New Triassic Dicynodonts from South America, Their Origins and Relationships

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NEW TRIASSIC DICYNODONTS FROM SOUTH AMERICA, THEIR ORIGINS AND RELATIONSHIPS

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CONTENTS

Richly fossiliferous deposits have been found in the Ischigualasto region of Argentina in the last few years. The only known dicynodont from this area is the new genus *Ischigualastia*, of which a diagnosis and fully illustrated description are given. A specimen from Brazil, which had earlier been referred to the genus *Stahleckeria* as *S. lenzii*, is shown to be very similar to *Ischigualastia*, but not generically identical with it; this specimen is therefore placed in the new genus *Barysoma*.

The only South American dicynodont which had previously been fully described is *Stahleckeria*, from Brazil. A diagnosis and fully illustrated description are now given of the complete skeleton of the genus *Dinodontosaurus*, also from Brazil. Earlier Brazilian material which had been referred to the African genus *Dicynodon* is shown to belong to *Dinodontosaurus*.

A very large skull from the same deposits is identical with *Dinodontosaurus*, except that it has a much more massive snout and tusks, and a wider occiput. The dicynodonts are herbivorous, and may well have lived in herds; it is suggested that the massive skull may belong to the old male of such a herd of *Dinodontosaurus*, and it is therefore not given separate taxonomic status.

The skull of *Placerias*, the only dicynodont known from North America, had previously been restored by Camp & Welles (1956) from the broken remains of about forty individuals. Comparison of the restored skull with that of *Ischigualastia* has suggested various modifications in the reconstruction, and illustrations of the new reconstruction are given.

The relationships of the Triassic dicynodonts are discussed. It is suggested that, excluding the specialized genus *Lystrosaurus*, they show two main divergent adaptations, which are probably related to their mode of feeding. A pointed snout and high occiput is thought to characterize the family Kannemeyeriidae (which includes the forms *Kannemeyeria*, '*Kannemeyeria*' *vanhoepeni*, *Sinokannemeyeria*, *Parakannemeyeria*, *Ischigualastia*, *Barysoma* and *Placerias*). A blunt snout and wide occiput is thought to characterize the family Stahleckeriidae (which includes the genera *Stahleckeria* and *Dinodontosaurus*). A similar distinction is found today between the browsing black rhinoceros and the grazing white rhinoceros. The most primitive kannemeyeriids are found in the Lower Triassic of China, and these forms may also be ancestral to the stahleckeriids. The only other Triassic dicynodonts, *Shansiodon* and '*Dicynodon*' *njalilus*, may be placed in a separate family, the Shansiodontidae.

All these Triassic genera have two features in common: the presence of a separately ossified olecranon process on the ulna, and a shortened interpterygoid vacuity. It is possible that this may indicate a common ancestry for them all, but no Upper Permian or Basal Triassic genera now known appear to be possible ancestors for them.

The lack of any Middle Triassic vertebrate fauna in the northern hemisphere makes it very difficult to date the Argentinian and Brazilian faunas, which include gomphodont cynodonts, dicynodonts, rhynchosaurs, pseudosuchians and a few saurischians. It is not felt that the presence of rhynchosaurs necessarily indicates a Middle Triassic age, as the group is known from the mid-Norian of India. It is possible that the presence of several saurischians and of a pseudosuchian closely related to the German Norian genus *Aëtosaurus*, may indicate a Carnian age for the Argentine fauna. The Brazilian fauna is somewhat dissimilar to that of Argentina and contains no genera in common with it; it may therefore be of earlier, Ladinian, age.

The fauna of the Manda Beds of East Africa is similar in composition to that of Brazil, but contains no genera in common with it. It also lacks saurischians and includes a dicynodont, *Kannemeyeria*, that is otherwise typical of the Lower Triassic *Cynognathus* zone of South Africa. It may therefore be Anisian in age.

Introduction

The dicynodonts formed the bulk of the land vertebrate herbivore fauna of the Upper Permian, during which they are known from Africa, Europe and Asia. In the South African strata of this period, with its abundant fossils, dicynodonts contribute about 80% of the specimens. These specimens probably represent about fifty genera, and show a corresponding diversity in structure and possible habitat. The skulls range in length from 5 to 75 cm. Though teeth are never found on the anterior region of the premaxilla, different genera are known with a great variety of dental apparatus, from the extensive tooth row in some endothiodonts to the completely toothless *Oudenodon* with its extensive horny beak. Though the genera with cheek teeth are usually small, they include the genus *Endothiodon*, the skulls of which may be as large as 57 cm long and have an extremely complicated dental apparatus. The dicynodont fauna also includes the little burrowing form *Kistecephalus*.

The transition to the Triassic is accompanied by a dramatic reduction in the dicynodont fauna. This affects not only the number of specimens found but also the number of genera and the diversity of structure that is represented. Triassic dicynodonts with cheek teeth are unknown, so that the dentition is restricted to upper canine tusks or is completely absent.

In the Basal Triassic, only a few dicynodont genera are known, the best known being the aberrant semi-aquatic hippopotamus-like *Lystrosaurus*. In beds later than this *Lystrosaurus* zone, only twelve dicynodont genera are known—this includes those described in the present paper and in Cruickshank's papers (in preparation). Though this Triassic fauna has as wide a geographical range as the Permian dicynodont fauna, the individuals are all large, with skull lengths ranging from 24 to 68 cm.

Despite the abundance of Permian dicynodont specimens, articulated skeletons are very rare, so that many forms are based upon skulls alone. In addition to this restriction, only a relatively small amount of information on skull structure could be obtained with mechanical methods of preparation, especially on the smaller genera. As a result of these two factors, the interrelationships of the large number of varied Permian genera are at present almost entirely unknown. Most of the Triassic genera, on the other hand, are known from almost complete skeletons, and their large size makes investigation of their cranial structure far more easy. The aim of this paper is therefore to give as full an account as possible of the osteology of several undescribed Triassic genera from South America. This account is followed by a comparison of all the known Triassic dicynodont genera, which shows that they probably belong to several distinct families. The interrelationships of these families will probably remain uncertain until our knowledge of the dicynodonts of the Upper Permian and Lower Triassic of areas outside Africa has improved.

In order to facilitate comparison between different specimens, all paired bones have been drawn as though they were those of the left side; where necessary, bones of the right side have therefore been drawn as mirror images of themselves.

The abbreviation MCZ is used to indicate the Museum of Comparative Zoology at Harvard University

ISCHIGUALASTIA JENSENI, A NEW DICYNODONT FROM ARGENTINA

Apart from a fragment of the humerus of a dicynodont from the uppermost reaches of the Amazon in north-eastern Peru, identified by von Huene (1944), Brazil was until recently the only part of South America from which Triassic vertebrate remains had been described. However, during his South American collecting, von Huene (1931) had noticed fossil foot-prints in the Ischigualasto Valley region of San Juan Province, in western Argentina. Cabrera (1943) had found fragments of bone in this same region, and Heim (1949) gave a full description of the Ischigualasto beds, mentioning the abundant vertebrate remains and giving a photograph of a cynodont skull *in situ*. In 1958, acting on these indications, Dr A. S. Romer and Dr B. Patterson took an expedition to the Ischigualasto Valley which, they found, was exceedingly rich in vertebrate fossils (see Romer 1962).

The dicynodont material collected by this expedition consists of five specimens, which all came from about the same horizon. Four of these include both cranial and post-cranial material, the other comprises only an ilium. All appear to belong to the same new genus of dicynodont, which has been named *Ischigualastia jenseni*, after Mr James Jensen, who collected and prepared this material. A preliminary diagnosis of *Ischigualastia* has already been published (Cox 1962) and is repeated below.

Genus. *Ischigualastia* Cox.

Generotype. *Ischigualastia jenseni* Cox.

Generic diagnosis. Large dicynodont (type skull 55 cm long, 46 cm broad). No teeth in upper or lower jaws. Skull triangular in dorsal view, greatest width across occiput. Very wide interorbital region, very narrow intertemporal region. Tapering snout, without nasal ridges or bosses. No pineal boss, but a slight mound in front of pineal foramen. No postfrontal bone. Preparietal bone probably present. Interparietal forms whole of posterior half of intertemporal bar, widely separating squamosals from postorbitals. No sharp median intertemporal ridge. Zygomatic arches bowed outward. Sharp transition between dorsal and occipital surfaces. Occiput almost semi-circular in outline. No tabular bone visible. Stapes lacks stapedial foramen. Short interpterygoid vacuity. No ectopterygoid bone. Pterygoid broadly meets maxilla. Palatine and premaxilla meet, excluding maxilla from internal nares. Palatal surface of premaxilla bears pair of anterior ridges. Premaxilla extends some way anterior to maxilla. No lateral wing on dentary. Stout retro-articular process.

Five sacral ribs. Acromion process of scapula absent or vestigial. Coracoid foramen between precoracoid and scapula. Sternum constricted halfway along its length; dorsal surface bears bosses for attachment of ribs. Ulna has large olecranon process, with cartilaginous epiphysial union with rest of bone. Femur with well-developed head set off from rest of bone.

Holotype of I. jenseni. Number 18.055, Muséo Argentino de Ciencias Naturales, consisting of skull and partial skeleton.

Geological horizon and locality. Ischigualasto formation (Triassic), approximately 100 m above the base of the formation; about 2 km north of Agua de la Peña, Ischigualasto Valley, Department of Valle Fertíl, San Juan Province, Argentina.

Referred material. MCZ Nos. 3118, 3119, 3120, 3121.

Skull

The skull belonging to the holotype of *Ischigualastia* is almost complete and undistorted. Other skull material comprises two laterally compressed but largely complete skulls (specimens MCZ Nos. 3118 and 3119), and the premaxilla and braincase of a fourth skull (MCZ No. 3120).

Nearly all of the following description is based on the holotype skull. The following regions were damaged: the palatal edges of the premaxilla and maxillae, the pre-orbital part of the maxillae, and the anterior ends of the zygomatic arches. All these features have been restored from other skulls.

The holotype skull seems also to have been slightly distorted, as the anterior entrance to the cranial cavity was blocked by the ventral end of the descending part of the parietal. The apposition of these areas could have been caused by an upward and forward rotation of the lower end of the occipital plate, or by a downward compression of the dorsal roof in the parietal region. The skull is still bilaterally symmetrical and shows no obvious lines of breakage or distortion. However, the pterygoid region of the palate was damaged, and the quadrates lay in a position which appeared unnaturally close to the base of the zygomatic arch. As both these features could have resulted from a movement of the occipital plate, but not from a depression of the dorsal roof, it was felt that the former type of distortion was the more likely. Accordingly, the quadrates and the lower end of the occipital plate have been somewhat rotated back in the accompanying drawings.

Dorsal view (figure 1*A*). The greatest length of the skull is about 55 cm, its greatest breadth 46 cm. There is no sign of any nasal or pre-frontal bosses. There is a median ridge on the premaxilla, and a supra-orbital ridge. The upper edge of the orbit is somewhat rugose. There is a low mound just in front of the pineal foramen.

The inter-orbital region is extremely broad, so that the orbits are hardly visible in dorsal view. There is a large prefrontal, but no postfrontal. The frontal is triangular. It extends far anteriorly, so that the nasals have a very short midline suture. It extends

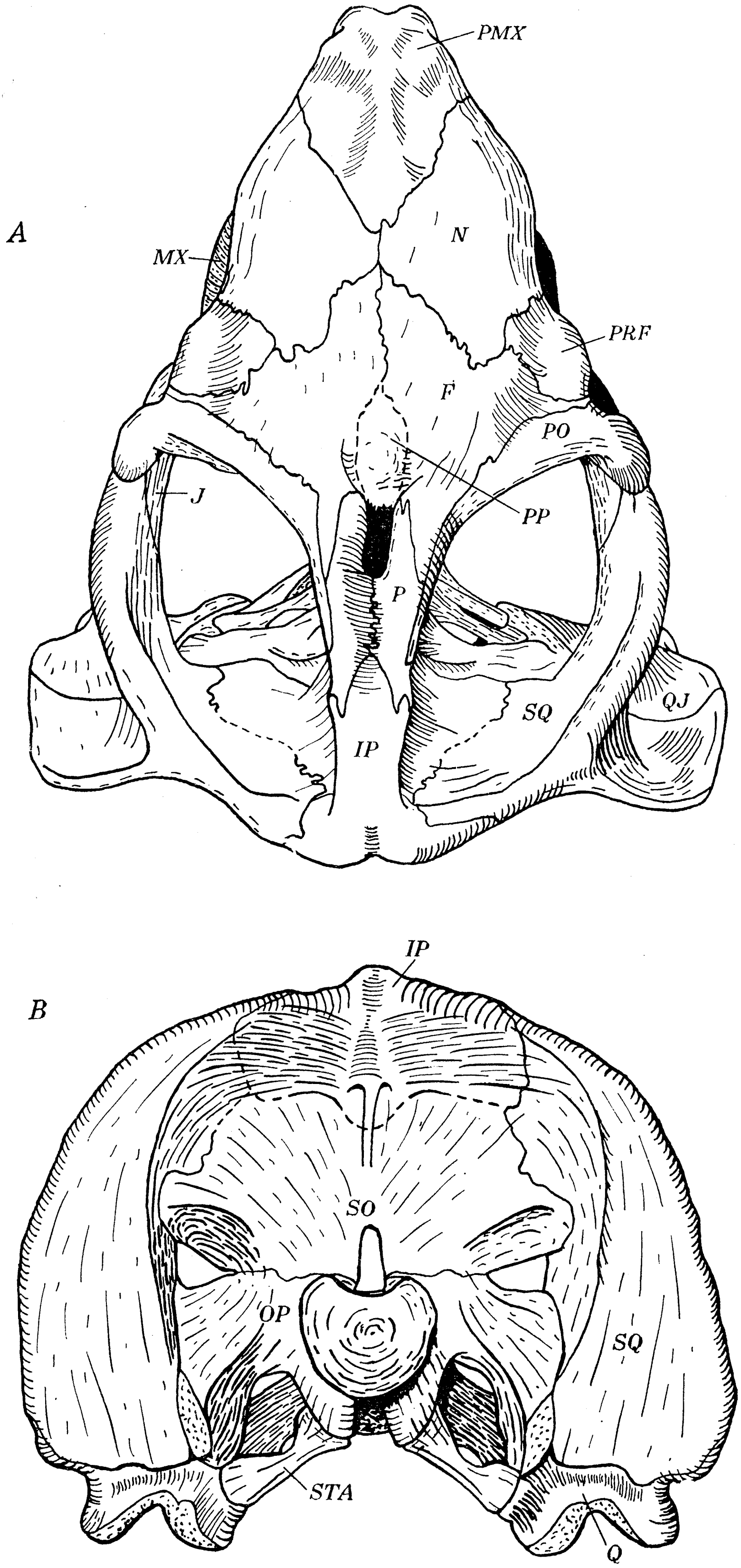

FIGURE 1. *Ischigualastia jenseni*, type specimen. *A*, Dorsal view of skull, × 2/9. *B*, Occipital view of skull, × 2/9. For abbreviations of names of bones see p. 514.

laterally until it just enters the edge of the orbit, and it also extends far posteriorly to a level just past the posterior end of the pineal foramen.

It is difficult to distinguish sutures in the region just in front of the pineal foramen. The sutures indicated in the figure as outlining a preparietal bone appear to be present, but it is impossible to be certain of this. The pineal foramen itself is long and narrow, with a smooth transition onto the frontals on either side of the low mound on the preparietal bone.

The great posterior extent of the frontal has filled in what is normally the angle between the post-orbital bar and the intertemporal region. The postorbital bone therefore runs postero-medially to continue along the side of the intertemporal bar, which is very narrow. The whole of the posterior part of the intertemporal bar is formed from the interparietal, and the postorbital and squamosal therefore do not meet.

The zygomatic arches are markedly bowed outward; this appears to be natural, not the result of distortion.

Occipital view (figure 1*B*). The occiput is almost semi-circular in outline. The interparietal occupies a fairly large area of the upper part of the occiput, and extends backwards to overhang the rest of the occiput. Much of the region of meeting of the interparietal and supraoccipital is damaged, so that the sutures here cannot be seen. Despite prolonged search both in superficial view and in sections, no trace of a tabular could be found.

There is a clear suture separating the supraoccipital from the more ventral bones, but the other elements of the occipital plate (exoccipital, opisthotic, basioccipital) are fused together. There is a clear region of muscle insertion in a hollowed area above and below the post-temporal fossa; this muscle was probably part of the obliquus capitis complex (see Cox 1959; Ewer 1961). The distal end of the paroccipital process bears a posteriorly directed process, the position of which is thus identical with that of the tympanic process described in *Kingoria* (Cox 1959).

The occipital condyle of the type skull is large and subcircular in outline, with no sign of division into exoccipital and basioccipital portions. In skull MCZ No. 3120 the condyle is more trifoliate in outline.

The foramen magnum appears to have been laterally compressed.

The squamosal has an interdigitating suture with the interparietal and supraoccipital, but only abuts against the distal end of the paroccipital process.

A ridge runs down the squamosal from near its dorso-medial corner to a level halfway down the paroccipital process. This may mark the outer limit to the area of the occiput which was occupied by muscle insertions.

Palatal view (figure 2*A*). The long secondary palate is formed almost exclusively by the premaxilla. This bone bears a pair of blunt ridges anteriorly, and a median posterior ridge which continues beyond the level of the internal nares and meets the vomer. The postero-lateral corners of the premaxilla meet the palatines, excluding the maxillae from the margin of the internal nares.

Behind the premaxillary secondary palate the air passage continues into a channel between the anterior rami of the pterygoids. The lateral walls of this channel are formed anteriorly by the palatines, posteriorly by the pterygoids. Its roof is not preserved, but it was probably formed by the vomer and palatines, as in other dicynodonts.

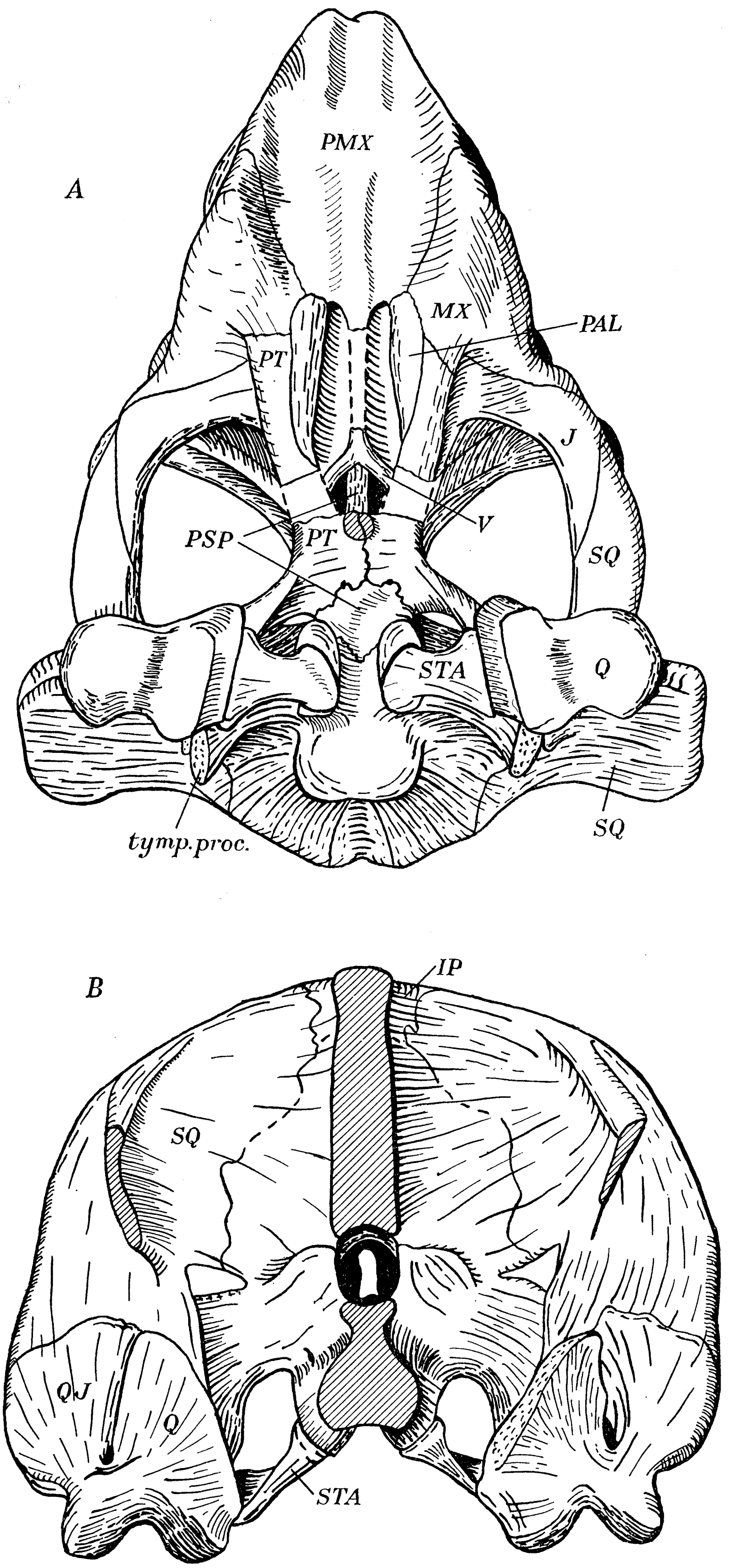

FIGURE 2. *Ischigualastia jenseni*, type specimen. *A*, Ventral view of skull, × 2/9. *B*, Anterior view of occipital plate, × 2/9. *tymp.proc.*, Tympanic process. For abbreviations of names of bones see p. 514.

The middle section of the vomer is lost, but its posterior end is preserved, where it forms the anterior border of the very short interpterygoid vacuity. Through this vacuity can be seen the ventral surface of the processus cultriformis of the parasphenoid.

The anterior rami of the pterygoids meet the maxillae anteriorly. Sutures are very difficult to distinguish in this region, but the pterygo-maxillary suture appears to lie more anteriorly on the right side than on the left side. No trace could be found of an ectopterygoid.

The pterygoids have an extensive meeting behind the interpterygoid vacuity. This region is very broad (8·0 cm). There is a raised broken surface here, which appears to be the remains of a median boss; specimen MCZ No. 3119 shows a similar structure. The foramina for the internal carotid arteries lie in the suture between the pterygoids and the parasphenoid.

The basisphenoid tubera are set rather close together and project downwards and only slightly outwards. As a result, the inner ends of the two stapes are only 2·8 cm apart. The stapes has a wide distal end, which rests against a ledge on the inner surface of the quadrate.

Anterior face of the occipital plate (figure 2*B*). The intertemporal region, above the cranial cavity, is very narrow, as are the posterior parts of the zygomatic arches.

The pilae antoticae were not preserved.

A groove runs inwards from the post-temporal fossa to a notch in the anterior wall of the braincase. This groove probably housed the vena capitis dorsalis (see Cox 1959).

In anterior view, no sutures can be seen between the bones of the braincase (supraoccipital, prootic, opisthotic, basisphenoid).

The quadratojugal does not extend very far dorsally. It lies on the anterior face of the squamosal, to which it is firmly attached. Its lower end is fused to the outer condyle of the quadrate. The quadrate rests in a pocket formed by the quadratojugal, the squamosal and the distal end of the paroccipital process.

Side view (figure 3). The septomaxilla and the palatal edges of the premaxilla and maxilla are restored from other specimens.

The premaxilla extends a considerable distance in front of the anterior end of the maxilla, and its paired anterior palatal ridges are visible in side view.

The maxilla bears no teeth. It meets the squamosal below the orbit.

The sphenethmoid and the anterior part of the parasphenoid-basisphenoid complex were not preserved and have not been restored in the side view of the skull.

The base of the epipterygoid is very high and covers most of the antero-lateral surface of the quadrate ramus of the pterygoid. The ascending portion is flattened, and about 1 cm wide. There appears to be an interdigitating suture between its dorsal end and the descending part of the parietal. If correct, this means that the dorsal end of the epipterygoid is not expanded to form any large part of the side wall of the braincase.

Lower jaw (figure 3*B*). None of the specimens includes a complete and undamaged lower jaw. That of the type consists of only the articular region and the dentary. The lower jaw of specimen MCZ No. 3120 is more or less complete, but the posterior end of the dentary is damaged. The exact position and angle of junction of the dentary with the post-dentary bones is therefore uncertain, so that the precise length of the lower jaw is not known. It has been restored to the minimum length allowed by the interleaving of the bones and by the markings of overlap which they bear.

The dentary is massive. It is notched posteriorly, so that it extends back as dorsal and ventral wings. In dorsal view, it tapers anteriorly to a blunt and slightly bilobed tip.

The details of the relationships of the post-dentary bones cannot be distinguished. The type shows a well developed retro-articular process.

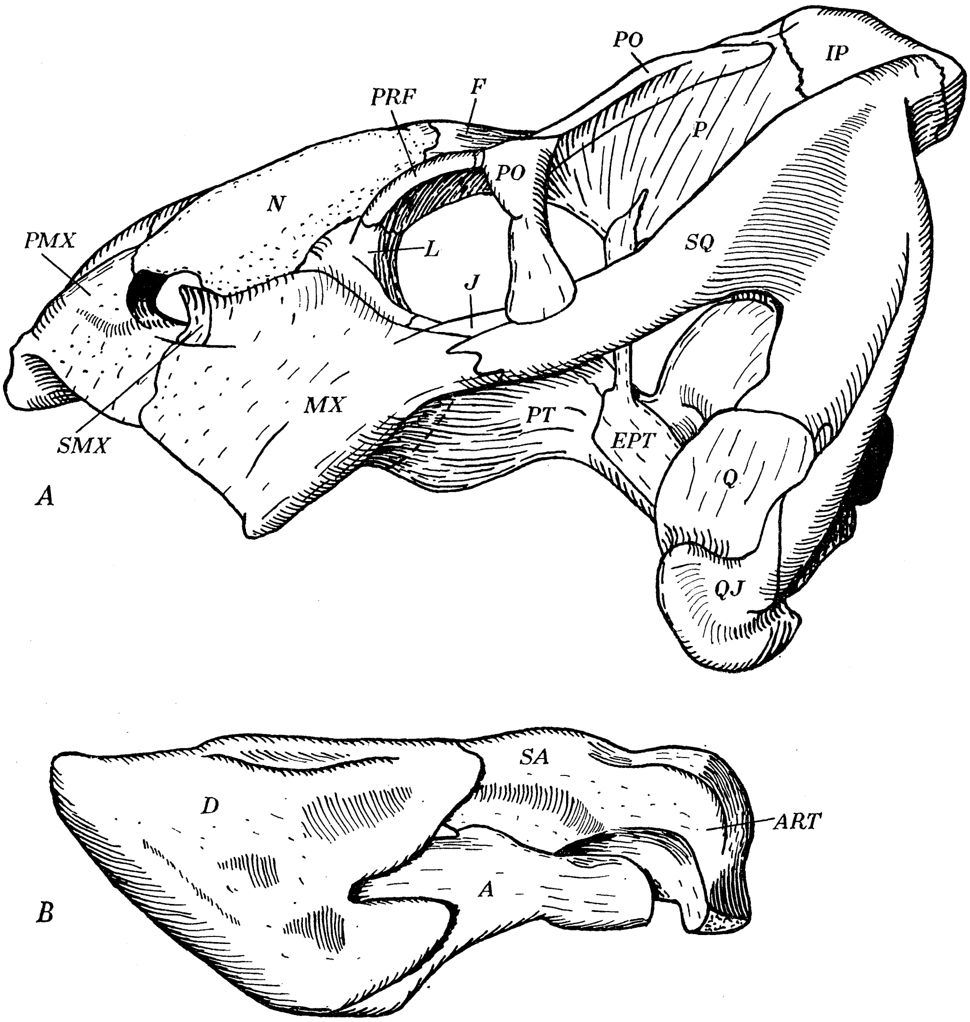

Figure 3. *Ischigualastia jenseni*. *A*, Lateral view of skull of type specimen, × 2/9. *B*, Lateral view of lower jaw, × 2/9, restored from dentary of specimen MCZ No. 3120 and post-dentary bones of type specimen. For abbreviations of names of bones see p. 514.

Post-cranial skeleton

Much of the post-cranial skeleton is represented in one or more of the five specimens of *Ischigualastia jenseni*. The best preserved specimen of each bone has been drawn in the accompanying figures, irrespective of which specimen it comes from. The humerus, radius, ilium and femur were drawn from those of the right side, and reversed in the figures.

Vertebral column (figure 4). Only a few more or less complete vertebrae were preserved. That shown in figure 4*A* to *C* is probably the most anterior, as its centrum is the shortest antero-posteriorly, the capitulum and tuberculum are well separated, and the neural spine has only a slight backward slope. Its prezygapophyses are wide and gently rounded, directed upwards and slightly inwards. In contrast to this, the postzygapophyses are narrow and flat and are directed ventro-laterally at a considerable angle. It is possible that this is the first dorsal vertebra, as in *Kingoria* (Cox 1959) this vertebra is similar in having considerable freedom of movement on the preceding last cervical vertebra, but little freedom of movement on the succeeding second dorsal vertebra.

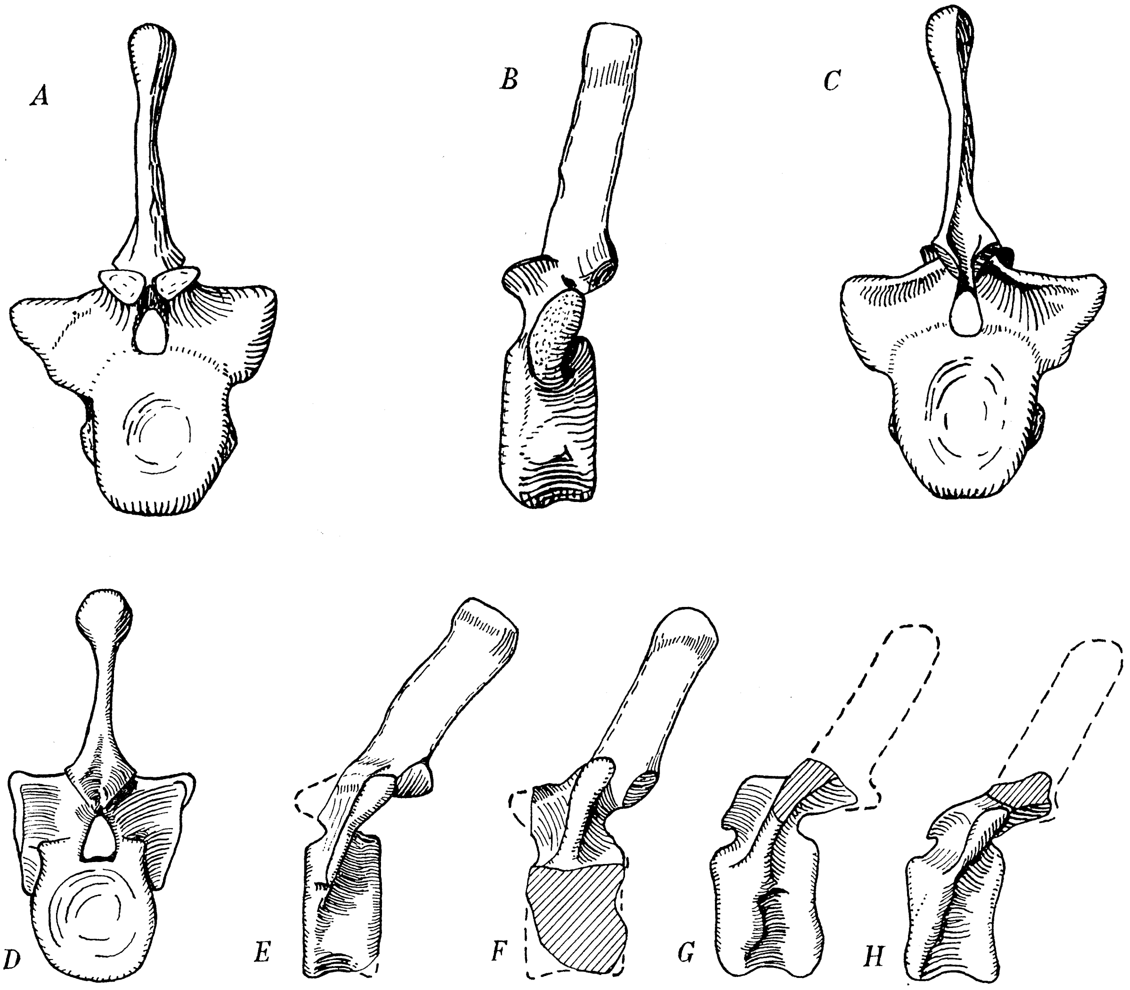

FIGURE 4. *Ischigualastia jenseni*, type specimen. Vertebrae, × 1/5. *A* to *C*, Possibly first dorsal vertebra, in *A*, anterior view; *B*, lateral view; *C*, posterior view. *D*, *E*, Another vertebra in *D*, posterior view; *E*, lateral view. *F* to *H*, Other vertebrae in lateral view.

There is not a sufficient number of other well-preserved vertebrae for it to be possible to put these in order. All show a long rib-facet extending down the outside of the transverse process and down on to the centrum.

Ribs (figure 5). Only a few complete ribs, and some other rib-heads, were preserved. The smallest rib, presumably cervical, is distinctly double-headed. It is too thin for it to be possible to remove the matrix, so only a sagittal section is figured (figure 5*A*). The remaining ribs form a series in which the largest has two heads separated by a small notch, while the smallest has only a single head. By comparison with other dicynodonts, it seems likely that the largest is one of the most anterior dorsals, and that the two heads become united as one moves posteriorly along the vertebral column.

The large double-headed rib (figure 5*B*) is complete, though somewhat flattened. It ends in a rounded surface beyond which the cartilaginous distal part of the rib presumably continued. This may also be true of a smaller, more posterior rib (figure 5*D*). The smallest rib (figure 5*E*) may be either a posterior dorsal or a caudal rib; it has a large groove running along its posterior surface.

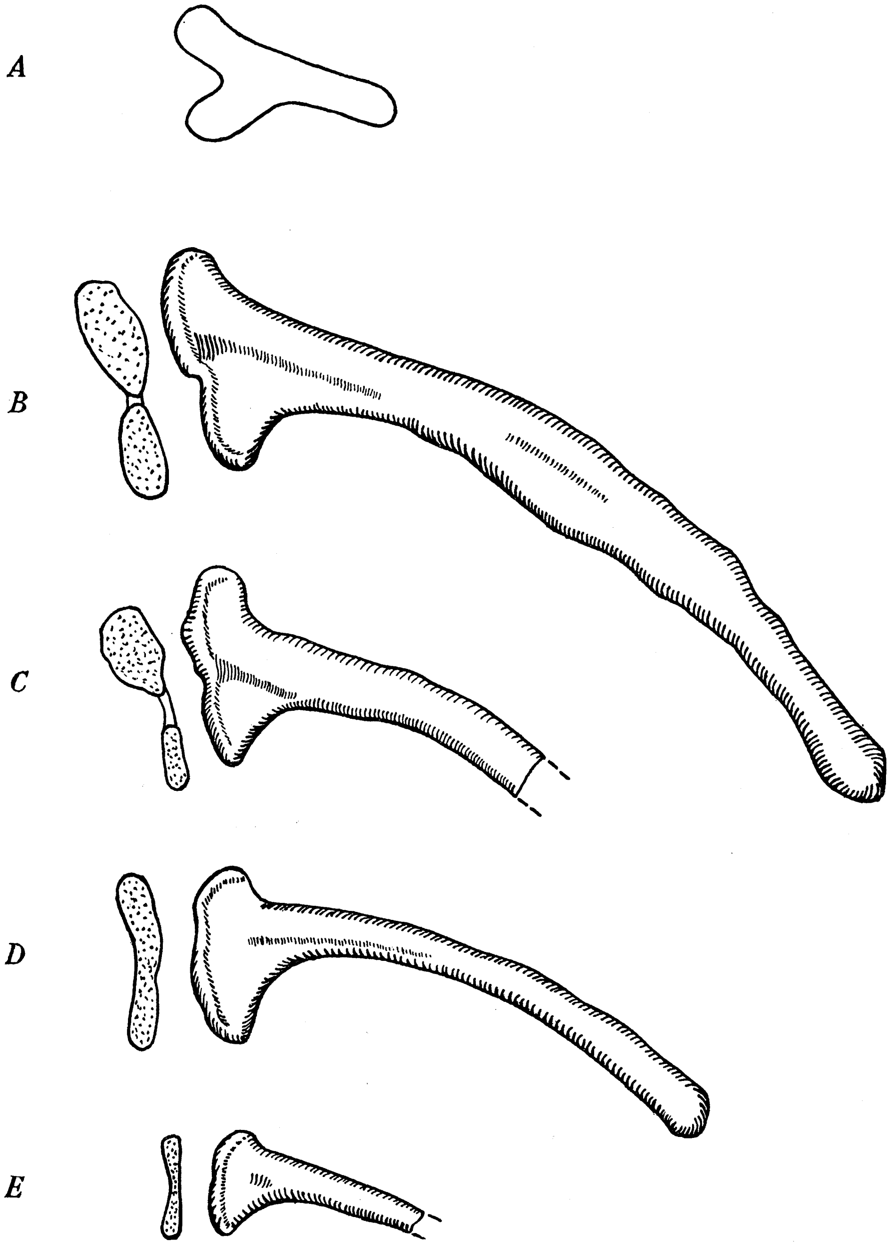

Figure 5. *Ischigualastia jenseni*, type specimen. Ribs, × 1/5. *A*, Outline of cervical rib. *B–E*, Anterior views of other ribs, and proximal views of their heads.

Pectoral girdle (figure 6). No cleithrum, clavicles or interclavicles were found. The scapula shows no facet for the attachment of the cleithrum, and this bone was probably absent, as in most dicynodonts.

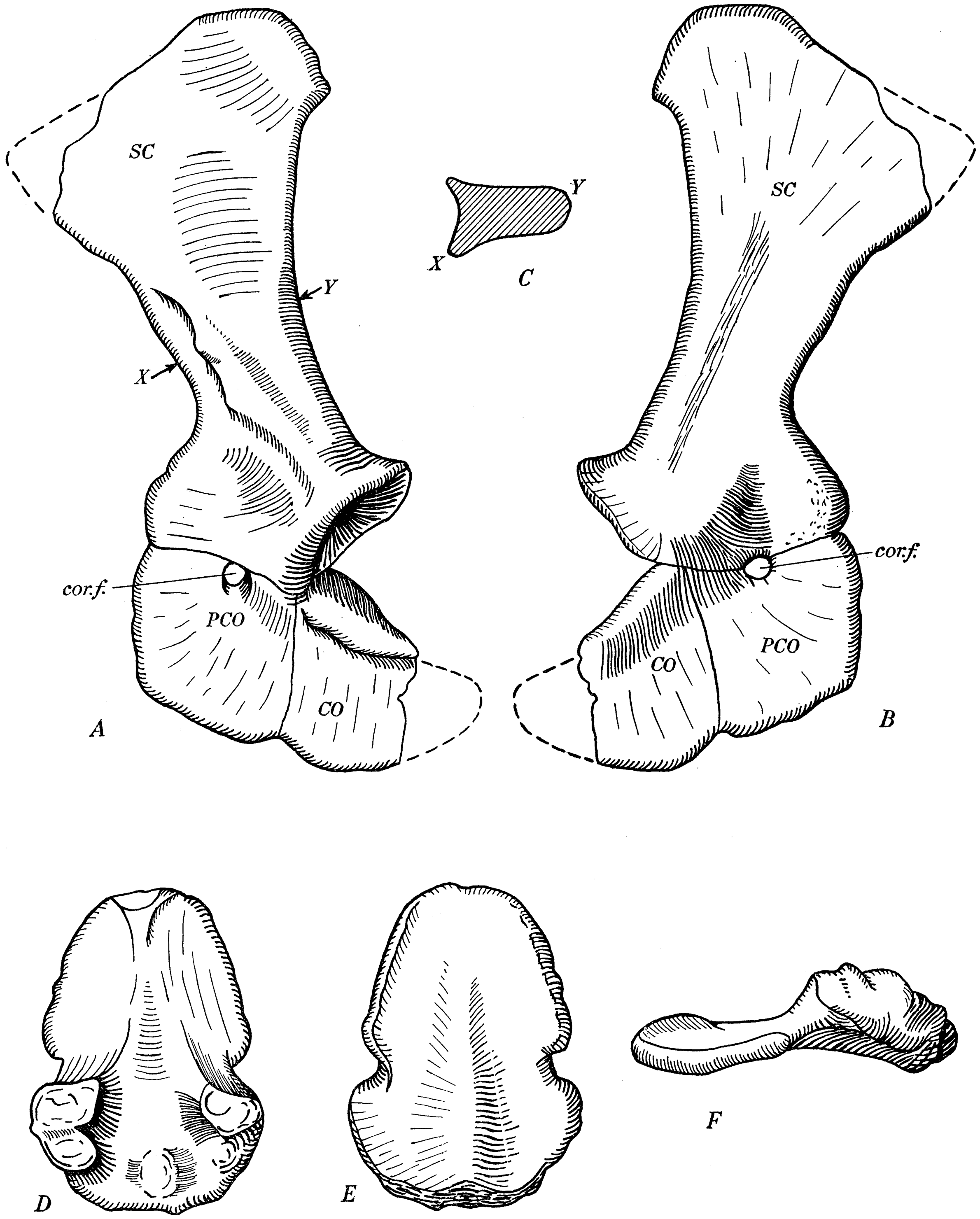

FIGURE 6. *Ischigualastia jenseni*. *A*, *B*, Scapulo-coracoid of type specimen in *A*, lateral view and *B*, medial view, × 1/5. *C*, Section across scapula at level *X*–*Y* in figure *A*, to show lack of acromion process. *D*–*F*, Sternum of specimen MCZ No. 3120 in *D*, ventral view; *E*, dorsal view; *F*, lateral view, × 1/5. *cor.f.*, Coracoid foramen. For abbreviations of names of bones, see p. 514.

Several scapulo-coracoids were available. As preserved, the scapula is slightly curved, and the coracoid plate is in nearly the same plane as the lower part of the scapula; this position of the coracoid plate is probably due to crushing. The scapula is unusual in lacking an acromion process; though a ridge runs down the outer side of the lower part of the bone near its front edge, this does not become an acromion process. The ridge is probably merely the division between the areas of attachment of the infraspinatus and supraspinatus muscles. The lack of an acromion is shown in several specimens, and it is therefore unlikely that it is due to breakage or weathering.

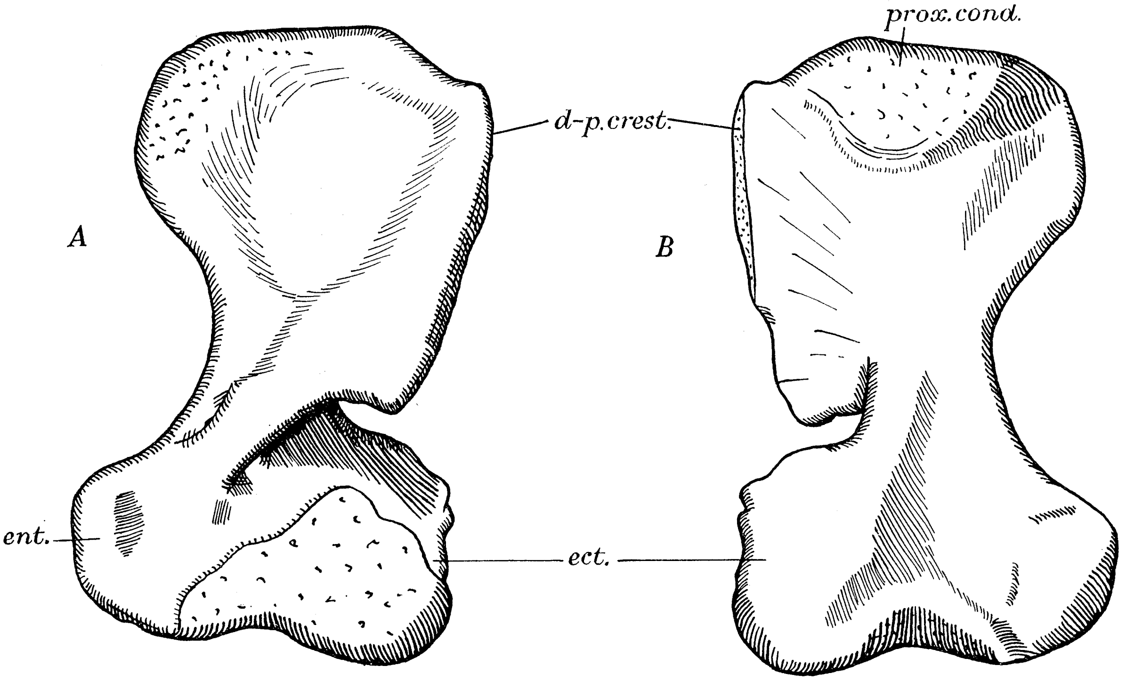

Figure 7. *Ischigualastia jenseni.* Humerus of specimen MCZ No. 3118, × 1/5, in *A*, ventral view and *B*, dorsal view. *d-p.crest.*, Delto-pectoral crest; *ect.*, ectepicondyle; *ent.*, entepicondyle; *prox.cond.*, proximal condyle.

The coracoid foramen lies between the precoracoid and the scapula. The precoracoid is excluded from the glenoid facet.

The sternum is unusual in having a constriction halfway along its length, anterior to the bosses which represent the points of attachment of ribs.

Fore-limb (figures 7, 8). The humerus has been badly flattened, so that the proximal and distal expansions of the bone lie in nearly the same plane. The condyles are fairly well ossified, and the delto-pectoral crest is well developed.

The olecranon process of the ulna has a cartilaginous epiphyseal union with the rest of the bone, and is missing in some specimens. It is missing from the ulna drawn in figure 8 and has been restored from specimen MCZ No. 3120. The semi-lunar facet of the ulna is very large; it runs completely across the width of the bone, and occupies about half its length. In the figured ulna a canal runs from a large foramen on the posterior side of the ulna and opens into a deep irregular groove on the semi-lunar facet. This canal is not present in other specimens.

The shaft of the ulna is short and slender in comparison with its enormous olecranon and semi-lunar facet.

The radius is short and its shaft is only slightly constricted. Its outer surface just below the proximal end bears a distinct swelling for the insertion of the radial head of the biceps muscle. The distal end of the radius is convex.

The more distal parts of the fore-limb were not found.

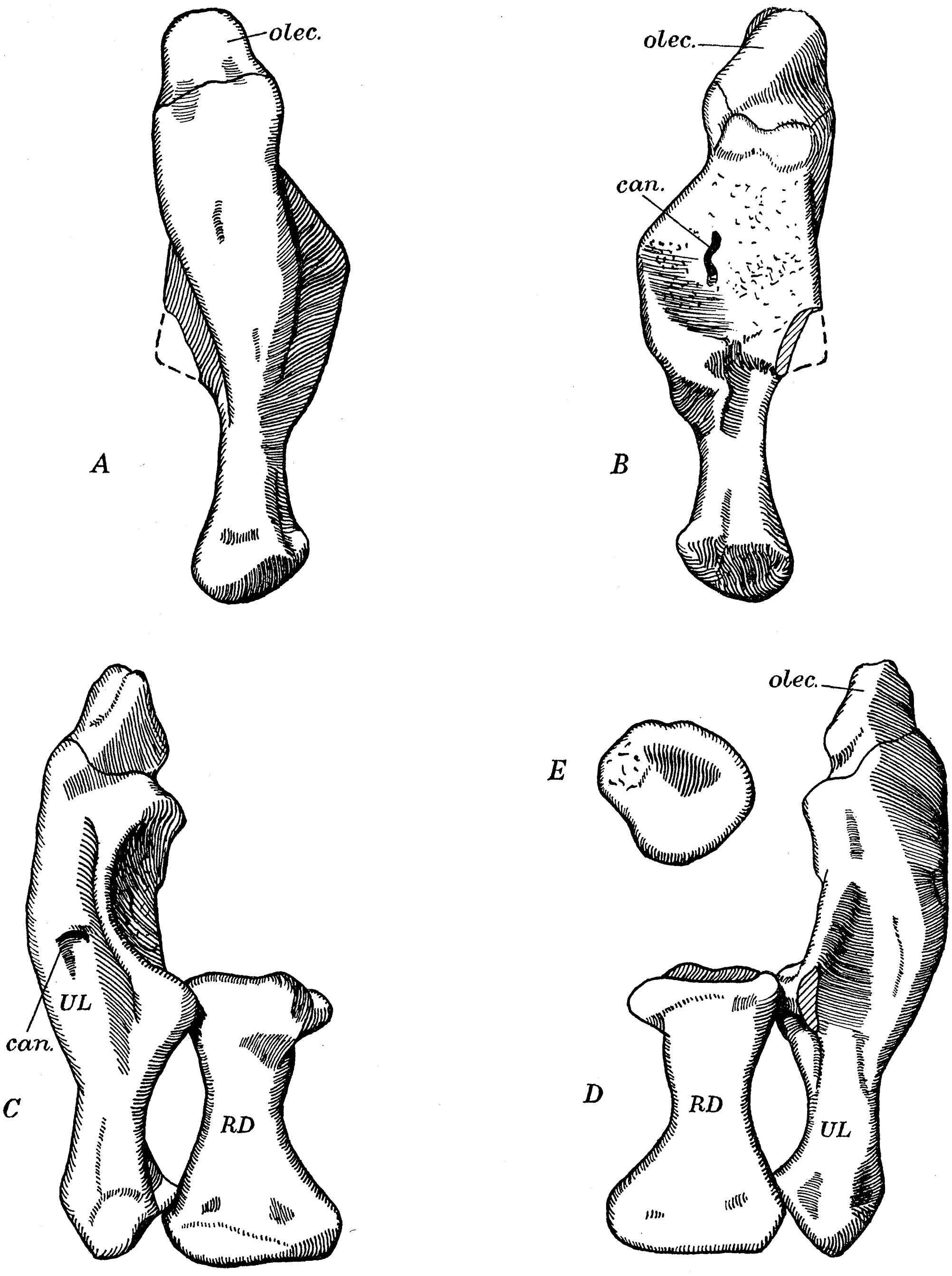

FIGURE 8. *Ischigualastia jenseni*, × 1/5. *A*, *B*, Ulna in *A*, lateral view and *B*, medial view. *C*, *D*, Radius and ulna in *C*, posterior view and *D*, anterior view. *E*, Proximal end of radius. (Ulna of type specimen, with olecranon restored from that of specimen MCZ No. 3120; radius of specimen MCZ No. 3120.) *can.*, Openings of canal perforating ulna; *olec.*, olecranon. For abbreviations of names of bones, see p. 514.

Pelvic girdle (figure 9). Two ilia were found, but only a very fragmentary portion of the ischiopubic plate. The anterior end of the ilium is expanded ventrally as well as dorsally.

The dorsal edge of the ilium does not form a single convex curve; the anterior half of the blade is expanded but, posterior to this, the blade is somewhat constricted dorso-ventrally. Its posterior region tapers to a blunt point.

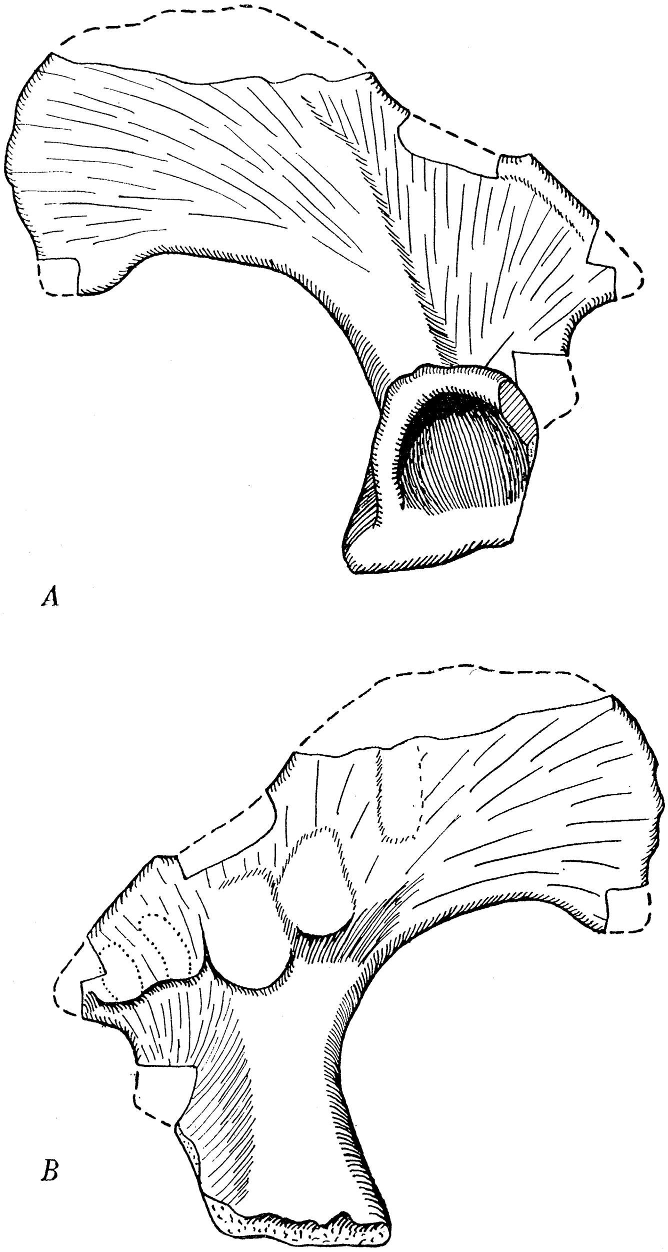

FIGURE 9. *Ischigualastia jenseni*, ilium of specimen MCZ No. 3121 in *A*, lateral view and *B*, medial view, × 1/5. Dotted outlines of attachments of posterior ribs restored from specimen MCZ No. 3119.

The ilium is fairly wide antero-posteriorly above the acetabulum. There is a strong supra-acetabular ridge. The facets for the ischium and pubis are at a considerable angle to one another.

The figured ilium was weathered out and clearly shows the areas of attachment of sacral ribs on its inner side. Another ilium was preserved with the crushed sacral vertebrae and ribs in place. It shows that there were five sacral ribs, and the areas of attachment of the two most posterior ribs are shown in dotted lines in the figure.

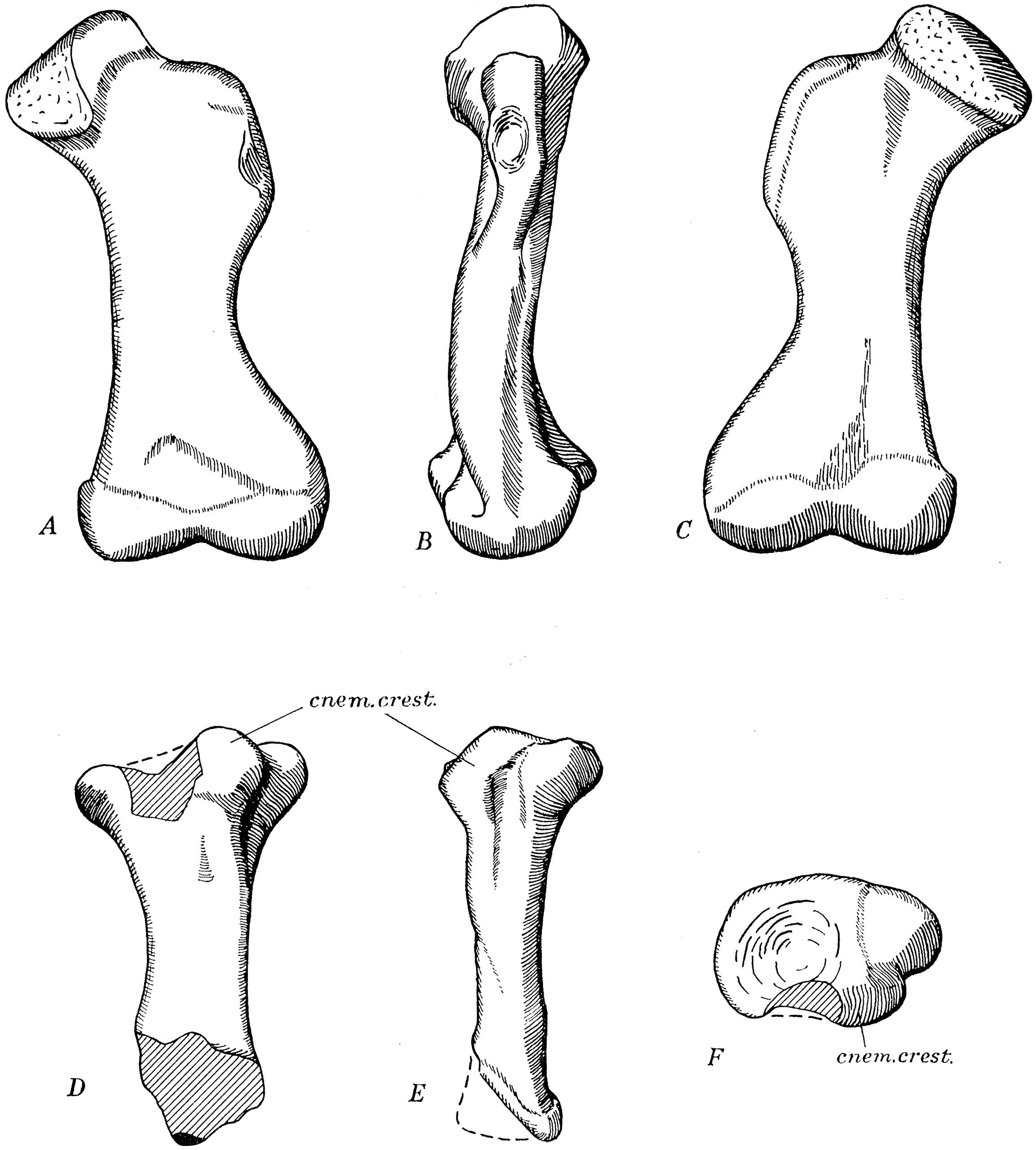

Figure 10. *Ischigualastia jenseni*, × 1/5. *A* to *C*, Femur of specimen MCZ No. 3120 in *A*, anterior view; *B*, lateral view; *C*, posterior view. *D* to *F*, Tibia of type specimen in *D*, anterior view; *E*, lateral view; *F*, proximal view; *cnem.crest.*, cnemial crest.

Hind limb (figure 10). The femur is very well preserved. It has a well-developed head which is set off medial to the shaft of the bone and separated from it by a distinct constricted neck. The greater trochanter is well developed, and its edge shows a distinct hollow.

The shaft of the bone is gently curved, with the anterior surface convex. The distal condyles for the tibia are well defined; the medial condyle is larger, especially in lateral view, and is set slightly lower than the lateral condyle. There is a distinct popliteal groove on the posterior surface of the bone above the condyles.

Most of the distal end of the tibia is missing. Its proximal end shows a large concave inner sulcus, which is separated by a ridge from the small and slightly convex outer sulcus. The ridge between the two sulci continues anteriorly onto a large rounded boss; this is the upper end of the cnemial crest, which runs from the boss downwards along the anterolateral aspect of the shaft.

Neither the fibula nor the more distal elements of the foot were found.

The status of Stahleckeria lenzii, *Romer & Price*

This Brazilian specimen, MCZ No. 1688, came from sanga no. 3, 15 km south of Candelaria (see p. 474). It was described by Romer & Price in 1944, at a time when the only other Triassic material from the western hemisphere available for comparison was *Stahleckeria*, also from Brazil. The new form was represented only by the occiput and braincase, plus a few elements of the post-cranial skeleton. Romer & Price noted that these elements showed several differences from *Stahleckeria potens*, and stated that the new form was quite possible generically distinct. However, since the specimen was very incomplete, they felt it better to retain it in the genus *Stahleckeria* as a new species, *S. lenzii*.

It is now possible to compare *S. lenzii* with a greater variety of Triassic dicynodonts, and it is immediately apparent that it is more closely related to *Ischigualastia* than to *Dinodontosaurus* or *Stahleckeria*. As in *Ischigualastia*, the occiput has a characteristic semi-circular shape, and the squamosal covers the lateral tip of the supraoccipital in posterior view. There appears to have been a relatively narrow intertemporal region as in *Ischigualastia*, but not in *Stahleckeria*, and the contours suggest that the interparietal took part in the formation of this crest, as in *Ischigualastia*.

Though the skull of '*Stahleckeria*' *lenzii* thus shows considerable similarity to *Ischigualastia*, the post-cranial skeleton shows several notable differences from it. One outstanding difference lies in size alone. Though their skulls are of very similar size (the width of the occiput is *ca.* 48 cm in each), the post-cranial skeleton of *Ischigualastia* is far smaller than that of *S. lenzii*. The difference is most noticeable in the limb-bones, as might be expected since they must bear the weight. The radius and ulna of *Ischigualastia* are only 65 % of the length of these bones in *S. lenzii*, and are far less massive—the weights of the radii are 5·5 and 32·5 lb respectively (2·5 and 14·7 kg). The scapula and largest vertebra do not show quite so marked a difference; their lengths are *ca.* 85 % of the lengths of these bones in *S. lenzii*.

Another difference between the post-cranial skeletons of *S. lenzii* and *Ischigualastia* is that the scapula of *S. lenzii* has a very well-developed spine along its outer surface near the anterior edge, and a well-developed acromion process. The scapula of *Ischigualastia* lacks both these features.

Though the suture is not shown in Romer & Price's figure (1944, Fig. 9), the olecranon is a separate ossification, with a sutural union to the ulna.

There is also some evidence of a difference between the skulls of *S. lenzii* and *Ischigualastia*. In their description of the occipital fragment of *S. lenzii*, Romer & Price found difficulty in identifying an area of bone near the dorsal midline of the occiput (see Romer & Price 1944, p. 471 and Fig. 1). Comparison with *Ischigualastia* and *Placerias* suggests that the unknown bone of Romer & Price is the parietal, which is covered antero-dorsally by the anterior end of the squamosal, and rests against the anterior surface of the interparietal. If this identification is correct, this region of the skull of *S. lenzii* is unlike that of *Ischigualastia*, in which the parietal and squamosal are widely separated by the interparietal. It seems instead to be more similar to *Placerias*, though the interparietal of *S. lenzii* was probably not as broad as that of *Placerias*.

From the above discussion it is apparent that *Stahleckeria lenzii* is in fact far removed from the genus *Stahleckeria*. It is more closely related to *Ischigualastia* and *Placerias*, but is generically distinct from these also. In view of its large post-cranial skeleton, it is therefore named *Barysoma lenzii* (Romer & Price), gen.nov., from the Greek *βαρυς* (massive) and *σωμα* (body).

DICYNODONTS FROM BRAZIL

The existence of terrestrial Triassic vertebrate fossils in South America was first recognized by Woodward (1907) who described some fragments of bone which had been sent to him from the Rio Grande do Sul, in southernmost Brazil. Further collections were sent to von Huene and described by him (1928, 1929) and von Huene himself collected in the Chiniquà and Santa Maria regions of Rio Grande do Sul in 1928–29. His paper (1935) on the dicynodonts he found was the first evidence of the group in South America. von Huene recognized a new genus of large dicynodont, *Stahleckeria*. He also described other remains which were so imperfect that they could not be distinguished from the common South African 'genus' *Dicynodon*, and which he therefore named *D. tener* and *D. turpior*.

A few years later, in 1936–37, more vertebrate material from the Triassic of Brazil was collected by L. I. Price and T. E. White during the course of an expedition of the Museum of Comparative Zoology, Harvard. The specimens came from the area south of the town of Candelaria, in the province of Rio Grande do Sul. The only specimens of this collection which have been described are two dicynodonts. A preliminary note on a mounted skeleton of a new genus, *Dinodontosaurus*, was published by Romer (1943). Romer & Price (1944) also described some remains of a very large dicynodont, *Stahleckeria lenzii*, the status of which has been discussed above.

Most of the specimens collected by Price and White came from five sangas (dry river courses) about 15 km south of Candelaria, near the township of Chico Morais. White's field notebook, in the Museum of Comparative Zoology at Harvard, gives a description of the strata in these sangas, as follows. The uppermost layer, immediately below the grass, was 20 ft. thick, composed of reddish clay with fairly numerous white calcareous concretions. The second layer, 20 ft. thick, was similar except that the clay was mauve in colour. The third layer, 10 ft. thick, was composed of white calcareous concretions with a very little reddish clay. The fourth layer, 20 to 25 ft. thick, was of bright red clay with reddish-white calcareous concretions. The full extent of the lowest, fifth, layer is unknown; its deepest exposure was 80 ft. It was of mauve clay with small concretions of barite discoloured by haematite; it also contained large black concretions downwards from a point about 20 ft. below its top.

Bones were found in layers 1, 2 and 4 and in layer 5 down to the level of the black concretions. They were often encased in calcareous layers or within calcareous nodules and are heavily impregnated and seamed with calcite.

Another locality which yielded dicynodonts was a sanga about 30 km south-west of Candelaria. This showed only three layers. The uppermost, 30 ft. thick, was of mauve clay with patches of red, and fairly numerous concretions, some with barite but mostly calcareous, and a few black concretions. This layer contained fairly abundant fossils, many very badly preserved but those from the patches of red clay being much better preserved. Below this layer was about 20 to 25 ft. of nodular clay, the nodules forming small dykes and seams. Fossils were scarce and very poorly preserved in this layer. Below this, about 15 ft. of red clay was exposed; it contained many calcareous nodules, but no fossils. White's notebook states 'There seems to be little in common between this sanga and those at Chico Morais. Even the fossils look different'. However, the dicynodonts appear to be identical with those from the Chico Morais area.

Genus Dinodontosaurus *Romer*

This dicynodont was very briefly described by Romer (1943), who published a photograph of a skeleton which had been mounted in the Museum of Comparative Zoology at Harvard, and a few facts about its skull morphology.

More than sixteen dicynodonts were collected by White and Price. With the exception of *Stahleckeria lenzii* (Romer & Price 1944), which is very distinct in both size and morphology, all appear to belong to *Dinodontosaurus*. They are of various sizes, with skull lengths ranging from a young one 78 mm long, through forms about 165 mm long and 275 mm long to several about 350 mm long and one large specimen (discussed in detail below) 400 mm long. In spite of this range in size, the proportions of the skulls are quite uniform, as are the sutural patterns where these are visible. Though damage, crushing or lack of preparation make it impossible to be sure, they all therefore appear to belong to a single species of *Dinodontosaurus*.

In his description of the new form, Romer (1943) names it *Dinodontosaurus oliveirai*. Other dicynodont material from Brazil had previously been described by von Huene (1935). This included the fairly complete remains of the new genus *Stahleckeria*, which is readily distinguishable from *Dinodontosaurus*. von Huene also mentioned and figured (1935, pp. 67–87 and Pl. 10, Figs. 6–18) the very incomplete remains of two smaller dicynodonts. Though these were obviously unlike *Stahleckeria*, the material available was not sufficient to distinguish them from the common and variable African genus *Dicynodon*. von Huene therefore named the smaller Brazilian forms *Dicynodon tener* and *Dicynodon turpior*. Comparison of *Dinodontosaurus* with von Huene's figures of the remains of *Dicynodon turpior* show them to be identical in their morphology, and this was confirmed by comparison with one of the humeri of von Huene's *D. turpior*, very kindly lent by the Tübingen Museum. The correct name of Romer's specimen is therefore *Dinodontosaurus turpior* (von Huene).

The type specimen must now be selected from amongst the remains described by von Huene (1935). Unfortunately, these contain very little skull material. The most complete collection of post-cranial material is that from 'digging 42' (von Huene 1935, p. 84) which appears to belong to a single individual. It comprises ten vertebral centra; a neural arch; ribs and sacral ribs; parts of both scapulae; both clavicles and humeri; the left ulna; the right radius; parts of both femora; the left tibia; the left fibula. The clavicle, radius, ulna, tibia and fibula were figured by von Huene (1935, Pl. 10). It seems best to define this collection from digging 42 as the lectotype material.

One of the most useful bones for comparative purposes is the humerus, and von Huene (1935, Pl. 10, Fig. 8) figures an almost complete humerus, which was lent by the Tübingen Museum as mentioned above. Though in the legend to von Huene's figure the humerus is stated to come from locality 1055, and the bone itself is marked 1055, the text relating to that locality (1935, p. 82) makes no mention of a humerus. However, a pair of humeri are described (1935, p. 85) from 'digging 42', and the dimensions and characteristics noted there do correspond with the figure (though the degree of completeness shown in the figure is there attributed to the left humerus, and the right humerus is said to lack both its ends). The figured humerus thus does appear to belong to the collection of type material from digging 42.

von Huene's (1935) species *Dicynodon tener* clearly also belongs to the genus *Dinodontosaurus*, and may be referred to that genus as *Dinodontosaurus tener* (von Huene); its position is discussed below (p. 494). Since the remains of *D. turpior* are far more complete than those of *D. tener*, it is preferable to define the former as the type species, and the genus may therefore be taxonomically and geologically defined as follows.

Genus. Dinodontosaurus Romer.

Generotype. Dinodontosaurus turpior (von Huene).

Generic diagnosis. Dicynodont of medium to large size (skull lengths 16·5 to 40 cm). Teeth absent except for upper canine tusks. In dorsal view, skull tapers slightly towards anterior end, greatest width across occiput. Wide interorbital region, narrow intertemporal region. Long pre-orbital region, forming nearly half of skull length. Snout almost rectangular in section, and ends bluntly anteriorly. No bony bosses on snout or pineal region. No postfrontal bone. Frontal forms only short section of border of orbit. Preparietal bone present, bordering anterior end of pineal foramen. Postorbitals and squamosals do not extend onto intertemporal bar, which is formed almost wholly by parietals. Intertemporal bar narrow, with cross-section like an inverted V; does not rise up as sagittal crest above level of rest of skull. Interparietal forms only the most posterior end of the intertemporal bar. Temporal openings very short. Squamosal extends far out lateral to root of zygomatic arch. Sharp transition between dorsal and occipital surfaces. Broad, low occiput. No tabular. Stapes lacks stapedial foramen. Short interpterygoid vacuity. Ectopterygoid may be present as thin sliver of bone on dorso-lateral surface of pterygoid. Maxilla just enters margin of internal naris. Paired anterior palatal ridges run back to meet long median posterior palatal ridge. Maxilla meets squamosal below orbit. Conical projection on dorsal surface of pterygoid just anterior to base of epipterygoid. No lateral wing on dentary. Stout retro-articular process.

Twenty-three or twenty-four presacral vertebrae; probably five cervical vertebrae; five sacral vertebrae; probably fifteen caudal vertebrae. Acromion process of scapula projects anteriorly from front edge of blade; no scapular spine. Coracoid foramen runs through precoracoid bone. No cleithrum. High median ridge on ventral surface of interclavicle. Rounded sternum. Humerus bears massive delto-pectoral crest; very marked condyles for radius and ulna; entepicondyle extends further distally than ectepicondyle. Separate olecranon ossification on ulna. Blade of ilium bears quite large posterior projection. Ischio-pubic plate lies postero-ventral to ilium. Strong pubic tubercle. Head of femur not very distinct from proximal end of bone.

Referred material. The specimens described by von Huene (1935, pp. 67–87) as *Dicynodon tener* and *Dicynodon turpior*, some of which were figured by him (1935, Text-figs. 15–19 and Pl. 10, Figs. 6–18) are referred to the genus *Dinodontosaurus*. These specimens are now in the Museum für Geologie und Paläontologie of Tübingen University; though they do not bear Museum numbers, they are marked with the number of the locality or digging in which they were found.

The material in the Museum of Comparative Zoology at Harvard University which is considered to belong to the genus *Dinodontosaurus* comprises the following specimens: MCZ Nos. 1628, 1677, 1678, 1679, 1687, 1692, 1757, 1758, 1759, 3105, 3106, 3107, 3108, 3109, 3112, 3114.

Geological horizons and localities. All the specimens came from the Santa Maria Formation, of probably Middle Triassic age, in the province of Rio Grande do Sul, southern Brazil. von Huene's specimens came from an area west of the town of Chiniquà (see von Huene 1935, Text-fig. 1, for sketch map), but more detailed information on the precise geological horizons of the different specimens is not available. White's field notebook gives details of the locations and, in some cases, the levels of discovery of some of the specimens collected by the MCZ expedition, as follows:

15 km south of Candelaria, near Chico Morais

Sanga no. 1	MCZ No. 1628, layer no. 5
	MCZ Nos. 1678, 1679, layer no. 4
	MCZ No. 1757
Sanga no. 2	MCZ No. 1670, layer no. 1
Sanga no. 3	MCZ No. 1677
Sanga do Janguta	MCZ No. 1687

30 km south-west of Candelaria

Sanga da Ribiero	MCZ Nos. 1692, 1758, 1759

Dinodontosaurus turpior (von Huene)

Romer (1943) described the mounted specimen (MCZ No. 1670), which is shown in figure 11. The skull of this specimen is the best preserved but, like nearly all the specimens, it is heavily impregnated and seamed with crystalline resistant minerals. The only skulls in which the sutures can be seen are the imperfect juvenile (MCZ No. 1677) and a badly distorted skull (MCZ No. 1687) of about the same size as MCZ No. 1670. Though MCZ No. 1670 therefore gives the best impression of the morphology of the species, it has been necessary to superimpose the sutural pattern from skull MCZ No. 1687. The following description therefore uses these two skulls as sources of these characteristics. Those sutures which are visible for skull MCZ No. 1670 are consistent with what has been added from skull MCZ No. 1687.

Skull

The greatest length of the skull is 364 mm, the greatest breadth is 322 mm.

Dorsal view (figure 12*A*). The most unusual feature of the skull is its extremely long pre-orbital portion and the angularity of this region in section. The top of the snout is wide and almost flat and the sides are at about a right-angle to it. The front of the snout is also wide and blunt.

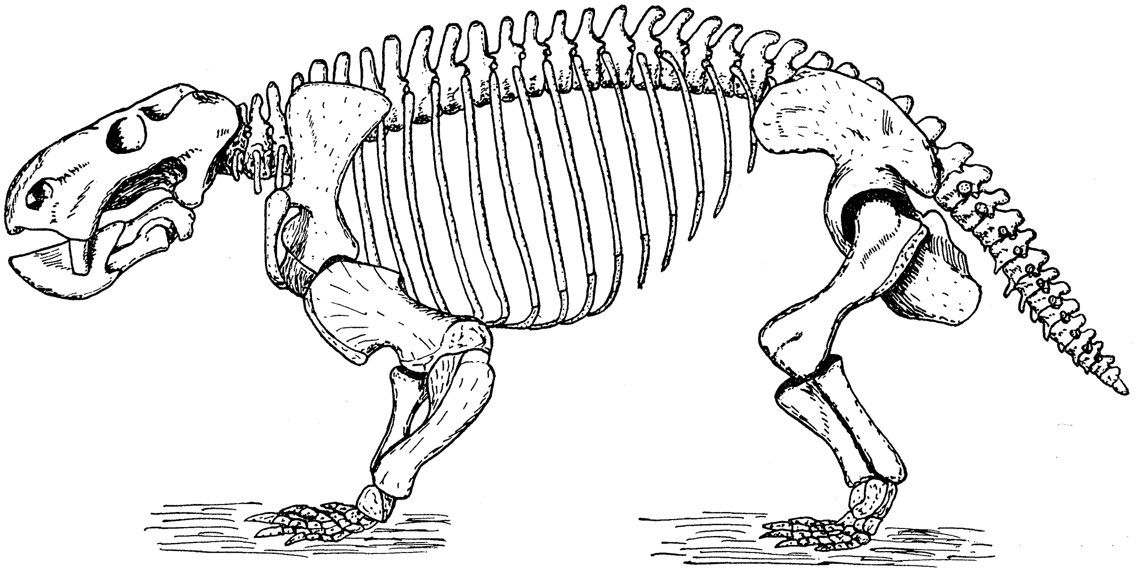

FIGURE 11. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Lateral view of skeleton, × 1/12. Slightly modified from photograph of mounted skeleton.

There are no bony bosses on the prefrontal or pineal regions. There is a large prefrontal but no trace of a postfrontal could be found. The interorbital region is wide, so that the orbits are hardly visible in dorsal view. Though this region is difficult to make out, the frontal does not appear to extend posteriorly beyond about halfway along the preparietal bone, where it meets the parietal in a transverse suture.

The temporal openings are extremely short, and this feature is one of the most noticeable characteristics of the genus. In most dicynodonts the temporal openings are longer than their breadth, but in *Dinodontosaurus* the openings are of about equal length and breadth. This, together with the long snout, makes the orbits appear to lie very far back in the skull, compared to most dicynodonts.

The intertemporal bar is narrow; in cross-section it is like an inverted V, the parietals rising up fairly steeply to a median ridge. The postorbital does not extend far back along the intertemporal bar, and the squamosal does not reach the posterior end of the bar, so that the postorbital and the squamosal are widely separated here.

The zygomatic arches originate from about halfway across the transverse, occipital portion of the squamosal, so that a considerable part of the squamosal lies lateral to the

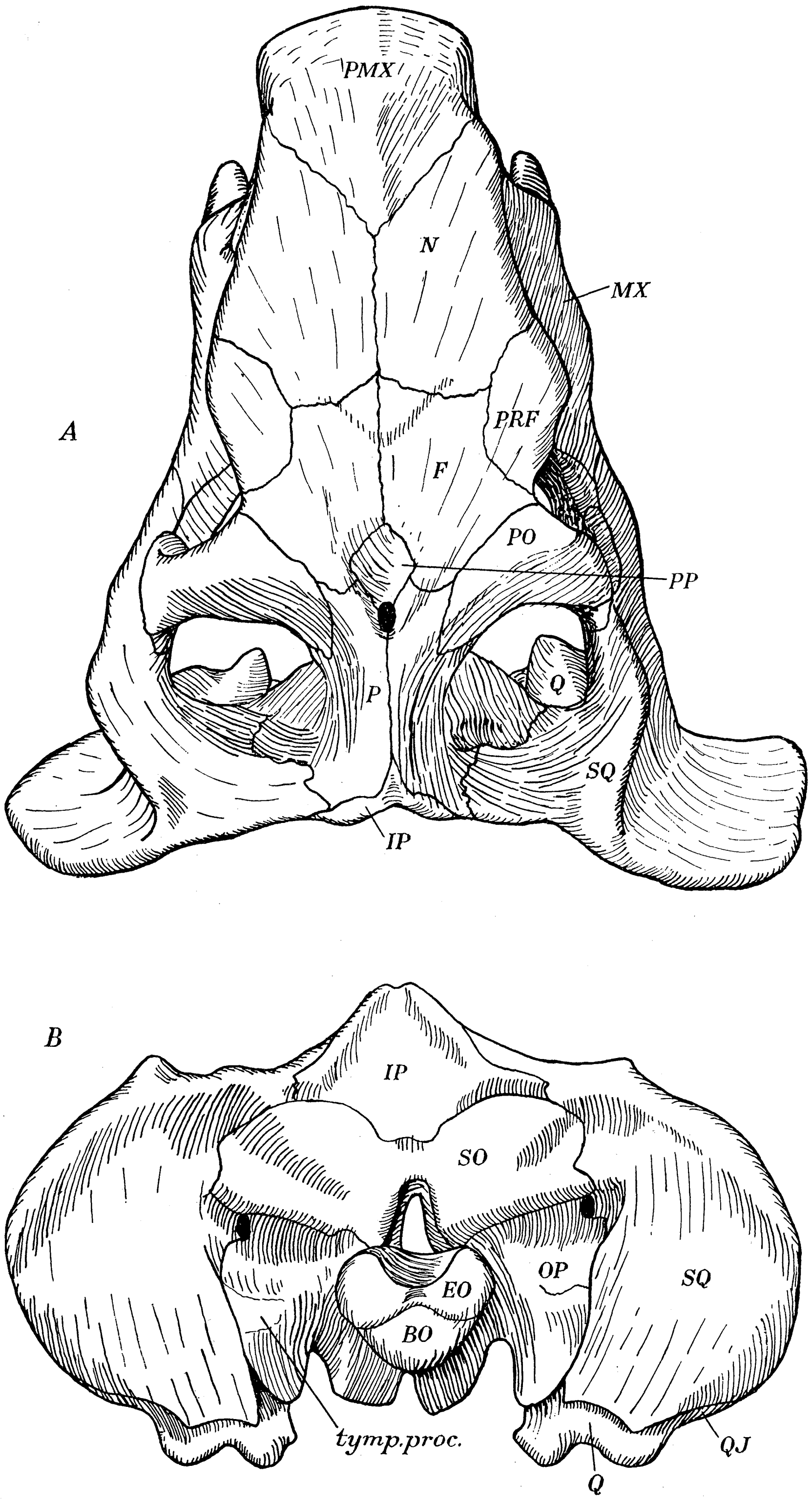

FIGURE 12. *Dinodontosaurus turpior*, specimen MCZ No. 1670. *A*, Dorsal view of skull, × $\frac{1}{4}$. *B*, Occipital view of skull, × $\frac{1}{4}$. *tymp.proc.*, Tympanic process. For abbreviations of names of bones, see p. 514.

root of the zygomatic arch. The anterior ends of the zygomatic arches may have been crushed inwards slightly.

Occipital view (figure 12*B*). The occiput is low and rather broad, the squamosals contributing a considerable part of the breadth. All the bones of the brain-case are fused. The interparietal forms the dorsal apex of the occiput, and forms the whole thickness of the posterior end of the intertemporal bar. Ventrally it overlaps the supraoccipital, and it also extends quite a long way laterally, covering the posterior surface of part of the squamosal. Its extreme lateral tip is covered posteriorly by the squamosal. The paroccipital process of the opisthotic bears, near its meeting with the squamosal, a well developed tympanic process (see Cox 1959).

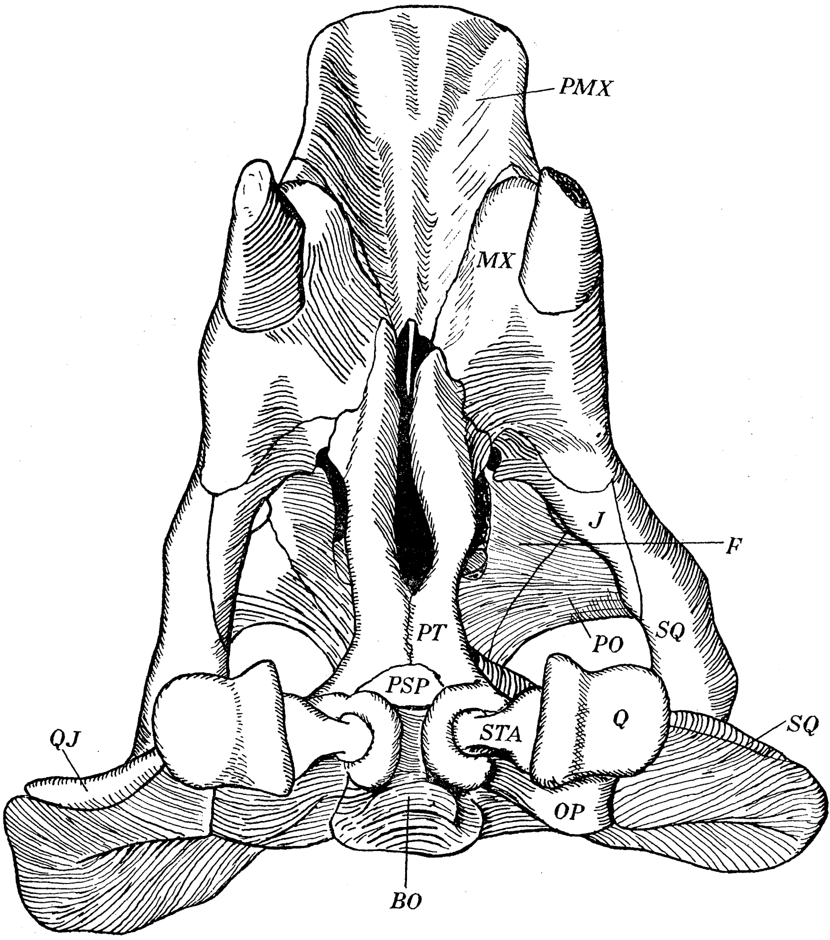

FIGURE 13. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Ventral view of skull, × $\frac{1}{4}$. For abbreviations of names of bones, see p. 514.

The occipital condyle is tripartite, but the lateral (exoccipital) components are better developed than the ventral (basioccipital) component, so that functionally it is almost a double condyle. The upper surface of the condyle, leading into the foramen magnum, slopes rather strongly upwards and forwards.

Palatal view (figure 13). The secondary palate is formed almost exclusively by the premaxillae. The paired anterior palatal ridges run back to meet the long median posterior palatal ridge. This median ridge meets the vomer posteriorly. The maxillae appear to enter the margin of the nares.

The more posterior region of the palate is damaged, and the two anterior rami of the pterygoids have been crushed together. The relationships of the pterygoids and palatines cannot be distinguished on specimens MCZ Nos. 1670 and 1687, but a further specimen (MCZ No. 1758) is better preserved in this region. In it the palatines lie on the inner sides of the slightly diverging anterior rami of the pterygoids. The specimen also shows what appears to be a thin, splint-like ectopterygoid lying on the dorso-lateral surface of the anterior ramus of the pterygoid, meeting the maxilla anteriorly. The interpterygoid vacuity is shown only by specimen MCZ No. 1758, in which it is short. The quadrates and stapes of specimen MCZ No. 1670 are damaged, but are of normal dicynodont structure.

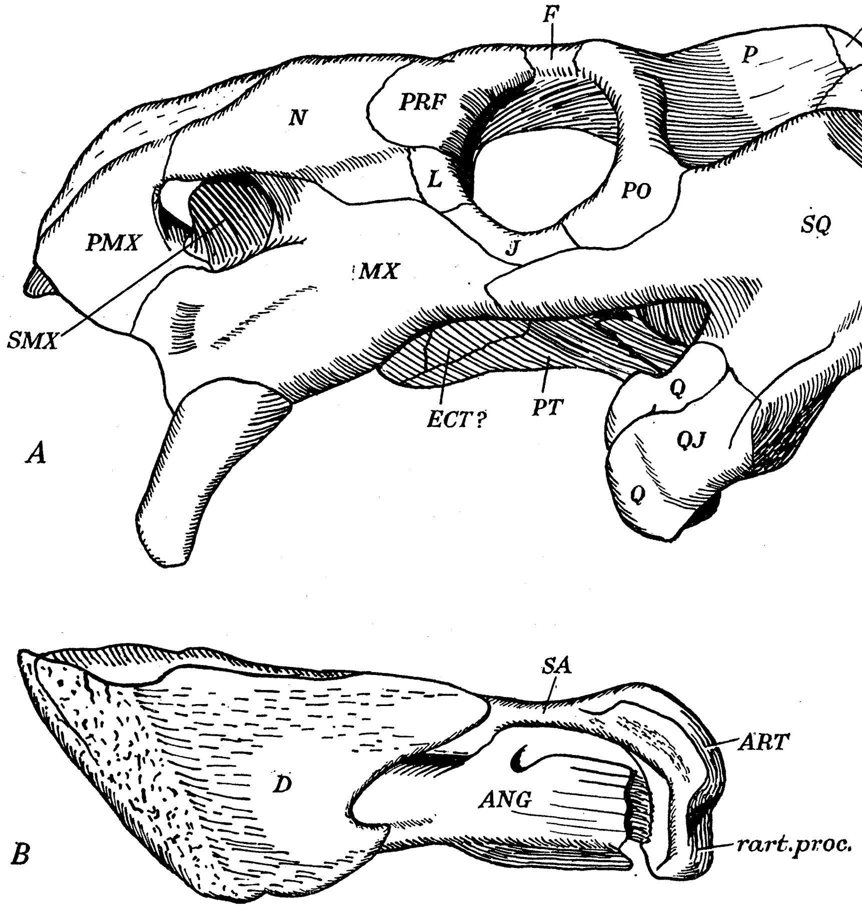

Figure 14. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Lateral view of skull and lower jaw, × ¼. *rart.proc.*, Retro-articular process. For abbreviations of names of bones, see p. 514.

Side view (figure 14). The long pre-orbital region and short post-orbital region are very noticeable in side view.

A ridge runs back along the maxilla from the antero-ventral corner of the naris. The maxilla meets the squamosal posteriorly.

In specimen MCZ No. 1687 there is a strong rounded projection on the pterygoid, just in front of the base of the epipterygoid (see also figure 24*B*). von Huene (1935) found a similar development in *Stahleckeria*, but believed that it represented an anterior portion of the base of the epipterygoid which had become fused to the pterygoid. Ewer (1961) found a similar boss in the South African *Daptocephalus*; cracks made the interpretation of this region very difficult, and she tentatively suggested that the boss and a more anterior region (Ewer 1961, Fig. 5, 'C') all represented an anterior extension of the base of the epipterygoid. However, the boss in *Dinodontosaurus* is clearly part of the pterygoid, and it seems more likely that this was also the case in *Daptocephalus*. The more anterior region in *Daptocephalus* may be a dorsal exposure of the palatine bone. The boss appears to be common in large dicynodonts, and it was probably associated with the origin of part of the pterygoideus musculature.

As already mentioned, the pterygoids are damaged and distorted in specimen MCZ No. 1670, which also shows little detail of the braincase and bones in the midline. Those features which can be discerned show that this region is similar to that of a large specimen, MCZ No. 1628, whose position and structure are discussed below.

Lower jaw (figure 14). The lower jaw of MCZ No. 1670 is damaged and that of MCZ No. 1687 has been figured instead. This is distorted, but clearly shows the relationships of the various bones.

The dentary forms a blunt transverse anterior edge. Its anterior surface, and the anterior part of its lateral surface, are rugose. This presumably marks the area covered by the horny beak in life. The upper edge of the dentary bears a groove along its anterior region. This groove is bounded by two sharp-edged ridges, the inner of which is higher than the outer. The posterior border of the dentary is notched where the angular runs medial to it. The angular has a well-developed reflected lamina, which extends in under the ramus of the jaw as well as extending on the lateral surface to near the articular bone. There is a well-developed retro-articular process, whose posterior surface is set slightly forward underneath the posterior end of the outer articular condyle.

Post-cranial skeleton

The bones of the right side of specimen MCZ No. 1670 have been carefully prepared for use in the mounted skeleton. In order to facilitate comparison with other Triassic dicynodont remains, these right-side bones have been reversed in the drawings so as to appear as left-side bones.

Vertebral column and ribs. Most of the vertebrae and ribs are somewhat crushed and distorted, and they have therefore not been figured in detail. Though the mounted specimen has twenty-three presacral vertebrae, there appear to be twenty-four in specimen MCZ No. 1687.

Cervical vertebrae and ribs. In specimen MCZ No. 1759, two small rod-like bones lie pressed against the ventral side of the axis centrum. These have at some time been labelled 'atlantal ribs'. The atlas arches are missing. These rod-like bones are certainly smaller than the axis ribs, but show no sign of the double head which is normally found in cervical ribs. However, the modification of the atlas pleurocentrum to form the odontoid process of the axis might well cause the atlas rib to be single-headed. Comparative data are lacking since atlas ribs have not been reported in any other dicynodont. It is, alternatively, possible that these bones are displaced elements of the hyoid skeleton.

Though the first four vertebrae of specimen MCZ No. 1670 are badly crushed, it can be seen that the axis spine was thick and had a concave posterior face. The ribs of the axis and next three vertebrae are small, but the ribs of the sixth vertebra are much more massive. This suggests that the sixth vertebra bore the first rib which made contact with the sternum, so that there were only five cervical vertebrae. In specimen MCZ No. 1687 it can be seen that the postzygapophyses are much wider in vertebra 5 than in vertebra 6, and that the transverse process becomes larger in vertebra 6; these features also indicate a possible change in function at the sixth vertebra. The only other dicynodont in which the number of cervical vertebrae is known is *Kingoria* (Cox 1959) in which there were six.

The ribs of the axis and cervicals 3 to 5 are double-headed.

Dorsal vertebrae and ribs. In specimen MCZ No. 1670 the length of the centra of the dorsal vertebrae increases posteriorly; that of the first dorsal is 26 mm long, while that of the last (18th) dorsal is 36 mm long. In the anterior vertebrae the transverse process projects laterally, but further back it comes to project more dorso-laterally, and its distal end rises above the rib-head to form a metapophysis (see Cox 1959).

Though the rib-heads are not very well preserved, those of the anterior three or four dorsal vertebrae are two-headed, while the remainder are single-headed.

Sacral vertebrae and ribs. The sacral vertebrae of specimen MCZ No. 1670 are badly crushed, but specimen MCZ No. 1687 clearly shows five sacral vertebrae.

Caudal vertebrae and ribs. In specimen MCZ No. 1670 only the first six caudal vertebrae are preserved, and these are badly damaged. The first seven caudal vertebrae are preserved in specimen MCZ No. 1687. Specimen MCZ No. 1759 shows what seems to be the last twelve caudal vertebrae, there being a gap in the sacral region. Comparison of these specimens suggests that these were originally fifteen caudal vertebrae.

In specimen MCZ No. 1687 the first two caudal ribs have distal ends which are elongated antero-posteriorly so that they touch one another distally, while the first caudal rib similarly touches the last sacral rib. The third caudal rib is very massive with a blunt distal end.

Pectoral girdle (figure 15). The scapula is about 29·5 cm high. There is a well-developed acromion process projecting forwards, but there is no spine on the outer surface of the blade.

The coracoid foramen runs through the precoracoid bone and is continued antero-dorsally in a groove up its inner face. The precoracoid is excluded from the glenoid. The edges of both precoracoid and coracoid are thickened. The postero-dorsal part of the coracoid swings in medially as a strong ridge with a blunt posterior end, to which muscles were presumably attached.

There is no trace of a cleithrum in any specimen.

The clavicles run from the acromion process of the scapula to cover the under side of the anterior end of the interclavicle.

The interclavicle and sternum are best shown in specimens MCZ Nos. 1759 and 1692. The former shows the anterior part of the interclavicle and its relation to the clavicles, and also the general shape of the rest of the interclavicle and of the sternum. Though the details of these elements are obscured by damage and by parts of the ribs, they are shown by specimen MCZ No. 1692.

The interclavicle is expanded anteriorly, where it lies dorsal to the median ends of the clavicles. It is rather short and wide. It has a median ridge on both dorsal and ventral surfaces; the ventral ridge forms a high narrow tab-like projection 2·1 cm high. This ventral ridge can be seen also on the mounted specimen. The posterior end of the interclavicle forms a series of small rugose knobs.

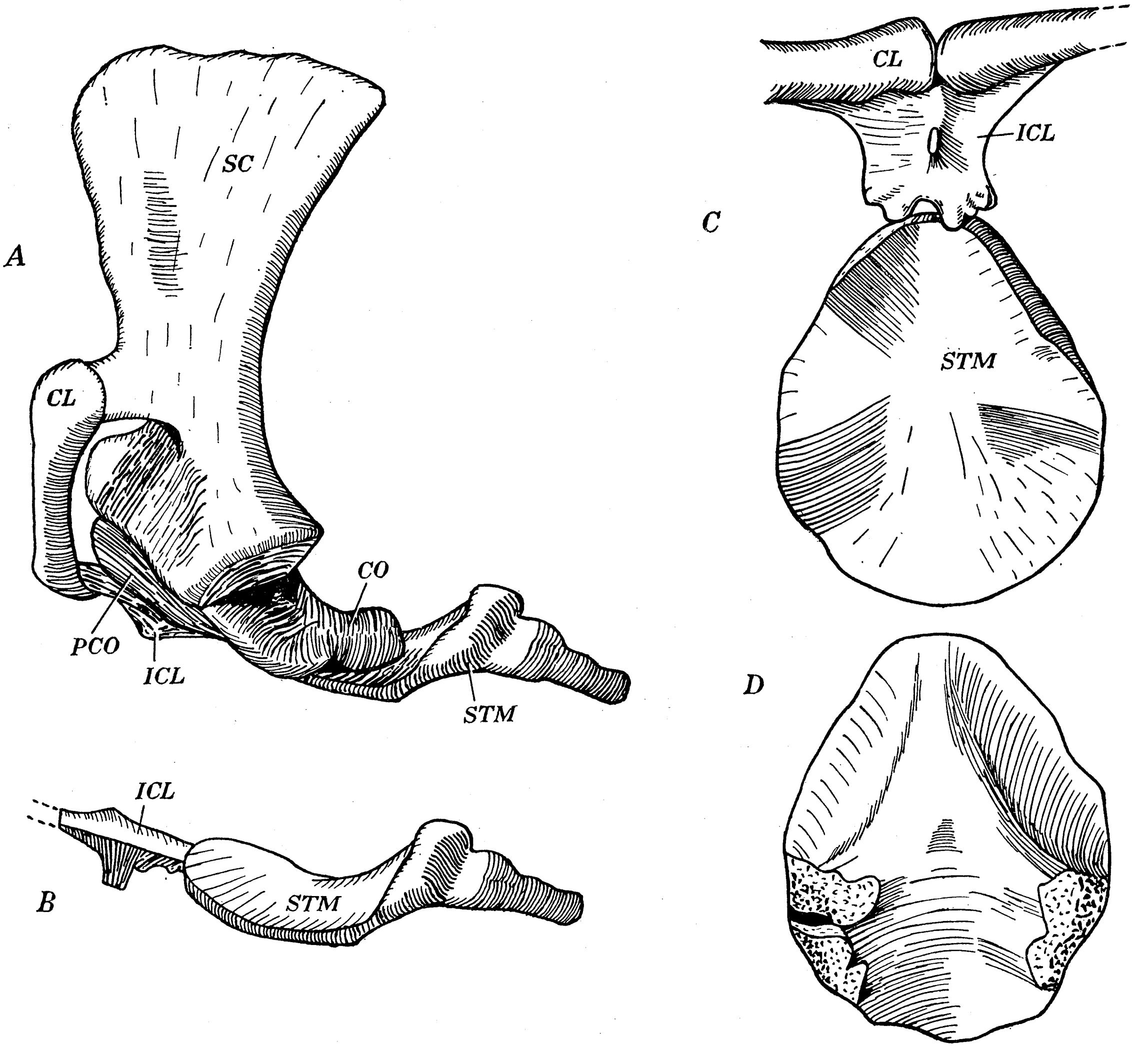

Figure 15. *Dinodontosaurus turpior*, pectoral girdle, × ¼. *A*, Lateral view of complete pectoral girdle. *B*, Lateral view of interclavicle and sternum. *C*, Ventral view of sternum, interclavicle and medial ends of clavicles. *D*, Dorsal view of sternum. (Sternum in all figures from specimen MCZ No. 1692. Interclavicle in *B* and *C* from specimen MCZ No. 1759. All other bones from specimen MCZ No. 1670.) For abbreviations of names of bones, see p. 514.

The sternum is of rounded shape. Its ventral surface is concave from side to side in its anterior region and is also hollowed in its postero-lateral regions. Its dorsal surface is greatly thickened postero-laterally, where the ribs attached. These thickenings run antero-medially and join to form a wide rounded median ridge along the anterior part of the dorsal surface. The sterna of specimens MCZ Nos. 1759 and 1692 are both 17·8 cm long, while the sternum of the mounted specimen is somewhat longer, 20·2 cm.

Fore-limb (figures 16 and 17, *A* to *D*, 18 *A*). The humerus has been somewhat crushed, so that the delto-pectoral crest lies more nearly in the plane of the distal condyles. Its greatest length is about 29 cm.

In dorsal view, the low proximal condyle can be seen. The entepicondyle extends further distally than does the ectepicondyle. Between these two lies the thickening which forms the dorsal portion of the ulnar condyle.

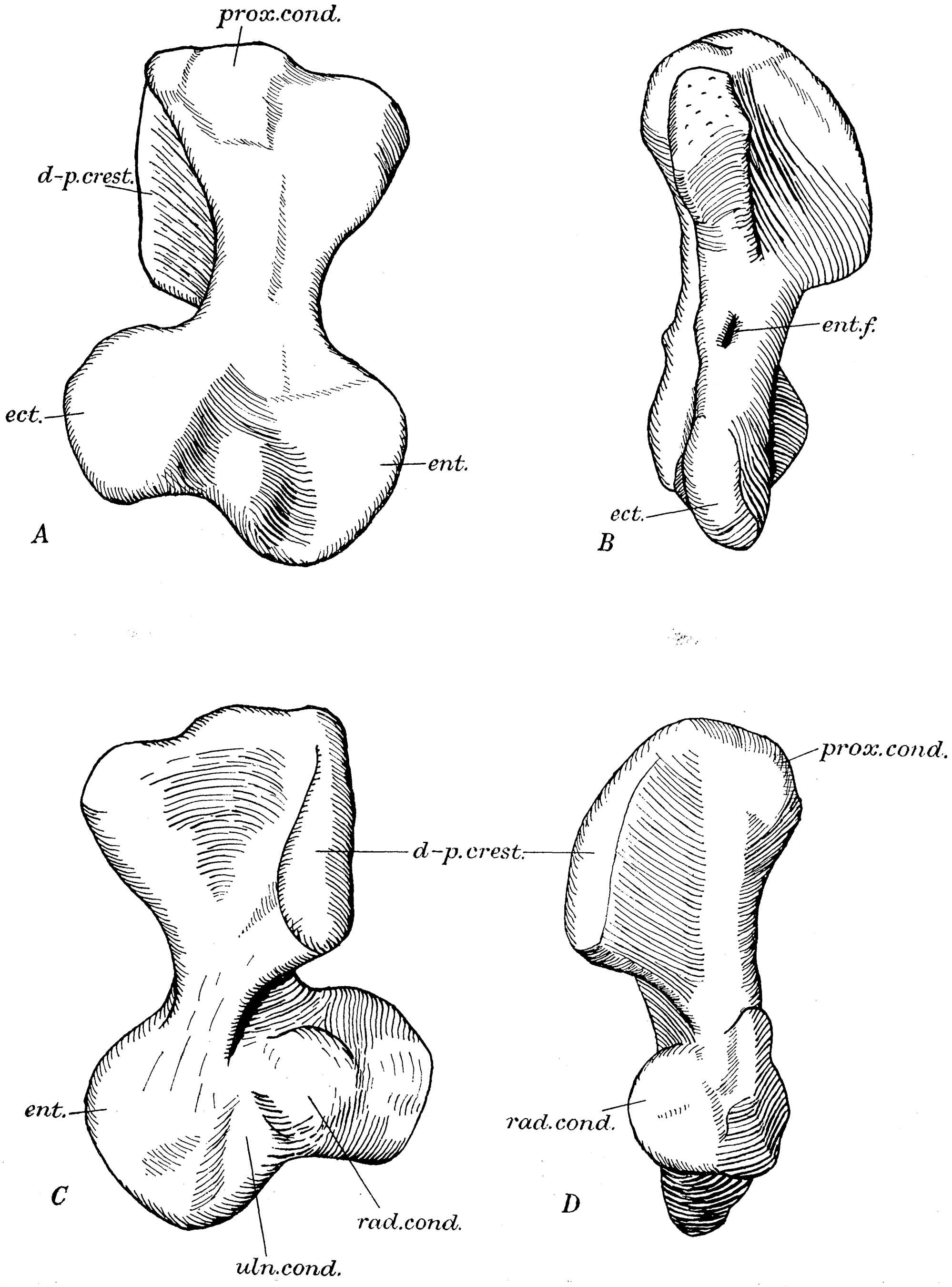

FIGURE 16. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Humerus, × $\frac{1}{4}$. *A*, Dorsal view; *B*, posterior view; *C*, ventral view; *D*, anterior view. *d-p.crest.*, Delto-pectoral crest; *ect.*, ectepicondyle; *ent.*, entepicondyle; *ent.f.*, entepicondylar foramen; *prox.cond.*, proximal condyle; *rad.cond.*, radial condyle; *uln.cond.*, ulnar condyle.

In ventral view, the thick edge of the delto-pectoral crest can be seen; this is up to 4·4 cm thick. There is a very pronounced rounded radial condyle and a more elongate ulnar condyle.

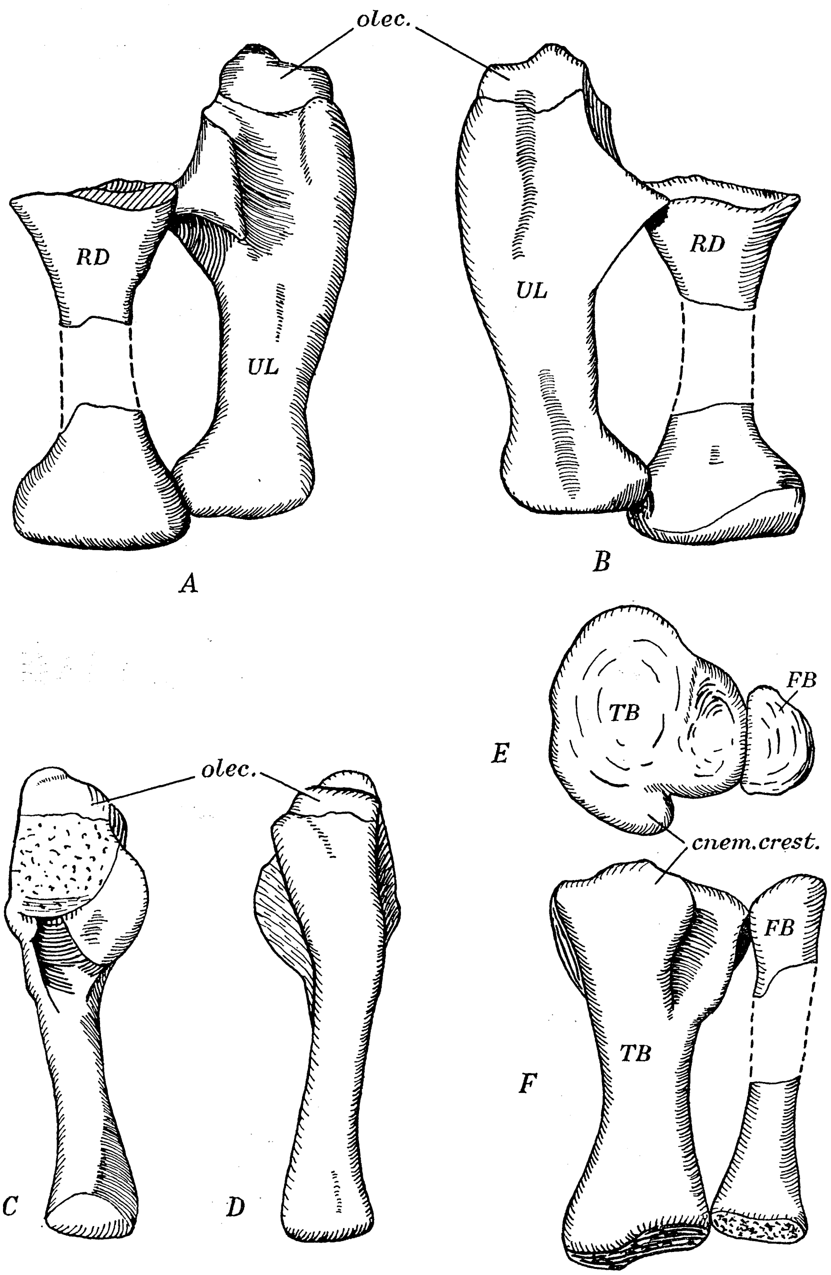

FIGURE 17. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Radius, ulna, tibia and fibula, $\times \frac{1}{4}$. *A*, *B*, Anterior and posterior views of radius and ulna. *C*, *D*, Medial and lateral views of ulna. *E*, *F*, Proximal and anterior views of tibia and fibula. *cnem.crest.*, Cnemial crest; *olec.*, olecranon. For abbreviations of names of bones, see p. 514.

The ulna is about 25 cm long. The olecranon process is a separate ossification. It appears to be complete, with a rugose proximal end; if so, it is short. The anterior surface in front of the sigmoid notch has a facet which receives the head of the radius when the limb is swung back. There is a deep hollow below this facet.

The middle portion of the radius is missing. It has an expanded concave proximal end which articulates with the radial condyle on the ventral surface of the humerus.

The preserved bones of the manus of the mounted skeleton comprise the ulnare, radiale, two other centralia and all the metacarpals and phalanges. Since these elements are all set in plaster, and no notes of their original interrelationships before preparation survive, it is not possible to be sure of the identities of the two centralia. Figure 8*A* therefore merely shows the manus as it appears in the mounted specimen.

Pelvic girdle (figure 19). The pelvic girdle figured here is not that of the mounted specimen. Most of the dorsal border of the ilium and ischium is missing in the mounted specimen, and the ischio-pubic plate has been incorrectly mounted, so that the pubic tubercles project medially and meet in the midline.

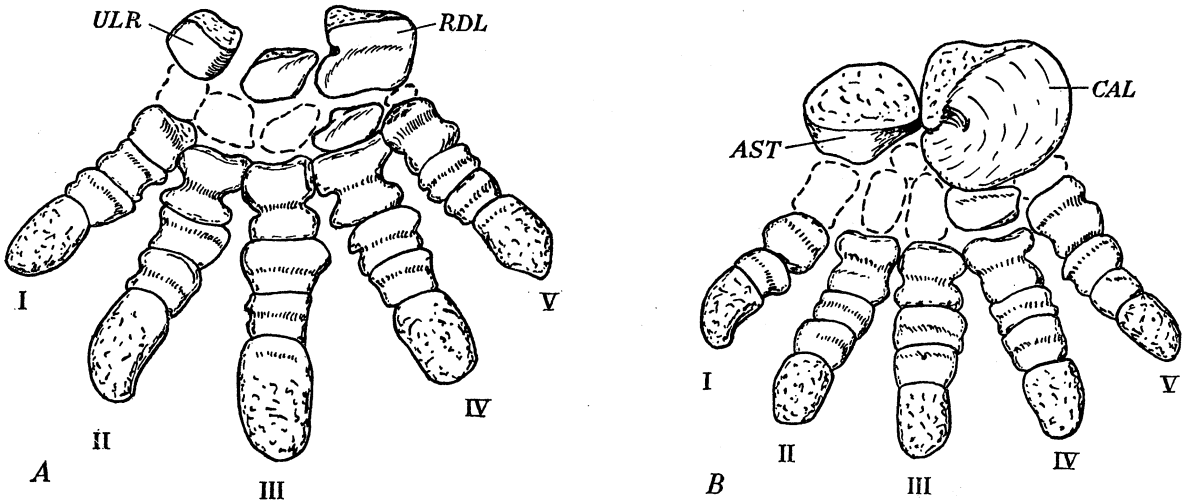

FIGURE 18. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Antero-dorsal views of *A*, manus and *B*, pes, ×$\frac{1}{4}$. Dotted elements have been reconstructed in plaster. For abbreviations of names of bones, see p. 514.

The ilium shown in figure 19*A* is that of MCZ No. 1687; this lacks only the extreme anterior end, which has been restored from the complete ilium of MCZ No. 3108. The ischio-pubis figured is that of MCZ No. 1759. The pelvic girdle as restored is smaller than that of the mounted specimen; the restored ilium is 27·3 cm long, while that of the mounted specimen is 33·0 cm long.

The ilium of MCZ No. 1687 is remarkable for the swollen character of the acetabular region; this is particularly noticeable in posterior view (figure 19*B*). This characteristic is not present in all the ilia (e.g. MCZ No. 3108, see figure 19*D*) but it does not appear to be a post-mortem effect, and it may be either an individual or a pathological character. The ilia which lack this feature are otherwise similar.

The dorsal edge of the blade is thick toward the anterior end and is notched about two-thirds of the way back on both right and left ilia. The posterior expansion of the blade emerges rather abruptly from the swollen acetabular region, but this might be due to crushing.

The ischio-pubic plate is also unusual. The dorsal part of the ischium is turned inwards to lie slightly more medially than the blade of the ilium. The pubis forms a downwardly directed projection; though narrow in lateral view, this is merely the edge of a flange which sweeps in medially and then posteriorly to join the ischium. The suture between the pubis and the ischium could not be distinguished. As in other dicynodonts, there is no median bony pelvic symphysis (see Cox 1959).

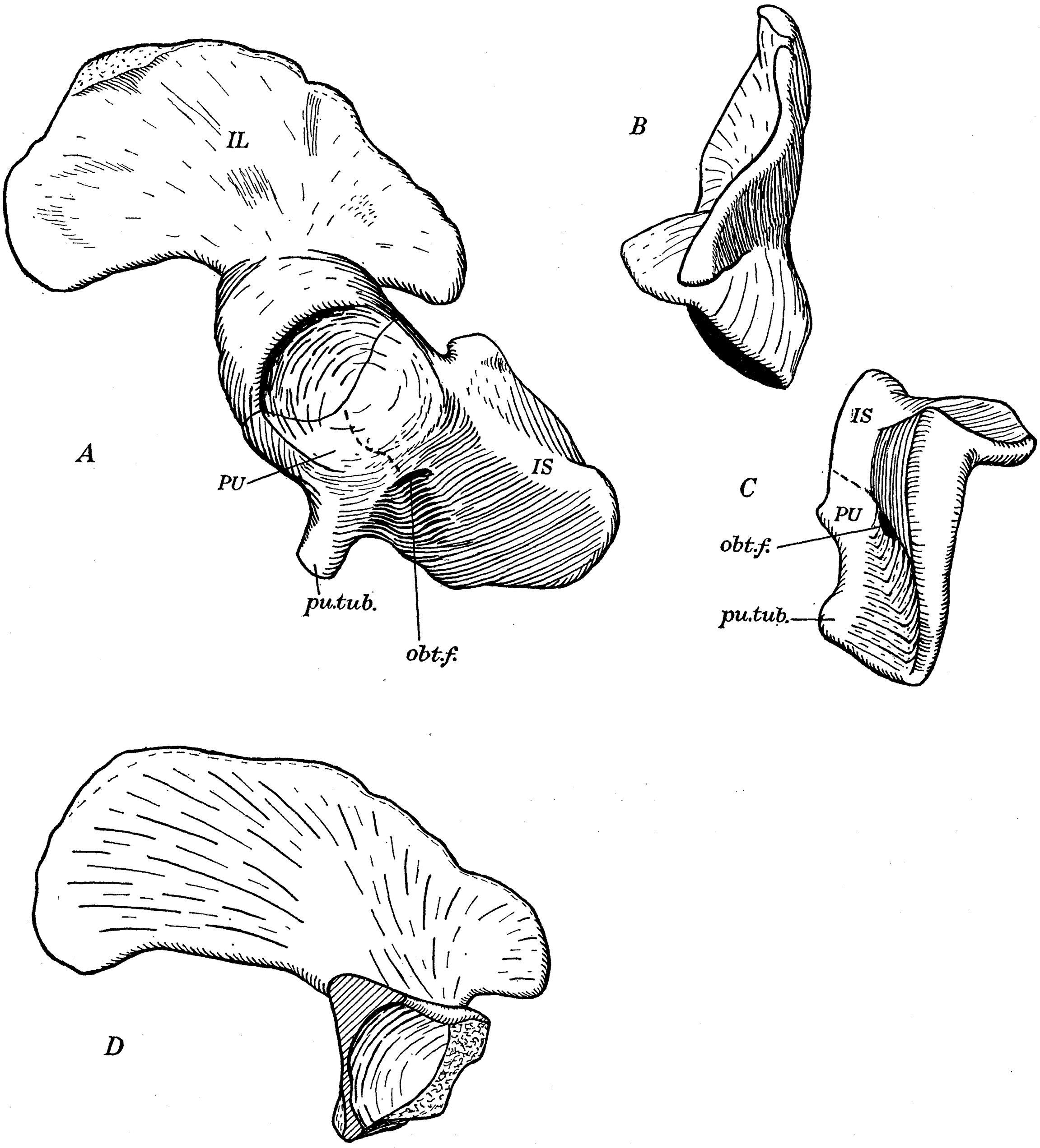

FIGURE 19. *Dinodontosaurus turpior*. *A*, Lateral view of pelvic girdle, × $\frac{1}{4}$. *B*, Posterior view of ilium, × $\frac{1}{4}$. *C*, Posterior view of ischio-pubis, × $\frac{1}{4}$. (Ilium from specimen MCZ No. 1687, ischio-pubis from specimen MCZ No. 1759.) *D*, Lateral view of ilium of MCZ No. 3108, × $\frac{1}{4}$. *obt.f.*, Obturator foramen; *pu.tub.*, pubic tubercle. For abbreviations of names of bones, see p. 514.

Hind limb (figures 17, *E* and *F*, 18*B* and 20). The femur is about 30 cm long. Its head is quite well developed, but is not separated from the proximal end of the bone by any distinct neck. The great trochanter is moderately well developed. The shaft of the femur is almost straight. The distal condyles are well defined; they face downwards and towards the posterior side of the bone.

The tibia is 21 cm long. Its proximal end bears two concave facets for the femoral condyles, that for the inner condyle being the larger. The cnemial crest runs up the proximal part of the front surface of the bone and ends proximally in a large rounded prominence. The distal end bears two faces, a lower medial one for the astragalus and a higher lateral one for the calcaneum.

The middle part of the fibula is missing and has been restored. Its proximal end is damaged, but appears to have been concave and to have completed the other half of the facet for the outer femoral condyle. The fibula bears on its antero-distal surface a facet for the fibulare.

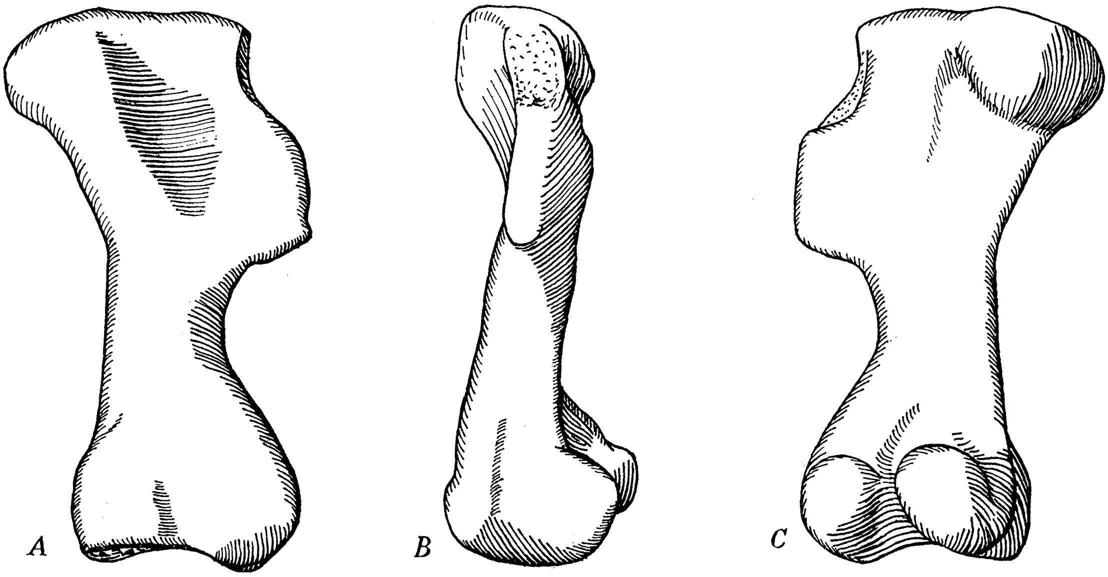

Figure 20. *Dinodontosaurus turpior*, specimen MCZ No. 1670. Femur, ×$\frac{1}{4}$. *A*, Anterior view; *B*, lateral view; *C*, posterior view.

The preserved bones of the pes of the mounted skeleton comprise the tibiale, fibulare, one other centrale and all the metatarsals and phalanges. As in the manus, all that it has been possible to do is to figure the pes as it appears in the mounted specimen (figure 18*B*).

Specimen MCZ No 1628

This consists of a skull, plus a few pieces of vertebrae and limb-bones. The skull lacks both quadrates and quadratojugals, and also the left zygomatic and post-orbital arches. It is slightly distorted: the dorsal surface has been shifted slightly to the left, the occipital wing of the left squamosal has been widened, and the palatal rami of the pterygoids have been bowed somewhat apart. The right zygomatic arch and posterior end of the right squamosal have also been pressed slightly downwards. However, it has been possible to correct these distortions with little chance of significant error and this has been done in the accompanying figures.

Dorsal view (figure 21). The greatest length of the skull (taken in the midline from the anterior end of the snout to a line drawn between the posterior margins of the squamosals) is 40 cm. Its greatest breadth, also 40 cm, is at the occiput, measured across the lateral wings of the squamosals.

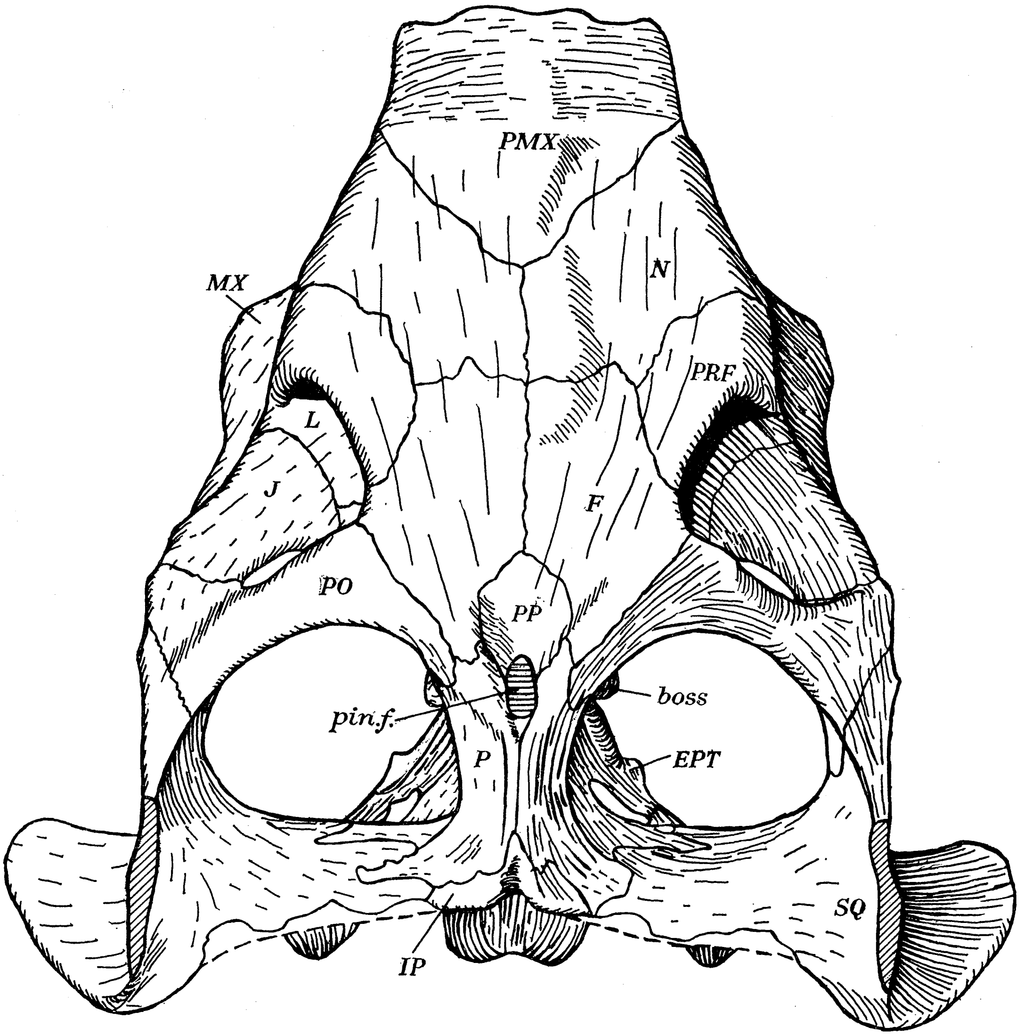

FIGURE 21. *Dinodontosaurus turpior*, specimen MCZ No. 1628. Dorsal view of skull, × ¼. *boss*, Projection from pterygoid, probably for part of pterygoideus musculature; *pin.f.*, pineal foramen. For abbreviations of names of bones, see p. 514.

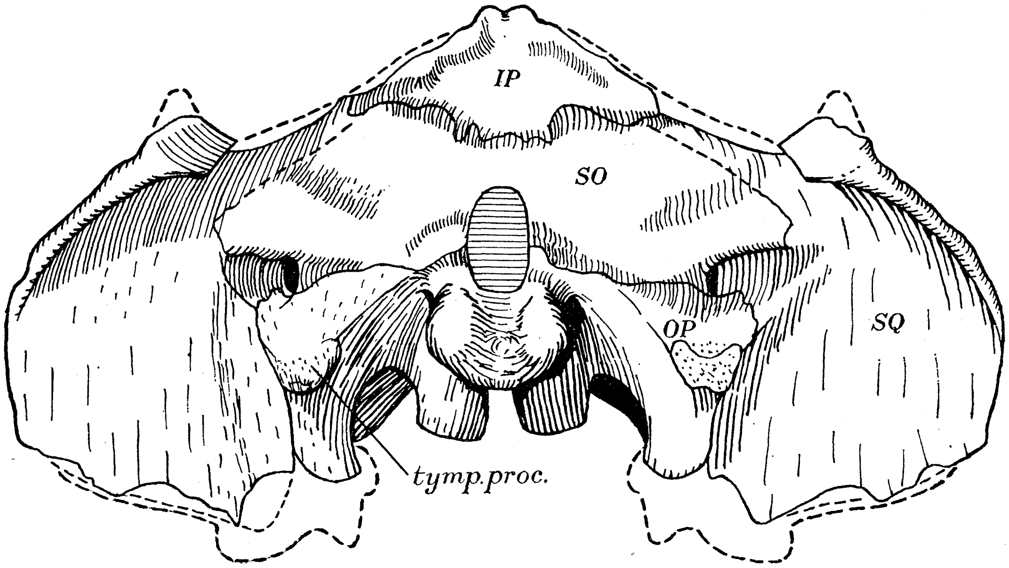

FIGURE 22. *Dinodontosaurus turpior*, specimen MCZ No. 1628. Occipital view of skull, × ¼. *tymp.proc.*, tympanic process. For abbreviations of names of bones, see p. 514.

The general shape of the skull, square posteriorly and tapering to a wide, blunt muzzle, can be seen from the figure. The interorbital bar is fairly broad, but not so broad as to obscure the orbits in dorsal view. There is a large, broad preparietal bone, forming the anterior margin of the oval pineal foramen which is 2·5 cm long and 1·3 cm broad.

Occipital view (figure 22). The occiput is noticeable for its great width, a considerable part of which is due to the lateral expansion of the occipital portion of the squamosal.

The suture between the supraoccipital and the opisthotic can be seen, but opisthotic, exoccipital and basioccipital are fused together.

Palatal view (figure 23). The palate is almost 15 cm long, i.e. nearly 40% of the total length of the skull. Another remarkable feature is the position of the very large canines. These are unusually far back, and also placed far out to the side in very pronounced lateral swellings of the maxillae. The canines are both broken off, but the portion embedded in the maxilla is 3·3 cm wide.

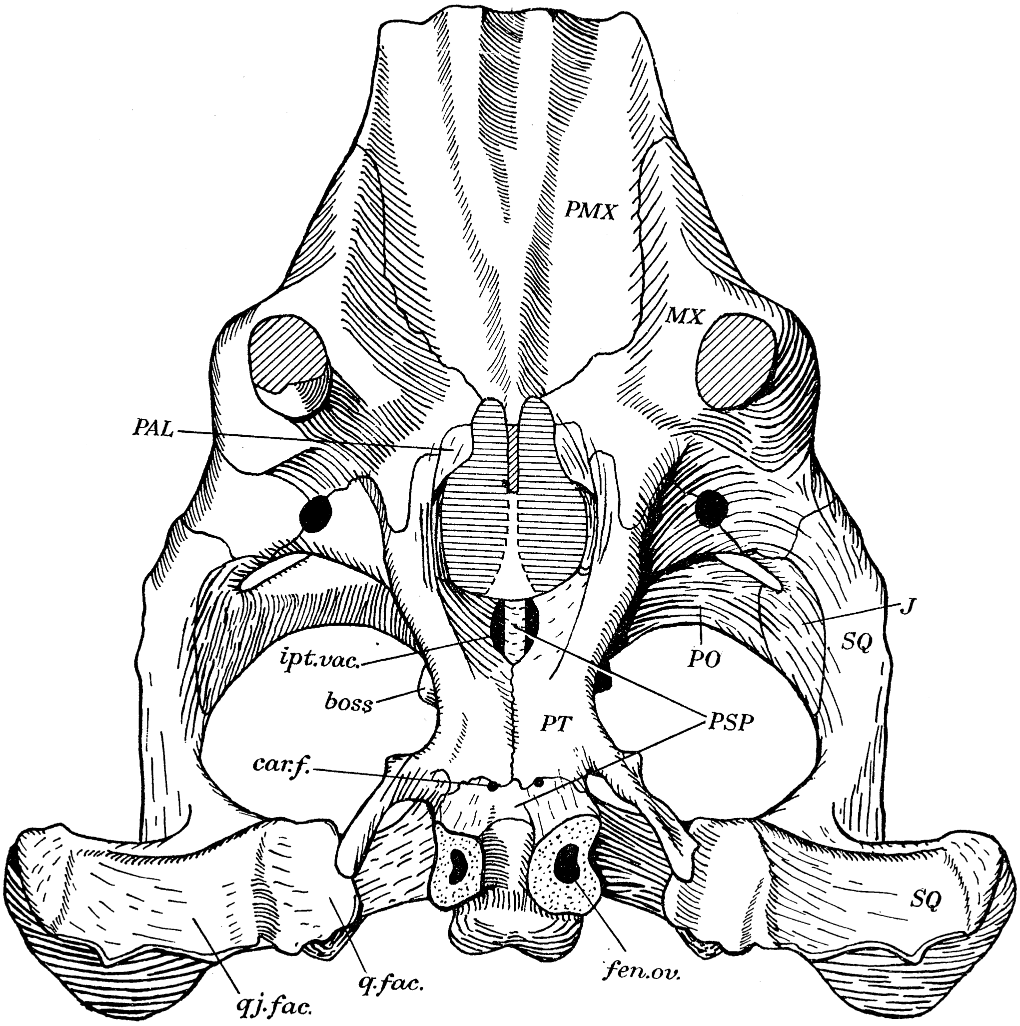

FIGURE 23. *Dinodontosaurus turpior*, specimen MCZ No. 1628. Ventral view of skull, ×¼. *boss*, Projection from pterygoid, probably for part of pterygoideus musculature; *car.f.*, carotid foramen; *ipt.vac.*, interpterygoid vacuity; *q.fac.*, facet for quadrate; *qj.fac.*, facet for quadratojugal; *fen.ov.*, fenestra ovalis. For abbreviations of names of bones, see p. 514.

The edge of the maxilla in front of the canine tusk, and of the premaxilla itself, is quite sharp. This edge, and also the ridges on the palatal surface of the premaxilla, continue to the anterior end of the snout. The anterior end of the premaxilla, seen from in front, therefore has a jagged outline. The palatine is thickened anteriorly and projects inwards, but it does not appear to meet the premaxilla.

The two pterygoids have a long and firm midline suture and are 6 cm wide at this point. The quadrate ramus of the pterygoid is high but thin. The internal carotid foramen can be seen entering between the pterygoid and the parasphenoid. The parasphenoid itself

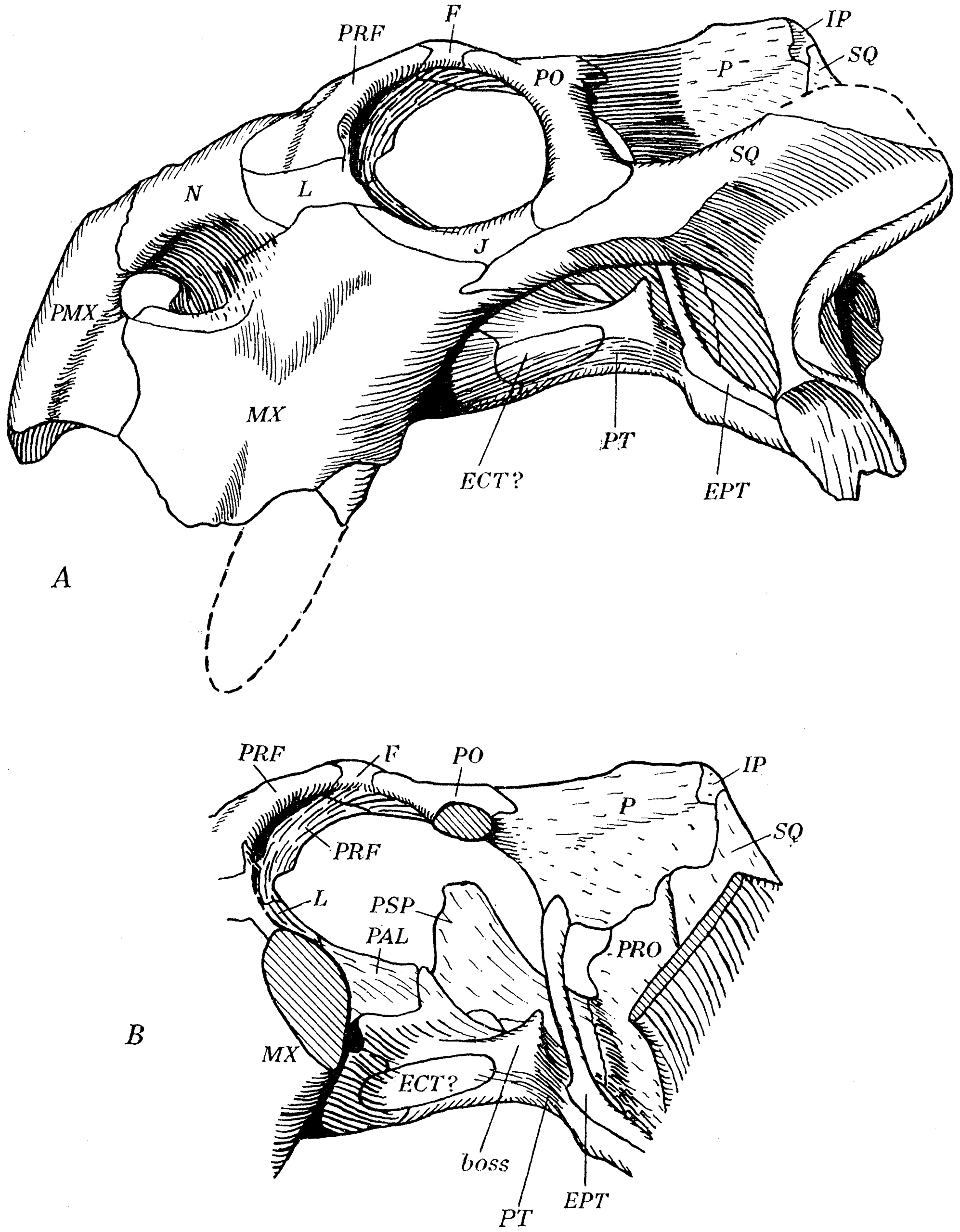

FIGURE 24. *Dinodontosaurus turpior*, specimen MCZ No. 1628. *A*, Lateral view of skull, $\times \frac{1}{4}$. *B*, Lateral view of braincase, after removal of post-orbital and zygomatic arches, $\times \frac{1}{4}$. *boss*, Projection from pterygoid, probably for part of pterygoideus musculature. For abbreviations of names of bones, see p. 514.

has a short but wide ventral exposure where it forms the anterior surfaces of the pair of basisphenoid tubera. Each tuber is strong, about 2 cm high, and surrounds a fenestra ovalis about 7 mm in diameter. No clear suture can be seen between the basisphenoid and the basioccipital. Both stapes are missing.

As already mentioned, the quadrate and quadratojugal are missing. The original extent of these bones is clearly indicated by markings and grooves on the anterior face of the squamosal. The depression for the quadratojugal is rather shallow; the bone formed the lower lateral edge of the occiput and extended medially for about 10 cm from this point. Though it is thus very wide, it is only about 6·5 cm high and does not extend even up to the level of the lower border of the post-temporal fossa. This depression for the quadratojugal is bounded medially by a strong ridge, separating it from the rounded pocket for the quadrate. This pocket has about the same dorsal extent as the depression for the quadratojugal. As in other dicynodonts, the squamosal interposes itself between the quadrate and the distal end of the paraoccipital process.

Side view (figure 24*A*). The heavy snout, somewhat sharply truncated, and the posterior position of the canine are very noticeable in side view.

The sutures of the septomaxilla with the surrounding bones cannot be distinguished. The external naris is sunk into a deep hollow. Its lower border is formed of a high ridge, projecting above the level of the floor of the external naris. This ridge is continuous anteriorly with the base of the anterior border of the naris; posteriorly it curves slightly upwards and dies out.

The maxilla is a very massive bone. In front of the canine, its edge extends further ventrally than the base of the tooth. Posteriorly, the maxilla meets the anterior tip of the squamosal and covers the outer side of the jugal.

Both the lachrymal and the prefrontal have a considerable exposure on the face. The anterior wall of the orbit is formed by the prefrontal, which meets the lachrymal ventrally. The lachrymal does not have a very large exposure on the floor of the orbit, for it is overlapped posteriorly by the jugal and internally by the palatine.

The pterygoid is a very extensive bone in lateral view. The sutural pattern at its anterior end is very difficult to make out. There is a thin sheet of bone on the outer side of each pterygoid. This sheet meets the maxilla anteriorly and appears to be the ectopterygoid, which is reduced or lost in all other large or late dicynodonts.

There is a large foramen between the anterior end of the pterygoid and the maxilla. This is found in all dicynodonts which have large canines, and presumably transmitted nerves and blood vessels to the root of the canine tusk (Pearson 1924*a*). Above this foramen the pterygoid meets another bone, presumably the palatine, which runs forward to meet the lachrymal.

In front of the base of the epipterygoid is a strong conical projection of the pterygoid, 26 cm high. This spur is also visible in dorsal and ventral view. The epipterygoid itself extends antero-dorsally as a fairly solid bar of bone. It does not appear to form any large part of the dorsal wall of the braincase, but merely meets the ventral edge of the parietal.

Braincase (figure 24*B*). The inside of the braincase is not accessible, and the different bones of the braincase are fused.

The lateral wall of the front part of the braincase is formed largely by the parietal. Below this, the front edge of the braincase shows a projection which is presumably the pila antotica. In front of this, the parasphenoid-basisphenoid complex rises up antero-dorsally in the midline. Its suture with the prootic region cannot be distinguished, but it has a good lateral suture with the pterygoid, from which it is also separated for a short distance by the interpterygoid vacuity.

No details of the sphenethmoid region can be discerned.

Taxonomic position of specimen MCZ No. 1628

At first sight, this specimen appears to be very different from *Dinodontosaurus turpior*, though obviously closely related to it. Specimen No. 1628 differs in having a much heavier, stronger snout, and canines which are very large and are more posteriorly placed than in *D. turpior*. Though the snout is wider than in *D. turpior*, the width of the inter-orbital region is the same, so that far more of the floor of the orbit is visible than in *D. turpior*. The occiput is wider than in *D. turpior*, largely as a result of a much greater lateral extent of the squamosal. The pterygoid regions of the two forms are not readily comparable, as that of *D. turpior* is laterally compressed and badly damaged, while that of specimen No. 1628 has been bowed outwards.

These are the only observable differences between specimen No. 1628 and *Dinodontosaurus turpior*. They are not such as to merit generic status. They may be regarded as indicating either a specific difference or a sex difference. The extremely numerous herbivorous dicynodonts may well have formed herds for all or part of the year, and specimen No. 1628 can easily be interpreted as the 'old bull' of such a herd, distinguished by his more heavily built skull and canine tusks. A very similar sex variation, including an example of an unusually large and massive male skull, is shown today in various seals and sea-lions, e.g. *Otaria byronia* (Hamilton 1934, 1939). It is impossible to distinguish infra-specific variation from sexual variation in most fossil vertebrates. In the ultimate analysis it matters little whether specimen No. 1628 is regarded as a sexual variant or as a separate species, as long as its morphology is adequately known. Since it can reasonably be explained as a large male form of *Dinodontosaurus turpior*, it seems unnecessary to add further to the already crowded array of dicynodont species.

Dinodontosaurus tener (von Huene)

This species was founded by von Huene (1935) as *Dicynodon tener*. The greater part of the remains of the species consisted of a collection of associated fragments from his digging no. 39 at Chiniquà; these comprised the preparietal, frontals, jugal, postorbital, maxilla, supraoccipital, sphenethmoid, dentary, two vertebrae, a few ribs, both scapulae and the left humerus. von Huene also referred to this species a few other remains from other localities; these remains included a maxilla, two squamosals, a right ilium and a few other fragments of a humerus, vertebrae and ribs.

These remains certainly demonstrate the presence of specimens of *Dinodontosaurus* considerably smaller than the type material of *D. turpior*. All the material is imperfect and damaged, and only the associated preparietal and frontals, the humerus and the scapulae are sufficiently well preserved to be of assistance in defining the species. By the kindness of

Dr F. Westphal of the Tübingen Museum, these elements have been borrowed and figured (figure 25).

The associated preparietal and frontals (figure 25*A*) were figured by von Huene (1935, Fig. 15, 1). They show that the skull had an interorbital breadth of 5·3 cm, which compares with that of 10·8 cm in the mounted specimen of *D. turpior*. The frontals of *D. tener* contribute much more to the margin of the orbit than in *D. turpior*. The frontals of *D. tener* show the sutural facets where they met the prefrontals and nasals, and the pattern of meeting of these bones is somewhat different in the two species (compare figures 12*A* and 25*A*). The frontal of *D. tener* also sends back a rather slender process alongside the preparietal; this process is not present in *D. turpior*. The frontal of *D. tener* shows a curved facet along its postero-lateral margin; this facet was probably for the postorbital bone, rather than for a postfrontal as believed by von Huene (1935, p. 68). Finally, the pineal foramen of *D. tener* is proportionately much larger than that of *D. turpior*, and it is bordered laterally by the preparietal bone, while in *D. turpior* it lies behind the preparietal and is bordered laterally by the parietals.

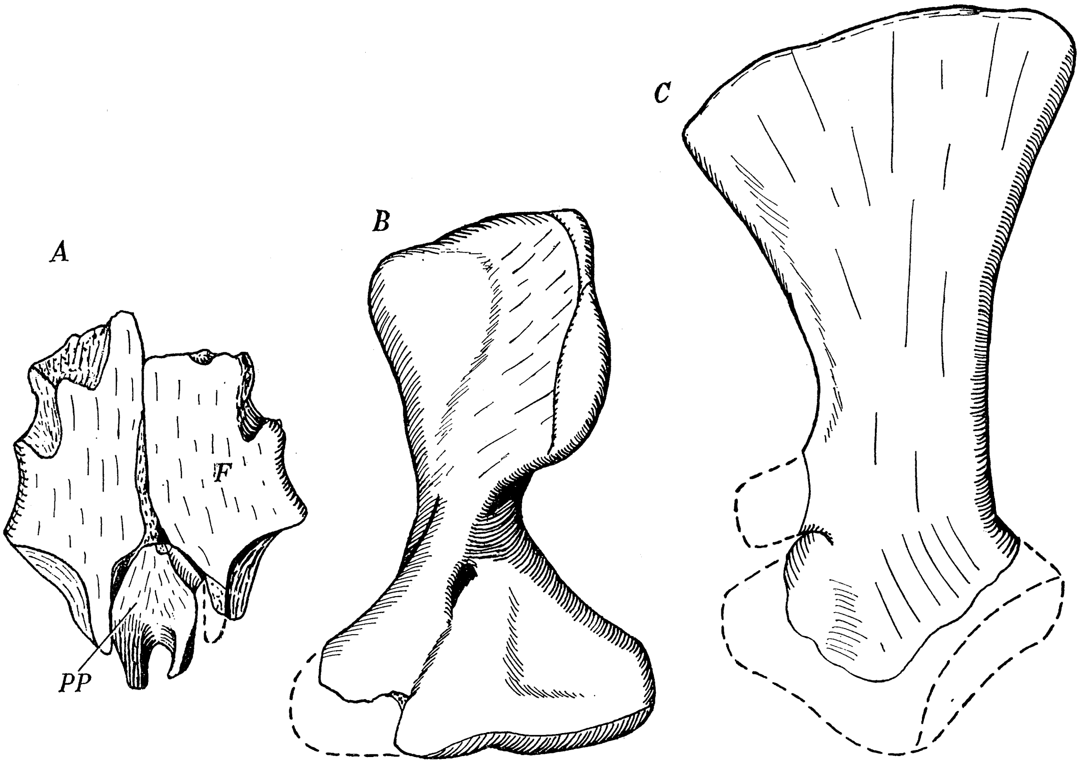

FIGURE 25. *Dinodontosaurus tener*. *A*, Dorsal view of preparietal and frontals, × $\frac{2}{3}$. *B*, Ventral view of humerus, × $\frac{2}{3}$. *C*, Lateral view of scapula, × $\frac{2}{3}$, composite restored from left and right scapulae. All specimens are from von Huene's digging no. 39 (see von Huene 1935). For abbreviations of names of bones, see p. 514.

The humerus of *D. tener* (figure 25*B*) is 10·5 cm long, whilst the humerus of von Huene's type specimen of *D. turpior* is about 18·0 cm long. The humerus of *D. tener* differs from that of *D. turpior* in the following respects: the bridge across the entepicondylar canal is much narrower, the condyles for the radius and ulna are not visible at all, and the entepicondyle does not appear to have projected beyond the ectepicondyle.

The scapulae of *D. tener* (figure 25*C*) are both damaged and lack the acromion process and ventral region. The blade of the scapula does not appear to be appreciably different from that of *D. turpior*; as in that species, the acromion process projects from the front margin of the blade. However, the curvature of the blade of the scapula is more marked than in *D. turpior*.

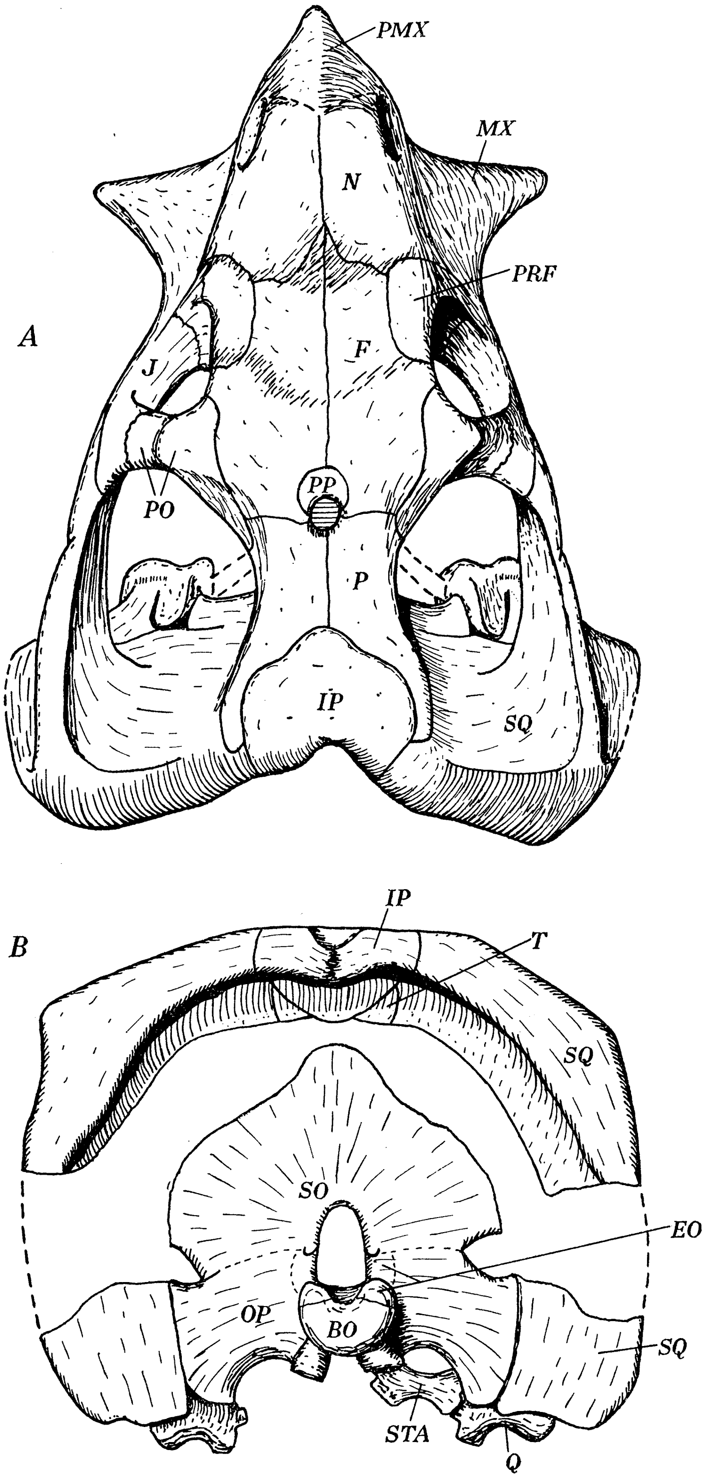

FIGURE 26. Restored skull of *Placerias gigas* in *A*, dorsal view and *B*, occipital view, × $\frac{1}{6}$. For abbreviations of names of bones, see p. 514.

The differences between *D. tener* and *D. turpior* thus consist only of a difference in size, some differences in the relationships between the frontals and the pineal foramen and the surrounding bones, and differences in the curvature of the scapula and in the degree of development of the articular surfaces of the humerus. These differences are such that it remains possible that *D. tener* is merely a young form of *D. turpior*. Indeed, a juvenile *Dinodontosaurus* skull (specimen MCZ No. 1677) shows a very similar pattern in the frontal and pineal region. However, without considerably more work on the smaller specimens in the Museum of Comparative Zoology at Harvard, it is impossible to be sure that this is so. It therefore seems advisable for the present to retain the species as *Dinodontosaurus tener* (von Huene). The associated remains from von Huene's digging no. 39 at Chiniquà, described and figured by him (1935, pp. 67–72 and Fig. 15) may be regarded as the type material.

A NEW RESTORATION OF THE SKULL OF *PLACERIAS*

Placerias is the only known North American dicynodont and the only known Upper Triassic dicynodont, coming from the Lower Chinle of Arizona. First named from a humerus described by Lucas (1904) as *Placerias hesternus*, the genus is best known from the large number of fragments described by Camp & Welles (1956) as *Placerias gigas*. Their description is based upon a collection of more than 1600 skull and skeletal elements from a quarry near St Johns, Arizona. These elements represent the incomplete remains of at least 39 individuals, whose bodies appear to have been trodden into the mud of a large pond. The bones of each carcass are thus scattered and mingled with those of other carcasses, while the skull elements have been almost entirely macerated along suture lines and widely separated.

The total of 815 skull elements catalogued, derived from at least 39 individuals, represents only about one-third of the skull elements which these individuals must originally have possessed. Measurements of the commonest elements, the postorbitals and jugals, show that the smallest specimen was only about half the size of the largest. Finally, many of the skull elements are damaged. All these factors make the restoration of the skull of *Placerias gigas* unusually difficult. As stated by Camp & Welles (1956, p. 287), 'Parts of at least nine individuals from the quarry have been put into this restoration, and the result is correct in the relations of the elements, but the proportions and attitudes of some of the parts are inaccurate'. An attempt has been made below to correct some of these inaccuracies and to provide a new restoration of the skull of *P. gigas*. This was made possible by the kindness of Drs Camp and Welles, who allowed the writer to study the material and to make alterations to the composite restoration, drawings of which were then made by Mr Owen J. Poe. The accompanying figures are based upon these drawings and upon photographs taken by Dr Welles.

The basic change that was found to be necessary, as suggested by Camp & Welles (1956, p. 287), was to swing back the braincase and lower portion of the occipital plate and to shorten the quadrate ramus of the squamosal. This change is possible because this region of the restored skull is not connected by preserved bone to either the dorsal region of the occiput or to the palatal region of the skull. As will be seen, this change corrects several other errors found in the previous restoration and noted by Camp & Welles (1956, p. 287).

First, this change moves the quadrates back from their previous position extremely close to the maxillae. It also makes the whole of the articular surfaces of the quadrates accessible to the articular condyles of the lower jaw—previously, the anterior section of the quadrate condyles was not in contact with the lower jaw condyles at any stage of the movement of the latter. The change in the position of the quadrates also makes it necessary to increase the length of the lower jaw. This larger lower jaw is also more in keeping with the distance between the quadrate condyles, which was too great for the previous, smaller, lower jaw.

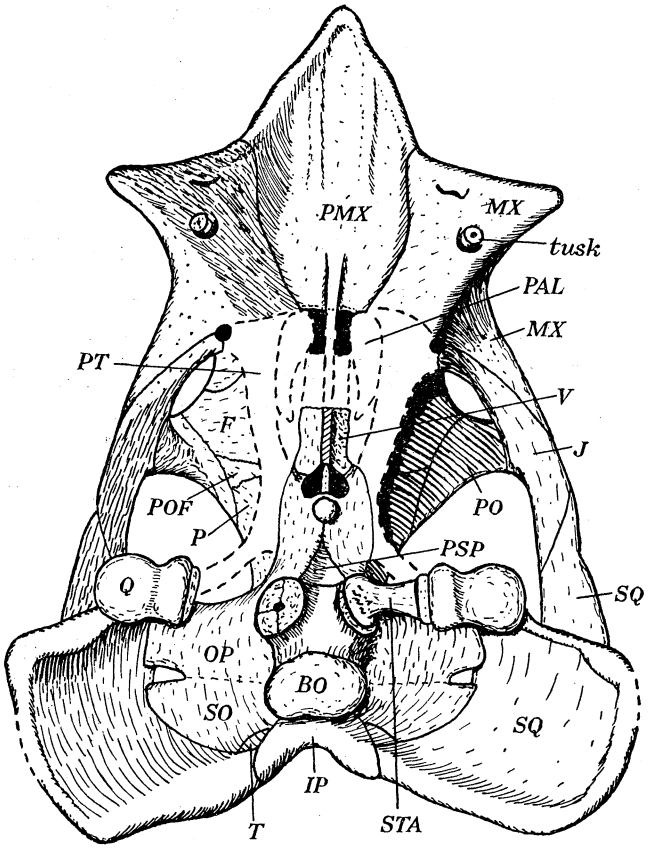

FIGURE 27. Restored skull of *Placerias gigas* in ventral view, × $\frac{1}{6}$. Palatines, anterior portion of vomer and all except body of pterygoid, restored. For abbreviations of names of bones, see p. 514.

The posterior shift in the position of the braincase makes it necessary to increase the length of the palate. There is no difficulty in doing this, as the region between the posterior end of the premaxilla and the anterior end of the interpterygoid vacuity was almost entirely unrepresented in the preserved material. This region had also seemed excessively short in the previous restoration.

The only other change which was made was to replace the maxillae, which bore extremely large caniniform processes, with maxillae bearing smaller processes. These seemed to match the premaxilla equally well, and to match the rest of the skull far better. The maxillae have also been inserted so that the caniniform processes project more ventrally than in the previous restoration. This was necessary to allow the anterior end of the pterygoid to meet the appropriate facet on the maxilla. In the previous restoration

(Camp & Welles 1956, Pl. 31) the pterygoid facet of the maxilla projects too far ventrally and laterally for any such meeting to be possible.

One or two other features in the accompanying new restorations of *Placerias gigas* are worth mentioning. In palatal view, it is worth emphasizing again that hardly anything is known of the pterygoid, palatine and vomer. No trace has been found of an ectopterygoid and this element may well have been absent, as in most large or late dicynodonts. Triassic dicynodonts also always have a very short interpterygoid vacuity, as is well shown by *Placerias*. Just behind this, the pterygoids in *Placerias* bear a very well-developed median boss. The small spike of parasphenoid which is visible within the interpterygoid vacuity is not merely the ventral surface of the cultriform process of the parasphenoid, as is normally the case in dicynodonts. It is, instead, a short antero-ventral projection from the cultriform process.

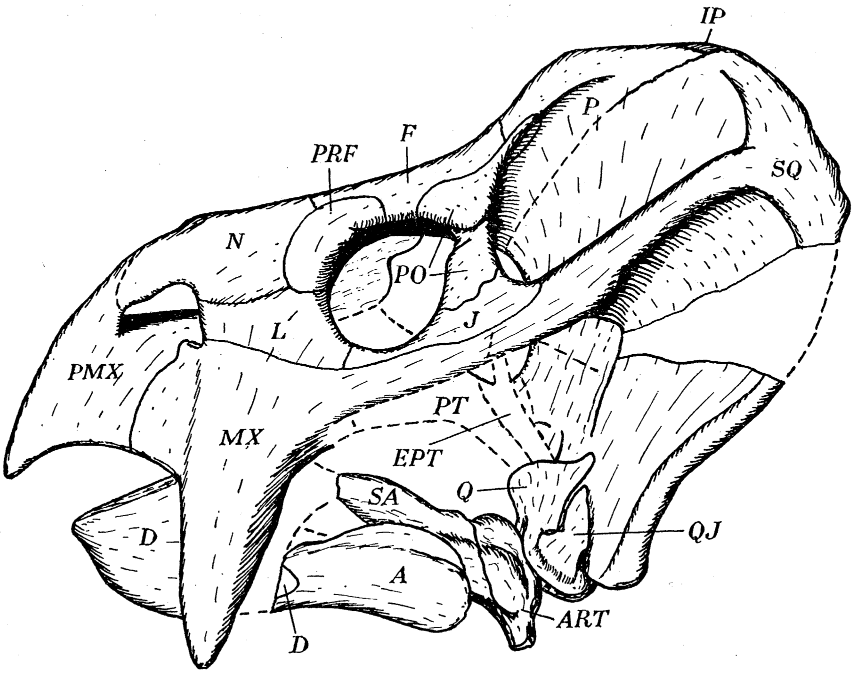

FIGURE 28. Restored skull and lower jaw of *Placerias gigas* in lateral view, × $\frac{1}{6}$. For abbreviations of names of bones, see p. 514.

In lateral view, a rod-like epipterygoid has been added, rising to the parietal from a footplate on the quadrate ramus of the pterygoid. This is the normal dicynodont condition, and traces of it are visible in some specimens of *P. gigas*.

The lower jaw has been lengthened in the figures, as mentioned previously. A slight change has also been made in the relationship between the posterior end of the angular and the surangular and articular, following preparation of a specimen showing these elements almost undisturbed. However, the restored lower jaw is still felt to be unsatisfactory in its abnormally large Meckelian fossa between the dentary and post-dentary bones, and in the angle between the biting dorsal edge of the dentary and the surface of the palate. It is possible that a larger dentary would prove more suitable.

The relationships of the Triassic dicynodonts

Table 1 gives the names of all the well-known Triassic dicynodonts which have so far been described, together with the principal sources of anatomical information for each genus, and its geological stratum and probable age.

Table 1. The triassic dicynodonts

Basal Triassic

Myosaurus (Haughton 1917) *Lystrosaurus* Zone, South Africa
Prolystrosaurus (Haughton 1917) *Lystrosaurus* Zone, South Africa
Lystrosaurus (van Hoepen 1913; Broom, 1932; Brink, 1951) *Lystrosaurus* Zone, South Africa
Lystrosaurus (Young 1935, 1939) Tsan-jang-kan Series, Sinkiang, China
Lystrosaurus (Robinson 1958) Panchet Beds, India

Lower Triassic

Kannemeyeria (Haughton 1915; Pearson 1924*a*, *b*) *Cynognathus* Zone, South Africa
'*Kannemeyeria*' *vanhoepeni* (Camp 1956; Cruickshank in preparation) *Cynognathus* Zone, South Africa
Sinokannemeyeria (Young 1937; Sun 1963) Er-ma-ying Series, Shansi, China
Parakannemeyeria (Sun 1960, 1963) Er-ma-ying Series, Shansi, China
Shansiodon (Yeh 1959) Er-ma-ying Series, Shansi, China
Rhadiodromus (Efremov 1938, 1951) zone VI, European Russia

Middle or Upper Triassic

'*Dicynodon*' *njalilus* (von Huene 1942; Cruickshank, in preparation) Manda Formation, Tanganyika
Kannemeyeria (Cruickshank, in preparation) Manda Formation, Tanganyika
Stahleckeria (von Huene 1935) Santa Maria Formation, southern Brazil
Dinodontosaurus Santa Maria Formation, southern Brazil
Barysoma Santa Maria Formation, southern Brazil
Ischigualastia Ischigualasto Formation, northern Argentina
Placerias (Camp & Welles 1956) Chinle Formation, Arizona, U.S.A.

Table 2. Distribution of the dicynodont genera

	Africa	Europe	India	Asia	South America	North America
Upper Permian	*ca.* 50	3 (1)	—	2	—	—
Basal Trias	3	(1)	1	1	—	—
Lower Trias	2 (2)	1 (1)	(1)	3	—	—
Middle or Upper Trias	1 (5)	1 (1)	—	—	4 (1)	1

Numbers in parentheses refer to additional genera known but not yet described.

Brachybrachium and *Eubrachiosaurus* are genera based on very fragmentary material from the Upper Triassic of North America, described by Williston (1904); they are too incomplete to merit further consideration here, and will be disregarded. Dicynodonts are also known from the Basal Triassic zone V, the Lower Triassic zone VI and the Middle Triassic zone VII of European Russia (Olson 1957) but, with the exception of *Rhadiodromus* (Efremov 1938, 1951), no account of them has yet appeared.

At least three new genera of dicynodont were collected in the summer of 1963 by the British Museum and London University Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika (Attridge, Ball, Charig & Cox 1964). Two of these genera were collected from the Ntawere Formation of Northern Rhodesia, from a level that may be of Lower or Middle Triassic age. The other new genus was collected from the Middle Triassic Manda Beds of Tanganyika. Descriptions of these new genera will be published as soon as possible.

The known distribution of the dicynodonts is best shown in the form of a table (table 2). Two features of this are worth noting. First, the extreme abundance of dicynodont genera in the Upper Permian of Africa is confined to that period and area. Secondly, the absence of known dicynodonts in the Upper Permian to Lower Triassic of North and South America may be only a reflection of the lack of terrestrial vertebrates from these beds, and it cannot be assumed that they were in fact absent.

The attempt to define the relationships of the Triassic dicynodonts may be divided into two stages. First, one may examine the Lower, Middle and Upper Triassic genera, and try to discover features which may indicate the existence of one or more lineages within these genera and, by inference, the primitive features that would have been possessed by the earlier members of such lineages. Secondly, one may then compare these hypothetical 'earlier members' with the known genera from the Basal Triassic or Upper Permian in an attempt to discover actual connexions.

The relatively complete post-cranial skeletons of the Triassic genera gave some hope of showing the existence of recognizable lineages, and these were therefore first compared in detail, with results which may be outlined as follows.

The scapulae of *Sinokannemeyeria*, *Parakannemeyeria*, *Kannemeyeria* and *Placerias* are all rather tall and very narrow, while that of *Dinodontosaurus* is unusually low and wide. The development of the acromion process and scapular spine is very variable. Where the acromion process is directed more or less anteriorly, the scapular spine is either lacking (*Sinokannemeyeria*, *Parakannemeyeria*, *Kannemeyeria*,* *Placerias*, *Dinodontosaurus*, *Shansiodon*) or very poorly developed (*'Dicynodon' njalilus*). Where the acromion process is directed more antero-laterally, a well-developed scapular spine is present (*Stahleckeria*, *Barysoma*). *Ischigualastia* is unusual in showing hardly any trace of an acromion process, and the shoulder girdle is also unlike that of the other forms in that the precoracoid foramen runs between the scapula and the precoracoid bone (instead of piercing the precoracoid bone), and in the peculiar waisted shape of the sternum.

It has been suggested (Camp 1956) that the humeri of *Kannemeyeria* were more primitive than those of some other Triassic genera in having less well-ossified condyles. However, the humeri of *Kannemeyeria* in the British Museum (Natural History) studied by Pearson (1924*b*) appear to have ben badly crushed, so that the condyles have been flattened. There do not appear to be any significant differences in the degree of ossification of the condyles of the humerus in the other Triassic genera, and Sun (1963) finds that the degree of development of the condyles is variable in *Parakannemeyeria youngi*. It may further be noted that the entepicondyle is unusually large in *Dinodontosaurus*, while the ectepicondyle is unusually large in *Placerias* and is larger than the entepicondyle in *Shansiodon*, *Parakannemeyeria* and *Ischigualastia*. The radial condyle is well separated from the other condyles only in *Shansiodon*, *Dinodontosaurus* and *Stahleckeria*. The radius itself is more slender in

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* In *Kannemeyeria* there is a very low incipient scapular spine which runs up near the front edge of the bone for a short distance. This condition was interpreted by Watson (1917) as being the margin of the area of attachment of a cleithrum. However, the straight bone which he interpreted as a cleithrum has a shaft of oval section, does not fit into the front edge of the scapula, and bears marks of bone overlap at both ends. The specimen is probably a clavicle—an element which is otherwise unrepresented in the material of *Kannemeyeria*. The cleithrum is known in the Dicynodontia only in *Kistecephalus* (von Huene 1942) *Diictodon* and *Diictodontoides* (Watson 1960), and there in so reason to suppose that it was present in *Kannemeyeria*.

Sinokannemeyeria, *Parakannemeyeria*, *Kannemeyeria*, *Shansiodon* and '*Dicynodon*' *njalilus* than in the other genera. One notable feature found in all the Triassic genera is the presence of a separately ossified olecranon process on the ulna; this character has already been described in all the Triassic genera except *Kannemeyeria*, and several ulnae of this genus in the British Museum (Natural History) (e.g. specimen No. R 3740) also show it. This point will be mentioned again later.

Apart from the unusually swollen ilium found in some specimens of *Dinodontosaurus*, there does not seem to be any great variation in this bone in the Triassic genera. A well-developed pubic tubercle is commonly present, as is the in-turning of the dorsal edge of the ischium.

The femora of *Shansiodon* and '*Dicynodon*' *njalilus* are more slender than those of the other genera. A pronounced lateral head, separated from the rest of the femur by a narrow neck, is shown in Yeh's (1959) figure of *Shansiodon*, but it seems very likely that much of the proximal end of the bone has been lost by weathering. A less pronounced laterally developed head is found in *Ischigualastia*. The trochanter is unusually well developed in *Dinodontosaurus*.

As can be seen, this comparison of post-cranial features does not provide any immediately apparent pattern of relationships between the genera, except perhaps that the genera *Sinokannemeyeria*, *Parakannemeyeria*, *Kannemeyeria* and *Placerias* all have scapulae of similar shape and with a similar orientation of the acromion process. The comparison does also suggest that one feature, the presence of a separately ossified olecranon process on the ulna, is a feature common to, and therefore possibly primitive for, the Triassic genera as a whole.

With these points in mind, one may now turn to compare the skulls of these Triassic genera (figures 29 and 30). These skulls do not show any of the peculiarities occasionally found in the Permian genera, such as nasal, frontal or pineal bosses. The preparietal and postfrontal bones are somewhat variable in occurrence, but variation in these bones is well known (see Sun 1963) and is unlikely to be of taxonomic significance.

The shape of the skull is overwhelmingly conditioned by its adaptations to the diet and manner of feeding. These aspects of its mode of life will directly affect the shape of the snout and lower jaw, and also the shape of the posterior end of the skull, which accomodates and provides attachment for the jaw musculature. The most obvious contrast in these characters is to be seen if the skulls of *Kannemeyeria* (figures 29*E*, 30*G*) and *Stahleckeria* (figures 29*H*, 30*D*) are compared. In *Kannemeyeria* the snout tapers anteriorly to a blunt point. The jaw muscles originate from the front face of an occipital plate which has been greatly heightened postero-dorsally. As a result, the temporal vacuity appears quite long in dorsal view, and the intertemporal bar in lateral view projects above the level of the rest of the skull as a high median crest. The occiput is as high as it is broad.

In *Stahleckeria* the snout is extremely wide and blunt. The jaw muscles originate from the front face of an occipital plate which has been greatly widened by the lateral extension of the squamosals. As a result, the temporal opening appears comparatively short in dorsal view, and the intertemporal bar in lateral view hardly projects above the level of the rest of the skull. The occiput is wide but low.

Having recognized the divergent adaptations of *Kannemeyeria* and *Stahleckeria*, it becomes apparent that several of the other Triassic forms are similar to one or other of these two genera. The pointed snout, long temporal opening, high intertemporal crest and high occiput are all to be found in both *Ischigualastia* and *Placerias*; what is known of *Barysoma* indicates that it is close to *Ischigualastia* and belongs to the same group. A clue as to the earlier history of this group is given by '*Kannemeyeria*' *vanhoepeni*. As shown by Cruickshank (in preparation), this form is sufficiently distinct from the other species of *Kannemeyeria* to merit generic status, and appears to be slightly more primitive than *Kannemeyeria* in having a wider and slightly concave intertemporal bar, in which there is a wider exposure of the interparietal, and in having a rather wider snout.

It is possible that an even earlier stage in the evolution of the *Kannemeyeria* group is represented by two of the Chinese genera, *Sinokannemeyeria* and *Parakannemeyeria*. The four species *S. yingchiaoensis*, *P. ningwuensis*, *P. youngi* and *P. dolichocephala* form a series in which the snout becomes more pointed, the intertemporal bar becomes narrower, the temporal opening becomes longer and the occiput becomes higher (see Sun 1963, Fig. 51 and p. 97); all these features are thus progressing towards the *Kannemeyeria* condition. It is interesting to note that *Sinokannemeyeria* comes from a slightly lower level than *Parakannemeyeria* (Sun 1963, Table 8 and p. 108). It is impossible at present to decide whether the Chinese *Sinokannemeyeria-Parakannemeyeria* fauna is earlier in time than the African *Cynognathus* zone fauna which contains *Kannemeyeria*, but the two Chinese dicynodonts in general appear to be more primitive than the African forms though, as pointed out by Bonaparte (1964), they are also specialized in having an unusually long pre-orbital region.

It may be recalled here that the genera *Sinokannemeyeria*, *Parakannemeyeria*, *Kannemeyeria* and *Placerias* were earlier shown to be similar in the shape of their scapulae and the angle of insertion of the acromion process. The scapula of *Ischigualastia* is widened dorsally, but is otherwise similar in shape to those of the above group of genera.

The wide snout and occiput, short temporal opening and level intertemporal bar, features of *Stahleckeria*, are all found in rather less exaggerated form in its companion in the Brazilian Triassic deposits, *Dinodontosaurus*. Furthermore, these features are also found in the most primitive member of the *Kannemeyeria* group, *Sinokannemeyeria*. The genus *Sinokannemeyeria* is thus a possible structural ancestor for the stahleckeriids as well as for the other kannemeyeriids. In view of the far better series of forms linking the different genera, it seems best to place all the forms *Sinokannemeyeria*, *Parakannemeyeria*, *Kannemeyeria*, '*Kannemeyeria*' *vanhoepeni*, *Ischigualastia*, *Barysoma* and *Placerias* together in the family Kannemeyeriidae. Even though they may have evolved from an early kannemeyeriid, *Dinodontosaurus* and *Stahleckeria* are separated from it by a considerable gap in time and space, and may conveniently be placed in a separate family, the Stahleckeriidae.

The only other genera from the Lower, Middle or Upper Triassic which have been fully described are the Chinese Lower Triassic genus *Shansiodon* (figures 29*A*, 30*A*) and the East African Triassic '*Dicynodon*' *njalilus* (figures 29*F*, 30*B*). These two forms are alike in possessing a rather short, blunt snout, a fairly narrow interorbital bar and a very narrow intertemporal bar. They are thus sufficiently alike for it to be possible, for the present, to take the convenient course of placing them together in a separate family, the Shansiodontidae.

The divergent differences noted above between the forms placed in the families

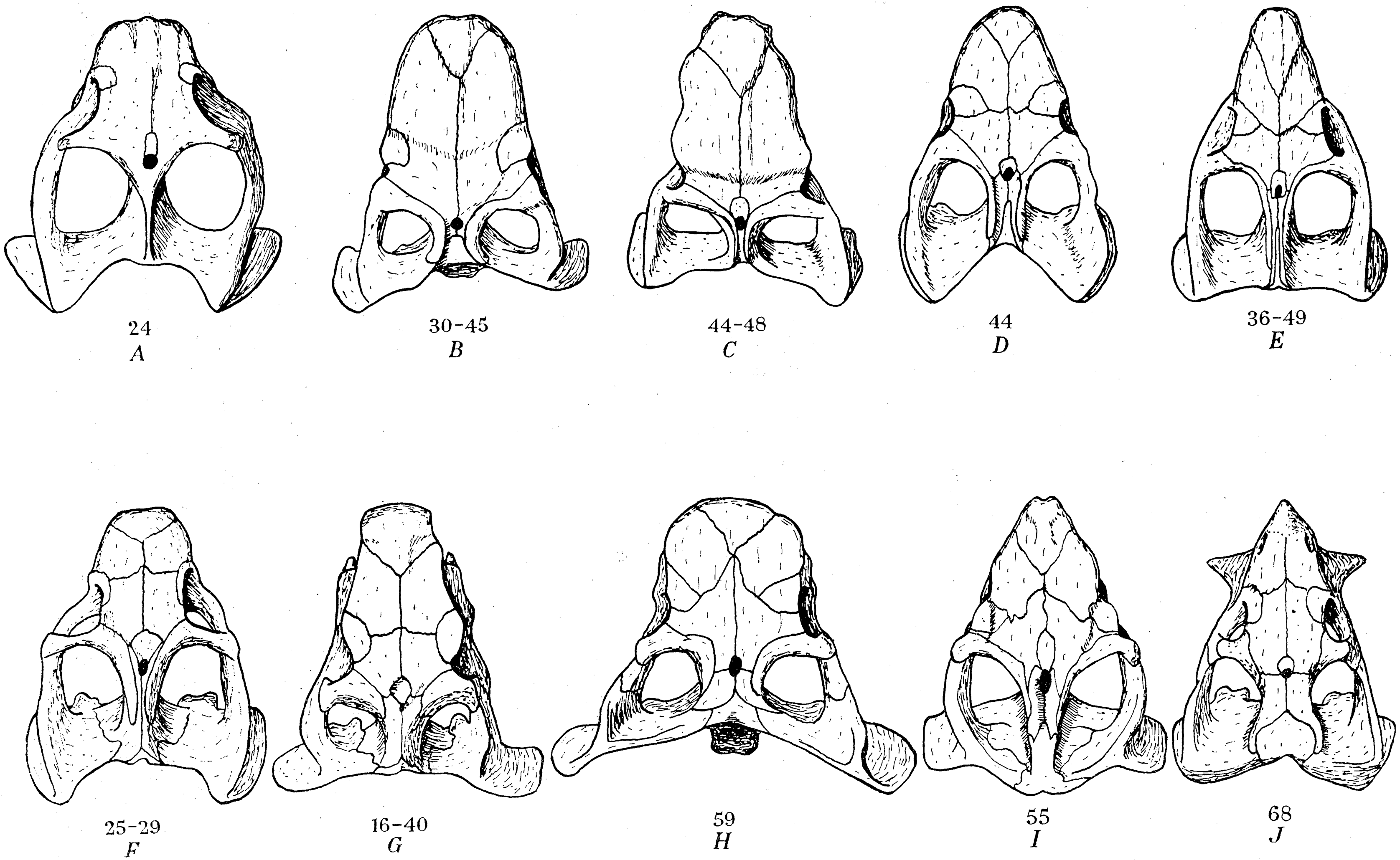

FIGURE 29. Skulls of Triassic dicynodonts in dorsal view, all reduced to same length. Figures beneath each skull indicate actual skull lengths, in centimetres. *A*, *Shansiodon wangi*; *B*, *Sinokannemeyeria yingchiaoensis*; *C*, *Parakannemeyeria ningwuensis*; *D*, '*Kannemeyeria*' *vanhoepeni*; *E*, *Kannemeyeria simocephalus*; *F*, '*Dicynodon*' *njalilus*; *G*, *Dinodontosaurus turpior*; *H*, *Stahleckeria potens*; *I*, *Ischigualastia jenseni*; *J*, *Placerias gigas*. [*A*, after Yeh (1959); *B*, *C*, after Sun (1963); *D*, *E*, *H*, after Camp (1956); *F*, after von Huene (1942), modified according to Cruickshank, in preparation.]

Kannemeyeriidae and Stahleckeriidae must surely be correlated with differences in their diet and mode of feeding. A similar difference is known today between the black and the white rhinoceros in Africa. The white rhinoceros (*Diceros* [*Ceratotherium*] *simus*) has a square lip and feeds entirely on grass, while the black rhinoceros (*Diceros bicornis*) has a pointed lip

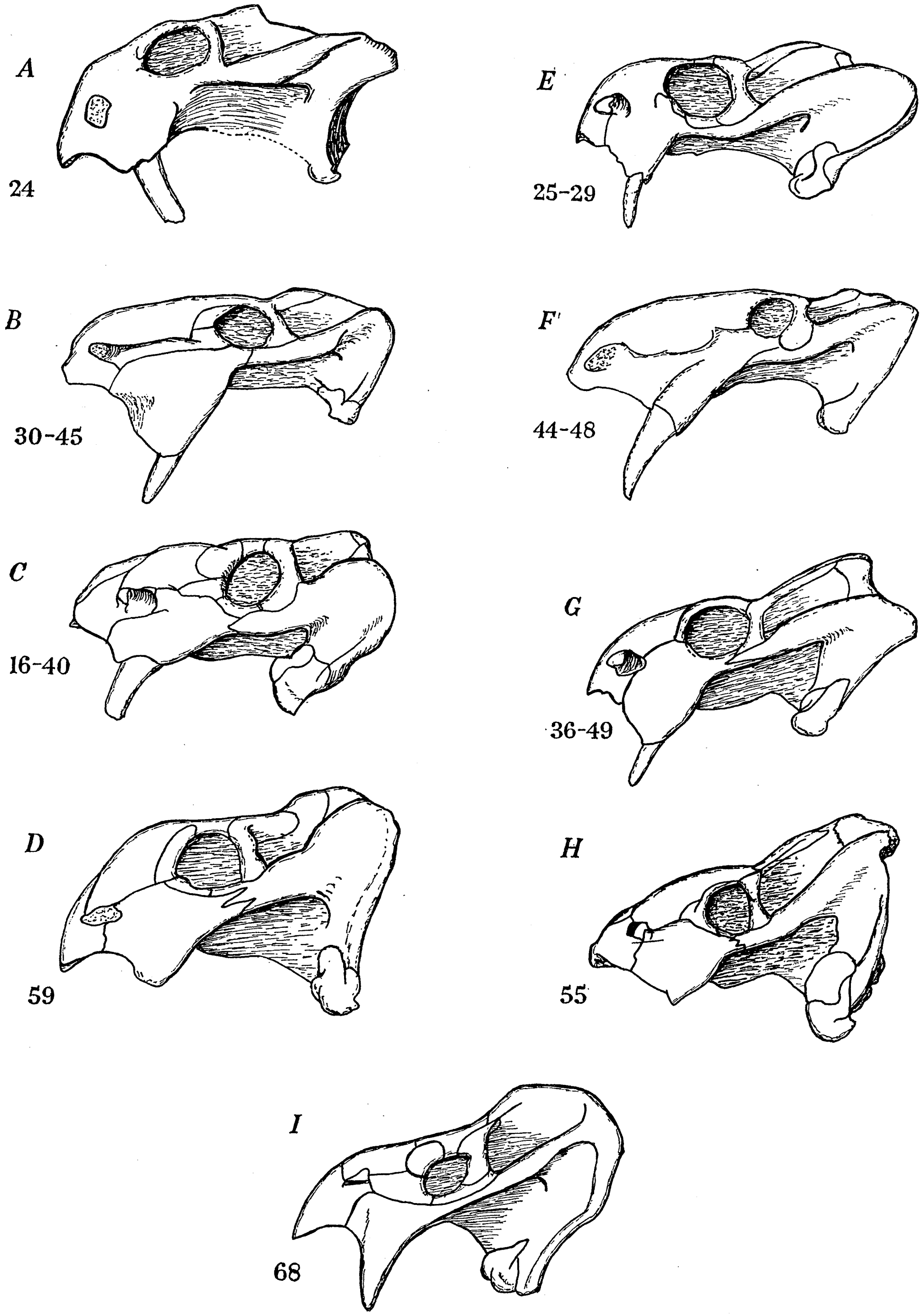

FIGURE 30. Skulls of Triassic dicynodonts in lateral view, all reduced to same length. Figures beneath each skull indicate actual skull lengths, in centimetres. *A*, *Shansiodon wangi*; *B*, *Sinokannemeyeria yingchiaoensis*; *C*, *Dinodontosaurus turpior*; *D*, *Stahleckeria potens*; *E*, '*Dicynodon*' *njalilus*; *F*, *Parakannemeyeria ningwuensis*; *G*, *Kannemeyeria simocephalus*; *H*, *Ischigualastia jenseni*; *I*, *Placerias gigas*. (Origins of figures as in figure 29.)

and feeds on leaves as well as on grass. Zeuner (1936) has also pointed out that the angle of carriage of the head is also affected by the feeding habits, and that this in turn affects the angle between the occiput and the palate. It is noticeable that the occiputs of *Stahleckeria* and *Dinodontosaurus* are almost at right angles to the plane of the palate, whilst those of the Kannemeyeriidae are much more obliquely inclined.

It may be objected that the divergent adaptations of the black and white rhinos have occurred in forms that are quite closely related, whilst a similar difference has here been used to separate families of dicynodonts. However, the differences between the black and white rhinos have at present affected only the mobile fleshy lips; there is only a slight difference between the shapes of the bony lips and angles of the occiputs, and the skulls in general are extremely similar. In the dicynodonts, on the other hand, the overall shapes of the skulls are quite different.

The proposed classification is also open to criticism on the ground that it is based on adaptive features (the modifications of the skull to specific diets), so that forms which have been classified together may merely be forms of unrelated ancestry which have become convergent in structure through feeding on a similar diet. However, the suggested families Kannemeyeriidae and Stahleckeriidae differ in the shape of the jaws, in the relative length of the temporal vacuity, in the development of a parietal crest and in the shape and angle of the occiput. It seems unlikely that quite unrelated lines could converge to this extent without retaining any other characteristics which might betray their differing origins. The almost complete absence of teeth, which in many groups are of such use in tracing lineages and convergences, makes the discernment of these relationships of particular difficulty in the dicynodonts. Whether it is 'true' or not, the classification suggested here seems to provide a reasonable interpretation of the facts at present known, and it may therefore be used unless and until further work shows modification of it to be necessary.

Having thus suggested that the dicynodonts of the Lower, Middle and Upper Triassic may be classified into three families, two of which diverge from the genus *Sinokannemeyeria*, one may now turn to the second stage of this investigation into the relationships of the Triassic genera—the origins of these lineages. Two questions need to be answered: is there any evidence that the two lineages (the family Shansiodontidae, and *Sinokannemeyeria* with its two descendant lines) are of a single origin; and how are they related to the known Basal Triassic and Upper Permian dicynodonts.

Two features, the olecranon process and the interpterygoid vacuity, appear to link the two lineages. A separately ossified olecranon process to the ulna is now known in all the Lower, Middle and Upper Triassic genera, and it is not known in any earlier genera. Though this may well be a significant feature, it should be pointed out that the presence of a suture between the ulna and the olecranon had been missed by earlier workers on the large genera *Barysoma* and *Kannemeyeria*, and that it is even more likely that it would have been missed on the smaller Permian genera.

The interpterygoid vacuity is elongate in Permian dicynodonts, but has been greatly shortened from in front in all the Triassic dicynodonts (the condition of this region is unknown only in *Shansiodon*). It is possible that this shortening is related to the large size of most of these genera; the large form *Daptocephalus* from the *Kistecephalus* zone of South Africa also has a shortened interpterygoid vacuity, though it is not as short as that of the

Triassic genera. However, the Triassic form '*Dicynodon*' *njalilus* is of only moderate length and has a shortened interpterygoid vacuity, whilst the Upper Permian genus *Aulacephalodon* is of similar size but has an elongate vacuity, and the little Upper Permian burrowing dicynodont *Kistecephalus* has a very small interpterygoid vacuity.

It does not seem possible, on the basis of these two characters alone, to come to any decision as to whether these Triassic dicynodonts are of a single origin. From an abstract point of view, it would be somewhat surprising if all except one line of the considerable diversity of Upper Permian dicynodonts became extinct at the end of the period, and that this one line then radiated through the world. Nevertheless, the facts known at present do not exclude this possibility.

Whether these two lineages are of single origin or not, we may finally consider their relationships to earlier forms. The dicynodonts that are nearest to them in time are those of the *Lystrosaurus* zone beds of South Africa, which were probably laid down in Basal Triassic times. In the uppermost parts of these beds have been found skulls of the small dicynodont *Myosaurus* (Haughton 1917). The skulls are very small, only 48 mm long, lack both canine and post-canine teeth, and have a very wide intertemporal bar, reminiscent of that of *Kistecephalus*. It seems unlikely that this little tuskless dicynodont is related to the large, tusked dicynodonts of the later Triassic.

The commonest fossil of the *Lystrosaurus* zone is *Lystrosaurus* itself and the closely related, possibly ancestral form, *Prolystrosaurus* (Haughton 1917). *Lystrosaurus* is known also from the Panchet Beds of India, and from Sinkiang, China. It is a very specialized dicynodont: the snout is elongated and downwardly directed, but the nostrils have remained dorsally placed and the orbits project somewhat above the level of the rest of the skull roof. These features, together with the fact that the carpus and tarsus are largely cartilaginous, have led many workers to suggest that *Lystrosaurus* was semi-aquatic, and that it was probably similar in habit to the modern hippopotamus.

As might be expected in a Basal Triassic genus, *Lystrosaurus* shows many features that are primitive when compared with the genera of the later Triassic. It is not surprising that, as pointed out recently by Cruickshank (1964), *Lystrosaurus* possesses all the features which Camp (1956) listed as to be expected in any ancestor to these later genera; it also has the relatively short temporal opening found in *Sinokannemeyeria* and its descendants. As stated by Camp (1956, p. 327): 'An ancestor of *Lystrosaurus* before the acquirement of aquatic specializations would perhaps have been close' to the line of ancestry of the later genera. It seems very unlikely, however, that any form showing the specialized aquatic features and thus meriting the name *Lystrosaurus* could have been actually ancestral to the later Triassic genera. *Lystrosaurus* may therefore be left, with *Prolystrosaurus*, in its own family the Lystrosauridae, as suggested by earlier writers; the poorly known Russian Lower Triassic genus *Rhadiodromus* (Efremov 1938, 1951) may also belong in this family.

The classification of the Triassic dicynodonts proposed above may be summarized as follows:

Family Lystrosauridae. *Prolystrosaurus* (Basal Triassic *Lystrosaurus* zone of South Africa); *ystrosaurus* (Basal Triassic *Lystrosaurus* zone of South Africa and China; Panchet formation of India); ? *Rhadiodromus* (Lower Triassic zone VI of European Russia).

Family Shansiodontidae. *Shansiodon* (Lower Triassic Er-ma-ying formation of Shansi, China); '*Dicynodon*' *njalilus* (Manda Beds of East Africa).

Family Kannemeyeriidae. *Sinokannemeyeria* and *Parakannemeyeria* (both from the Lower Triassic Er-ma-ying formation of Shansi, China); '*Kannemeyeria*' *vanhoepeni* and *Kannemeyeria* (both from the Lower Triassic *Cynognathus* zone of South Africa, the latter also from the Manda Beds of East Africa); *Ischigualastia* (Ischigualasto formation of Argentina); *Barysoma* (Santa Maria formation of Brazil); *Placerias* (Upper Triassic Lower Chinle formation of Arizona, U.S.A.).

Family Stahleckeriidae. *Stahleckeria* and *Dinodontosaurus* (both from the Santa Maria formation of Brazil).

Finally, one may briefly indicate the problem of the origins of the Triassic dicynodonts from the Upper Permian genera. It is possible that one of the tusked forms from the Upper Permian, such as *Aulacephalodon* or one of the many species of the vast 'genus'-assemblage *Dicynodon*, might be ancestral to one or both of the Triassic lineages. The Shansiodontidae are not dissimilar to these Permian forms, but none of the latter appear to show the very short temporal opening that is so characteristic of *Sinokannemeyeria* and its descendants.

THE AGES OF THE SOUTH AMERICAN TRIASSIC FAUNAS

Apart from dicynodonts, the vertebrate fauna of the Santa Maria formation of Brazil also contains gomphodont cynodonts, rhynchosaurs, pseudosuchians, all described by von Huene (1928, 1935–42), and a procolophonid (Price 1947). Dicynodonts, cynodonts, primitive rhynchosaurs and pseudosuchians are all found also in the *Cynognathus* zone fauna of South Africa, which is generally agreed to be of Scythian (Lower Triassic) age. However, the Brazilian representatives of all these groups include forms which are more advanced than those of the South African fauna. On the other hand, the Brazilian fauna does not include metoposaurid amphibians or phytosaurs, which are both known from the Norian faunas of Germany and North America, and it contains only one probable example of the saurischian dinosaurs, which form a prominent element in these Norian faunas. These facts indicate that the age of the Brazilian fauna is somewhere in the Carnian, Ladinian or Anisian, but any more accurate dating seems to be extremely difficult at present. The main difficulty lies in the absence of any Ladinian or Anisian vertebrate fauna in the northern hemisphere, while even the Carnian Schilfsandstein and Gipskeuper of Germany have a terrestrial vertebrate fauna restricted to a few pseudosuchian or saurischian fragments. Since it is therefore impossible to date the South American deposits by a comparison of their overall fauna, one can only attempt a dating based on the possible significance of the individual components of the fauna and of their relative abundances.

Romer (1960) has argued that rhynchosaurs are essentially a Middle Triassic group, since they are not found in the Upper Triassic Keuper beds of Germany. As Romer admits, rhynchosaurs are also present in the Keuper sandstones of Great Britain, but he suggests that these may be of Lower Keuper (Carnian) age and that the rhynchosaurs had become extinct before the time of the more richly fossiliferous Upper Keuper (Norian) deposits of continental Europe. However, the British rhynchosaurs are found with pseudosuchians such as *Stagonolepis*, which is extremely closely related to *Aëtosaurus* of the German

Norian Stubensandstein (Walker 1961). Furthermore, a rhynchosaur is also known from India, where it is associated with a metoposaurid amphibian, a phytosaur and with fragments that may belong to coelurosaurian and prosauropod saurischians; this fauna appears to be of Carnian to mid-Norian age (Jain, Robinson & Chowdhury 1964).

The distribution of the rhynchosaurs in time and space is thus far from clear.* (Their recent discovery in Nova Scotia (Baird 1962) may be noted here.) It might be suggested that the rather poor nature of the terrestrial vertebrate fauna of the German Lower Keuper may explain the absence of the group from these beds, and that the presence of the group in the mid-Norian Maleri beds of India might be explained as a relict phenomenon, the group persisting in an Indian continent which appears at that time to have been still in a more southerly and perhaps isolated position than it is today. However this may be, it cannot be denied that the rhynchosaurs persisted into Carnian times, and their occurrence in the South American beds therefore does not restrict these beds to an Anisian or Ladinian age.

Colbert (1963, p. 252) states that 'all available evidence would seem to indicate that the saurischian dinosaurs did not arise from their pseudosuchian ancestors until the beginning of late Triassic time'. He therefore believes that the presence of saurischians in the Brazilian beds indicates that these must be of Carnian age. However, much of the archosaurian material, both from Brazil and from the deposits of Carnian age in Germany, is so fragmentary that it is often impossible to be sure whether it is pseudosuchian or saurischian in nature. It is therefore difficult to be certain as to just how varied the saurischians had already become in Carnian times, and correspondingly difficult to estimate what length of previous history the group must have had prior to the Carnian. If Colbert's opinion is nevertheless accepted, it would indicate a Carnian age for the Ischigualasto deposits, from which Reig (1963) has described a carnosaurian and two genera of coelurosaurian saurischians. Such an Upper Triassic date for this fauna is also supported by the presence of a pseudosuchian, *Aetosauroides*, which Casamiquela (1961) considers to be closely related to *Aëtosaurus* from the Norian of Germany.

Comparison of the Argentinian and Brazilian faunas shows several differences (See table 3). First, no genera are known to be common to the two areas; since the areas are on the same continent and not a great distance apart, this suggests that they may be of somewhat different age. Secondly, the faunas are slightly different in composition: the only certain saurischian from Brazil is that reported, but not yet described, by Colbert (1963), while the Brazilian fauna also contains more genera of pseudosuchians and dicynodonts than the Argentinian fauna. Though these may merely be due to chance or to ecological factors, it may be significant that these differences are all just what would be expected if the Brazilian fauna were earlier than the Argentinian fauna. This is supported by the cynodonts, Bonaparte (1962) having concluded that *Exaeretodon* from Argentina is more advanced than the Brazilian cynodonts. The Brazilian dicynodonts do not help in this respect; though

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* The rhynchosaurs seem to be particularly sporadic in occurrence. For example, they are found in one of the three Brazilian localities (Santa Maria), where dicynodonts are not found, but are absent from the other two localities (Chiniquà, Candelaria), where dicynodonts are found instead. It is possible that the explanation lies in the rhynchosaurs having had a rather narrow ecological preference, as is also suggested by their extremely specialized jaws and teeth.

Dinodontosaurus has, for example, a rather primitive pectoral girdle, *Barysoma* does not appear to be very different from the Argentinian genus *Ischigualastia*.

TABLE 3. TRIASSIC REPTILIAN FAUNAS OF EAST AFRICA AND SOUTH AMERICA

	East Africa	Brazil	Argentina
Procolophonids	—	*Candelaria*	—
Rhynchosaurs	*Stenaulorhynchus*	*Scaphonyx*	Gen. indet.
Pseudosuchians	*Teleocrater*, *Stagonosuchus*, *Mandasuchus*, *Parringtonia*	*Hoplitasuchus*, *Rauisuchus*, *Rhadinosuchus*, *Prestosuchus*, *Procerosuchus*, *Spondylosoma*, *Cerritosaurus*	*Aetosauroides*, *Argentinasuchus*, *Saurosuchus*, *Cuyosuchus*
Saurischians	—	Gen. indet. (*fide* Colbert 1963)	*Triassolestes*, *Ischisaurus*, *Herrerasaurus*, gen. indet.
Crocodilians	Gen. indet.	—	*Proterochampsa*
Dicynodonts	*Kannemeyeria*, '*Dicynodon*' *njalilus*, gen. indet.	*Stahleckeria*, *Dinodontosaurus*, *Barysoma*	*Ischigualastia*
Cynodonts	*Aleodon*, *Scalenodon*, *Cricodon*, *Theropsodon*, cf. *Gomphodontosuchus*	*Gomphodontosuchus*, *Chiniquodon*, *Belesodon*, *Traversodon*	*Exaeretodon*, *Colbertosaurus*, gen. indet.

If the Brazilian fauna is now compared with that of the Manda Beds of Tanganyika, East Africa, rather more pronounced differences can be seen. No saurischians at all have been found, though some of the pseudosuchians are quite advanced. Most significant, however, is the presence of *Kannemeyeria*, a dicynodont that is otherwise typical of the Lower Triassic *Cynognathus* zone of South Africa, and the dicynodonts certainly appear to be more primitive than those of Brazil.

The presence of *Kannemeyeria* suggests that the Manda Beds may be of immediately post-Lower Triassic, i.e. Anisian, age. This would in turn suggest that the Brazilian fauna, which seems to be younger than that of East Africa but older than that of Argentina (which has above provisionally been assigned to the Carnian) might conveniently be considered as Ladinian in age.

A fauna which includes dicynodonts, gomphodont cynodonts and archosaurs has also been discovered recently in the Ntawere Beds of Northern Rhodesia (Drysdall & Kitching 1963). This fauna may also be of Anisian age. However, rhynchosaurs are not at present known from these beds; if their absence is confirmed after more extensive collecting, it would suggest that the beds were older than the Manda Beds of Tanganyika, possibly of uppermost Lower Triassic age. Alternatively, the absence of rhynchosaurs might be merely ecological.

Though they had previously been considered non-fossiliferous, a few specimens of gomphodont cynodonts have now been found in the Molteno Beds of Basutoland, South Africa (Boonstra 1947; Crompton & Ellenberger 1957). This fauna is therefore comparable in age with those discussed above but, until other elements of the fauna are discovered, its age cannot be more closely determined.

The evidence on which the above datings have been suggested is indirect, since the standard German sequence does not provide any Middle Triassic terrestrial fauna with which these faunas might be compared, neither can they be related to the ammonite zones of the French Alpine sequence. The datings must therefore be regarded as provisional. The case for a difference in age between the faunas of East Africa, Brazil and Argentina is somewhat stronger than the evidence for distributing them among the Carnian, Ladinian and Anisian. For example, if the saurischians evolved from the Pseudosuchia earlier than the beginning of the Carnian (and the advanced nature of some of the Manda pseudosuchians makes one suspect that this might well be true), then these three faunas might be placed within a shorter time-span, i.e. within the Ladinian and Anisian. It might further be suggested that the differences between the faunas of East Africa and Brazil resulted from the fact that these faunas were on different continents, that of Africa being for some reason rather more conservative than that of South America. In this case the East African and Brazilian beds might both be regarded as Ladinian, while that of Argentina would be placed in the Anisian. The recent advances in geological fields such as palaeomagnetism and the study of the pattern of the oceanic ridge-system, have given a new respectability to the concept of continental drift. This drift is envisaged as having begun in the Mesozoic and, though it is still uncertain exactly when the separation of Africa and South America began to take place, Creer (1964) has recently suggested that it may have begun in the Upper Permian.

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List of the abbreviations of the names of bones, as used in the figures

A	angular
ART	articular
AST	astragalus
BO	basioccipital
CAL	calcaneum
CL	clavicle
CO	coracoid
D	dentary
ECT	ectopterygoid
EO	exoccipital
EPT	epipterygoid
F	frontal
FB	fibula
ICL	interclavicle
IL	ilium
IP	interparietal
IS	ischium
J	jugal
L	lachrymal
MX	maxilla
N	nasal
OP	opisthotic
P	parietal
PAL	palatine
PCO	precoracoid
PMX	premaxilla
PO	postorbital
POF	postfrontal
PP	preparietal
PRF	prefrontal
PRO	prootic
PSP	parasphenoid-basisphenoid complex
PT	pterygoid
PU	pubis
Q	quadrate
QJ	quadratojugal
RD	radius
RDL	radiale
SA	surangular
SC	scapula
SMX	septomaxilla
SO	supraoccipital
SQ	squamosal
STA	stapes
STM	sternum
T	tabular
TB	tibia
UL	ulna
ULR	ulnare
V	vomer