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A NEW METOPOSAURID AMPHIBIAN FROM THE UPPER TRIASSIC MALERI FORMATION OF CENTRAL INDIA

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[Plates 1 to 3]

CONTENTS

Improved methods of collection have led to the discovery of much better amphibian fossils from localities in the Upper Triassic Maleri formation of the Pranhita Godavari Valley. Some preliminary observations regarding the Maleri sediments and their relationship with the overlying and underlying rocks are noted.

A composite restoration of the skull is given. The pattern of the dermal roofing bones, the shape of the skull and the position of the orbits clearly indicate that the material belongs to a metoposaurid amphibian. A new metoposaur species, *Metoposaurus maleriensis* is proposed and a description is given of its skull, braincase and palate. The presence of a prominent additional nasal bone on each side, exposed on the skull roof in one of the skulls of *M. maleriensis* and its absence in other skulls of this metoposaur is noted and the possible explanation for this condition is put forward. The position of the orbits varies according to the size of the skull; a comparison is made between the two more complete specimens to show that the orbits are more posteriorly placed in larger skulls. It is suggested that this difference in orbital position is probably due to the relative rate of activity of two zones of intensive growth in the skull, anterior and posterior to the orbits.

Postcranial material includes three clavicles, interclavicle, humerus, ischium and eight intercentra including that of an atlas. These have also been assigned to *M. maleriensis* on the basis of close association and osteological characters.

Study of the Maleri metoposaur and its comparison with the other adequately known genera, *Metoposaurus* from the Keuper of Europe and '*Eupelor*' from the Upper Triassic of North America, has demonstrated the weak foundation on which metoposaur genera are based. The position of the lacrimal bone has been used as one of the main morphological characters distinguishing between the previously recognized metoposaur genera. However, this character is variable within a subspecies recognized by Colbert & Imbrie, which suggests caution in its use in distinguishing between genera. The recognition of this feature further emphasizes the extremely close similarity between the metoposaur genera, already commented on by previous authors. The suggestion is made that these genera are morphologically indistinguishable and a revised taxonomy of the metoposaurs is put forward.

The upper and lower stratigraphic limits of the metoposaurs are examined, and it is found that the metoposaurs are restricted to horizons equivalent to Carnian and Norian. The fauna associated with the metoposaurs in different parts of the world is discussed, and it is concluded that the age of the Maleri fauna is not younger than Middle Norian and probably not older than Carnian.

INTRODUCTION

The Maleri formation, a member of the Indian Gondwana Group, occurs in the Pranhita–Godavari Valley and has long been known for its fish and tetrapod remains. Fossils were first discovered in 1856 by the Rev. Hislop (King 1881, p. 28), in red clays near the small village of Maleri. Hislop's collections, and those made subsequently, consisted of fragments and were described by Oldham (1859), Miall (1878), Lydekker (1885) and Huene (1940). The vertebrate fauna, as far as it is identifiable from the fragments available, has been reported in previous literature, and consists of the Dipnoan *Ceratodus*, three types of labyrinthodonts possibly Metoposauridae, *Paradapedon*, *Brachysuchus*, *Massopondylus* and Coelurosauria. A similar fauna is known from the Tiki beds, the Maleri equivalent in South Rewa, where *Massospondylus* and Coelurosauria are apparently absent but Pseudosuchian fragments are thought to occur.

The incomplete nature of the material representing the Maleri fauna has been reflected in the fact that, out of fourteen different forms noted by Huene (1940), only five have been named. Regarding the metoposaurid amphibians Romer (1947) noted that three types appear to be represented (Huene 1940), but the material is too fragmentary for systematic description. Colbert & Imbrie (1956) further noted that 'von Huene did not attempt to give these fossils (metoposaurs) a formal name, a sound decision in view of the incomplete nature of the fossils'. The reason for the incomplete nature of the fossils is that the collections were mainly made from surface accumulations and none were found *in situ*. An interesting feature of the Maleri fauna is the apparent association of metoposaurs and phytosaurs with rhynchosaurs. In all other localities known these forms do not occur together.

During 1958, and again in 1959, the Indian Statistical Institute despatched successive expeditions to the Maleri area under the guidance of Dr Pamela L. Robinson. A careful and systematic search by members of the party in the Maleris was rewarded by the discovery of better material *in situ*. The new fossil material consisted of partial skulls and shoulder girdles of a metoposaur and parts of a skull and associated postcranial skeleton of a rhynchosaur. Metoposaur and rhynchosaur specimens have been excavated within a few hundred yards of one another. No good material of the phytosaur has yet been found, but individual bones occur within a few hundred yards of the metoposaurs and rhynchosaurs. Judging by fragmentary material, which is more common, this homogeneous fauna extends right across the main outcrop of the Maleri formation.

The purpose of the paper is an attempt to study the metoposaurs of the Maleris on the basis of much better material available now; to attempt a reconstruction and a comparison with the metoposaurs well known from North America and Germany. In a concluding section the question of the age of the Maleri fauna, by a comparison of it with faunas known elsewhere in the world, will be considered.

Some observations on the Maleri formation

The Gondwana group of rocks of the Pranhita Godavari Valley

The Gondwana group consists of sediments deposited in a series of elongated troughs on an eroded land surface of pre-Cambrian rocks. Sedimentation commenced with a glacial boulder bed of probable Upper Carboniferous age, followed by a thick series of fluviatile and lacustrine deposits ranging in age from Permian to Cretaceous (Aptian). The present-day valleys of the rivers Pranhita and Godavari partly coincide with a much more ancient valley in which Gondwana group sediments accumulated (figure 1).

The only systematic geological work in this area was carried out by King (1881), who worked out the sequence of Gondwanas as follows:

Upper Gondwanas	Chikiala formation
	∼Unconformity∼
	Kota formation
	∼Unconformity∼
	Maleri formation
∼∼∼∼Unconformity∼∼∼∼	
Lower Gondwanas	Kamthi formation
	∼Unconformity∼
	Barakar formation
	∼Unconformity∼
	Talchir formation
	Unconformity
	Pre-Gondwanas

The Maleri formation

The Maleri rocks crop out mainly in the north-western part of the basin, as demarcated by the river Godavari in the south and the river Pranhita in the east (figure 2). The main exposures are around the village of Maleri, but they extend over an elongate strip of country with a N.W.–S.E. trend and about 40 miles long and between 4 to 10 miles wide. There are also two outlying exposures of the Maleri formation; one to the south and the other to the north of the main outcrop.

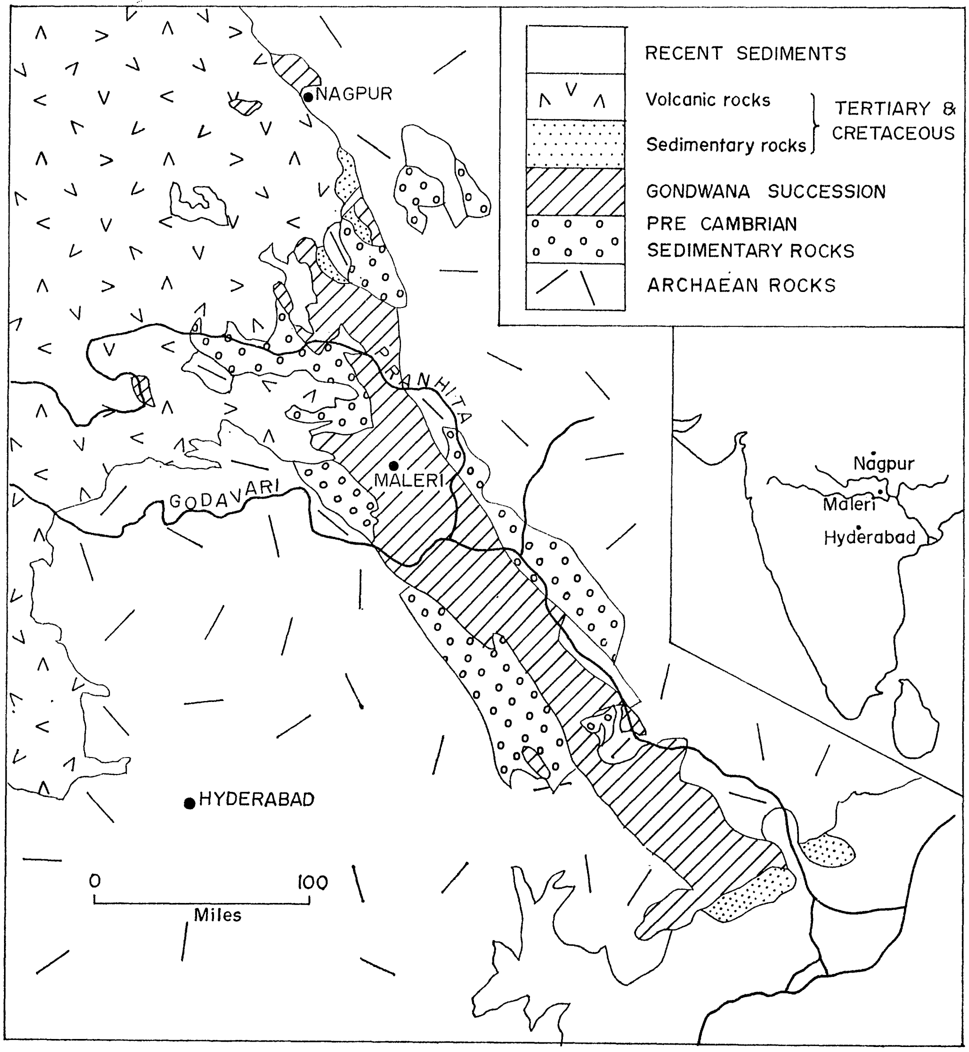

Figure 1. Inset, map of India to show the river Godavari and its tributaries, and the two principal towns in the region. Generalized geological map of the region of the river Godavari and its tributaries to show the lie of the Gondwana Group outcrop.

The Maleri formation is a series of variegated, light-coloured open textured and rather soft sandstones with intercalated broad bands and lenses of bright red and vermilion coloured clays. King (1881) gives a short description of this formation as it is seen around the village of Maleri:

'...there are bright red and vermilion-coloured clays, showing very rarely in sections, and then only poorly bedded and laminated. Generally these clays show merely as wide

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undulating fields of red clayey soil which has been smoothed down by weathering and cultivation.'

The nature of the Maleri lithology, the physiography of the area and its limited accessibility impart some difficulties in working out the geology properly. King (1881) observed that 'owing partly to the tendency of the Gondwana beds, and especially of the higher groups, to disintegrate at the surface and to form a thick mass of soil and subsoil, which

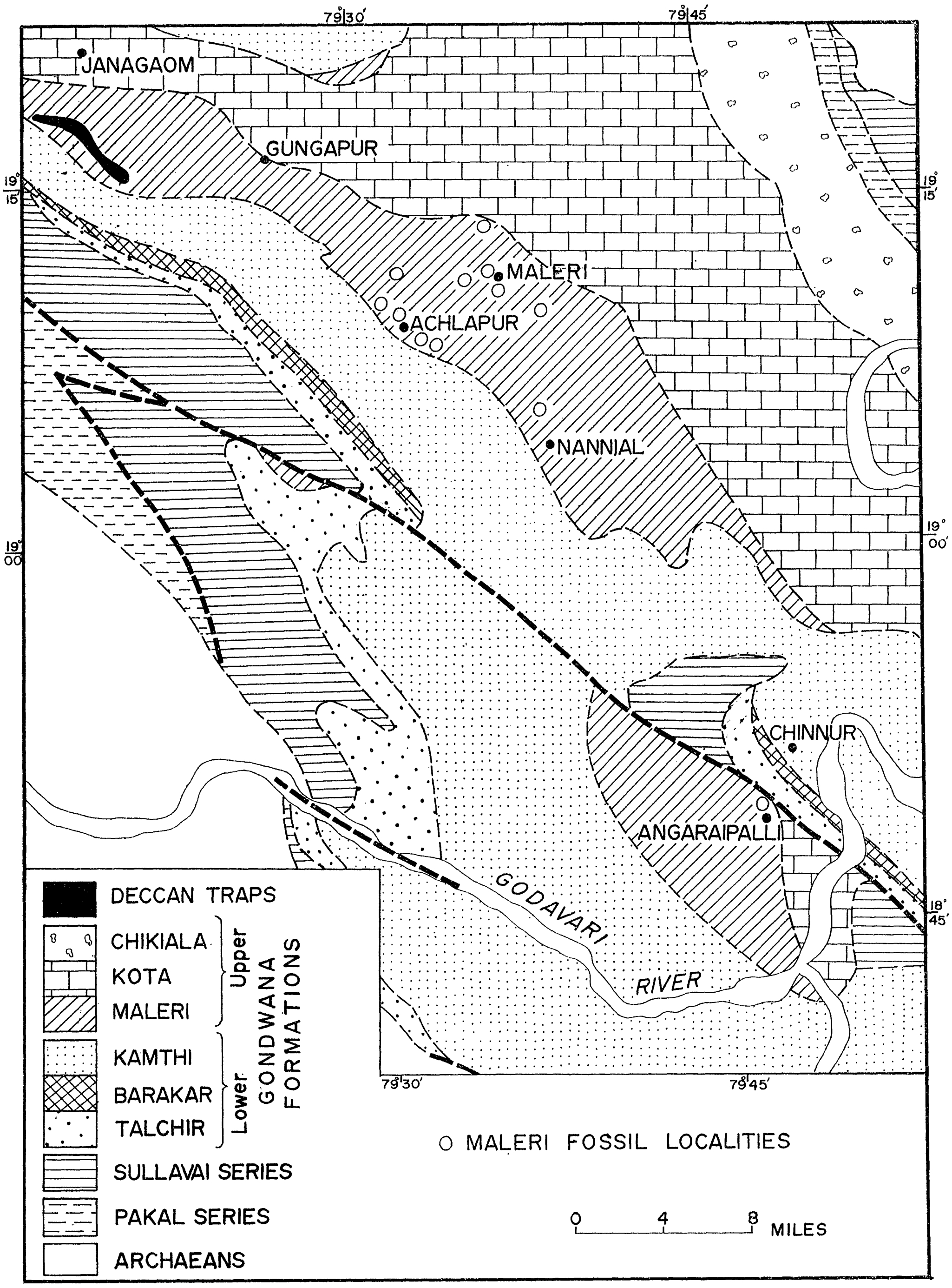


FIGURE 2. Geological map of part of the Pranhita Godavari Valley after King (1881) showing fossil localities.

conceals all the beds, partly to the flatness of the country—a circumstance in itself connected with the deficiency of hard bands of rock—partly to the existence of thick and widely spread deposits probably of fluviatile origin, and partly to the prevalence of forests, the tract of country around Maleri and Kota presents unusual difficulties....Even in the streams, it is very rare to find good and continuous sections; everything is masked and concealed by surface accumulation of sand, clay and gravel'.

Some new observations

During the Indian Statistical Institute expeditions, along with the palaeontological work, a few preliminary geological observations were made in the main Maleri area by Dr Robinson and the author, and are presented here pending a more detailed study of the Maleri formation.

The Kamthi/Maleri boundary

In the north-west part of the main outcrop, near its junction with the underlying Kamthis, the Maleris are mainly soft sandstones. The author has examined the Kamthi/Maleri boundaries best displayed in a few stream sections. In these small streams, the Maleris, occurring within a few yards of the brownish, well jointed Kamthi sandstones, are mainly pale coloured, white to pale green, unjointed sandstones of varying grain size. Occasionally clay galls are present in these sandstones. There is undoubtedly an unconformity between the Maleris and the Kamthis, as the Maleris are lapping round and baying in and out round a low ridge of Kamthi sandstone. There is no development of a conglomerate at the junction of the Maleris with the Kamthis. It seems probable that during the commencement of Maleri sedimentation, the topography of the region was more or less flat and the relief low enough not to lead to the formation of coarse clastics.

Lithology of the Maleris

North-east of the basal Maleri sandstones occurs a wide strip of red clays, usually structureless with streaks and patches of green. The most common variant within the red clays are impersistent beds of lime-pellet rocks. In these the calcareous concretions are commonly pale green or grey and vary in size from about a centimetre to a few millimeters in diameter. Sometimes they are well cemented together and may form a moderately hard rock up to 10 ft. thick, though of no great lateral extent. Often these rocks are current bedded; occasionally the clays also show current bedding. The mode of deposition of the line pellets is not in doubt, being obviously fluviatile. The process by which the pellets are formed is less obvious, but is under study and will be published in a separate paper by Dr Robinson. Lenses of soft white sandstone are not uncommon within the clays. Beyond the clay strip, farther north-east, the sandstones again appear to be the dominant rock types with subordinate clay. These sandstones can be recognized at once from their topographic expression as low ridges covered with scrub, but can best be seen in the stream sections. The sandstones invariably have a calcareous cement. Characteristically they contain a great number of small rounded galls of soft red clay. Sometimes they lack any gall or conglomerate content and are moderately fine grained and much current bedded. Further clay belts are seen around Maleri and extend northwards to the boundary with the overlying Kotas, with occasional ridges of sandstones.

In the south-eastern part of the basin, according to King, the bottom beds are yellow and red friable sandstones with purple sandy clay bands, and these gradually change upwards into dirtier beds with red and green clay-galls, slightly calcareous, until the more calcareous grey rubbly rock, with red and green clay galls, is reached. These last are not of any thickness, though there must be separate beds of 2 or 3 ft. Then the red clays come in, with gradually thinning bands of calcareous rocks. The relation between different rock types within the Maleris has always been difficult to ascertain. It has only been possible to obtain reliable dips in the Maleris from two places—both of them, however, point in the same direction—a few degrees east of north.

Although the Maleris mainly consist of sandstones and red clays with lime-pellet rocks, it has not been possible to work out a proper succession of different lithologies. Exposures are few in the area, and good sections are even fewer, but we were able to establish that there are no regular repetitions of sequence of the three main Maleri lithologies. It is not possible to trace any stratum as a persistent horizon to be used as a marker bed. On the other hand, the beds seem to die out after a distance giving the impression that the Maleris are mainly formed of superimposed lenses of varying dimensions. About half a mile west-south-west of the village of Maleri are red clays with abundant coprolites and above this comes a white sandstone forming a low ridge, and about 20 ft. thick at its greatest development, but which thinned off and disappeared westward within a 100 yards or so, leaving an unbroken succession of red clays. The impersistent nature of the lime-pellet rocks occurring within the red clays can be seen in a section not very far from the Maleri village. It is, therefore, difficult to make any estimate of the thickness of the Maleri formation, and, if the Maleris are cut-and-fill continental sediments such estimates would have little meaning.

Conditions of deposition of the Maleris

It is evident, from the lithology and also from the fauna and flora obtained from the Maleris, that we are dealing with a series of sediments deposited under fluviatile conditions. It is not difficult to conceive of a system of river valleys with a series of river beds with broad flood plains alongside, the sands being accumulated in the river beds themselves and the clays being deposited on the flood plains under quieter conditions. Current bedding measurements indicate that the general direction of drainage was from south to north. The nature and the relationship of the sediments suggest that the river bed or the series of river beds shifted from time to time.

Relationship with overlying Kota formation

The relationship of the Maleris with the overlying Kota formation is far from simple. Hughes (1877) included both Maleri and Kota in one geological unit. But in the opinion of King (1881), also supported by Cotter (1917) and Fox (1931), there is a stratigraphical and palaeontological break between the Maleri and Kota formations. King (1881) described, as Gungapur beds, a group of sediments which he included in the Kotas, but he regarded these beds as transitional to the latter from the Maleris. The Gungapur beds mainly consist of hard, massive, pale sandstones, stained brown down the well-developed joints, much current bedded and with thin beds of well-rounded pebbles. The pebbles, up to several centimetres in diameter, are of quartzite, quartz, chert and feldspar. Within the soft sandstones there are a few intercalated bands of hard brown or purple sandstones with a haematitic matrix which weathers black. There is also, near the top of the succession, a development of red and violet clays with greenish streaks. A single dip direction, a few degrees east of north, was obtained from the Gungapur sandstones. The north dip of the Maleri sandstones, and the continuation of the same in the Gungapur beds, suggests that the two are in conformity and the real relation between these two rock units may be from south to north. Previously, the Maleris have been regarded as younging from south-west to north-east. This is because the overlying Kotas contain three bands of well-bedded limestone which seem to be striking north-west/south-east. The Gungapurs, whether or not they prove to be conformable with the Maleris, differ from the latter in the complete absence of clay galls in the sandstones, in the presence of a large number of well-rounded pebbles, in the lack of any bands of lime-pellet rock so characteristic of the Maleris, and in the complete absence of vertebrate fossil remains in the red clays. Therefore, there are reasons to regard the Gungapur beds of King, although they may be in conformity with the Maleris, as a unit distinct from the latter, probably belonging to a slightly different facies.

A REVIEW OF THE PREVIOUS WORK ON METOPOSAURID AMPHIBIANS

The metoposaurid amphibians are known exclusively from the upper Triassic rocks of distantly separated countries of the world. They are known from the Keuper of Germany and Austria, the upper Triassic of eastern and western North America and from the upper Triassic of central India. There are reports of their occurrences in the Rhaetic of Bristol in Great Britain and in the Triassic of China, but such reports are based on fragments and lack confirmation.

The earliest mention of metoposaurid amphibians dates back to 1842, when von Meyer (1842) described the dorsal view of the skull roof of a labyrinthodont from the Keuper Schilfsandstein of Feuerbacher Haide near Stuttgart. Subsequently, von Meyer (1844, 1855) dealt with the same specimen in greater detail and attempted a reconstruction of the skull roof. Von Meyer (1842) named the specimen *Metopias diagnosticus*, the type for the genus *Metopias*.

Miall (1874) gave a complete reconstruction of the skull roof showing the sensory canals. His figure was based on a specimen in the British Museum which came from the Keuper Schilfsandstein of Feuerbacher Haide, near Stuttgart.

Fraas (1889) got hold of an excellent collection from the Schilfsandstein of Hühnerdiehaide, Hanweiler and Feuerbacher Haide, all near Stuttgart. Fraas had at his disposal four skulls (including von Meyer's type), one of which was associated with several vertebrae and the thoracic armour, a scapula, a humerus and a few isolated vertebral intercentra. The entire lot was designated as *M. diagnosticus*. All the material described by von Meyer and Fraas is in the Stuttgart Museum except the articulated specimen from Hanweiler, which is in Tübingen University. Lydekker (1890) renamed the genus *Metoposaurus*, the name *Metopias* not being valid owing to preoccupation. Watson (1919), on the basis of the skull specimen in the British Museum, reconstructed the occiput and the palate, his reconstruction differing in detail from that given by Fraas.

Besides the type species, Fraas (1913) described *Metoposaurus stuttgartensis* from the Keuper Lehrbergstufe of Sonnenberg, near Stuttgart. His description was based on an interclavicle and the left clavicle, some ribs and vertebrae, now in the Stuttgart Museum. Koken (1913) also described *M. santaecrucis* from the middle Keuper Raibl beds of south Tyrol, Austria. His description is based on a partial skull of small size found in a locality north of Heiligenkreuz, now in the University Museum of Tübingen. Lastly, Kuhn (1932) described *M. heimi*, known from a complete skull from the middle Keuper Blasensandstein near Ebrach in Upper Franconia. The specimen is now in the Museum of Palaeontology and Historical Geology, Munich. The only other European genus, known from rather poor material from the lower Keuper Lettenkohle of Kölleda, Germany, is *Trigonosternum latum*, described by Schmidt (1931). The form is known only from an incomplete interclavicle, now in the University collection of Jena.

The first fossil metoposaur from North America was discovered by Emmons in 1854, from the Upper Triassic Newark Group of North Carolina in the Appalachian region. The specimen was described by Leidy (1856) as *Dictyocephalus elegans*, but was based on rather fragmentary material consisting of a partial skull roof, showing the parietal foramen and part of the right otic notch. Cope (1866) described some teeth and two girdle bones (which he thought of as 'portions of two crania') from the Newark Group of eastern Pennsylvania as belonging to *Mastodonsaurus durus*, but two years later (Cope 1868) he assigned the material to a new metoposaur genus *Eupelor*, the type being *M. durus*. Later Cope (1869) again reconsidered *Eupelor durus* and came to the conclusion that the teeth should not be assigned to *E. durus* but rather to the Thecodontia. Von Huene (1921) re-examined the specimens and restricted *E. durus* to a tooth, a left clavicle and an interclavicle; the rest of the material was reaffirmed as belonging to Thecodontia. All the specimens mentioned in the above paragraph are now in the American Museum of Natural History.

Lucas (1904) described an interclavicle from the upper Triassic Chinle formation of north-east Arizona (located 5 miles east of Tanner's Crossing, Little Colorado river), now in the United States National Museum, which he referred to as *Metoposaurus fraasi*; the name, however, was discarded by Branson & Mehl (1929) in favour of *Kalamoiketor* (?) *fraasi*. Branson (1905) described the material collected by the University of Chicago field party from the upper Triassic Popo Agie formation of Wyoming. The collection included fragments of vertebrae, 'breast plates', ribs, limb bones and a few complete skulls. On the basis of the skulls Branson established a new metoposaur genus *Anaschisma* with two species, *A. browni* and *A. brachygnatha*. These fossils are catalogued in the Chicago Museum of Natural History. Subsequent collections were made from the upper Triassic Popo Agie formation of Wyoming and from the upper Triassic Chinle formation of Arizona. All these collections are now in the University of Missouri Vertebrate Palaeontology collection. Branson & Mehl (1929) made a study of these metoposaurids, which, besides the reconsideration of the previously known *Anaschisma*, led them to establish three new genera. They are (i) *Koskinonodon* from the Popo Agie formation; the type and only species *K. princeps* is based on a skull. To this genus is also assigned an interclavicle, a clavicle, and an ilium. (ii) *Borborophagus*, from the Popo Agie formation; the type for the genus is *B. wyomingensis*, known from a skull, a clavicle, an interclavicle and three vertebrae. Another interclavicle somewhat larger in size, has been assigned to *Borborophagus* sp. (iii) *Kalamoiketor*, from the Chinle formation; the type for the genus is *K. pinkleyi*, based on the posterior half of a skull. The only other species of this genus is *K.* (?) *fraasi*, based on an interclavicle described by Lucas (1904) as *Metoposaurus fraasi*.

Another North American metoposaur genus *Buettneria* has mainly been described by Case (1922, 1931, 1932). Most of these materials were collected from the upper Triassic Dockum formation of Texas.

The genotype *B. perfecta* is known from a complete skull, clavicles, interclavicles and a few other fragmentary post cranial elements. The other well-known species is *B. bakeri*, which is also known from a skull, clavicle, interclavicle and a femur. A less well-known species, *B. jonesi*, is only based on associated clavicles and interclavicles. Branson & Mehl (1929) described a right clavicle and a vertebral centrum from the Chinle formation as *B.* (?) *major*. Most of the material of *Buettneria* is in the museum of Palaeontology, University of Michigan. Wilson (1941) gave an excellent description of the cartilages and other soft parts of the skull of *Buettneria*. Sawin (1945) described *B. howardensis* from a collection made from the Dockum beds of Howard county, Texas. The material consisted of cranial and postcranial elements which enabled Sawin to reconstruct the skull in detail and the complete animal in general. The specimens are now in the University of Texas Museum. Besides these more or less well-known forms, Sinclair (1917) described one left mandibular ramus from the upper Triassic Newark group of Buck county, Pennsylvania as a new metoposaur, *Calamops paludosus*. The specimen is in the Museum of Princeton University.

There are excellent collections of metoposaur remains in the Museum of Comparative Zoology at Harvard from the Chinle formation of New Mexico, which according to Romer (1939), belong to *Buettneria perfecta*. A large block containing several skulls and postcranial parts from the same locality is in the United States National Museum. The last collection on record was made in 1954 from Potter county, Texas (Colbert & Imbrie 1956) which yielded a series of skulls, jaws and postcranial parts. These fossils are now housed in the University of Canyon.

Colbert & Imbrie (1956) made a review of the Triassic metoposaurid amphibians, especially those from North America. In their study, the validity of most of the metoposaur genera, known from North America, was questioned. Their biometric study of North American metoposaurs suggested the following taxonomy:

Dictyocephalus Leidy 1856.
  Dictyocephalus elegans Leidy 1856,

    Newark Group, North Carolina.
  Eupelor, Cope, 1868
  Eupelor durus (Cope) 1868 Pennsylvania New Jersey.
    Probable Synonym: *Calamops paludosus* Sinclair 1917.

  Eupelor fraasi fraasi (Lucas) 1904, Chinle formation, Arizona, New Mexico, Utah.
    Synonyms: *Buettneria major* Branson & Mehl 1929.
      Kalamoiketor pinkleyi Branson & Mehl 1929.

Eupelor fraasi jonesi (Case) 1922, Dockum formation, Texas.
Synonyms: *Buettneria perfecta* Case 1922.
Buettneria bakeri Case 1931.
Buettneria howardensis Sawin 1945.

Eupelor browni (Branson), 1905, Popo Agie formation, Wyoming.
Synonyms: *Anaschisma brachygnatha* Branson 1905.
Koskinonodon princeps Branson & Mehl 1929.

The earliest study on metoposaurs in India was made by Lyddeker (1882) when he figured a discoidal vertebral intercentrum from the Maleri beds of Central India, which he regarded as affording evidence of the existence of a laybrinthodont with fully ossified vertebrae in the Maleri beds. A few years later the same author (1885) described a fragment of the right maxilla from the Tiki beds, one right squamosal (supratemporal) from the Maleris, along with a few other cranial and mandibular fragments, which he regarded as being very similar to *Metoposaurus* and *Capitosaurus*. Huene (1940) described some more rather fragmentary material from the Maleris and Tikis, and realized their undoubted similarity to the metoposaurs. Three types appeared to be represented, but the material was 'too fragmentary for systematic description'. All the fossils are housed in the Indian Museum at Calcutta, excepting a few pieces which are in the British Museum (Natural History).

THE MATERIAL AND METHOD OF COLLECTION

The nature of the fossils and methods of collection

The Maleri terrain is undulating country, the sandstones forming the low wooded ridges and the clays forming broad valleys where small rivulets meander through the paddy and millet fields, occasionally exposing the clays. The sandstones are usually barren of vertebrate remains. Fossils are mainly found in the clays and occur throughout the red clay belts. Since 1856 many collectors, mainly from the Geological Survey of India, have made collections from this area. The method of collection adopted by previous collectors can be found in King's (1881) descriptions:

'Virapa, the native sent down by Mr Hislop in the first instance, must have made a clean sweep of this remarkable field, working as he did over untrodden ground. We only came a few years later, before there had been time for fresh accumulations to be gathered to any extent in the gullies or on the fields; nevertheless, thanks to a novel mode of beating across these fields with his men in a long line at a few yards from each other, Mr Hughes managed to pick up many good things and, only a few months later, when we went over the same ground together on a similar beat, our search was rewarded with some teeth of *Ceratodus*, and some fine bones of a parasuchian crocodile'. The kind of result obtained by such methods quoted above is well illustrated by remarks made by von Huene (1940) in his monograph:

'The preservation of the material is not satisfactory as it mostly consists of fragments and small pieces collected on the surface and not *in situ*. Some of the fragments were adjacent, and were joined together at Tübingen, but others, being isolated, could not be so treated.'

During recent expeditions, attention was given to actual exposures of the clays rather than to the ploughed fields. Such exposures occur mainly on the slopes of slight rises and ridges, the latter produced by the presence of underlying sandstone lenses. The ground is cut by stream courses, usually dried up during winter. Careful search in the unploughed waste grounds and gullies on these ridge-slopes was rewarded by the discovery of more complete specimens than any found hitherto. Quite a few of the specimens were excavated *in situ* from the clays by standard palaeontological techniques. Some of the specimens were collected from the surface but not far removed from their places of actual occurrence. Bone fragments scattered over a limited area on a particular slope were carefully collected and it was found that the pieces belonged to one particular fossil skull or skeleton which was just in the process of disintegration. These fragments were then fitted together like the pieces of a jig-saw puzzle. One of the skull specimens thus assembled consists of forty-five separate bone pieces (figure 3 and plate 1). The specimens collected came, mainly, from the red clays (localities on figure 2) and they were washed and prepared in the laboratory by mechanical means.

List of specimens of metoposaurs

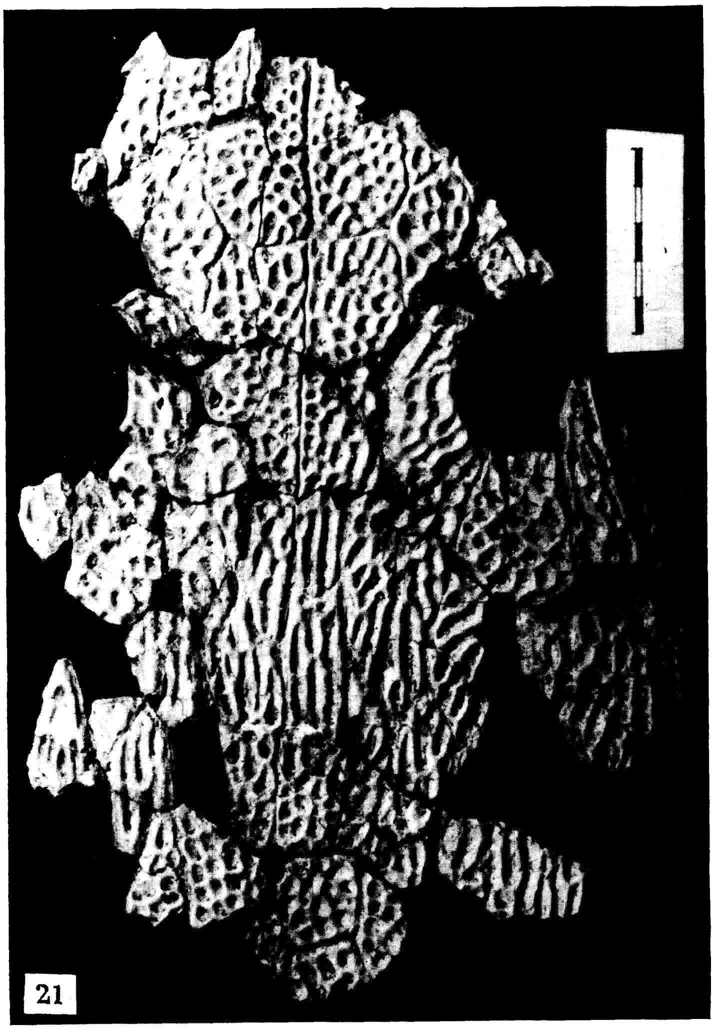
A complete list of the best of the new metoposaur specimens, connected with the present study, together with the localities from which they were collected, is given below. Gampalpalli is the circle immediately north-west of Achlapur shown in figure 2.

specimen number	nature of the specimen	locality	figure and plate no.
I.S.I. A. 1	part of a skull	Achlapur No. 2	figure 14
I.S.I. A. 2	part of a skull	Achlapur No. 2	
I.S.I. A. 3	part of a skull	Achlapur No. 2	figure 5
I.S.I. A. 4	part of a skull	Achlapur No. 2	figure 3; figure 21, plate 1
I.S.I. A. 5	left squamosal	Achlapur No. 2	figure 6
I.S.I. A. 6	part of a skull	Achlapur No. 2	figure 8
I.S.I. A. 7	part of a skull	Achlapur No. 1	figures 7 *a–c*; figure 22, plate 1
I.S.I. A. 8	part of a skull	Gampalpalli	figure 4
I.S.I. A. 9	interclavicle	Achlapur No. 2	figure 19
I.S.I. A. 10	left clavicle	Achlapur No. 2	
I.S.I. A. 11	left clavicle	Achlapur No. 1	figures 23, 24, plate 2
I.S.I. A. 12	right clavicle	Gampalpalli	figure 18; figure 25, plate 2
I.S.I. A. 13	atlas vertebra	Achlapur No. 2	figure 28, plate 3
I.S.I. A. 14	four vertebrae	Achlapur No. 2	figures 29–34, 37–42, plate 3
I.S.I. A. 15	three vertebrae	Achlapur No. 1	figures 35, 36, 43, 44, plate 3
I.S.I. A. 16	right ischium	Achlapur No. 2	figure 20
I.S.I. A. 17	left humerus	Achlapur No. 2	figures 26, 27, plate 2

RESTORATION OF THE SKULL

Introductory

The specimens listed above were collected mainly from the lower part of the Maleri formation and the three main localities of their provenance fall within the same stretch of the clays and are separated from each other by a distance of less than 4 miles. The more complete specimens of the skull indicate their undoubted metoposaurid affinity from the position of the orbits and the extreme flatness of the skulls, and those specimens which lack orbits have a sculpture and suture pattern very similar to the more complete skulls. But there is a noticeable variation in the size of the orbits and in the antorbital part of the



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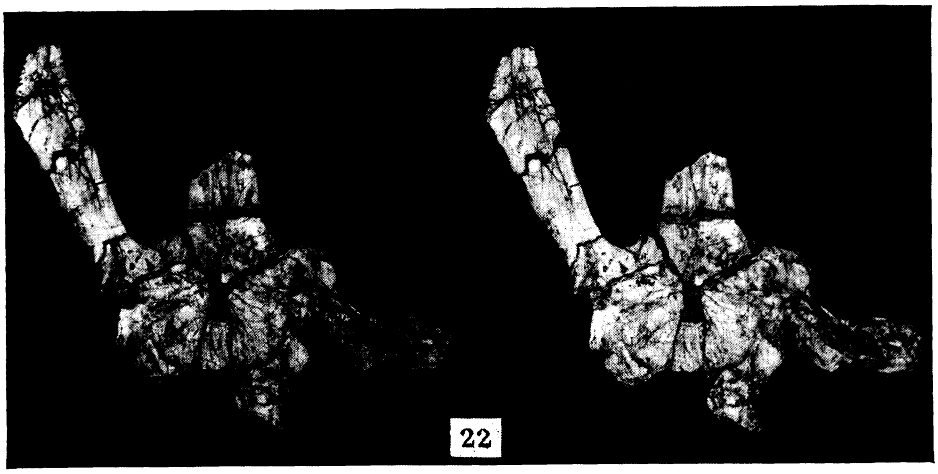

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Metoposaurus maleriensis n.sp.

FIGURE 21. Part of the skull roof in dorsal view, showing the right orbit, a part of the left orbit and external naris, slime canals, ornament, pineal foramen, and sutures demarcating many of the bones. Holotype specimen I.S.I. A. 4. × $\frac{1}{5}$.

FIGURE 22. Dorsal surface of part of the palate, and floor of the braincase. Specimen I.S.I. A. 7. × $\frac{1}{2}$.

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Metoposaurus maleriensis n.sp.

Figure 23. Dorsal view of clavicle I.S.I. A. 11. ×$\frac{1}{3}$.

Figure 24. Ventral view of clavicle I.S.I. A. 11. ×$\frac{1}{3}$.

Figure 25. Dorsal view of clavicle, cleithral spine incomplete. I.S.I. A. 12. ×$\frac{1}{3}$.

Figure 26. Dorsal view of humerus I.S.I. A. 17. ×$\frac{2}{3}$.

Figure 27. Ventral view of humerus I.S.I. A. 17. ×$\frac{2}{3}$.


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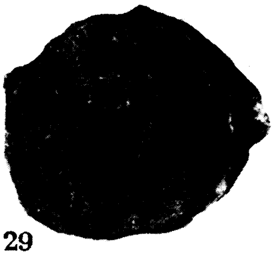
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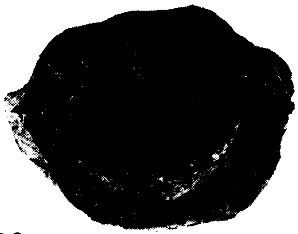
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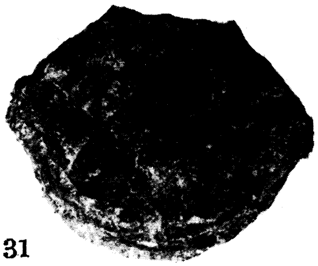
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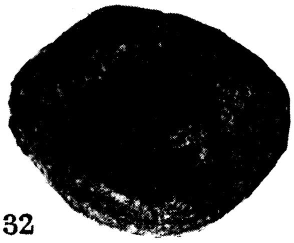
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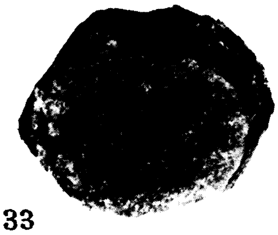
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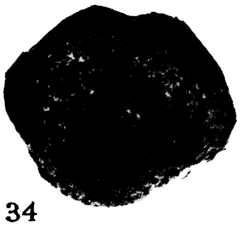
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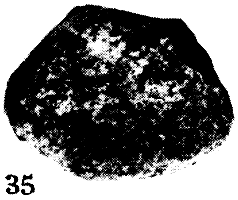
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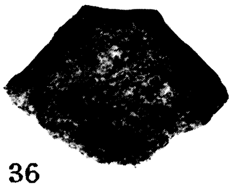
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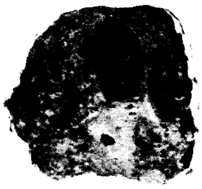
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Metoposaurus maleriensis n.sp.

FIGURE 28. Anterior view of the incomplete atlas intercentrum I.S.I. A. 13. × $\frac{2}{3}$.

FIGURES 29 TO 34. Anterior views of six dorsal intercentra I.S.I. A. 14*a*, *b*, *c*, *d*, and I.S.I. A. 15*a*, *b*. All × $\frac{2}{3}$.

FIGURES 35 AND 36. Anterior views of two caudal intercentra I.S.I. A. 15*c*, *d*. × $\frac{2}{3}$.

FIGURES 37 TO 42. Left lateral views of six dorsal intercentra I.S.I. A. 14*a*, *b*, *c*, *d*, and I.S.I. A. 15*a*, *b*. × $\frac{2}{3}$.

FIGURES 43 AND 44. Left lateral views of two caudal intercentra I.S.I. A. 15*c*, *d*. × $\frac{2}{3}$.

skulls, which must be either due to the different growth stages each individual represents within a species or due to the presence of more than one genus and species of metoposaurs. It is not possible to study in detail whether the variation due to growth among individuals is intraspecific, interspecific or intergeneric with such a small number of complete specimens. The difficulty can be overcome by considering the distribution of metoposaur species in areas where they are known from a large number of specimens. In North America, no less than eight genera and fourteen species of metoposaurs have been erected on specimens from Upper Triassic horizons. The close similarity between all these forms led Romer (1947) to comment that 'there is little reason to believe that these forms are all generically distinct'. Three genera were described (Bransen & Mehl 1929) from the Popo Agie formation of Wyoming and Romer (1947) again gave the opinion that 'it is none too probable that three genera (*Anaschisma*, *Borborophagus* and *Koskinonodon*) existed at the same time in Wyoming.' Subsequently Colbert & Imbrie (1956) came to the conclusion, after an extensive revision which included biometric study, that the variation within the North American metoposaur skull specimens is intrageneric, and that the metoposaurs from North America belong mainly to a single genus and three species, each occupying a distinct geographical area.

It can therefore be assumed that the Indian metoposaurs, collected from such a small area of the Maleri formation, must have formed part of a geographical and taxonomic unit and that the variations noted among them are intraspecific. The reconstruction of the skull and description which follows is based on this assumption that we are dealing with a single genus and species.

Composite restoration

The new Maleri metoposaur skull specimens, though incomplete, together provide fairly complete information about the skull. By combining all the specimens, and making corrections for size differences, it is possible to make a composite restoration.

Dorsal view of the skull (figure 9)

Five skull specimens were most useful for restoration of the dorsal view of the skull.

1. Specimen I.S.I. A. 4 (figure 3; figure 21, plate 1).
2. Specimen I.S.I. A. 8 (figure 4).
3. Specimen I.S.I. A. 3 (figure 5).
4. Specimen I.S.I. A. 5 (figure 6).
5. Specimen I.S.I. A. 7 (figure 7).

For the purpose of reconstruction of the dorsal view of the skull, specimen I.S.I. A. 4 has been taken as the master specimen because it shows many important skull features, such as the orbit, nostril and parietal foramen. The orbits and the posterior border of the left nostril can be fixed without difficulty. To complete the skull margin, specimen I.S.I. A. 8 was reduced to the same size as specimen I.S.I. A. 4 by matching the suture and lateral line pattern behind the orbits which the two specimens have in common.

The size difference between the two specimens does not seem to impair the correctness of reconstruction for the following reasons.

1. Specimen I.S.I. A. 8 is not very much larger than specimen I.S.I. A. 4.
2. Features like the lateral line canals and suture lines matched up fairly well when the two specimens were brought to the same scale.

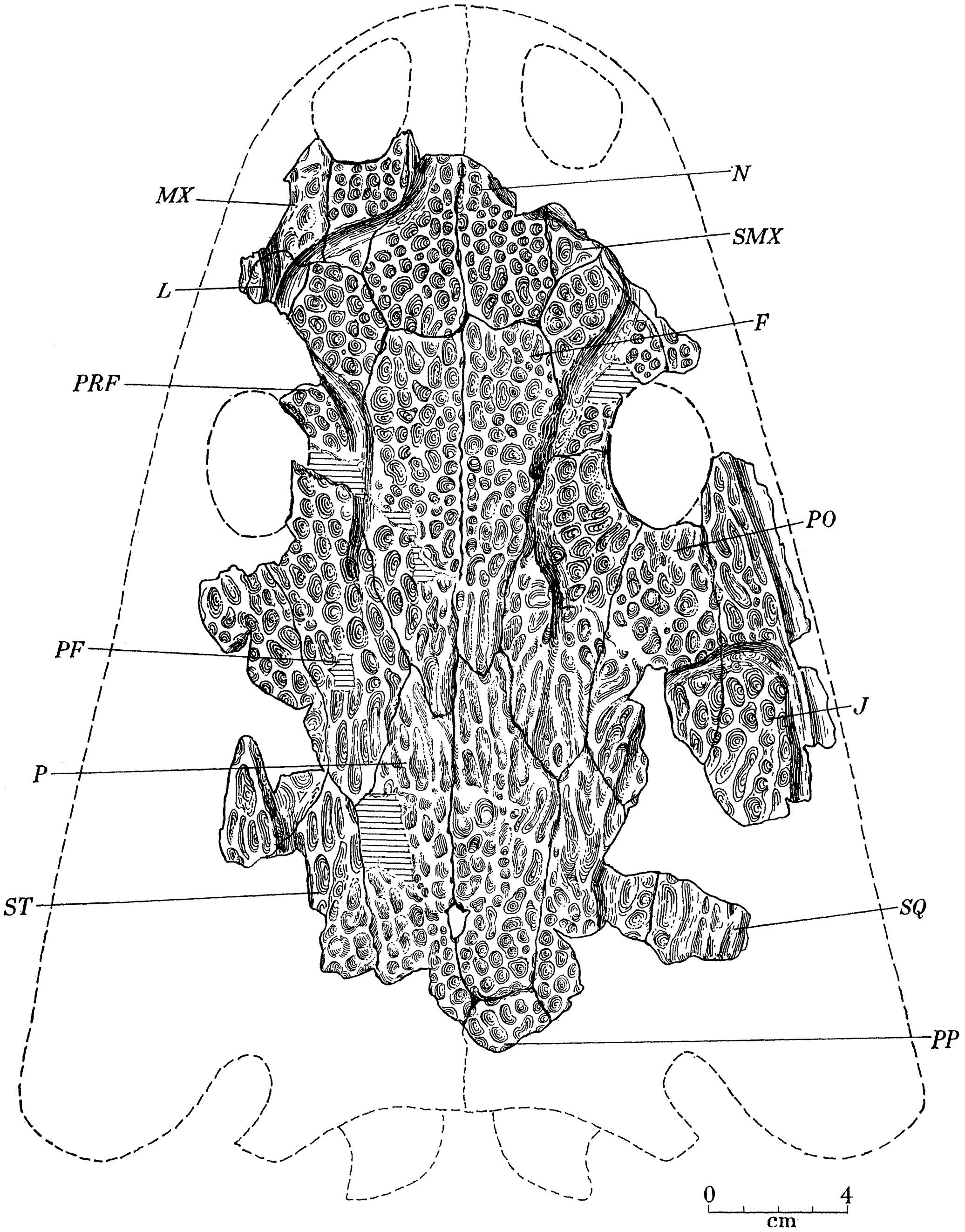


FIGURE 3. Skull I.S.I. A. 4. (Magn. × ½.) Dorsal view. For abbreviations see p. 52.

The composite drawing of the two specimens gives us the complete outline of the antorbital and cheek region of the skull, the position of the orbits and nostrils, the lateral line canals, the skull bones and the sutures between them.

The region between the parietal foramen and back of the skull was reconstructed mainly by superimposing the information obtained from specimens I.S.I. A. 3 and I.S.I. A. 7 on specimen I.S.I. A. 4. A combined drawing of I.S.I. A. 3 and I.S.I. A. 7

gave all the details of the region between the parietal foramen and back margin of the skull table up to the otic notches. The common features present in I.S.I. A. 3, I.S.I. A. 7 and in specimen I.S.I. A. 4 are:

1. The parietal foramen.
2. The lateral line grooves on the supratemporals.
3. Sutures between the common bones.

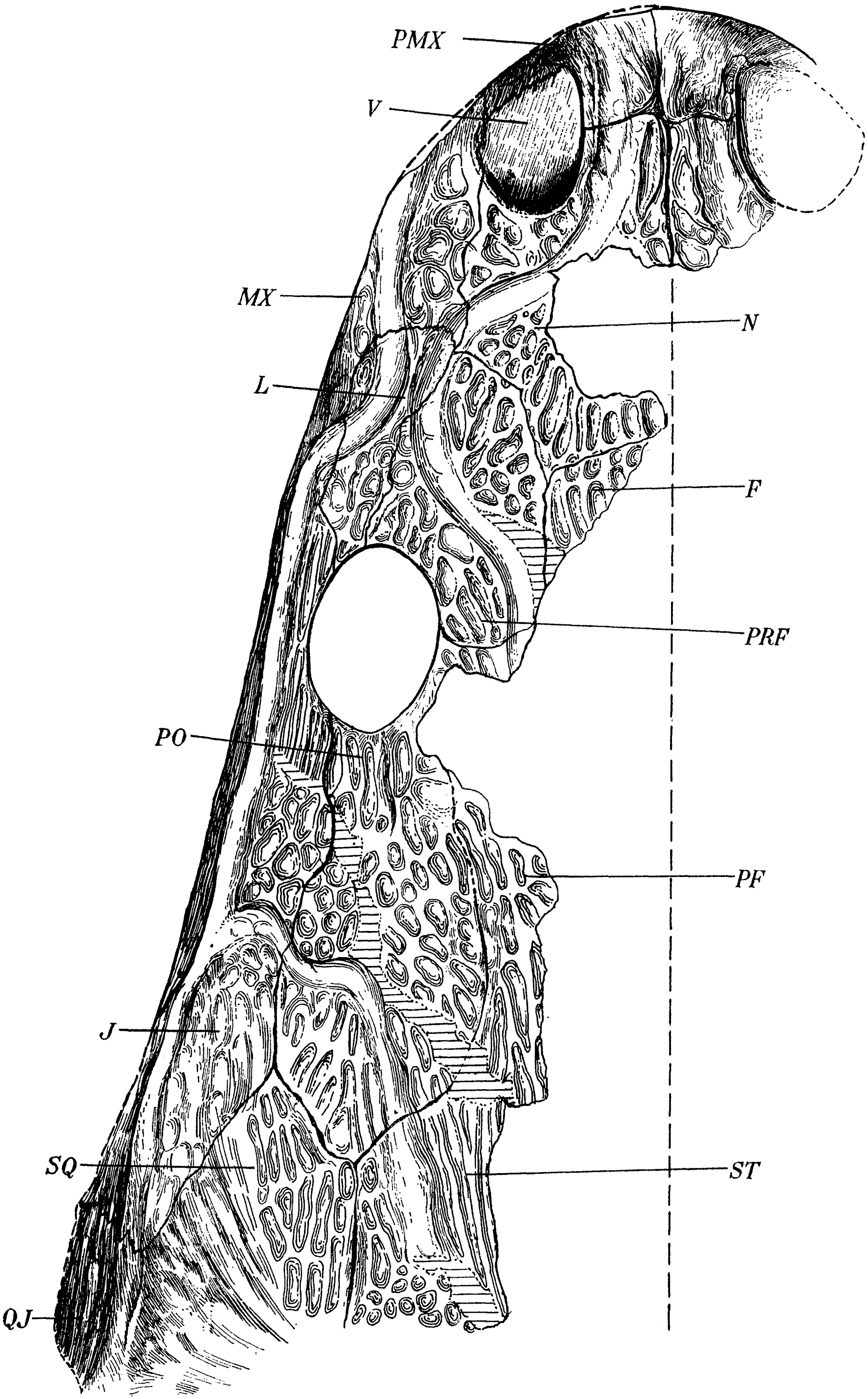


FIGURE 4. Skull I.S.I. A. 8. (Magn. × ½.) Dorsal view.

There is thus sufficient overlap between the parts present in the three specimens to allow their accurate comparison. A part of the missing cheek region was filled in with the help of specimen I.S.I. A. 5, a complete left squamosal. This specimen was also useful in completing the otic notch.

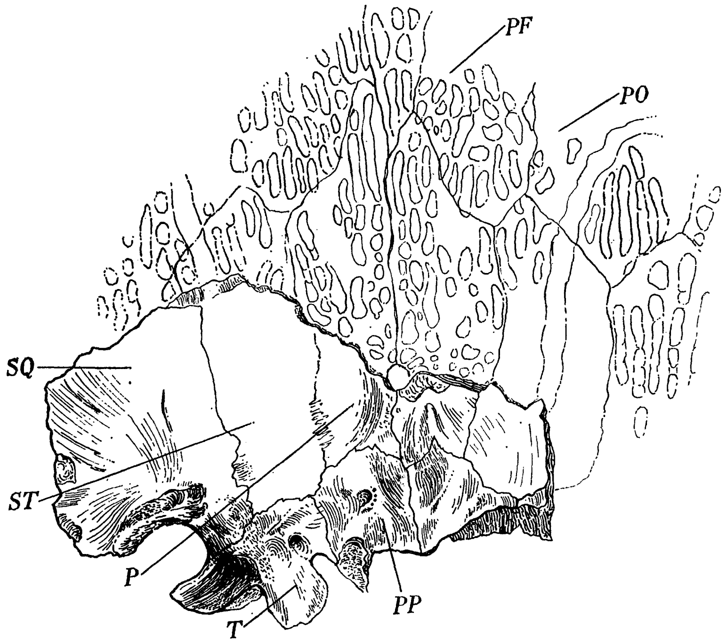


Figure 5. Skull I.S.I. A. 3. (Magn. × ½.) Ventral surface of the skull roof.

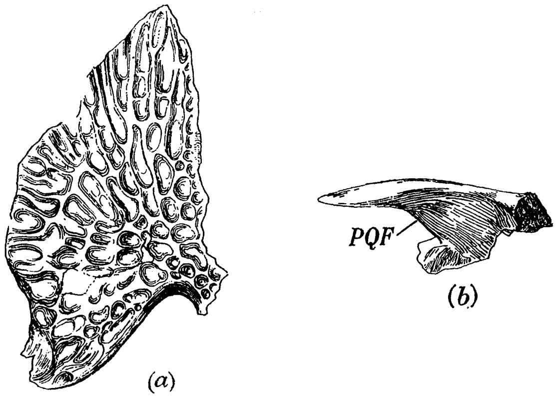


Figure 6. Skull I.S.I. A. 5. (Magn. × ½.) Left squamosal; (a) dorsal view, (b) posterior view.

The only part of the skull roof about which no information exists is the extreme postero-lateral margin. The crushed region of I.S.I. A. 8 skull gives the portion of the suture between the squamosal and quadratojugal, but it has not been possible to trace the latter bone right back to the posterior margin of the skull roof.

Palatal view

The palate (figure 10) has been reconstructed mainly from specimens I.S.I. A. 7 (figure 7) and I.S.I. A. 6 (figure 8). The size given here represents that of the former specimen because it has more of the palate preserved than the other. The condyles, back

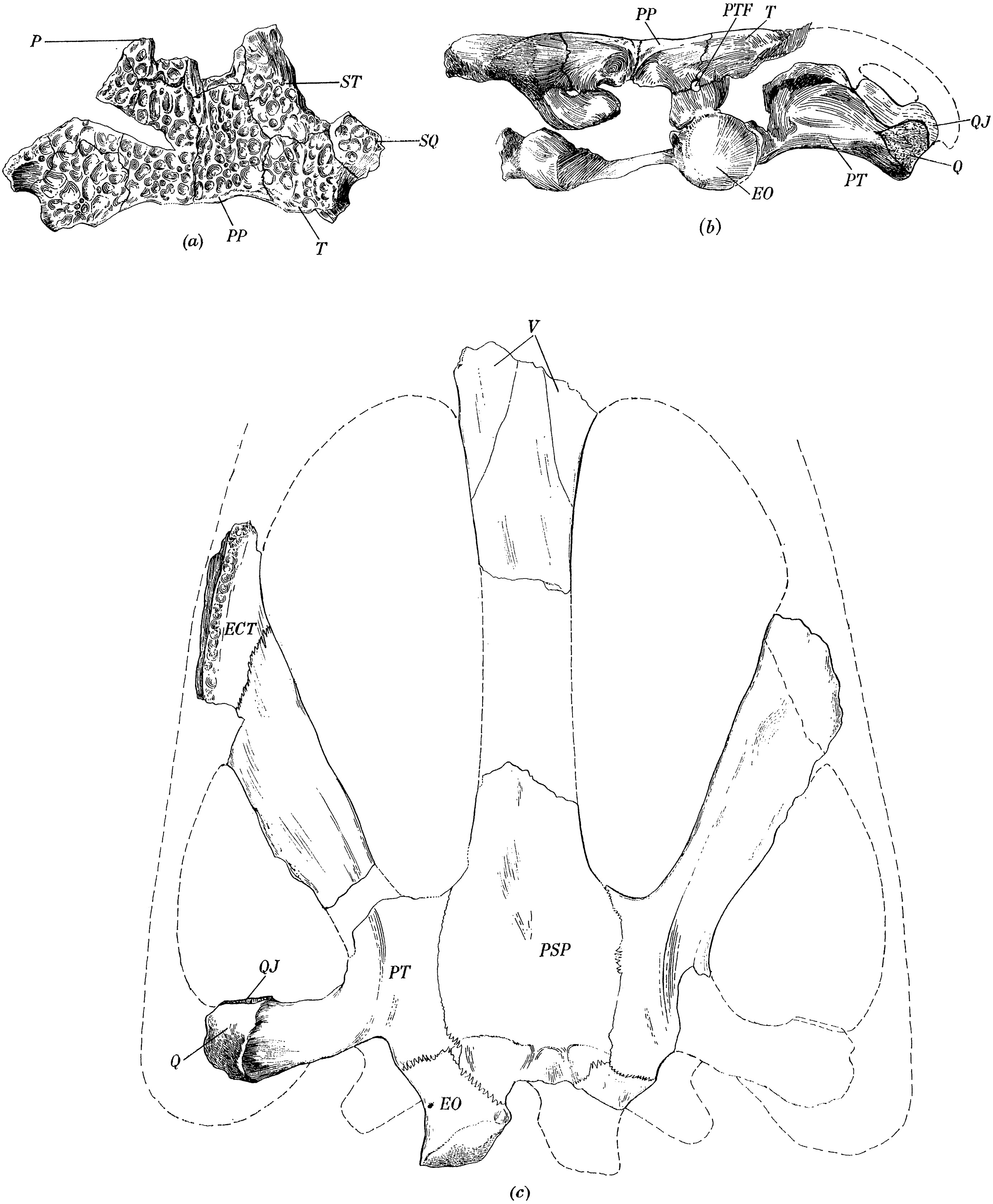


FIGURE 7. (*a*) Posterior portion of skull I.S.I. A. 7, dorsal view. (Magn. × ½.) (*b*) Skull I.S.I. A. 7. (Magn. × ½.) Occipital view. (*c*) Skull I.S.I. A. 7. (Magn. × ½.) Palatal view.

of the palatal margin up to the quadrate, pterygoid, parasphenoid including the cultriform process, ectopterygoid and part of the vomer are present on one side or the other of specimen I.S.I. A. 7. The asymmetry noted in the specimen has been kept in the figure. The palatines, the position of the internal nostril on the palate, and the position of the orbit in relation to the palate, have been adopted from I.S.I. A. 6 which is the larger of the two specimens. The part of the palate anterior to the internal nostril could not be restored for want of an adequate specimen. The anterior marginal outline, where it was missing, has been restored from the outline of the skull roof brought to the same scale. The only other specimen which has parts of the palate preserved is I.S.I. A. 2. and a few characters of the palatal dentition shown well in this specimen have been incorporated in the reconstruction.

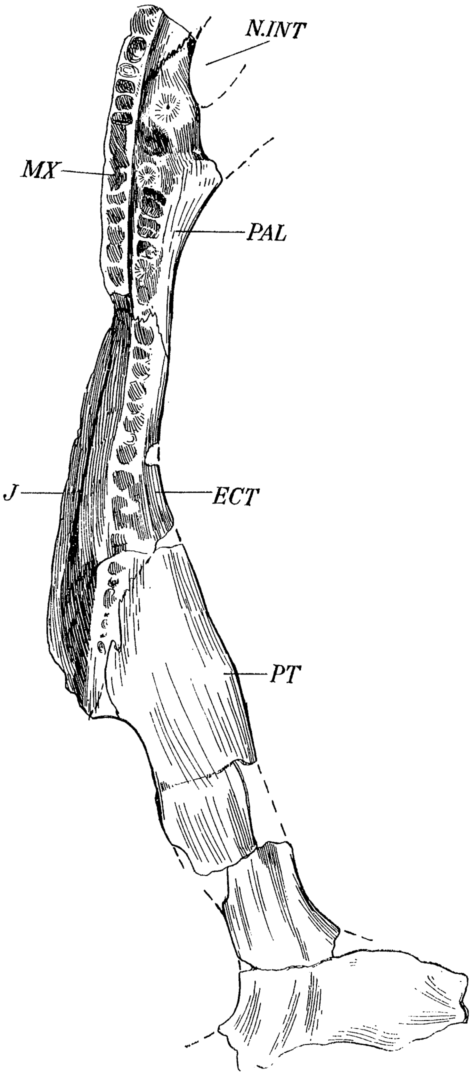


Figure 8. Skull I.S.I. A. 6. (Magn. × $\frac{1}{2}$.) Part of the skull in palatal view.

Occiput

The occipital view (figure 11) is mainly based on specimen I.S.I. A. 7 (figure 7) drawn to the scale of the dorsal view of the skull. The squamosal part has been taken from specimen I.S.I. A. 5. (figure 6*b*).

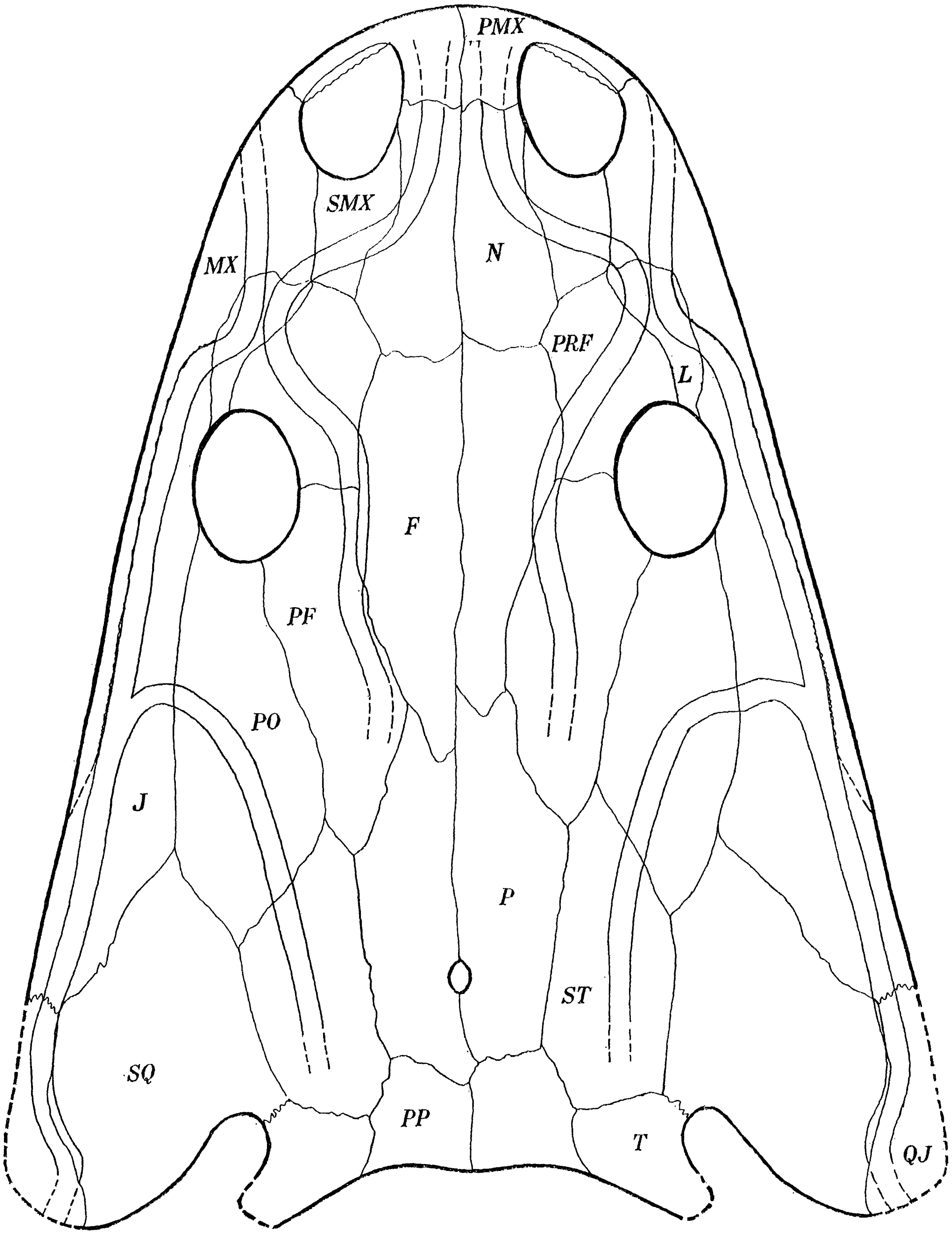


FIGURE 9. Composite restoration of the skull. (Magn. × ½.)
Dorsal view. (Size based on skull I.S.I. A. 4.)

SYSTEMATIC DESCRIPTION

For the purposes of description it is convenient to name the Maleri metoposaur now, even though a proper assessment of the taxonomy, a diagnosis, will have to be deferred until the Maleri specimens have been compared with the forms found outside India in a later section of this paper.

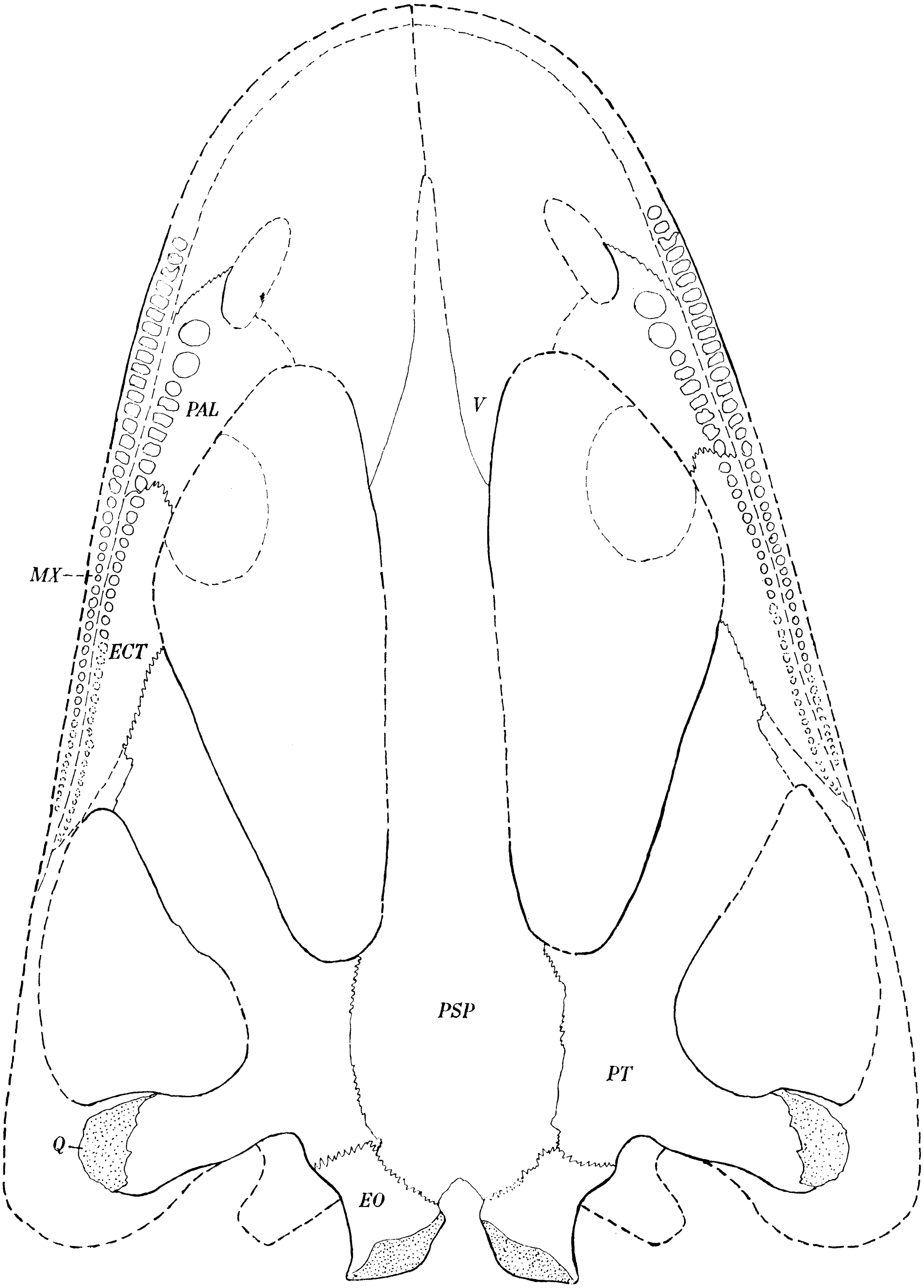


Figure 10. Composite restoration of the skull. (Magn. × $\frac{1}{2}$.) Palatal view. (Size based on skull I.S.I. A. 7.)

Metoposaurus maleriensis n.sp.

Holotype—specimen number I.S.I. A. 4; part of a skull. Collection at the Geological Museum, Indian Statistical Institute, Calcutta.

Paratypes—remainder of the specimens listed in p. 12, in the collection at the Geological Museum, Indian Statistical Institute, Calcutta, and specimens K33/638, K33/616*a*, *b*, K33/630*a*, K33/606*a*, K33/611*a*, K33/602*a* in the Indian Museum Calcutta.

Type locality—Achlapur, Pranhita Godavari Valley, Andhra Pradesh, India.

Horizon—Maleri formation of the Gondwana Group, Upper Triassic.

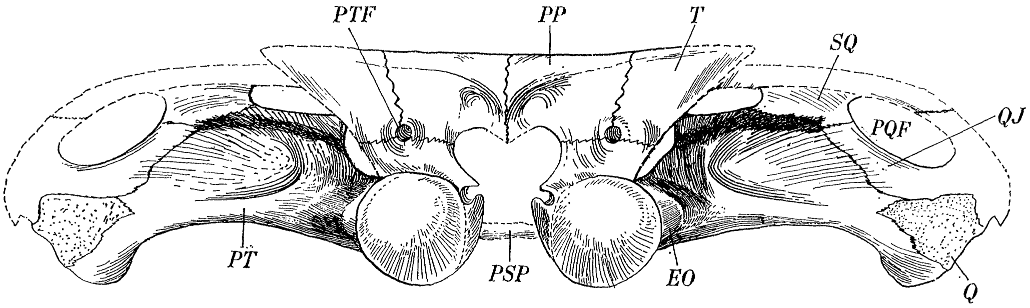


FIGURE 11. Composite restoration of the skull. (Magn. × ½.) Occipital view. (Size based on skull I.S.I. A. 4.)

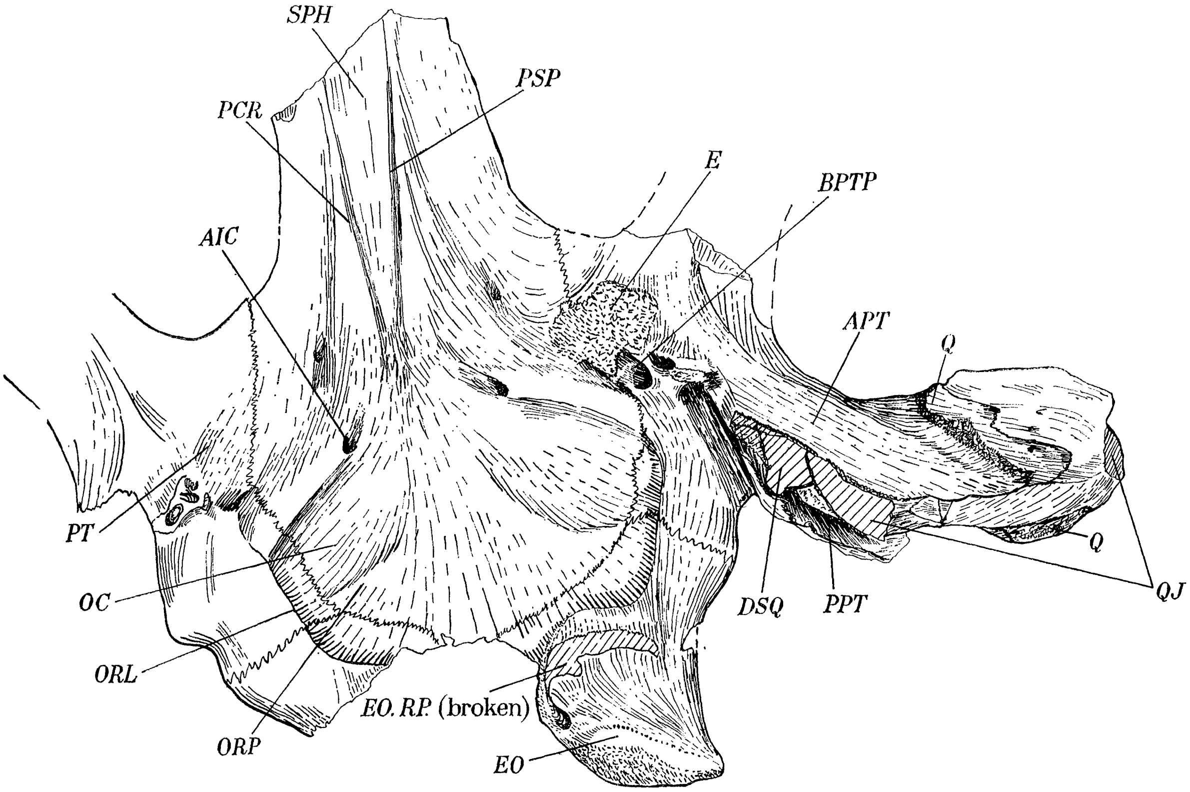


FIGURE 12. Skull I.S.I. A. 7. (Magn. × ½.) Dorsal surface of the palate showing the floor of the braincase.

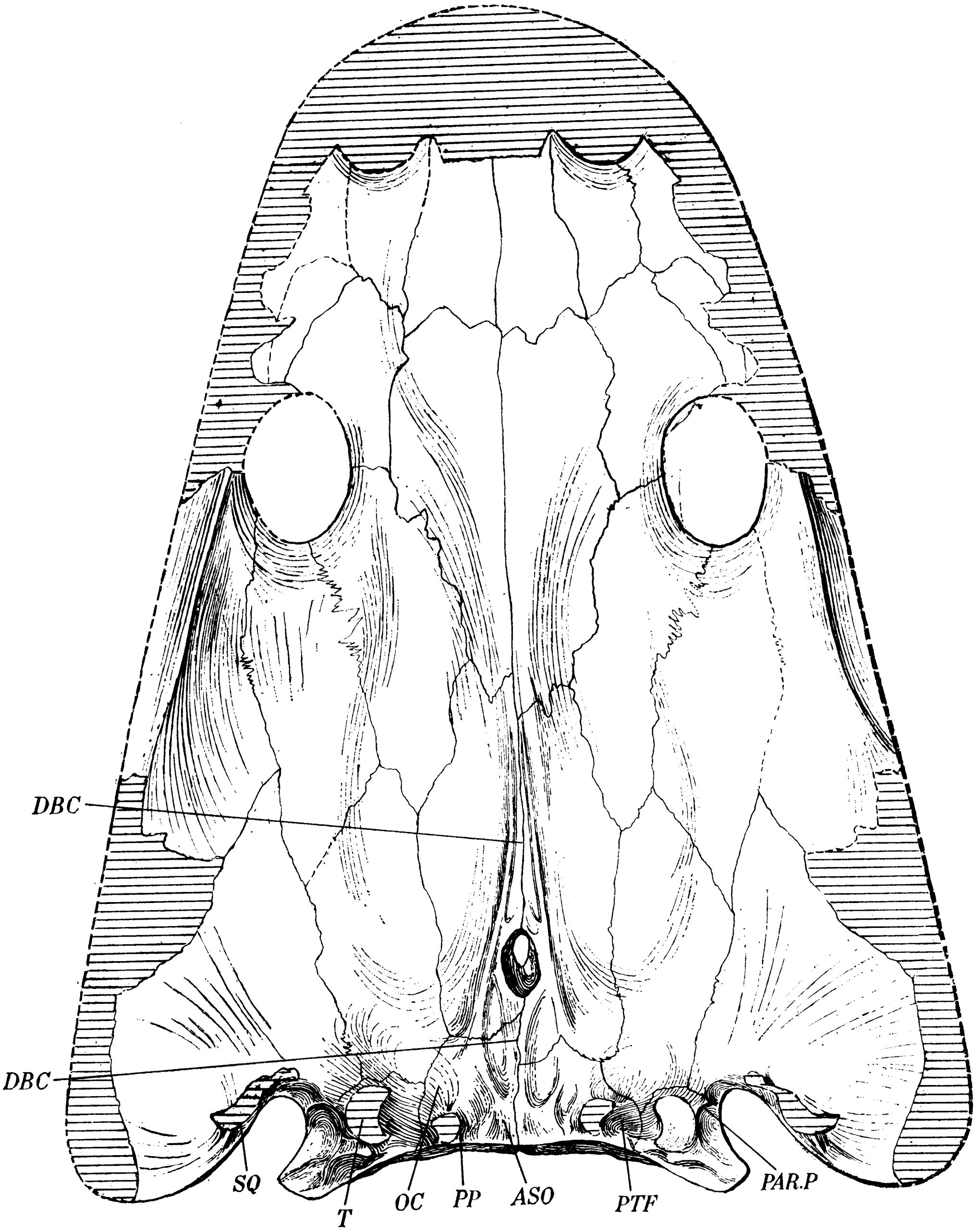


FIGURE 13. Ventral surface of the skull roof. (Magn. × ½.) Restored. (Size based on skull I.S.I. A. 4.)

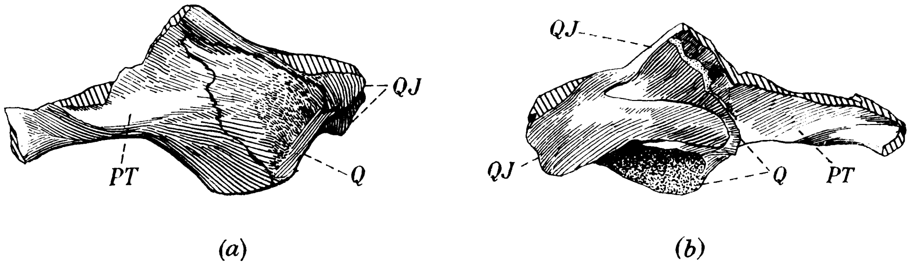
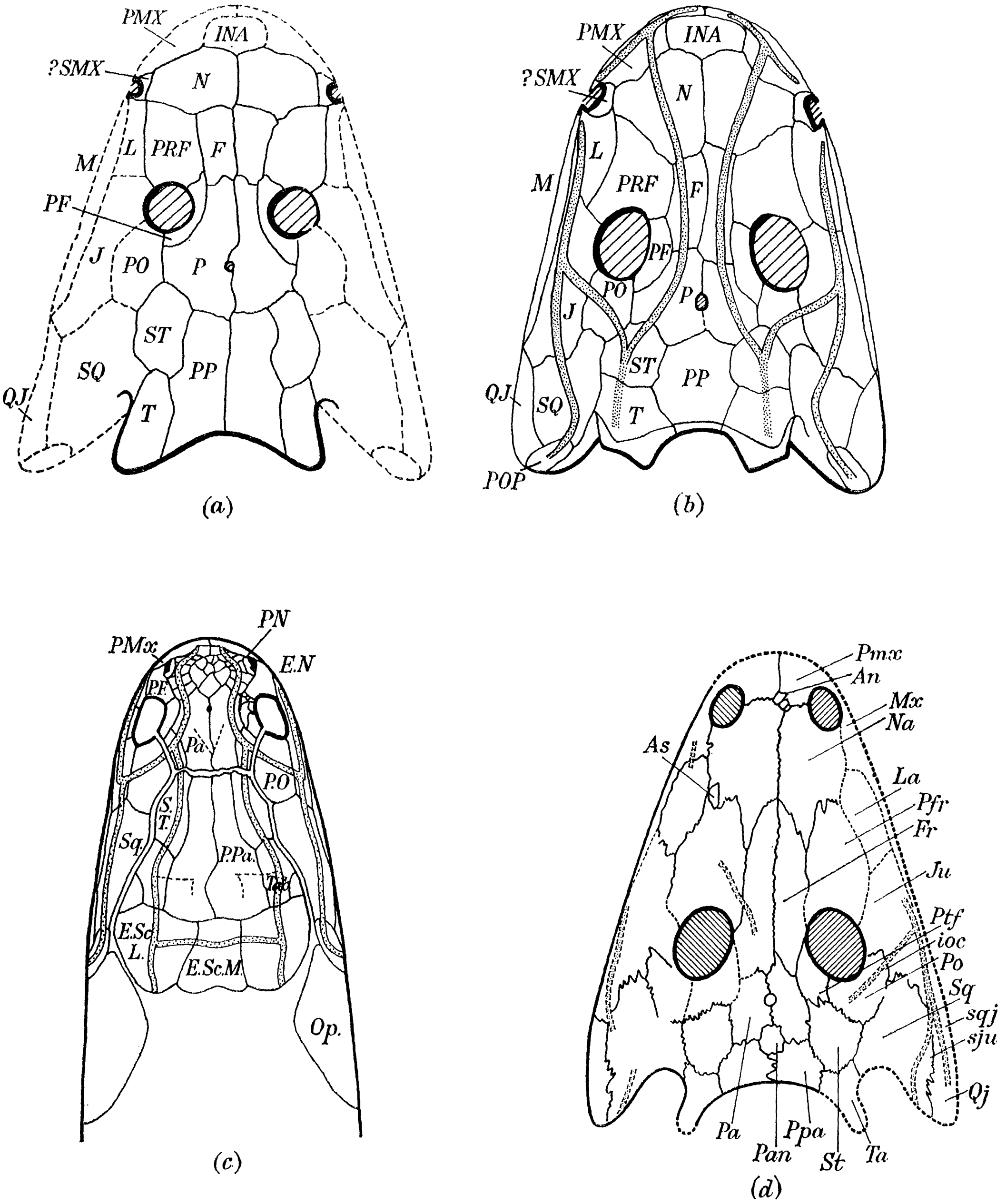


FIGURE 14. Skull I.S.I. A. 1. (Magn. × ½.) Quadrate region. (a) Posterior view. (b) Anterior view.

General features of the skull

The fossil material belonging to *Metoposaurus maleriensis* consists of several individuals, of which the most complete skull has been selected as the holotype. All but one of the specimens (Huene's Form III, 1940, plate 7, figure 3) previously collected from the Maleri formation, and figured, are referred to the same species because of their close similarity in osteological characters and sculpture, and because of their provenance from the same localities in the Maleri formation. In the description which follows all cranial measurements refer to the reconstructed skull, based on I.S.I. A. 4, unless otherwise stated. As



(*a*) (*b*) (*c*) (*d*)

FIGURE 15. Skull roofs of (*a*) *Elpistostege*, (*b*) *Ichthyostega*, (*c*) *Osteolepis* showing the septomaxillae; skull roof of (*d*) *Benthosuchus* sp. showing the supplementary bones (*As* and *An*). (*a*) and (*b*) after Romer (1947); (*c*) after Westoll (1943); (*d*) after Lehman (1961).

the anatomy and shape of metoposaurid skulls is well known, only the salient characters of the Indian form need be described, especially as illustrations are given of all the important specimens as well as a reconstruction.

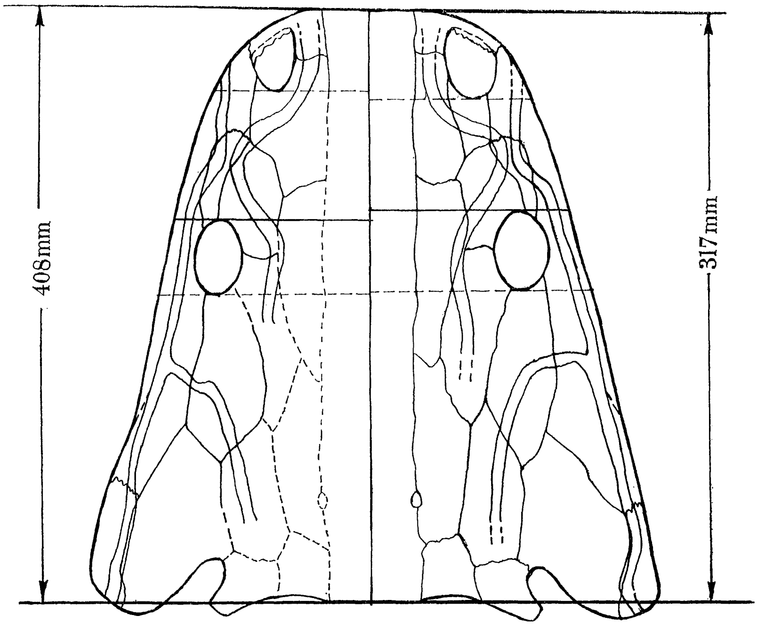


Figure 16. Skulls I.S.I. A. 8 (left) and I.S.I. A. 4 (right) brought to same scale to show the position of the orbits in relation to the skull length.

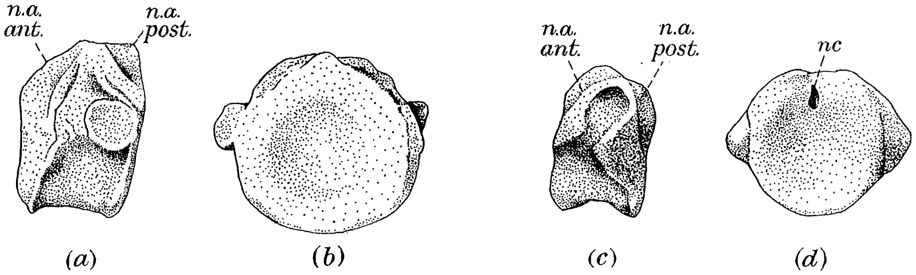


Figure 17. Vertebrae I.S.I. A. 14*a* and I.S.I. A. 15*a*. (Magn. × ½.)
(*a*), (*c*) Lateral views. (*b*), (*d*) Posterior views.

Dorsal aspect

The skull roof (figure 9) is extremely flat, the length (317 mm) is greater than the width (255 mm), and the length-width ratio is 1:0·81. The greatest width is at the posterior end of the skull, across the quadratojugals. The occipital margin has prominent otic notches formed by the squamosals laterally and tabulars medially. The central portion of the occipital rim of the skull is nearly straight between the tabular tips, but with a gentle concavity facing posteriorly. The external nostrils are placed very anteriorly and moderately close to the midline of the skull. The posterior margin of the external nostrils is set well above the dorsal surface of the vomers but the narial margin gradually slopes forward to the level of the narial floor. The orbits are comparatively small with a maximum diameter of 42 mm, and face upwards. The openings are oval in shape with the longer axis oriented anteroposteriorly. The lacrimals enter the orbital margins at the anterolateral corners of the orbits. The parietal foramen, placed quite posteriorly between the parietals, is nearly circular with diameter of 8 mm.

The sculpture on the dorsal side of the skull roof consists of polygonal, generally pentagonal pits separated by narrow raised ridges. In the zones of intensive growth, the pits become elongated, and this is most extensive in the area between the orbits and the parietal foramen. The elongated pits are situated in a crescent shaped band, the central part of the crescent occupies the posterior part of the frontals and the anterior part of the parietals; the lateral part extends through the posttemporal and postorbital on to the squamosal and jugal. There is a less pronounced area of slightly elongated pits in the antorbital region near the suture between the nasal and frontal. The thickness of the bones is variable; in section the bones are thickest (11 mm, I.S.I. A. 4) towards the posterior margin, and along the midline, and gradually become thin, both laterally and anteriorly. The thinnest bones (4 mm, I.S.I. A. 4) are near the snout. On the skull roof, the left-hand member of a pair of bones is slightly posteriorly placed in comparison to the right hand one.

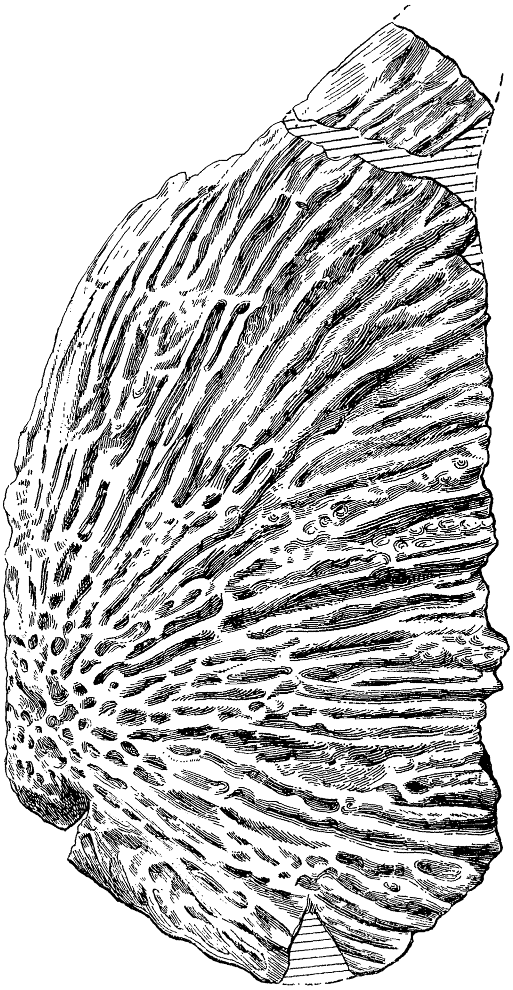


Figure 18. Clavicle I.S.I. A. 12. (Magn. × $\frac{1}{2}$.) Right clavicle. Ventral view.

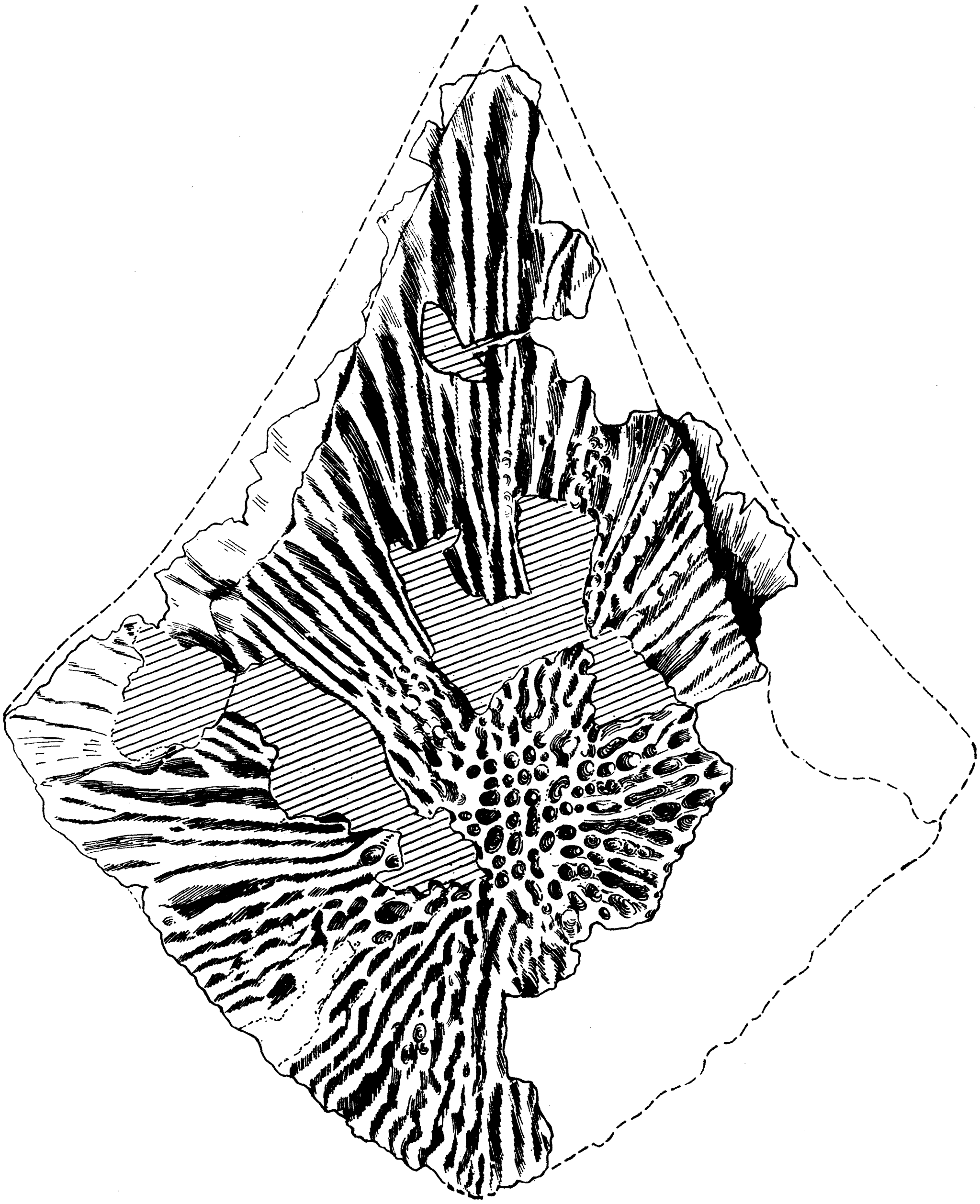


FIGURE 19. Interclavicle I.S.I. A. 9. (Magn. × ½.) Ventral view.

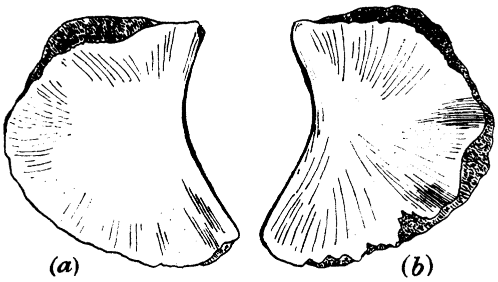


FIGURE 20. Ischium I.S.I. A. 16. (Magn. × ½.) Right ischium; (a) dorsal view, (b) ventral view.

A system of grooves carrying the lateral line canal is present on the skull. The grooves vary in width between 6 and 9 mm, and are usually 2 to 3 mm deep. The supraorbital grooves run very close to the skull midline in between the external nostrils but they expand to form a 'lyra' between the nostrils and the orbits, running from the nasals to lacrimals, then to the prefrontal and along the sutures between frontals and postfrontals, finally fading out in the posterior parts of the postfrontals. The infraorbital grooves commence from that portion of the maxilla which lies lateral to the external nostrils, and come very close to the supraorbital grooves in the lacrimals; then they swing outward and run backward to the jugals, where they receive the supratemporal grooves. The posterior continuation of the infraorbital grooves follow the sutures between the jugals and quadratojugals and then run along the sutures between the squamosals and quadratojugals up to the posterior margin of the skull roof. The grooves for the supratemporal canal commence from the posterior part of the supratemporals and move forward into the postorbitals where they turn outward through a right angle before entering the jugals.

Occipital view

The occipital view (figure 11) emphasizes the flatness of the skull and shows the general shape of the back of the skull. The width–height ratio of the skulls is 1:0·20 as usually expected for a flat-skulled form. The occiput forms a single structure, for the sutures of the component bones, though discernible, are usually co-ossified. The paired condyles are made entirely of exoccipitals and are set apart from each other by a distance of 23 mm. Above the condyles the foramen magnum is large and surrounded by the postparietals and exoccipitals. Its dorsal border is heart shaped and the foramen opens below in a gap probably occupied in life by a cartilaginous basioccipital. Lateral to the dorsal border of the foramen magnum, on each side of the skull, there is a posttemporal fenestra, circular in outline, with a diameter of 5 mm, and which opens internally, probably above the cartilagenous opisthotic. Near the dorsal end of the posterior rising process of the pterygoid, on each side, there is a canal running forward and downward to a position just behind the epipterygoid and probably served for the passage of some nerve or blood vessel during life. From its position and direction, it seems unlikely that it lodged the stapes. This canal might possibly have conducted the chorda timpani branch of the seventh (facial) nerve. The dorsal part of the occiput is placed slightly forward of the ventral part; so that behind the skull table the occipital surface slopes slightly posteroventrally and the condyles project behind the skull roof.

Palatal aspect

The anterior part of the palate, i.e. most of the vomers, is not represented by any specimen in the present collection, and is mainly adopted from other known metoposaurid palates similar in size and proportion. The palate is extremely flat (figure 10). The interpterygoid vacuities are very large, broad anteriorly and separated by the cultriform process of the parasphenoid. The subtemporal fossa for the lower jaw muscles are present in their usual positions, in the posterolateral part of the palate. The lateral and posterolateral borders of the subtemporal fossa are not represented in the Maleri specimens, but must have been made by the jugals and quadratojugals. The paired occipital condyles form the most posterior part of the palate and the quadrate condyles lie a little in front of them. The quadrate condyle faces ventrolaterally and its medial border hangs slightly below the level of the rest of the palate. The parasphenoid forms the main floor of the braincase and extends forward along the skull midline as a broad but relatively thin cultriform process. Ventrally the process has a very shallow concave surface. There are some ridges at the base of the cultriform process, reminiscent of skull ornament but much more slightly developed. In its most anterior extremity, situated in front of the palatal vacuities, the cultriform process terminates as a V-shaped process wedged in between the vomers and on the same plane. The main body of the parasphenoid extends laterally forming a firm sutural connexion with the basal parts of the pterygoids. The posterior margin of the parasphenoid is bounded by the exoccipitals, except in the central part, where the bone has a free margin forming a notch in between the condyles. Probably a cartilaginous basioccipital was housed here. The pterygoid meets the exoccipital at a transverse suture, and these two bones and the parasphenoid all lie in the same horizontal plane. There is a double row of teeth present along the margin of the skull anterior to the subtemporal fossa. The outer row consists of maxillary teeth and must have continued on the premaxilla. It seems that there were more than sixty teeth present on the maxilla in each side. Medial to and parallel with the maxillary row, the second row consists of palatal teeth extending from the posterior end of the ectopterygoid on to the palatine as far as the hinder part of the internal nostril. There are at least twenty-two teeth on the ectopterygoid and ten teeth on the palatine. These increase progressively in size anteriorly, but the two most anterior teeth are very large fangs showing an abrupt increase in size when compared to those behind.

Braincase and associated structures

Very little of the braincase is actually preserved. The reason for this is twofold. First, the loss of ossification of the braincase has reached an advanced level in all the late Triassic stereospondyls, and the metoposaurs are no exception to this. Secondly, the chances of preservation of some of the poorly ossified parts are rather small as they tend to become detached or crushed. The exoccipitals are the best ossified parts of the braincase and are usually well preserved in fossil specimens. Although only partly ossified, the pro-otic and opisthotic and a well-developed epipterygoid have been noted in some of the North American metoposaurs (Case 1931; Wilson 1941; Sawin 1945); none of these bones was found preserved in *M. maleriensis*, nor has a stapes been found. It is, however, possible to get an adequate idea about the braincase from the traces and impressions left by the different elements on the adjacent dermal bones of the palate and skull roof, and from the positions of the cartilage bones and impression of cartilages of the palatoquadrate.

The dorsal surface of the palate (figure 12), particularly the parasphenoid, adjoining parts of the pterygoid and exoccipital are useful for consideration of the braincase floor. Lateral to the suture of the parasphenoid with the pterygoid and exoccipital, the latter two bones form a thick ridge. The mesial face of this ridge and the dorsal surface of the parasphenoid form a broad shallow depression which presumably housed the otic capsules and floor of the cranial cavity. The most posterior part of this depression, formed by the parasphenoid and exoccipitals, is centrally placed and limited posterolaterally by relatively thick unfinished mesial faces of the exoccipitals. This posterior depression on the parasphenoid and the unfinished edges of the exoccipitals strongly indicate the presence of a cartilaginous basioccipital. It is not possible to demarcate the anterior limit of the basioccipital region. On the mesial face of the rising process of the exoccipital there is a foramen probably for the passage of the hypoglossal nerve (XII) which emerges through an opening on the lateral surface of the exoccipital, in front of the occipital condyle.

Although the otic region was entirely cartilaginous, its position is indicated by a shallow depression on each side of the parasphenoid anterolateral to the basioccipital region. The floor of the otic region is demarcated from the basioccipital region by a faint transverse prominence on the parasphenoid (see figure 12). The anterior limit of the otic depression is demarcated by a transverse ridge which houses the tunnel for the internal carotid artery. The internal carotid artery enters the tunnel a little anterior to the pterygoid/exoccipital suture. The tunnel extends forward and inward through the parasphenoid and opens fairly close to the midline, marking the probable position of the pituitary fossa. The inner face of the occipital flange, formed by the tabular and postparietal, has a shallow depressed area, which can be interpreted as the position for the cartilaginous opisthotic. The cartilaginous basisphenoid probably had a narrow posterior part situated between the otic regions, and probably extended anteriorly about as far as the openings for the internal carotid arteries. In front of the tunnel for the internal carotid artery the basisphenoid must have extended laterally into a basipterygoid process, as the recess for the latter is well marked on the pterygoid close to the suture with the parasphenoid. The dorsal limits of the braincase are defined by a pair of ventrally projecting ridges and a few prominent depressions on the ventral surface of the skull roof (figure 13). The ventrally projecting ridges are found close to the skull midline, on the ventral surface of the posterior part of the frontals and on the parietals, but die away before reaching the postparietals. As the ridges are traced backwards from the frontals they diverge, reaching a maximum distance apart of about 30 mm (skull I.S.I. A. 8) just behind the pineal foramen, at the position where the ridges die out in the posterior part of the parietals. Behind the region of the divergent ridges, on the ventral surface of the postparietals, there is a slight median depression. The depression is limited posteriorly by a transverse bony ridge at the level of the descending flanges of the postparietals. The transverse ridge presumably marks the posterior limit of the cartilaginous neurocranium. Posterior and a little lateral to this depression, there is a distinct rugose area which probably afforded attachment to the cartilaginous supraoccipital, forming the posterodorsal wall of the cranial cavity. The supraoccipital extended up to the dorsal margin of the foramen magnum. Placed lateral to the depression for the roof of the neurocranium, behind the line of the pineal foramen, there is a shallow depression on each side occupying the undersurfaces of the postparietal, tabular and supratemporal which probably marks the dorsal limit of the otic capsule. There are rugosities surrounding the depression, which are probably attachments for the cartilages of the otic region but the limits of the different elements are difficult to infer. It seems that the impressions of the otic capsule and the brain case are separated by a very small ridge, beneath which the narrow supraotic fossa or fossa bridgei was presumably situated. Lateral and posterolateral to the depression for the otic capsule there is an area of prominent rugosity on the undersurface of the tabular, probably for attachment of the cartilaginous paroccipital process. The next prominent landmark is the pineal foramen placed rather posteriorly in the parietals. Anterior to this must be the dorsal part of the sphenethmoid region, the limit of which is present as the ventrally projecting ridges already mentioned. The two ridges slightly converge anteriorly and die away in the posterior part of the frontals. The dorsal impression of the nasal capsule is not very clear.

Cartilage bones and cartilages of the primary palatoquadrate

Two ossifications of the primary palatoquadrate arch, the epipterygoid and quadrate are present. Only a part of the former is ossified, as a patch of spongy bone (figure 12) on the dorsal surface of the palate. This patch of bone, probably part of the basal portion of the epipterygoid, is roughly triangular in outline and rests a little behind the posterior border of the palatal vacuity, on, and partly co-ossified with, the dorsal surface of the pterygoid, close to its suture with the parasphenoid. The quadrate is wedged in between the quadrate ramus of the pterygoid and the quadratojugal. The relationship of the quadrate with adjoining dermal bones of the skull is complicated. In metopossaurs this relationship has partly been noted by previous workers (Watson 1919; Case 1922). The specimens I.S.I. A. 7 (figure 7*c*) and I.S.I. A. 1 (figure 14) shows the relationship of the quadrate with the adjoining bones of the skull very well. Dorsally and laterally the quadrate is in contact with the quadratojugal; posteriorly and posterolaterally it abuts against the quadrate ramus of the pterygoid. The ventral surface of the quadrate is free to form a somewhat triangular condyle for the articulation of the lower jaw. The articular face is saddle shaped. Mesially the quadrate forms the lateral part of the inner surface of the occiput and terminates against the quadrate ramus of the pterygoid by an unfinished edge; the further continuation of this edge was probably the cartilaginous commisura quadro-cranialis basalis (Wilson 1941). On the lateral part of the anterior face, the quadrate receives a mesially projecting thin lamina of the quadratojugal.

Fragments of the skull described in previous literature

Besides the skull specimens mentioned above, some highly fragmentary skull elements have been described by Lydekker (1885) and Huene (1940) as belonging to metoposaurs. None of these fragments are even complete single bones, but all were collected from localities near Achlapur, Gampalpalli and Maleri. The sculpture pattern of these fragments is exceedingly similar to the more complete new specimens, as is the detailed structure of the two isolated exoccipital bones. There is no reason to doubt that all these fragments from previous collections represent the same genus and species as the new material. Three fragments representing parts of interclavicles and a fragment of the clavicle, all from Maleri, have also been figured by Huene (1940), and will be discussed with the description of the postcranial skeleton.

Discussion of special features of the skull

The bones in the nasal region

Specimen I.S.I. A. 8 of the skull of *Metoposaurus maleriensis* shows the normal condition of the nasal bone in metoposaurs. The nasal forms the posterior border of the external nostril, has lateral contacts with the maxilla and lacrimal and bears a part of the supraorbital lateral line canal. Though a portion of the bone is missing in the specimen the remaining ornament suggests that the bone has a single centre of growth. In specimen I.S.I. A. 4 there are two bones occupying the place of the normal nasal on each side of the skull. One lies more mesially, making contact with its fellow of the opposite side at the midline, in normal nasal fashion. The other is an extra bone lying more laterally and bearing the supraorbital lateral line canal. The sutures along the margin of this extra bone are extremely clear and can be traced both on the dorsal and the ventral surfaces of the skull roof. The bone forms the posterior margin of the external nostril, makes a lateral contact with the maxilla, touches the lacrimal posterolaterally, meets the prefrontal posteriorly, and is bounded by the nasal medially. The identity and significance of this extra bone is a problem requiring discussion.

It may be suggested that this extra ossification is a secondary anamestic element. Lehman (1955, 1961) noted the presence of such supplementary bones in the snout region of *Benthosuchus* sp. (figure 15*d*) from the Eotriassic of Madagascar. One supplementary bone is present between the left nasal and prefrontal and three supplementary bones are present between the premaxilla and the nasal near the skull midline. But the so-called supplementary bones in *Benthosuchus* sp. are asymmetrically disposed and very small, whereas the extra bones in skull I.S.I. A. 4 are paired, symmetrical, and relatively large. Moreover, they bear part of the supraorbital lateral line groove. The presence of lateral line grooves tends to give permanence to the bones which develop round them in ontogeny, according to theories of evolution of dermal bone patterns (cf. Parrington 1948). It is therefore unlikely that anamestic bones would bear lateral line grooves.

Since the space occupied by the extra bone in the nasal region of the skull of I.S.I. A. 4 of the Maleri metoposaur is usually occupied by the nasal, it is possible to suggest that it is a homologue of the oesteolepid postnarial. This would imply that the tetrapod nasal originated as a compound bone formed by the fusion of postnarial and nasal elements and that the condition seen in I.S.I. A. 4 is an atavism. The postnarial (Westoll's terminology, 1943) or anterior tectal (Jarvik's terminology, 1942) of an ostelepid such as *Osteolepis* (figure 15*c*) or *Eusthenopteron* (Jarvik 1942, fig. 34) lies above and continues behind the external nostril, meets the frontonasal series, premaxilla, prefrontal, and often the lacrimal.

But no sign of a compound origin for the nasal bones of recent amphibia has ever been recorded. In those species of fossil amphibians in which a good growth series has been studied (e.g. *Benthosuchus*, *Dvinosaurus*), the smallest (presumably youngest) specimens also show no sign of compound nasal bones. If the osteolepid forerunners of amphibia are considered, these all have several small bones present in the nasal region. The derivation of the single pair of nasals can be achieved by the fusion of the several elements present in the osteolepid nasal region following the theory put forward by some authors (Säve-Söderbergh 1935). Bystrow (1938, fig. 14*d*) has shown the presence of two centres of ossification in the postorbital of *Dvinosaurus*, which can be regarded as a possible example of fusion of dermal bones in the amphibian skull. The concept of dermal roof evolution by fusion has, however, been strongly criticized by many authors (Westoll 1943; Romer 1947; Parrington 1956). These authors suggest that some of the small elements in the nasal region were eliminated by atrophy and their place taken up by more rapid growth of an adjacent centre of ossification. However, whichever theory be adopted, Westoll (1943) has pointed out that the common pattern of dermal bones of the skull shown by primitive amphibians like *Elpistostege* (figure 15*a*) and Ichthyostegalia (figure 15*b*) is strong evidence that the amphibians were derived from an ancestral type in which this process (of fusion) had been completed. If this is true, it would be most unlikely that a separate ossification in the nasal region, reflecting the emergence in a single individual of a condition seen in such remotely ancestral forms, would occur in such late forms as metoposaurs.

In fossil amphibians the position of this extra ossification is sometimes occupied by the septomaxilla, when preserved. Among rhachitomes, a septomaxilla has been noted in *Edops*, *Chenoprosopus*, a few trematosaurs and a few benthosuchids. In all the above-mentioned forms the septomaxilla is small, and is excluded from the prefrontal, a phenomenon which, according to Westoll (1943), is probably due to the lengthening of the snout. The septomaxilla is not so well known among the short-faced stereospondyls. The reason for this is probably that this bone is usually situated within the narial activity, perhaps due to the extreme shortening of the snout region, and does not make a dorsal exposure; the adjoining bones, particularly the nasal, spreading over its dorsal surface. Moreover, as suggested by Romer (1947), the septomaxilla might be destroyed in preparation when present, or could even drop out before fossilization, and these may be reasons why it has not been recorded in metoposaurs, and in many other labyrinthodonts. Watson figured (1956, figs. 1, 5) a septomaxilla in *Bothriceps* and in *Batrachosuchus*, as a very small bone partly situated within the narial cavity and partly exposed dorsally, and in *Batrachosuchus* making a contact with the prefrontal. Romer (1947) opined that in short-faced forms the pointed anterior tip of the prefrontal may exceptionally touch the septomaxilla.

The Maleri metoposaur is a moderately short-faced form, and the extra bone behind the external nostril in skull I.S.I. A. 4 has the same relations with neighbouring bones as a septomaxilla. It may be objected that the extra bone has an exceptionally large dorsal exposure as compared to other septomaxillae. But this could be due to accelerated growth during ontogeny in this specimen, which has limited the nasal to a more medial position and smaller size, and has caused the septomaxilla to make an exceptionally large contribution to the skull roof.

A second objection may be raised to the identification of the extra bone as a septomaxilla. The extra bone bears part of the supraorbital lateral line groove, a condition not known in any other septomaxilla. This objection requires a consideration of the origin of the tetrapod septomaxilla.

In osteolepid fishes the bone termed the prenarial by Westoll (1943), or lateral rostral by Jarvik (1942) has been considered to be the homologue of the tetrapod septomaxilla. In external view the prenarial lies posteroventrally to the external nostril, has a broad contact with the premaxilla and meets the lacrimal; in many cases it meets the nasal series. The prenarial is very commonly pierced by the infraorbital lateral line canal in osteolepid fishes. If the extra bone of skull I.S.I. A. 4 is to be regarded as a septomaxilla homologous with the osteolepid prenarial, the presence of a supraorbital, rather than infraorbital, lateral line canal in the former becomes a serious obstacle. However Jarvik (1942) made an excellent study of the septomaxilla in fossil amphibians and suggested that it consists of three parts; a facial part, a medial process projecting inward into the nasal cavity, and a palatal part. Although such a complex bone has been thought to be homologous with a single osteolepid element, namely, the prenarial (lateral rostral), its facial part, as exposed in the skull roof, shows extreme similarity with the osteolepid postnarial (anterior tectal). The postnarial is pierced by the supraorbital lateral line canal in some crossopterygians (*Latimeria*), though this condition is not known, so far, in osteolepids. It is quite possible that the tetrapod septomaxilla is a true homologue of the osteolepid prenarial (lateral rostral); but it may be additionally possible that a part of the tetrapod septomaxilla, the facial part, is homologous with the osteolepid postnarial. If that is the case, the fusion of the pre- and postnarial must have been completed in the ancestral forms from which the amphibians were derived. From the discussion given above it is possible to suggest that the extra bone in skull I.S.I. A. 4 is a septomaxilla, and an accelerated rate of growth during ontogeny can perhaps explain the unusually large dorsal exposure which it makes on each side of the skull roof in I.S.I. A. 4.

Growth pattern of the skull roof

The skull roof of *Metoposaurus maleriensis*, as well as all other metoposaur species, shows two major zones of elongated sculpture pattern; one antorbital zone between the orbits and the nostrils, and one postorbital zone between the orbits and the pineal foramen. Bystrow (1935) has suggested that this elongate sculpture demonstrates a zone of intensive growth. He has shown that for most temnospondyls the activity of these two zones affects the skull proportions in various ways as size increases. The way in which growth affects the skulls of *M. maleriensis* can readily be seen in figure 16. The lengths of the restored outlines of the two skulls (I.S.I. A. 8 and I.S.I. A. 4) have been brought to the same scale in the figure. A comparison shows that the smaller skull (I.S.I. A. 4), presumably the younger of the two, has a slightly shorter antorbital length than the larger and presumbly more mature skull (I.S.I. A. 8). It can, therefore, be concluded that during the growth interval represented by the difference in size of the two skulls, the Maleri metoposaur seems to develop a relatively longer antorbital region. Whether or not this is true for the entire span of growth during life history can only be ascertained by measurements made on a large sample of skulls, and this is not yet available.

TABLE 1. MEASUREMENTS OF THE SKULLS (IN MM)

	I.S.I. A. 4	I.S.I. A. 8	I.S.I. A. 6
1. length of the skull roof	317*	408*	—
2. antorbital length (line across anterior margins of orbits to anterior)	118·5*	146	—
3. average length of orbits	42	52	—
4. postorbital length (line across anterior margins of orbits to posterior)	208·5*	262*	—
5. greatest width	255*	234*	—
6. height from base of condyles	—	—	58

* Measurement from restoration.

In the smaller skull of *M. maleriensis*, I.S.I. A. 4, the region of intensive growth in the postorbital region is indicated by a series of very elongate pits—or rather grooves. There is no indication of such a zone of intense growth in the antorbital region of this specimen, grooved ornament being completely absent. In the larger skull, I.S.I. A. 8, there is a grooved zone of ornament in the antorbital region as well as in the postorbital one. These two specimens allow the suggestion to be made that during ontogeny intensive growth begins first in the postorbital region of the skull, and then, after reaching a size of approximately 318 mm in length, the antorbital growth zone becomes active. If this were true the position of the orbits would vary during the growth-life of an individual, moving a little anteriorly, relatively, as the postorbital growth zone became active and then shifting posteriorly as the anterior zone began intensive growth. However, it is dangerous to assume that the two zones are active only when apparent as a region of groove ornament, for another factor must be considered, namely the rate at which the cross-bars are laid down, which convert the grooves to a series of pits. This rate may perhaps differ both intraspecifically and interspecifically during the ontogeny of the individuals of populations. It seems wisest, therefore, to rely wholly on measurements to assess changes in the orbital position and proportions of a skull with increase in size.

Postcranial skeleton

Vertebrae

There are nine vertebrae, including one atlas (figures 28 to 44, plate 3), all collected from Achlapur. None of the vertebrae was found associated. Each vertebra is represented only by its centrum; the neural arches are missing in all cases. All the centra, except that of the atlas, are circular or subcircular disks, slightly narrow dorsally and bear parapophyses. On some of them, facets for the reception of the neural arches can be seen. The atlas centrum is roughly oval transversely; its anterior face shows two concave facets for the occipital condyles. The dorsal part of the atlas is missing and so is the lateral part of the right condylar facet. No authentic information is available on the number of vertebrae present in a metoposaur vertebral column. Recognition of regional differentiation is difficult because of lack of comparative associated material. Out of the six centra which are provisionally regarded as presacral, two are circular (figures 29, 30, 37 and 38, plate 3) and opisthocoelous, with no trace of the notochordal pit. The parapophyses are placed well up on the posterior edge of the centrum. The remaining four presacral centra (figures 31 to 34, and 29 to 42, plate 3) are subcircular in outline, platycoelous to amphicoelous and the parapophyses extend across the adjacent vertebra to assume an intercentral position. Some have a small notochordal pit (figure 17*b*) placed dorsally on both articular faces. Two centra (figures 35, 36, 43 and 44, plate 3) are regarded as probable caudals. They are triangular in outline and are somewhat thickened ventrally. One of the caudals (figure 36, plate 3) has a short rib fused with the parapophysis.

Paired facets for the reception of the neural arches can be seen at each end of the dorsal surfaces of the more well preserved centra (figure 17) and perhaps indicate that each neural arch sat astride two adjacent centra. The characters of the dorsal centra indicate that we are dealing with stereospondylous vertebrae derived from the intercentra of earlier rhachitomous type. Panchen (1959), however, concluded that in plagiosaurs, single centra with notochordal pits and free intervertebral neural arches are pleurocentra, since each neural arch actually articulated with the centrum placed immediately behind it. None of the centra of the Indian metoposaur associated with neural arches, nor even a dissociated neural arch is available. Hence, it is rather difficult to ascertain the exact relationship between the centrum and the neural arch. However, the posterior facets for the neural arch on the centrum (figure 17) are distinct triangular areas separated by a small median ridge. Each facet is limited laterally by a distinct ridge sloping posteriorly. The anterior area for the reception of the neural arch, on the other hand, is rather smooth and less well defined. It appears, therefore, that the neural arch articulated with the centrum in front of it. Romer (1947, fig. 12) has noted a more or less similar condition in North American metoposaurs.

The presence of a notochordal pit high up on the articular faces of the centrum has been noted in *M. maleriensis* as well as in some North American metoposaurs (Case 1932). The position of the notochordal pit in the centrum may be useful to suggest whether the centrum is an intercentrum or a pleurocentrum. The intercentrum ossification, always unpaired, lies below the notochord, whereas the pleurocentral ossifications lie on either side of the notochord. Therefore, increase in ossification of either of the two centra, i.e. intercentrum or pleurocentra, tends to trap the reduced notochord in different positions within the centrum. The intercentrum would grow mainly upwards, pushing the notochord well dorsally before finally trapping it by the encircling growth of its lateral parts. The pleurocentra would grow in a more encircling way, because of their position in relation to the notochord, thus placing the notochord more or less in a central position, but much constricted to a mere remnant. In embolomerous vertebrae the intercentral growth cannot push the notochord dorsally because the pleurocentra, because of their position relative to the notochord, achieve an early cross-connexion above the notochord which thickens in a ventral direction. This opposes the tendency of the intercentrum to push the notochord dorsally because the intercentrum is thickening in a dorsal direction. The result of the balance between the growth of the two centrum elements is that both are pierced centrally by the notochord, constricting it, and form amphicoelous disks.

The presumed posterior position of the neural arch on the centrum and the dorsal position of the notochordal pits are strong indications that the metoposaur centra are intercentra.

Clavicles (figure 18; figures 23 to 25, plate 2)

There are two left clavicles (I.S.I. A. 10 and I.S.I. A. 11) and one right clavicle (I.S.I. A. 12) in the collection. The preservation is good and the clavicles are nearly complete; the cleithral process is best seen in specimen I.S.I. A. 11 (figure 23). The clavicles are triangular in shape; the length is approximately twice that of the width. There is a striking difference in general shape between I.S.I. A. 11, which is long and narrow, and the other two clavicles (I.S.I. A. 10 and I.S.I. A. 12) which are, comparatively broader than the former. This marked difference between a broader and a narrower type warrants a careful consideration as to whether they belong to the same species or to two distinct species, even though the specimens come from localities situated close to each other. The narrowest clavicle (I.S.I. A. 11; figure 23 and 24) has a length/width ratio 1:0·45 and the widest clavicle (I.S.I. A. 12, figure 25) has a length/width ratio 1:0·56 (see table 2). This marked difference between a broader and a narrower form of clavicle has also been noted in other metoposaur genera. Case (1932) has eleven clavicles of *Buettneria bakeri* (*Eupelor fraasi jonesi*—vide Colbert & Imbrie 1956) from the Dockum formation in Scurry County, Texas, and their length/width ratio varied between 1:0·42 to 1:0·54 with intermediate stages making a very good series. Another collection of forty-eight clavicles of *Eupelor* (Colbert & Imbrie 1956) collected from the Dockum formation in

Potter county, Texas, gave the same kind of result. The length/width ratio varied between 1:0·43 to 1:0·56 and there seem to be all gradations between. The same kind of results were obtained from the clavicles known from the Dockum formation in Howard county, Texas (1:0.48–1:0·54), from the Chinle formation near Lamy, New Mexico (1:0·40–1:0·51), and from the Popo Agie formation, Wyoming (1:0·48–1:0·67). It has been proved beyond doubt that the clavicles belonging to a single metoposaur species or collected from a single locality are highly variable. Under such circumstances it is not at all improbable that all three clavicles from the Maleri formation belong to a single species in spite of differences in shape and proportions.

TABLE 2

specimen number	clavicle length	clavicle width	length/width ratio
I.S.I. A. 11	260	117	1:0·45
I.S.I. A. 10	234	129	1:0·55
I.S.I. A. 12	242	136	1:0·56

Ventrally the surface of the clavicle (figure 18) is ornamented with grooves and ridges. In the posterolateral part, where the centre of ossification lies, the ornament consists of polygonal or rounded pits, but becoming elongated into grooves towards the periphery. The outer or anterolateral border is smooth and thick, more or less straight in specimen I.S.I. A. 11, but swings inward anteriorly in specimen I.S.I. A. 12, which is broader than the former. The posteromesial margin is thinner and somewhat irregular, and fits into the anterolateral margin of the interclavicle by overlapping surfaces. The posterolateral margin consists of two portions, one posterior, one almost lateral, and which meet at an angle. The posterolateral margin is smooth and finished except the posterior third, where the margin is irregular to fit the recess on the interclavicle. The anterolateral part of the clavicle is relatively thick and the dorsal or cleithral process (figure 23, plate 2) rises from the dorsal surface near the posterior part of the anterolateral margin as a blade-like sheet of bone. The cleithral process swings mesially and then curves upward to lie roughly at 70° to the clavicular surface. The posterolateral corner of the cleithral process is produced into a spine, extended laterally and dorsally. The relatively thin, main portion of the sheet-like cleithral process has a concave surface facing dorsally, and which, as it approaches the anterolateral border of the clavicle, develops into an elongate narrow groove. The groove is 70 mm long and 22 mm wide and presumably afforded attachment for a musculus cleidomastoidius (cf. Watson 1958).

The dorsal surface of the clavicle immediately mesial to the cleithral process is shallowly concave, but this concavity gradually dies out anteriorly. The anterior part of the clavicle, anterior to the cleithral process, is flat. Roughly parallel to the lateral portion of the posterolateral margin and placed anteriorly to it, there is a ridge running across the dorsal surface. The ridge ends in an expansion which forms the angle at which the posteromesial margin meets the posterolateral one. This angular expansion corresponds to an indentation of the clavicular border of the interclavicle. The ridge corresponds to a laterally placed ridge on the interclavicle, and the attachment between the clavicles and the interclavicle is strongest in this region, both bones being very thick here, broadly overlapping and indented.

Interclavicles

There is only one interclavicle in the collection (Specimen no. I.S.I. A. 9), which comes from Achlapur, locality no. 2. To this may be added one interclavicle (specimen no. K33/638 from Maleri) figured by Huene (1940, plate 1, figure 1) which he referred to as his metoposaurid type of sculpture no. 1, but which agrees in all essentials with the new specimen. Both the interclavicles are fairly complete. They are bilaterally symmetrical bones, and the two sides of specimen I.S.I. A. 9 are sufficiently well preserved to allow a restoration to be made (figure 19). Like all other known metoposaur interclavicles, these are typically diamond shaped in outline and longer than they are broad. One of the diagonals is in the longitudinal axis of the animal and bisects the interclavicle down its length, while the other diagonal is at right angles to the former and divides the interclavicle into two unequal portions, of which the anterior part is larger than the posterior part. The posterior portion of the bone is very thick (23 mm) but it thins down anteriorly and anterolaterally (4 mm at the most anterior tip). The maximum thickness is, however, at the 'centre', that is at the intersection of the two diagonals, accentuated by a prominent boss on the dorsal surface of the bone.

The ventral surface of the interclavicle is ornamented with grooves and ridges. Near the centre of ossification the ornament consists of polygonal or rounded pits; while towards the periphery the ornament elongates to form grooves which may become bifurcate. The ornament extends right up to the posterolateral margins, whereas the anterolateral extensions of the sculptured area stop before reaching the margins, and the bone steps sharply and deeply down from the level of the sculpured surface to form a thin shelf-like recess on each side for the reception of the clavicle. This unornamented recess for the clavicle is broadest posteriorly, where the margin of the thick sculptured area swings mesially. This broad part of the 'recess', particularly its posterior portion, forms a strong abutment against the thickest part of the clavicle. Anteriorly the 'recess' gradually narrows down and extends beyond the most anterior tip of the sculptured surface.

TABLE 3. MEASUREMENTS OF THE TWO INTERCLAVICLES (IN MM)

specimen number	length	width	length of the sculptured area	width of the sculptured area	length of the posterior end (from 'centre' to posterior tip)
I.S.I. A. 9	332	270	315	250	102
K33/638	—	—	243	216	86

The dorsal surface of the interclavicle is smooth and without any sculpture. There is an elevated boss at the centre. Two ridges extend from the boss on each side, one laterally and one posterolaterally. In between the lateral and posterolateral ridges there is a depression. Posterocentrally placed, and between the two posterolateral ridges, there is another depression. The posterolateral ridge, on either side, bifurcates near the margin to form a small depression in between its two branches. Anterior to the boss the bone surface slopes gently into a concavity, then becomes flat without any marked undulations.

Humerus

The humerus, a left one, although found isolated in the field, occurred very close to other metoposaur specimens. It is obviously a stegocephalian and belongs to *Metoposaurus maleriensis*. The ossified portion of the humerus (figures 26 and 27, plate 2) is a somewhat short and wide bone, built on the tetrahedral pattern as in all large primitive tetrapods. The proximal and distal planes of the bone are typically 'twisted' in this specimen at an angle of 50° to each other. There is hardly any shaft region and the bone consists of two gradually spreading extremities terminated by unfinished ends indicating cartilaginous extensions. The surface of the proximal end or head is somewhat flattened laterally with its anteroventral part narrower than the posterodorsal part to give a more or less triangular, curved area. The convexly curved surface of the distal end, on the other hand, is expanded anteroposteriorly, thickened anteroventrally to accommodate a cartilaginous extension bearing the articular surface for the radius; anterodorsally it forms the ectepicondylar process. On the anterior edge of the humerus, immediately proximal to the facet for the articular surface for the radius is a narrow cartilage-bearing area which is the abbreviated supinator process. The posterior extension of the distal end of the humerus is thinner and spreads out into an entepicondular process, which was continued in cartilage. The anterior face of the humerus is broader proximally and narrow distally. Its ventral margin forms the deltoid ridge which expands distally into a rugose area and is separated from the supinator process by a notch. Near the ventral margin and proximal to the notch there is a rugosity for the pectoral crest. The dorsal face is narrow proximally but becomes expanded distally into a fan-shaped centrally depressed entepicondylar surface. Neither ent- nor ectepicondylar foramina are present. The dorsal border of the posteroventral face forms a curve which runs between the head and the entepicondylar process.

Ischium

The ossified portion of the ischium (figure 20) of the right side is a small crescent-shaped bone and all its margins except the posterior margin have unfinished edges indicating cartilaginous extensions. The thickened anterolateral margin has two facets, one was probably connected with the ilium by cartilage and the other formed part of the acetabulum. Its anterior border is comparatively thin and straight and probably extended as cartilage to meet the right pubis. The medial margin is gently convex; thicker anteriorly but gradually becomes thin posteriorly. This face is also rugose and extended as cartilage to meet the ischium of the other side along the midline. Posteromedially the ischium is narrow and thin. Posteriorly the ischium has a finished concave border. The dorsal surface of the bone is probably oriented horizontally with a centrally depressed area which slopes gently upward anterolaterally to the region of thickened iliac contact. Ventrally the central portion of the ischium is slightly convex compared to the lateral portion but there is a prominent thickening near the medial border. There are a few nutrient foramina facing laterally on the ventral surface.

Metoposaurus maleriensis n.sp. compared with other metoposaurids

The fossils included in the family Metoposauridae are known from rocks of distantly separated countries of the world. *Metoposaurus diagnosticus* is known from the Upper Triassic of Germany; a large number of metoposaurs are known from the Upper Triassic of North America and these have been assigned to three species of *Eupelor* by Colbert & Imbrie (1956). (The taxonomy of the North American metoposaurs as given by Colbert & Imbrie has already been mentioned and need not be elaborated again.) *M. maleriensis*, the new species from the Upper Triassic of India described in the present paper, constitutes another adequately known member of the family. Two other genera are usually included in the Metoposauridae, *Dictyocephalus* from North America and *Trigonosternum* from Germany, but both these forms are known from material which is quite inadequate for detailed comparison and identification. Comparison must therefore be restricted to the adequately known members, namely *Metoposaurus diagnosticus*, the three species of *Eupelor* and *Metoposaurus maleriensis*.

The most striking feature of the metoposaur members lies in their extreme similarity. As Romer (1947) pointed out in his 'Review of the Labyrinthodontia': 'It is indisputable that the metoposaurs form a compact group...between which there are but minor generic differences, and which have many common features contrasting strongly with other Labyrinthodonts'. One of the main differences that has so far been recognized between the German and North American metoposaurs is that the lacrimal bone forms a part of the orbital margin in the latter, whereas in the former the lacrimal is excluded from the orbit. This difference in the position of the lacrimal in relation to the orbit has generally been regarded as a means of generic distinction (cf. Colbert & Imbrie 1956) and has sometimes been taken to distinguish the rank of sub-family (Säve-Söderbergh 1935). But this difference becomes less clear-cut when the individual skulls of species within each genus are considered. The position of the lacrimal seems to be well displayed in two of the six skulls of *Metoposaurus diagnosticus* (Meyer 1856, plate 61, figure 3; Fraas 1889, plate 12). Turning to the species of North American genus *Eupelor*, and using the taxonomy of Colbert & Imbrie (1956), it can be seen that in all figured skulls of *E. browni* and *E. fraasi fraasi*, the lacrimal enters the orbital margin. The condition of the lacrimal is not constant in the skulls of *E. fraasi jonesi*, known from the Dockum formation in Texas. As many as thirteen skulls have been described or figured from three localities; two from Crosby County ('*Buettneria perfecta*' Case), five from Scurry County ('*B. bakeri*' Case) and six from Howard County ('*B. howardensis*' Sawin); each of the three localities being separated from one another by a distance of nearly 40 miles. The skulls from Crosby and Howard Counties have the lacrimal touching the anterior margin of the orbits but four of the five skulls from Scurry County ('*B. bakeri*' Case 1932, figures 2–5), have been well figured and in each skull the lacrimal is clearly excluded from the orbit margin, a condition seen in *Metoposaurus diagnosticus*. While it is useless to argue that the Scurry County metoposaurs are more closely akin to German metoposaurs than to their North American relatives, it can be stated that the position of the lacrimal may not only vary within a genus but also within a species, even though that species occurs within a relatively small area. It also brings out the wide latitude of variation within a metoposaur species and draws attention to the very close similarity between the two well-known genera, separated by a distance of 4 to 5 thousand miles. The necessity of a reconsideration of the taxonomy of the metoposaurs does not seem to be unjustified under such circumstances and will be taken up later.

Now turning to the comparison of the Indian metoposaur species, the following differences have been noted between *M. maleriensis* and *M. diagnosticus*:

1. In *M. diagnosticus* the lacrimal is rather small and excluded from the margin of the orbit. In *M. maleriensis* the lacrimal is narrow and long and enters the margin of the orbit.
2. The postparietals in *M. diagnosticus* are always proportionately longer than those in *M. maleriensis*.
3. The interclavicle of *M. diagnosticus* has a long prolongation posteriorly from the centre of the bone. In *M. maleriensis* this posterior extension is shorter.
4. In *M. diagnosticus* the clavicles make a long contact anterior to the interclavicle but in *M. maleriensis* where is no sign of such a long contact.
5. The clavicles and interclavicles of *M. diagnosticus* have smaller areas of rounded sculpture compared to *M. maleriensis*.

These differences are used to distinguish the Indian metoposaur *M. maleriensis* as specifically distinct from *M. diagnostisus*.

When the North American genus *Eupelor* is considered, the comparison based on the above characters does not hold good. In fact there is such a close similarity between the Indian metoposaur and *Eupelor*, that it is not easy to find any single gross morphological character which can be used to distinguish between them generically. Differences between species within the genus *Eupelor* are based on characters which become significant only when studied biometrically, based on the large samples available from North American localities. A biometric study of the Indian metoposaur is not yet possible as only a few specimens are available and none of the skulls is complete. In the absence of such a study it is not possible to say whether or not the Maleri metoposaur departs sufficiently strongly from *Eupelor* on various characters of skull proportion, orbital position, etc., to warrant even a specific distinction. Nevertheless the Indian metoposaur is geographically 8 or 9 thousand miles distant from *Eupelor* (though the supporters of the continental drift theory would reduce this distance by most of the width of the Atlantic) and a certain amount of geographic isolation is implied by the presence of Tethys and a proto-North Atlantic. It seems safest to consider the Indian form as specifically distinct from *Eupelor*, at least provisionally, until sufficient specimens are available for closer study.

Although so few specimens of the Indian metoposaur are available, it is interesting to note certain suggestive features and compare them with the conditions seen in *Eupelor*. First, there is a qualitative difference in the sculpture of the skull-roof. In the Indian form the elongation of the sculpture into grooves is well marked in larger skulls whereas in *Eupelor* such grooves are not so pronounced in the zones of intensive growth. Secondly, Colbert & Imbrie (1956) have shown that various species of *Eupelor* differ in the position of the orbits and elongation of the skull, which are dependent on the growth pattern during ontogeny. The changes seen among the different species of *Eupelor* can be tabulated as follows.

		position of the orbits		
		very little change	moving anteriorly	moving posteriorly
skull elongation	very little change	*Eupelor fraasi fraasi*, Arizona		*Eupelor fraasi fraasi*, New Mexico
	skull becoming narrower			
	skull becoming wider	*Eupelor fraasi jonesi*, Texas	*Eupelor browni*, Wyoming	

It has already been emphasized in a previous section that the relative growth shown by two specimens of *Metoposaurus maleriensis* indicates a posterior movement of the orbits during ontogeny with very little change in skull elongation. This probably indicates that the Indian metoposaur is more similar to the New Mexico forms as far as relative growth of the skull is concerned.

A diagnosis of *M. maleriensis* has been avoided. The reason is that most of the observable morphological characters are variable both within and between the metoposaur species and the fossil sample of *M. maleriensis* is too small to assess the modal condition of these characters. To make a diagnosis, or even a definition (see Simpson 1961, p. 138), biometric study would be necessary. As this is not possible the new species can only be characterized by giving a description, geographic location, and horizon of the specimens, as has been done in an earlier section.

Taxonomy

The account of *Metoposaurus maleriensis* and its comparison with other well-known metoposaur members demonstrate its close relationship with *Metoposaurus* on one hand and *Eupelor* on the other. Moreover, the very close similarity noted between *Metoposaurus* and *Eupelor* raises serious doubts whether these two forms are generically distinct. The most important difference that has so far been used for regarding *Eupelor* as generically distinct from *Metoposaurus* is in the position of the lacrimal bone in relation to the orbit. In *Metoposaurus*, the lacrimal is never in contact with the orbital margin. In the North America forms, according to Colbert & Imbrie (1956, p. 418), this bone always enters the orbital border. But it has been shown in the previous section that individual skulls within a species of *Eupelor* show lacrimal position exactly similar to that of *Metoposaurus*. Therefore it becomes difficult to use the position of the lacrimal as a character for distinguishing genera. The other differences between *Metoposaurus* and *Eupelor* such as the way in which the clavicles meet in front of the interclavicle and in the area covered by rounded pits on shoulder girdle bones are not important differences (cf. Colbert & Imbrie 1956) and may even indicate age characters. It is more appropriate to consider these metoposaurs as belonging to a single genus and discussion therefore centres upon the question of priority between generic names.

The first metoposaur to be described was *Metopias diagnosticus*, from the German Keuper, named by von Meyer in 1842. Subsequently Lydekker substituted the name *Metoposaurus* for *Metopias*, this latter name having been preoccupied. The other described European metoposaurs are regarded as synonymous with *Metoposaurus diagnosticus*. The North American genus *Eupelor* was described by Cope in 1866 and all the metoposaurs subsequently described from North America have been assigned to *Eupelor*. There can be no doubt, therefore, that the material assigned to *Metoposaurus diagnosticus*, the type for the genus *Metoposaurus*, has priority over all other metoposaur genera subsequently described. Since there is no morphological evidence to regard *Eupelor* as a genus distinct from *Metoposaurus* it is more appropriate to consider the former name synomymous with the latter. It is realized that the elimination of the genus *Eupelor* may cause a temporary confusion, but it is also true that many of the North American metoposaur genera have already been dropped in recent years. It is hoped that the revised taxonomy of the Family Metoposauridae given below will help in avoiding the need of a future change of nomenclature.

I. Family ***Metoposauridae*** Watson 1919

Genus *Metoposaurus* (Meyer 1842) Lydekker 1890 (*pro Metopias* Meyer 1842 *nom. imperf.*)

Synonyms: *Metopias* Meyer 1842
Eupelor Cope 1866
Anaschisma Branson 1905
Calamops Sinclair 1917
Buettneria Branson & Mehl 1929
Borborophagus Branson & Mehl 1929
Kalamoiketor Branson & Mehl 1929
Koskinonodon Branson & Mehl 1929

Metoposaurus diagnosticus (Meyer) 1842, Keuper, central Europe

Synonyms: *Metoposaurus stuttgartiensis* Fraas 1913
Metoposaurus santaecrucis (Koken) 1913
Metoposaurus heimi Kuhn 1932

Metoposaurus durus (Cope) 1866, Newark group, North America

Synonym: *Eupelor durus* Cope 1866
Probable synonym: *Calamops paludosus* Sinclair 1917

Metoposaurus fraasi fraasi (Lucas) 1904, Chinle formation, North America

Synonyms: *Metoposaurus fraasi* Lucas 1904
Buettneria major Branson & Mehl 1929
Kalamoiketor pinkleyi Branson & Mehl 1929

Metoposaurus fraasi jonesi (Case) 1922, Dockum formation, North America

Synonyms: *Buettneria perfecta* Case 1922
Buettneria bakeri Case 1931
Buettneria howardensis Sawin 1945

Metoposaurus browni (Branson) 1905, Popo Agie formation, North America

Synonyms: *Anaschisma browni* Branson 1905
Anaschisma brachygnatha Branson 1905
Borborophagus wyomingensis Branson & Mehl 1929
Koskinonodon princeps Branson & Mehl 1929

Metoposaurus maleriensis n.sp., Maleri formation, India

II. Genera doubtfully assigned to Family ***Metoposauridae***

Genus *Dictyocephalus* Leidy 1856

Dictyocephalus elegans Leidy 1856, Newark group, North America

Genus *Trigonosternum* Schmidt 1931

Trigonosternum latum Schmidt 1931, Lettenkohle, Central Europe

Probable age of the Maleri fauna with reference to the upper and lower limit of the metoposaurs

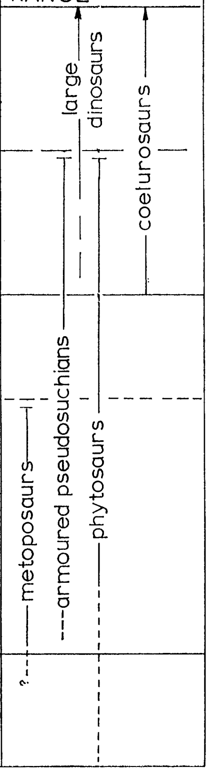
A review of the different views on the age of the Maleri fauna (Oldham 1859; Blanford 1878; Cotter 1917; Fox 1931; Huene 1940) reveals that opinion has varied from Middle Triassic to Jurassic. There are a number of reasons for these differences of opinion. First, the fossil material was fragmentary in nature and only a few of the fragments could be identified with precision. Secondly, the beds underlying the Maleris, the Kamthis, have so far proved barren of fossils, and although the overlying Kota rocks have provided good index fossils of Liassic age there is an unconformity between the Kotas and the Maleris. Thirdly, the nature of the Maleri fauna has a somewhat peculiar composition which needs careful consideration. Fourthly, there has always been some uncertainty in age determination and correlation of the Triassic continental sediments and their faunas. There is a well dated sequence up to the *Cynognathus* zone in the South African Karroo formation, which reaches as far as the base of the Middle Triassic. The rocks immediately overlying the *Cynognathus* zone in South Africa (Molteno beds) have not provided us with an equally good fauna. Upper Triassic faunas are known from formations widely scattered in different parts of the world and hence their correlation has always been somewhat uncertain. But with increasing knowledge of the Upper Triassic faunas and with the discovery of undoubted metoposaurs from the Maleri formation, it is perhaps possible to make a further contribution on the age of the Maleri fauna.

The present discussion is mainly confined to two problems: (1) the lower and upper limits of the range in time of the metoposaurs, and (2) the probable age of the Maleri fauna.

The metoposaurs, besides the Indian occurrences, are known from the Upper Triassic of Germany and North America. In Germany undoubted metoposaur remains come from the Schilfsandstein, Lehrbergstufe and Blasensandstein of the Swabian Keuper and the Raibl beds of Upper Franconia. An interclavicle impression of metoposaurid affinities has been recorded from the Lettenkohle of Thuringia, but the specimen is incomplete and must be regarded as a very doubtful record of metoposaur occurrence because not determinable taxonomically (Romer 1947; Colbert & Imbrie 1956).

The Keuper of southwestern Germany is the standard for the Upper Triassic and includes all deposits from the Lettenkohle through the Rhät sandstones, ranging in age from the upper part of Ladinian to Rhaetian (Bubnoff 1935; Brinkmann 1960). The succession with its faunas and their marine equivalents is tabulated in table 4. The Lettenkohle, although regarded as Lower Keuper by German authors, contains the typical Muschelkalk mollusca *Alloceratities schmidti* and *Myophoria goldfussi* in a marine band near its top and has been excluded from the Keuper by some workers (c.f. Neaverson 1955; Gignoux 1955). The Rhatsandstein (Upper Keuper of German authors) is also quite distinct from the underlying Keuper (Middle Keuper of the German authors) and in some parts of the world, such as Britain, the Rhaetic is always excluded from the Keuper. To avoid confusion in using the term Keuper and its subdivisions, the author prefers to use the standard marine zonal equivalents when referring to the subdivisions of the Keuper of Germany. The Schilfsandstein is underlain by Gipskeuper, which has, in Silesia and Poland, a marine band near its base containing *Myophoria kefersteini* indicating Carnian age (Gignoux 1955). The Raibl beds also have a Carnian fauna including *M. kefersteini* (Gignoux 1955). The Schilfsandstein has a rich Keuper flora and may be regarded as representing the upper part of the Carnian. A direct correlation of the Blasensandstein and Lehrbergstufe with the standard marine succession is not possible. However, the Blasensandstein is usually equated with the lower part of the Norian (Bubnoff 1935; Brinkmann 1960). The position of Lehrbergstufe, which underlies the Blasensandstein in Upper Franconia, is rather uncertain and may be partly Carnian and partly Norian. Higher up in the succession, the Stubensandstein is probably roughly equivalent to the middle part of Norian (Walker 1961). It has a good vertebrate fauna, but no metoposaurs have been found in it although plagiosaurs and capitosaurs are present. The Knollenmergel overlies the Stubensandstein and represents the upper part of the Norian. Above the Knollenmergel comes the Rhätsandstein of undoubted Rhaetian age. So in Germany, if the doubtful Lettenkohle occurrence is omitted, the metoposaur range from horizons equivalent to Gipskeuper up to Blasensandstein, that is from Carnian to lower part of Norian and have disappeared before the middle Norian. Of the other amphibians associated with the metoposaurs, the capitosaurs extend from Lettenkohle to Stubensandstein and the plagiosaurs from Lettenkohle to Rhätsandstein.

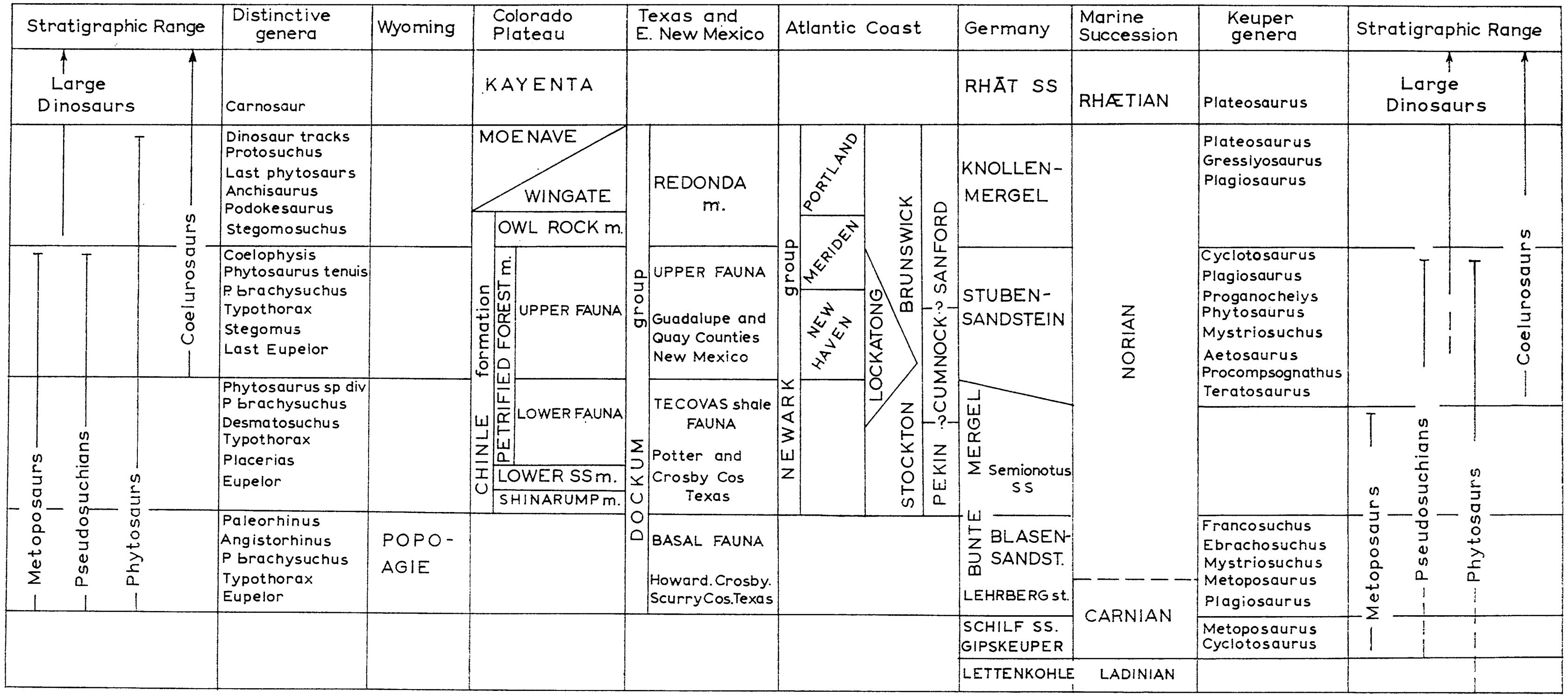
TABLE 4

MARINE SUCCESSION	CHARACTERISTIC MARINE FOSSILS	"KEUPER" SUCCESSION		AMPHIBIANS	REPTILES	STRATIGRAPHIC RANGE
RHÆTIAN	Avicula cantorta	RHÄTSANDSTEIN		Gerrothorax	Tritylodonts Plateosaurus	
NORIAN		KNOLLENMERGEL		Plagiosaurus	Plateosaurus Gresslyosaurus	
		STUBENSANDSTEIN		Cyclotosaurus Plagiosaurus	Phytosaurus Mystriosaurus Aetosaurus Teratosaurus Procompsognathus Proganochelys	
		SEMIONOTUS-SANDSTEIN	BUNTE MERGEL			
		PLATTENSANDSTEIN				
		BLASENSANDSTEIN		Metoposaurus Cyclotosaurus Plagiosaurus	Franchonosuchus Ebrachosuchus Mystriosaurus	
CARNIAN		LEHRBERGSTUFE				
		SCHILFSANDSTEIN	RAIBL BEDS	Metoposaurus Mastodonosaurus Capitosaurus Cyclotosaurus	Phytosaurus Dyoplax	
	Myophoria kefersteini	GIPSKEUPER		Metoposaurus "Mastodonosaurus"	Henodus	
LADINIAN	Myophoria goldfussi Alloceratites schmidti	LETTENKOHLE		Mastodonosaurus Plagiosuchus Plagiosternum ?Trigonosternum	Nothosaurus Plesiosaurus Zanclodon	

In North America, the metoposaurs are known from the Upper Triassic Dockum group of Texas and New Mexico, Popo Agie member of the Chugwater formation of Wyoming, Chinle formation of the Colorado plateau, and Newark group of eastern North America. The Dockum group has four faunal zones (table 5) defined on the basis of characteristic phytosaurs (Gregory 1957). The metoposaurs are common in the lower two zones, become less prominent in the third and are not present in the uppermost zone (Redonda member). The Popo Agie member of the Chugwater formation contains metoposaurs and the fauna as a whole is regarded as closely related to the basal Dockum, this opinion being based on the close similarity between the phytosaurs present in the two formations. The Chinle formation has a fauna comparable with the middle two faunal zones of the Dockum and the metoposaurs are also extremely similar in both. Metoposaurs from the Brunswick formation of the Newark group are less well known, but they are present as in earlier faunal horizons of the west. No Upper Triassic amphibians, other than the metoposaurs, are known from North America. All the North American metoposaurs are very closely related to one another and belong to one genus.

Although the metoposaurs from North America and Germany are very similar and suggest the possibility of near contemporaneity of the rocks in which they are found, it is necessary to consider in greater detail whether or not the range in time of North American metoposaurs is similar to that in Germany. To achieve this it is essential to attempt a correlation of the metoposaur-bearing horizons of North America with the German succession by a careful comparison of the total faunas found in each. Three main archosaur elements in the faunas require consideration—phytosaurs, armoured pseudosuchians and dinosaurs. All these considerations regarding the age of the continental Upper Triassic of North America, relative to the standard German Triassic sequence are also relevant to the determination of the age of the Maleri fauna, but this will be taken up later on. The phytosaurs occur throughout the Dockum and some evolutionary trends among the phytosaurs have been established (Gregory 1962). The armoured pseudosuchians are also an important component of Upper Triassic faunas. The dinosaurs, although absent in the lower part of the Upper Triassic, appear higher up in the succession. Colbert & Gregory (1957) have discussed in some detail the correlation of the North American Upper Triassic sediments by vertebrate fossils and Gregory (1957) has made an attempt to establish their relationship with the German Keuper succession. It is quite likely that the Popo Agie member of the Chugwater formation and the Basal Dockum are roughly equivalent to the Blasensandstein (Lower Norian) on the basis of the close similarity between the associated phytosaurs; the North American genus *Palaeorhinus* agreeing in all essential characters with *Franchonosuchus* from the Blasensandstein. Gregory (1957) has considered the above mentioned North American deposits to be later than Schilfsandstein (Carnian), largely 'on the negative evidence of absence of phytosaurs' in the latter. But a jaw fragment belonging to *Phytosaurus* (*P. arenaceus*, Fraas 1896) has been reported from the Schilfsandstein and it indicates that the lower limits of Basal Dockum and Popo Agie might have extended down into the Schilfsandstein. The upper faunas of the Chinle and Dockum and the lower part of the Brunswick formation of the Newark group are the last horizons where metoposaurs are found in North America. The phytosaurs and armoured pseudosuchians associated with them are very closely comparable with the Stubensandstein (middle Norian) fauna of Germany. The phytosaur *Mystriosuchus* from the Stubensandstein is comparable to North American genera *Phytosaurus* and *Rutiodon*. *Aetosaurus*,

TABLE 5



Stratigraphic Range	Distinctive genera	Wyoming	Colorado Plateau	Texas and E. New Mexico	Atlantic Coast	Germany	Marine Succession	Keuper genera	Stratigraphic Range
Large Dinosaurs	Carnosaur		KAYENTA			RHÄT SS	RHÆTIAN	Plateosaurus	Large Dinosaurs
	Dinosaur tracks Protosuchus Last phytosaurs Anchisaurus Podokesaurus Stegomosuchus		MOENAVE WINGATE OWL ROCK m.	DOCKUM group REDONDA m.	NEWARK group PORTLAND	KNOLLEN-MERGEL	NORIAN	Plateosaurus Gresslyosaurus Plagiosaurus	
Coelurosaurs	Coelophysis Phytosaurus tenuis P. brachysuchus Typothorax Stegomus Last Eupelor		CHINLE formation PETRIFIED FOREST m. UPPER FAUNA	UPPER FAUNA Guadalupe and Quay Counties New Mexico	MERIDEN NEW HAVEN LOCKATONG BRUNSWICK PEKIN ?CUMNOCK ? SANFORD	STUBEN-SANDSTEIN		Cyclotosaurus Plagiosaurus Proganocheiys Phytosaurus Mystriosuchus Aetosaurus Procompsognathus Teratosaurus	Coelurosaurs
Metoposaurs Pseudosuchians Phytosaurs	Phytosaurus sp div P brachysuchus Desmatosuchus Typothorax Placerias Eupelor		LOWER FAUNA LOWER SS m. SHINARUMP m.	TECOVAS shale FAUNA Potter and Crosby Cos Texas	STOCKTON	MERGEL Semionotus SS			Metoposaurs Pseudosuchians Phytosaurs
	Paleorhinus Angistorhinus P brachysuchus Typothorax Eupelor	POPO-AGIE		BASAL FAUNA Howard. Crosby. Scurry Cos. Texas		BUNTE BLASEN-SANDST. LEHRBERG st.	CARNIAN	Francosuchus Ebrachosuchus Mystriosuchus Metoposaurus Plagiosaurus	
						SCHILF SS. GIPSKEUPER		Metoposaurus Cyclotosaurus	
						LETTENKOHLE	LADINIAN		

the armoured pseudosuchian from the Stubensandstein is close to *Typothorax*, common in Chinle and Dockum, and to *Stegomus* of the Newark group (Gregory 1957; Walker 1961).

In North America, therefore, the metoposaurs have a longer geological history and extend up to horizons which are probably homotaxially equivalent to the German Stubensandstein. It can, therefore, be concluded that, on the evidence available at present, metoposaurs are restricted to the continental horizons equivalent to Carnian and lower and middle Norian. Miall (1874) reported a lower jaw from the Rhaetic of Aust Cliff in Britain as probably a metoposaur, a suggestion which has lately been disproved (Dr R. J. G. Savage, personal communication).

This study presents definite evidence of the existence of metoposaurs in the Maleri formation; so it is necessary to reconsider the age of the Maleri fauna. The close similarity between the metoposaurs from the Maleri formation with those from Germany and North America has already been discussed. The vertebrate fauna of the Maleri formation, as determined by previous workers, is as follows:

Fishes—Order—Dipnoi
- *Ceratodus hunterianus*
- *Ceratodus hislopianus*
- *Ceratodus virapa*

Labyrinthodontia—Family Metoposauridae
- Form No. 1
- Form No. 2
- Form No. 3

Reptilia—
1. Subclass—Lepidosauria
    - Order—Rhynchosauridae
        - *Paradapedon huxleyi*
        - *Paradapedon* (?) *indicus*
2. Subclass—Archosauria
    - A. Order—Thecondontia
        - Suborder—Phytosauria
            - *Brachysuchus* (?) *maleriensis*
            - Form No. 2
            - Form No. 3
            - cf. *Typothorax* (?) sp.
    - B. Order—Saurischia
        - (i) Suborder—Coelurosauria
            - Form No. 1
            - Form No. 2
        - (ii) Suborder—Prosauropoda
            - c.f. *Massospondylus* sp.

The fauna listed above has been described by Miall (1878), Lydekker (1885) and Huene (1940). The fossils are extremely fragmentary and collected from the surface. The dipnoan *Ceratodus* is known only from teeth. It has already been shown that only one form of metoposaur, *Metoposaurus maleriensis*, is present in the Maleris. It seems that the rhynchosaurs are the best known members of the fauna, although known very incompletely. Huene (1940) believed that four types of phytosaurs are present; one of them compares favourably with *Brachysuchus*, but he ascribed to phytosaurs some scutes very similar to *Typothorax*, because Huene regarded *Typothorax* as a phytosaur. Two forms of coelurosaur have been based on three broken fragments, a vertebral centrum, distal part of a left femur and head of a right tibia. The presence of a prosauropod similar to *Massospondylus* has been based on two vertebrae; both of them are broken. In an unpublished work Charig (Ph.D. thesis 1956) has shown successfully that some pseudosuchians during the Triassic had assumed many dinosaurian characters without becoming true dinosaurs. Romer (1960) seems to have supported Charig's findings. It is, therefore, difficult for the author to accept the fragments mentioned above as evidence for the presence of dinosaur characters and they may belong to advanced pseudosuchians. Collection of better material of the Maleri archosaurs is urgently needed. At present the Maleri fauna can be identified as follows:

1. Fishes
   Dipnoi—*Ceratodus hunterianus*, *C. hislopianus*, *C. virapa*
2. Amphibians
   Metoposaurs—*Metoposaurus maleriensis*
3. Reptiles
   Rhynchosaurs—*Paradapedon huxleyi*, *P.* (?) *indicus*
   Phytosaurs—*Brachysuchus* (?) *maleriensis*
   Pseudosuchia—some scutes similar to *Typothorax*
   Coelurosauria } very doubtful fragments
   Prosauropoda }

Ceratodus has a long range; it appears in the Triassic and continues as far as Upper Cretaceous. The rhynchosaurs, although dominant in the Middle Triassic (Romer 1956, 1960) have some Upper Triassic representatives. Walker (1961) noted the occurrence of *Stagonolepis*, a pseudosuchian from the same horizon as the rhynchosaur *Hyperodapedon* from the Triassic of Elgin, which he correlated with the Stubensandstein in Germany. Baird (Walker 1961) has discovered rhynchosaurian remains from the Wolfville sandstones of Nova Scotia, incidentally the first report of the presence of rhynchosaurs in North America. Baird & Take (1959) have provisionally correlated the Wolfville sandstones with the New Haven arkose of Connecticut Valley and the Lower Brunswick formation of New Jersey. The latter have a reptilian fauna closely comparable with that of the Stubensandstein and the Elgin sandstones. The Maleri rhynchosaur *Paradapedon* appears to be extremely similar to *Hyperodapedon*, although differing from the latter in minor features such as a second row of teeth in the lower jaw. According to Huene (1940), the skull of *Paradapedon* has developed extravagant extoses, and so possibly indicates a terminal stage. These extravagant extoses may indicate a very old individual. Thus the discoveries in North America and the restudy of the Elgin fauna suggest that rhynchosaurs may extend to horizons as high as the middle Norian Stubensandstein and its equivalents, so that the Maleris may also extend up this horizon.

The presence of a metoposaur strongly indicates the age of the Maleris from Carnian to roughly Middle Norian. This has already been discussed in detail.

Phytosaur remains from the Maleri formation include a large animal aff. *Brachysuchus maleriensis* (Huene 1940) and fragments of two smaller types which Huene did not name.

Gregory (1962) commented that 'the specimens are most unsatisfactory, for the lack of critical portions, for comparisons with other phytosaurs. Some or all may well pertain to *Phytosaurus* or some may represent *Rutiodon*'. Both *Phytosaurus* and *Rutiodon* are known from the Upper Triassic of North America.

Before coming to a conclusion about the possible equivalence of the Maleris with other better known faunal horizons of the world, a marked change in the Upper Triassic continental faunas is worth mentioning.

The faunas known from Schilfsandstein, Blasensandstein and Stubensandstein and their North American equivalents consist mainly of phytosaurs and armoured pseudosuchians, besides the amphibians. The coelurosaurs appear near the top. In the succeeding horizons of Knollenmergel and their probable equivalents in North America there is a noticeable change in the fauna. The armoured pseudosuchians are absent; the phytosaurs become rare and the large dinosaurs become the most prominent archosaurian element of the fauna.

The fauna of the Maleri formation, based on its *reliably* determinable members tends to indicate an age older than the Knollenmergel and its equivalents. The upper limit of the Maleri fauna, therefore, can be fixed as Middle Norian (Stubensandstein and its equivalent). This must be regarded as strictly provisional, as if a prosauropod should prove to be present, this might require a reconsideration of views on the sequence of the Upper Triassic faunas in other parts of the world. The lower limit of the age of the Maleri fauna cannot be fixed without doubt. It is not easy to correlate or specify Middle Triassic terrestrial faunas owing to the highly peculiar nature of the German Muschelkalk faunas which are mainly aquatic, and owing to the absence of mammal-like reptiles from the whole German Triassic sequence. However, the composition of the Maleri fauna definitely indicates similarity with horizons as old as Schilfsandstein and its equivalents in North America, which are of undoubted Carnian age (see p. 46). So it can be concluded that the age of the Maleri fauna is probably Carnian or lower to middle Norian. Discovery of good material of the phytosaurs may allow a more exact correlation within Carnian–Middle Norian.

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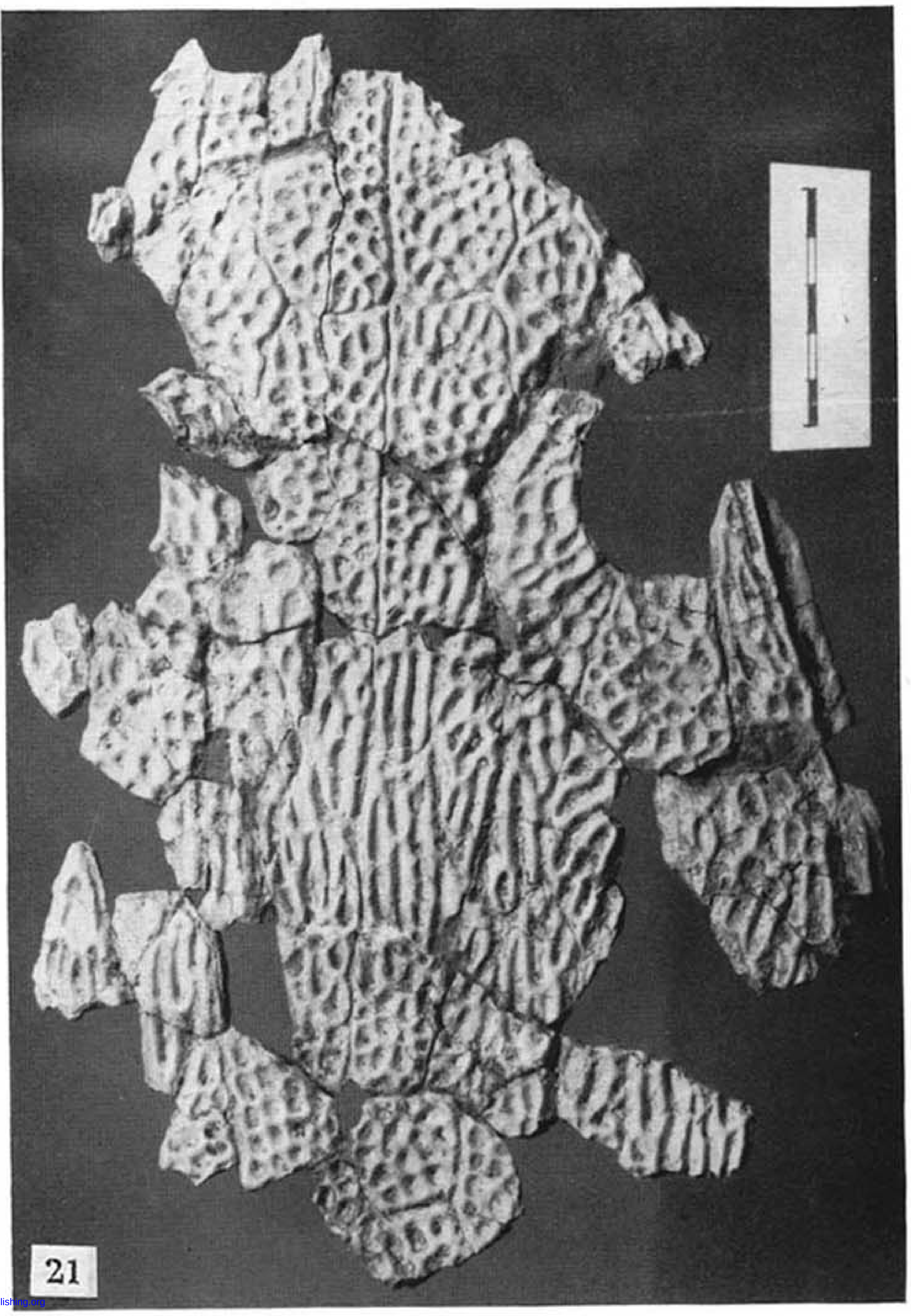
EXPLANATION OF ABBREVIATIONS

AIC	anterior foramen for the internal carotid.
APT	anterior rising process of quadrate ramus of the pterygoid.
ASO	attachment for the supraoccipital.
BPTP	recess for the basipterygoid process.
DBC	dorsal side of the cartilaginous brain-case.
DSQ	descending flange of the squamosal.
E	trace of the epipterygoid.
ECT	ectopterygoid.
EO	exoccipital.
EO.RP	rising process of exoccipital
F	frontal.
INA	internasal.
J	jugal
L	lacrimal.
M	maxilla.
N	nasal.
N.INT	internal nerves.
n.a. ant.	anterior neural arch facet.
n.a. post.	posterior neural arch facet.
nc	notochordal pit.
OC	otic capsule.
ORL	ridge bounding otic region laterally.
ORP	ridge bounding otic region posteriorly.
P	parietal.
PAL	palatine.
PAR.P	trace of paroccipital process.
PCR	ridge on cultriform process of parasphenoid.
PF	postfrontal.
PMX	premaxilla.
PN	postnarial.
PO	postorbital
PP	postparietal.
PPT	posterior rising process of the quadrate ramus of the pterygoid.
PQF	paraquadrate foramen.
PRF	prefrontal.
PSP	parasphenoid.
PT	pterygoid.
PTF	posttemporal fossa.
Q	quadrate.
QJ	quadratojugal.
SMX	septomaxilla.
SPH	seating of cartilaginous sphenethmoid.
SQ	squamosal.
ST	supratemporal.
T	tabular.
V	vomer.



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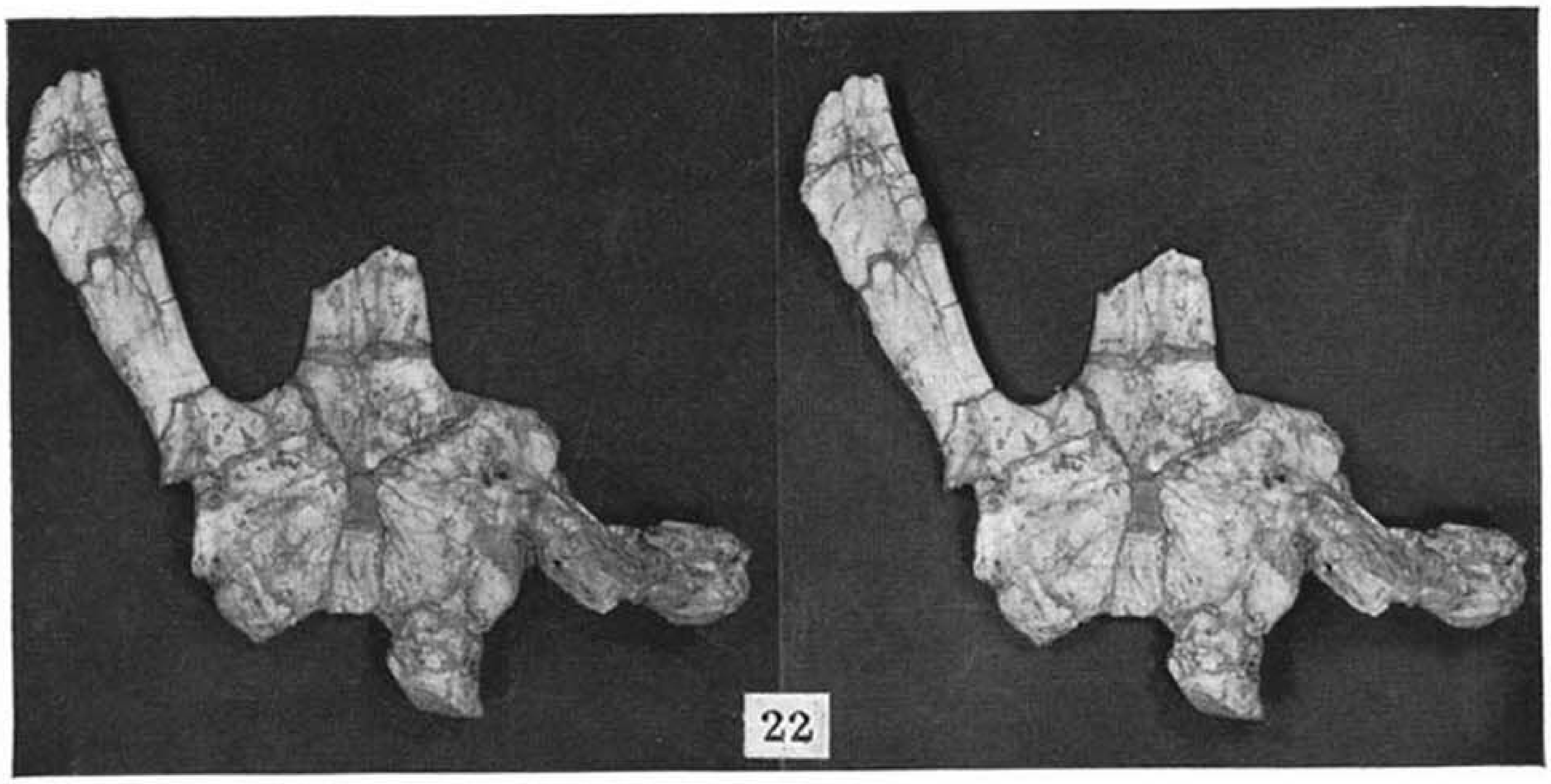
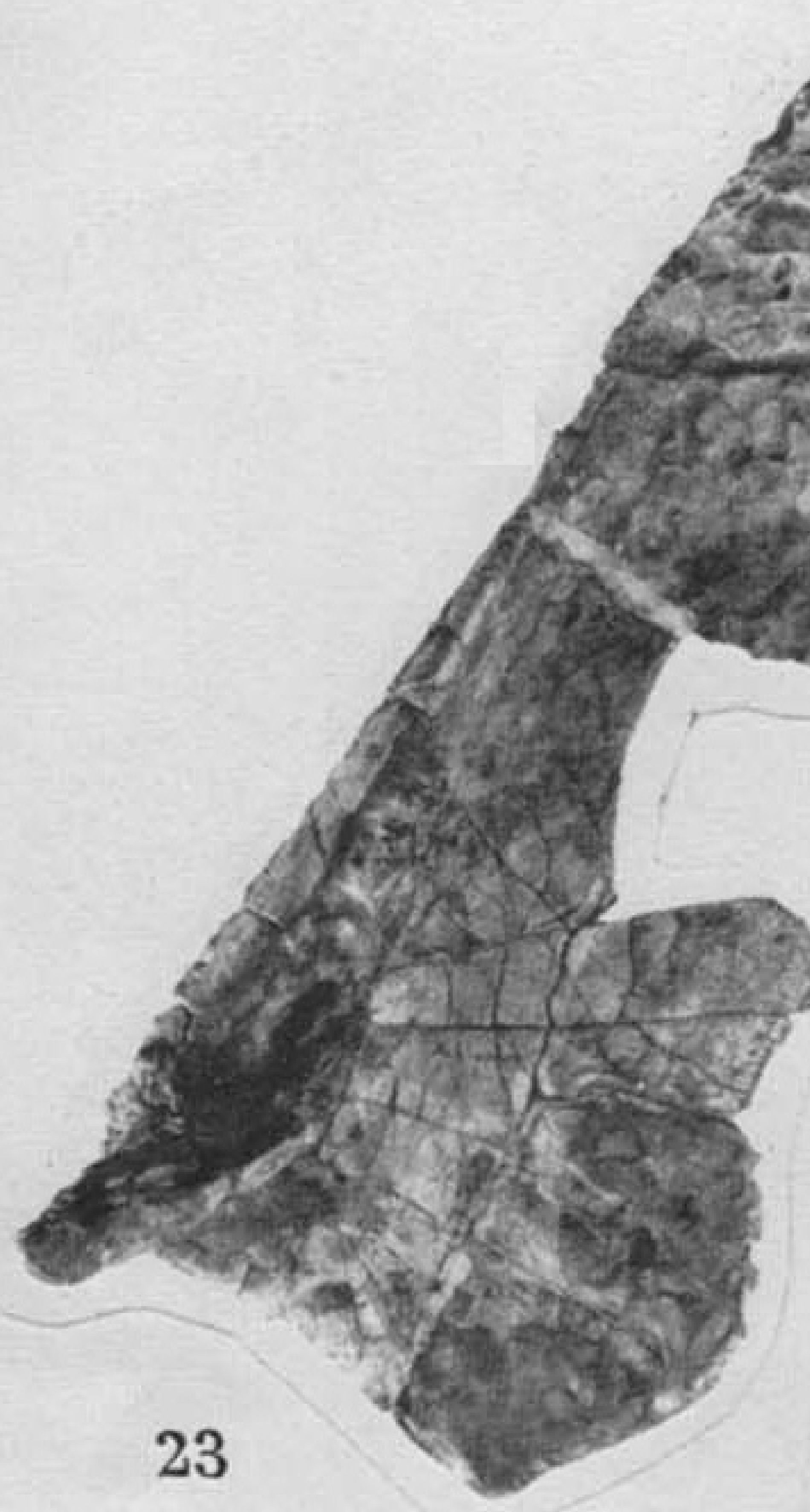


Metoposaurus maleriensis n.sp.

FIGURE 21. Part of the skull roof in dorsal view, showing the right orbit, a part of the left orbit and external naris, slime canals, ornament, pineal foramen, and sutures demarcating many of the bones. Holotype specimen I.S.I. A. 4. × $\frac{1}{5}$.

FIGURE 22. Dorsal surface of part of the palate, and floor of the braincase. Specimen I.S.I. A. 7. × $\frac{1}{2}$.



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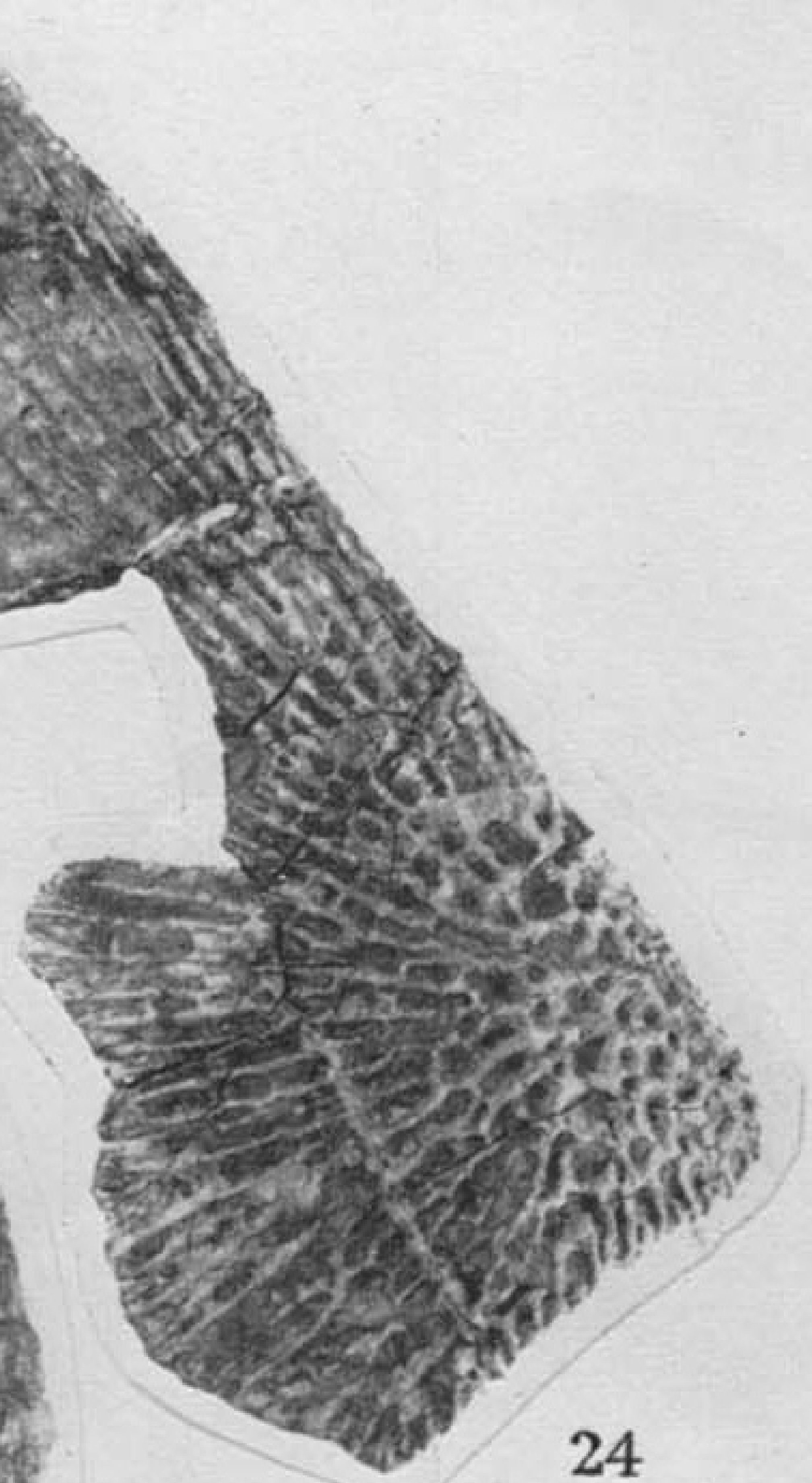

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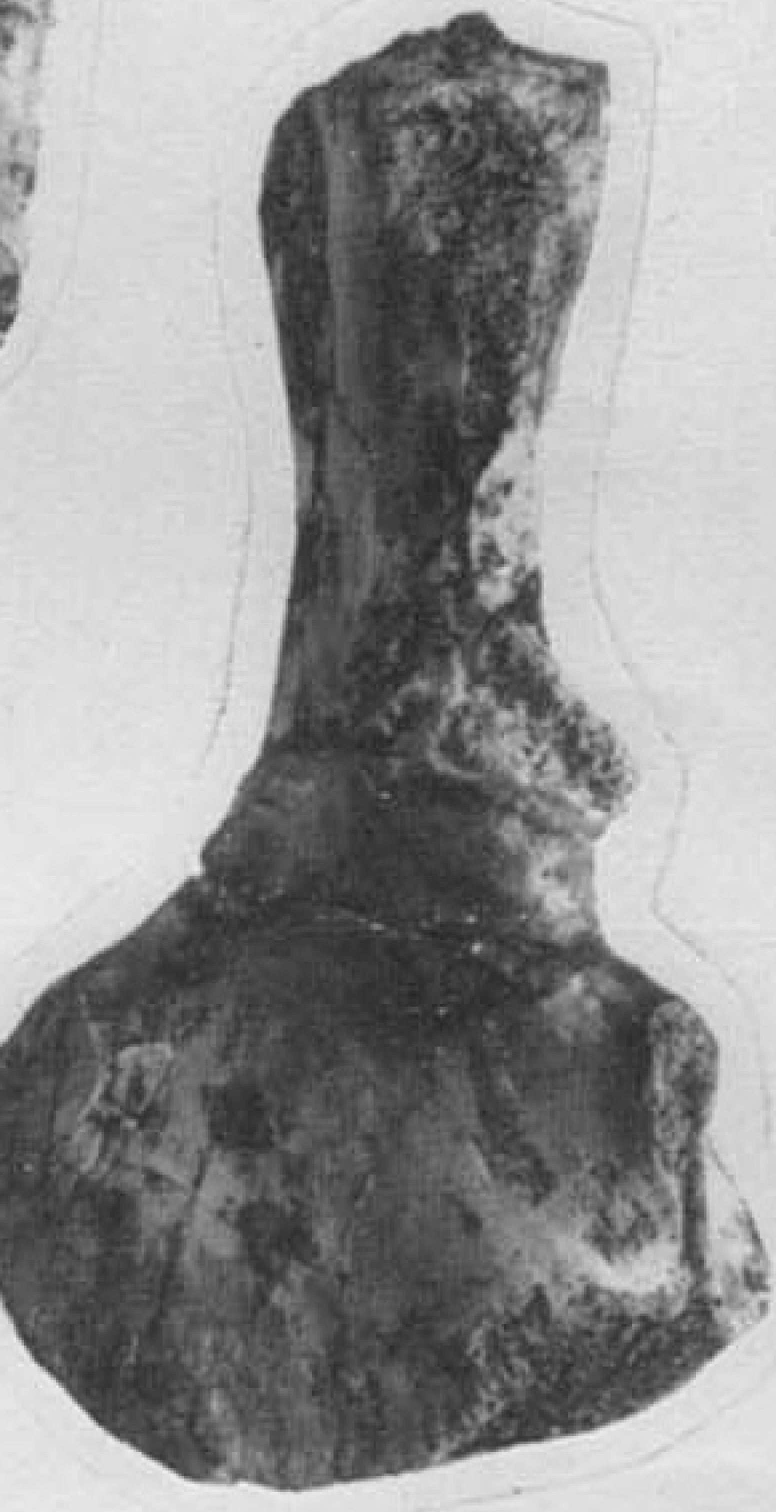

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Metoposaurus maleriensis n.sp.

FIGURE 23. Dorsal view of clavicle I.S.I. A. 11. × $\frac{1}{3}$.

FIGURE 24. Ventral view of clavicle I.S.I. A. 11. × $\frac{1}{3}$.

FIGURE 25. Dorsal view of clavicle, cleithral spine incomplete. I.S.I. A. 12. × $\frac{1}{3}$.

FIGURE 26. Dorsal view of humerus I.S.I. A. 17. × $\frac{2}{3}$.

FIGURE 27. Ventral view of humerus I.S.I. A. 17. × $\frac{2}{3}$.


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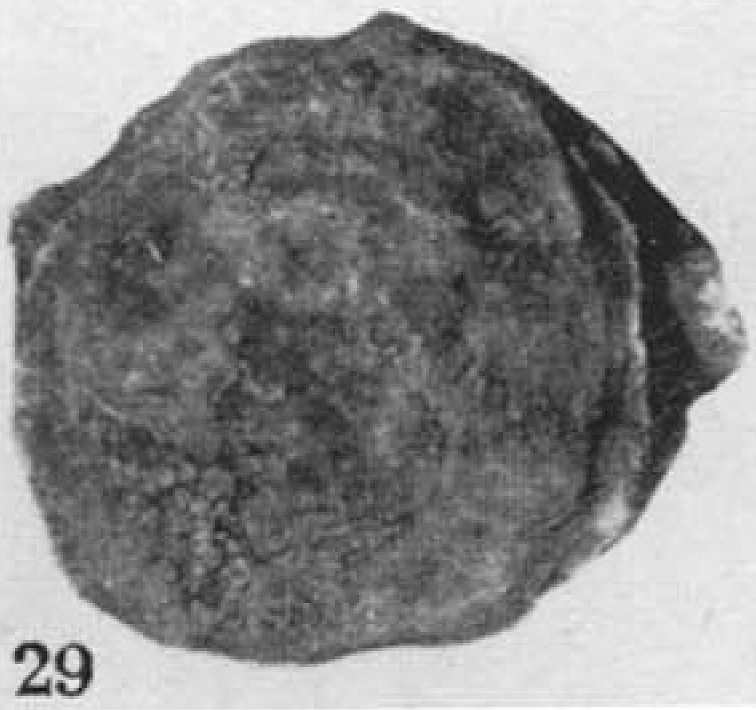
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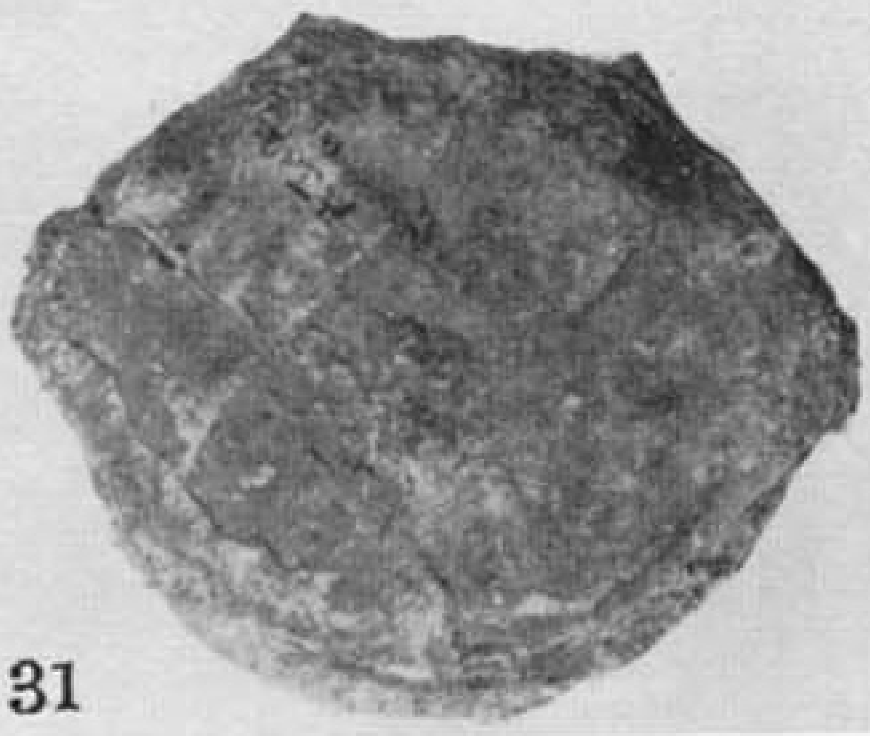
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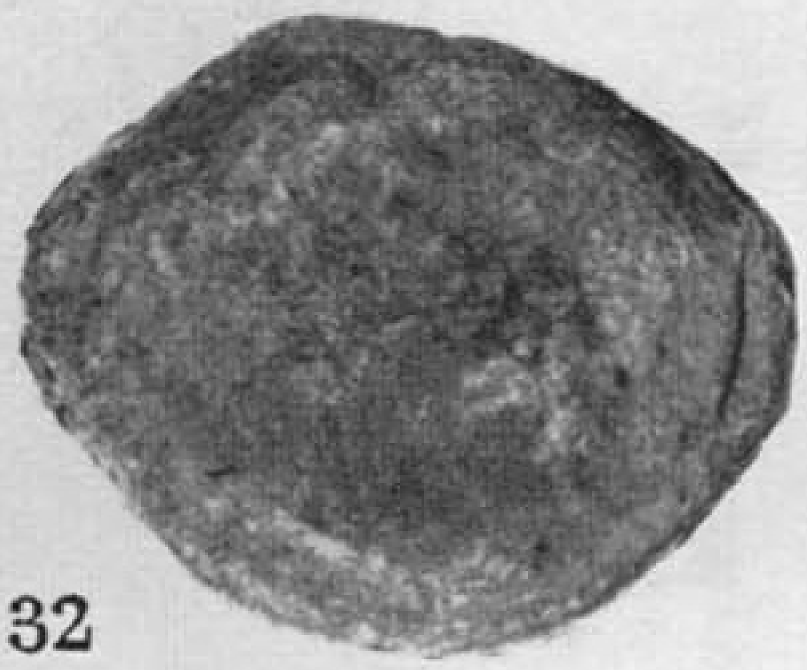
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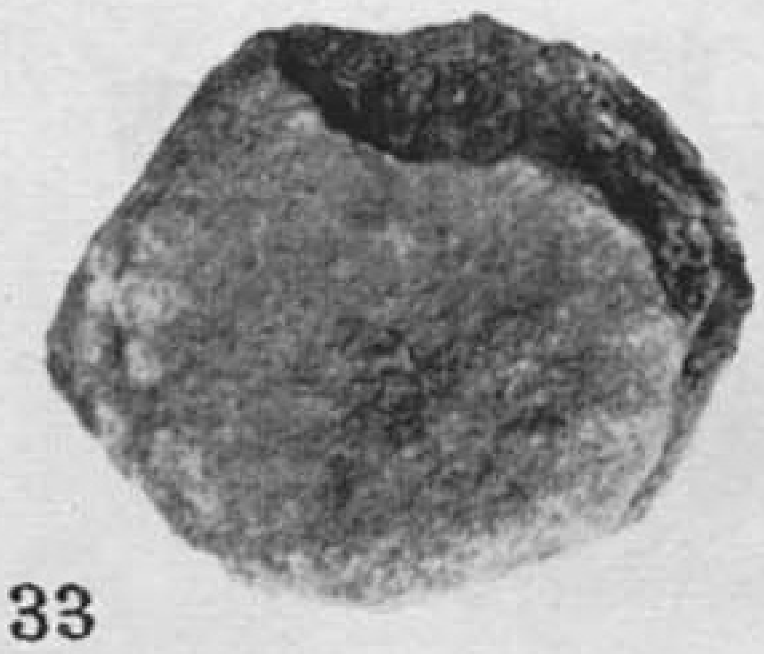
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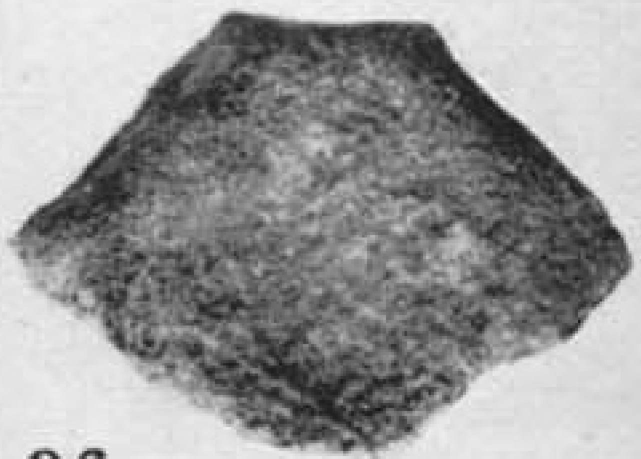
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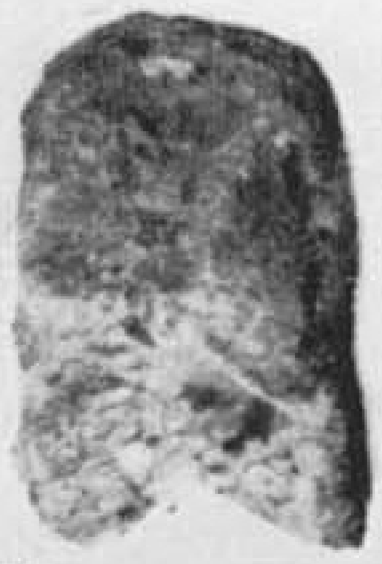
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Metoposaurus maleriensis n.sp.

FIGURE 28. Anterior view of the incomplete atlas intercentrum I.S.I. A. 13. × $\frac{2}{3}$.

FIGURES 29 TO 34. Anterior views of six dorsal intercentra I.S.I. A. 14*a*, *b*, *c*, *d*, and I.S.I. A. 15*a*, *b*. All × $\frac{2}{3}$.

FIGURES 35 AND 36. Anterior views of two caudal intercentra I.S.I. A. 15*c*, *d*. × $\frac{2}{3}$.

FIGURES 37 TO 42. Left lateral views of six dorsal intercentra I.S.I. A. 14*a*, *b*, *c*, *d*, and I.S.I. A. 15*a*, *b*. × $\frac{2}{3}$.

FIGURES 43 AND 44. Left lateral views of two caudal intercentra I.S.I. A. 15*c*, *d*. × $\frac{2}{3}$.