shaped; the rib and vertebra could well be interpreted as the first caudal were it not for its position opposite the posterior tip of the iliac blade (S6, Fig. 2A). While it is apparent that the width between the distal ends of this pair of ribs (20 mm) is much less than that of the fourth and fifth sacrals (27 mm), the intervening gap could well have been completed by ligaments. This interpretation of the sixth sacral vertebra and ribs may be open to future modification, but on present evidence appears to be the most probable.

Only the first three caudal ribs are preserved. All are synostosed, their shafts directly posterolaterally. The first is only 8 mm long (Cdl, Fig. 2A), with two blunt processes on its terminus resembling a stunted version of the last sacral rib. As far as can be determined, terminal processes were not developed on the second and third caudal ribs, which are 5 mm or less in length. Ribs on succeeding vertebrae must have been very small and probably did not occur in the posterior caudal series.

## Shoulder Girdle

Available interclavicles of *Massetognathus pascuali* are incomplete, although there is sufficient material to conclude that the morphology is very similar to that in *Thrinaxodon liorhinus* and different from that in *Exaeretodon* sp. In outline the interclavicle is cruciate with an elongate posterior ramus (pr, Fig. 5A). The entire bone, although basically a flat plate, is bowed ventrally from front to back. Two ridges, one longitudinal, the other transverse, divide the ventral surface of the interclavicle into quadrants. The two anterior quadrants (c c, Fig. 5A) are shallow concavities for reception of the proximal ends of the clavicles. The ridges are

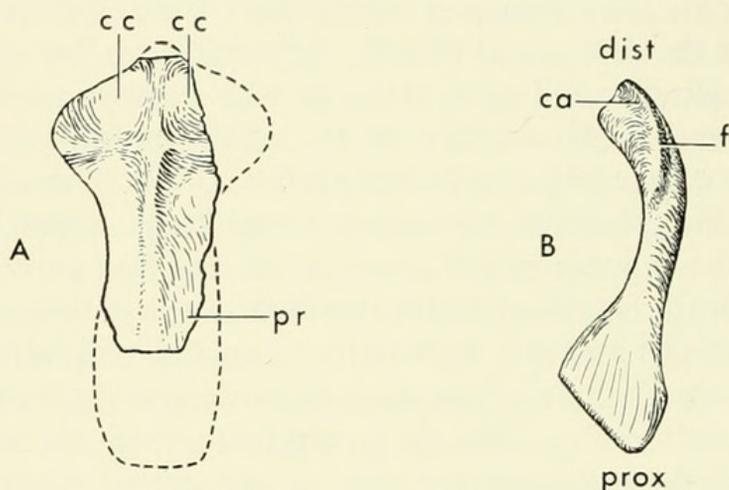


Figure 5. *A*, The interclavicle and *B*, the right clavicle of *Massetognathus pascuali*, both in ventral view.  $\times 1$ . Abbreviations: ca, concavity for acromion; c c, concavity for proximal end of the clavicle; dist, distal end of clavicle; f, ventral flange on distal end of clavicle; pr, posterior ramus of interclavicle; prox, proximal end of clavicle.

most prominent at their intersection. With the exception of the posterior part of the longitudinal ridge, which gradually fades out, the ridges become more salient toward the margins. There is no evidence that the longitudinal ridge was a deep keel as in *Exaeretodon* sp. (Bonaparte, 1963a). The posterior ramus in *M. pascuali* is similar in length and form to that in galesaurids, and is unlike the very short ramus of *Exaeretodon* sp.

The *Massetognathus pascuali* clavicle is robust. The proximal two-thirds are more or less straight (Fig. 5B), the distal third curving sharply posterodorsally. The broad, flat plate on the proximal end articulates with the previously described concavity (c c, Fig. 5A) in the interclavicle. Along the ventral aspect of the distal

third runs a flange (f, Fig. 5B) similar to that noted in African Triassic cynodonts (Jenkins, in press) and *Exaeretodon* sp. (Bonaparte, 1963a). This flange continues to the distal end where it contributes to the formation of a concavity (ca, Fig. 5B) for reception of the acromion. The clavicle is essentially identical to that in galesaurids.

The scapula, coracoid, and procoracoid in *Massetognathus pascuali* are firmly synostosed, although the joints can readily be distinguished (Fig. 6A). The scapular blade, elongate and narrow, bears a distinct concavity on its lateral surface—a fossa presumably for the supracoracoideus muscle, the infraspinatus homologue of mammals. The anterior margin of the blade is reflected sharply laterally, the posterior margin somewhat less so. An acromion process as such is not preserved on any of the scapulae; this absence may be due to postmortem damage to a delicate process or to the fact that the clavicular concavity simply fitted to the convex edge of the anterior scapular base (ac, Fig. 6A). The scapular half of the glenoid is a hemicircular and slightly convex facet that faces posteroventrally and somewhat laterally.

The coracoid is basically triangular in lateral view (co, Fig. 6A). The posterior end forms an elongate, attenuated process terminated by a tubercle for the origin of the coracoid head of the triceps (co tr, Fig. 6A). The process is morphologically similar to the same feature in *Pascualgnathus polanskii* and in African Triassic cynodonts, but differs in form from that in *Exaeretodon* sp. as interpreted by Bonaparte (1963a). Between the glenoid and the triceps tubercle, the superior margin of the coracoid is about 2 mm wide and is slightly concave from front to back. The slightly convex inferior margin is, in contrast, extremely thin bone, and, as a consequence, is invariably damaged postmortem. A saddle-shaped facet, concave dorsoventrally and convex transversely, constitutes the coracoid half of the glenoid.

The procoracoid (pr, Fig. 6A) appears to be an irregularly shaped, flat plate, but in no available specimen are the free margins complete. There are so many basic similarities in the scapulocoracoid of *Massetognathus pascuali* and African cynodonts that a complete procoracoid of the former would probably have the same oval shape characteristic of the latter. A crescentic depression on the lateral aspect along the inferior margin may represent the biceps origin. Above lies the round procoracoid foramen (f pr, Fig. 6A) sculptured in a ventrolateral direction to facilitate passage of its nerve and blood vessels. The evidence as to whether the procoracoid participated in the glenoid is equivocal. I

believe that the procoracoid probably supported articular cartilage at the very anterior extremity of the glenoid (see left glenoid, Fig. 6A), but there is no certainty of the procoracoid contributing to the shoulder joint as there is for some African Triassic cynodonts.

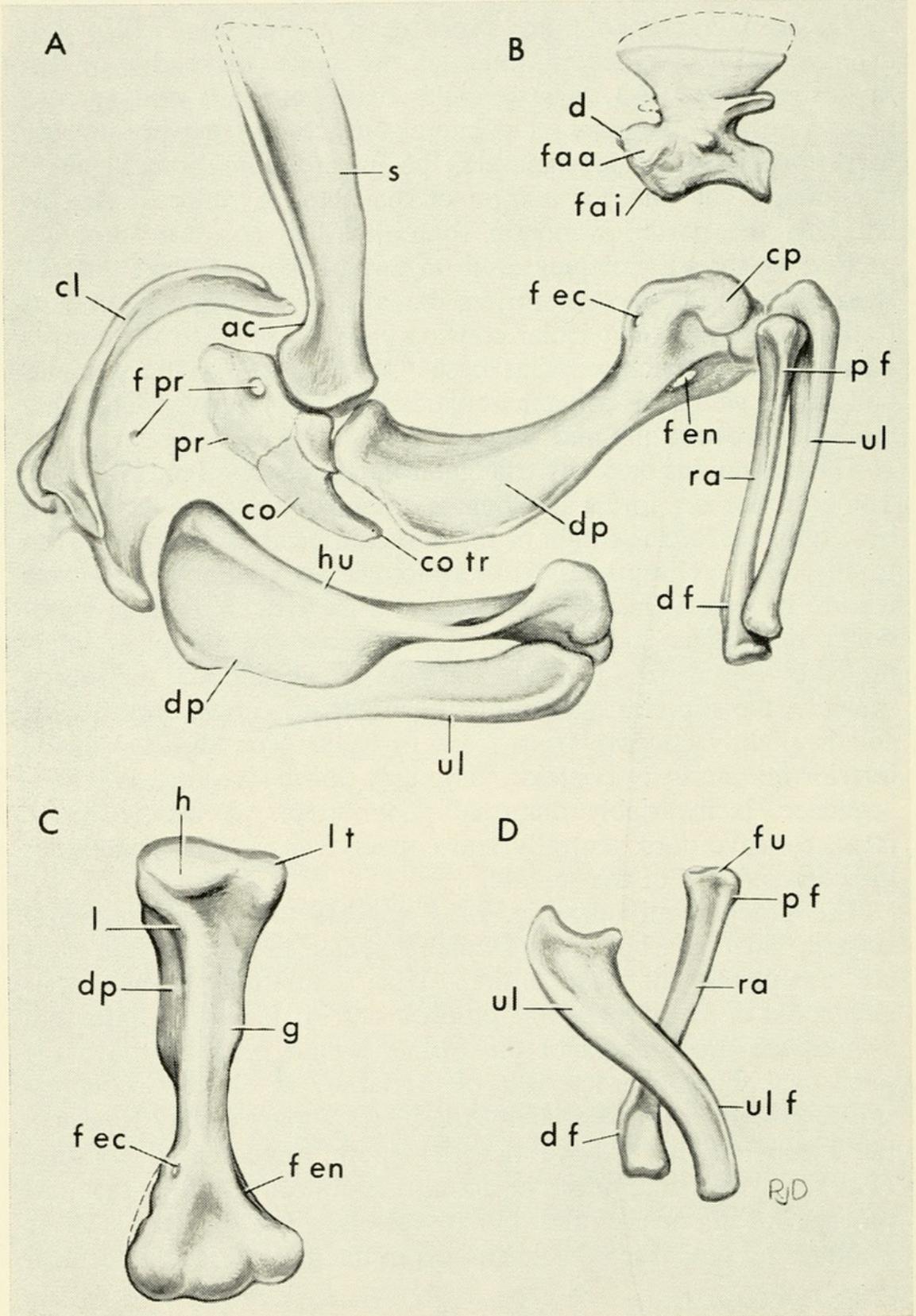


Figure 6. Elements of the postcranial skeleton of *Massetognathus pascuali*, drawn as preserved *in situ*. *A*, Incomplete left shoulder girdle and forelimbs seen from the left side. *B*, Lateral view of axis. *C*, Dorsal view of left humerus. *D*, Medial view of left radius and ulna. All  $\times 1$ . Abbreviations: ac, area of clavicular articulation (distinct acromion process not developed); cl, clavicle; co, coracoid; co tr, tubercle for coracoid head of triceps; cp, capitellum; d, dens; d f, distal flange on radius; dp, deltopectoral flange; f a a, atlas centrum facet for atlas arch; f a i, atlas centrum facet for atlas intercentrum; f ec, ectepicondylar foramen; f en, entepicondylar foramen; f pr, procoracoid foramen; g, groove possibly representing teres major insertion or the origin of one of the humeral triceps heads; h, humeral head; hu, humerus; l, ridge possibly representing insertion of the teres minor; l t, lesser tuberosity; p f, proximal flange on radius; pr, procoracoid; ra, radius; s, scapula; ul, ulna; ul f, ulnar flange.

## Forelimb

Principal characteristics of the humerus of *Massetognathus pascuali* are the relatively broad expansion of the proximal and distal ends, and the large deltopectoral flange. The proximal end of the shaft is bowed dorsally and the head is oriented to a more dorsal position. The well-rounded head (h, Fig. 6C) possesses greatest curvature along its dorsoventral axis. As preserved, the articular surface is confluent medially with the lesser tuberosity (l t, Fig. 6C) and laterally with the proximal margin of the deltopectoral flange. The greater tuberosity presumably arose in the mammalian lineage between the head and the proximal margin of the deltopectoral crest, but in *M. pascuali* there is no evidence of a distinct tubercle. The greatest width of the proximal end, from the lesser tuberosity to the region of the presumptive greater tuberosity, measures approximately one-third the total length of the humerus. The broad deltopectoral flange is slightly more than half the total length of the humerus. The free edge of the flange thickens and everts (laterally) at its proximal and distal extremities, but along the middle part is rather thin and flat. From the region of the presumptive greater tuberosity a low, bony ridge runs obliquely across the flange toward the shaft (l, Fig. 6C). An identical ridge on the humeri of certain African Triassic cynodonts has been interpreted as possibly representing the insertion of a teres minor (Jenkins, in press). On the posterodorsal aspect of the shaft is a groove possibly representing the insertion of the teres major or the origin of one of the humeral triceps heads (g, Fig. 6C); Bonaparte (1966b) interpreted a rugosity at this site in *Pascualgnathus polanskii* as the origin of the medial triceps head.

The distal end of the humerus is triangular in dorsal view, its maximum breadth being approximately 40 per cent of the humeral length. Arising from the robust ectepicondylar region, a thin supracondylar flange runs proximally as well as somewhat dorsally. The flange, pierced in its proximal half by a small ectepicondylar foramen (f ec, Fig. 6A, C), becomes a low crest at the middle of the shaft and is continuous with the ridge (l, Fig. 6C) described above. A stout bar of bone arising from the entepicondylar region encloses an elongate, oval entepicondylar foramen (f en, Fig. 6A, C). The capitellum (cp, Fig. 6A) is bulbous and contributes to the thickness of the ectepicondylar region. The trochlea immediately adjacent is a broad, shallow groove; the principal axis of this groove is dorsoventral, as expected, but it is also slightly oblique—the dorsal part being more laterally situated than the

ventral part. Morphologically, the humerus of *M. pascuali* is essentially identical to that in *Pascualognathus polanskii* and galesaurids; apparent differences with galesaurids, e.g., the greater roundness of the head and capitellum, are due to the better ossification in *M. pascuali* and *P. polanskii*. As Bonaparte (1963a) noted, the humerus of *Exaeretodon* sp. is more similar to the dicynodont or gorgonopsid pattern than to that typical of galesaurids, and thus stands in contrast to the conventional cynodont humerus of *M. pascuali*.

The radius has a slight sigmoidal curvature (which facilitates its crossing over the anterior aspect of the ulna) and expanded proximal and distal ends. The nearly circular proximal articular facet forms a shallow concavity, in which the greatest curvature is anteroposterior (as is its reciprocal surface on the capitellum). On the posteromedial aspect of the proximal end is an excrescence that bears a facet (f u, Fig. 6D) apparently for articulation with the ulna. From this excrescence, a distinct flange (p f, Fig. 6D) runs distally to about the midpoint of the shaft. On better preserved material of African Triassic cynodonts, I interpreted a similar flange as possibly being associated with the biceps insertion and the radio-ulnar interosseous ligament (Jenkins, in press). Bonaparte (1963a) interpreted a similar feature in *Exaeretodon* sp. as marking the position of the interosseous ligament. The distal end of the radius expands gradually to the distal articular facet which is oval (long axis transverse) and shallowly concave. A distal flange (d f, Fig. 6D) arises near the midpoint of the shaft essentially as a continuation of the attenuating proximal flange described above. Beginning on the posterior aspect of the shaft, the distal flange takes a spiral course toward the lateral aspect as it enlarges distally. Its position is suggestive of the attachment of an intermuscular septum separating flexor and extensor muscle groups.

The ulna, like the radius, is sigmoidally shaped but is expanded only at its proximal end (Fig. 6D). The relatively shallow semilunar notch represents the typical cynodont condition—basically oval in outline, but with a rather straight medial margin and a nearly hemicircular lateral margin. An olecranon process is not present or at least was not ossified; the proximal end of the ulna, where such a process would be developed, is broad and rugose. The transversely narrow shaft of the ulna bears on its anteromedial aspect a flange (ul f, Fig. 6D) that extends from the semilunar notch to the distal articular facet. In all probability this flange represents the ulnar attachment of the interosseous ligament. The lateral surface of the shaft reveals one large, spoon-shaped fossa proximally, and on the medial surface two fossae, one proximal, the other distal. All three fossae are well represented in African

Triassic cynodonts, and I have proposed (Jenkins, in press) that they represent origins of various manual flexor and extensor muscles. The distal articular facet, convex from front to back, is broad anteriorly and narrow posteriorly and thus is triangular in outline. Both the radius and ulna of *M. pascuali*, as far as available material permits comparison, are extremely similar to their counterparts among galesaurids and in *Pascualgnathus polanskii*. Although definite similarities exist with the antebrachial elements of *Exaeretodon* sp., the essential identity of the *M. pascuali*-galesaurid pattern is incontrovertible.

Only an incomplete and disarticulated series of seven or eight carpals of *Massetognathus pascuali* is known, but these are so poorly preserved, and good comparative material is so scanty, that no constructive observations on the manus can be made at this time.

### Pelvis

A complete pelvis of *Massetognathus pascuali* is not yet available, although enough is known of the ilium and ischium for preliminary description and comparison with other forms. The ilium bears an elongate, vertical blade, spatulate in front and lanceolate behind (il, Fig. 2). The lateral aspect of the blade is concave, especially anteriorly. The shape of blade, as well as the relative proportions of the pre- and postacetabular regions, is most similar to that in *Pascualgnathus polanskii* and is comparable to that of galesaurids, cynognathids, and diademodontids; *Exaeretodon* sp., on the other hand, has an iliac blade quite unlike the foregoing (Bonaparte, 1963a). The base of the iliac blade in *M. pascuali* is constricted into a short neck, below which are medial and lateral processes. The medial process (m p, Fig. 2B) bears two articular surfaces—one each for the pubis and ischium—which intersect at an angle of about  $150^\circ$ . The lateral process bears a nearly circular, concave facet that represents the iliac contribution to the acetabulum (a il, Fig. 2B). The facet is oriented principally in a posteroventral direction but with a slight lateral eversion.

Only the dorsal half of the ischium is available for examination (is, Fig. 2). The concave acetabular surface faces anterolaterally and is oriented essentially vertically. The postacetabular part of the ischium constitutes a broad plate that ventrally meets its counterpart of the opposite side. A longitudinal groove (gr, Fig. 2) on the dorsal margin of this plate terminates posteriorly at an ischial tuberosity (is t, Fig. 2).

Available pubes have been extensively damaged postmortem.

The pubic contribution to the acetabulum is considerably smaller than that of the ischium. Neither the obturator fenestra nor the ventral aspect of the pelvic basin is preserved.

The bony acetabulum is relatively shallow—a little more than 5 mm deep. The continuous, sharp rim around the acetabulum defines a more circular socket than that known in African Triassic genera. In all other details, the pelvis of *Massetognathus pascuali* appears to be morphologically similar to that in *Pascualgnathus polanskii*, galesaurids, and even larger African Triassic forms.

### Hindlimb

The femur (Figs. 7, 8A) is a moderately slender bone, except for the expanded proximal end, which bears robust trochanters. The femoral head, bulbous and almost hemispherical as in mammals, is reflected medially but also somewhat dorsally by virtue of the dorsal bowing of the proximal end of the shaft (Fig. 8A). The protuberant trochanter major (tr mj, Figs. 7, 8A) measures about 5 mm in thickness. A pear-shaped area of smooth bone on its apex may represent the principal site of muscle attachment or of a subtendinous bursa. The bone surface immediately adjacent to the apex is rugose. The trochanter minor (tr mn, Figs. 7, 8A) forms an elongate flange that arises abruptly near the intertrochanteric

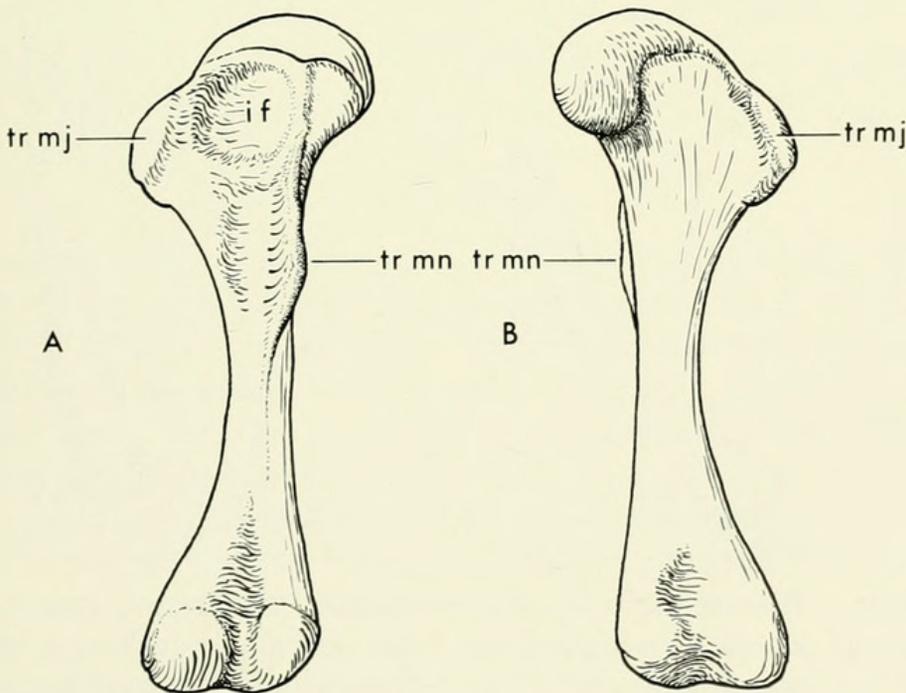


Figure 7. Reconstruction of a left femur in *Massetognathus pascuali* in A, ventral, and B, dorsal views.  $\times 1$ . Abbreviations: i f, intertrochanteric fossa; tr mj, trochanter major; tr mn, trochanter minor.

fossa (i f, Fig. 7) and gradually disappears slightly distal to the shaft's midpoint. In cross-section, the middle of the shaft is essentially rectangular; its thickness from extensor (dorsal) to flexor (ventral) surfaces is about 6 mm, from the medial to lateral surfaces 4.5 mm. The distal end of the femur expands gradually but asymmetrically, the lateral condyle being broader and farther offset from the femoral axis than the medial. The medial condyle projects more ventrally than does the lateral condyle. The fibula appears to have articulated on the lateral epicondylar region where a shallow groove (f f, Fig. 8A) occurs. The femur of *Massetognathus pascuali* is morphologically comparable to the femora of *Pascualgnathus polanskii* and even the larger African genera in which ossification of the extremities was well developed (Jenkins, in press). In smaller forms, such as galesaurids, the femur appears to be different because of the lack of ossification of the extremities and trochanters.

The tibia is a transversely slender bone, bowed somewhat anteriorly. The two proximal articular facets, oval in outline and shallowly concave, are separated by a low, median ridge. The

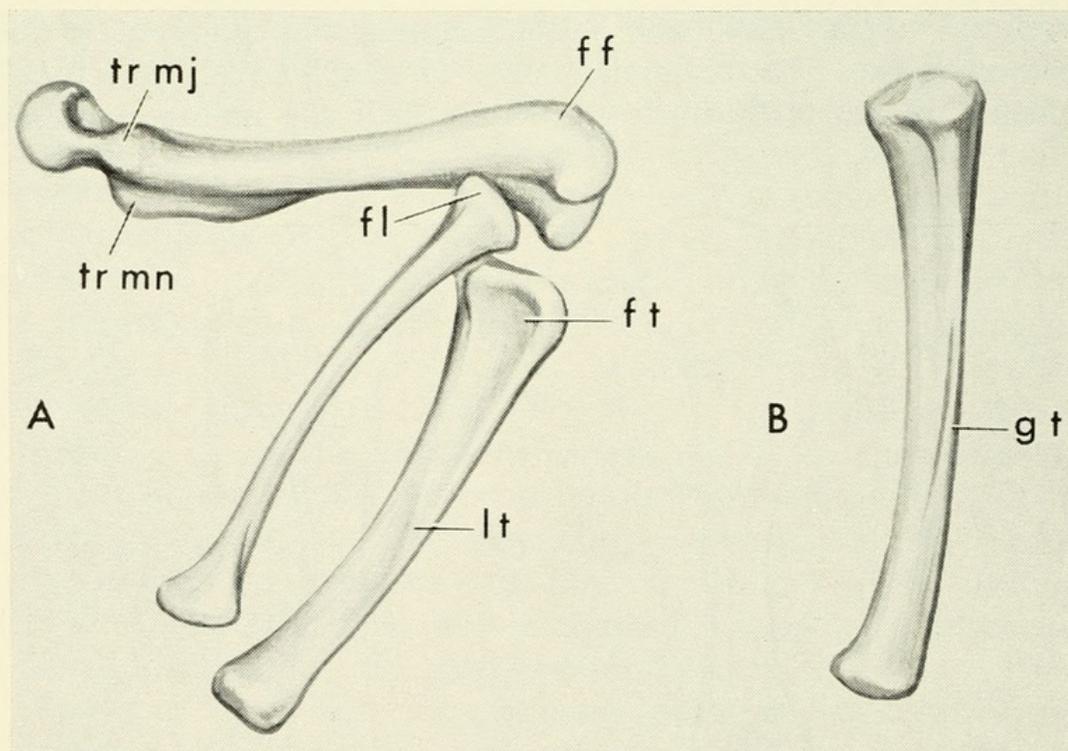


Figure 8. Elements of the hindlimb of *Massetognathus pascuali*, drawn as preserved *in situ*. A, Right femur, tibia and fibula in lateral view. B, Left tibia in medial view. All  $\times 1$ . Abbreviations: f f, facet for articulation with fibula; fl, fibular flange for femoral articulation; f t, lateral tibial fossa of uncertain significance; g t, groove on medial aspect of tibia; l t, lineation on lateral aspect of tibia; tr mj, trochanter major; tr mn, trochanter minor.

lateral margin of the lateral facet is thickened and protuberant, and it appears likely that part of the proximal fibula articulated here. On the proximal end of the lateral aspect of the shaft is a deep fossa (f t, Fig. 8A) of uncertain significance; from the posterior margin of this fossa a faint lineation (l t, Fig. 8A) runs obliquely across the shaft to merge with the narrow anterior margin of the shaft. Also of uncertain significance is a slightly curved groove (g t, Fig. 8B) along the middle of the shaft's medial aspect. The distal extremity of the tibia has a marked lateral expansion that sufficiently widens at the terminus to accommodate a broad, slightly convex facet for the astragalus.

The fibula, a very slender-shafted bone with enlarged extremities, is bowed laterally. The shaft appears to have been wider transversely than anteroposteriorly. On the one complete specimen, a shallow groove running the length of the shaft along its medial aspect can be detected. A flange on the proximal end (fl, Fig. 8A) probably contacted a groove on the lateral epicondylar region of the femur; the remainder of the proximal fibula articulated with the tibia. The distal end, like the proximal, broadens anteroposteriorly and is inflected somewhat medially. All features of both tibia and fibula found in *Massetognathus pascuali* are duplicated in galesaurids and even in the larger African Triassic genera. The tibia and fibula of *Exaeretodon* sp., by contrast, depart from the uniform pattern of other cynodonts by being proportionally more massive.

Nothing can be described of the pes of *Massetognathus pascuali* from the available material.

### Discussion

*Massetognathus pascuali*, about 50 cm in length from head to tail, was a cynodont of relatively slender build (Fig. 9). The shortness of the limbs relative to the approximated trunk length gives the body a "low-slung" appearance. The head seems disproportionately large for the body, but a relatively massive head is a common cynodont characteristic.

The postcranial skeleton of *Massetognathus pascuali* is basically like that in galesaurids, diademodontids, cynognathids and *Pascualgnathus polanskii*. Limited morphological diversity appears to be the rule for the postcranial skeletons of Triassic cynodonts. *Exaeretodon*, however, is an exception; the postcranial skeleton in this genus differs in major details from the pattern characteristic of other Triassic cynodonts. Bonaparte (1963a) recognized postcranial specializations in his original description and implied that

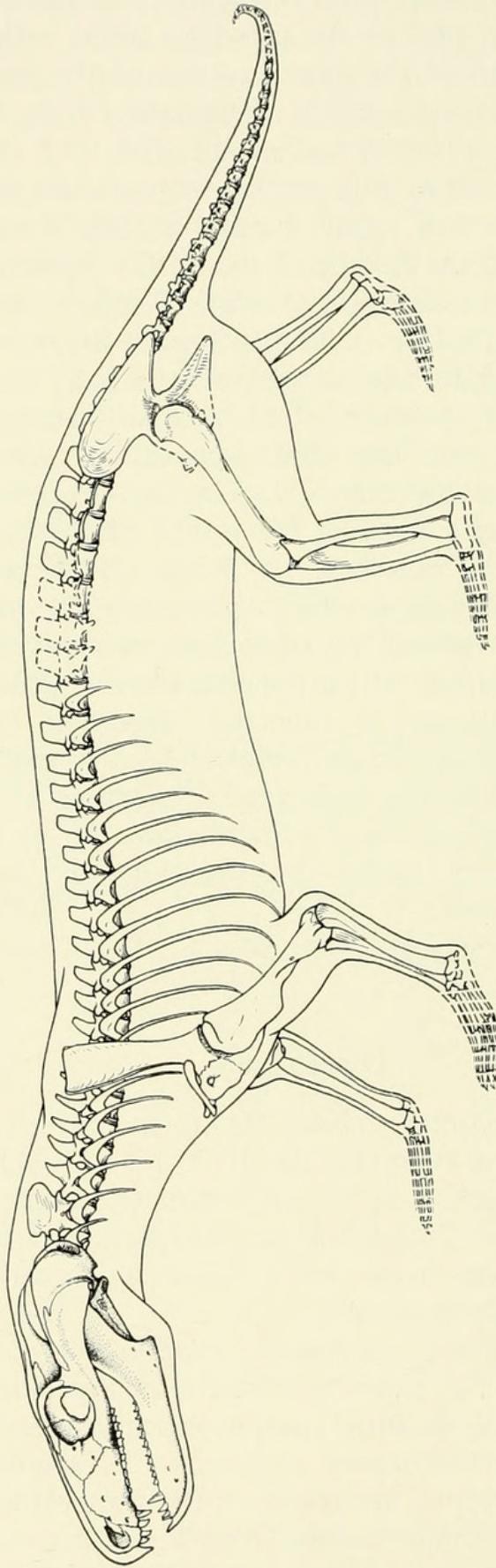


Figure 9. Skeletal reconstruction of *Massetognathus pascuali*,  $\frac{1}{3}$  natural size. Skull modified after Romer (1967). Dashed lines indicate areas of uncertain morphology.

similar features might also be characteristic of other traversodontids. From similarities between the genera *Exaeretodon* and *Leavachia*, Bonaparte further inferred that traversodontids possibly evolved from procynosuchids in a lineage separate from that giving rise to other cynodont families. These conclusions, credible on evidence available in 1963, now require modification, because *P. polanskii* and *M. pascuali* demonstrate that *Exaeretodon* is a specialized traversodontid. Such specialization is not surprising in view of the fact that this genus lived later in the Triassic than any form with which it has been compared. Limb bones in *Exaeretodon* sp. are more robust than in other cynodonts (Fig. 10), no doubt in relation to its unusually large size. Some *Exaeretodon* features are unknown in other cynodonts. For example, a deep, sagittal keel occurs on an unusually short interclavicle; an extra trochanteric process runs distally from the trochanter major along the ventral aspect of the femur (Bonaparte, 1963a; a similar process, identified as a trochanter minor by Parrington (1961), is known in a whaitsid therocephalian and in a scaloposaurid bauriamorph). Furthermore, the lack of rib specialization is a unique feature for a Triassic cynodont. Thus, as a specialized traversodontid, *Exaeretodon* is no longer as relevant to the problem of traversodontid origins as it was when other traversodontid genera were poorly known.

Two facts bear on the problem of traversodontid origins. First, morphological similarities between the postcranial skeletons of *Massetognathus pascuali*, *Pascualgnathus polanskii*, and African Triassic cynodonts are evidence of close phylogenetic relationship. Similarities between the skull and specialized ribs of *P. polanskii* and *Diademodon* (see Bonaparte 1966b) raise the likelihood that traversodontids and diademodontids were derived from a common stock. Second, the paucity of information available on the procynosuchid postcranial skeleton does not appear to be useful in evaluating relationships with other cynodont families. Bonaparte (1963a) compared the postcranial morphology of *Exaeretodon* sp. and *Leavachia duvenhagei* and on this basis suggested the possibility that traversodontids and procynosuchids were directly related. The difficulty of this approach may be illustrated with respect to the forelimb in which, for example, Bonaparte noted similarity between the radius and ulna of *Exaeretodon* sp. and *L. duvenhagei*. The radius and ulna of *L. duvenhagei* are, in fact, poorly known and in relative proportions do not resemble those in *Exaeretodon* sp. more than those of African Triassic cynodonts (Fig. 10). Similarities cited by Bonaparte between the manus of *Exaeretodon* sp. and

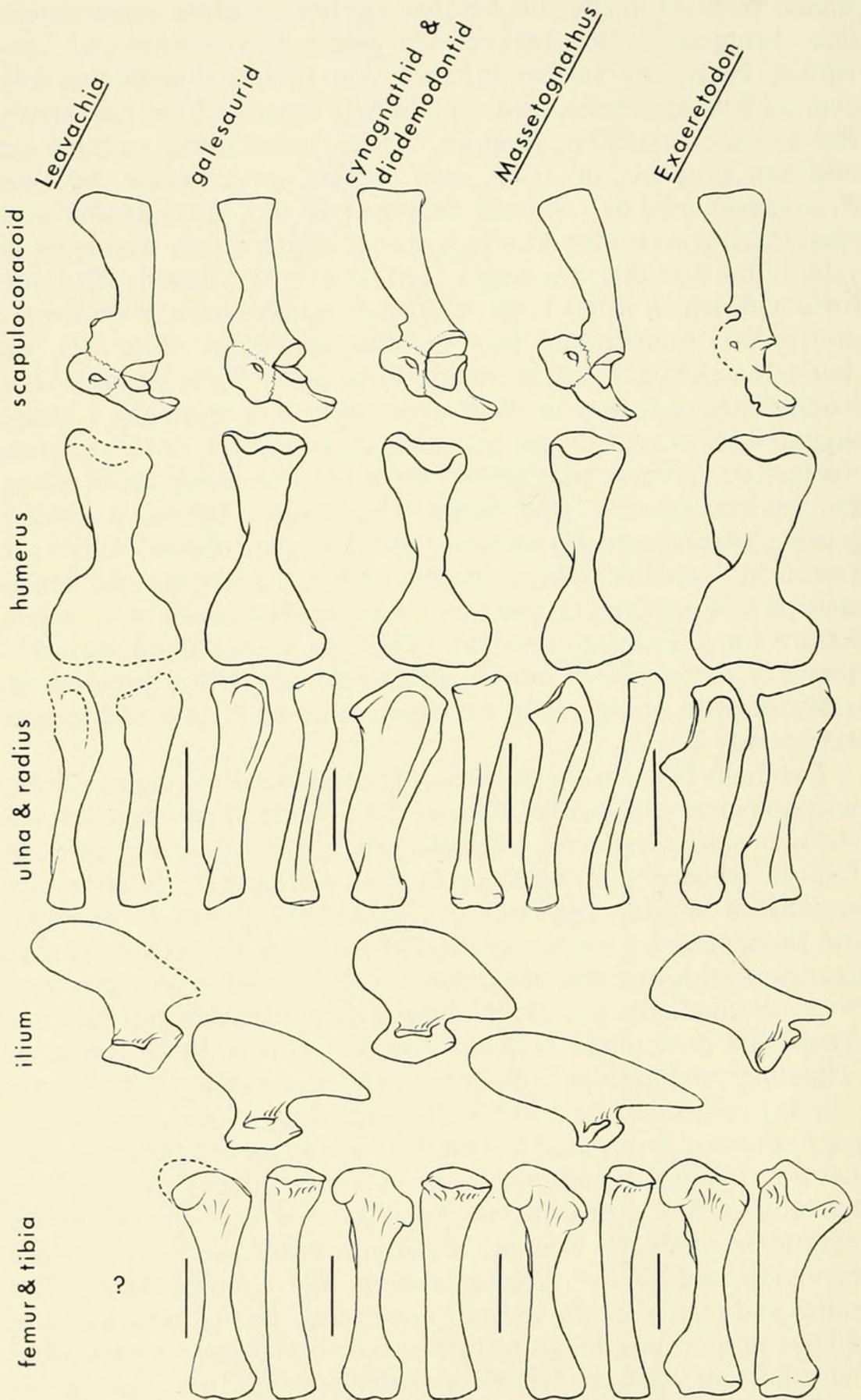


Figure 10. Diagrammatic comparison of postcranial bones in various major groups of cynodonts. *Leavachia*, in part modified from Broom (1948) and in part drawn from stereoscopic photographs, represents Procynosuchidae. The galesaurid and cynognathid–diademodontid patterns are taken from Jenkins (in press); cynognathids and diademodontids are sufficiently alike in their postcranial morphology to be represented here by a single pattern. The *Exaeretodon* material is drawn from Bonaparte (1963b). All bones have been reduced to a standard dimension to illustrate proportional differences.

*L. duvenhagei* are of equivocal significance in view of the almost total lack of information on the manus of other cynodonts. Bonaparte's contention that the humeri of *Exaeretodon* sp. and *L. duvenhagei* are proportioned alike is valid, but the dissimilarity to those in other cynodonts is not so great as to make this comparison especially significant (Fig. 10). Bonaparte admitted that the scapulocoracoid of *Exaeretodon* sp. is more like that in *Cynognathus* sp. than that in *L. duvenhagei*. This resemblance, in Figure 10 at least, is not particularly marked, although the specialized character of the scapulocoracoid in *Exaeretodon* sp. is evident. Thus, comparisons between forelimb features of several cynodont families provide no evidence of special affinity between traversodontids and procynosuchids.

The iliac blade of *Massetognathus pascuali* has a long posterior process like that in African Triassic cynodonts (Fig. 10) and *Pascualgnathus polanskii*. In contrast, the same process in *Exaeretodon* sp. is relatively short (Fig. 10), and as a consequence the blade as a whole has a more mammalian shape (Bonaparte, 1963a). The iliac blade in the type of *Leavachia duvenhagei* appears to have a short posterior process (Fig. 10; Broom, 1948) but also appears to be somewhat damaged. Thus a long posterior process may have existed in procynosuchids, and on present evidence, at least, the ilia of *Exaeretodon* sp. and *L. duvenhagei* do not indicate special affinity between the two.

Bonaparte (1963a) cited the absence of specialized ribs in *Exaeretodon* sp. and *Leavachia duvenhagei* as possible evidence of a close relationship between traversodontids and procynosuchids. The subsequent discovery of specialized ribs in *Massetognathus pascuali* and the reclassification of *Pascualgnathus polanskii* (which has specialized ribs of the *Diademodon* pattern) make this observation no longer significant. It is interesting, however, that in the type of *Leavachia duvenhagei* (Rubidge Collection No. 92, Graaf Reinet, South Africa) the last dorsal rib appears to be laterally oriented (Fig. 4C), much as in *M. pascuali* and in other cynodonts with specialized ribs. On the dorsal aspect of the shaft is a ridge (b, Fig. 4C) comparable in position and orientation to a similar ridge in *M. pascuali*, cynognathids, and diademodontids (b, Fig. 4A, B). Furthermore, Konjukova (1946) figured a specimen of the procynosuchid *Permocynodon*, incompletely prepared from the ventral aspect. The posterior dorsal ribs are directed anterolaterad (as in *Thrinaxodon*, for example) and the shafts appear to be wider than those of more anterior dorsal ribs. The capitular articulations of posterior dorsal ribs in *Permocynodon* are relatively broad, a feature typical of cynodonts in which the posterior dorsal

ribs are synostosed. On this incomplete evidence, it appears possible that rib specialization was already underway in procynosuchids and was further modified in the various cynodont families descended from them.

Hopson and Crompton (1969), in a discussion of the origin of mammals, observe that galesaurids such as *Thrinaxodon liorhinus* would be ideal candidates for mammalian ancestors were it not for the presence of specialized ribs. These authors suggest that *Exaeretodon* is relevant to this problem because its nonspecialized ribs may represent a reversion from a specialized pattern, and similar trends may have occurred in galesaurids. There is now substantial evidence favoring the view that rib specialization was gradually lost in traversodontids. *P. polanskii*, the earliest traversodontid for which ribs are known, has a costal morphology of a *Diademodon* pattern. *M. pascuali*, temporally intermediate between *P. polanskii* and *Exaeretodon* sp., has ribs with less extensive specialization. Thus the ribs of *Exaeretodon* sp. apparently represent a reversion to a nonspecialized condition, and are not primitively nonspecialized as originally suggested by Bonaparte (1963a). That such a loss occurred in one family of cynodonts increases the possibility that a similar reversion occurred in advanced galesaurids—or their descendants—during the reptile–mammal transition.

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