THE OSTEOLOGY AND RELATIONSHIPS OF AQUATIC EOSUCHIANS FROM THE UPPER PERMIAN OF AFRICA AND MADAGASCAR

by

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ABSTRACT

Tangasaurid eosuchians are represented by hundreds of specimens from the Permo-Triassic strata of Madagascar and Africa. The confusion surrounding the identification and anatomy of these reptiles is resolved by comparative anatomy and relative measurements, and three genera, Thadeosaurus, Tangasaurus and Hovasaurus, are described. Extensive growth series present a unique opportunity to study differences in growth strategies in two closely related Permian genera, one that was terrestrial (Thadeosaurus) and the other aquatic (Hovasaurus). The vertebrae of Youngina have a derived character state that indicates close relationship with the tangasaurids. A new genus and species of eosuchian, Acerosodontosaurus piveteaui, has a specialized feature in the carpus that is found in the Tangasauridae. The relationships between tangasaurids and other eosuchians are considered.

EXTRAIT

Les éosuchiens tangasauridés sont représentés par plusieurs centaines de spécimens des strates Permo-Triassiques de Madagascar et d'Afrique. La confusion concernant l'identification et l'anatomie de ces reptiles se résout par comparaison anatomique et mesures relatives, et trois genres, *Thadeosaurus*, *Tangasaurus*, et *Hovasaurus* sont décrits. De longues séries de croissances offrent une chance unique d'étudier les différences de stratégie de croissance dans deux genres permiens étroitement liés, un qui était terrestre (*Thadeosaurus*) et un autre aquatique (*Hovasaurus*). Les vertèbres de *Youngina* possèdent un état de caractère dérivé qui indique une proche relation avec les tangasauridés. Un nouveau genre et espèce d'éosuchien, *Acerosodontosaurus piveteaui*, est doté d'un trait specialisé dans la carpe qui se retrouve chez les Tangasauridae. Une nouvelle classification des tangasauridés et genres étroitement liés est proposée.

PREFACE

This thesis is presented in the style of Palaeontologia Africana with the intention of submitting section V to that journal in the near future. Sections I and II have already been accepted for publication (Currie, 1980, 1981), and section IV is being reviewed for possible publication by the South African Museum. These sections were rewritten for integration into the body of the thesis. All parts of the thesis as presented are interconnected and interdependant, but publication as a unit would not have been possible because of the length.

Complete descriptions are given for Hovasaurus, a poorly understood genus represented by more than 300 well preserved specimens, and a new genus of eosuchian from Madagascar. Only those characters that were previously unknown or misunderstood are described in the sections on Youngina, Thadeosaurus and Tangasaurus. All descriptive sections are based on original research on the specimens unless otherwise credited in the text. Three systems of relative measurement were utilized to distinguish and define the genera, and to determine the biological significance of the relative sizes of elements to growth, habits and ecology. Much of the Introduction and section VI is based on the published research of other workers. These sections summarize a large body of published data, and indicate where further research is needed.

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INTRODUCTION

Reptilian classification is traditionally based on the configuration of openings in the temporal region of the skull (Romer, 1956). The three major lineages of reptiles--anapsids, synapsids and diapsids--were already distinct by the end of the Palaeozoic era. The anapsid condition is the most primitive (fig. 49a), and is characterized by the absence of fenestra in the temporal region. Synapsid reptiles have a single opening in the side of the skull behind the orbit. In general, diapsid reptiles have lateral and upper temporal fenestra (fig. 49c). Lizards, snakes, crocodiles, dinosaurs, pterosaurs, plesiosaurs and birds are branches of the successful diapsid lineage.

In 1914, Robert Broom announced the discovery of a new type of diapsid reptile from the Upper Permian Karroo beds of South Africa. <u>Youngina</u> (fig. 49) had the characteristic lateral and dorsal temporal fenestra in the skull, but overall had a more primitive level of organization than any diapsids known until that time. Broom created a new reptilian suborder, the Eosuchia, for <u>Youngina</u>.

Since Broom's original description of <u>Youngina</u>, a large number of genera from around the world have been referred to the Eosuchia. The earliest record, according to Reisz (1981), is Petrolacosaurus from the Upper Pennsylvanian strata of Kansas. The greatest diversity appears to have been in Late Permian times, and there was a gradual decline during the Triassic when derived groups rose in prominence. Two eosuchians, Champsosaurus (Erickson, 1972) and Simoedosaurus (Russell-Sigogneau and Russell, 1978), survived until the Eocene, about 60,000,000 years ago.

By the Late Permian, some 230,000,000 years ago, at least three major lines of eosuchians had evolved. One line, characterized by Prolacerta (Gow, 1975) and Protorosaurus (Watson, 1957), was long thought to have been the ancestral stock of lizards. This is no longer accepted by most palaeontologists, but the line appears to have led to the highly specialized Tanystropheus of the Middle Triassic of Europe (Wild, 1973). Research by Carroll (1975a, b, 1977) has shown that paliguanids are more suitable lizard ancestors than prolacertiform eosuchians. Carroll considers paliguanids to be primitive lizards, but in a horizontal classification they would be classified as eosuchians. The third major line of eosuchians had radiated in the Permian into a diverse and successful assemblage of terrestrial forms like Youngina (Gow, 1975) and aquatic forms such as Tangasaurus

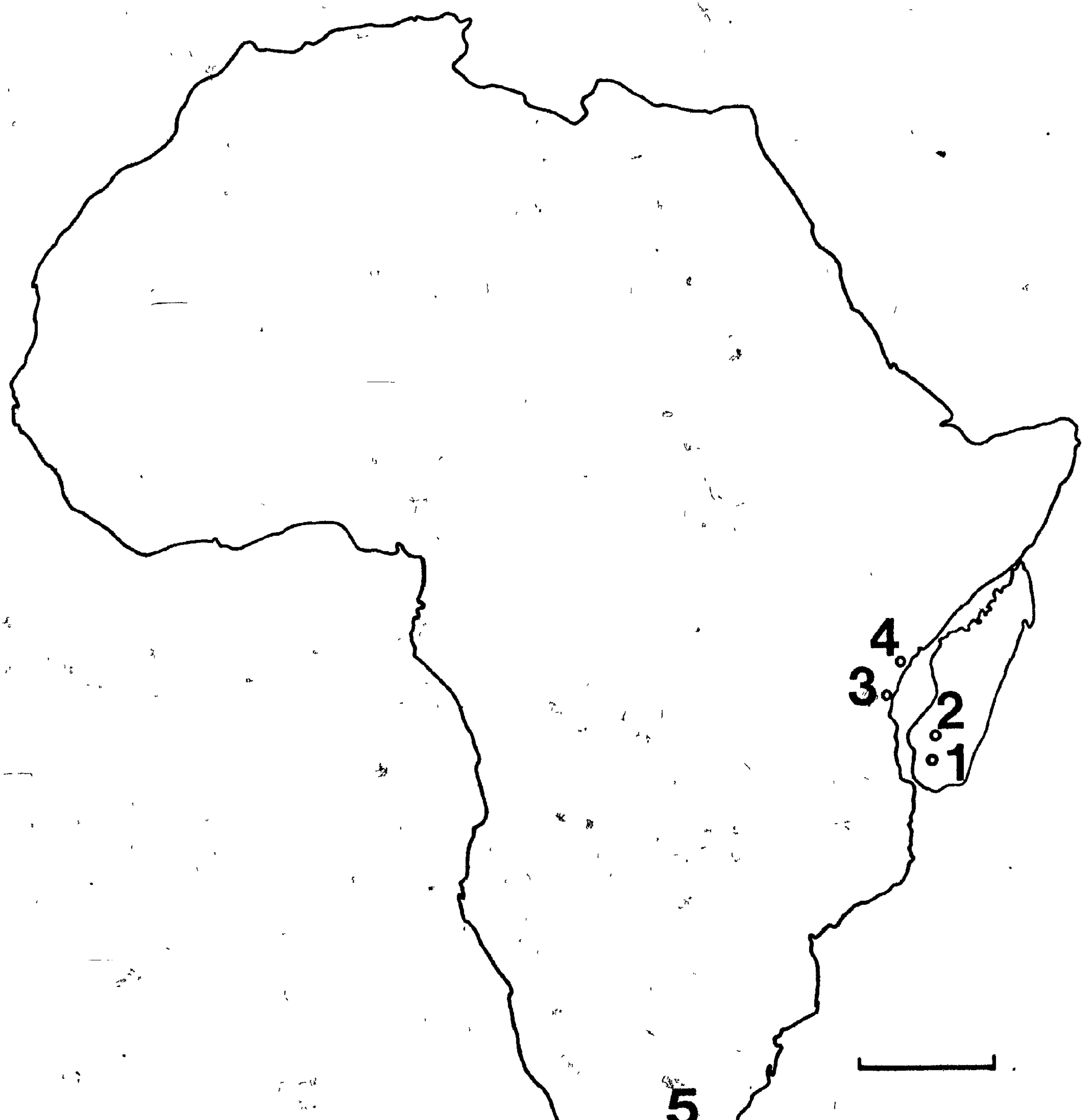
(Haughton, 1924). This line appears to have given rise to archosaurs (Carroll, 1976a) and sauropterygians (Carroll, 1981).

Many genera of eosuchians independently became adapted for an aquatic existence. The Tangasauridae were close relatives of Youngina that lived in Africa and Madagascar during Permo-Triassic times. The family includes both terrestrial and aquatic forms, presenting a unique opportunity to study the diversification within a well-defined unit of eosuchians.

Tangasaurus was a small, lizard-like reptile that was described by S.H. Haughton in 1924. The genus was based on two specimens from Upper Permian strata in the vicinity of Tanga, Tanzania (fig. 1). The specimens are poorly preserved, but Haughton (1924) felt that several characters indicated that this genus was a swimming reptile.

Numerous well preserved specimens from the Upper Permian of Madagascar were identified as Tangasaurus by Piveteau (1926). During the Permian, Madagascar was much closer to Tanzania (fig. 1) than it is now, and the Mozambique Channel had just started to open (Bambach et al, 1980). This region has been referred to as the Tangasaurid Province of the ancient continent Gondwanaland (Anderson and Cruickshank, 1978).

Figure 1. Eosuchian localities of Africa and Madagascar. Madagascar has been moved on the map to its probable position at the end of the Permian. 1, Mount Eliva. 2, Ranohira. 3, Tanga, Tanzania. 4, Mariakani, Kenya 5, Youngina Localities. Scale = 1,000 km.


1
2
3
4
5

Unfortunately, reexamination of the specimens from Madagascar previously identified as Tangasaurus has shown that they represent a different genus, Thadeosaurus (Carroll, 1981), known only from the Upper Permian of Madagascar.

The most commonly recovered eosuchian from the Upper Permian of Madagascar is Hovasaurus (Piveteau, 1926). After Haughton's paper of 1930 demonstrated the anatomical similarities between Tangasaurus and Hovasaurus, these genera were usually included as the only known representatives of the Tangasauridae (Camp, 1945; Piveteau, 1955; Romer, 1956, 1966; Orlov, 1964; Kuhn, 1969).

Kenyasaurus from the Lower Triassic of Kenya was assigned by Harris and Carroll (1977) to the Tangasauridae on the basis of general body form, the presence of a sternum and particularly the anatomy of the foot.

Piveteau (1926) tentatively referred several specimens collected in Madagascar to the European genus Datheosaurus. However, Datheosaurus is a junior synonym of Haptodus, the name given to a sphenacodont pelycosaur (Currie, 1979). The specimens from Madagascar belong to an eosuchian, and have been renamed Thadeosaurus (Carroll, 1981). The fossils from Madagascar that were identified as Tangasaurus are now referred to as Thadeosaurus.

The tangasaurids are the focal point for this investigation. A further specimen in the collections of the Muséum National d'Histoire Naturelle (Paris) had been identified as Tangasaurus, but is in fact a new genus of eosuchian. A description of this animal is included here for comparison with tangasaurid anatomy. The scope of the investigation was further extended when the type specimen of Youngina was found to have a derived character in the vertebrae that unites it with the tangasaurids.

Papers by Carroll (1975a, b, 1976a, b, 1977, 1978, 1981), Currie (1980, 1981), Erickson (1972), Gow (1975), Harris and Carroll (1977), Reisz (1977, 1981), Russell-Sigogneau and Russell (1978) and Wild (1973) have substantially increased our knowledge of primitive diapsid reptiles, and it is appropriate to consider the relationships of tangasaurids to other eosuchians.

Historical résumé

In 1902, E.F. Gauthier mentioned the presence of a "bande triasique" on the island of Madagascar. The first fossils were collected from this region in 1908 by Captain J. Colcanap, who sent at least two specimens to Boule in Paris. Boule (1908) announced the discovery of reptiles from the Sakamena River Valley, and pointed out that the association with Glossopteris fronds suggested that the beds were Permian in age. The first two specimens sent are now known to represent Thadeosaurus (MNHN 1908-5-1) and Daedalosaurus (MNHN 1908-5-2). The second shipment (MNHN 1908-11) included the counterpart of the Daedalosaurus specimen sent in the first mailing, plus specimens of Atherstonia, Coelurosauravus (Carroll, 1978) and Thadeosaurus (Carroll, 1981). It would appear that all specimens collected up to that time were from a single locality because no subsequent collections have turned up the articulated remains of the three reptiles. Two more shipments totaling more than 125 specimens collected by Colcanap in the Sakamena River Valley reached Paris in 1908. Almost every identifiable reptile specimen belongs to the aquatic genus Hovasaurus, except for one specimen that will be described as a distinct eosuchian genus.

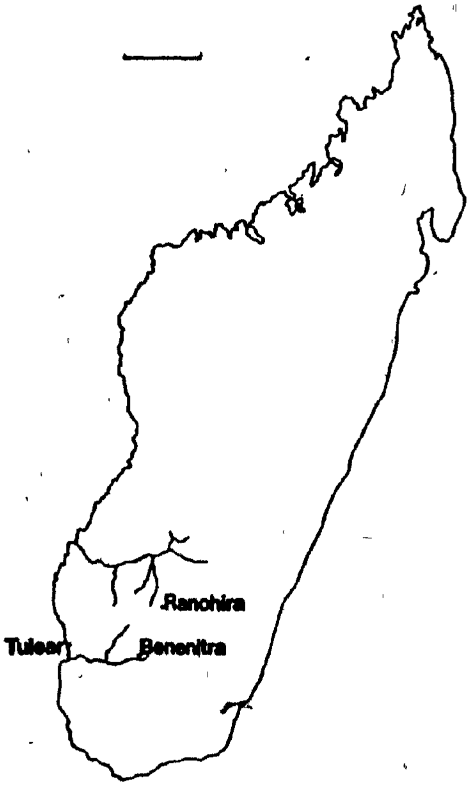
More than 90 isolated amphibian and reptile bones were sent by Colcanap to Paris in 1909. The elements recovered from numerous sites in the Benenitra area (fig. 2) have been identified as the ancestral sauropterygian Claudiosaurus (Carroll, 1981), Acerosodontosaurus (Currie, 1980) and therapsids. An amphibian jaw found north of Ranohira was the strongest evidence used until recently for correlating the fossil beds of Madagascar with those of South Africa.

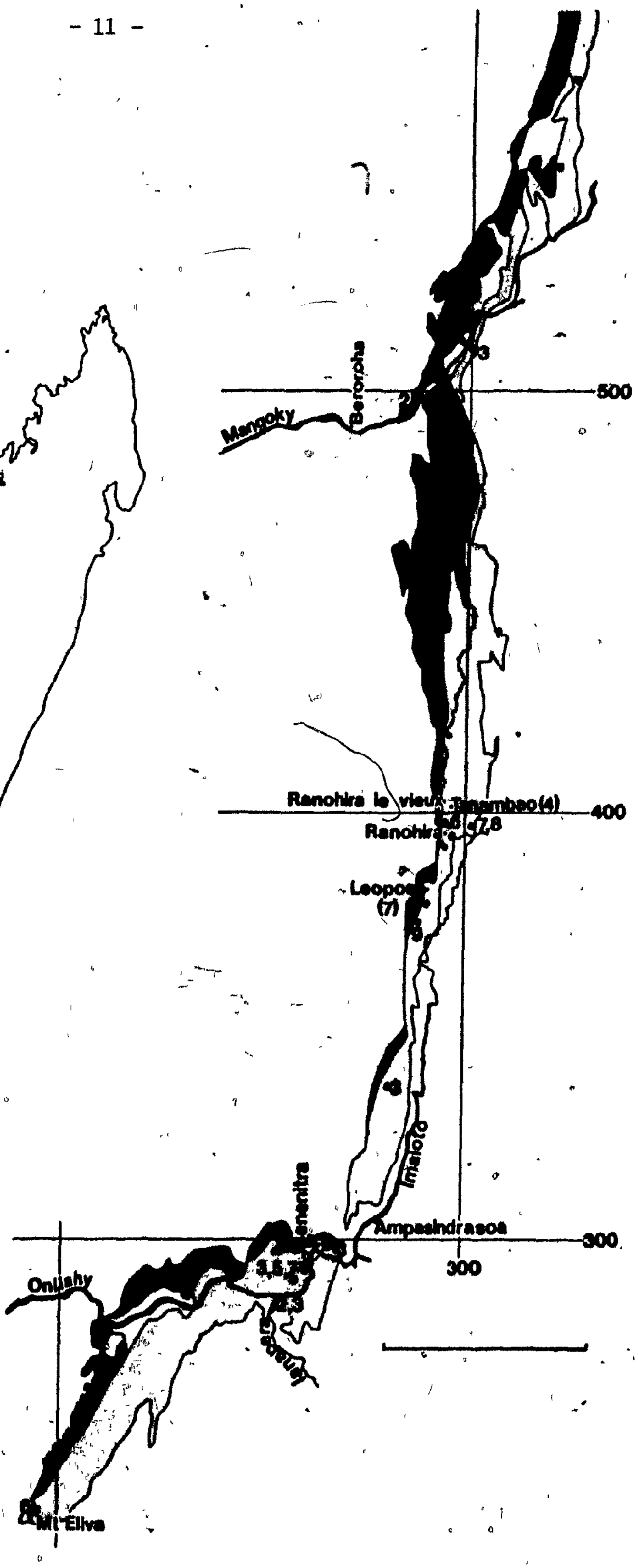
H. Perrier de la Bathie sent a fine collection of fossil plants to Zeiller (1911), who concluded that the flora was Triassic in age. Amongst the plant fossils was a single specimen of Claudiosaurus (MNHN 1910-33-1) that had been collected on the Sakamanigy River east of Ranohira (figs. 1, 2) five metres above the contact with the Precambrian shield.

Piveteau (1926) collected more than 200 fossils from the Permo-Triassic beds of Madagascar in 1925. Most of these seem to have been collected at Mt. Eliva (fig. 2) and represent Hovasaurus. Isolated bones collected from the Benenitra and Ranohira regions represent the same genera found in the Colcanap collections. Piveteau published the first major paper on the eosuchians of Madagascar, and included the first rigorous observations on the Permian strata of the Sakamena River Valley.

Figure 2. Upper Permian collecting sites in Madagascar. Left, the island of Madagascar. Right, collecting localities for amphibians and reptiles of the Lower Sakamena Formation. Circle, collecting site; square, geographic location; 1, Rhinesuchus; 2, isolated bones of ?labyrinthodont amphibians; 3, isolated bones of reptiles; 4, Barasaurus besairiei Piveteau; 5, ?Acerosodontosaurus; 6, Hovasaurus boulei Piveteau; 7, Claudiosaurus germaini Carroll; 8, ?Daedalosaurus; 9, articulated, unidentified reptile remains in nodules. Hovasaurus remains were recovered also from unknown localities in the lower courses of the Sakamena and Ianapera Rivers. Thadeosaurus, Coelurosauravus and Daedalosaurus collected from a site in the Sakamena River Valley. Isolated therapsid remains are probably from the Benenitra area. Scale is 50 kilometers. After Piveteau, 1926, Tortochaux, 1950 and Besairie, 1953.

Yellow, lower Sakamena; green, Middle and Upper Sakamena Formation.


Ranohira
Tulear
Benenitra


3
500
Berorpha
2
Mangoky
Ranohira le vieux
Tanambao (4)
400
Ranohira
7,8
Leopo
(7)
Imaloto
Benenitra
Ampasindrasoa
300
300
Onilahy
3,5,7
2,3
Isanasy
Mt Eliva

Between 1926 and 1929, H. Besairie studied the stratigraphy of the Permian formations south of the Onilahy River (fig. 2). Specimens of Hovasaurus collected at Mt. Eliva were sent to Paris (Basse, 1934) and the South African Museum. The reptile-bearing beds were named the Lower Sakamena Formation.

In 1929, L. Barrabe recognized that the Sakamena beds of the south of Madagascar extended as far north as Cape St. André.

E. Basse (1934) studied the Permo-Triassic outcrops between the Onilahy and Mangoky Rivers. She did not collect any vertebrate fossils, but did find pelycopods that were studied by Cox (1936).

From 1945 to 1949, F. Tortochaux (1949, 1950) examined the Permo-Triassic beds between the Onilahy River and Cape Saint André. Many specimens of vertebrates were collected and sent to Paris, but their present location is unknown. The published identifications of the fossil reptiles are unreliable.

Detailed studies on the stratigraphy and tectonics of the Upper Permian of Madagascar were undertaken by P.S. Hirtz (1949) and P. Cliquet (1950, 1951, 1952) for the Syndicat d'Études et de Recherches Pétrolières.

In clearing an area to set up a drilling rig, a large number of reptiles were found in nodules at the top of the Lower Sakamena Formation (C. Germain, 1953) near Leoposa (fig. 2). These have been described as Claudiosaurus (Carroll, 1981), a reptile with eosuchian affinities, and features expected in an ancestor of nothosaurs and plesiosaurs.

The most recently described collection of Permian reptiles from Madagascar included the type specimen of the procolophonid Barasaurus (Piveteau, 1955a) from the vicinity of Ranohira.

In 1973, R.L. Carroll examined the eosuchians from Madagascar in the collections of the South African Museum and the Muséum National d'Histoire Naturelle, and initiated the first detailed studies of these reptiles (Carroll, 1978, 1981; Currie, 1980) since Piveteau's paper in 1926.

The known specimens of tangasaurids from Africa are few in number. The type specimens of Tangasaurus were found in the Mzimbazi River near Tanga, Tanzania by F.P. Mennell in 1922. Although Haughton described two specimens from this site, Mennell (1930) reported that he had found a "number of nearly complete skeletons of a lizard-like reptile...two being embedded in the ordinary shale and six in concretions". The whereabouts of these other specimens is unknown. Janensch (1927) noted that reptilian bone fragments were discovered by Reck in the Tanga beds in 1913. There is no other record of finds from this area.

The only known specimen of Kenyasaurus was found in Lower Triassic beds 25 miles from Mombasa, Kenya (Harris and Carroll, 1977). No other reptile fossils have been reported from this region.

Stratigraphic Distribution of the Tangasauridae

The Karroo series of Madagascar was divided into three groups by Besairie (1930), which are separated by discordances. The lowest is the Sakoa group, which was deposited during Early and Middle Permian times. This is unconformably overlain by the Sakamena Group, which in turn is overlain by the Upper Triassic to Middle Jurassic deposits of the Isalo Group.

The Sakamena is usually divided into six members south of the Onilahy River. From bottom to top, these members are:

1. Basal Conglomerates.
2. Shales and sandstones with limestone intercalations.
3. The Vohipanana-Ambatokapika limestone.
4. Upper shales and sandstones.
5. Marine shales with septarian nodules.
6. The upper red series.

Members one to four are considered to be the Lower Sakamena Formation, five is the middle Sakamena and six is the Upper Sakamena Formation. All records of reptiles from the Lower

Sakamena are from the fourth horizon. Tortochaux (1950) reported Tangasaurus specimens from the Middle Sakamena Formation. However, his identification cannot be confirmed and he included the upper level of Horizon 4 in the Middle Sakamena Formation, a practice not followed by anyone else.

The Sakamena followed a tectonic phase, which explains the discordance between the Sakoa and Sakamena Groups. The basal conglomerate is not always present, but is widespread. The Sakamena can lie on Sakoa beds, or directly on the shield. The basal facies are isotopic but not synchronous.

The combined shale and sandstone complex of Horizons 2, 3 and 4 is thick and extensive. The lithology has been described in detail by Besairie (1930), Tortochaux (1949, 1950), Hirtz (1949) and Cliquet (1950), and summarized by Besairie (1971). The complex is 870 metres thick in the Iambiky-Benaha region (Tortochaux, 1950), 950 m in the region of Antsoakaky (Cliquet, 1950) and more than 1,500 m south of the Onilahy River (Hirtz, 1949). A borehole drilled into the Sakamena Group north of the Onilahy River and west of Benenitra (fig. 2) traversed more than 2,500 m of Lower Sakamena strata without reaching the lower limit (Besairie, 1971). This suggests that the formation has a tendency to be thicker away from its eastern borders at the shield. The Lower Sakamena thins out towards the north, where the Middle Sakamena Formation becomes thicker.

Piveteau (1926) felt that the Lower Sakamena sediments could have been deposited in lagoons. Some petroleum geologists (Hirtz, 1949; Cliquet, 1950, 1951, 1952) have expressed their belief that the Lower Sakamena Formation is mainly of marine or estuarine origin. The limestones at the base of the formation are unquestionably marine. Goubin (1965) concluded on the basis of microfossils that there are typical marine intercalations (with acritarchs, dinoflagellates and foraminiferans) throughout the formation, but that most of the formation is continental in origin. Most authors consider the Lower Sakamena formation to be primarily of continental origin because of the presence of terrestrial plants and vertebrates.

Fossilized reptile remains can be found at many levels in Horizon 4. Articulated remains are found in nodules, and usually lack head and tail. The bone is softer than the fine grained sandstone of the nodules, and for the most part is eroded out after the nodules split. The majority of specimens are natural moulds of the animals, and it is necessary to make high fidelity latex or silicone rubber casts as an aid in study (Baird, 1951). The nodules are common only at certain sites. Disarticulated bones are frequently found in these beds of coarse gravel.

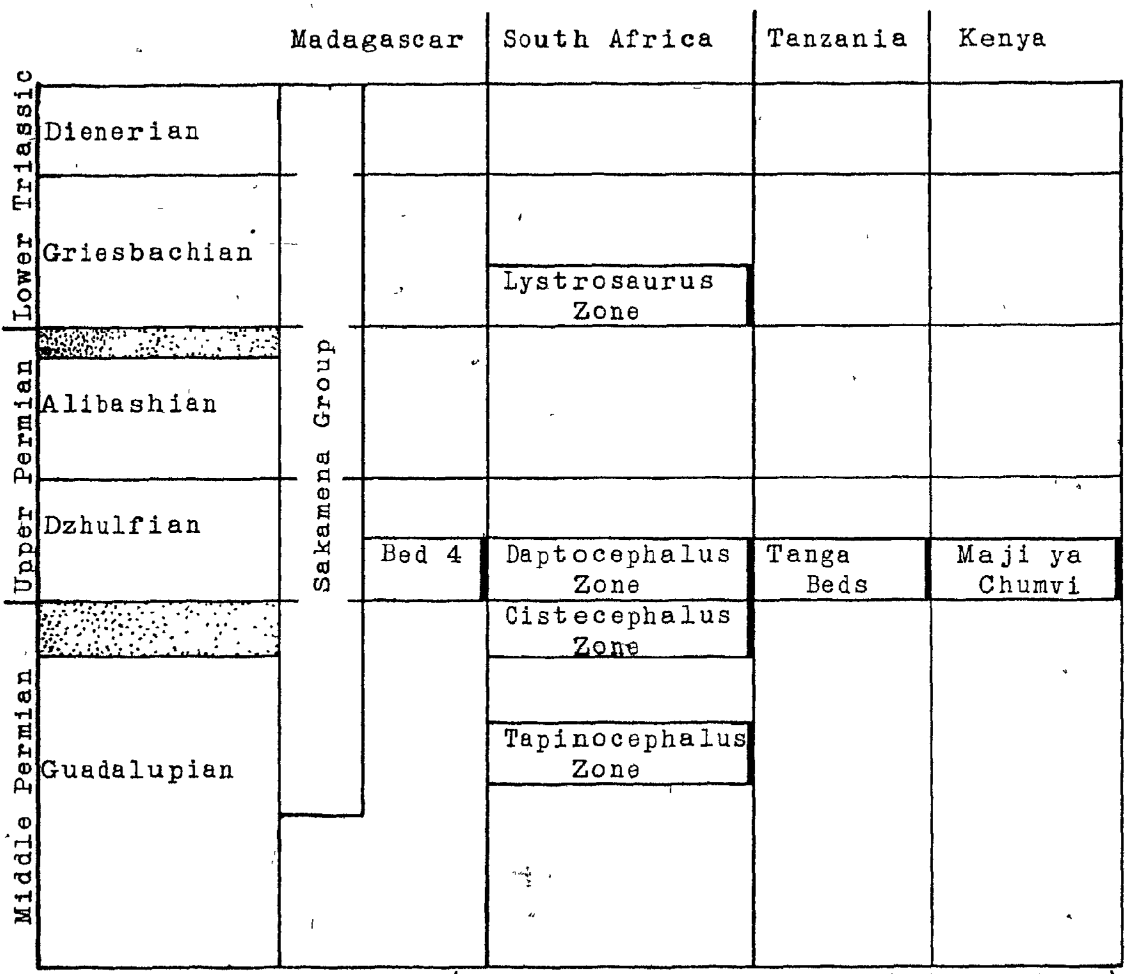
Age of the Tangasaurid-bearing Sediments

The Sakamena Group includes both Upper Permian and Lower Triassic strata (fig. 3). The Lower Sakamena Formation has been referred to the Triassic by some authors, but is generally considered as uppermost Permian.

Pollen has been used by Jekhowsky and Goubin (1964), Goubin (1965), Hart (1969) and Anderson and Anderson (1970) to show that the Lower Sakamena Formation is Permian. Hart (1969) correlated the formation with the Russian Tatarian (Dzhulfian Standard Stage). Goubin (1965) divided the Lower Sakamena Formation into three palynological zones south of the Menamaty River. The zonation was not as clear in the northern sample area. The dominant pollen types in the lowest zone, IA, are Platysaccus praevius and Platysaccus fuscus. Gluttulapollenites hannonicus and incertae sedis B dominate IB, and Vittatina striata, Lueckisporites virrkiae and Gluttulapollenites gondwanensis are most common in IC. Alisporites papillo is characteristic of all of Zone I. Anderson and Anderson (1970) feel Vittatina is equivalent to Paravittatina of the Permian of Pakistan.

The palynological zones correspond roughly with the lithological separation between the Lower and Middle Sakamena Formations at most sites. At Saloanivo (Madagascar geographic grid co-ordinates X=289, Y=223, fig. 2), the top of pollen

Figure 3. Stratigraphic correlation showing relative age of known genera of younginid and tangasaurid eosuchians.



		Madagascar		South Africa	Tanzania	Kenya
Lower Triassic	Dienerian	Sakamena Group				
	Griesbachian			Lystrosaurus Zone		
Upper Permian	░					
	Alibashian					
	Dzhulfian		Bed 4	Daptocephalus Zone	Tanga Beds	Maji ya Chumvi
Middle Permian	░			Cistecephalus Zone		
	Guadalupian			Tapinocephalus Zone		

(After Anderson and Cruickshank, 1978)

zone IC is in the Middle Sakamena, at Antsokaky (X=317, Y=273) it is 213 metres below the contact between the Lower and Middle Sakamena Formations, at Ambalabe (X=462, Y=275) it is in the Middle Sakamena, and at Leoposa (fig. 2) it is almost exactly at the contact. Pollen and spore dispersal tends to be widespread and is usually a better indicator of absolute time than lithology. This suggests that the lithological contact between the Lower and Middle Sakamena Formations is not synchronous throughout southern Madagascar.

Among the collections made by Colcanap in southern Madagascar, there were specimens of *Glossopteris*, which led Boule (1908) to the conclusion that these beds were Permian in age. At least one reptile specimen (MNHN 1908-5-1) from the Sakamena River Valley is associated with a frond of *Glossopteris* (Haughton, 1930). *Glossopteris* has also been reported from Tambohazo (X=628, Y=326; Carpentier, 1935), Ranohira (uppermost levels of the L. Sakamena; Besairie, 1957), Lola (X=352, Y=288; Tortochaux, 1950), northern Madagascar (Besairie, 1971) and many other localities in the lower Sakamena Formation.

Carpentier (1935, 1936) described and illustrated plant fossils from several sites. His identifications were amended by Townrow (1966, 1967) and Anderson and Anderson (1970). *Glossopteris* sp., *Baiera* sp., and *Voltziopsis africana* are recognized from Tambohazo (X=628, Y=326), and Anderson and

Anderson (1970) suggested the bed there to be Upper Permian. Thinnfeldia callipteroides, Lepidopteris madagascarensis, Taeniopteris sp., Rissikia media, Voltziopsis africana and V. wolganensis are known from Amboriky (X=695) and other localities. Anderson and Anderson 1970) feel the flora of Amboriky can be used to correlate the Lower Sakamena Formation with the lowermost Narrabeen (probably Upper Permian) of Australia.

Another typical member of the Glossopteris flora, Schizoneura gondwanensis, has been identified from numerous sites (Zeiller, 1911). Basse (1934) noted that these were the best preserved plant remains between the Onilahy and Menamaty Rivers. Unfortunately, none of the specimens were illustrated, and therefore the identification has not been included in recent palaeobotanical reviews of the Madagascar Permian.

The Vohipanana-Ambatokapika limestone horizon south of the Onilahy River is rich in Syringopora and Cladochonus (Besairie, 1930), two corals that are not known from beds younger than the Upper Permian. Cladochonus is known also from a limestone bed just above the conglomerate level near Bena (X=335, Y=287), 5 km south of Antsokaky (Tortochaux, 1950) and near Ambohitra south of the Onilahy (Tortochaux, 1950).

Basse (1934) discovered a two metre thick lamellibranch bed near Bena at the confluence of the Bena (= Benaha) and Imaloto Rivers. The bed is above the conglomerate and not far below the "Rhinesuchus" horizon. Numerous specimens from this locality were studied by Cox (1936). Gervillia elianae and Modiolopsis stockleyi are known from the Lower Sakamena Formation of Madagascar, and from Tanzania, but from nowhere else. The lamellibranch fossils therefore cannot be used as reliable stratigraphic indicators. Cox (1936) concludes, however, that the Tanzania lamellibranchs have Permian, not Triassic, affinities. He also suggested that Gervillia and Modiolopsis were freshwater genera.

Middle Sakamena beds of northern Madagascar have been correlated with beds in southern Madagascar on the basis of lithology and fish fossils. Underlying horizons in the north near Ankitokazo are considered to be the top of the Lower Sakamena Formation, are of marine origin, and include the Upper Permian (Guadalupian and Dzhulfian) ammonites Cyclolobus and Xenaspis (Brenon, 1972). Lower horizons in the Lower Sakamena beds of the north include the Middle Permian brachiopods Productus and Spirifer.

Articulated fish-remains are uncommon in the Lower Sakamena Formation. Colcanap collected four specimens of the palaeoniscoid Atherstonia (Boule, 1910) in the Sakamena

River Valley, presumably at the same site as Thadeosaurus, Coelurosauravus and Daedalosaurus. Atherstonia colcanapi was described by Priem (1924) on the basis of these specimens. Piveteau recovered a good specimen (MNHN 1925-5-2) of Atherstonia colcanapi at Mt. Eliva. Dr. Brian Gardiner (letter to Dr. R.L. Carroll, March 8th, 1976) reexamined these specimens, confirmed their generic identification, and pointed out that the genus is known only from the Upper Permian. Palaeoniscoid scales have been reported from numerous sites in the Lower Sakamena Formation (Tortochaux, 1950), but could represent genera other than Atherstonia. A palaeoniscoid recovered from Ranohira (Besairie, 1971) appears to be a Lower Triassic genus (B. Gardiner, personal communication).

Boule (1910) was the first to report on the remains of amphibians from Madagascar, referring to the mandible of a labyrinthodont. Piveteau (1926) identified the jaw as Rhinesuchus cf. senekalensis, a species known from the Daptocephalus Zone (uppermost Permian) of South Africa. Besairie (1949) felt that the jaw probably came from Middle Sakamena beds, but all other workers seem to consider the jaw as being from the uppermost levels of the Lower Sakamena.

Barasaurus besairei (Piveteau, 1955a) is a procolophonid that was found in Lower Sakamena strata 1,500 m northeast of Ranohira (Besairie, 1971). It is closely related to, and possibly synonymous with, <u>Owenetta</u> of the <u>Daptocephalus</u> Zone of South Africa, which is considered to be Dzhulfian (fig. 3).

Cliquet (1957) has suggested on the basis of tectonic evidence that sediments in the Early Sakamena depositional basin between Benenitra and the Mangoky River are somewhat older than those of the Sakamena River Valley.

Even though the Lower Sakamena Formation may have been deposited over a long period of time and at different times in different areas, most fossils indicate that the formation is probably Upper Permian. The two best types of fossils for dating, pollen and ammonites, indicate that the Lower Sakamena Formation is best referred to the Dzhulfian Standard Stage, with an estimated age of 225 to 230 millian years.

Across the Mozambique Canal from Madagascar, the type specimens of <u>Tangasaurus</u> were found in the Middle Division of the Tanga series of northeastern Tanzania. The supposed presence of <u>Tangasaurus</u> in the Lower Sakamena Formation of Madagascar was the strongest evidence for correlating this formation with that in Tanzania. The Middle Division of the Tanga series is more than 1,000 m thick (McKinlay, 1956), and has been compared lithologically with the Lower Sakamena (McKinlay, 1960a). Plants recovered from these strata include several species found in the Lower Sakamena Formation (Seward, 1934), and have been referred provisionally to the Upper Permian

(MacKinlay, 1960b).

Kenyasaurus was recovered from the upper part of the Maji ya Chumvi Beds of Kenya, which are usually correlated with the Middle Division of the Tanga Beds (Miller, 1952; Caswell and Baker, 1953; McKinlay, 1960a). A marine shale in the middle of the Maji ya Chumvi beds includes the remains of Boreosomus gillioti, also known from the Middle Sakamena Formation, which is considered to be Lower Triassic. Most authors, including Harris and Carroll (1977), consider the upper part of the Maji Ya Chumvi as Triassic, but the evidence is inadequate. Anderson and Cruickshank (1978) refer Kenyasaurus to the Dzhulfian Standard Stage, but do not state their reasons for doing this.

Youngina, a close relative of the Tangasauridae, is found in the Daptocephalus zone of the Karroo of South Africa. Like the Lower Sakamena Formation, this is considered to be equivalent to the Dzhulfian Stage of the Upper Permian (Anderson and Cruickshank, 1978).

In summary, the tangasaurids Hovasaurus and Thadeosaurus from Madagascar are known only from Dzhulfian times of the Late Permian. Tangasaurus and Kenyasaurus from Africa could have been contemporaries, although some weak evidence suggests that the latter genus lived during the Early Triassic.

Youngina, an animal close to the ancestral stock of the tangasaurids, apparently also lived in Dzulfian times and could not have been directly ancestral unless it had originated earlier.

Distribution of the Tangasauridae

During the Late Permian, the known sites for tangasaurid eosuchians in Madagascar, Tanzania and Kenya were geographically close (fig. 1). Tangasaurus and Kenyasaurus are known from only one site each, whereas fossil reptiles are known from many Upper Permian sites in Madagascar (fig. 2, Appendix I). The precise location of Colcanap's discoveries is unknown; there are discrepancies between locality names in the catalogues and the literature, and reptiles from some sites have been misidentified. It is important to clear up some of these problems if we are to interpret the depositional environment that contributed to the preservation of the tangasaurids of Madagascar, and to understand the palaeoecology of the Lower Sakamena environments.

As previously mentioned, the first collection made by Colcanap included the tangasaurid Thadeosaurus associated with Glossopteris, Atherstonia, Coelurosauravus and Daedalosaurus. This material probably came from a single site in the Sakamena River Valley, but not Mt. Eliva as Piveteau (1926) assumed.

The absence of Hovasaurus is noteworthy because both Atherstonia and Glossopteris are found with Hovasaurus at Mt. Eliva, suggesting that both sites are probably synchronous. A single rib of Daedalasaurus was found in a nodule with a skeleton of Claudiosaurus near Ranohira, but Thadeosaurus and Coelurosauravus have not been found in any other localities.

Piveteau collected more than two hundred fossils in 1925 from the Permian beds between Mt. Eliva and Ranohira. The Paris catalogues state that 40 specimens were collected near the village of Besakoa on the lower course of the Sakamena River, 45 specimens were from the lower course of the Ianapera near the village of Vohibory, 60 were from Mt. Eliva and 30 from the Imaloto River near Ampasindrasoa and Ranohira. However, Piveteau (1926) only mentions Mt. Eliva and shows neither Besakoa nor Vohibory on his maps. Villages of these names are not marked on any recent maps of the lower courses of the Sakamena or Ianapera Rivers. It seems possible that all of Piveteau's specimens were recovered from the Mount Eliva region and that the catalogues are in error. There are two reasons for this assumption. The lower course of the Sakamena passes through Lower Triassic beds where one would not expect to find Hovasaurus. Although the Lower Sakamena Formation is exposed along the lower courses of the Ianapera River, only disarticulated bones were found there by Tortochaux (1950).

A large number of disarticulated bones were collected from numerous sites in the Lower Sakamena Formation by Tortochaux (1950). Most were identified as Tangasaurus and Hovasaurus on the basis of erroneous criteria, and the identifications have been published by Tortochaux (1949), Besairie (1971) and others. Because the identifications of the specimens are questionable and their present location unknown, most localities cited by Tortochaux are meaningless.

The most common eosuchian in the Lower Sakamena Formation is Hovasaurus. Colcanap collected many specimens of this genus somewhere in the Sakamena Valley in 1908, Piveteau recovered more from the foot of Mt. Eliva and about a kilometre to the west of the rest stop named Sakamena in 1925, and Besairie collected at least eight from Mt. Eliva between 1926 and 1929.

Near Ranohira (fig. 2), west of the junction of the Beroroha-Ihosy routes, there is a bed of siltstone nodules containing reptile and plant remains. The bed was first noticed by Gence in 1938 (Tortochaux, 1950). Quartz pebbles are found in the abdominal region of the partial skeletons. The sternum is ossified, the humerus is curved with a greatly enlarged distal end, and the tail is specialized for swimming. These are all diagnostic characteristics of Hovasaurus.

A specimen of Hovasaurus (AMNH 5333) collected at Kalivari on Madagascar is in the collections of the American Museum of

Natural History. Kalivari is not on any of the maps of Madagascar that I have access to, and the specimen has no other information.

Palaeoecology of Tangasaurids

The known fauna and flora of the Lower Sakamena Formation are summarized in Appendix II. The specimens were collected from strata representing many different depositional environments. The formation is extensive, both horizontally and vertically. The number of specimens collected from each site and the associated data are usually inadequate. Even so, faunal differences can be seen at different sites.

Many plant genera considered typical of the Glossopteris flora of the southern hemisphere are not found in Madagascar, and the flora lacks variety. The low diversity and the presence of growth rings in silicified wood suggests seasonal variability. Seasonal stress is expected because the study area was located at a high latitude, 60° South during Permian times (Bambach et al, 1980).

The remains of reptiles are the most commonly preserved vertebrates in the Lower Sakamena Formation. The reptile fauna, dominated by eosuchians, strongly contrasts with the contemporary faunas of South Africa where therapsids are the dominant vertebrates. For a long time it seemed that therapsids were not present in Madagascar, but a single vertebra was recovered recently from the red beds of the underlying Sakoa formation (Besairie, 1971). A number of isolated therapsid bones were found in collections from the Lower Sakamena Formation of the Benenitra region (Carroll, personal communication, 1975). These have been tentatively identified as a dicynodont vertebra and tusk, and the anterior end of the dentary of a carnivorous therapsid. It appears highly probable that the rarity of therapsids in the Lower Sakamena can be attributed to a different habitat from that represented by the Karroo System of South Africa.

The osteology of Thadeosaurus and its association with Coelurosauravus and the gliding reptile Daedalosaurus suggests that this animal could have been terrestrial. Fish remains found at the site show that the depositional environment was aqueous, but the articulated nature of the terrestrial specimens suggests that is was not far from land. The absence of the aquatic tangasaurid Hovasaurus is interesting because it appears to have been a contemporary of Thadeosaurus (both genera are associated with Glossopteris and Atherstonia).

Hovasaurus is common in Lower Sakamena strata at Mt. Eliva, and is probably also present at a site near Ranohira. At this time, it can be associated with only two other animals from the Sakamena River Valley -- one specimen of the palaeoniscoid fish Atherstonia and a single specimen of the eosuchian Acerosodontosaurus.

The type specimen of Acerosodontosaurus is associated with a large number of Hovasaurus specimens from the Sakamena River Valley. Some isolated bones found in association with the aquatic reptile Claudiosaurus at Benenitra probably represent Acerosodontosaurus. The association with aquatic genera suggests that Acerosodontosaurus could have been an aquatic reptile, whereas its rarity at the two sites could mean that its remains were washed in from a terrestrial environment.

The remains of Claudiosaurus are common at Benenitra and Leoposa, and one specimen was found near Ranohira. Because Acerosodontosaurus is associated with both Claudiosaurus and Hovasaurus, it seems likely that the latter two genera were contemporaries. This view is supported by the fact that Claudiosaurus fossils have been found at stratigraphic levels above and below the Hovasaurus level at Ranohira. The apparent absence of Hovasaurus from sites where Claudiosaurus is abundant implies that these two swimming reptiles inhabited two distinct aquatic environments in the same general region during early Sakamena times.

Clearly any conclusions made concerning Lower Sakamena depositional environments and palaeoecolocy are speculative at this time. The data is suggestive of at least four distinct palaeoenvironments distinguished by the following faunal associations:

1. Marine invertebrates. No identifiable reptiles.
2. Dominated by terrestrial reptiles (Thadeosaurus, Daedalosaurus, Coelurosauravus). The palaeoniscoid Atherstonia makes up 25% of the specimens.
3. Strongly dominated by Hovasaurus (97-99%). Acerosodontosaurus and Atherstonia present.
4. Dominated by Claudiosaurus. Associated terrestrial elements include Acerosodontosaurus, Daedalosaurus and the therapsids.

Fieldwork concentrating on the detailed stratigraphy, taphonomy and palynology of fossiliferous sites is necessary to confirm the significance of these associations.

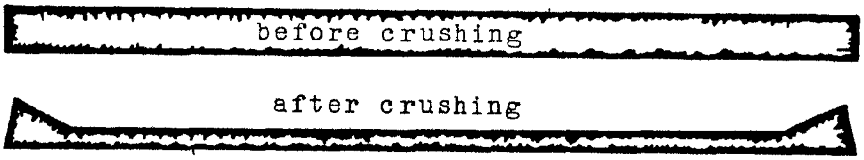
Measurements

Specimens of Acerosodontosaurus, Thadeosaurus and Hovasaurus are preserved in siltstone nodules with calcareous, siliceous cement (Tortochaux, 1950). When collected, most of the bone had eroded out of the split modules, leaving only the natural moulds of the bones in the counterpart blocks. High fidelity latex or silicone rubber casts were made from the moulds as an aid in studying the specimens. All measurements were taken from the casts for consistent results, even though the nodules were available for some of the specimens. A hundred comparative measurements were made between the original specimens and casts to determine how much shrinkage had occurred in the reproductions. It was found that the average shrinkage in latex casts was 1.2%, while in casts of silicone rubber shrinkage was 1.0%. This amount of shrinkage is negligible for the majority of measurements because of the small size of the bones, hence no attempt was made to add a correction factor to measurements made from casts.

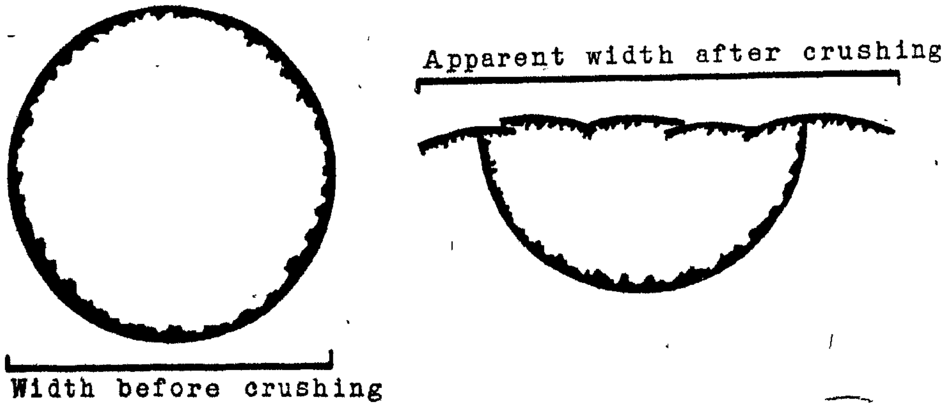
All measurements were made by means of a calliper to the nearest tenth of a millimetre. Because of the large number of specimens involved and the large number of measurements per specimen, most measurements were made only once. Bivariate graphs were made, comparing the length or width of the element being studied (y) with the average length of a dorsal centrum (x) (fig. 4). Any points on the graphs that were inconsistent with the general trends were noted. Once the list was long enough to eliminate all memory of why a particular point was inconsistent, the measurements of the inconsistent points were taken again. This time each dimension was measured four times and the average measurement was taken as the final figure. In most cases there was not a significant difference from the original measurement, but some mistakes were found.

Lengths were measured between perpendiculars to the longitudinal axes of the bones, and widths between lines parallel to the longitudinal axes. Limb bone measurements of length, proximal width and distal width were made between the points of greatest separation, whereas shaft width was taken from the narrowest region of the shaft.

In general, the skeletons had collapsed into a single plane, but show signs of crushing and distortion only in the largest bones. Crushing has little effect on the length measurements of limb elements. In longitudinal section, the upper and lower surfaces of a limb bone are almost parallel and crushing forces are not severe enough to do more than collapse the upper surface.

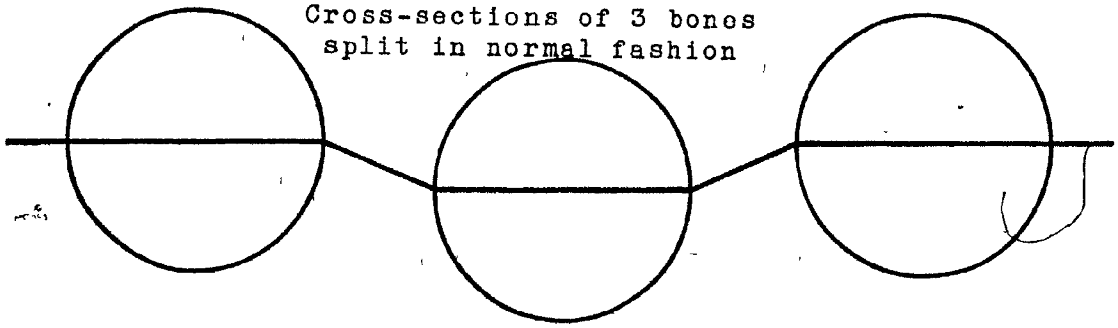


Width measurements are more variable. In cross-section a limb bone is an ellipse or circle, the circumference of which is greater than the width (diameter). When crushed, the apparent width can increase up to one half the circumference of the outer surface, although this is never reached because of curved, overlapping sections.



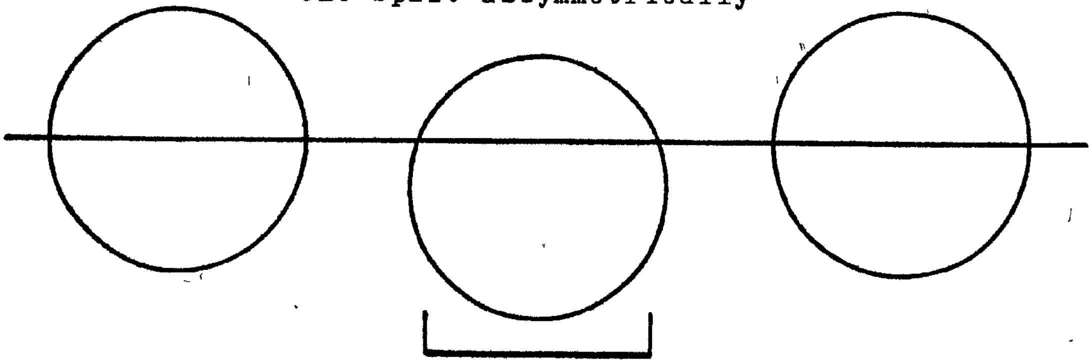
The curvature of the bone contributes to the higher variability of width measurements in another way. Almost every bone is split when a nodule is cracked open. In most cases, the longitudinal division of a bone occurs at the level where the bone is widest.

Cross-sections of 3 bones split in normal fashion



If split above or below this level, the diameter or width of the bone at the level of division will be less than the maximum diameter. In most cases, only one half of each nodule was recovered and it is impossible to know whether or not the full width is represented.

Cross-sections of 3 bones, one split assymmetrically



Apparent width of bone if only upper portion found

Comparison of measurements is one way to answer questions of identification or relationship of extinct and living taxa. This proved critical in this study because Hovasaurus and Thadeosaurus are so similar anatomically that many specimens could only be identified by comparative measurements. It was only after the identifications were made that it became apparent that the genera are locality specific. There are many ways to analyse the measurements made on specimens, and each method has some advantages.

Multivariate analysis summarizes large numbers of observations into a small number of axes (Gould, 1967). There are numerous programs possible that can be analysed quickly by computer. Multivariate analysis has been used with pelycosaurs (Gould, 1967; Gould and Littlejohn, 1973) and modern reptiles (Dodson, 1975a, b), and proved useful for establishing general trends. However, it did not provide information specific enough for detailed comparisons between genera, and therefore was not used in this investigation.

More specific comparisons are possible if they are bivariate, provided a suitable standard for comparison can be established. Romer and Price (1940) developed a standard of measurement that allowed them to compare objectively the relative dimensions of bones of animals of different sizes. The standard was based on half the transverse width of a vertebral centrum (r) from the middle or posterior dorsal region. The orthometric linear unit, $\underline{r}^{2/3}$ (Romer, 1948), is proportional to the weight of the animal when it was alive, and appears to be the ideal yardstick for measuring bones. If the length of a bone is divided by the orthometric linear unit (OLU), the resulting figure is called the unit measurement. This measurement should be constant for any bone in closely related adult animals, regardless of differences in their absolute size.

However, Currie (1978) has pointed out that the OLU is based on only isometric, interspecific size changes in its derivation, and should therefore be restricted to these same dimensions in its application. The orthometric linear unit should not be used in studying sub-mature specimens because the coefficient of allometry is not the same in ontogenetic and interspecific series when $\underline{r}$ is used as the basis for comparison. Therefore, this system of unit measurement cannot be used directly with Thadeosaurus and Hovasaurus because most specimens are immature.

Unit measurement based on the OLU is useful for intergeneric comparisons of mature animals. The largest known specimens of Thadeosaurus and Hovasaurus are mature but incomplete specimens. However, if the allometric equation for growth is known for any element, an estimated mean value for the length or width of this element can be calculated from the known value of $\underline{r}$ of the largest specimen (Tables 3, 8). The unit length can then be calculated by dividing the estimated length by the OLU, and this can be compared with the unit lengths of the same element in other reptiles.

Because of its relationship to the OLU, the ideal standard of measurement for ontogenetic series in Thadeosaurus and Hovasaurus would have been $\underline{r}$. The unit measurements could have been solved by simply substituting the values of b' and k' of the ontogenetic power equation and $\underline{r}$ of a mature animal into the equation

$$b \text{ (unit measurement)} = b'\underline{r}^{k'-2/3} \quad \text{(Currie, 1978).}$$

Unfortunately, $\underline{r}$ can be measured directly in very few specimens.

The length of a dorsal centrum can be measured easily in most specimens, and has a simple, direct relationship to $\underline{r}$. Where it could be measured, it was found that in Hovasaurus the width ($2\underline{r}$) of the dorsal centrum was on the average 84% the length of the centrum regardless of the animal's age at the time of death. Furthermore, the relative lengths of dorsal centra are far more consistent in relation to $\underline{r}$ in eosuchians than length of cervical vertebrae, length of limb bones, width of any element or total body length. For these reasons, the dimension selected to be the standard of measurement in this investigation is the average length of a dorsal centrum, $\underline{x}$.

Both Thadeosaurus and Hovasaurus are represented by specimens ranging from juveniles to adults. The length of an average dorsal centrum of the largest known specimen of Thadeosaurus is 2.8 times the length of the same dimension in the smallest known specimen (Table 3). The ratio is 3.5 in Hovasaurus (Table 6). It is evident from the ossification of the largest specimens that these were mature animals when they died. The size ratio of adults to hatchlings for 38 species of lizards and crocodylians was compared with the corresponding adult body length using the least squares method. These measurements were extracted from the literature specifically for this investigation. The correlation coefficient is high (.98), and the ratio of adult to hatchling length can be defined as 2.70 + .003 (adult length in mm) mm^{-1}. Tangasaurids probably laid eggs and had the same type of metabolism as extant species of lizards and crocodylians. Therefore it seems reasonable to assume that growth rates and adult to hatchling size ratios would have been similar to those of living reptiles. The expected adult to hatchling length ratio for Thadeosaurus (adult length 400 mm) is 4.0 (95% confidence interval is 3.8-4.3), and that for Hovasaurus (adult length 550 mm) is 4.6 (95% confidence interval is 4.3-4.8). Although these ratios were calculated for total length, vertebral length at any age is directly proportional to total length because the total number of vertebrae does not change and there is no evidence that vertebral growth rates are variable in different regions of the body. The adult to juvenile length ratios of the vertebrae indicate that the smallest known specimens of both Thadeosaurus and Hovasaurus were not very old when they died, but were not hatchlings. Because reptiles generally double their length within the first year of life, the smallest specimens of both genera would have been less than one year old.

The power formula can be adapted to describe growth in Thadeosaurus and Hovasaurus. Simpson, Roe and Lewontin (1960) point out that the relative growth of two dimensions is a basic characteristic of a species. The individual animals of either species could have had different rates of growth, but a random sample of individuals could give measurements that represent simple power equations of growth.

In the equation $y = b'x^{k'}$, y is the length or width of the element being studied, x is the average length of a dorsal centrum, and b' and k' are constants. The length of the centrum is not dependent on weight in ontogenetic development, so growth is isometric when $k' = 1.0$ (Currie, 1978). The constant b' and k' were solved for length and width measurements of every tangasaurid element for which the sample was large enough to be statistically significant (Tables 3, 8).

The length of the skeletal elements will be used to differentiate growth strategies in Tangasaurus and Hovasaurus. For example the logarithm of humerus length was plotted against the logarithm of x for six specimens of Thadeosaurus and 22 specimens of Hovasaurus where both these dimensions are known (fig. 4). The points on the scatter diagram are consistent in their alignment for each genus, the correlation coefficients being .997 in Thadeosaurus and .991 in Hovasaurus. The coefficient of allometry, k_{yx}' (calculated by the least squares method), is significantly higher than 1.0 in both genera. However, positive allometric growth is greater in Hovasaurus. Consequently, although the humerus of Hovasaurus is relatively shorter in juveniles than it is in Thadeosaurus, it becomes relatively longer in adults.

As in the humerus, the correlation coefficients of other dimensions are high. This is a reflection of the excellent size range available for most elements. The correlation coefficients of width measurements tend to be lower than those of length, relating directly to greater distortion in bone widths as discussed previously.

The measurements do not include the complete length of the bone because the cartilaginous ends are not preserved. In mature specimens, the amount of cartilage would be negligible. However, cartilage makes up a much higher percentage of the length of any limb bone in juveniles. The ossified portions of adjacent limb bones are separated by the cartilaginous ends of the bones. The unossified region is represented by gaps between adjacent bones in the fossils of articulated skeletons. The separation between the humerus and forearm was measured in the smallest specimens of both genera. If it is assumed that half the distance represents the cartilaginous distal end of the

Figure 4. Relationship between length or width of a limb element (y, ordinate) and length of associated thoracic centrum (abscissa) in _Thadeosaurus_ (circles) and _Hovasaurus_ (squares). a) Length of humerus. b) Length of femur. c) Shaft width of femur. All measurements converted to logarithms. Data from Tables 3 and 6.

Fig. 4a

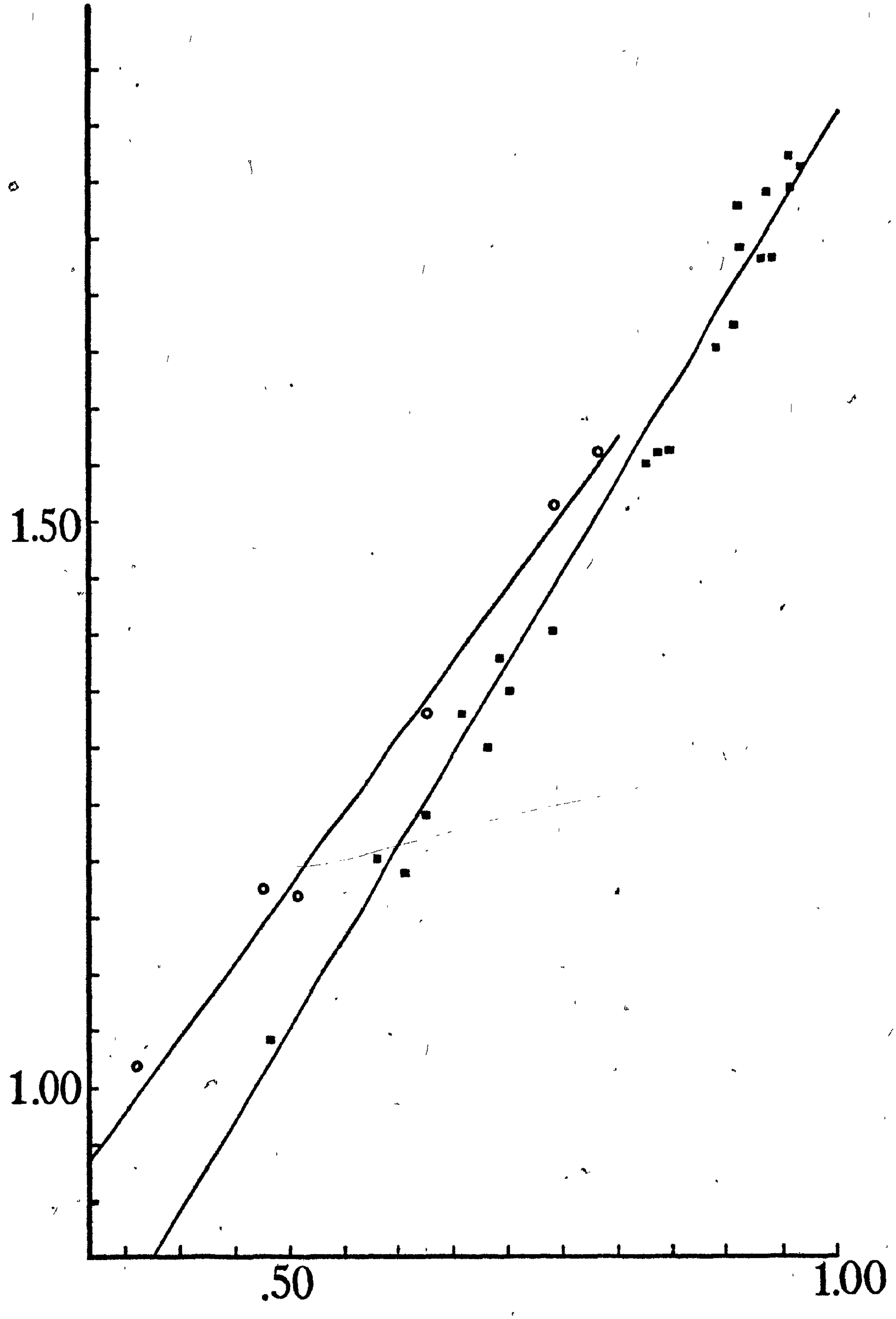


Fig. 4b. Length of Femur

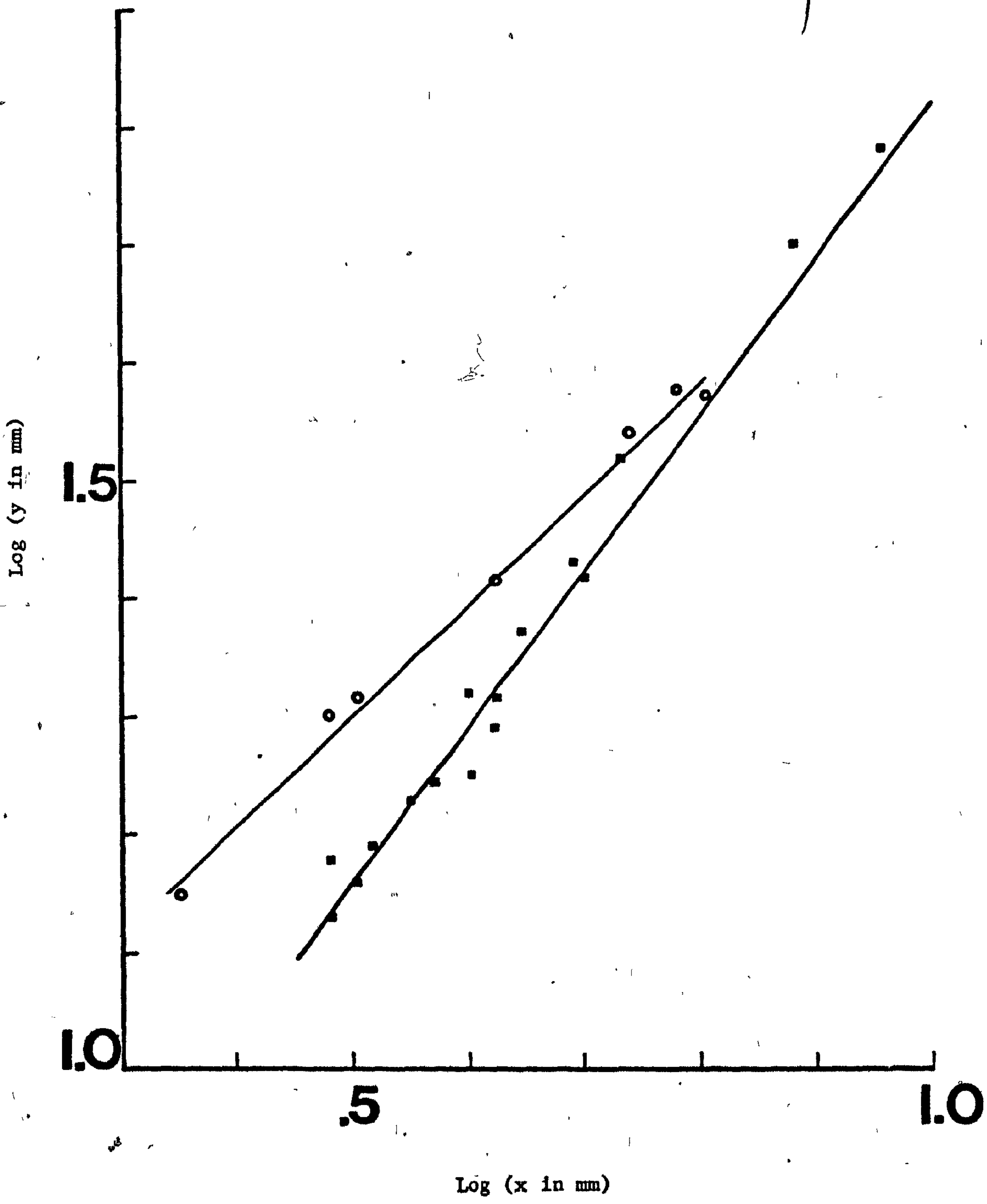
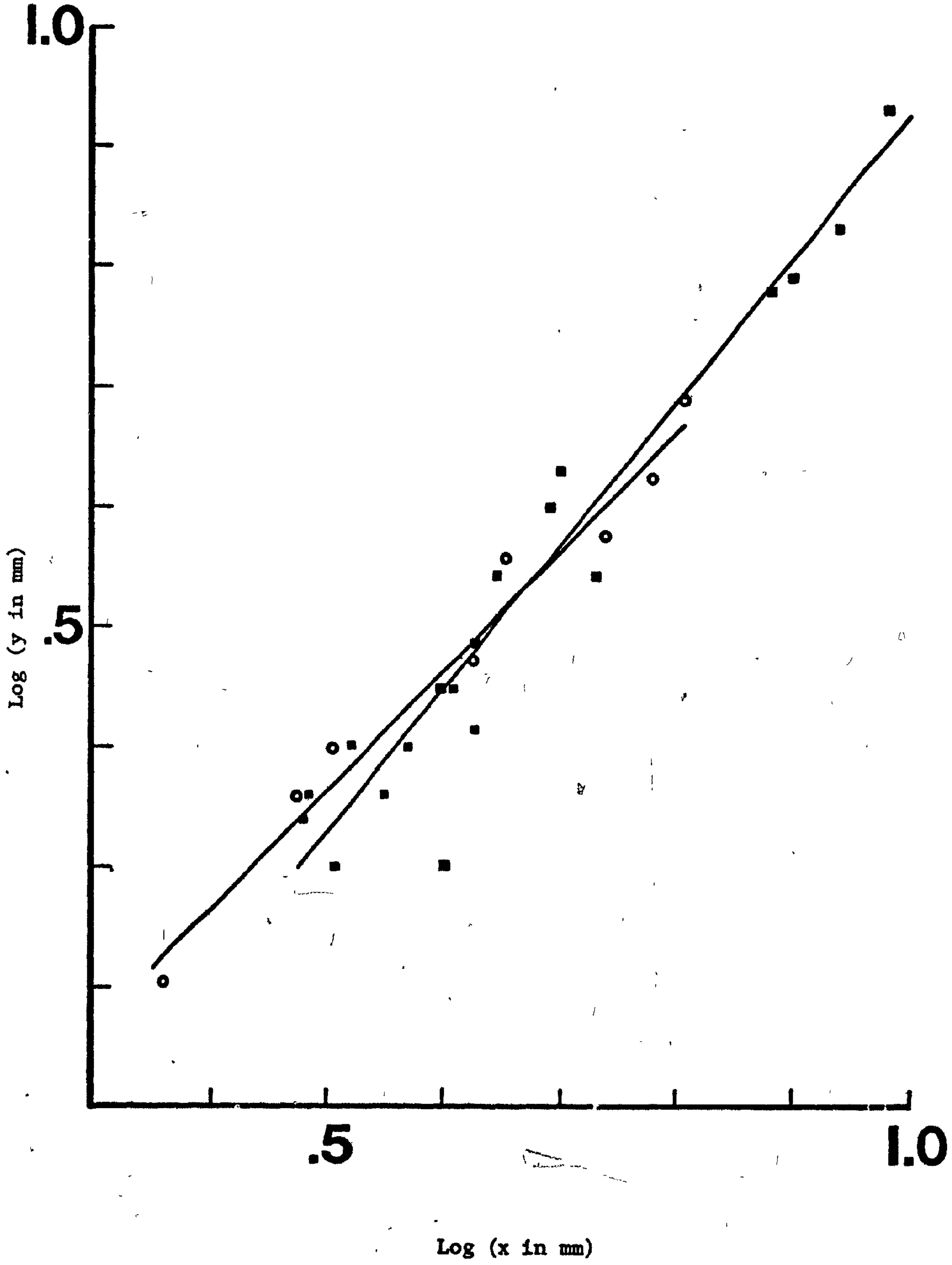


Fig. 4c. Femur, Shaft Diameter



humerus, and that the cartilage of the proximal end would have been about the same length, then an estimate can be made of the percentage of total length of the humerus formed by cartilage. On the average, 16.2% of the total length of the humerus was cartilaginous in juveniles of life stages A and B (Table 6) of Hovasaurus. The average (15.5%) cartilaginous composition for the same bone in Thadeosaurus is not significantly different.

Allometric growth rates are frequently referred to in this study. The growth rates calculated are for the ossified lengths of the bones, and not the total lengths. In most cases the amount of cartilage cannot be estimated. There would have been none in the dermal bones, and the percentage in endochondral bones would vary. The difference in growth rate of the total bone and growth rate of the ossified portion can be estimated for the humerus. The coefficients of allometry for ossified lengths of the humeri of Hovasaurus and Thadeosaurus are 1.61 and 1.30 respectively. If we assume that the total length of the humerus is 16% cartilage in the smallest specimens and 1% at maturity, the coefficients of allometry for total bone lengths are calculated to be 1.50 in Hovasaurus and 1.16 in Thadeosaurus. Because the percentages of cartilage in the bones of the two genera are apparently the same at equivalent life stages, differences in the growth rates of the ossified portions of the bones are biologically significant.

In summary, the large number of well preserved tangasaurid specimens permits quantitative studies to supplement morphological information. Thadeosaurus and Hovasaurus are closely related, contemporary genera that had different habitat preferences. Comparative measurements make it possible to identify many partial skeletons that lack diagnostic morphological features. In the past, new fossil genera were often established on the basis of relative limb proportions that differ from those of known genera. Study of the growth series of tangasaurids is another indication of how much relative proportions can change in the life of a reptile. Relative limb proportions in adult animals can be used to indicate habitat preferences. Comparative study of growth rates indicates significant differences between the genera that reflect different life styles (prey preference, dispersal, etc.). These will be discussed in detail in subsequent sections.

I

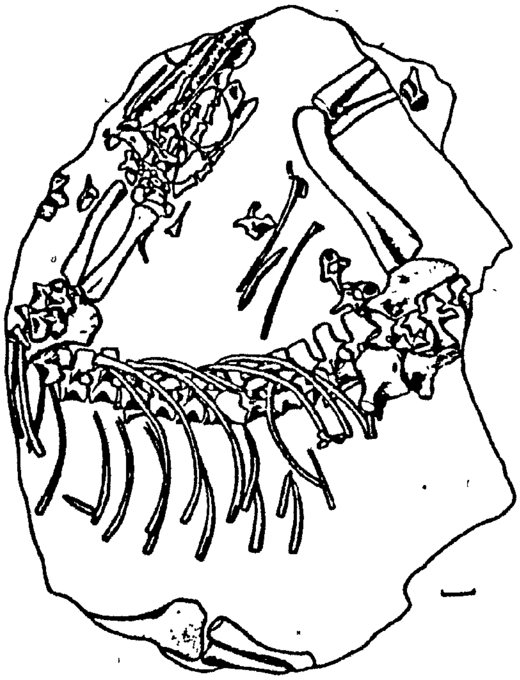
A NEW GENUS OF YOUNGINIFORMES (REPTILIA: EOSUCHIA) FROM THE UPPER PERMIAN OF MADAGASCAR

In re-examining the tangasaurids of Africa and Madagascar, it was discovered that one of the specimens (MNHN 1908-32-57) in the Paris collections labeled tentatively as Tangasaurus is a new genus of younginiform. Most specimens that have been described and attributed to the Younginiformes are either poorly preserved or juveniles. The new specimen provides a better understanding of the anatomy of primitive eosuchians, and increases the known diversity.

The specimen was preserved in a nodule of fine-grained sandstone. Most of the bone had eroded out of the split nodule, leaving only the natural molds of the bones in the counterpart blocks. Unfortunately, one of the blocks was chipped in the region of the skull, and the imprint of most of the outer surface of the skull was lost. Latex casts were made from the molds as an aid in studying the specimen (Baird, 1951).

The skull, trunk, front limbs, pelvic girdle and part of the left hind limb are preserved (fig. 5). The body of the animal had settled into the mud on its right side, and had started to decay before it was buried by sediment. The skull settled on top of the right manus and became disarticulated. The bones on the right side of the skull remained in

Figure 5. *Acerosodontosaurus piveteaui*.
Specimen drawing of MNHN 1908-32-57a,
holotype. Ventral scales omitted
from drawing. Scale = 1 cm.



association, but those of the left side drifted away. Of the left side of the skull, only the lacrimal and the postfrontal bones have been found in the nodule. The braincase had drifted beyond the limit of nodule formation. Some of the cervical and anterior dorsal vertebrae and ribs became disarticulated and were carried a short distance from their original positions. The current that removed these bones appears to have been gentle, and there is no evidence of macrophagous scavenging.

In life, the animal would have been lizard-like in appearance. The snout-vent length was approximately 30 cm, and the length of the whole body was probably between 60 and 70 cm.

A number of features suggest that the animal was still immature when it died. The skull is disarticulated. Sutures are still visible between the centra and the neural arches. The ectepicondylar foramen of the humerus is open. The separation between the head of the femur and the internal trochanter is indistinct. The well-ossified quadrate, articular and carpus, the presence of muscle scars on the limb bones, and other characters indicate that the animal was close to adult size.

Systematics

Class Reptilia

Order Eosuchia

Suborder Younginiformes

ACEROSODONTOSAURUS Currie 1980

Diagnosis

Diapsid reptile of the suborder Younginiformes. Differs from Youngina, Heleosaurus and Galesphyrus in having larger number of maxillary teeth. Marginal teeth slender and sharply pointed in contrast to the blade-like teeth of Heleosaurus or the peg-like teeth of Galesphyrus. Skull wider in the antorbital region than Youngina. Cervical centra shorter than the thoracic centra, whereas in Heleosaurus the centra are about the same length throughout the column; neural spines taller and longer than those of Youngina, Galesphyrus, Heleosaurus or Heleosuchus. Ventromedial-dorsolateral width of the pubis greater than its length, distinguishing it from Youngina, Galesphyrus and Heleosaurus; iliac blade extends relatively farther caudad than that of Youngina. Radius has twisted appearance characteristic of Champsosaurus, but not known in any other primitive diapsid; ulna (excluding olecranon) longer than radius, whereas in Youngina and Galesphyrus, the radius is longer; intermedium and ulnare relatively shorter than in Galesphyrus; medial centrale smaller than lateral centrale. Acerosodontosaurus is distinctive from Thadeosaurus (Carroll, in press) in that it possesses a more gracile humerus, has an ulna that is longer than the radius and has a pubis with different proportions.

ACEROSODONTOSAURUS PIVETEAUI CURRIE 1980

Etymology—Latin "aceros" - needle-shaped, Greek "odônt" - tooth, Greek "sauros" - lizard; piveteaui in honour of Dr. Jean Piveteau, the first person to study the eosuchians of Madagascar.

Holotype—MNHN 1908-32-57a, b. Muséum National d'Histoire Naturelle, Paris, France.

Horizon and Locality

Lower Sakamena Formation, Upper Permian. Sakamena River Valley, southern Madagascar. Exact locality not recorded.

Diagnosis

Same as for genus.

Description

The state of ossification in the skull suggests that this animal was immature at the time of death. The dermal bones were not co-ossified, and had become disarticulated before burial. Only two endochondral bones, the right quadrate and the right articular, are well-ossified. Ossification of endochondral bones occurs late in the development of reptilian skulls (Howes and Swinnerton, 1901).

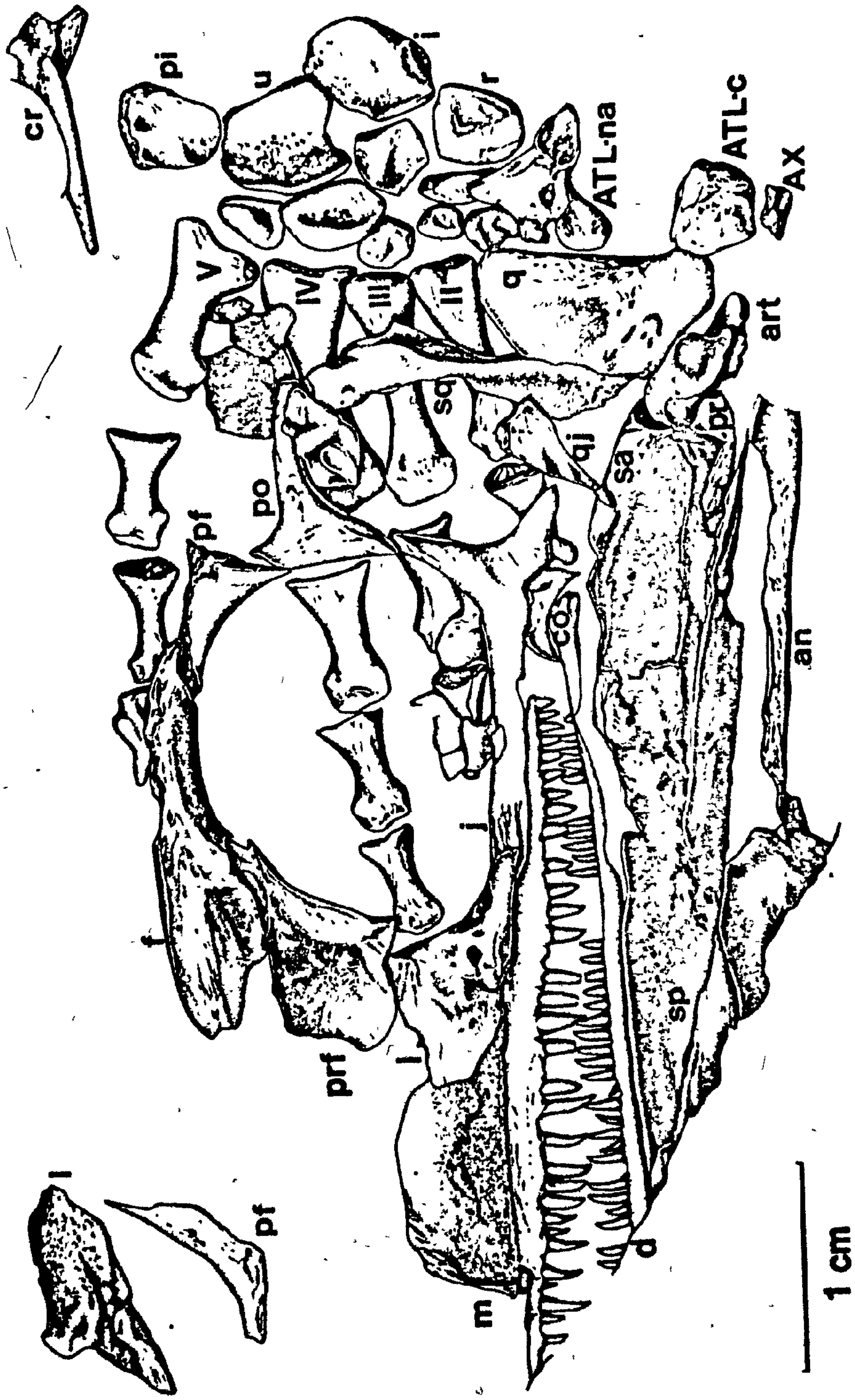
Most of the bones of the right side of the skull have retained the proper relationships to each other, but can be seen in internal view only (fig. 6). A maxilla, both lacrimals, prefrontal, frontal, jugal, both postfrontals, postorbital, squamosal, quadratojugal, ectopterygoid, quadrate, dentary, splenial, coronoid, angular, surangular, prearticular and articular have been identified in the specimen. A number of thin bones in the orbital region could be the remains of scleral ossicles.

The right side of the skull is disarticulated enough to reveal the full extent of most of the bones. It is therefore possible to make a reasonable reconstruction of the skull in external view (fig. 8). The teeth would appear slightly shorter in external view than they would in internal view.

An accurate estimate of the length of the skull cannot be made because of the absence of the premaxilla. If the reconstruction is correct, the skull would have been about 55 mm in length, or approximately six times the length of a dorsal centrum.

Figure 6. *Acerosodontosaurus piveteaui*, holotype. Internal view of right side of skull and dorsal view of right manus.

Figure 7. *Acerosodontosaurus piveteaui*, holotype, MNHN 1908-32-57b. Ventral view of right manus.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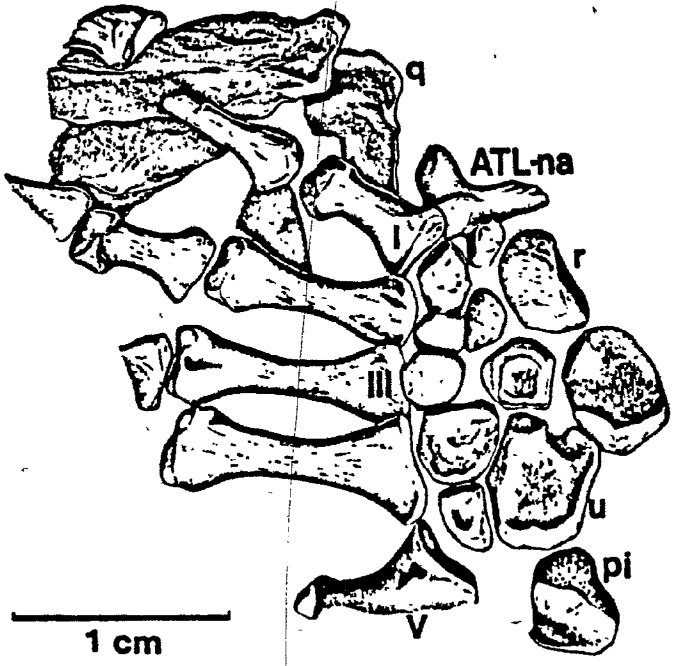
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1 cm

The preorbital region is long, almost one half the length of the skull.

The lower margin of the skull shows little curvature in the maxilla, but turns ventrad in the postorbital region. The finished anterior edge of the maxilla indicates that the narial opening was probably large. The orbit is large, reflecting the relatively small size of the animal. It occupies approximately one third the length of the skull, and most of the height. The orbit is oval in shape, about ten per cent longer than it is high. The lateral temporal fenestra is relatively large. Only one bone of the palate, the ectopterygoid, is preserved. The shape of this bone and the position of the suture for the palatine on the maxilla indicates that the internal naris and the suborbital fenestra are elongate, as they are in most primitive diapsids.

The maxilla is a long, moderately high bone, with a length almost five times its height. It extends posteriorly to the mid-orbital region. The anterior edge rises sharply from the premaxillary ramus. The bone is thickened along this edge ventrally. The ventral edge of the maxilla extends medially as a narrow palatal shelf above the marginal tooth row. A rugose region above the twelfth to fourteenth teeth marks the point of attachment to the palatine. A recess in the dorsal surface of the palatal shelf anteriorly, and a facet at the base of the thickened anterior edge of the dorsal process of the maxilla could represent the point of contact with the septomaxilla. There is no medial buttress of bone supporting and strengthening the central part of the maxilla as reported by Gow (1975) in Prolacerta.

The lacrimal forms the anteroventral portion of the orbital rim. It does not extend anteriorly to the external naris like the lacrimal of Petrolacosaurus (Reisz, 1977), the earliest known diapsid, but is larger than the lacrimals of most other early diapsids. The posterior end of the lacrimal is overlapped laterally by the jugal and the maxilla. A heavy internal buttress on the lacrimal in this region braces the maxilla against the orbital rim of the prefrontal. The lacrimal overlaps the prefrontal, but not to the extent seen in Eocaptorhinus (Heaton, 1979). The dorsal and ventral lacrimal puncti can be seen on the posterior surface of the orbital rim of the right lacrimal. The canaliculi from the puncti merge to form the common osseous canal of the lacrimal duct, which pierces the heavy buttress of bone. The course of this canal can be seen on the left lacrimal where the medial wall of the canal has collapsed.

The prefrontal forms the anterodorsal rim of the orbit. A wide orbital rim extends medially from the main body of the bone. A ridge on the medial surface of the orbital rim marks the attachment of the fibrous orbitonasal membrane. The external surface of the bone is strongly convex in cross-section, indicating that the prefrontal must have been exposed equally in dorsal and lateral aspects. The strong curvature extends from the prefrontal onto both the lacrimal and the maxilla. That the skull of *Acerosodontosaurus* was broader in the antorbital region than that of *Youngina* is indicated by the curvature and dimensions of the prefrontal. Posterodorsally, the prefrontal overlaps a sutural surface on the frontal.

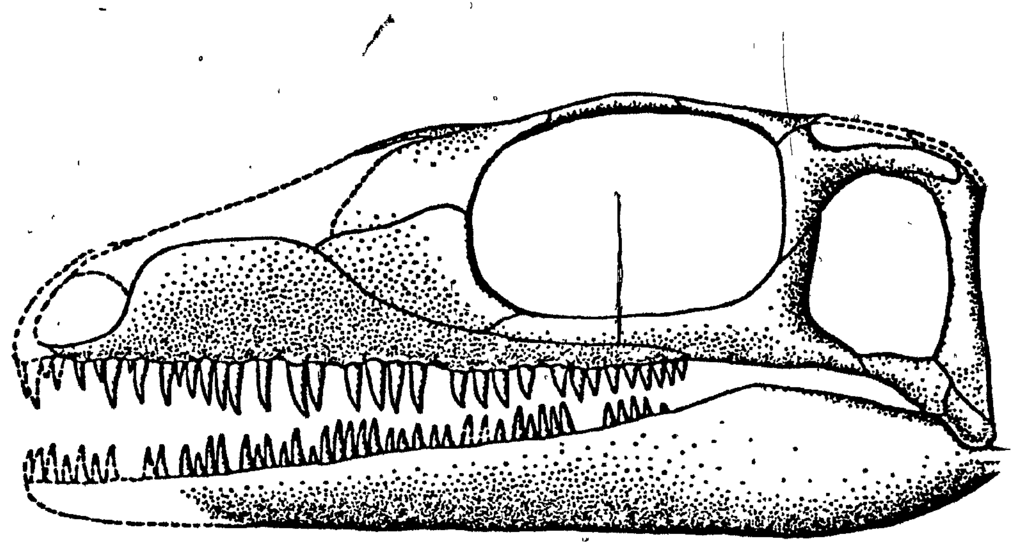
Most of the ventral and part of the posterior portion of the orbital rim is formed by the jugal. Ventrally, the jugal is excluded for more than half its length from the ventral margin of the skull by the maxilla. The suborbital ramus is low but strong, as would be expected for a relatively small reptile with large orbits. The postorbital ramus of the jugal overlaps the end of the jugal ramus of the postorbital. The subtemporal ramus is a thin plate of bone that curves posteroventrally.

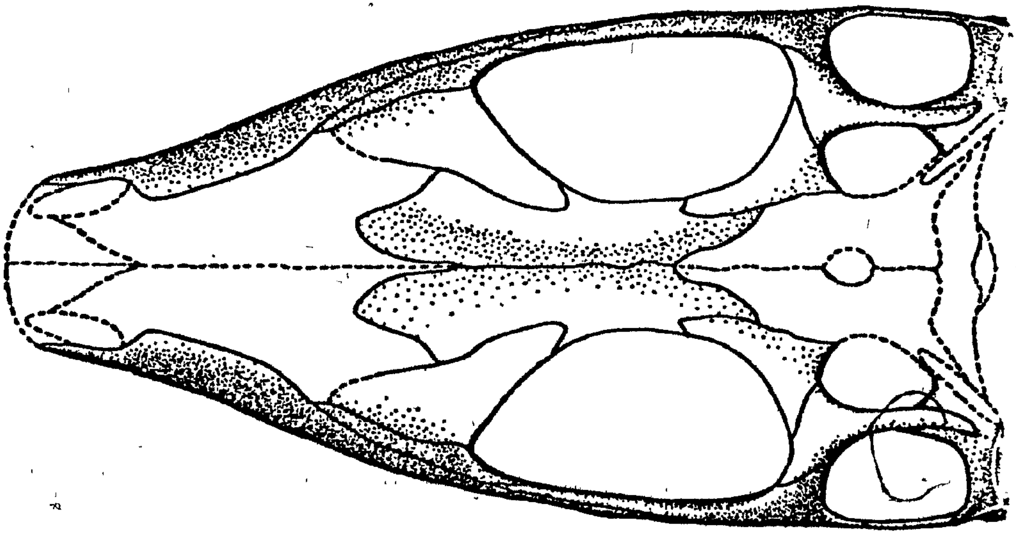
The quadratojugal is a small, triangular bone, similar in shape to that of Youngina (Gow, 1975, fig. 2) and Heleosaurus (Carroll, 1976a, fig. 2). In MNHN 1908-32-57, the bone has shifted slightly from its original position, making it difficult to determine the original relationship to the quadrate and squamosal. It appears that it extends posteriorly to contact the quadrate, for there is a pronounced posteromedial sutural surface. The quadratojugal is overlapped laterally by the squamosal, and appears to have overlapped the jugal anteriorly as in Heleosaurus (Carroll, 1976a). As in Petrolacosaurus and Youngina, the quadratojugal forms part of the ventral border of the lateral temporal fenestra.

The squamosal has the same basic configuration as that of Petrolacosaurus (Reisz, 1977) and Youngina (Gow, 1975). It makes up most of the posterior border of the lateral temporal fenestra, and descends to the ventral skull margin. A robust ridge extends dorsoventrally along the mesial surface of the bone. An elongate concavity posteromedial to the ridge cradled the lateral edge of the quadrate.

The frontal is a long, narrow bone that is dorsoventrally thickened in the orbital region and that thins between the prefrontals. Anteriorly, the frontals expand laterally, another indication that the skull is broad in the antorbital region. The

Figure 8. Acerosodontosaurus piveteaui. Reconstructions of the skull in lateral and dorsal views. Scale = 1 cm.





frontals of Youngina (Carroll, 1977, fig. 13) may have expanded laterally at the anterior end in a similar manner, though not to as great an extent. Posteriorly, the frontals diverge to receive the joined anteromedial processes of the parietals. On the ventral surface, a robust ridge exists as a continuation of the internal edge of the orbital rim of the prefrontal. Posterolaterally, the frontal is emarginated for its contact with the postfrontal, and is partially overlapped by the sutural surface of the latter bone. In Prolacerta, the frontal overlaps the postfrontal in this region (Gow, 1975, fig. 14).

The postfrontal forms the posterodorsal corner of the orbit, and part of the anterior rim of the superior temporal fenestra. An oblique sutural contact with the postorbital extends from the orbit posterodorsally to the superior temporal fenestra. The contact twists so that the postfrontal overlaps the dorsal tip of the postorbital slightly as in Youngina (Gow, 1975). There is a relatively long contact with the parietal, which underlies the posterior corner of the postfrontal. As in Youngina, the postfrontal separates the parietal and postorbital, and forms part of the anterior rim of the superior temporal fenestra. This is not the case in

Petrolacosaurus (Reisz, 1977) or Prolacerta (Gow, 1975).

The postorbital is triradiate and similar in outline to that of Youngina. The nature of its contact with the squamosal cannot be seen clearly, although it probably overlapped the latter bone in the same manner as in Youngina and other primitive reptiles (Heaton, 1979; Currie, 1979).

The ectopterygoid is a small bone located between the jugal and the coronoid in MNHN 1908-32-57, and is seen in posterodorsal view. As in Petrolacosaurus (Reisz, 1977), it formed part of the anterior boundary of the subtemporal fenestra, and the posterior margin of the suborbital fenestra.

The quadrate is a large bone with extensive immovable contacts with the squamosal, quadratojugal and pterygoid. In MNHN 1908-32-57, the quadrate can be seen only in external (posterior) view. The posterolateral surface is heavily scarred where it was sutured to the occipital flange of the sqamosal. It is evident from the orientation of the articular that each of the articular condyles would have been on almost the same horizontal plane during life. In outline, the quadrates of Acerosodontosaurus and Heleosaurus (Carroll, 1976a) are similar.

Thin bones found in the orbital region may be the remains of scleral ossicles. These are known in many primitive reptiles, including Prolacerta

(Camp, 1945).

The mandible is long and slender, with a low coronoid process. The toothed margin is only slightly concave in lateral view.

Detailed description of the mandibular elements is not possible because of crushing. The splenial forms the anterior half of the internal surface of the lower jaw. The angular forms much of the ventral margin of the mandible, and the floor of the Meckelian canal. Anteriorly, it tapers to a point that is overlapped medially by the splenial. The medial surface of the angular is deeply scarred anteriorly, presumably for muscle attachment. The dorsal edge of the surangular is thickened medially into a ridge that forms the dorsal margin of the adductor foramen. Anteriorly this ridge continues onto the posterodorsal portion of the coronoid. The ridge becomes a prominent buttress posteriorly, where it forms a posteromedially oriented facet connecting with the articular. The coronoid is a relatively small bone that forms the posterior part of the roof of the Meckelian canal. Anteroventrally, there is a simple butt joint with the prearticular. Unlike the condition in Petrolacosaurus (Reisz, 1977) and Prolacerta (Gow, 1975), the coronoid does not extend ventromedially to form part of the anterior rim of the adductor foramen. There is no coronoid in Heleosaurus (Carroll, 1976a).

The dorsal surface of the articular is convex anteriorly. Approximately halfway along its length, the outline of the bone turns sharply ventrad to form a pair of concavities that articulate with the quadrate. The lateral concavity is more pronounced than the medial one. The entire dorsal surface of the articular is unfinished bone, suggesting that the surface was covered by a cap of cartilage. A small area of finished bone is exposed anteromedially between the dorsal convexity and the prearticular suture. The retroarticular process is minute.

The marginal teeth are subconical structures that curve posteriorly and slightly lingually near the tips. The teeth are sharply pointed in contrast to the peg-like teeth of Galesphyrus (Carroll, 1976b), and lack serrations and cutting edges such as are found in Heleosaurus (Carroll, 1976a) or Prolacerta (Gow, 1975). They are protothecodont in implantation, that is, set in shallow sockets with relatively higher walls labially.

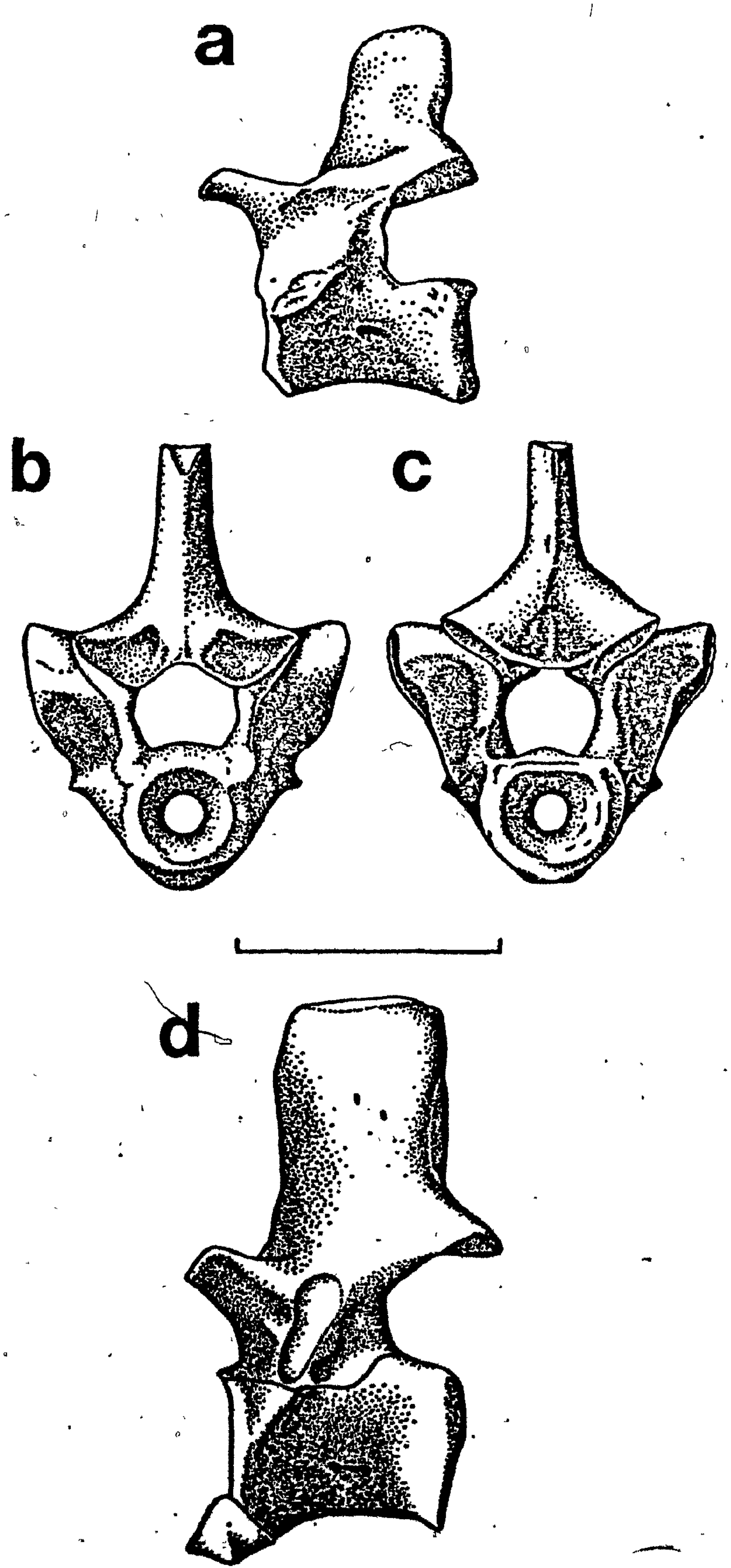
The preserved portion of the maxilla of MNHN 1908-32-57 bears 31 teeth, and about six empty alveoli. It is probable that a few more teeth were present in the anterior tip of the maxilla, which is not preserved. This is a higher number than has been reported in any other early diapsid with the exception of Petrolacosaurus, which has up to 31 (Reisz, 1975). Youngina has approximately 20 functional teeth (Gow, 1975), and Heleosaurus has about twelve. The total number of teeth in Galesphyrus is unknown. However, Carroll (1976b) estimated that B.P.I. 4286 would have had smaller and more numerous teeth than Youngina. Acerosodontosaurus has more maxillary teeth than later eosuchians such as Askeptosaurus (Kuhn-Schneider, 1952) and Champsosaurus (Russell, 1956), which have maxillary tooth counts of 12 and 29 respectively. The teeth at the front of the maxilla of Acerosodontosaurus tend to be relatively longer and more slender than the posterior ones. However, as in all known early diapsids except Petrolacosaurus, there are no conspicuous caniniform teeth. An accurate count of mandibular teeth cannot be made. Thirty-two teeth are preserved, but there would have been more than this. Nevertheless, the number is higher than that of other early diapsids.

Twenty-one presacral vertebrae are preserved. The anterior vertebrae have become disarticulated and scattered, and some are missing. It is doubtful that the total presacral count differed much from the typical early diapsid counts of 24 to 26. For convenience, it is being assumed in this paper that there were 25 presacrals. Two sacral vertebrae are preserved, and it is unlikely that there was a third.

The centra are notochordal, and each has a strong, longitudinal ventral ridge. Well defined lateral pits (foramina subcentralia) mark the junction of the ventral ridge and the lateral surface of the notochordal sheath in the presacrals. The ridge is sharply defined as a keel in the cervical vertebrae, but is more rounded in the dorsal vertebrae. The suture between the neural arch and the centrum is visible in the posterior dorsals (fig. 9d). As in most primitive reptiles, the neural arch forms part of the anterior intervertebral articular surface of the vertebra.

The average length of the last nine presacral centra is 9.0 mm. This length is used as a standard of measurement for comparison with other genera, and is represented throughout this paper as "x." There is a decrease in length of progressively more anterior centra as in Youngina. The measured length of one cervical centrum is 7.8 mm (.87x), and it appears that none of the cervical centra were elongated as

Figure 9. Acerosodontosaurus piveteaui. a, cervical vertebra; b, anterior view of anterior dorsal vertebra; c, posterior view of anterior dorsal vertebra; d, posterior dorsal vertebra and intercentrum. Scale = 1 cm.


a
b
c
d

they are in Petrolacosaurus (Reisz, 1975) or Prolacerta. In Heleosaurus, cervical and dorsal centra are about equal in length (Carroll, 1976a).

Centra width, measured across the posterior intervertebral articulation, appears to be constant throughout the presacral column. The width of each of two cervical centra and of the last presacral centrum is 5.3 mm. The orthometric linear unit (Romer, 1948; Currie, 1978) was calculated from this. Unit measurements, represented by OLU in this paper, were calculated for the lengths of bones by dividing the absolute lengths by the orthometric linear unit ($(5.3 \times \frac{1}{2})^{2/3} = 1.91$).

Centra height, measured at the posterior intervertebral articulation, increases posteriorly. Two cervical centra have a height of 5.0 mm, whereas the most posterior presacral centra are 5.8 mm high.

In the cervical vertebrae, the dorsal surface of the transverse process is at the same level as the dorsal limits of the articular surfaces of the zygapophyses. In relation to the zygapophyseal level, the transverse processes become more ventral in position in the mid and posterior dorsal vertebrae. In the last presacral vertebra, the transverse processes are below the level of the ventral limits of the zygapophyses. The transverse processes do not extend laterally much farther than the lateral limits of the zygapophyses. The width across the transverse processes of one of the posterior cervical vertebrae is 11.8 mm (1.3x). The articulating surface on the transverse process is wide and rounded dorsally where it articulated with the tubercular section of the rib head, tapers anteroventrally, and then expands somewhat for the capitular articulation. This shape is typical for early diapsids, protorothyridids and primitive pelycosaurs (Currie, 1979). The rib articulations of the dorsal vertebrae are entirely on the neural arch. A ridge on the anterior rim of the centrum extends posterodorsally to support the lower edge of the transverse process. The transverse process is joined dorsally to the zygapophyses by ridges.

The zygapophyses extend laterally beyond the centrum. In the dorsal vertebrae, the articular surfaces are inclined at an angle of approximately 30^0 to the horizontal. The anterior zygapophyses are joined posteromedially by a thin horizontal shelf of bone. There is no pronounced swelling above the posterior zygapophyses. They are joined anteromedially by a thin horizontal shelf of bone that forms the ventral margin of a pronounced pocket in the posterior surface of the neural spine (fig. 9c).

The thoracic neural spines are well developed, and are almost rectangular in lateral view. In contrast, the spines of Galesphyrus (Carroll, 1976b), Heleosuchus (Owen, 1876) and paliguanids (Carroll, 1975a) are short and triangular. The greatest dorsoventral height of the neural spines of Acerosodontosaurus is reached in the eighteenth to twenty-second presacral vertebrae, where the average height is 11.8 mm (1.31x, 6.18 OLU). This is relatively and absolutely higher than the neural spines are in Youngina (Watson, 1957), Heleosaurus (Carroll, 1976a) or Kenyasaurus (Harris and Carroll, 1977). Neural spines undergo positive allometry in growth, so it should be pointed out that the lower relative height of the spines of Youngina is possibly a factor of the immaturity of the known specimens. The only genus of primitive diapsid that has relatively taller neural spines in the dorsal region is Hovasaurus (Currie, personal observation). The height of the neural spines decreases anteriorly, and is 8.5 mm (.94x) in one of the anterior dorsals.

The greatest anteroposterior length of a neural spine is found in the eighteenth to twenty-second presacrals, where the average length is 6.9 mm (.76x). This length is reduced in more anterior vertebrae. In the isolated cervical it is 4.1 mm (.46x). The neural spines in the mid and posterior dorsal region have their lowest longitudinal and lateral dimensions at a point where the anterodorsally oriented ridges from the posterior zygapophyses meet. Above this point, the neural spines expand, although not to the degree seen in tangasaurids. In the cervical and the anterior dorsal vertebrae, the neural spines are inclined dorsoposteriorly, but are vertical in the mid and posterior dorsals. There is no evidence to suggest that dermal ossicles were present as they are in Youngina (Gow, 1975) and Heleosaurus (Carroll, 1976a).

Three bones of the atlas-axis complex have been identified (figs. 6, 7). The atlantal centrum, like that of Heleosaurus (Carroll, 1976a), is poorly defined, and lacks finished bone surfaces. It is excluded from the ventral margin of the vertebral column by the atlantal and axial intercentra. In lateral view, it is roughly triangular, flat dorsally and tapering ventrally. It is not fused to the axial intercentrum. The atlantal neural arch can be seen clearly only in medial view (fig. 6), because it is largely obscured by other bones in lateral view (fig. 7). There is an anterodorsal facet on the lateral surface of the atlantal neural arch for articulation with the proatlas. The articular facet for the centrum is at the ventral end of a robust pedicel. In lateral view, the caudally directed spine is poorly developed relative to those of most primitive reptiles, but may not have been ossified at the time of death. A posteroventrally oriented ridge presumably ended in a facet for the rib articulation. The only other element of the atlas-axis complex that is preserved is the crescentic axial intercentrum.

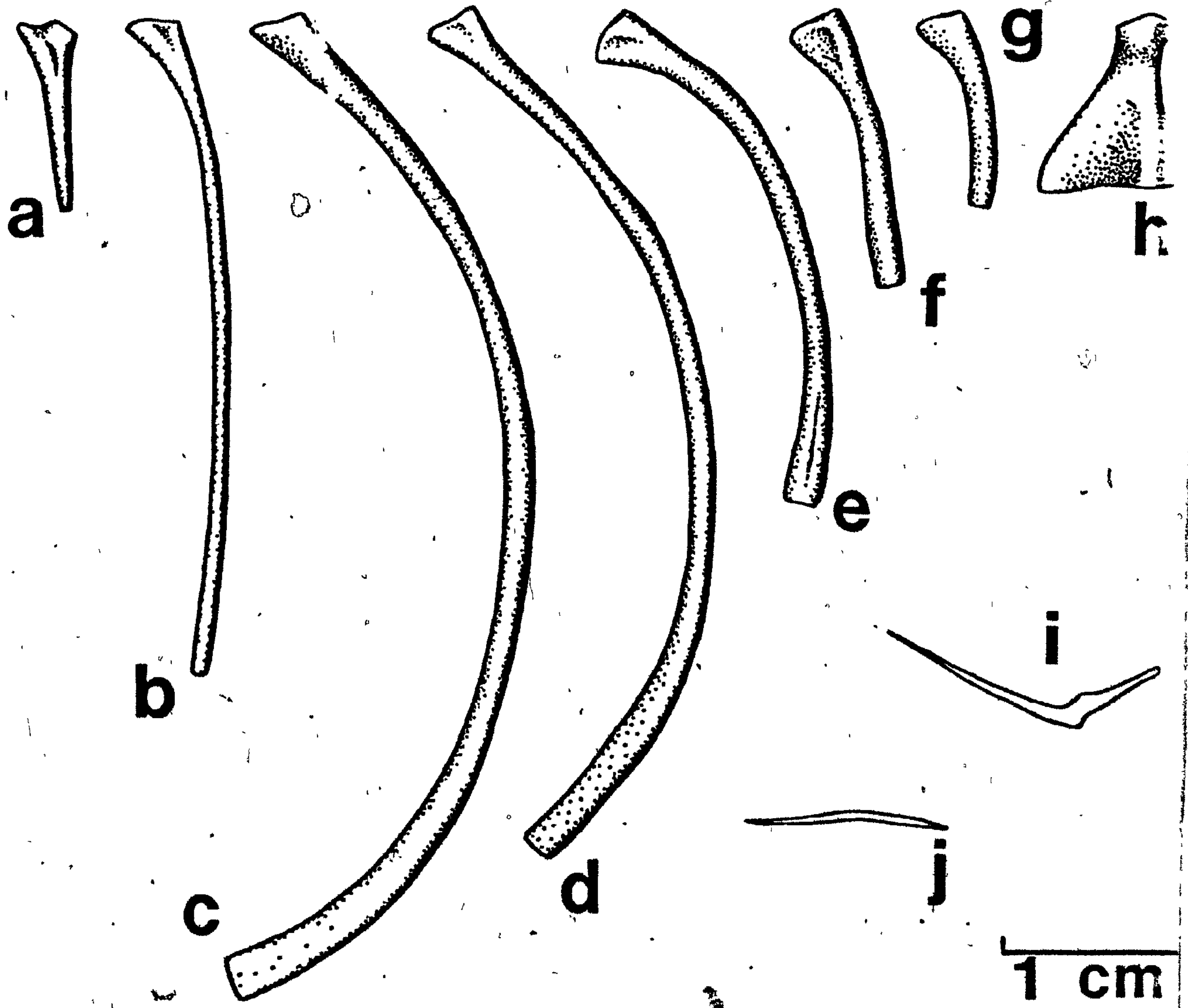
The rib articulations on the sacral vertebrae are present on both the neural arches and the centra.

A single caudal centrum, 8.2 mm (.91x) in length, and attached rib is preserved. The suture with the neural arch is visible. Although the neural arch reached the front of the centrum, it did not participate in the intervertebral articulation. Most of the suture with the rib is on the centrum, but extends onto the neural arch. From the lengths of the centrum and the caudal rib, it is estimated that this is one of the fifth to tenth caudal vertebrae.

Ossified intercentra (fig. 9d) are found throughout the presacral column as in most early diapsids. They do not articulate with the ribs. The intercentra are 2.5 mm (.28x) long.

Only one cervical rib is preserved (figs. 5, 6, 10a). It is 11.7 mm in length, and is presumably the

Figure 10. _Acerosodontosaurus_ _piveteaui_. a, cervical rib; b, anterior dorsal rib; c, 14th (?) presacral rib; d, 17th (?) presacral rib; e, 21st presacral rib; f, 23rd presacral rib; g, 24th presacral rib; h, 1st sacral rib; i, median ventral scale; j, lateral ventral scale.


a
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1 cm

the third or fourth rib (based on comparisons with other primitive diapsids). There are distinct capitular and tubercular heads, of which the former is more pronounced. The shaft of the rib is nearly straight, and tapers distally.

There were at least nineteen pairs of dorsal ribs (figs. 5, 10). Two disarticulated, anterior dorsal ribs are long (40 mm) and nearly straight. The mid-dorsal ribs are up to 70 mm (7.78x) long and curved throughout their length. This indicates that the trunk of the animal was broad and rounded in cross-section, as it was in Youngina (Gow, 1975) and Kenyasaurus (Harris and Carroll, 1977). Although the dorsal ribs are holocephalous, the articular surfaces have distinct capitular and tubercular portions joined by a thin bridge of bone. The posterior trunk ribs are short and somewhat curved.

The specimen includes two pairs of sacral ribs, but only the first is well enough preserved for description. It is 10.3 mm (1.14x) in length with an iliac suture 8.8 mm in anteroposterior length, and almost 5 mm in height at the posterior end. There is a horizontal groove in the posterior face at the distal end of the first sacral rib. This groove cradled the anterior edge of the second sacral rib. The sacral ribs are sutured to the vertebrae.

The only caudal rib preserved is 5.8 mm long, flat and bluntly pointed. The longitudinal axis of the rib is oriented posterolaterally. This rib is sutured to the vertebra.

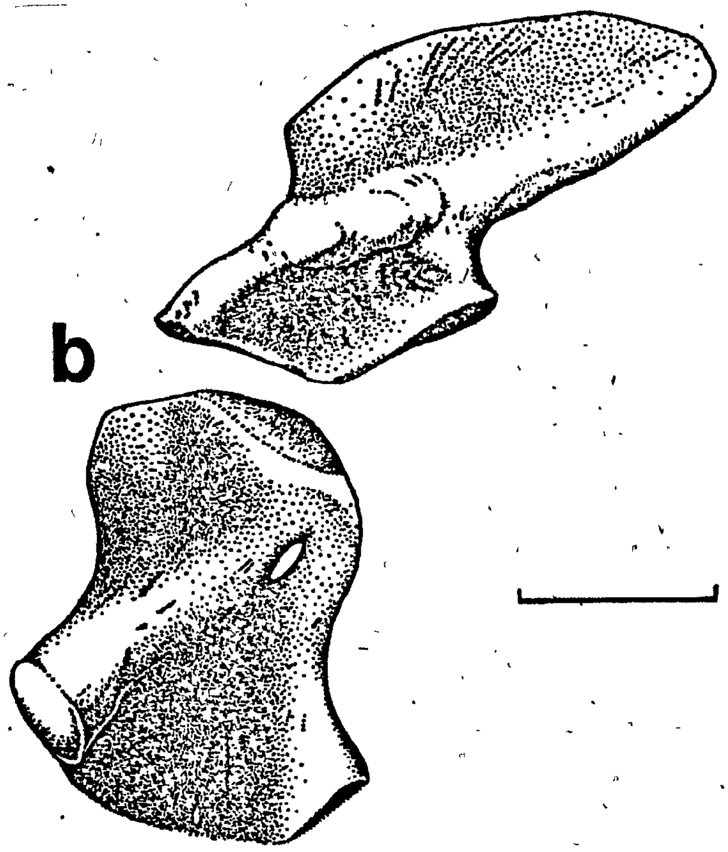
An isolated bone which may be the only representative of the pectoral girdle (fig. 11a) is probably a cleithrum. It is 23.4 mm measured on the outside of the curvature. The bone is gently curved, with tapering ends and a central constriction.

The proximal ends of the humeri (figs. 12a, c) are not preserved, and the total lengths of these bones are unknown. The diameter of the shaft is 8.0 mm, and the distal end expands to 20.5 mm. The distal articular surface is incompletely differentiated into capitular and "trochlear" regions, but there is no ossified capitulum. The ectepicondylar foramen is only partially closed. The entepicondyle is not as well developed as that of tangasaurids.

Both right and left radii and ulnae are preserved (figs. 12a, b, c). The radius is 33.9 mm in length (17.7 OLU). In medial and lateral views, this bone is strongly arched so that the posterior outline is convex. There is a pronounced ridge running from the posterior edge of the lateral surface to the mid-lateral surface of the distal end. The proximal articular surface is concave. In anterior or posterior

Figure 11. Acerosodontosaurus piveteaui. MNHN 1908-32-57. a, cleithrum (?) in lateral and medial views; b, left ilium and pubis in external view. Posteromedial outline of pubis restored from right pubis. Scale = 1 cm.

b



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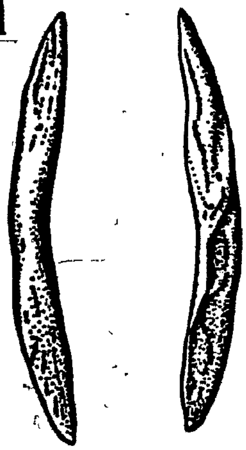


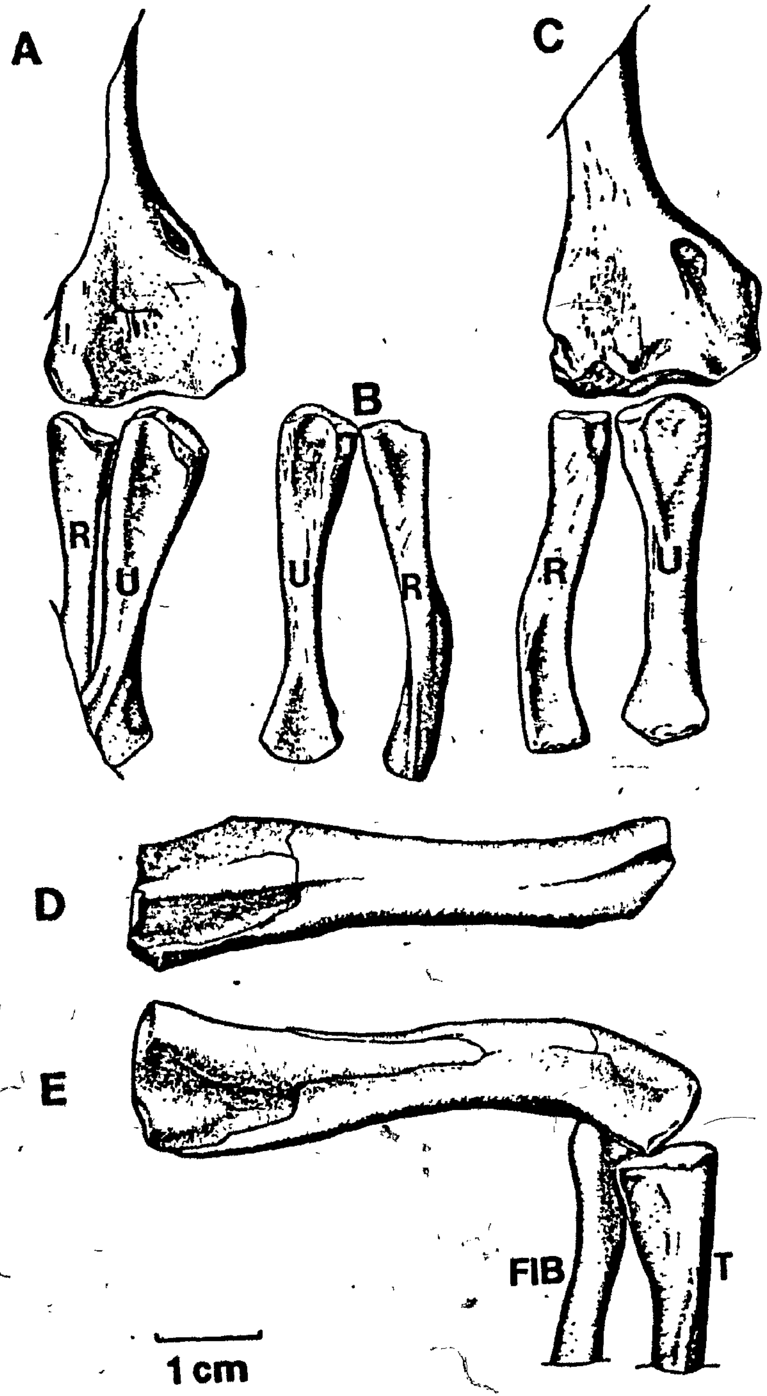
view, the proximal end has an outline similar to that of the ulna. The distal articular surface is oval and has prominent ridges that suggest that the movement at the articulation with the radiale was restricted. In lateral or medial view, the radius is twisted in appearance, looking very much like the radius of a champsosaur (Russell, 1956; Erickson, 1972). It is interesting to note that Champsosaurus also has a prominent ridge on the lateral surface of the radius.

The ulna is 34.7 mm (3.9x, 18.2 OLU), less than one millimeter longer than the radius. In Youngina (Gow, 1975), Galesphyrus (Carroll, 1976b) and tangasaurids, the radius is always longer than the ulna. The olecranon process was not ossified when the animal died, and the entire proximal end of the bone is unfinished.

The right carpus is preserved in dorsal (fig. 6) and ventral (fig. 7) views. It is similar to those of most primitive reptiles. There are eleven elements. The radiale is triangular in dorsal view, tapering medially. The articulation with the radius is broad and flat. The distal articular surface is broad and rounded. The entire lateral surface articulated with the lateral centrale, and there appears to have been no contact with the intermedium. The intermedium is not elongate as in many primitive reptiles (e.g. Petrolacosaurus, Reisz, 1975; Captorhinus, Holmes, 1977), and is only about 15% longer than it is wide. The proximal articulation with the ulna is extensive and oriented somewhat ventrally, as is the articulation with the ulnare. The ulnare is the most prominent bone of the carpus. It is wider than it is long. In Petrolacosaurus (Reisz, 1975) and Galesphyrus (Carroll, 1976b), the ulnare is longer than it is wide. The pisiform is well developed. There is an extensive proximal articular surface for the ulna and ulnare. When properly articulated, the pisiform would have projected primarily posteriorly. The medial centrale is smaller than the lateral centrale, and relatively smaller than that of primitive reptiles (Holmes, 1977), Petrolacosaurus, or Galesphyrus. It did not contact the third distal carpal, in contrast with that of Captorhinus (Holmes, 1977), Petrolacosaurus or Galesphyrus. The first distal carpal articulates as much with the second metacarpal as it does with the first. It is larger than the second distal carpal. The fifth distal carpal articulates primarily with the fifth metacarpal, but also contacts the fourth metacarpal.

All of the metacarpals and eleven of the phalanges of the right manus are preserved. The unguals

Figure 12. Acerosodontosaurus piveteaui, MNHN 1908-32-57. a, left humerus (dorsal view), radius (posterior view), and ulna (posterior view); b, right ulna (anterior view) and radius (lateral view); c, right humerus (ventral view), radius (medial view) and ulna (posterior view); d, left femur (posterior view); e, left femur (anterior view), fibula, and tibia.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are recurved and sharply pointed. The penultimate phalanges of the first and fifth digits are about the same length as metacarpal I and the first phalanx of the fifth digit respectively. This characteristic has been noted in many primitive reptiles and extant lizards, but its significance is unknown at present.

MNHN 1908-32-57 includes the ilia and pubes, but no ischia. The left ilium and pubis had separated, whereas the right ilium and pubis remained firmly sutured together. The iliac blade extends posterodorsally far beyond the acetabulum, and is more extensive than that of Youngina. The ilium, measured between the anteriormost point of the puboiliac suture to the most distal point of the ventral edge of the iliac blade, is 31.5 mm (3.5x, 16.5 OLU) in length. The lateral surface of the iliac blade has extended anterodorsally from the primive position seen in Petrolacosaurus (Reisz, 1975). As in other younginiform eosuchians, the pubis makes up only a small part of the acetabular surface (fig. 11). The pubis extends 22 mm ventromedially from its suture with the ilium. The maximum anteroposterior length is 18 mm. The proportions of the pubis suggest that the animal was relatively broad and low in its proportions. In Youngina, Galesphyrus and Heleosaurus, the anteroposterior length is greater than the height. The posterior margin of the pubis is emarginated, suggesting that there could have been an incipient thyroid fenestra. There is a powerful "pectineal" tubercle that terminates in unfinished bone. The obturator foramen is located close to the dorsoposterior corner.

The entire length of the left femur is preserved (fig. 12). It is 55 mm (6.1x, 28.8 OLU) long. As in most eosuchians, the articular head turns markedly dorsally, and the distal end curves ventrally. the entire proximal end of the bone is unfinished bone, but had already differentiated into a head and trochanter when the animal died. The femur is similar to that of Heleosaurus (Carroll, 1976a).

Only the proximal ends of the left tibia and fibula are preserved (fig. 12).

The ventral scales are disarticulated, and it is not possible to know how many rows and how many ranks of scales there are. There are median, chevron-shaped scales (fig. 10I) and straight, tapering lateral scales (fig. 10J).

Discussion and Conclusions

Acerosodontosaurus can be grouped with Youngina in the suborder Youngeniformes primarily on the basis of cranial similarities. Comparisons of the postcranial skeleton are difficult because of the immaturity of the Youngina material.

The type specimen of Acerosodontosaurus was one of a group of one hundred reptile specimens sent to Paris in 1908 from the Sakamena Valley of Madagascar. There is no assurance that all the specimens were collected at the same locality, but it seems likely that they were. Twenty-five of the best specimens of that group were examined by the author, and with the exception of MNHN 1908-32-57, every specimen is attributable to Hovasaurus, a tangasaurid that was highly specialized for an aquatic existence. The presence of so many specimens of Hovasaurus suggests that the depositional environment could have been a large body of water. Sediments of the Lower Sakamena Formation accumulated rapidly in rift valleys (Cliquet, 1957). The environment could have been near-shore marine (P.L. Cliquet, personal communication, 1977; Carroll, 1981). Disarticulated bones are recovered from the region of Benenitra (fig. 2). Most of the bones are attributable to another aquatic genus, Claudiosaurus. However, an isolated pubis (MNHN 1925-5-83) is identical to that of Acerosodontosaurus, as are a number of other, less diagnostic bones.

The association with aquatic genera suggests that Acerosodontosaurus could have been an aquatic reptile, whereas its rarity at these two localities suggests that its remains could have been washed in from a terrestrial environment. The significance of the similarity between the radii of Champsosaurus and Acerosodontosaurus is not apparent, but could indicate functional similarities. There are no other osteological features that can be used to indicate that Acerosodontosaurus was adapted to an aquatic existence.

Acerosodontosaurus is a relatively primitive younginiform eosuchian that lacks most of the derived characters that are shared by Youngina and the tangasaurids. It is one of the few Permian eosuchians with a reasonably well preserved skull. Unlike Youngina, the limb elements are well ossified and details can be seen that were previously unreported in Permian eosuchians. As will be seen in subsequent sections, Acerosodontosaurus represents a stage of morphological evolution that is intermediate between protorothyridid captorhinomorphs and tangasaurids.

II

THE VERTEBRAE OF <u>YOUNGINA</u>

(REPTILIA: EOSUCHIA)

In 1914, Broom established the genus Youngina on the basis of a specimen collected from the Daptocephalus Zone of the Karroo of South Africa. He recognized that the animal represented the most primitive level of diapsid reptile found up to that time, and proposed a new suborder, the Eosuchia, for Youngina. The Eosuchia, a diverse assemblage of terrestrial, aquatic and gliding reptiles, has generally been accepted as the basal stalk from which all later diapsids probably evolved. Youngina is represented by more than a dozen skulls (Gow, 1975), which are relatively unspecialized, and provide the basis of our concept of the cranial anatomy of the Eosuchia.

The postcranial skeleton of Youngina is known from three partial specimens, none of which were sufficiently ossified at the time of death to permit an adequate knowledge of the postcranial osteology. Recent examination of the type specimen indicates that the vertebrae are more complicated than was suggested by the previous descriptions. Because the presence of specialized, or derived, features is important in determining the relationships of animals, precise understanding of anatomical details is important.

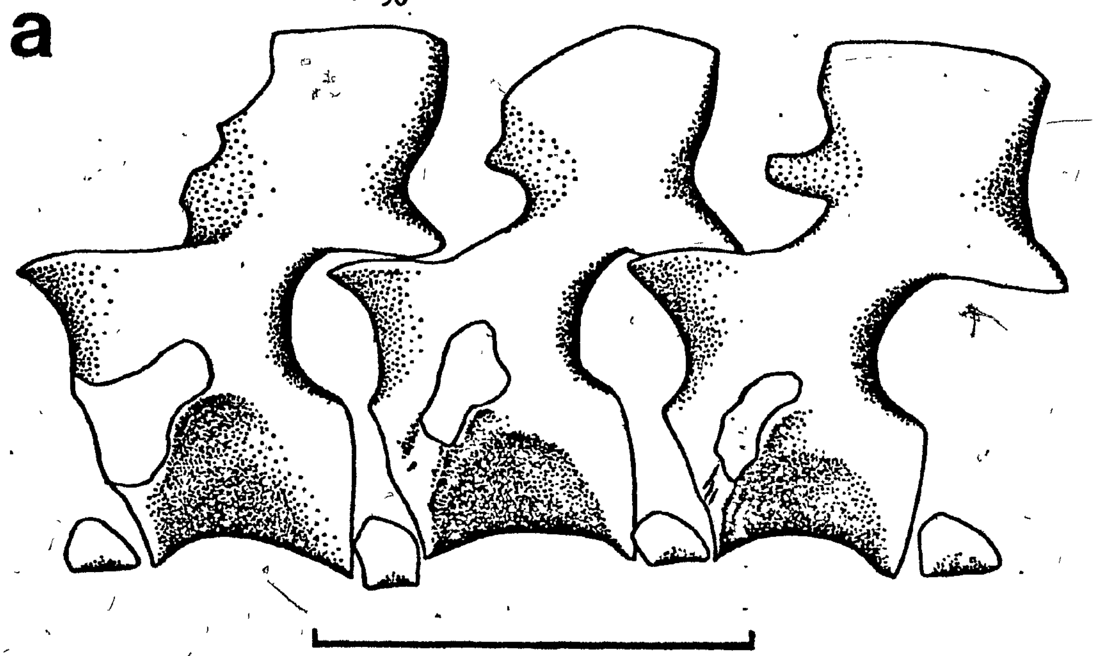
The type specimen of Youngina, consisting of a skull and vertebral column, is in the collections of the American Museum of Natural History (AMNH). A second specimen (Broom, 1922) from the same locality was damaged during collection, but there were a large number of notochordal vertebrae, mostly imperfect. Broom (1922) noted that the caudal vertebrae are elongate, and lack chevrons. In his examination of the early history of sauropsid reptiles, Watson (1957) reexamined the vertebrae of the type specimen (AMNH 5561) and figured the vertebral column. He pointed out that the articular surfaces of the zygopophyses are wide and nearly horizontal. Youngina capensis specimens prepared in acid were figured by Gow (1975).

The vertebral column preserved in the type specimen includes the last twelve presacral vertebrae, two sacrals and six caudals. The total number of presacral vertebrae in Youngina is unknown, although Gow (1975) shows 23 in his reconstruction. In contrast, most eosuchians have 24-26 presacrals.

The average length of a dorsal centrum of AMNH 5561 (figs. 13a, 14) is 5.4 mm, and the average height is 4.2 mm. The neural spines are relatively low, 5.5 mm on the average (Table 1), and anteroposteriorly long (5.2 mm). There are two sacral vertebrae (Watson, 1957: Gow, 1975). The total number of caudals is unknown.

The zygopophyses extend laterally beyond the lateral limits of the centra, and the articular surfaces are

Figure 13. Youngina capensis, type specimen (AMNH 5561). a, dorsal vertebrae (20th, 21st and 22nd?); b, ventral view of 20th (?) intercentrum; c, section through front end of second caudal and posterior portion of the neural spine of the first caudal (left side restored); d, third caudal. Scale = 1 cm.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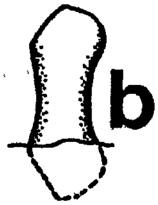
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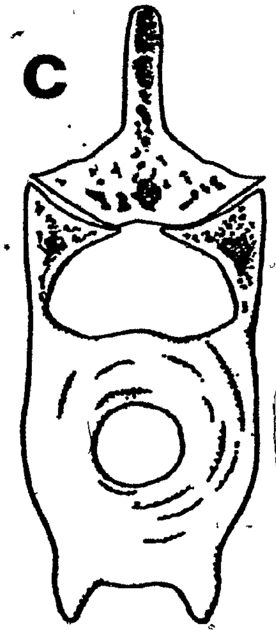
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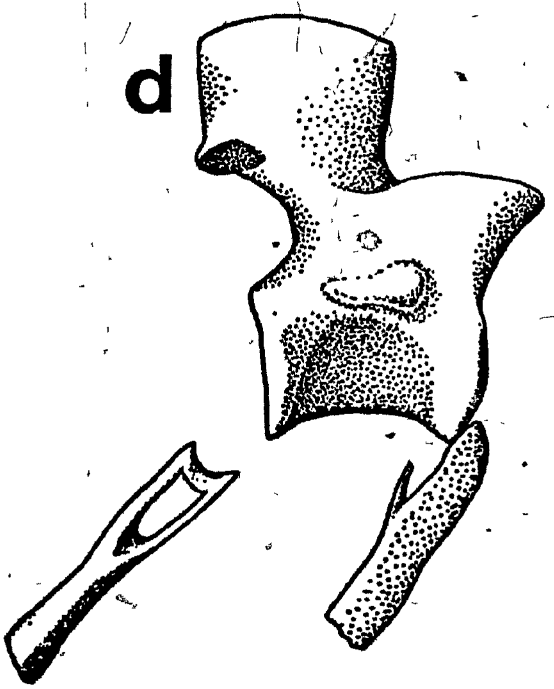
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inclined at a low angle from the horizontal (Watson, 1957; Gow, 1975) in the presacral series. In the caudals (fig. 13c), the zygopophyseal articulating surfaces are inclined at an angle of more than 35^{o} from the horizontal.

Intercentra are present throughout the dorsal series, and are constricted anteroposteriorly on the midline (fig. 13b).

The specimen described by Broom (1922) does not have haemal spines in the tail. However, haemal spines are found posterior to the first two caudals in the type specimen. Gow (1975) reconstructs the first five caudals as lacking haemal spines. Perhaps Broom's specimen included only anterior caudals.

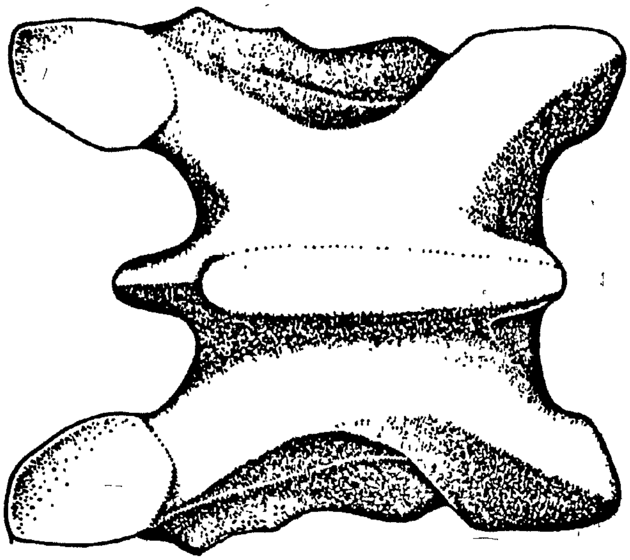
A feature that has gone unnoticed is the presence of an extra intervertebral articulation between the pairs of zygopophyses. These processes show in Watson's figure of the vertebral column, although it appears he did not recognize them for what they are. He neither described them nor did he include them in his reconstruction of the vertebrae in dorsal view. These processes would have been easy to miss because they are small, the specimen was only partially prepared, and because they could have been interpreted as being the medial surface of the unexposed, right anterior zygopophyses.

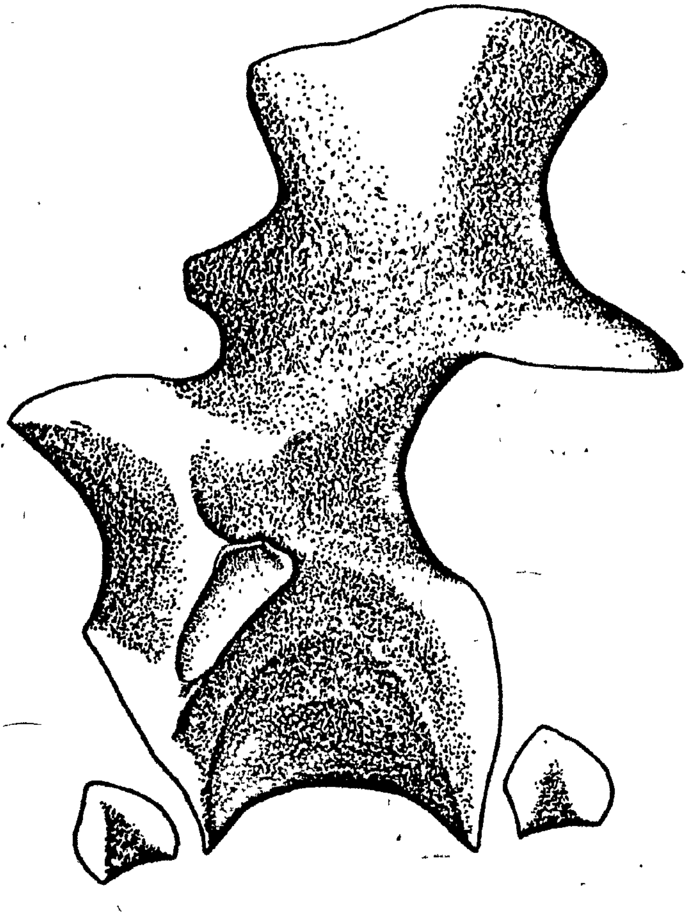
In the mid-dorsals (fig. 13a), there is a very thin rectangular process on the anterior edge of the neural spine on the midline. It appears to be long enough to contact the posterior face of the neural spine of the preceding vertebra.

The cervical vertebra (fig. 15f) figured by Gow (1975) shows there was a posterior, midline expansion at the base of the neural spine.

As will be seen in a subsequent section, the neural spines of Hovasaurus articulate by means of such processes. It was found that these processes are quite variable throughout the column and between different individuals of the same species as well. However, it appears that throughout the vertebral column there is some form of contact of the neural spines in between the zygopophyseal contacts, and in some cases this contact can extend vertically far up the neural spine. In the anterior dorsals, the extension is on the posterior surface of the neural spine (fig. 15g), whereas in the posterior dorsals the expansion is on the anterior surface (fig. 15h). The accessory contacts of the mid-dorsals are transitional in form between the patterns seen in the anterior and posterior presacral vertebrae. Although the processes are more complex in Hovasaurus, the same basic pattern of a posterior extension of the neural spine in the anterior part of the column (fig. 15f) and an anteriorly directed process in the posterior dorsals (fig. 15) is found in Youngina also.

Figure 14. Youngina capensis. Reconstruction of mid-dorsal vertebra in dorsal and lateral views. Based on AMNH 5561.



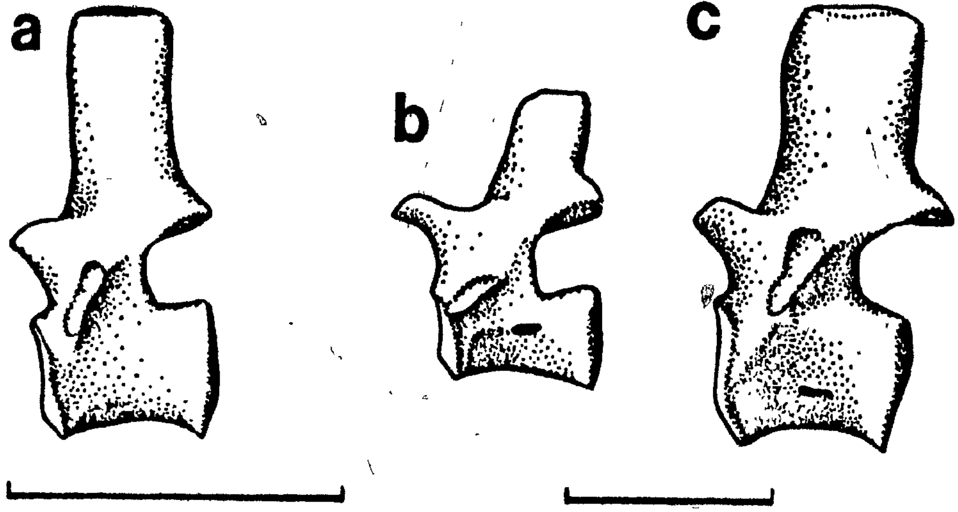


A similar pattern of intervertebral articulation is found in some other eosuchians. Kenyasaurus (fig. 15e) seems to have an extra, anteriorly directed process in the mid and posterior presacral vertebrae, as does an animal from the Upper Permian of Madagascar that Piveteau (1926, p 171) referred to as "Datheosaurus" (Carroll, 1981). The type specimens of Tangasaurus, although badly preserved, seem to show the same adaptations.

Contact between the neural spines in addition to the zygopophyseal articulations would tend to restrict dorsoventral motion, as would the large, almost horizontal zygapophyses in Youngina. As in modern snakes and Sphenodon, there would be no restriction on the lateral flexibility of the column. The reason for restricting the vertical flexure of the column is not clear in Youngina, although in Hovasaurus it is clearly part of a highly specialized system to control lateral undulations for propulsion in water.

Accessory intervertebral articulations are not found in protorothyridids (fig. 15a), the ancestral stock of eosuchians. Heleosaurus (Carroll, 1976) and Acerosodontosaurus (Currie, 1980) were referred to the Younginidae, but neither have accessory intervertebral articulations (figs. 15b,c), suggesting they are not closely related to Youngina. Midline articular processes have not been reported on the neural spines of other lines of eosuchians. They appear to be a derived character that suggests,

Figure 15. Presacral vertebrae of some primitive reptiles: (a) Protorothyris, dorsal vertebra, after Heaton and Reisz (unpublished manuscript); (b,c) cervical and dorsal vertebrae of Acerosodontosaurus, after Currie (1980); (d) Heleosaurus, dorsal vertebra, after Carroll (1976); (e) posterior dorsal vertebra of Kenyasaurus, after Harris and Carroll (1977); (f) cervical vertebra of Youngina, after Gow (1975); (g) anterior dorsal of Hovasaurus, based on SAM 9463; (h) posterior dorsal vertebra of Hovasaurus, based on MNHN 1908-32-60; (i) dorsal vertebra of Youngina. Each scale represents 1 cm, p = accessory articulating process.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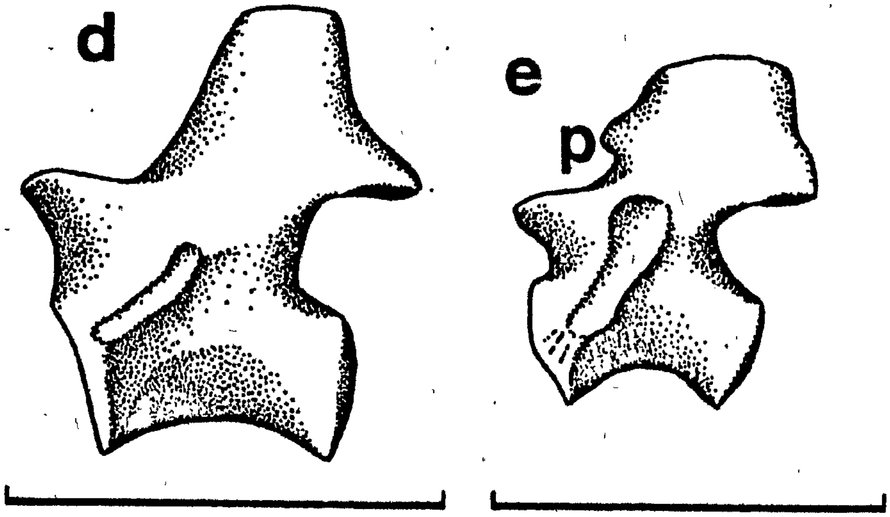
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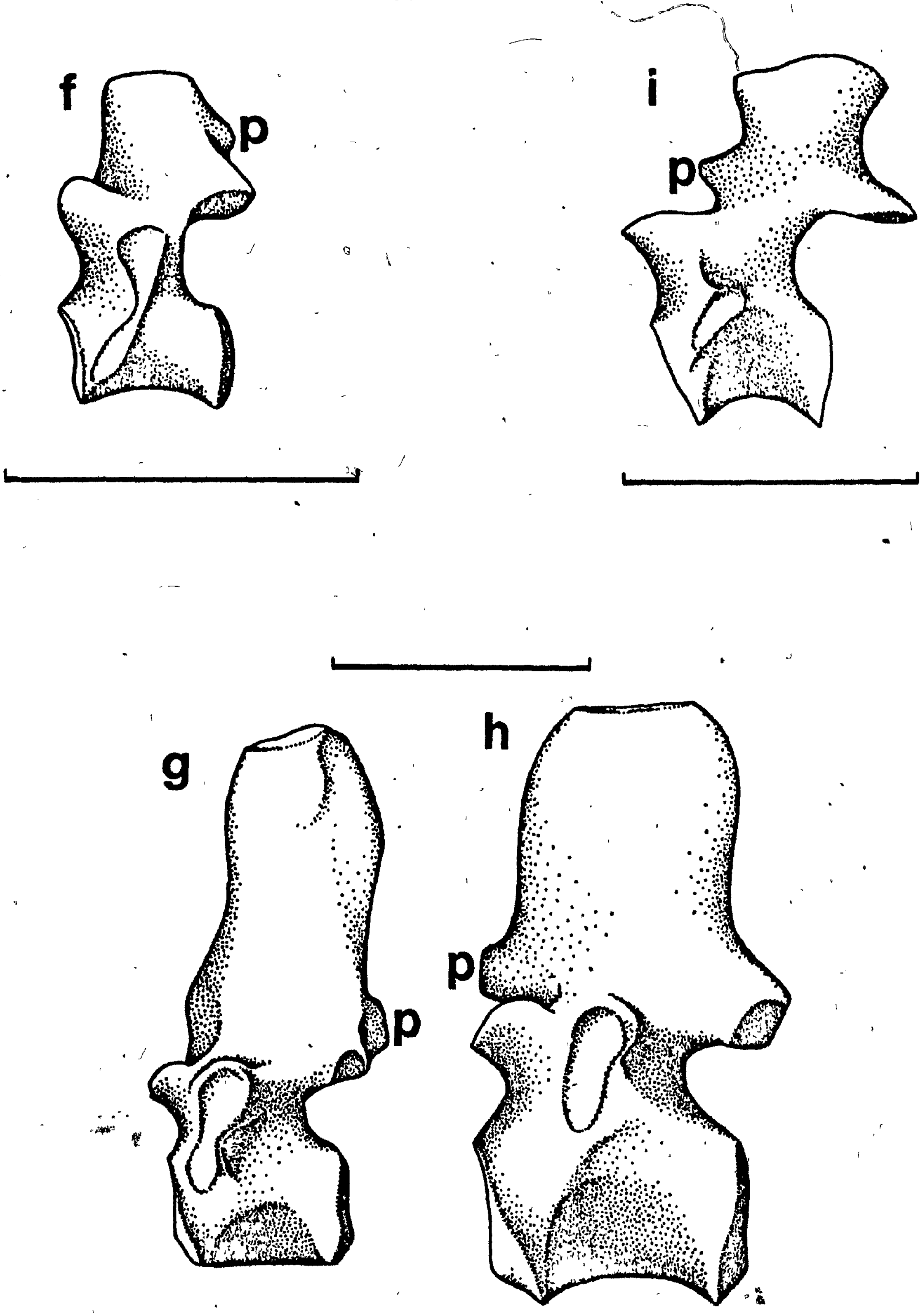
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along with other characters, close relationships among Youngina, Thadeosaurus, Kenyasaurus, Tangasaurus and Hovasaurus. It also suggests that Youngina is too specialized in the vertebrae to be an ideal ancestral morphotype for other eosuchians, eolacertilans or archosaurs.

III

NEW DATA ON THE TANGASAURID EOSUCHIAN <u>THADEOSAURUS</u> FROM THE UPPER PERMIAN OF MADAGASCAR

INTRODUCTION

In 1926, J. Piveteau described the remains of several reptiles from the Upper Permian strata of southern Madagascar. One animal was referred to *Tangasaurus*, a reptile previously described (Haughton, 1924) from the Upper Permian of Tanzania. A second was tentatively referred to as *Datheosaurus*, a genus based on a single specimen from the Lower Permian of Europe. A new genus, *Hovasaurus*, was detailed on the basis of abundant material. Haughton (1930) showed that *Tangasaurus* and *Hovasaurus* are closely related eosuchians. They were united into a single family, the Tangasauridae. A third genus, *Kenyasaurus*, from the Lower Triassic of Kenya was recently referred to this family (Harris and Carroll, 1977).

Carroll (1981) recently redescribed the two specimens of *Datheosaurus* from Madagascar (that Piveteau originally described) as a new genus of younginid eosuchian, *Thadeosaurus colcanapi*. At the same time, Currie was studying the tangasaurid specimens, and discovered that *Tangasaurus* from Tanzania is a distinct animal from the "*Tangasaurus*" specimens of Madagascar. The redescription of *Thadeosaurus* was in press before it was realized that the Madagascar specimens of "*Tangasaurus*" were *Thadeosaurus*.

Younginids and tangasaurids are closely related (Currie, 1981), and are distinguishable by relatively few osteological characteristics. The newly recognized specimens of Thadeosaurus indicate that this animal is a tangasaurid rather than a younginid. There are, however, no features in the skeleton of this animal to suggest aquatic habits, in contrast with the closely related genus, Hovasaurus. A growth series of nine specimens is now known for Thadeosaurus, and more than seventy specimens of Hovasaurus were available for study. Characteristics in the growth series of the two genera are different, and can be correlated with differences in habitat preference.

Class REPTILIA Linnaeus 1758

Subclass LEPIDOSAURIA Dumeril and Bibron 1839

Order EOSUCHIA Broom 1914

Suborder YOUNGINIFORMES Romer 1945

Family TANGASAURIDAE Camp 1945

Subfamily KENYASAURINAE Currie 1981

THADEOSAURUS Carroll 1981

Diagnosis. --- Can be distinguished from its closest relative, Kenyasaurus, by taller dorsal neural spines and lower number of caudal ribs and transverse processes (19 pairs compared with 28 in Kenyasaurus). There is no small tuberosity on the fifth metarsal for insertion of the brevis branch of the peronaeus muscle as there is in Kenyasaurus.

THADEOSAURUS COLCANAPI Carroll 1981

Holotype --- MNHN 1908-11-8, MNHN 1908-11-21, counterpart slabs in the Muséum National d'Histoire Naturelle, Paris.

Referred specimens --- see Table 3.

Horizon and Locality --- Lower Sakamena Formation, Upper Permian. Sakamena River Valley, southern Madagascar. All specimens seem to be from a single site, but the exact locality is not recorded.

Diagnosis -- same as for genus.

DESCRIPTION

Thadeosaurus appears to have been primarily terrestrial reptile that would have been lizard-like in appearance. The skull is known from only one specimen. The neck is very short, as it is in Youngina and Hovasaurus. The snout-vent length of a mature animal would have been 19 to 22 centimetres, assuming there was no elongate rostrum. The tail was long, about 32 centimetres at maturity.

Measurements

The length of an average dorsal centrum of the largest known specimen of Thadeosaurus is 2.8 times the length of the same dimension (x) in the smallest known specimen (Table 3). There is no evidence to show that any portion of the vertebral column increased in length during growth at a different rate than that of the dorsal series. Therefore, the length of the vertebral column has a direct relationship to the total length of the body. A change in the relative length of the skull, if it existed, would have had little affect on total body length because the skull makes up only 10% of the total body length and any changes in relative skull length would have been only a fraction of that 10%. It is therefore reasonable to assume that the total length of the largest specimen of Thadeosaurus is about three times the total length of the smallest known specimen. Comparison with adult to hatchling length ratios in living reptiles (page 39) suggests that an adult to hatchling length ratio would have been about 4.0 for Thadeosaurus. It is evident from the ossification of the largest specimens that these were mature animals when they died, so presumably the smallest known specimens were not hatchlings.

For convenience of reference, the series of Thadeosaurus specimens has been divided into life stages A to G on the basis of vertebral length. It should be pointed out that the word "stages" is used in a loose sense, because each subdivision represents a .6 millimetre interval of continuous growth of the dorsal vertebrae. If an equivalent portion of the life span is represented by those specimens as that shown by

Hovasaurus, the life stages in the two genera should be almost equivalent. These subdivisions based on size do not correspond to those used by Piveteau (1926) and Haughton (1930), which were based on specimens from three distinct genera (Table 2).

Several standards of relative measurement can be used to compare elements of different genera. The orthometric linear unit (OLU) should give a unit measurement independent of the animal's weight provided it is used only on mature animals (Currie, 1978). In many cases the OLU cannot be calculated because the diameter of the dorsal vertebrae cannot be measured. Therefore, a second system, based on the ratio of the dimension being considered to the average length of a dorsal centrum (x), is also used.

Skull.

Very little cranial material is known for Thadeosaurus. Some fragments were described by Carroll (1981). The only other skull material is provided by one of the juvenile specimens (MNHN 1908-11-16, fig. 16). This fossil seems to have suffered somewhat from erosion, because definition of many of the bones is poor.

The skull is exposed in ventral aspect. Although the anterior bones cannot be seen, the degree of tapering suggests that the skull would not have had an elongate rostrum, and that the skull would have been less than eighteen millimetres long.

This is 5.6 times the average length of a dorsal centrum (x), which is close to the skull length of Tangasaurus (fig. 17) and Acerosodontosaurus (Currie, 1980). Most Permian reptiles have relatively longer skulls than this. In Youngina, the skull is almost twice the length at 10.6x (Gow, 1975). Prolacerta (Gow, 1975) and Palaeagama (Carroll, 1975) have cranial lengths in excess of 7x.

The maxilla, jugal, frontal, palatine, epipterygoid, basisphenoid-parasphenoid complex, basioccipital, exoccipital, quadrate, prootic, opisthotic and ceratobranchiale I are represented in MNHN 1908-11-16 (fig. 16).

The ventral margin of the left maxilla can be seen in external aspect. No teeth are visible, but were probably lost when the skull disarticulated before burial. The external surface of the bone is shallowly sculptured. Anteriorly the maxilla formed the lateral margin of the internal naris.

The jugal is a triradiate bone, which is larger compared with the quadrate (a bone well preserved in both genera) than the jugal of Hovasaurus. Only the postorbital ramus can be seen clearly, but the base of the subtemporal branch is visible. The presence of a subtemporal ramus indicates that there was probably a complete lower temporal bar.

Only the orbital margin of the frontal can be seen in ventral view. As in Hovasaurus (fig. 26), an anterolateral projection of the frontal excludes the posterior end of the prefrontal from the orbital rim. The frontals appear to have tapered anteriorly along the midline to separate the posterior ends of the paired nasals. The frontals are very narrow between the orbits as in Hovasaurus.

A portion of the palatine is visible where it forms the medial and posterior margin of the internal naris.

The pterygoid cannot be seen in this specimen, but in MNHN 1908-11-8 it bears two rows of small, sharp palatal teeth (Carroll, 1981).

The epipterygoid has broad base and long columella. Compared with other reptiles, the base is relatively small, which indicates that much of the bone was still cartilaginous when the animal died.

Both quadrates are exposed in external aspect, which is unusual because the rest of the skull is exposed in ventral view. The condyles are oriented anteriorly, whereas most specimens disarticulate so that the condyles face caudally. The same type of disarticulation occurs in Hovasaurus, where additional evidence indicates that the quadrate probably sloped anteroventrally. It is highly probable that the jaw articulation of Thadeosaurus was anterior to the occipital condyle. The quadrate is a broad, relatively low bone with a width to height ratio of greater than .8 as in Hovasaurus (fig. 26). The quadrate of tangasaurids would have been somewhat taller in mature specimens. The dorsal margin of the quadrate of tangasaurids is concave in posterior aspect and would have been extended by cartilage. In most reptiles, including Youngina (Olson, 1936), the quadrate is a tall, narrow bone. A ridge extends from the medial condyle to the dorsal margin on the external surface as in Hovasaurus (fig. 26) and Youngina (Olson, 1936). The pterygoid would have overlapped the concave surface medial to the ridge. A pronounced stapedial boss extends posteriorly from the ridge above the condyles. The cartilaginous end of the stapes would have passed dorsal to this knob.

The parasphenoid-basisphenoid complex is well preserved, with the exception of the cultriform process. It is similar to but distinct from the complex in Hovasaurus (Piveteau, 1926, Pl. XIV, fig. 1). The base of the cultriform process is swollen laterally anterior to the basipterygoid tubercles, whereas this region is narrow in Hovasaurus (fig. 31c). A low ridge runs along the midline of the cultriform process, and ends posteriorly in a rounded hump of bone between the basipterygoid processes. A pair of ridges continue posterolaterally from this boss along the crests of the crista ventrolateralis. There are no carotid foramina visible in ventral aspect. The complex is vaulted between the crista. A caudally directed, rectangular process on the midline would have overlapped the ventral surface of the basioccipital. In contrast with Hovasaurus, the crista ventrolateralis extend posteriorly well beyond the posterior margin on the midline. They would have reached the exoccipitals distally and prevented any contact between the basioccipital and opisthotic. The ossified portion of the crista of Hovasaurus do not extend much beyond the basioccipital suture, but could have been continued distally in cartilage.

Only the bases of the exoccipitals are visible. These bones did not form any portion of the occipital condyle.

As in Hovasaurus, the semicircular notochordal "pit" indents the posterodorsal margin of the occipital condyle. A pair of basioccipital tubercles diverge anterolaterally from the ventral margin of the occipital condyle. A ventral depression between the tubercles would have been covered by the posterior midline process of the basisphenoid-parasphenoid complex. A slight depression in the ventrolateral margin of the basioccipital could represent an area of muscle insertion.

Few details of the prootic and opisthotic can be seen in the specimen. The posterior surface of the opisthotic is convex like that of Hovasaurus, and the paroccipital process is short.

A pair of hyoid bones (Ceratobranchiale I) are indistinguishable in outline from those of Hovasaurus (fig. 27), Heleosaurus (Carroll, 1976a), Prolacerta (Camp, 1945) and many

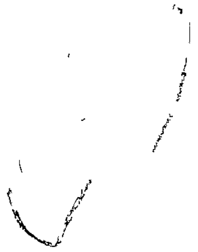
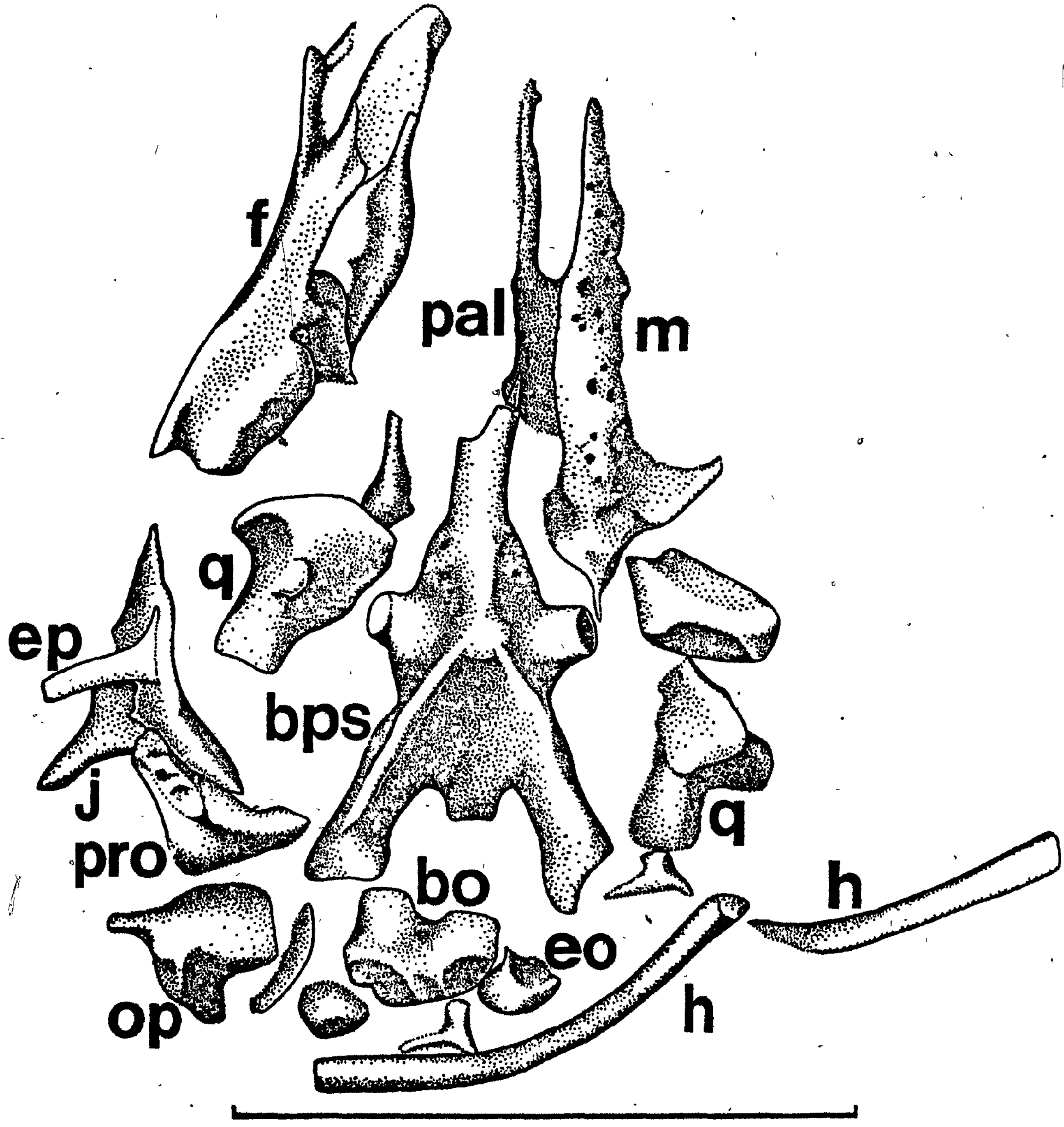


Figure 16. Thadeosaurus colcanapi, MNHN 1908-11-16.
Ventral view of skull. Scale = 1 cm.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other primitive reptiles. It is a long slender rod that has a concave posterior end for the cartilaginous Epibranchiale I.

Vertebrae and Ribs

Most of the vertebral column of MNHN 1908-11-16 can be seen, and suggests that there were no fewer than 25 vertebrae and no more than 26.

The cervical vertebrae are shorter than the dorsals. Where details can be seen they are identical to those of *Hovasaurus*. The atlantal centrum of MNHN 1908-11-16 is about .4*x*. The atlantal neural arch has a caudally directed spine as in all primitive reptiles. There is a relatively small atlantal intercentrum, and a larger axial intercentrum with a length of .3*x*. The axis is not well exposed. The third centrum is approximately 85% the length of a dorsal centrum, and the fourth is 88%. The articular facets for the ribs extend down onto the centrum from the neural arch in the cervicals. The neural arch seems to have been firmly sutured to the centrum in this specimen (stage B). The fourth intercentrum is ossified, whereas it is not in specimens of *Hovasaurus* at the same life stage.

Short crescentic intercentra are present throughout the trunk by stage B, whereas these do not ossify in *Hovasaurus* until stage F.

In the dorsal region, sutures between the two sides of the neural arch are still visible at stage B (MNHN 1908-11-4) and the attachment to the centrum is still visible at stage D

(MNHN 1908-11-5). Both types of sutures are no longer visible by late in stage D (MNHN 1908-11-15). The neural spines increase in size during growth with high positive allometry. The coefficient of allometry (1.8) is greater than that of Hovasaurus (1.2), although the spines are relatively lower at any life stage in Thadeosaurus.

Altough there are no zygosphenial joints, accessory articulations are found along the midline of the neural spines of the presacral vertebrae. These do not appear until stage F, and are simply butt joints dorsal to the neural canal. No known specimen of Thadeosaurus has an accessory articulation as complex as that seen in Hovasaurus (figs. 32, 33). The presence of accessory articulations is a derived character that is also found in Youngina (fig. 13a), Kenyasaurus (fig. 15e) and probably Tangasaurus.

The neural spines are constricted anteroposteriorly above the level of the accessory articulations, but expand slightly at the distal end in mature specimens. The anteroposterior length of the neural spine of the mid-dorsals of MNHN 1908-5-1 is .77x. As in Hovasaurus, the neural spines are relatively thick laterally at the distal end in large specimens.

MNHN 1908-11-16 is a series of 33 caudal vertebrae in three sections with two missing intervals. The most anterior vertebra would have been between the fifteenth and twentieth caudals, and the two missing sections would have included at least a half dozen vertebrae. This specimen seems to have had approximately 55 caudal vertebrae, in contrast with 47 in MNHN 1908-11/19 (Carroll, 1981). The length of the tail appears to be variable in Thadeosaurus, and can be as long as that of Kenyasaurus (Harris and Carroll, 1977). Nevertheless, it was much shorter than the tail of Hovasaurus, which has a minimum count of 70 vertebrae.

The neural spines of the caudal vertebrae are shorter than those of the dorsals in contrast with Tangasaurus and Hovasaurus. The caudal neural spines of Thadeosaurus are rectangular, and have a posterodistal slope (fig. 17c). The length of the haemal arch and spine exceeds the length of the neural arch and spine by more than 60%.

There is no evidence of an atlantal rib. The axial rib is short (.9x) and triangular. The fourth and fifth cervical ribs are relatively straight rods of bone that expand slightly distally (MNHN 1908-11-16). The fourth is 1.1x in length, and the fifth is 1.5x.

The dorsal ribs are not pachyostotic like those of Hovasaurus, but are otherwise indistinguishable.

The anterior caudal ribs either taper throughout their length (MNHN 1908-11-13/19, 1908-5-1, 1908-11-15) or expand slightly distally (MNHN 1908-11-4, 1908-11-5). The anterior caudals of Hovasaurus are expanded distally to a greater degree.

The first caudal rib of Thadeosaurus extends laterally beyond the tip of the ilium, rather than anterolaterally as it does in Hovasaurus.

At least 19 caudal vertebrae have pointed lateral processes (Carroll, 1981), compared with a maximum of 12 in Hovasaurus and 28 in Kenyasaurus (Harris and Carroll, 1977). Most of these lateral processes are fused caudal ribs, but the most posterior ones would be transverse processes. The caudal ribs of the juveniles have not coossified with the centra, and are distinct as far back as the sixteenth caudal in MNHN 1908-11-4.

Pectoral Girdle and Limb

The scapular blade is short in tangasaurids, including Thadeosaurus. The scapula has a large ventral exposure (MNHN 1908-11-5) and forms part of the screw-shaped glenoid. There is no supraglenoid ridge, nor is there a supraglenoid foramen. A depression in the supporting ridge anterodorsal to the glenoid is also seen in Hovasaurus and Champsosaurus (Sigogneau-Russell, 1979), and could have served as part of the origin of the subcoracoscapularis. The scapula is not fused to the coracoid by stage D (MNHN 1908-11-5), but fusion must have occurred shortly after. Coosification seems to occur at the same stage in Hovasaurus.

The interclavicle (MNHN 1908-11-5) has a t-shaped head as in Saurosternon (fig. 53c) and Hovasaurus (fig. 39). The width of the head is more than 2x, and the maximum width of the shaft is approximately .6x. There is a well defined ridge along the midline on the central surface of the anterior part of the shaft.

A pair of sternal ossifications are present in all specimens except the smallest (MNHN 1908-11-7). The allometric growth curves (for the ossified portions) suggest that the sternum should have started to ossify at an earlier age than this, so the sternal plates may have been lost before burial. The length and width of each ossified sternal plate undergoes high allometric growth (k_{yx} exceeds 2.2). The sternal elements do not fuse into a single element until stage G. In Hovasaurus, the coefficients of allometry for length and width of the sternal plates are lower than those of Thadeosaurus, but the plates coossify by stage F. Otherwise, the sternum is not distinguishable amongst tangasaurids. Carroll (1981) reported that there were three pairs of processes along the lateral margins for attachment of the ribs. As in Hovasaurus (fig. 41), a pair of facets with unfinished bone can be seen in dorsal aspect behind the articulation with the coracoid. Another pair of ribs probably attached here. The spacing also indicates that another point of attachment would have been present near the posterior end as in Hovasaurus. Therefore, there are 5 pairs of facets on the sternum for attachment of ribs.

In juveniles, the humerus is less than 75% the length of the femur. Allometric growth is positive in the humerus and isometric in the femur, so that at maturity the ratio of humerus to femur length exceeds 1.1. The radius is 70% the length of the humerus in juveniles, but because of the higher growth rate in the humerus, the radius to humerus length ratio is less than .60 in adults. The tibia to femur length ratio changes from .87 to .90 as the animals matures, and the ratio of radius to tibia increases from .60 to .73. The changes in limb proportions parallel those seen in Hovasaurus, Although the epipodials are shorter in the more aquatic genus. The two specimens of Tangasaurus show the same trends as Hovasaurus.

The changes in limb proportions in Thadeosaurus also parallel those of nothosaurs but not those of terrestrial reptiles. The similarities suggest that Thadeosaurus could have spent a great deal of time in the water, even though there is no morphological evidence in the skeleton to suggest swimming habits. Among living swimming lizards, the marine iguana shows few skeletal adaptations even though it spends a great deal of time in the water.

The coefficient of allometry in the humerus is high (1.3), but not as great as that of Hovasaurus (1.6). At maturity, the humerus is relatively long (25.8 OLU, 6.7x), although it is significantly shorter than that of Hovasaurus (27.5 OLU, 7.2x). In more primitive reptiles, the humerus tends to be much shorter. The length of this bone is 19 OLU (5x) in Palaeothyris (Carroll, 1970) and 5.4x in Petrolacosaurus (Peabody, 1952). The humeri of known specimens of Youngina are very short (4.8x, Gow, 1975), but this seems to be related to delayed ossification of the limb elements despite an advanced stage of ossification in the vertebrae.

The entepicodylar foramen is not enclosed distally by bone in MNHN 1908-11-4 (stage B). although both the entepicondylar and ectepicondylar grooves are visible. The ectepicondylar foramen is enclosed in bone by stage F, but in Hovasaurus is not closed distally until stage G. Except for its smaller size at maturity, the humerus of Thadeosaurus cannot be distinguished from that of Hovasaurus.

The radius shows moderate positive allometry in its growth. At maturity its length (15.1 OLU, 3.9x) is greater than that of Hovasaurus (14.4 OLU, 3.7x) but not significantly so. The radius is shorter in Palaeothyris (11.4 OLU, 3x), but relatively longer in terrestrial forms like Petrolacosaurus (6.5x) and Prolacerta (19.4 OLU, 4.1x, Gow, 1975).

The ulna (excluding the olecranon) is shorter than the radius, a characteristic of most eosuchians. The olecranon process was either not developed or unossified. The presence of longitudinal striations on the lateral surfaces of the proximal end of the ulna marks the insertion of the tendinous sheet of the triceps musculature. This muscle normally inserts onto the olecranon (Holmes, 1977), so its point of attachment in tangasaurids extends more distally than in captorhinids.

No carpal ossifications are present in the smallest specimen (MNHN 1908-11-7), but four have appeared by stage B (MNHN 1908-11-4). By stage D (MNHN 1908-11-5, 1908-11-15), the full complement of eleven carpal elements have ossified. The medial centrale is a wide bone that articulates with distal carpals I to IV. In captorhinomorphs and most eosuchians, the medial centrale is separated from the fourth distal by the lateral centrale and third distal carpal. The derived state seen in Thadeosaurus is also present in Hovasaurus (fig. 60j) and probably Tangasaurus (Haughton, 1924).

At maturity, metacarpal IV is significantly longer (6.1 OLU, 1.6x) than the same element in Hovasauarus (5.2 OLU, 1.3x). Digit IV is as long as the radius, and relatively longer than the fourth digit of Hovasaurus (13.3 OLU, 3.5x). The first digit, including the metacarpal, is 44% the length of the fourth digit, the second is 61%, the third is 84% and the fifth is 63%. On the average, the fifth digit is 74% the length of the third. The relative proportions of digits I to V in Thadeosaurus are primitive, whereas the central digits are shortened in Hovasaurus to form a more efficient swimming appendage. Growth in metacarpal IV is isometric, while the length of the fourth digit (excluding the metacarpal) increases with negative allometry ($k_{yx}' = .7$).

Pelvic Girdle and Limb

The morphology and relative dimensions of the ilium are not significantly different from those of Hovasaurus.

The major dimensions of the pubis increase isometrically with age in Thadeosaurus. A mature pubis is wider (9.6 OLU, 2.5x) than long (6.8 OLU, 1.7x), and the ratio of width to length is greater than in any other known eosuchian. The relative length of the pubis of Hovasaurus is greater, so the ratio of width to length is lower. The obturator foramen is open in small specimens until stage B, as in Hovasaurus.

The length of the ischium increases at a slightly higher rate than the width during growth. The length (9.7 OLU, 2.5x) and width (7.6 OLU, 2.0x) are significantly shorter than the same dimensions in Hovasaurus. The suture with the pubis is strong in MNHN 1908-5-1, and there is no evidence of a thyroid fenestra.

The femur shows weak negative allometry ($k_{yx}' = .9$) in its growth. At maturity it is 23.2 OLU (6.0x) in length, which is not significantly different in the femur of Hovasaurus. The femora of Palaeothyris (19.6 OLU, 5.2x), Petrolacosaurus (5.7x) and most more primitive reptiles are shorter than those of tangasaurids. Prolacerta (28.5 OLU) and Acerosodontosaurus (28.8 OLU) have relatively longer femora. The mature femur of Thadeosaurus (MNHN 1908-5-1) cannot be distinguished from those of Hovasaurus (fig. 48j), Acerosodontosaurus (fig. 12d) and Heleosaurus (Carroll, 1976a).

Three ossifications appear in the tarsus at stage A. These represent the astragalus, calcaneum and probably the fourth distal tarsal. Two more ossifications, the centrale and third distal tarsal, have appeared by stage B, and all seven elements are present by stage D. In contrast the tarsus of Hovasaurus does not have a full complement of ossifications until stage F. As in Hovasaurus (fig. 62), Kenyasaurus (fig. 62) and Tangasaurus (fig. 17), the fifth distal tarsal has been lost as a discrete element. This characteristic distinguishes tangasaurids from Youngina (Broom, 1922).

The length of metatarsal IV (11.6 OLU, 3.0x) is attained through isometric growth, and is not significantly different in Hovasaurus.

There is no small tuberosity on the fifth metatarsal for insertion of the brevis branch of the peronaeus muscle as there is in Kenyasaurus (Harris and Carroll, 1977).

There are only two specimens of Thadeosaurus with complete fourth digits, and both are less than half grown. Because of the small sample size and the closeness in size, the calculated coefficient of allometry (1.3) is not statistically significant. The ratio of length of digit four to that of the tibia is 1.16 in one specimen and 1.17 in the other. In Hovasaurus, this ratio changes only slightly with age, and it is reasonable to assume that the same would have been true in Thadeosaurus. If so, the length of digit IV in a mature specimen of Thadeosaurus could have been 24.3 OLU (6.3x). This calculation can be checked by an independent method because digit V and part of digit IV are preserved in MNHN 1908-5-1, the largest specimen of Thadeosaurus. The length ratio of digit IV to digit V (excluding metatarsals) is 1.16 in the Thadeosaurus juveniles and 1.20 in Hovasaurus, and multiplication of the length of digit V of MNHN 1908-5-1 by these ratios will give two estimates for the length of digit IV. These work out to be 22.2 OLU (5.8x) and 22.9 OLU (5.9x). None of the three estimates are significantly different from the length of digit IV in Hovasaurus, but are relatively longer than this digit in Tangasaurus (4.9x).

Gastralia (ventral dermal scales) cover the ventral surface of the abdomen between the posterior end of the interclavicle and the middle of the pubis (between the pectineal tubercles). The median segments cannot be seen clearly in any of the specimens. At least 35 segments can be counted in MNHN 1908-11-4, for an average of almost four per rib segment. Each includes two lateral segments in addition to the median element. The most distal segment is closely appressed to the anterior edge of the more medial lateral segment.

Gastroliths are present in the posterior portion of the abdominal cavity of two specimens. The well rounded pebbles in MNHN 1908-11-5 (Piveateau, 1926, Pl. XI, fig. 2) are up to 2.5x in length, and 1.3x wide, but are not numerous. Although not well exposed in MNHN 1908-5-1 (Piveteau, 1926, Pl. XII) it appears that there was a pebble mass in the abdomen as large as in many specimens of Hovasaurus. The mass of pebbles does not extend anteriorly beyond the level of the seventeenth presacral vertebra.

DISCUSSION

Characteristics can be seen in the specimens recently identified as Thadeosaurus that clearly indicate its close relationship to Hovasaurus, Tangasaurus and Kenyasaurus. The skull of Thadeosaurus is similar to that of Hovasaurus in all details known for the incomplete skulls. It is relatively short apparently, is narrow between the orbits, has an anteroventrally sloping jaw suspensorium, has a relatively low, broad quadrate, and has a short paroccipital process. The loss of contact between the lateral centrale and the third distal carpal is a derived character state of tangasaurids that is also found in Acerosodontosaurus (Currie, 1980). Loss of the fifth distal tarsal as a discrete element is another specialized character that identifies Thadeosaurus as a tangasaurid rather than a younginid.

The neural spines of Thadeosaurus are relatively longer (1.1x) than those of Kenyasaurus (.75x) in the dorsals of animals of the same absolute size. Thadeosaurus has only 19 pairs of caudal "ribs" compared with 28 in Kenyasaurus. No other significant differences are presently known to distinguish these genera, which have been united in the subfamily Kenyasaurinae.

Kenyasaurine tangasaurids are distinguishable from the Tangasaurinae (Tangasaurus, Hovasaurus) by the specialization of the tail as a swimming appendage in the latter subfamily.

Although Thadeosaurus does not have any osteological characteristics to indicate a clear preference for aquatic habitats, several features suggest that such may have been the case. Its close relationship to aquatic genera is one clue. The limb proportions are closer to those of Hovasaurus, Tangasaurus and nothosaurs than to more primitive, terrestrial forms. The ossified portion of the scapular blade is very low, and the ventral portion of the pectoral girdle is proportionally larger. This trend is common in aquatic reptiles and is most highly developed in plesiosaurs to lower the centre of gravity for stability and increase the area available for muscle attachment. The presence of ingested pebbles in the abdominal cavity could also serve to lower the centre of gravity and increase the specific gravity of the animal. Associated fossils, two fish and three unquestionably terrestrial reptiles, provide no evidence of the habitat preference of Thadeosaurus. Regardless of the weak evidence that may indicate Thadeosaurus spent part of its life in the water, this genus was clearly not as well adapted for swimming as Hovasaurus.

In summary, newly recognized specimens of Thadeosaurus show that this genus is closely related to Kenyasaurus, Tangasaurus and Hovasaurus. Features seen in partial skulls of Thadeosaurus and Hovasaurus are distinctive when compared with other eosuchians. There are additional shared derived characters in the vertebrae, manus and pes that can be used to define the Tangasauridae. No anatomical specialization in either Thadeosaurus or Kenyasaurus indicate unequivocally that these genera were aquatic like Tangasaurus and Hovasaurus. Growth series representing most of the life spans of Thadeosaurus and Hovasaurus can be compared, and indicate that there are significant differences in the growth rates of limb elements. These can be correlated with differences in habitat preference, which will be discussed in a subsequent section.

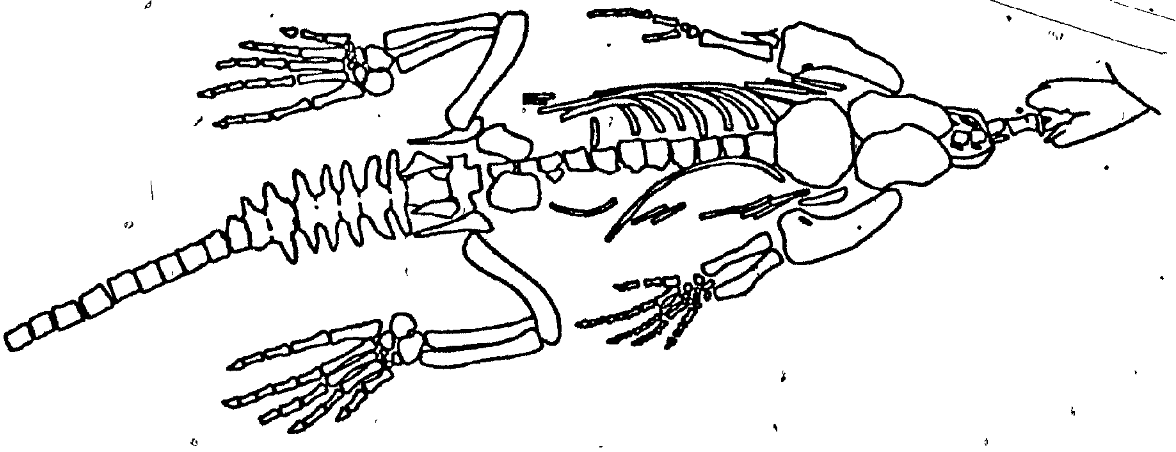
IV

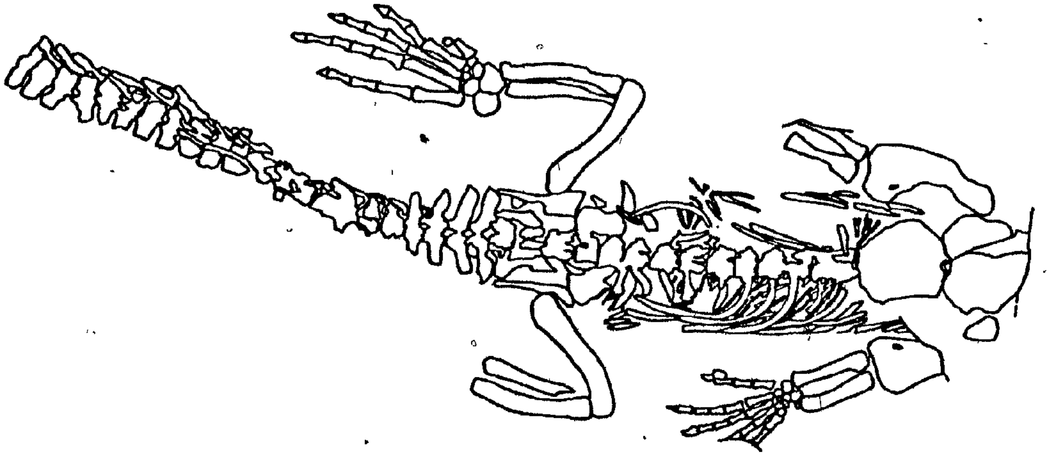
THE OSTEOLOGY AND RELATIONSHIPS OF
TANGASAURUS MENNELLI HAUGHTON
(REPTILIA: EOSUCHIA)

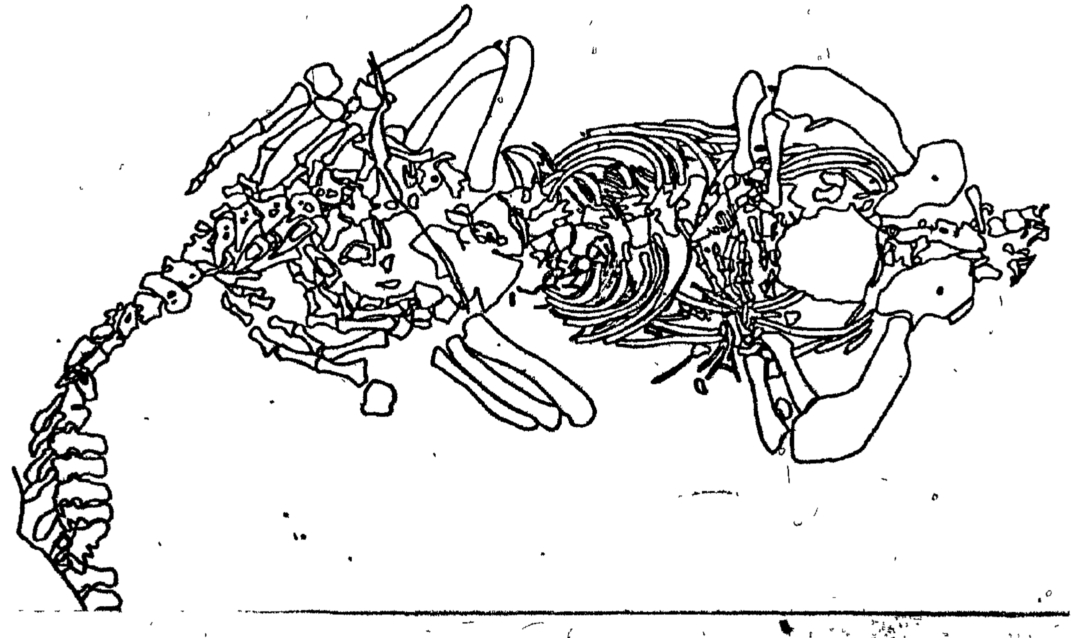
In 1924, S.H. Haughton described two fossil reptile specimens that had been collected from Upper Permian strata in the vicinity of Tanga, in what is now Tanzania. These were recognized as a previously unknown taxon and named <u>Tangasaurus</u> <u>mennelli</u>. Although the specimens were designated as co-types, the smaller, better preserved one (fig. 17a) is here considered as the lectotype. It resides in the museum in Bulawayo, Zimbabwe, while its counterpart (SAM 6231, fig. 17b) and the larger specimen (SAM 6232, fig. 17c) are in the South African Museum, Cape Town. Another half specimen in the South African Museum has not been described (R.L. Carroll, personal communcation). On the basis of postcranial characteristics, Haughton (1924) felt that <u>Tangasaurus</u> was probably a diapsid reptile that, because of the long, powerful, flattened tail, had become adapted for an aquatic existence.

Numerous specimens of small reptiles had been collected in beds of approximately the same age along the Sakamena River of southern Madagascar. One of the animals collected was described as <u>Broomia</u> <u>madagascariensis</u> (Piveteau 1925), but was referred the following year by Piveteau to <u>Tangasaurus</u> <u>menelli</u> (<u>sic</u>). Contrary to Haughton's conclusions, Piveteau felt that <u>Tangasaurus</u> was a primarily terrestrial animal. Following Nopcsa (1924), he considered it to be related to <u>Araeoscelis</u>,

Figure 17. Tangasaurus mennelli, syntypes. a, Ventral view of skeleton in Bulawayo Museum, Zimbabwe; b, SAM 6231, counterpart of preceding specimen, after Harris and Carroll, 1977; c, SAM 6232.







Kadaliosaurus, Broomia, Saurosternon and Pleurosaurus.

Haughton restudied Piveteau's specimens from Madagascar, and in 1930 published his observations. He concluded that Tangasaurus and Hovasaurus were allied, and that both were diapsids. Hovasaurus was recognized as a reptile adapted to an aquatic existence through reduction of the fore-limb and coracoid, and retarded ossification and elongation of the body. Tangasaurus was considered to be intermediate morphologically between Youngina and Hovasaurus.

Other specimens described by Piveteau (1926) were not associated with Tangasaurus and Hovasaurus until recently. A large number of caudal sections were recovered along the Sakamena River of Madagascar. The caudal vertebrae have high neural spines, and the haemal spines are long and plate-like. Piveteau recognized these as belonging to a reptile adapted to swimming, but did not have any other skeletal elements associated with the caudal vertebrae. These are now known to belong to Hovasaurus.

A third genus recognized by Piveteau (1926, p. 171-172) was assigned with doubt to the European genus Datheosaurus, now considered to be congeneric with Haptodus (Currie 1979), a sphenacodont pelycosaur. The specimens referred to this genus were redescribed recently by Carroll (1981) as Thadeosaurus. Morphologically this animal appears to be close to the ancestral stock of Tangasaurus and Hovasaurus.

Kenyasaurus mariakaniensis from the Lower Triassic of Kenya (Harris and Carroll, 1977) was considered to be most closely comparable with Tangasaurus and Hovasaurus on the basis of general body form, the presence of a sternum and particularly the anatomy of the foot.

In re-examining the anatomy of tangasaurids, it became obvious that there is a great deal of confusion concerning the identification and anatomy of these animals. The anatomy of Tangasaurus and Hovasaurus is very similar, and there are few characters to distinguish the genera. Although more than three hundred specimens were collected in Madagascar, in almost every case two of the most diagnostic parts of the tangasaurid body--the skull and the tail--were missing. The problem is compounded by poor preservation of the type specimens of Tangasaurus, which generally were ignored in favour of the better preserved specimens from Madagascar. Finally, many of the specimens were misidentified because they are immature and show few distinctive characters. As part of a revision of tangasaurid anatomy, the majority of specimens that have been figured were re-examined and, in many cases, reidentified (Table 2). Hopefully, the confusion concerning the identification of tangasaurids has been resolved. This will permit more accurate conclusions concerning evolutionary and developmental lineages, palaeoecology, evolutionary and developmental lineages, palaeoecology, distribution and stratigraphy.

Tangasaurid eosuchians were relatively small reptiles, lizard-like in appearance. Hovasaurus is the largest of the known tangasaurids, with an estimated maximum snout-vent length of about 35 cm. The largest specimen of Tangasaurus is 20% smaller than the largest Hovasaurus, but the ends of the limb bones are not well ossified which suggests that larger specimens probably existed. The linear dimensions of a mature specimen of Thadeosaurus are about 35% smaller than the same dimensions in Hovasaurus.

Hovasaurus and Kenyasaurus are valid genera. Use of the name Tangasaurus in this paper is restricted to the two specimens from Tanzania. When referring to generic characters attributed by Piveteau (1926), Haughton (1930) and others to specimens from both Tanzania and Madagascar, the name Tangasaurus will be used in quotation. Most of the specimens from Madagascar that Piveteau (1926) identified as Datheosaurus and Tangasaurus are now referred to as Thadeosaurus.

Class REPTILIA Linnaeus 1758

Subclass LEPIDOSAURIA Dumeril and Bibron 1839

Order EOSUCHIA Broom 1914

Suborder YOUNGINIFORMES Romer 1945

Family TANGASAURIDAE Camp 1945

Subfamily TANGASAURINAE Piveteau 1926

TANGASAURUS Haughton 1924

Types species: Tangasaurus mennelli Haughton 1924, p. 3

1925 Tanganasaurus Piveteau, p. 155

1926 Tangasaurus menelli Piveteau, p. 78

1937 Tangasaurus minelli Payer, p. 115

Diagnosis. Tangasaurid eosuchian. Differs from Thadeosaurus and Kenyasaurus in specialization of tail as a swimming appendage by enlargement of neural and haemal spines. Height of neural spine of mid-caudal vertebra about 35% greater than length of associated centrum, and about 75% length of associated haemal arch and spine. In contrast, the neural spine of a mid-caudal in Hovasaurus is at least 125% greater than length of associated centrum and 90% length of associated haemal arch and spine.

Lectotype -- Skeleton in Bulawayo Museum, Zimbabwe, and its counterpart, South African Museum SAM 6231.

Referred specimen -- SAM 6232.

Horizon and Locality -- Middle Division of Tanga series, Upper Permian. Vicinity of Tanga, northeastern Tanzania.

DESCRIPTION

SKULL

Cranial anatomy is poorly known in tangasaurids. One of the two known specimens of Tangasaurus has a poor skull preserved in palatal aspect. The bone is crushed flat, and seems little better than a film of carbon. Further preparation of the specimen seems unfeasible. The anterior portion of the skull was not collected, but the preserved portion is 38 mm in length. Haughton (1924) felt that the full length of the skull would have been between 50 and 60 mm. In light of the anterior tapering of the skull, there was probably no elongate snout, and it is doubtful that the skull would have exceeded 45 mm (6.8x). The only bone that can be identified with any degree of certainty is the basisphenoid-parasphenoid complex. The cultriform process is long and tapering, and the basipterygoid processes appear to be short. The complex is concave ventrally in transverse section between the tuberosities. Haughton (1924) made observations on the pterygoid and various palatal vacuities, but none of these can be seen clearly enough in the specimen to merit further description. The basioccipital can be seen at the back of the skull, but shows no distinctive characters. Von Huene (1926) identified one bone as either stapes or quadrate, but whatever it is, the bone gives us no better understanding of the skull.

The contours and proportions of the parasphenoid-basisphenoid complex of Hovasaurus are similar to those of Tangasaurus.

VERTEBRAE AND RIBS

Haughton (1924) estimated that there were eighteen presacral vertebrae in the lectotype (SAM 6231) of Tangasaurus mennelli. This number is much less than that of other eosuchians, and it is assumed that he had not included the anterior presacrals in his total. Because he stated that there were seven or fewer anterior vertebrae obscured by bones of the pectoral girdle, his estimated presacral count can be raised to a maximum of 25. This is the number of vertebrae found in Hovasaurus. As in Hovasaurus, the neck of Tangasaurus is short--probably including only five vertebrae.

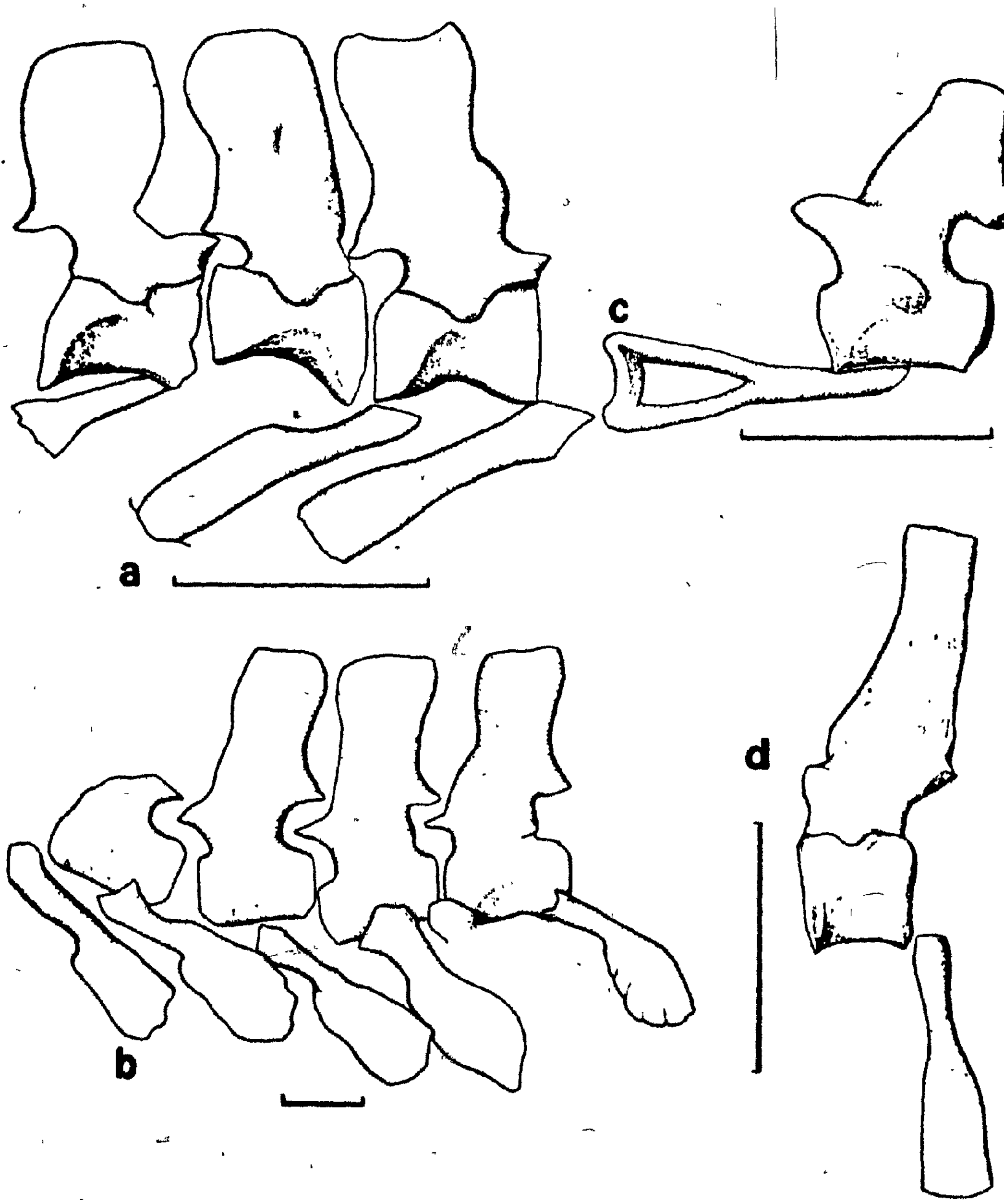
Primitive diapsid reptiles characteristically have two sacral vertebrae. Haughton (1924, p. 3) stated that one specimen of Tangasaurus mennelli (SAM 6231) had three fused sacral vertebrae. However, preservation in the sacral region of this specimen is poor, and it is likely that he misinterpreted the first caudal rib as a sacral. In a later paper (Haughton, 1930), he implied that SAM 6231 has two sacrals.

The total length of the tail is known in few eosuchians. Twenty-four caudal vertebrae are preserved in the lectotype of Tangasaurus, and 28 in SAM 6232. The tail was clearly much longer than this however. Thadeosaurus has at least 45 caudals (Carroll, 1981) and Hovasaurus probably had more than seventy.

Details of the dorsal vertebrae are difficult to delineate in the type specimens of Tangasaurus. In Hovasaurus, there is a process at the base of the neural spine that acts as an extra intervertebral articulation. A similar accessory process appears to be present in at least one of the dorsal vertebrae of the larger specimen of Tangasaurus. Contact between the neural spines has also been noted in Youngina (Currie, 1981), Thadeosaurus and Kenyasaurus.

Specimens of Tangasaurus (figs. 18a, b) have caudal vertebrae that are specialized as an adaptation for propulsion in the water. The neural spines are high, and the haemal spines of the mid-caudals are higher than the presacral neural spines, but are not as long as the haemal spines. The specialization is not as great as in Hovasaurus (fig. 18d) in that the spines are relatively lower, only about 35% greater than the length of the associated centrum compared with more

Figure 18. Caudal vertebrae. a, Tangasaurus (Bulawayo Museum), 19th to 21st; b, Tangasaurus, SAM 6232, 20th to 23rd; c, Thadeosaurus, MNHN 1908-5-1; d, Hovasaurus, MNHN 1908-32-64, 14th caudal. Each scale is 1 cm.


a
b
c
d

than 125% in the same region of the tail of Hovasaurus. Nevertheless, the caudal specializations suggest that Tangasaurus and Hovasaurus are closely related. Specimens of Thadeosaurus have unspecialized caudal vertebrae with low neural spines (fig. 18c).

The dorsal ribs of Tangasaurus have a single head and are not pachyostotic. In Hovasaurus, moderate pachyostosis can be seen in the ribs of large individuals, but it is usually not apparent in juveniles.

An exact count of caudal ribs is not possible because of the poor preservation of the Tangasaurus specimens. The maximum number would have been twelve. There is a maximum of twelve pairs of caudal ribs in Hovasaurus, which are replaced posteriorly by two pairs of transverse processes. In mature animals the ribs are fused to the caudal centra and cannot be distinguished from the transverse processes. Nineteen pairs of caudal ribs and transverse processes are found in Thadeosaurus and 28 pairs in Kenyasaurus.

APPENDICULAR SKELETON

Both Piveteau (1926) and Haughton (1924, 1930) recognized that the relative lengths of elements of the appendicular skeleton change with age. More precise calculations have helped show that "Tangasaurus" specimens of Madagascar are juveniles of Thadeosaurus and that the growth rates for Thadeosaurus and Hovasaurus are different (fig. 4).

The two specimens of Tangasaurus represent animals of different ages, and therefore show some differences in limb proportions. Comparison can be made with Hovasaurus by means of the allometric growth equations. The constants b' and k_{yx}' of power equation $y = b'\underline{x}^{k_{yx}'}$ (Currie, 1978) were solved to describe a growth series of Hovasaurus boulei. The average length of a dorsal centrum which serves as the base for comparison is represented by $\underline{x}$, while the length of the element being compared is represented by y. From this information, the expected mean length (in millimetres) of each element was computed for Hovasaurus specimens the same size as the Tangasaurus specimens SAM 6231 ($\underline{x}$ = 6.6 mm) and SAM 6232 ($\underline{x}$ = 8.0 mm). With the exception of the length of metatarsal IV of SAM 6231 and the length of digit IV of the pes of SAM 6232, all measurements fell within the 95% confidence intervals for these dimensions in Hovasaurus (Table 4). This shows that the relative lengths of limb elements are almost the same in Tangasaurus and Hovasaurus.

In the smaller specimen of Tangasaurus (SAM 6231), the humerus is shorter than the femur, whereas the femur is the shorter of the two in the larger specimen. This suggests that the humerus grew faster than the femur as the animal increased in size. The same thing happens in both Thadeosaurus and Hovasaurus where more complete growth series are known. Haughton (1930) stated that the limbs of "Tangasaurus" are longer relative to the body than those of Hovasaurus. However, it is now known that the humerus of Tangasaurus is 5.8 times the length (x) of a dorsal centrum, that of a mature Thadeosaurus is 6.7x, and that of a mature specimen of Hovasuaurus is 7.1x. Similarly, other limb elements of Tangasaurus have slightly smaller relative lengths than the same elements in Hovasaurus.

In Tangasaurus, the radius is 60% the length of the humerus, whereas in Hovasaurus it is only 52% at maturity. In the relatively unspecialized Thadeosaurus the radius is 54% the length of the humerus at maturity. Relative to the length of a dorsal centrum however, the length of the forearm of Tangasaurus is only 3.3x, whereas that of Hovasaurus is the same as Thadeosaurus (3.7x). Haughton's statement (1930) that the forearm is relatively shorter in Hovasaurus, is true only for immature specimens.

The tibia is 85% the length of the femur in Tangasaurus and Hovasaurus at maturity, and 90% in Thadeosaurus.

Many eosuchians, including Youngina (Broom, 1922), Tangasaurus (fig. 17), Hovasaurus (fig. 40), Thadeosaurus (Carroll, 1981) and Kenyasaurus (Harris and Carroll, 1977), have ossified sterna. The dimensions and outline of the sternum of Tangasaurus fall within the range of Hovasaurus.

The coracoids of Tangasaurus and Hovasaurus are similar in outline. Haughton (1930) stated they are distinguishable on the basis of proportions, but the coracoids of the type specimens of Tangasaurus are too poorly preserved to confirm this statement.

The humeri of Tangasaurus are identical in outline to those of many mature specimens of Hovasaurus. Well ossified humeri of Tangasaurus, Hovasaurus and Thadeosaurus are distinctive in that the entepicondyle is greatly expanded. The width of the distal end is up to 40% the length of the humerus. It is worth pointing out that all of the described humeri of Youngina are from immature animals and consequently do not show a well ossified entepicondyle. The curvature at the base of the entepicondyle and the position of the entepicondylar foramen suggest that the humerus of Youngina also had a greatly expanded entepicondyle at maturity.

A specialized character uniting Tangasaurus (Haughton, 1924, fig. 1), Hovasaurus and Thadeosaurus is found in the carpus. The medial centrale contacts the fourth distal carpal, thereby preventing the primitive contact between the lateral centrale and third distal carpal. This condition has been reported in Acerosodontosaurus (Currie, 1981), but was not present in protorothyridids (fig. 60a), Galesphyrus (fig. 60f), Claudiosaurus (fig. 60k) or any other eosuchians.

The tarsus is specialized in Tangasaurus, Hovasaurus, Kenyasaurus and Thadeosaurus in the loss of the fifth distal tarsal as a discrete element. Harris and Carroll (1977) refer to a specimen of Hovasaurus (MNHN 1908-21-10) and suggest that the fifth fuses to the fourth distal tarsal at maturity.

DISCUSSION

Tangasaurus mennelli is represented by two known specimens from the Tanga region of Tanzania. Specimens from Madagascar that have been attributed to this species represent a distinct genus, Thadeosaurus.

Four genera from Africa and Madagascar have been assigned to the Tangasauridae. They can be distinguished from Youngina, Acerosodontosaurus and other eosuchians by a relatively shorter skull, a low scapular blade, a large ventral scapulocoracoid plate, by limb proportions (particularly the humerus to femur ratio which exceeds 1.0), and loss of the fifth distal tarsal as a discrete element. As in Acerosodontosaurus and Youngina, the medial centrale of tangasaurids contacts the fourth distal carpal. Youngina and tangasaurids have a shared derived character in the accessory articulating processes on the neural spines.

Thadeosaurus and Kenyasaurus can be distinguished from Tangasaurus and Hovasaurus by differences in the caudal skeleton, and are accordingly being assigned to different subfamilies. The Kenyasaurinae have unspecialized tails that carry 19 to 28 pairs of caudal ribs and transverse processes, all of which taper distally. The caudal neural spines are shorter than the dorsal neural spines, and are not expanded anteroposteriorly. The haemal spines are rod-like and do not expand into platelike structures. The Tangasaurinae includes Tangasaurus and Hovasaurus, which have a maximum of twelve pairs of caudal ribs and transverse processes. The anterior caudal ribs are expanded distally. The neural spines in the proximal and mid-caudal regions are taller than those of the dorsal vertebrae. The haemal spines of tangasaurines are large and platelike.

V

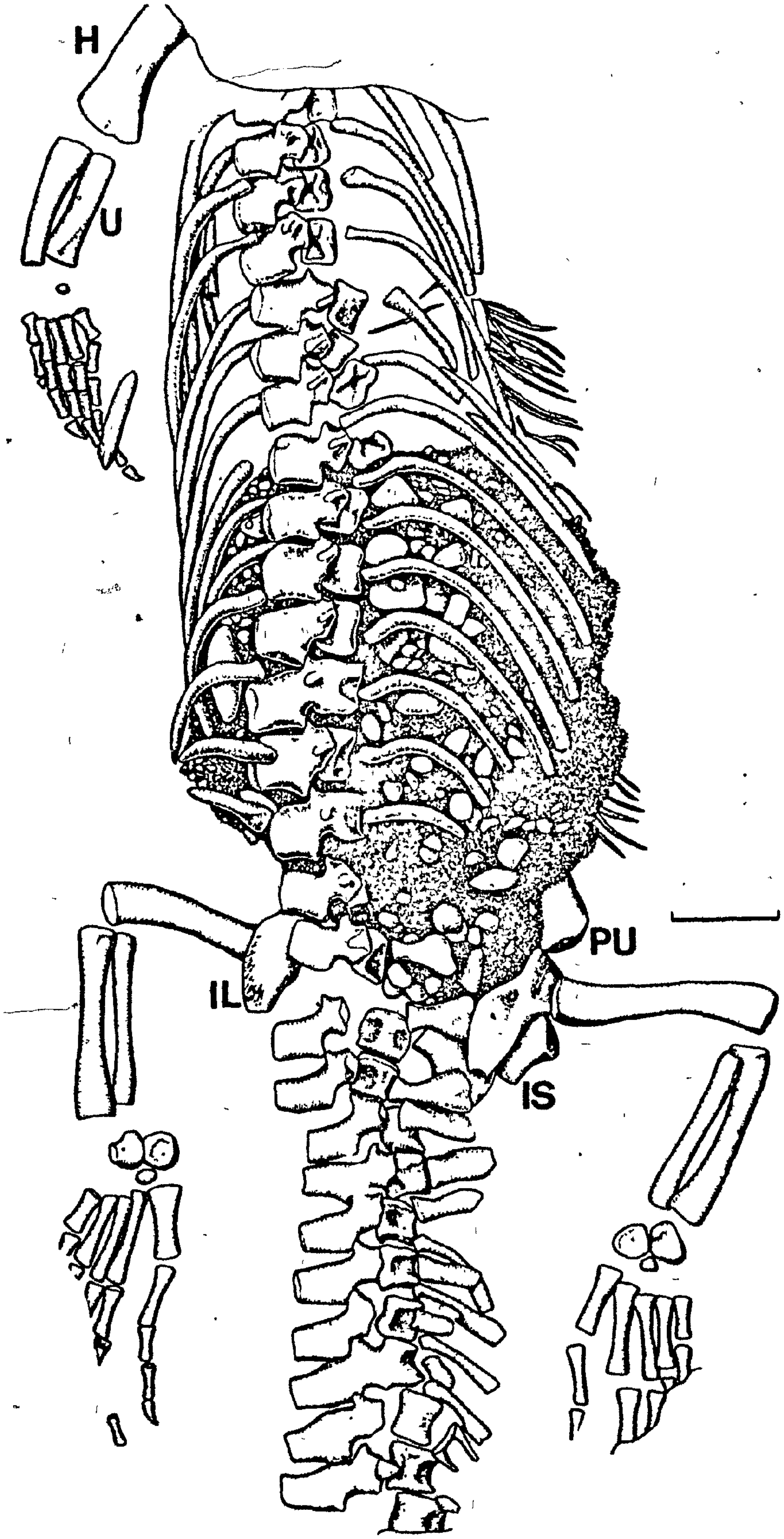
HOVASAURUS BOULEI, AN AQUATIC EOSUCHIAN FROM THE UPPER PERMIAN OF MADAGASCAR

In 1926, J. Piveteau established the genus Hovasaurus on the basis of a large collection of specimens from the Upper Permian of Madagascar. The paper was well illustrated with photographic plates and line drawings, but because of the nature of the specimens and lack of comparative material the description was based on only seven of the several hundred specimens in the Muséum National d'Histoire Naturelle (Paris). Although Hovasaurus was recognized as an aquatic reptile, it was assumed to be related to Mesosaurus. The specimens were studied in Paris by S.H. Haughton who published on his results in 1930. Since that time, Hovasaurus and Tangasaurus have been recognized as closely related eosuchian genera. Subsequent papers by other researchers have mentioned Hovasaurus, but no detailed description has been undertaken, and this genus has remained poorly understood.

Hovasaurus boulei is represented by more than three hundred specimens representing most of the life span, which permits the study of morphological variation and the changes undergone during growth in a single species. The length of an average dorsal centrum of the largest known specimen of Hovasaurus is 3.5 times the length of the same dimension in the smallest known specimen (Table 6). It is evident from the ossification of the largest specimens that these were mature animals when they died. Comparison with adult to hatchling length ratios in living

Figure 19. Hovasaurus boulei, lectotype. MNHN 1908-21-2. Scale = 1 cm.

Figure 20. Hovasaurus boulei, MNHN 1908-21-7, counterpart of MNHN 1908-21-2. Scale = 1 cm.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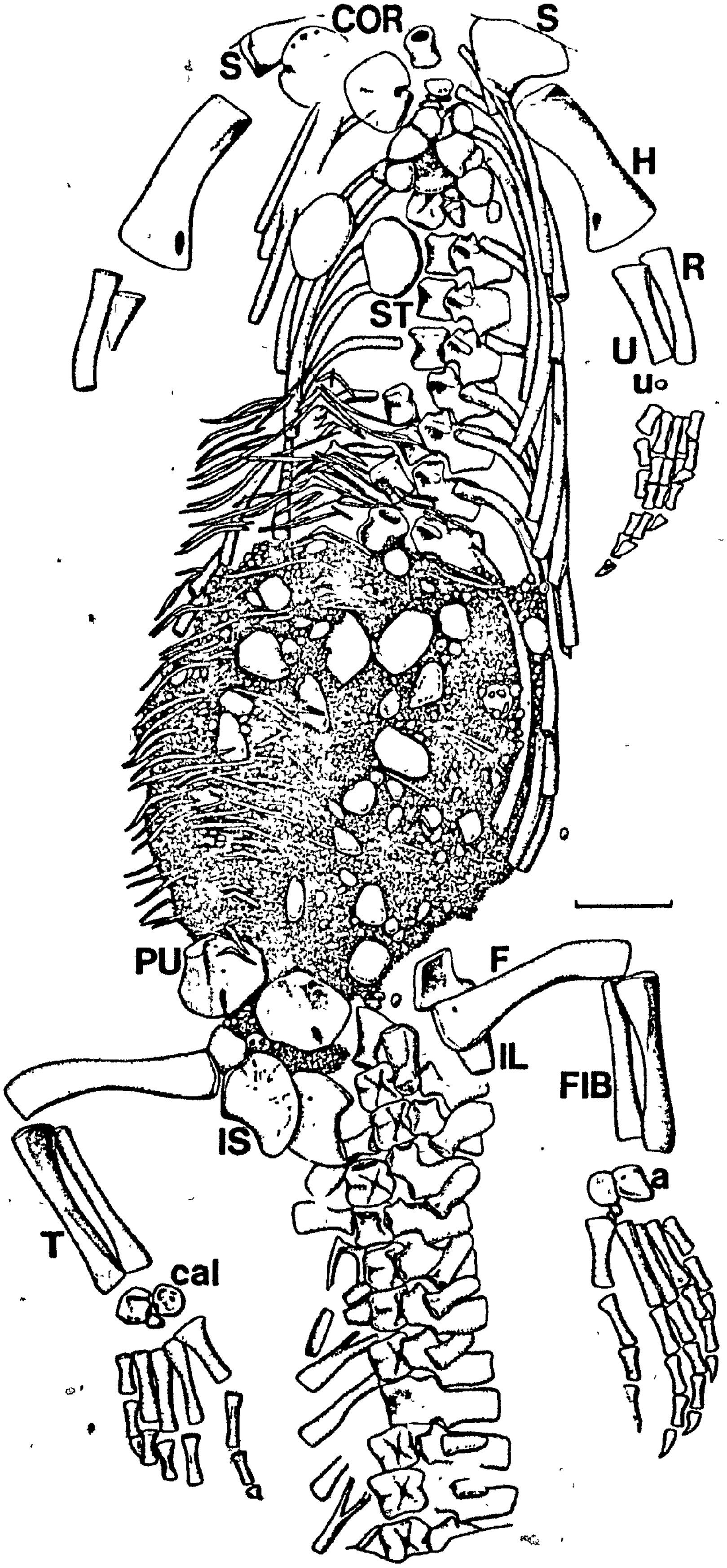
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reptiles suggest that the smallest specimens of Hovasaurus were less than a year old (page 39).

For convenience of reference, the series of Hovasaurus specimens has been subdivided into life stages A to G on the basis of vertebral length (Table 6). In most cases these do not correspond to life stages A to E used by Piveteau (1926) and Haughton (1930), which were based on an irregular size progression representing only the early stages of the life history.

Thadeosaurus, a closely related genus, is known from a smaller number of specimens. However, essentially the same range of life stages is represented. This provides a unique opportunity to study differences in allometric growth, relative dimensions and variability in closely related Permian genera that are exploiting different ecosystems.

Several standards of relative measurement are used to compare elements of animals of different sizes. The orthometric linear unit (OLU) should give a size independent unit measurement provided it is used only on mature animals (Currie, 1978). The type specimens of Tangasaurus had not reached full size before they died, so they are compared with Hovasaurus by regression analysis (Table 4). A commonly used system of comparison is based on the ratio of the dimension being considered to the average length of a dorsal centrum (x).

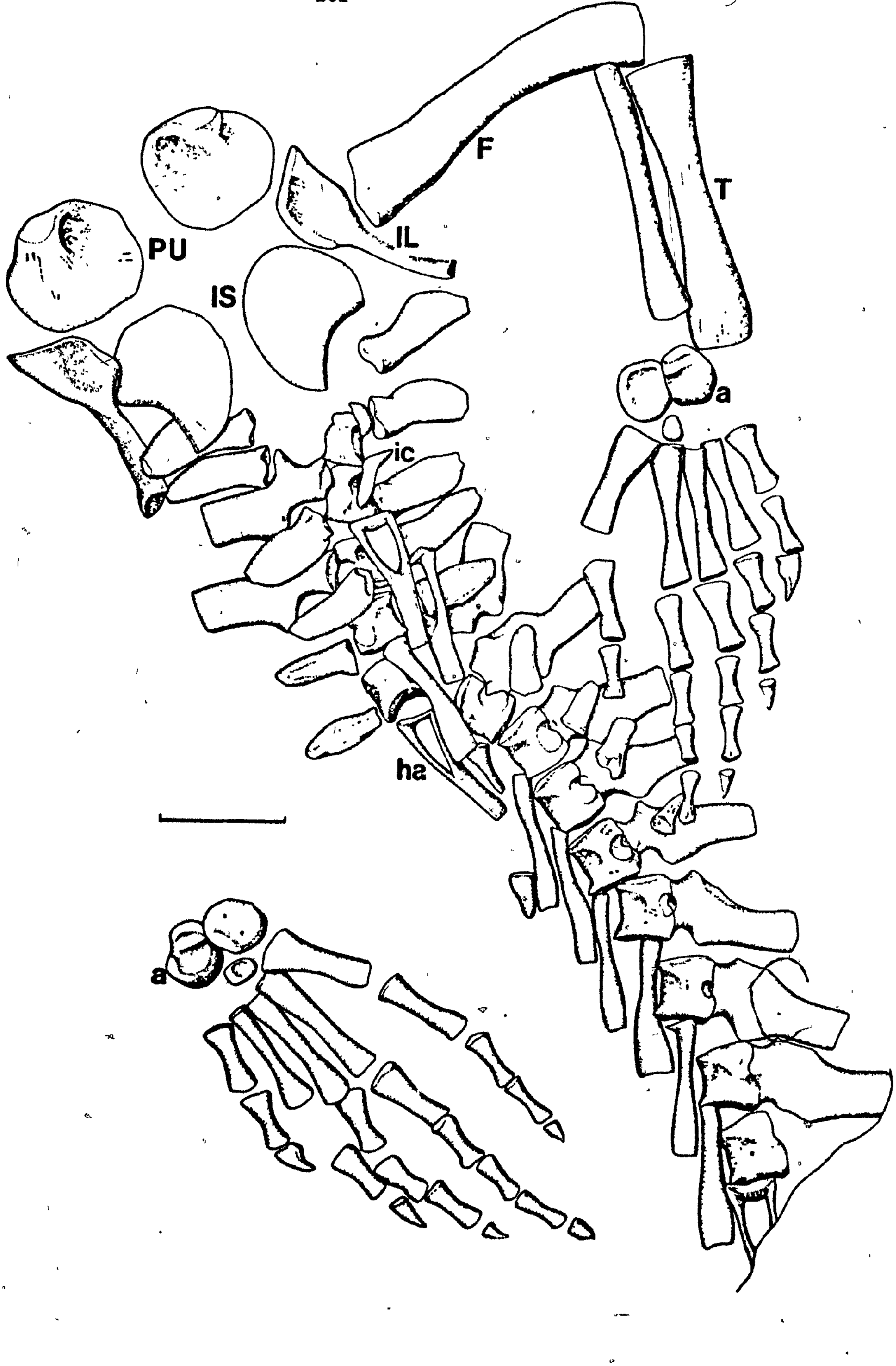
All known specimens of Hovasaurus were found in finely laminated nodules of siltstone. The abdominal cavity was the centre of nodule formation, possibly because of the digestive acids released during decomposition of the animal. The action of nodule formation usually did not persist long enough for the head and tail to be included, and these portions of the body are almost invariably lost. In most cases, only part of each nodule was recovered, and the soft split bone had already eroded out. Latex and silicone rubber casts were made from the high fidelity, natural molds as an aid in studying the specimens (Baird, 1951).

The orientations of the nodules are unknown. The centre of gravity would have been low in Hovasaurus, so most of the specimens probably settled upright in the mud. The disarticulation pattern of the skeleton supports this supposition in most specimens. For example, in MNHN 1908-32-24, the ventral bones have maintained their correct relationship to each other, but the dorsals appear to have collapsed. The scapular blades protrude dorsally above the vertebrae and ribs. The mid-dorsal vertebrae with their high neural spines have fallen on their side, but the sacrals and anterior caudals have remained upright because of the fused ribs that extend laterally from the centra.

It appears that in all cases the connective tissues disintegrated and the bones collapsed into a single plane before the cadaver was covered to any appreciable depth by the fine

Figure 21. Hovasaurus boulei, MNHN 1908-32-77.

Scale = 1 cm.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sediments. There is no evidence of macrophagous scavenging of any of the specimens, and the relatively minor amount of disarticulation evident can be accounted for by settling and gentle currents in the water.

Class REPTILIA Linnaeus 1758

Subclass LEPIDOSAURIA Dumeril and Bibron 1839

Order EOSUCHIA Broom 1914

Suborder YOUNGINIFORMES Romer 1945

Family TANGASAURIDAE Camp 1945

Subfamily TANGASAURINAE Piveteau 1926

HOVASAURUS Piveteau 1926

Diagnosis. -- The most highly specialized tangasaurid for an aquatic existence. The ratio of interorbital to intertemporal width is .4, compared with 1.1 in Youngina; jaw suspension slopes anteroventrally as in Thadeosaurus; triradiate jugal is relatively smaller than in Thadeosaurus or any other eosuchian known; supratemporal as long as but broader than in other eosuchians; distinctive rod-like, anteroventrally sloping ramus on squamosal; quadrate ramus of the pterygoid less than half the length of palatal ramus whereas it is more than half in Youngina; quadrate almost as wide as it is high as in Thadeosaurus but in contrast with Youngina where the width is half the height; external surface of opisthotic convex between main body and paroccipital process rather than concave as in most eosuchians. Accessory intervertebral articulations on midline of neural spines more complex than in Youngina or other tangasaurids; mid-dorsal neural spines up to double the length of centra, and are relatively higher than in any other eosuchian known; anterior and mid-dorsal neural spines thickened dorsally by mammillary processes; caudal neural spines distinctive in outline and up to 2.2 times the length of the centrum compared with 1.4 times in Tangasaurus; haemal spine expanded into large plate of bone that mimics neural spine in shape and size. Mid-dorsal ribs curved throughout their length; unlike other younginiform eosuchians, ribs pachyostotic in mature animals; up to 12 pairs of caudal ribs compared with 12 in Tangasaurus, 19 in Thadeosaurus and 28 in Kenyasaurus; anterior caudal ribs expanded distally. Ossified portion of scapular blade much shorter than Youngina and extends less than 50% up body wall; balance of scapulocoracoid almost horizontal; prominent process on scapula for long head on triceps lateralis. Cleithrum more strongly curved than in other eosuchians. Metacarpals II, III and IV subequal in length. Abdominal cavity usually includes more substantial ingested mass of pebbles than Thadeosaurus.

HOVASAURUS BOULEI Piveteau 1926

Lectotype ---- MNHN 1908-21-2, MNHN 1908-21-7, counterpart slabs in the Muséum National d'Histoire Naturelle, Paris.

Referred specimens --- see Table 6.

Horizon and Locality --- Lower Sakamena Formation, Upper Permian. Sakamena River Valley, southern Madagascar. Exact locality not recorded for lectotype, but probably from Mt. Eliva.

Diagnosis --- same as for genus.

Description

More than three hundred specimens in the Muséum National d'Histoire Naturelle, the South African Museum and the American Museum of Natural History may be identified as Hovasaurus boulei. This study is based on seventy of the best specimens (Tables 5, 6, 7). The specimen selected as the lectotype (figs. 19, 20) is more complete than the other specimens of the series on which the original description of Hovasaurus was based (Piveteau, 1926).

In life, Hovasaurus would have been lizard-like in general appearance. The snout-vent length of a mature animal would have been 30 to 35 centimetres assuming it did not have an elongate rostrum. The tail was exceptionally long, and a conservative estimate of tail length in a large animal would be 60 centimetres.

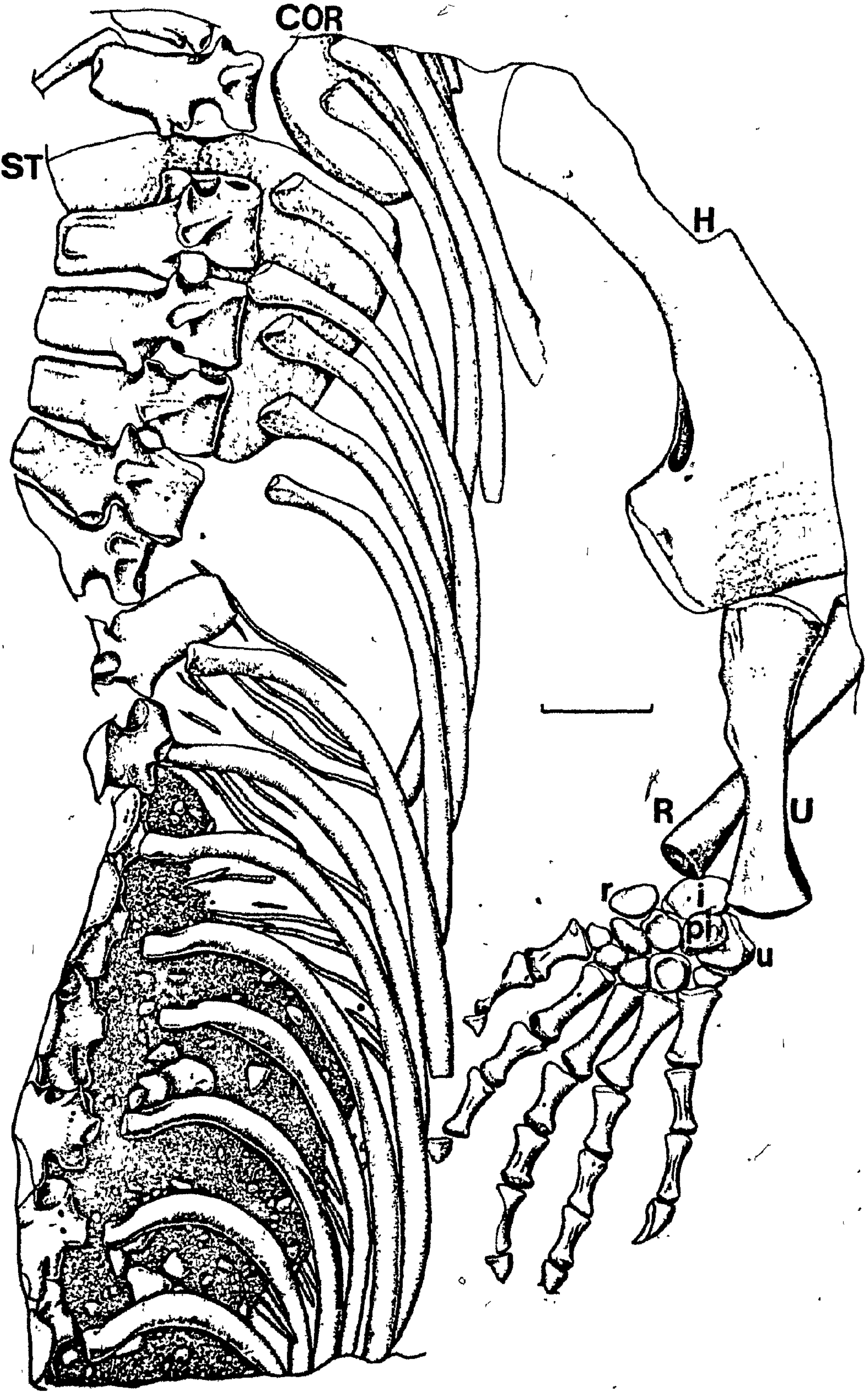
The majority of specimens assumed the same pose in death. The front limb is folded back against the body with the dorsal surfaces of the humerus and manus facing upward. The outer digit of the manus is closer to the body than the inner (figs. 19, 20, 23). Because of the position of the manus, the ulna lies parallel and medial to the radius, and has its anterior face turned upwards. The lateral side of the radius is usually seen from above. The femora tend to be directed outward (figs. 19, 20, 21, 24) with the posterior surface facing upward. The foot has turned so that the dorsal surface remains up, but the outer digit (V) lies closer to the tail than digit I. The tibia was strongly attached to the femur by ligaments and retains its proper orientation with that bone. However, the distal attachments of the fibula were stronger than the proximal so the bone tends to lie closer to the tail than the tibia and is exposed in anterior aspect. There appears to be little or no postmortem contortion of the spinal column such as commonly happened to crocodiles, dinosaurs and smaller reptiles and birds (Sternberg, 1970).

The most conspicuous diagnostic character of Hovasaurus is the presence of abundant pebbles in the abdominal cavity (figs. 19, 20, 22, 23, 24, 25). The majority of these are quartz and have a water-worn appearance. Some of the stones are larger than the vertebrae of the animal they are found in. Four specimens have pebbles up to 2x long, although the widths do not exceed 1.5x. The larger pieces are surrounded by smaller ones, most of which are between .5 and two millimetres in diameter (fig. 25). These are still much coarser than the fine grained silts that buried the specimens.

The pebble mass is completely enclosed within the abdominal cavity of most specimens. The ribs cover the mass dorsally, and

Figure 22. Hovasaurus boulei, MNHN 1908-32-59.

Scale = 1 cm.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the articulated gastralia underlie the mass. The pebble mass has a characteristic shape that tapers anteriorly and caudally. It does not fill the entire abdominal cavity, but in fourteen specimens is confined behind the sixteenth dorsal vertebra. In one specimen it extends anteriorly to the twelfth dorsal, and in the balance of the specimens studied the anterior limit cannot be seen. Posteriorly the pebble mass usually enters the pelvic canal dorsal to the pubis, but can extend caudally to the back of the ischium. The sausage-shaped pebble mass of one of the smallest specimens, MNHN 1925-5-25, fills the pelvic canal and extends back to the level of the third caudal vertebra. The well-defined margins of the pebble mass indicate that it was enclosed within a membrane of soft tissue before decomposition, which would also explain why the stones do not protrude through gaps between the ribs and pelvic bones.

The most logical explanation in light of the observations is that the pebbles were ingested when the animal was alive. The lectotype (fig. 20) has a small mass of pebbles in the pectoral region that it may have been in the process if swallowing when it died. Even the largest pebbles are less than a third the width of the skull in any of the individuals, so no special adaptations would have been necessary to ingest them.

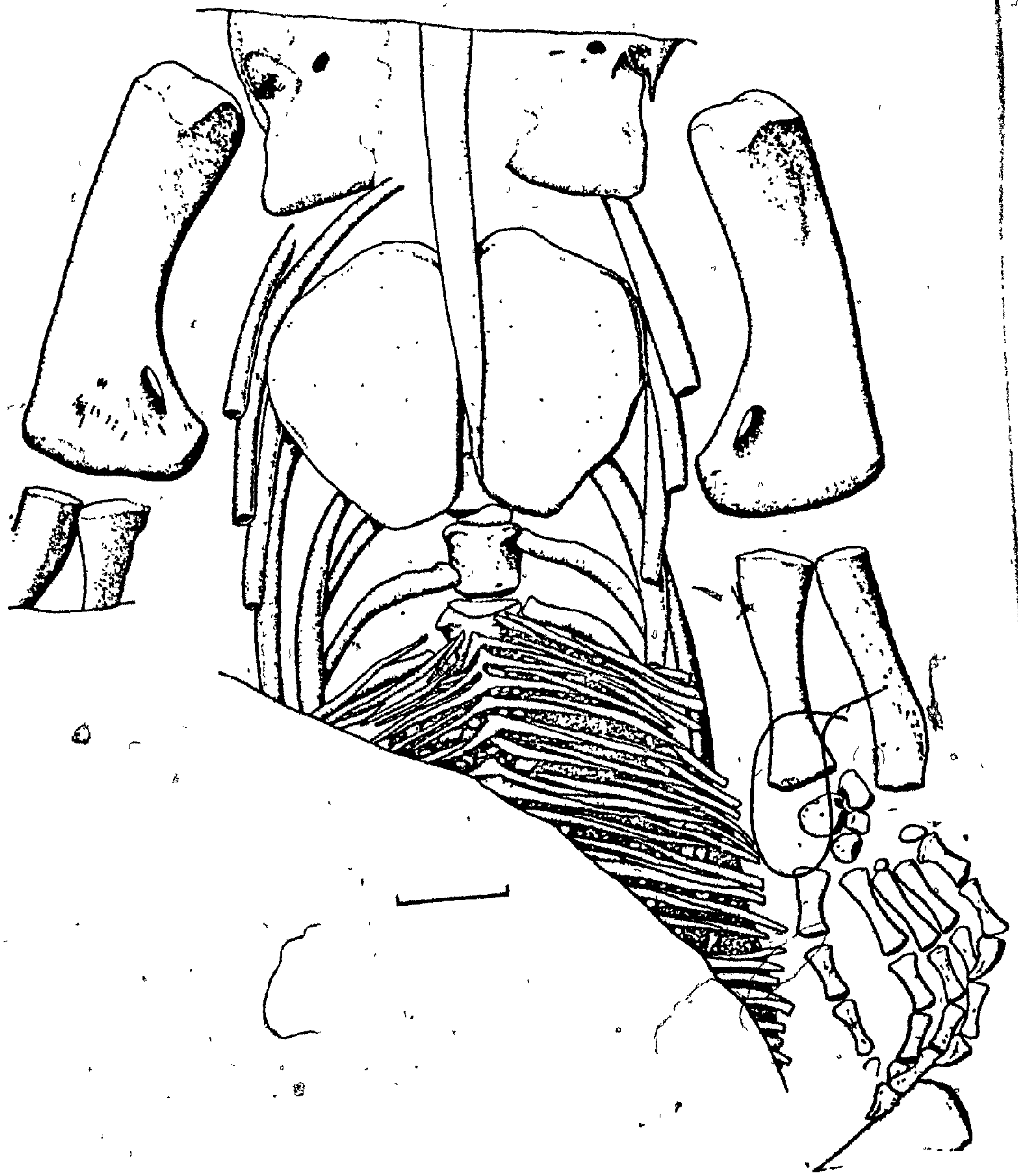
Haughton (1930) suggested that the stones were gastroliths. However, this is difficult to accept because of the large number present and their close packing. The small size of most would probably make them inefficient for grinding food, and they would pass out of the stomach with the food. Finally, they are too far back in the abdominal cavity to have been in the stomach. The consistent shape and position of the pebble mass suggests that they were in a blind sac along the digestive system that was adapted to hold them.

There are many possible alternative explanations. Perhaps they were ingested accidentally with the normal source of food. There are at least two specimens (MNHN 1908-21-6, 1925-5-60) without any stones in the abdomen between the ribs and gastralia, so their presence may not have been essential. Still, it seems that accidental acquisition of so many stones, including such large ones, is not a good explanation. Furthermore, the palatal teeth are slender, sharp and recurved, suggesting that Hovasaurus was an active predator that was not likely to ingest large amounts of gravel for the possible small organisms or detritus that it might include.

The most probably explanation for the pebble mass is that it functioned as ballast. Hovasaurus was an animal that spent a great deal of time in the water, using its long tail for propulsion. The symmetry of the tail suggests that it did most of its swimming underwater rather than on the surface. On the average, the specific gravity of reptiles is about 1.025 (Romer and Price, 1940), slightly denser than fresh water. The centre of gravity tends to be high in

Figure 23. Hovasaurus boulei, MNHN 1925-5-12.

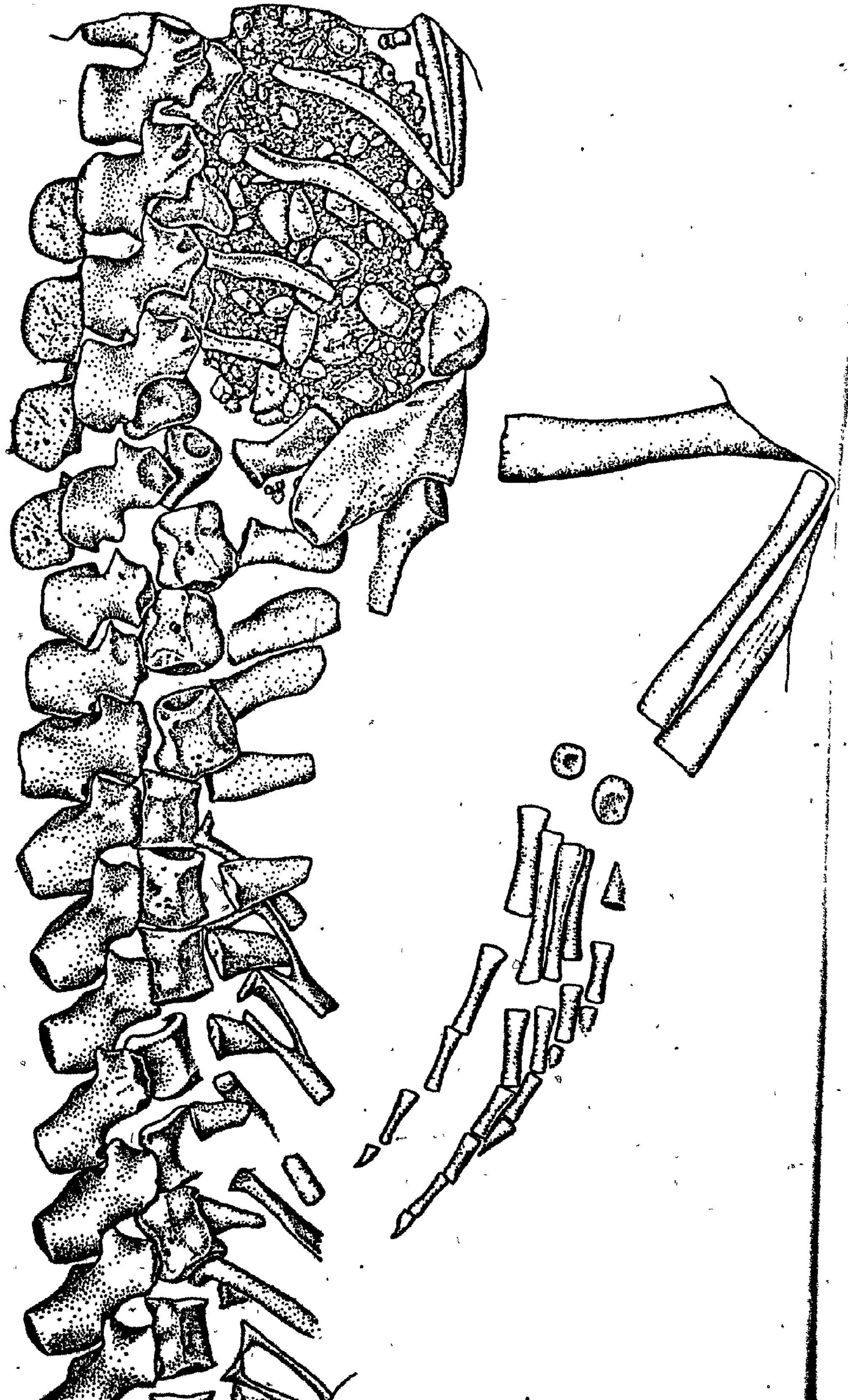
Scale = 1 cm.



the body, which has a tendency to roll over in the water. The reduction of the ossified portion of the scapular blade, the heavy ossification of the ventral part of the pectoral girdle, and the pachyostosis of the ribs would help to lower the specific gravity and the centre of gravity. However, the ribs in the posterior dorsal region are short, the ilium is not reduced like the scapular blade, and the puboischiatic plate is not as massively developed as the ventral part of the pectoral girdle. The main propulsion for swimming was provided by the long powerful tail. With the centre of gravity low in the anterior end of the body and the relatively low density of the posterior half of the body, a portion of the force provided by the tail would tend to lift the back of the body. A great deal of energy would have been expended in the maintenance of vertical stability. The pebble mass is in the perfect position to lower the specific gravity of the pelvic region and to shift the centre of gravity posteriorly to maximize the forward component of force provided by the tail.

It is possible to calculate the effect this pebble mass would have had on the specific gravity. The estimated weight of a mature specimen, using the radius of a dorsal centrum and a technique described by Romer and Price (1940), would have been approximately 10 kilograms. The same technique cannot be used with a juvenile because the radius of a centrum is not directly

Figure 24 . Hovasaurus boulei, MNHN 1925-5-20.
Scale = 1 cm.



related to weight until maturity. The lectotype would have been approximately 40 centimetres long including the tail. By multiplying the weight of the adult by the cubed ratio of juvenile to adult length, a crude weight estimate of 300 to 500 grams is reached for the lectotype. A cast was made of the three dimensional pebble mass of MNHN 1908-21-2/7 and the volume calculated by liquid displacement. The weight of the mass was calculated using the specific gravity of quartz (2.5), and amounted to 25 grams. This is enough to raise the specific gravity of the animal by five to ten percent, to the lower end of the specific gravity range of aquatic turtles (Zug, 1971).

The use of ingested stones for ballast is not a new idea. Cott (1961) presented data to show that the "gastroliths" function to lower the specific gravity and the centre of gravity in the Nile crocodile. Large masses of ingested stones, similar in abundance to <u>Hovasaurus</u>, are found in the abdomens of many plesiosaur specimens, and were probably used for ballast (Darby and Ojakangas, 1980).

Stomach stones are found in at least two specimens of <u>Thadeosaurus</u> (MNHN 1908-11-5, Piveteau, 1926, Pl. XI; MNHN 1908-5-1, Piveteau, 1926, Pl. XII, fig. 1) but are few in number and probably did serve as gastroliths. When present, the relative abundance of stomach stones is a quick way to distinguish <u>Hovasaurus</u> and <u>Thadeosaurus</u>.

Figure 25. Hovasaurus boulei, MNHN 1925-5-29. Ingested pebbles. Magnification approximately X3.7.

Absence of stones in the abdomen of Tangasaurus does not necessarily mean that this genus did not swallow pebbles. The gastralia have been lost, and the pebbles could have been lost by post-mortem rupture of the abdominal cavity.

Skull

General. The skull of Hovasaurus is poorly known. Only nine of the hundreds of specimens of this genus that have been collected have partial skulls. Two of the best specimens figured by Piveteau (1926, Pl. VII, fig. 3 and Pl. XIV, fig. 1) could not be relocated for study.

The most complete skull studied is that of MNHN 1925-5-34 (fig. 26). The skull has been disarticulated, and the skull roof is visible in ventral view only. Maxilla, jugal, frontal, postfrontal, parietal, pterygoid, epipterygoid and quadrate bones are represented. Elements of the lower jaw are present but are crushed and incomplete so that only the right surangular could be identified.

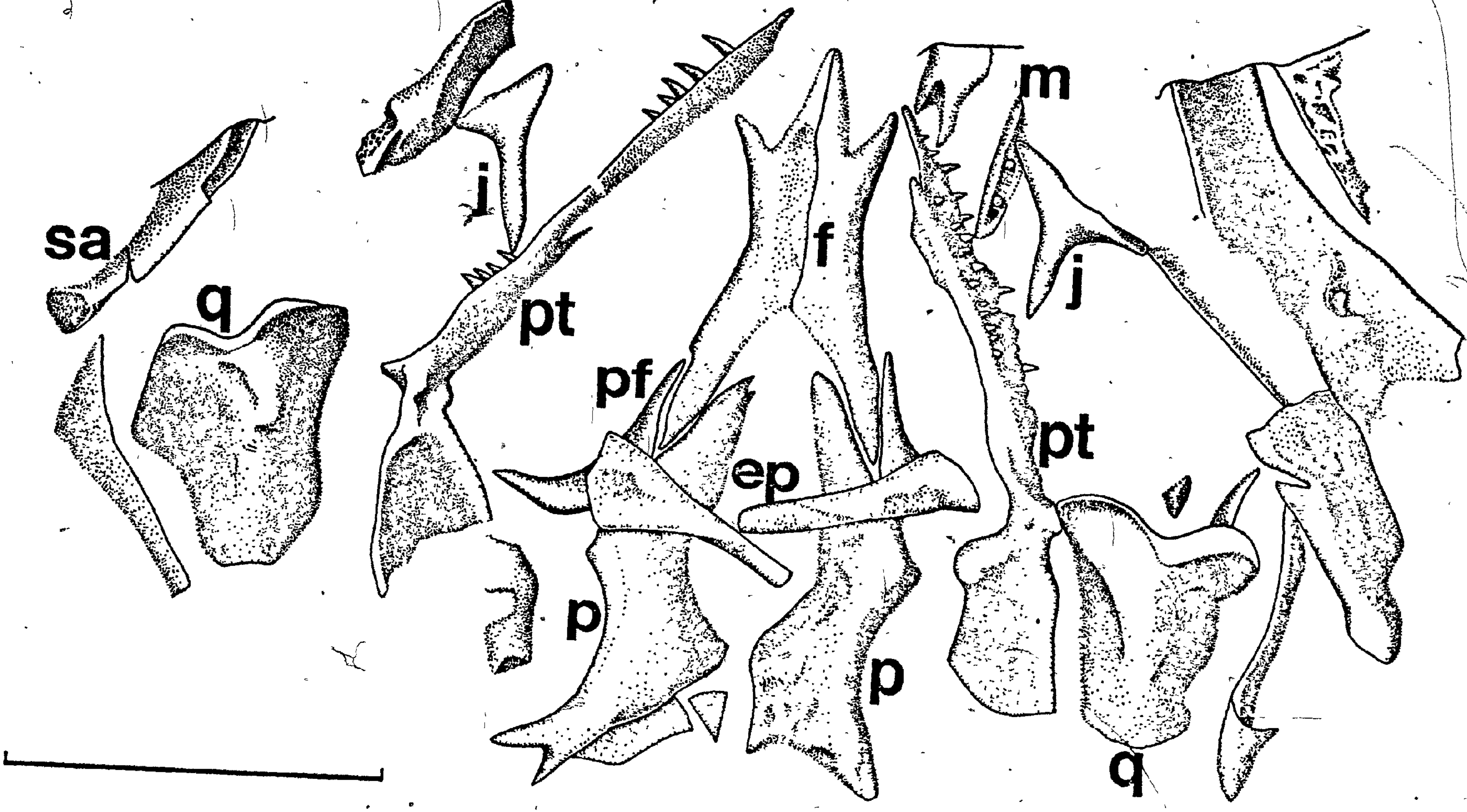
MNHN 1925-5-30 (fig. 27) includes part of the basisphenoid-parasphenoid complex, a prootic, opisthotics, a basioccipital and exoccipitals. The posterior ends of two hyoid bones are preserved.

Portions of the skull roof and occiput are visible in MNHN 1925-5-36 (fig. 29). Parietals, a postorbital, a squamosal, a quadrate, a supratemporal, a supraoccipital and a hyoid have been identified.

Figure 26. Hovasaurus boulei, MNHN 1925-5-34.

Ventral view of skull roof.

Scale = 1 cm.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The same region is exposed in MNHN 1908-32-99 (fig. 30) where parietals, a postfrontal, a postorbital, a squamosal, a supratemporal, an opisthotic and a stapes can be seen.

Three specimens, MNHN 1908-32-1, 1908-32-23 and 1925-5-49, have only portions of the most posterior bones of the skull and mandibles preserved.

The bones of all known skulls were disarticulated after death, suggesting that none of these animals were mature enough for the bones to have been firmly sutured. The largest specimen with a skull (MNHN 1925-5-36) is only three quarters of the maximum known size, and it is possible that the dermal bones were more strongly sutured in the largest animals. The endochondral cranial bones, which are the last to ossify in the ontogeny of modern reptile skulls (Howes and Swinnerton, 1901), are well formed in the smallest specimens.

Reconstruction of the postorbital region of the skull is possible in dorsal, lateral, ventral and occipital views (fig. 31). These restorations were based primarily on MNHN 1925-5-34, an animal that was intermediate in size to other specimens with skulls.

Cranial proportions can change during ontogenetic growth, so it is not a good policy to reconstruct a skull using animals of different ages. However, not enough data is available to calculate the coefficient of allometry for the postorbital region. Growth of the skull is more or less isometric in at least some reptilian genera (Currie, 1979). Furthermore, the largest specimen with a skull is less than twice the size of the smallest, and the reconstructed skull is intermediate. Finally the other skulls were scaled to the same size as MNHN 1925-5-34 on the basis of bones they have in common rather than on postcranial measurements. The effect of proportional changes due to growth should be minimal in the reconstruction.

The antorbital region of the skull is unknown. Piveteau (1926) stated that the skull was probably elongate as in Mesosaurus, but had no supportive evidence. A skull figured by Piveteau (1926, Pl XIII, fig. 5, Pl. XIV, fig. 1) is missing the anterior end, but appears to be tapering anteriorly at an angle that suggests there was no elongate snout.

As reconstructed, the skull is about 30 mm wide for an animal with a 6.4 mm long dorsal centrum. This is very close to the width of the skull of Heleosaurus (SAM 1070), an eosuchian with an average length of 6.5 mm for the dorsal centra. In dorsal aspect (fig. 31a), the skull seems to have been broader in the quadrate region than immediately behind the orbits. Both temporal openings are visible in dorsal view. The pineal opening is approximately equidistant from the front and back of the parietal along the midline, and is relatively large for an eosuchian. The skull is narrow between the orbits compared to the distance between the upper temporal fenestra. The ratio of interorbital to intertemporal width is .4 in Hovasaurus compared with 1.1 in Youngina (Broom and Robinson, 1948), and an estimated 1.0 in Acerosodontosaurus. The posterior margin of the skull table is emarginated centrally, but not to the degree seen in many Permian reptiles.

The skull is relatively low in lateral view (fig. 31b) which is considered a primitive characteristic (Reisz, 1981). The ratio of skull height in the orbital region to maximum skull width is the same as in the reconstruction of Acerosodontosaurus (fig. 8). The dorsal and posterior circumorbital bones show that the orbit is relatively large, and occupies most of the height of the skull. The lateral temporal fenestra was probably enclosed ventrally by a complete temporal bar, but a quadratojugal has yet to be identified with certainty. The jaw suspension apparently sloped forward, but did not extend much below the level of the tooth row.

Suborbital fenestrae are present in at least one specimen, but their size and shape is not well enough known to include in the palatal reconstruction (fig. 31c). The interpterygoid vacuity is of moderate size and the subtemporal fossae are large. The occipital condyle seems to have been located behind the jaw articulation. The basipterygoid articulation was located slightly anterior to the transverse process. Three toothbearing ridges radiate anteriorly, anterolaterally and laterally across the pterygoid from this region.

The skull appears relatively low and wide in occipital view (fig. 31d). A sharp inflection at the back of the parietal clearly delineates the dorsal limit of the occiput. The paroccipital processes are relatively short, but cartilaginous entensions would have formed the ventral margins of the relatively large posterior temporal fenestra.

Maxilla. The posterior end of the maxilla can be seen in ventral view in two specimens. The bases of several posterior teeth are preserved and have diameters of less than one millimetre. At least nine maxillary teeth can be seen in the partial maxilla figured by Piveteau (1926, Pl. XIV, fig. 1), but the total maxillary tooth count must have been more than double this number. The maxilla extended posteriorly to the back of the orbit.

Jugal. The jugal is a triradiate bone that seems to be relatively smaller than the same element in any other eosuchian (fig. 49). The suborbital ramus is short, and could not have extended anteriorly for more than half the length of the orbit. The bone is not thickened medially as the other circumorbital bones are. The ventral margin is straight below the orbit, but is inflected ventrally in the region of the subtemporal ramus. there is no evidence of a ventromedial tuberosity such as in Heleosaurus (Carroll, 1976a) and many other primitive reptiles

Figure 27. Hovasaurus boulei, MNHN 1925-5-30.
Cervical region and partial skull.
1, proatlas; 2, base of neural spine.
Scale = 1 cm.

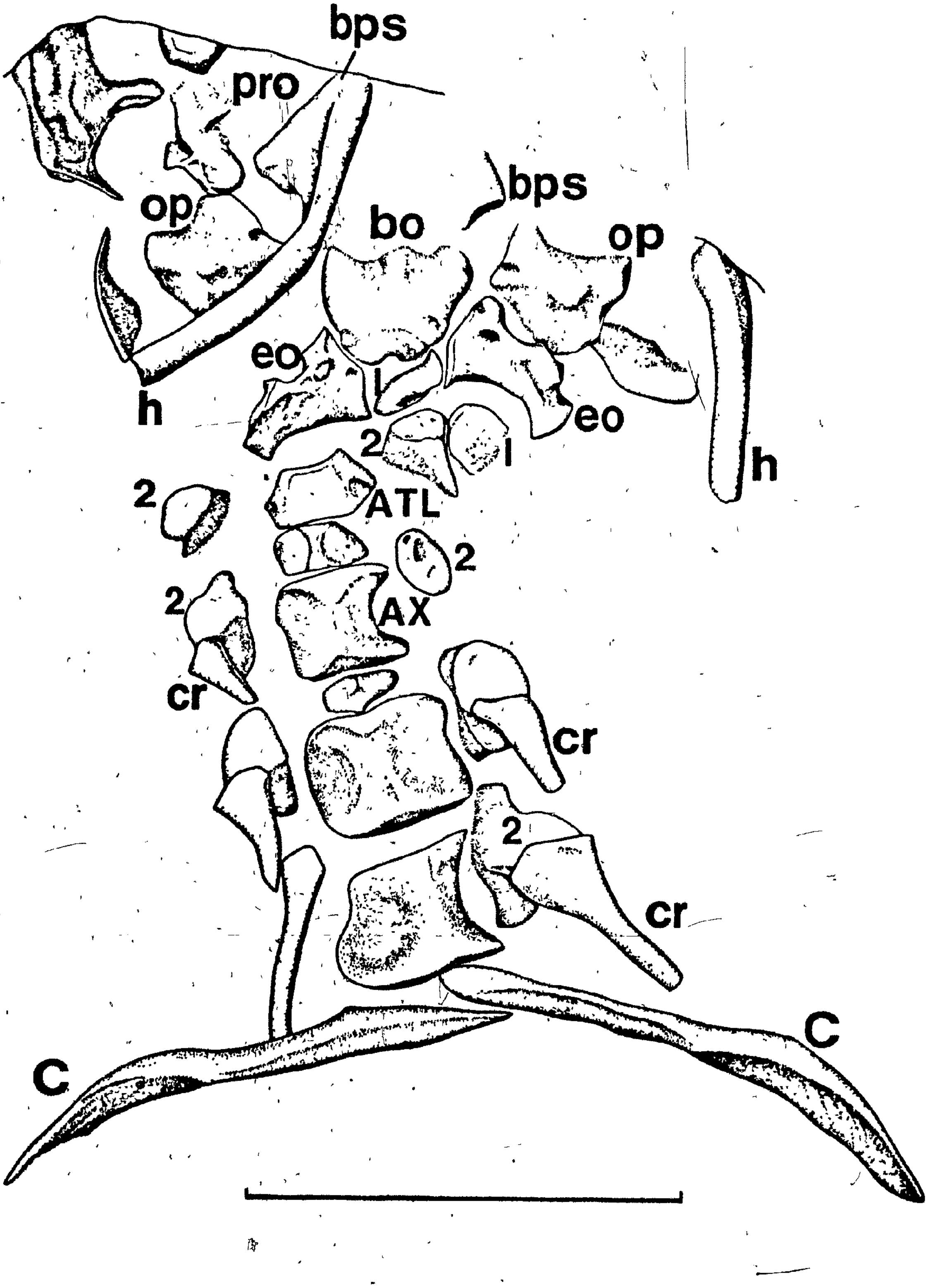
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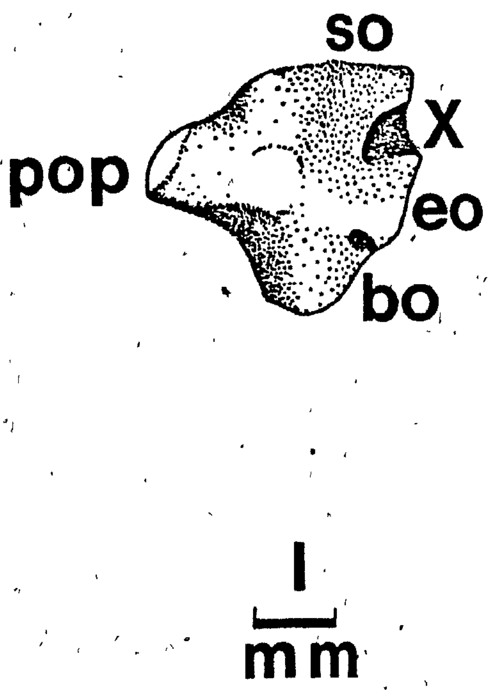
Figure 28. Hovasaurus boulei, reconstruction of left opisthotic (posterior view). Based on MNHN 1925-5-30. X, lateral margin of vagus foramen. Scale = 1mm.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(Romer and Price, 1940; Heaton, 1979). The subtemporal process is short and slender, but its presence suggests that the lower temporal bar was complete. Most of the postorbital ramus of the jugal is excluded from the margin of the orbit by the postorbital bone. There is a long diagonal contact with the postorbital which is twisted so that the dorsal end of the jugal overlaps the suture.

Frontal. The frontal (fig. 26) is distinctive in outline. Anteriorly, the paired frontals taper to a point on the midline to separate the posterior ends of the nasals as in *Youngina* (Gow, 1975). The frontal could have been overlapped externally by the nasal as it is in many primitive reptiles (Currie, 1977; Heaton, 1979). An anterolateral projection of the frontal excludes the posterior end of the prefrontal from the orbital rim. There is a narrow posterolateral emargination for the postfrontal. The paired frontals are separated posteriorly by the parietals. The tapered, posterior end of the frontal fits into a notch on the dorsal surface of the parietal. The same type of frontal-parietal suture is found in a probable petrolacosaurid from the Lower Permian of Oklahoma (Carroll, 1968) and in *Youngina* (fig. 50f) and *Claudiosaurus* (fig. 50h).

Parietal. A pair of parietals meet in a longitudinal, wavy suture anterior and posterior to the pineal opening. The bone is thickened into dorsal ridges along the margins of the pineal opening and the upper temporal fenestra. Another ridge borders the skull roof where it meets the occiput. The ventral surface of the parietal is vaulted between ventral ridges along the margins of the upper temporal fenestra. The parietal has distinctive contacts with the frontal and postfrontal that are identical to those described for Youngina (Broom and Robinson, 1948; Carroll, 1968; Gow, 1975) and Claudiosaurus (Carroll, 1981). The posterior end of the frontal is separated from the postfrontal by the parietal. A rostrally directed process of the parietal excludes the posterior end of the postfrontal from the margin of the upper temporal fenestra. The postfrontal does not overlap the parietal. This pattern appears to be primitive because it is found in protorothyridids. The similarity is particularly striking in Protorothyris (Clark and Carroll, 1973, fig. 2).

The posterolateral corner of the parietal is notched on its dorsal surface for the attachment of the supratemporal (figs. 29, 30). The posterior margin of the skull is embayed medially, and the parietals apparently extended onto the occiput for a short distance (fig. 30).

Postparietal, tabular. These bones are not seen clearly in any of the specimens. Fragments of one or both elements are present between the parietal and supraoccipital of MNHN 1925-5-36 fig. 29), so they have been included as a single outline in the reconstruction on the basis of information from the surrounding bones.

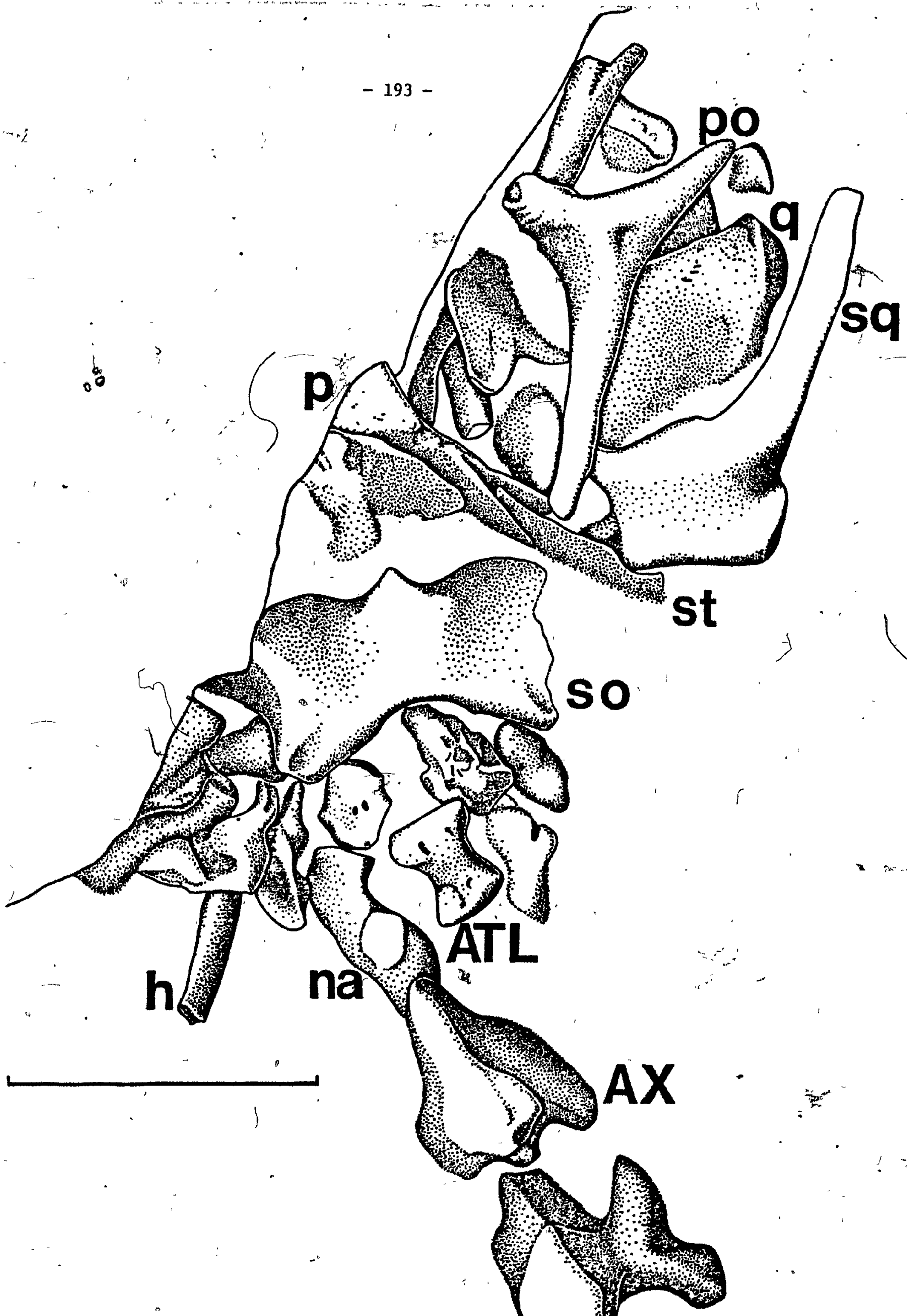
Supratemporal. The supratemporal is an elongate bone that tapers at both ends (fig. 30). It is relatively larger than in any other eosuchian or protorothyridid. There is no apparent adaptive significance for the enlargement of this bone in Hovasaurus, but it could be correlated with the anterior position of the mandibular articulation and the change in orientation of the quadrate and squamosal. The supratemporal fills a deep notch in the parietal (fig. 29), but becomes thinner where it overlaps the squamosal distally. It probably contacted the cartilaginous, lateral end of the paroccipital process.

Postfrontal. The postfrontal is an arched bone that forms portions of the margins of the orbit and the upper temporal fenestra. The ventrolateral end is tapered and overlaps the postorbital (fig. 30) as in most primitive reptiles except for Petrolacosaurus (Reisz, 1981). The postfrontal is not excluded from the margin of the upper temporal fenestra by the parietal and postorbital.

Postorbital. The postorbital is a triradiate bone with a long intertemporal ramus (fig. 30) that contacts the squamosal posteriorly in an overlapping suture. The weak curvature of the bone shows that both temporal fenestrae would be visible in lateral view.

Quadratojugal. The quadratojugal cannot be identified with certainty in any of the specimens. In the reconstruction,

Figure 29. *Hovasaurus boulei*, MNHN 1925-5-36.
Partial skull. Scale = 1 cm.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the postorbital length of the skull and the size of the lower temporal opening were determined by the skull roof and palatoquadrate elements. If the quadratojugal was present in Hovasaurus, it was apparently a large element, at least as long as that of Heleosaurus (Carroll, 1976a). Although the quadratojugal is present in all Permian eosuchians, it has lost contact with the jugal in the prolacertids, paliguanids and Claudiosaurus. The close relationship between Hovasaurus and Youngina is weak evidence that the lower temporal arch was complete in the tangasaurid. The presence of a subtemporal ramus on the jugal suggests that this bone contacted the quadratojugal, although a similar posterior extension of the jugal does not meet the quadratojugal in Prolacerta (fig. 49m) or Tanystropheus (fig. 49n). Haughton (1930) examined one of the missing skulls of Hovasaurus (Piveteau, 1926, Pl. VII, fig. 3) and felt that the lower temporal bar was complete on the left side of the specimen. Finally, Camp (1945) examined a cast of another specimen described by Piveteau (1926, Pl. IX, fig. 1) and tentatively identified a long, slim bone as the quadratojugal.

Squamosal. The posterior margins of the upper and lateral temporal openings are formed by the squamosal. There is an almost rectangular dorsal region with a distinct posterior process (fig. 29). This process is present, although it is not as prominent, in Youngina. This is the only portion of the squamosal of Hovasaurus that extends onto the occiput, where it possibly would have met the paroccipital process. A distinct, almost rod-like descending process of the squamosal is inclined anteroventrally, one indication that the jaw articulation has shifted anteriorly from its primitive position behind the occiput.

Palate. The palate illustrated by Piveteau (1926, Pl. XIV, fig. 1) is basically the same as that of Youngina in the configuration of the suborbital and subtemporal fenestra, and the interpterygoid vacuity. The palatine is present but lacks a visible suture with the pterygoid (Piveteau, 1926).

The palatal ramus of the pterygoid has two ventral ridges separated by a low vault (Haughton, 1930). Both ridges are tooth bearing, and the teeth on the medial ridge of MNHN 1925-5-34 are up to .8 mm long. The palatal teeth are randomly distributed on the crests of the ridges. Both pterygoids of MHNH 1925-5-34 can be seen in medial view (fig. 26). The medial edge of the palatal ramus of the pterygoid turns sharply dorsad anterior to the interpterygoid vacuity, and forms a low, vertical plate of bone.

The basipterygoid articulation is located anteromedial to the pronounced but low transverse process of the pterygoid.

The quadrate ramus of the pterygoid is relatively short, less than half the length of the palatal ramus, because of the anterior position of the jaw articulation. The medial surface of the quadrate ramus is concave above the medially thickened ventral margin. The anterodorsal border is strengthened by another ridge that terminates dorsally in a low process. The epipterygoid would have convered most of the anterodorsal margin of the quadrate process.

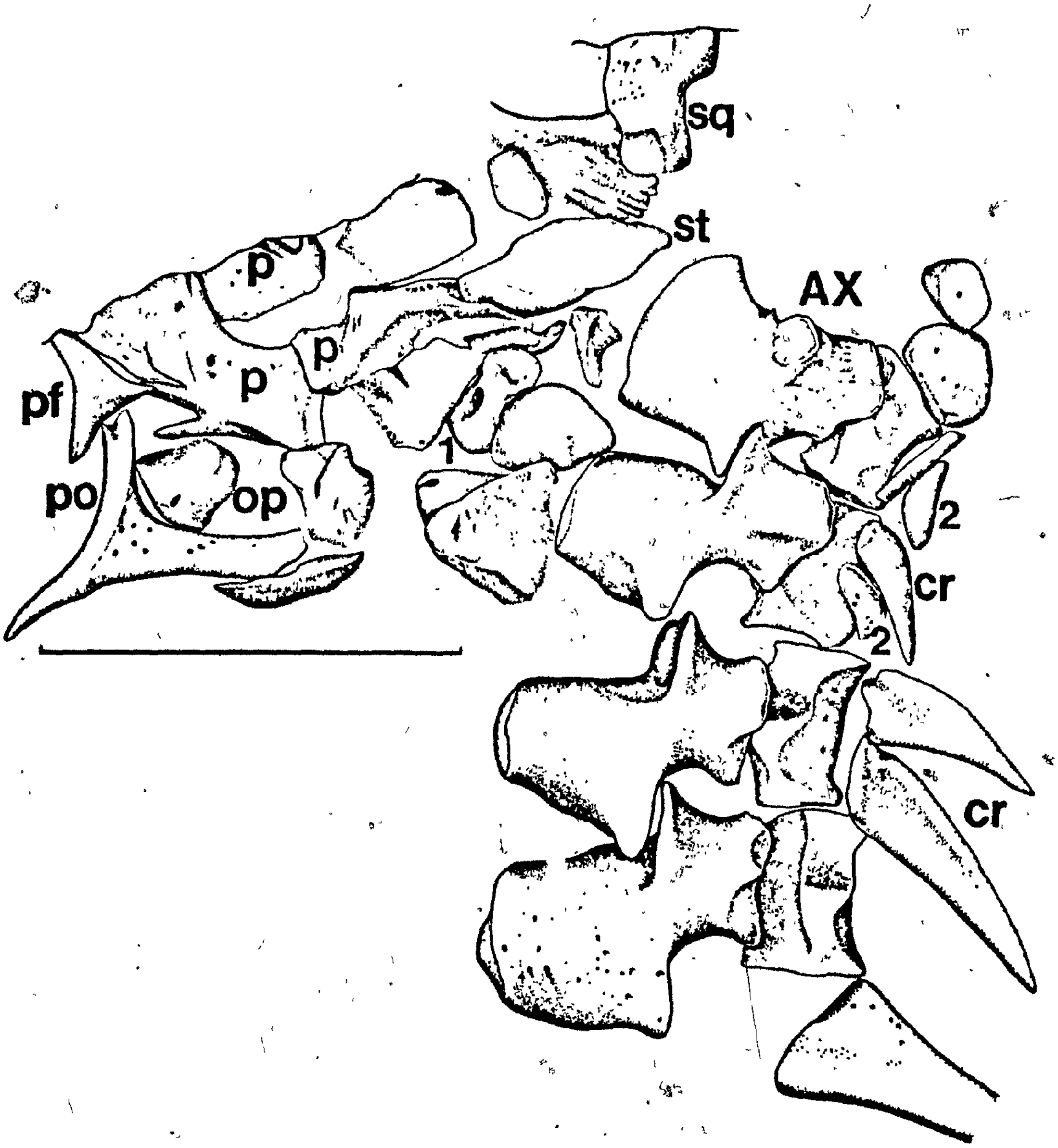
Epipterygoid. The epipterygoid has a broad base and a long, rod-like dorsal extension. The base is not completely ossified in MNHN 1925-5-34 (fig. 26) because of immaturity, so the basicranial articulation is not preserved. There is a distinct, triangular depression on the medial surface of the base, bounded anteriorly and posteriorly by ridges. The ridges converge and meet dorsally, and continue up the medial surface of the columella to terminate at the anterior edge halfway up.

Quadrate. Both quadrates of MNHN 1925-5-34 (fig. 26) are exposed in external aspect, which is unusual when the skull roof is exposed in ventral view. In most disarticulated reptile skulls from the Paleozoic, the quadrates lie behind the skull with the condyles facing caudad. The position of the quadrates in this specimen with the condyles oriented anteriorly suggests that in life the ventral end of the quadrate was anterior to the dorsal end. The condyles of the right quadrate of MNHN 1925-5-36 (fig. 29) are anterior to the squamosal, the ventral ramus of the squamosal is directed anteroventrally, and the quadrate ramus of the pterygoid is short, all of which supports the concept of the jaw articulation being anterior to the occiput.

The quadrate is a broad, relatively low bone that terminated ventrally in a pair of condyles for articulation with the mandible. The width to height ratio is .9, compared with .8 in Thadeosaurus and .4 in Youngina (Olson, 1936), although the dorsal end was unossified at death in MNHN 1925-5-34. The quadrate of Thadeosaurus is indistinguishable from that of Hovasaurus in shape, size and position. A ridge on the external surface of the quadrate extends from the medial condyle to the dorsal edge as in Youngina (Olson, 1936), and Thadeosaurus (fig. 16). Medial to the ridge is an extensive sutural surface for the pterygoid. A stapedial boss protrudes from the ridge above the condyles, and the cartilaginous distal end of the stapes would have passed dorsal to this knob. The quadrate of Hovasaurus is basically the same as those of Youngina, Thadeosaurus, Acerosodontosaurus and Heleosaurus.

Braincase. The parasphenoid and basisphenoid (Piveteau, 1926, Pl. XIV, fig. 1) are fused and will be treated as a unit. The maximum width of the complex is 28% of the total length. The elongate cultriform process makes up approximately two thirds of the total length. Anterior to the basipterygoid tubercles the rostrum is narrow at its base, expands somewhat anteriorly, and then tapers to a point. In Thadeosaurus it is swollen anterior to the tubercles (fig.16). A low ridge runs along the midline of the cultriform process, and ends posteriorly between the basipterygoid processes. The

Figure 30. <u>Hovasaurus</u> <u>boulei</u>, MNHN 1908-32-99.
Partial skull. 1, stapes, 2, intercentrum.
Scale = 1 cm.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basipterygoid tubercles are oriented anteriorly, ventrally and laterally, and are not fused to the palate. No carotid foramina are visible on the ventral surface (Piveteau, 1926). The complex is concave ventrally in transverse section between the crista ventrolateralis, and this region would have been lined in life by the pharyngeal membrane. There is a low, ventral ridge along the midline in the region where the complex overlaps the basioccipital. The crista ventrolateralis does not extend as far beyond the posterior margin of the bone on the midline as they do in Thadeosaurus.

The supraoccipital is a large, platelike bone (fig. 29). There is a crest along the midline of the posterior surface, extending from the foramen magnum to a pronounced medial process on the dorsal margin of the bone. Lateral to the margin of the foramen magnum, the ventral margin of the supraoccipital has an oblique, overlapping suture with the exoccipital. A ventrolaterally facing process abuts the dorsomedial portion of the opisthotic. A well-developed lateral ascending process extends dorsolaterally to contact the dermal roofing bones. Ventrolateral to this process, a concave region would have been continuous with the crista alaris of the prootic.

The exoccipital (fig. 27) is excavated medially by the foramen magnum and laterally by the vagus foramen. It is perforated by a single foramen for the hypoglossal nerve.

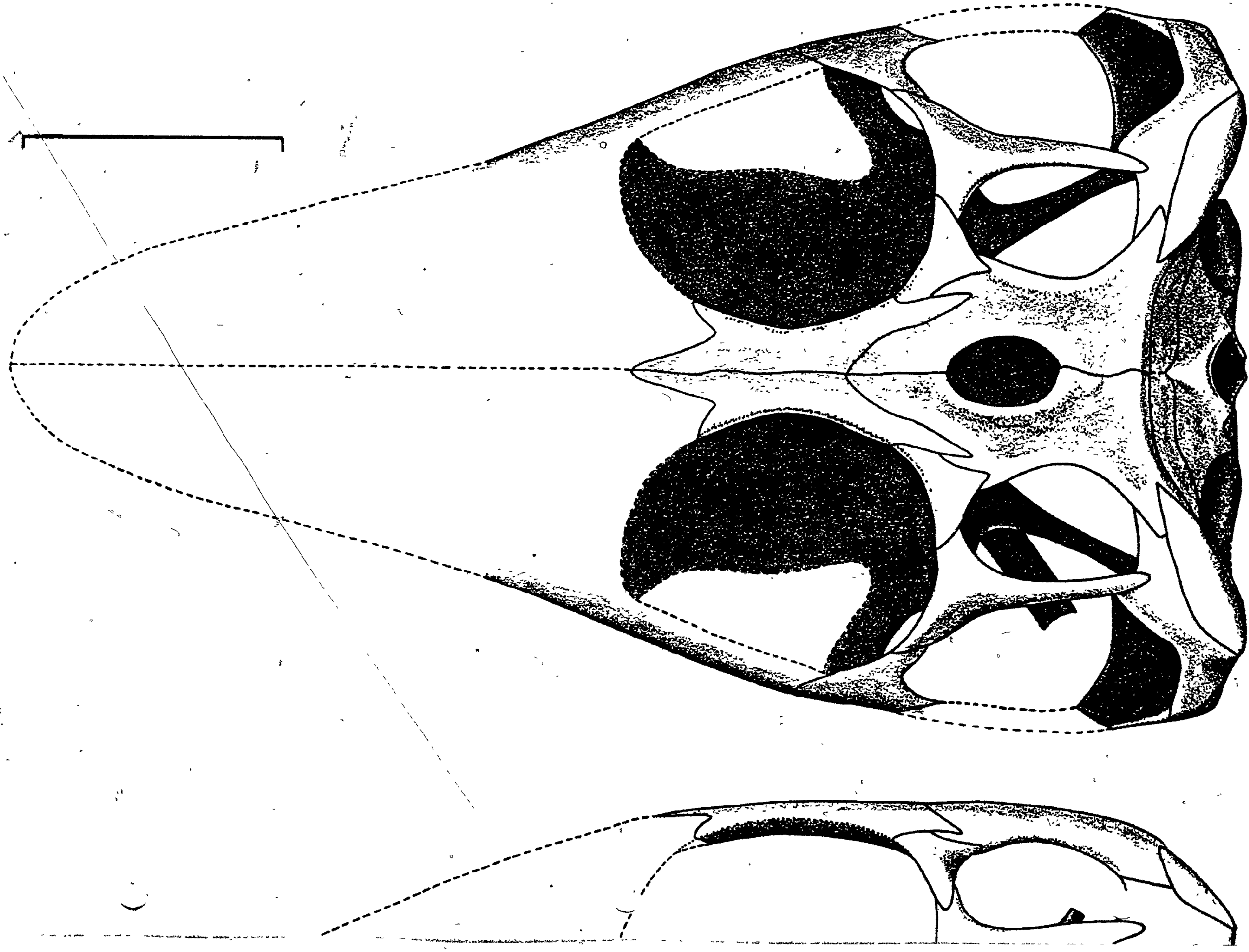
ventromedial to the vagus foramen. The vagus and hypoglossal foramina are separated by a well-defined ridge. There is a sharp inflection on the ventral margin of the exoccipital where it contacts the basioccipital. The exoccipital does not take part in the occipital condyle, and there is no facet visible for the articulation with the proatlas. The lateral margins dorsal and ventral to the vagus foramen are thickened for a strong suture with the opisthotic. The dorsal suture for the supraoccipital is relatively small, and the exoccipitals do not meet at the midline.

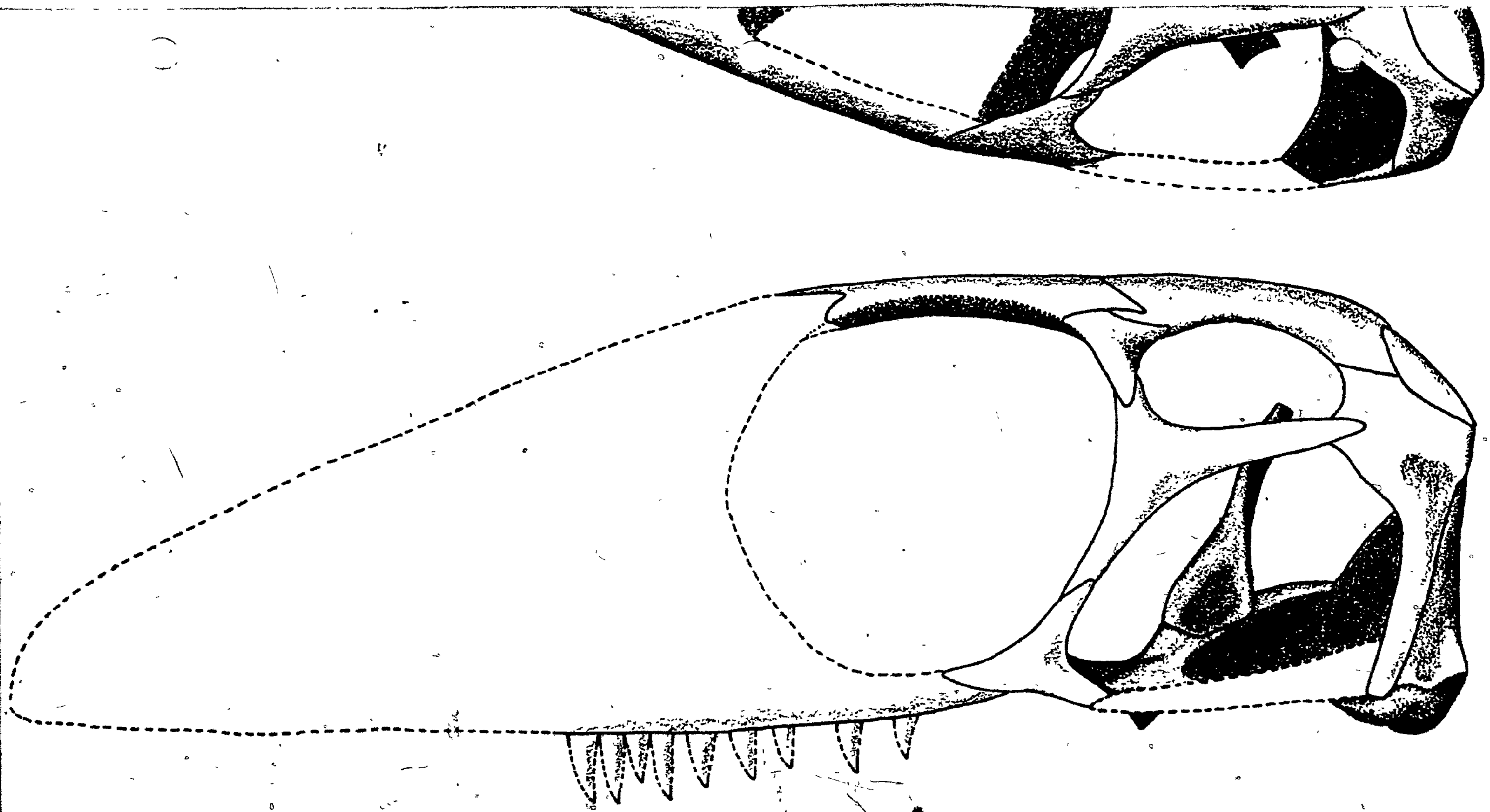
The basiocciptal (fig. 27) forms the hemispherical occipital condyle. It is concave dorsomedially where it forms the floor of the foramen magnum. A semicircular notochordal "pit" indents the posterodorsal margin of the occipital condyle. A pair of basioccipital tubercles diverge anterolaterally from the occipital condyle along the ventral surface. A pair of small concavities on the posterolateral surfaces of the tubercles possibly represent the insertions of the M. longissimus capitis transversalis cervicus. The basioccipital is thin and vaulted (except for a slight midline ridge) between the basioccipital tubercles. The region is overlapped ventrally by a thin posterior extension of the basisphenoid.

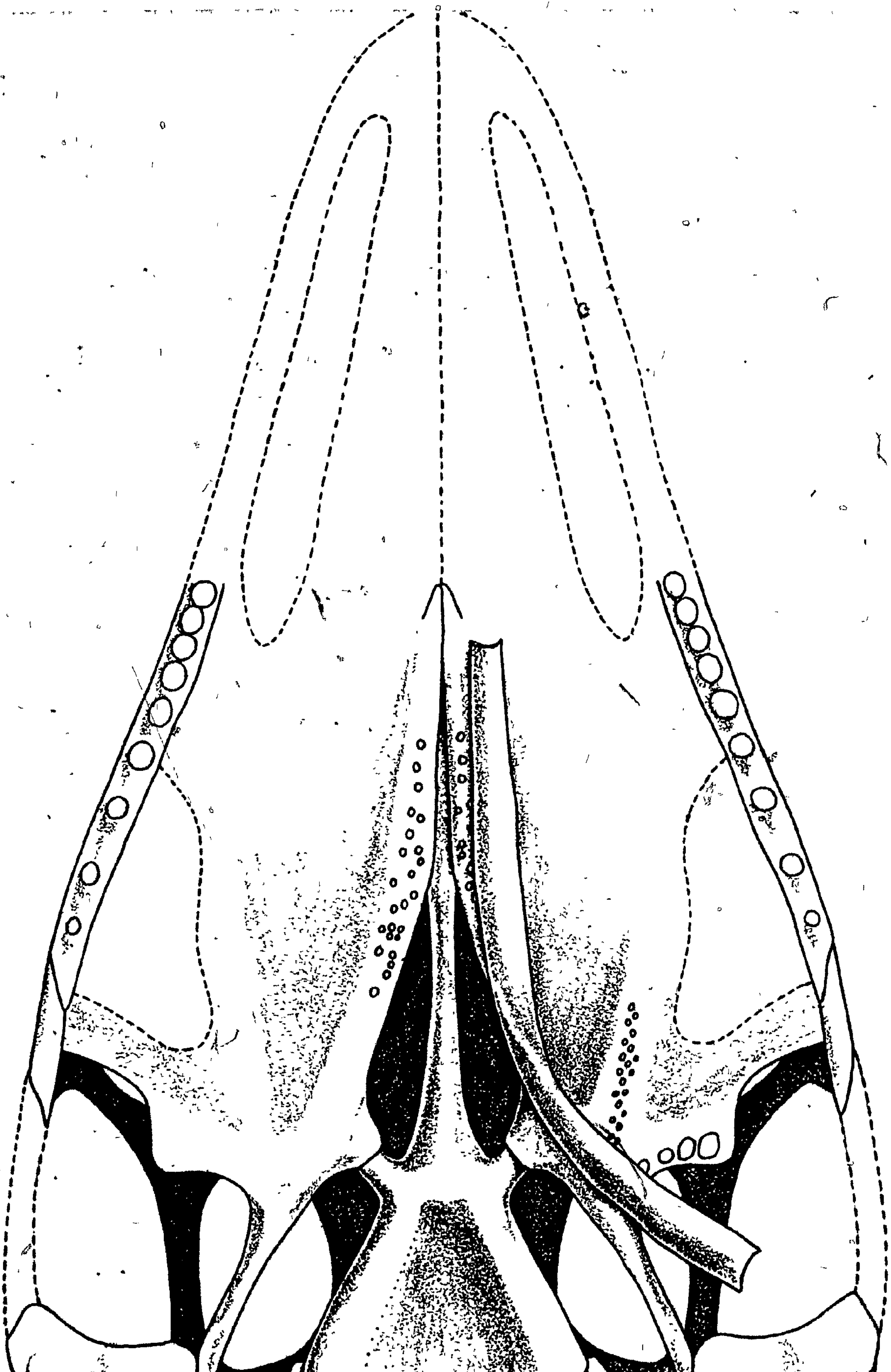
A partially exposed prootic can be seen in MNHN 1925-5-30 (fig. 27) in posterior view. Portions of two shallow grooves could have been for the vena capitis lateralis on the external surface and the subarcuate fossa on the posteromedial face.

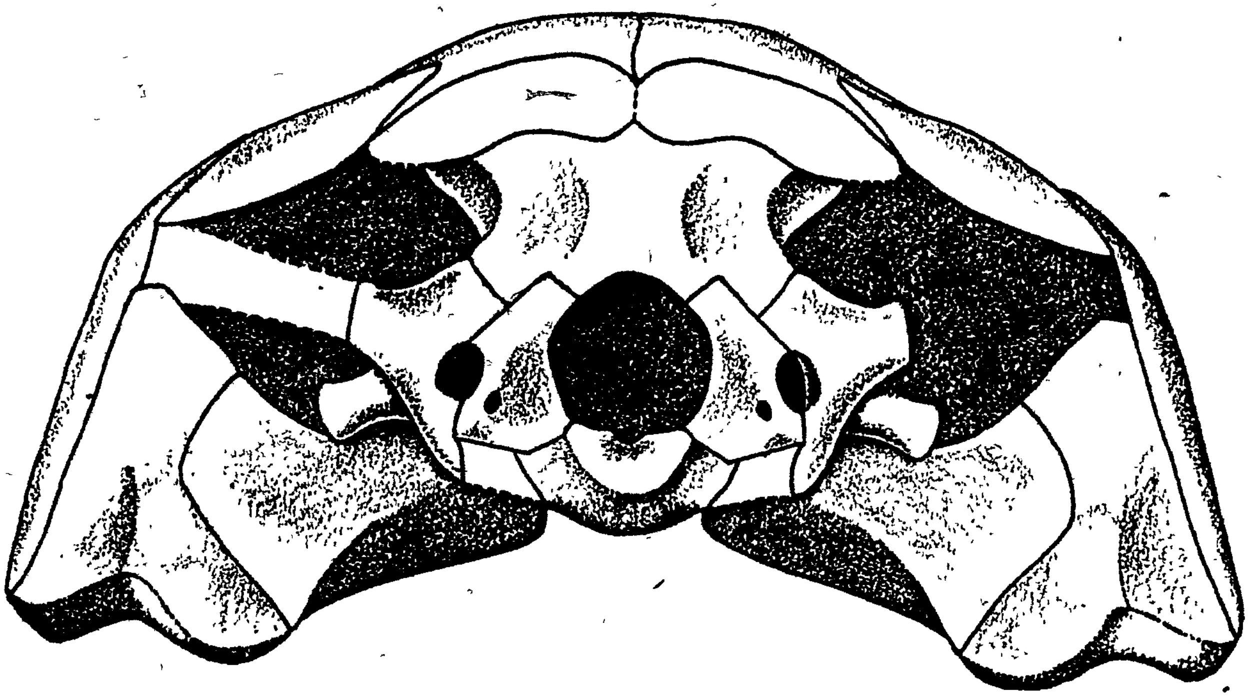
The opisthotic is visible in posterior view in MNHN 1925-5-30 (fig. 27) and MNHN 1908-32-99 (fig. 30), and in anterodorsal view in MNHN 1925-5-36 (fig. 29). The exoccipital sutures and lateral margin of the vagus foramen cannot be seen in any of the specimens but can be reconstructed from the exoccipital (fig. 28). As in Thadeosaurus, there is almost no development of an osseous paroccipital process in MNHN 1925-5-30. The distal end of the process is unfinished bone and would have been continued in cartilage. The paroccipital process would have been more extensive in large animals, and probably extended to the region where the supratemporal, squamosal and quadrate converge. A bony protuberence occupies a central position on the posterior surface of the opisthotic at the intersection of two low ridges The external surface of the bone is convex, whereas in most other reptiles it is concave posteriorly when viewed from dorsally or ventrally. This is further evidence indicating an anterior position for the quadrate in relation to the occipital condyle. There is a conspicuous but small foramen ventrolateral to the intersection

Figure 31. Hovasaurus boulei. Reconstruction of skull. a, dorsal view; b, lateral view; c, palatal view; d, occipital view. Scale = 1 cm.









of the opisthotic, exoccipital and basioccipital in all specimens that show this region. A branch of the fourth cranial nerve emerges from this region in crocodiles (Iordansky, 1973). The anterodorsal view of the opisthotic (fig. 29) shows broad sutural surfaces for the prootic and supraoccipital, and confirms that this bone enclosed portions of the posterior ampulla and posterior semicircular canal.

Stapes. The right stapes of MNHN 1908-32-99 (fig. 30) is protruding through the fragments of other bones. It is 2.8 mm in length, has a shaft diameter of less than 1 mm and expands distally to 1.5 mm. The footplate is partially obscured and cannot be measured. As in Youngina and most other primitive reptiles, the shaft is perforated by the stapedial foramen. There is no evidence of an osseous dorsal process. The distal end of the columella is unfinished bone, and must have been extended in cartilage to the quadrate.

Mandible. Details of only two bones of the mandible can be seen. The dorsal margin of the surangular is visible in one specimen (fig. 26). It is thickened medially into a ridge that forms the upper margin of the adductor foramen. Anteriorly this ridge is excavated dorsally for the coronoid. Posteriorly it becomes a prominent buttress where it supports a short, wide, posteromedially oriented facet that connects to the articular.

Piveteau (1926) noted that there was a short retroarticular process on the articular.

Hyoid. Hovasaurus has a pair of hyoid (ceratobranchial I) bones (figs. 27, 29; Piveteau, 1926, Pl. XIV, fig. 1) similar to those of Thadeosaurus (fig. 16), and many other primitive reptiles. The hyoid is a long, slender, curved rod of bone. The anterior portion is almost parallel to the longitudinal axis of the skull, and the posterior portion is inflected posterolaterally. The posterior end is cupped and probably had a cartilaginous extension (epibranchial I). The central region of the bone is somewhat flattened. A low ridge extends along the ventromedial surface of the anterior half of the bone, separating the insertion regions of two sets of hyoid musculature. The hyoid of MNHN 1925-5-30 is more than nine millimetres (2.4x) in length with a shaft diameter of about a millimetre.

Vertebrae

General. The vertebrae of Hovasaurus have notochordal centra (figs. 32, 34b) as do most primitive reptiles.

Piveteau counted 24 presacral vertebrae in one specimen of Hovasaurus (1926, Plate VII, fig. 3). A number of specimens, including MNHN 1908-32-99 (fig. 30) show that there are five cervical vertebrae, whereas others, such as MNHN 1908-32-24 (Piveteau, 1926, Pl. XIII, fig. 1) have 20 dorsals. This suggests that the presacral count is 25, and is confirmed by MNHN 1908-32-1 which has a complete presacral series. The number of presacral vertebrae falls within the range known for other genera of primitive eosuchians. Numerous specimens of Hovasaurus are known to have two sacral vertebrae (figs. 18, 19, 23). It would be easy to misinterpret the first caudal rib as a third sacral rib because it curves slightly anteriorly and almost touches the ilium. Most primitive reptiles have between fifty and seventy caudal vertebrae (Romer, 1956), but the total number is known in few eosuchians. Gow (1975) has shown only 30-35 caudals in his reconstructions of Youngina. However, none of the specimens he examined has a caudal series preserved in its entirety, so it can be assumed that the tail as reconstructed is too short. Carroll (1975a) estimated that the caudal count of Saurosternon approaches seventy. Fifty-six caudals are preserved in Kenyasaurus (Harris and Carroll, 1975) and 47 in Thadeosaurus (Carroll, 1981). In one specimen of Hovasaurus, MNHN 1908-32-58, the eighth to 53rd caudals are preserved, but do not include any distal caudals. SAM 9546 includes fourteen distal caudals, none of which are the terminal caudal. An estimate of seventy caudal vertebrae is probably conservative for Hovasaurus.

The presacral series can be divided into cervical and dorsal sections. Piveteau (1926) distinguished the cervicals by the absence of ribs. However, there are cervical ribs in Hovasaurus, which must have been inconspicuous in the specimen he was looking at. This specimen has been misplaced, and could not be relocated for study. Ribs have been disarticulated from the sterna in all known specimens of Hovasaurus, so relationship to the sternum cannot be used to define the dorsal region. The ribs of the sixth presacral segment are considerably longer than those of the fifth, and have the same basic form as more posterior ribs. For this reason, the sixth presacral vertebra is considered to be the first dorsal.

Cervical Vertebrae. The atlas-axis complex is preserved in ventral (fig. 27), dorsal (fig. 29) and lateral (fig. 30) views.

The proatlas is a small, paired element. The articulation with the exoccipital is at right angles to the articular facet for the atlas and is separated from it anteroventrally by a small area of finished bone (fig. 29). A small process on the dorsoposterior surface may represent a rudimentary neural arch.

The atlas centrum cannot be seen clearly in any specimens. It is preserved in dorsal view in MNHN 1925-5-36 (fig. 29) and possibly lateral view in MNHN 1908-32-99 (fig. 30). Unfortunately, the atlas-axis complex of the latter specimen is disarticulated, and the orientation of the atlas centrum is questionable. The close articulation between the centra of the atlas and axis suggests the former is being viewed in dorsal aspect. However, the bone exposed in this view is finished, suggesting that it is a lateral surface. The bone interpreted as the atlantal centrum in MNHN 1925-5-36 (fig. 29) is about 75% the length of the axial centrum, and shows articular facets on the dorsolateral surfaces for articulation with the neural arch. The atlantal neural arch is paired as in all primitive reptiles. There is a caudally directed spine, and an anterolateral facet that articulates with the proatlas (fig. 29). The atlantal intercentrum is large, about 50% the length of the axis centrum. The atlantal and axial intercentra meet ventrally, thereby excluding the atlantal centrum from the ventral margin of the vertebral column. In ventral aspect, the anterior margin of the intercentrum of the atlas is concave for its articulation with the occipital condyle. The centrum of the axis is relatively short, about sixty percent of the length of a dorsal centrum. More than half of the central length is excluded from the ventral margin of the vertebral column by the intercentra. There is a pronounced ventral keel (fig. 27), and the lateral walls of the centrum are concave. The suture between the axial neural arch and centrum is typical for most of the presacral column of primitive reptiles (fig. 30). The anterior edge of the neural spine curves strongly anterodorsally (figs. 29, 30). There is a pronounced facet for articulation with the neural arch of the atlas. The articular facet of the posterior zygapophysis is inclined only slightly from the horizontal plane. The facet on the neural arch for the attachment of the rib is inconspicuous in the specimens examined, and must have been minute. The neural spine is blade-like, with a thin anterior margin and a thick posterior edge (fig. 29). The axial intercentrum is a large element with a conspicuous mid-ventral, longitudinal ridge (fig. 27). In MNHN 1925-5-30, the bone is unfinished on the ventral midline. In lateral view, the intercentrum tapers dorsally and is not fused to the atlantal centrum in MNHN 1925-5-30 (fig. 27) and MNHN 1908-32-99 (fig. 30).

The centrum of the third cervical is longer than that of the axis, but is only 75% the length of the average dorsal. The rib facet is found near the front of the neural arch. It is relatively small, oval in shape, and faces ventrally. The transverse process is weak, and is located ventral to the zygopophyses. The neural spine curves posteriorly in large animals (MNHN 1925-5-49) and is relatively wide and anteroposteriorly short distally (fig. 29). The third intercentrum is the last one ossified in immature specimens. The midventral ridge is prominent anteriorly, and much weaker posteriorly. A slight posteroventral protuberance would have fit snuggly into a depression at the anterior end of the ventral ridge of the third centrum (fig. 27). This suggests that the third intercentrum and centrum were firmly attached and functioned as a unit.

The centrum of the fourth vertebra is about 85% the length of a dorsal centrum. The transverse process has become more prominent, and the neural spine is approximately two thirds the length of one of the dorsal spines. The transverse process is strengthened by strong anteroventral and posteroventral ridges, and a weaker dorsal process (MNHN 1925-5-49).

The fifth cervical is transitional in morphology between the more anterior cervicals and the dorsals. The centrum is almost the same length as a dorsal centrum. The transverse process has a longer articular facet for the rib, and is oriented more laterally. The neural spine is almost 75% the length of the neural spine of a mid-dorsal vertebra.

Dorsal Vertebrae. The basic structure of a notochordal centrum is hourglass shaped, constricted at the centre and expanding anteriorly and posteriorly into round, hollow ends that form the intervertebral articulations. The narrow waist is strengthened ventrally by a longitudinal ridge of bone. When viewed laterally, there is little curvature along the ventral ridge. The ventral edge of this ridge tends to be developed into a sharp keel in the cervicals, but becomes well rounded in the dorsals.

The width of a dorsal centrum is approximately 83% its length (Table 5), whereas the height of the centrum is only 65% the length.

There is a pair of strong dorsolateral ridges for the attachment of the neural arch. The centrum is widest dorsally across the ridges, and tapers ventrally. As in pelycosaurus (Romer and Price, 1940) and most other primitive reptiles, the dorsal part of each side of the posterior rim of the centrum is beveled so that the surface faces somewhat dorsolaterally as well as posteriorly (fig. 32). The anterior edge has complimentary dorsolateral expansions that articulate with the beveled surface of the adjacent centrum. The ventral rims of both anterior and posterior ends of the centrum are beveled for the intercentra.

The articulation for the rib does not appear to extend from the neural arch to the centrum in the dorsals. A strong ridge extends posterodorsally on the centrum to support the ventral edge of the transverse process (fig. 32). In large specimens, this ridge is longitudinally striated, presumable for ligaments that hold the rib in position.

The centrum forms the floor and part of the lateral walls of the neural canal. Between the supporting buttresses for the neural spine, the centrum is deeply excavated in young specimens, and the hourglass shape of the notochordal sheath can be made out clearly (figs. 20, 24). In more mature specimens, the region is only shallowly excavated, and there tends to be distinct pits close to the centre of the longitudinal axis. In adult specimens, it appears that the bottom of the neural canal was nearly flat when viewed laterally (fig. 34b).

The neural arch does not co-ossify with the centrum until late in life. In the smallest specimens, the right and left halves of each neural arch disassociated after death.

From the anterior margin of the centrum, the ventral edge of each pedicel of the neural arch curves posteroventrally to a point approximately one third the longitudinal distance of the centrum from the anterior edge of the centrum (figs. 19, 20, 24). Posterior to this point, the ventral edge curves posterodorsally until it reaches the dorsal limit of the centrum. The suture cannot be seen in large specimens (figs. 22, 32).

The anteroventral corner of each pedicel seems to reach the anterior edge of the centrum, and could have taken a limited part of the intervertebral articulation. Between this point and the base of the anterior zygopophysis, the anterior margin of the pedicel is shallowly concave, and forms the posterior margin of the intervertebral opening. The posteroventral corner of the neural arch is well forward from the posterior limit of the centrum, curves anterodorsally and then posterodorsally to the posterior zygopophysis. This rim forms the anterior margin of the intervertebral opening.

There is an extra intervertebral articulation between the pairs of zygopophyses. The terms zygosphene and zygantrum are inappropriate for these articulations for a number of reasons. In the sense used by Romer (1956), a zygosphene bears slanting articular surfaces on either side of an anteriorly projecting process. The accessory articulation is variable in Hovasaurus, but never bears ventrolaterally oriented facets, and is most prominent on the posterior edge of the neural spine.

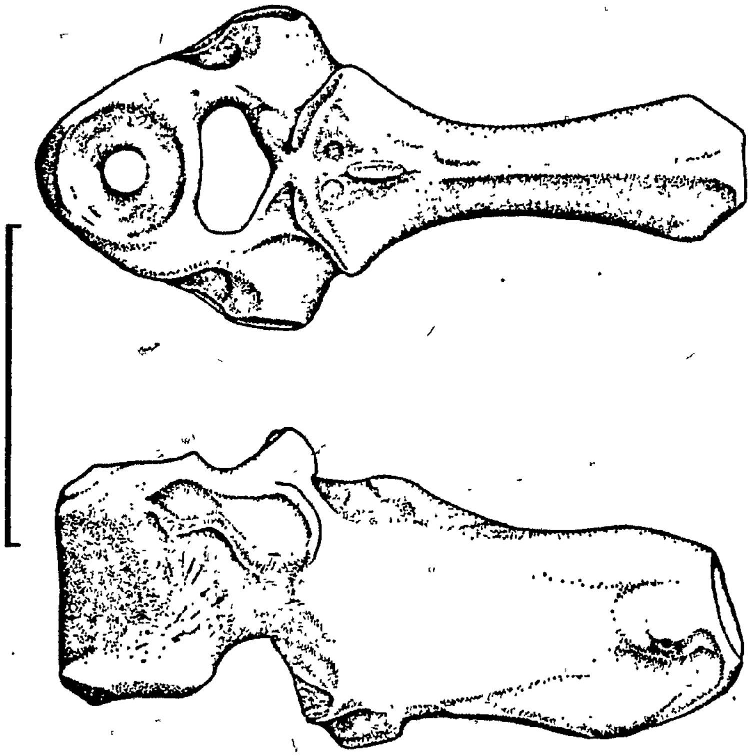
The accessory articulation is variable throughout the vertebral column (fig. 32), and apparently in different individuals as well. It could be that some of this variability is age specific, but more probably is just individual variation. However, throughout the vertebral column there is some form of contact of the neural spines, and in some cases this contact can extend vertically far up the neural spine. Because most specimens are split along the midline, details of the midline processes are poorly preserved in general. It is not possible to follow the changes undergone through the column for any single specimen.

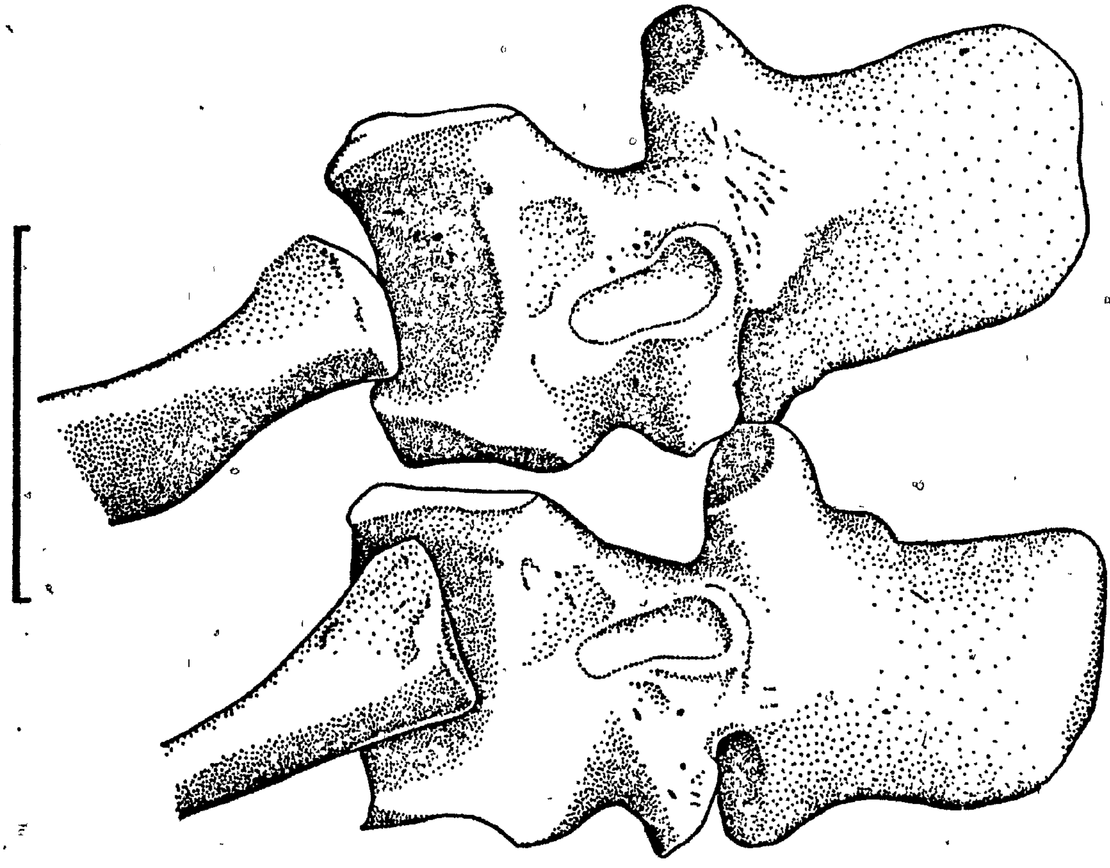
In the cervical region, it appears that the neural spines are in contact along the midline near the base of the neural spines, but there is no specialized articulation in this region.

There is a distinct process on the posterior surface of the neural spine in the dorsals. It does not seem to have extended caudally beyond the posterior limit of the posterior zygopophyses in the anterior dorsals. In the sixth presacral of SAM 9463, the process is represented by a low ridge that does not extend dorsally or caudally beyond the zygopophyses. The process is prominent in the ninth presacral of SAM 9461, but lies below the dorsal limit of the posterior zygopophyses. The size of the process continues to increase progressively, and is equally well developed in the eleventh and twelfth vertebrae of MNHN 1908-32-59. The largest rectangular process observed was in about the thirteenth presacral vertebra of SAM 9463 (fig. 32). It is relatively long dorsoventrally, extending dorsally above the articular surfaces of the zygopophyses. The rectangular process extends farther caudally than the posterior zygopophyses. Generally in more posterior dorsals, the process is reduced to a low ridge. By the eighteenth presacral of MNHN R146a, it is very small. The process seems to persist throughout the dorsal series for there is a minute nubbin of bone on the midline of the posterior surface of the neural spine of the 25th presacral of MNHN 1908-21-19.

There is a deep pit on the posterior surface of the neural spine on each side of the rectangular process in the anterior

Figure 32. Hovasaurus boulei, dorsal vertebrae. Left, SAM 9463, partially restored, posterior and lateral views of 13th dorsal vertebra; right, MNHN 1908-32-60, 16th and 17th dorsal vertebrae. Scale = 1 cm.





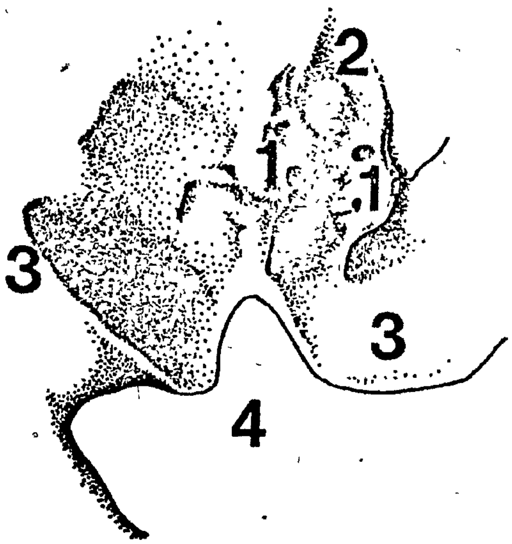
dorsals. This pair of pits (fig. 32) is close to the ventral level of the accessory process. The pits are separated by a low ridge that is continuous with the rectangular process dorsally, and which widens out ventrolaterally into a ridge joining the posterior margins of the posterior zygopophyses

In most vertebrae, a prominent ridge extends along the midline of the anterior surface of the neural spine. Near the base of the neural spine, this ridge is anterior to the posterior limits of the anterior zygopophyses. In the regions of the vertebral column where the neural spine of the proceding vertebra is extended posteriorly by a rectangular process, there had to be some way to accommodate the process or else the centra would not have touched. Most vertebrae are exposed only in lateral view, and the anterior view of this midline ridge cannot be seen. Fortunately it can be seen in several specimens. In an anterior dorsal of a juvenile specimen (MNHN 1925-5-28), there is a longitudinal depression along the crest of the anterior midline ridge. This depression is the right size and shape to accommodate the posterior rectangular process of the preceding vertebra. In a more mature specimen, MNHN 1908-32-24 (fig. 33), the complexity of these articulations is revealed. There is a distinct pit at the base of the anterior midline ridge of the twelfth presacral. It is higher than it is wide, and is large enough for the posterior rectangular process of the eleventh presacral to fit inside. Ventrolateral to the depression there are two bony protuberances that would have inserted into the pits ventrolateral to the posterior rectangular process of the preceding vertebra. Ventromedial to these protuberances is a shallow depression into which fits the ventral expansion of the ridge that is continuous dorsally with the rectangular process. The complex of anterior midline depressions and protuberances is symmetrical as a unit, but offset to the left of the midline.

In more posterior dorsals, a prominent process, the anterior midline process of the neural spine, develops dorsal to the contact with the posterior rectangular process of the preceding vertebra. The anterior midline process seems to reach its maximum size in the mid dorsals. Here it extends as far anteriorly as the anterior zygopophyses, and looks like a prominent tubular process. In the eighteenth presacral vertebra of MNHN 1908-32-24 there is a circular depression dorsal to a small posterior midline process for articulation with the anterior midline process of the nineteenth. Posterior to the 21st presacral, the anterior midline process rapidly diminishes in size, and has disappeared by the 24th presacral in MNHN 1908-32-24.

The contact between the bases of the neural spines along the midline is variable in the most posterior presacrals. The posterior midline ridge of the neural spine of the 25th presacral

Figure 33. Hovasaurus boulei, MNHN 1908-32-24. Accessory articulations on anterior surface of 12th neural spine. 1, processes; 2, pit; 3, anterior zygopophyses; 4, neural canal. X9.


2
1
1
3
3
4

of MNHN 1908-32-24 is divided ventrally by a depression into which fits the ventral end of the anterior midline ridge of the first sacral. The contact is different in MNHN 1908-21-19 where a minute posterior midline process of the 25th presacral articulates with a minute, flat facet at the base of the anterior midline ridge of the first sacral.

The presence of accessory articulations along the midline of the neural spines of presacral vertebrae is clearly a derived character that is not found in ancestral protorothyridids (Carroll and Baird, 1972), nor in most lines of eosuchians. In reexamining the type specimen of Youngina capensis, it was discovered that accessory articulations are present (fig. 13a). Kenyasaurus (fig. 15e) seems to have an anterior midline process of the neural spine in the mid and posterior thoracics, as does Thadeosaurus. Tangasaurus, although badly preserved, seems to show the same adaptation.

In juvenile specimens the anterior outline of the neural arch between the anterior zygopophyses and the posterior outline in the same plane are deeply embayed medially. This occurs because the ossification of the midline ridges cannot begin until the two halves of the neural spine coosify into a single unit.

The anterior zygopophyses are supported by a buttress oriented dorsomedially and slightly anteriorly from the base of the transverse process. The buttress of each side is joined by a thin shelf of bone above the neural canal. The articular surfaces extend onto this shelf, but do not meet. They are separated anteriorly by a medial notch, and posteriorly by the ventral end of the anterior midline ridge of the neural spine (fig. 33).

The posterior zygopophysis is supported by a strong ridge that extends dorsomedially, and to a lesser extent anteriorly, to the neural spine. The dorsolateral surface of this ridge is convex along its longitudinal axis, but concave where it meets the neural spine and near the posterolateral tip of the zygopophysis. In most dorsal vertebrae of mature animals, there is a narrow shelf of bone that connects the posterior zygopophyses ventromedially. The posterior edge of the articular surface is almost straight and perpendicular to the midline of the vertebral column in the anterior and mid dorsals. The articular surface is widest near its ventromedial limit and tapers as it extends dorsolaterally. The articular surface, on the average, is 60% as long anteroposteriorly as it is in the plane perpendicular to it. In the most posterior dorsals, the articular surface is diamond shaped with its widest expansion about half way between the lateral and medial borders. In end view (fig. 32), the ventrolateral outline of the zygopophysis is convex medially, but becomes concave laterally. The degree of curvature is variable throughout the presacral column.

Because of the curvature of the articular surfaces, it is difficult to determine the angle that the articular surface has been rotated from the horizontal. This is particularly true in the cervicals and anterior dorsals where the medial convex region is broad and the curvature is gentle. If a line is drawn from the ventromedial edge of the articular surface to the dorsolateral edge, this line is about 35° on the average from horizontal, but can be as high as 45° in the dorsals of some specimens. In the posterior dorsals, the average inclination to the horizontal is somewhat lower -- about 25°. In Youngina (Gow, 1975), the inclination is less than 30° in the anterior dorsals, whereas the inclination in most other primitive reptiles is closer to the condition seen in Hovasaurus.

The longest neural spines of the presacral column are found in the vicinity of the nineteenth to 22nd vertebrae. In large specimens, the neural spines in this region can be more than 50% greater than the maximum length of the centrum (Table 5). The shortest neural spine of the vertebral column is that of the axis, which in MNHN 1908-32-1 is less than half the height of the longest dorsal neural spine. The height of the neural spine increases gradually between the axis and mid dorsals, and then decreases in the posterior dorsals and sacrals.

Among closely related genera, the presacral neural spines of Youngina and Kenyasaurus are relatively low, while those of

Thadeosaurus and Tangasaurus are higher but still not as well developed as the neural spines of Hovasaurus.

The neural spines are constricted anteroposteriorly above the level of the midline processes of the neural spine. In mature specimens there is a slight expansion dorsal to this level. The maximum anteroposterior length of a neural spine of the mid and posterior dorsals is approximately 80% the greatest length of the corresponding centrum. Above this expansion, the neural spine tapers negligibly and ends in a plateau of unfinished bone (fig. 32).

The lateral thickness of the neural spines varies throughout the column. The neural spines of posterior dorsals, sacrals and caudals tend to be relatively thin. In the posterior dorsals of large animals (central length greater than 8 mm), the distal width of the spines is consistently almost three millimetres. The neural spines of the anterior and mid dorsals are greatly thickened distally by lateral ridges that end dorsally in mammilary processes. The width of the neural spine of the tenth presacral of MNHN 1908-32-59 is 4.5 mm, more than half the length of the associated centrum.

Sacral Vertebrae. The sacral centra are the same length as the posterior dorsals. In the two sacral vertebrae, the large articulations for the sacral ribs are found on both the neural arches and the centra. Because of these massive articulations, the ventral ridge of the centrum is pronounced. The average ratio of sacral spine height to maximum dorsal spine height for six specimens is .85. Neural spine length increases in the second sacral, and continues to increase through the proximal caudals. The sacrals do not coossify into a single unit in any of the specimens examined.

<u>Caudal Vertebrae</u>. The anterior caudal centra are either the same length as the dorsals, or are slightly shorter. The reduction in the length of the caudal centra is gradual. In the series of 45 caudals of MNHN 1908-32-58, the distal centra are only 10% shorter than the proximal centra.

The shape of a caudal centrum is different from that of a dorsal centrum. The anterior and posterior edges, as seen in lateral view, are nearly straight (fig. 34). The centrum is longest dorsally, and noticeably shorter along the ventral margin. The ventral edges of the rims are beveled where they articulate with the haemal arches. The width of the centrum is greatest dorsally, but tapers quickly below the level of the notochordal canal.

The midline ventral ridge is conspicuous in the anterior caudals, but becomes less prominent posteriorly, and disappears towards the end of the rib-bearing series. A pair of ventrolateral ridges appear on the centra of the rib-bearing caudals, become prominent by the end of the rib-bearing series, and continue on the remaining caudals.

The articular facets for the caudal ribs are found mainly on the centra, but also extend onto the neural arches (fig. 21).

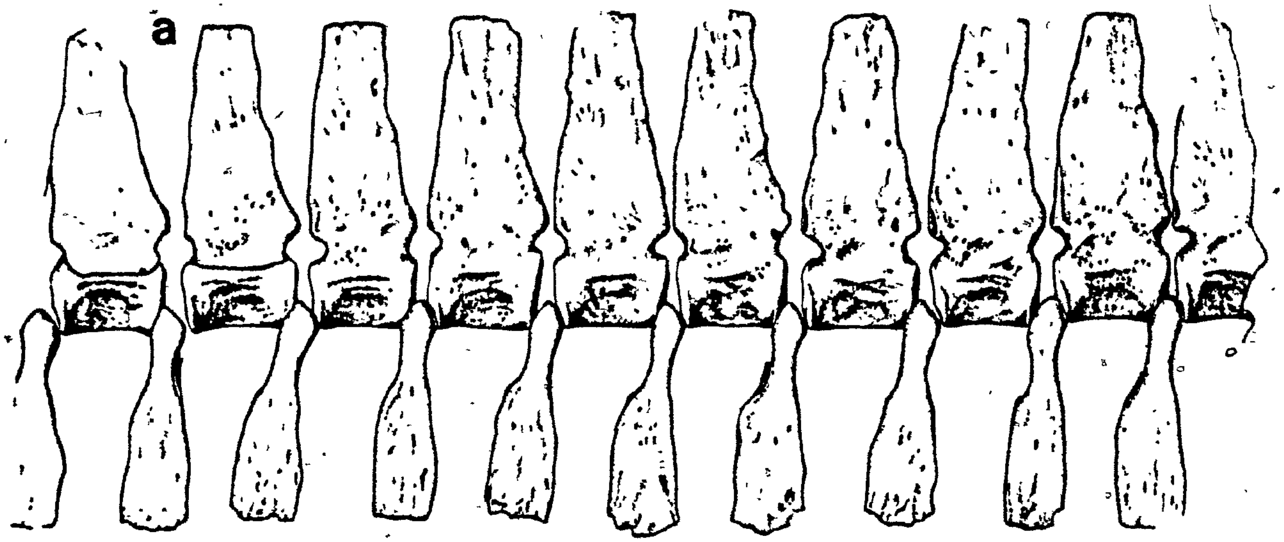
The ventrolateral outline of the pedicel of the neural arch is essentially the same in the cervical, dorsal, sacral and proximal caudal vertebrae. The outline changes in the anterior caudals however, and before the end of the rib-bearing series has taken on a more symmetrical form (fig. 21). The ventral margin is almost horizontal in lateral view, but close to the centre of the centrum there is a ventral process on each pedicel that fits into a corresponding socket in the centrum. The lateral surface of this process forms a relatively small part of the sutural facet on the vertebra for the caudal rib. The base of the pedicel of the neural arch does not take part in the intervertebral articulation.

The caudal neural spine is one of the most highly specialized features of Hovasaurus. It was tall to maximize force that the tail would produce in the water by its lateral undulations. Of the specimens examined, the highest ratio of caudal neural spine height to length of associated centrum was 2.7, and the ratio of maximum neural spine height to average length of a dorsal centrum is at least 2.5. In comparison, the same ratio of Tangasaurus is 1.35. The neural spines of the tail of Hovasaurus grow with high positive allometry (Table 5). Because the coefficient of allometry is higher in the caudals (1.43) than in the dorsal neural spines (1.34), the ratios of lengths of caudal neural spine to dorsal neural spine are 1.07 in juveniles and 1.19 in large animals. At all ages, the neural spines of the mid caudals are higher than the tallest preasacral neural spines.

The neural spine of the first caudal is taller than that of the second sacral, but is shorter than the highest neural spine of the presacral series. The second caudal has a neural spine taller than that of the first caudal; and, in all but the smallest specimens, taller than any dorsal spines. Neural spine height continues to increase from the third caudal to the mid caudal region. In MNHN 1908-32-58 and MNHN 1908-32-64/73, the tallest neural spines are those of the twelfth to 24th caudals. Neural spine height diminishes by seven percent over the next ten caudals (MNHN 1908-32-64/73). No specimen shows a complete caudal series. However, on the basis of morphological comparisons with MNHN 1908-32-58, it can be concluded that the first caudal preserved in SAM 9456 could not be more proximal than the 50th segment. In this region of the tail, neural spine height is reduced by 35% over the series of thirteen caudals preserved in SAM 9456. The height of the last neural spine preserved, estimated to be about the 63rd caudal, is 1.3 times the length of the associated centrum.

Figure 34. <u>Hovasaurus</u> <u>boulei</u>, caudal vertebrae. a, MNHN 1908-21-11, series of mid-caudal vertebrae (right lateral view); b. SAM 9462, mid-caudal vertebra, broken open to show neural and notochordal canals; c, SAM 9456, distal caudals, approximately 58th-63rd. Scale = 1 cm.

a



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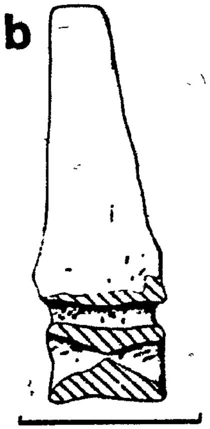

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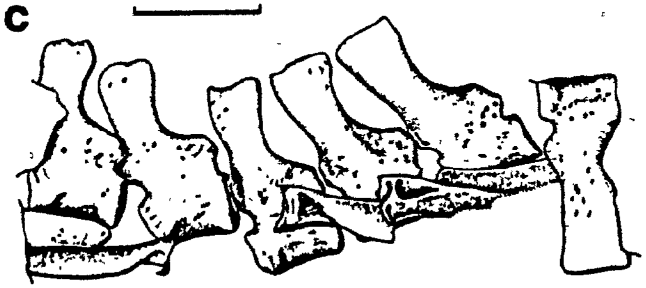


Three regions can be defined in the tail on the basis of morphology of the neural arch and spine. Proximal caudals can be defined by the presence of zygopophyses, but there is no sharp distinction between the mid caudal and distal caudal regions.

As in more anterior vertebrae, the posterolateral margin of the neural arch forms the largest portion of the border of the intervertebral opening in the proximal caudals. Proximal caudals (figs. 18d, 19, 20, 21, 24) have distinct zygopophyses. In MNHN 1908-32-64/73, the most caudad pair of posterior zygopophyses is found on the fourteenth caudal and the last anterior zygopophyses are on the fifteenth caudal. There is a pronounced anterior, midline ridge at the base of the neural spine that contacts the base of the neural spine of the preceding vertebra in a simple butt joint. Above this contact, the anterior margin of the neural spine curves posterodorsally, the amount of curvature decreasing until the margin is almost vertical distally. The posterior margin of the neural spine is almost straight, and is posterior to the centrum. The anteroposterior length of the distal end of the neural spine is about 70% the length of the centrum, and double the lateral width of the neural spine.

The mid caudals (figs. 34a, b) are more symmetrical in lateral view than the anterior and distal caudals. In contrast with the presacrals, sacrals and proximal caudals, the anterolateral margin of the neural arch forms as much of a border of the intervertebral opening as the posterolateral margin of the preceding neural arch does. The neural spines continue to articulate above the neural canal. This articulation, laterally wide at the base and tapering dorsally, can extend as much as 20% the height of the neural spine. In lateral view, the articular surface of the anterior midline ridge tends to be slightly convex, and the posterior margin tends to be concave. The neural spine tapers distally, and becomes laterally thin. The anterior margin of the neural spine tends to be slightly concave in lateral view and the posterior margin tends to be slightly convex. The centre of the neural spine is only slightly posterior to the centre of the centrum.

The intervertebral articulation at the base of the neural spine persists in the distal caudals, and can make up to 25% of the height of the neural spine. Above the midline articulations, the margins of the neural spine are concave in lateral view, but the curvature is more pronounced on the anterior margin (fig. 34c). The distal end expands to about 65% the length of the associated centrum. The centre of the neural spine lies over the posterior quarter of the centrum. The terminal caudals are presently unknown.

Intercentra

Intercentra ossify early in the life of Hovasaurus in the first three cervicals and in the caudals. It would appear that the remaining intercentra remained cartilaginous until the animal was more than half grown. In mature animals, they are present throughout the vertebral column.

The atlantal intercentrum is the largest of the series. Ossified intercentra of mature specimens of Hovasaurus (fig. 23) are long in an anteroposterior direction, and can be up to 45% of the length of a dorsal centrum in large animals. They broadly overlap the ventral surfaces of the adjacent centra, and extend dorsally more than halfway up the outer rims of the centra. The shape of the intercentra is basically the same as that of all primitive reptiles. The ventral surface is convex, both longitudinally and transversely.

Normal intercentra are found in the sacral segments (MNHN R146), and in association with the first two caudals (MNHN 1908-32-77). The third caudal vertebra is preceded by a crescentic intercentrum with a pair of parallel plates of bone projecting posteroventrally (MNHN 1903-21-7, MNHN 1908-32-77, SAM 9460). These plates do not meet distally, and each plate is less than two thirds the length that is required to enclose the haemal canal. The fourth caudal section is the first to bear a complete chevron.

There is no indication of separate centres of ossification in the chevrons of Hovasaurus such as seen in Sphenodon (Howes and Swinnerton, 1901). Furthermore, the crescentic basal portion of the chevron is found through the tail (figs. 19, 20, 21, 24, 34c).

In lateral view, the chevron is pointed proximally, with two facets for articulation with the adjacent centra. The haemal arch is oriented slightly posteriorly as well as ventrally (fig. 34a). In young specimens, the haemal canal occupies at least half of the dorsoventral length of the chevron in the proximal part of the tail. In more mature specimens, the haemal spine makes up a relatively larger percentage of the total length of the chevron. The dimensions of the haemal canal grow with negative allometry, whereas the haemal spine exhibits positive allometric growth (Table 5). Regardless of the age of the animal, the haemal canal decreases in size posteriorly in the tail. This feature was found to be useful in determining whether isolated series of caudal vertebrae were from proximal or distal parts of the tail.

The haemal spine expands posteriorly and to a lesser extent anteriorly from the haemal arch to form a large, distinctive plate of bone with a vertical axis (figs. 19, 20, 21, 34a). The distal expansion of the haemal spine has the same anteroposterior length as the distal end of the neural spine of the same segment.

In mature specimens, the haemal arch and spine are the same dorsoventral length (2.6x) as the neural arch and spine of the associated vertebra. This relationship is consistent throughout the tail.

Ribs

Ribs are present in all but the atlantal segment of the presacrum, in both sacrals, and the proximal caudals.

The second rib is short, somewhat less than the length of the associated axial centrum (figs. 27, 30), and tapers distally to a point. There are distinct tubercular and capitular heads (MNHN 1925-5-49), the latter extending to the intercentrum. The rib of the third cervical is longer than its centrum, recurved (fig. 30) and dichocephalous (fig. 27; MNHN 1925-5-49). The fourth cervical rib is one third longer than the associated centrum and about twice the length of the axial rib. The capitular head is still distinct but is very small relative to the tubercular head (MNHN 1925-5-49). There is a flange extending from the tubercular head along the outside curve of the rib shaft (fig. 30). The next rib is apparently holocephalus, with a continuous, dumbell-shape articular surface that articulated with the transverse process of the fifth cervical (MNHN 1925-5-49). The fifth rib is approximately double the length of the associated centrum, is not as strongly curved as the more anterior cervicals, but still tapers to a point distally.

The rib of the sixth vertebra is the first dorsal. The head has a larger circumference than any other region of the rib, and is distinct in outline from more anterior ribs (fig. 30). The articular surface is continuous, but is constricted in the centre so that capitular and tubercular portions of the head can be distinguished. This pattern is found in all but the last dorsal. The primitive condition, as exemplified by *Hylonomus* (Carroll, 1964), is to have a notch separating the capitular and tubercular heads. The shaft of the sixth rib of *Hovasaurus* is almost straight, and is more than five times the length, *x* of the dorsal centrum in MNHN 1908-32-1.

The anteroposterior length to height ratio of the proximal rib articulation increases from 1/3 in the anterior dorsals to more than ½ in the posterior dorsals.

There is a progressive increase in length from the sixth to tenth dorsal ribs. The eleventh to seventeenth ribs are approximately 7.5*x*, measured along the outside of the curvature. The maximum rib length is 7.8*x* in *Acerosodontosaurus* (Currie, 1980), and 7.0*x* in *Thadeosaurus* and *Tangasaurus*. In *Hovasaurus* there is a gradual reduction in length of more posterior ribs up to the 21st, and a rapid reduction in length from the 22nd to 25th dorsals (figs. 19, 23). The last dorsal rib is only about 1.5*x* in length.

The anterior dorsal ribs are curved for the proximal third of the shaft, and almost straight distally. Ribs of the mid and posterior dorsal regions are curved throughout their length, suggesting that Hovasaurus was a relatively broad bodied animal like Acerosodontosaurus (Currie, 1980), Youngina (Gow, 1975), Kenyasaurus (Harris and Carroll, 1977) and Tangasaurus (fig. 17c). The 25th rib does not curve ventrally, but extends laterally and curves slightly anteriorly (fig. 23, MNHN R146, MNHN 1908-32-4, MNHN 1908-32-24, MNHN 1908-32-67).

The dorsal ribs of Hovasaurus juveniles are indistinguishable from those of other younginoid genera. The ribs of the adults are visibly pachyostotic (fig. 22), although not to the degree seen in Champsosaurus and Mesosaurus. The distal expansion of the twentieth dorsal rib of a juvenile (MNHN 1908-21-2/7) is .30x whereas in MNHN 1908-32-67, an adult, the diameter of the same rib is .43x. The maximum shaft diameter of a dorsal rib in Tangasaurus is .30x. Pachyostosis is more discernible in the posterior dorsals, which are banana-shaped ribs in adults. The maximum shaft diameter is 12% the length of the 23rd rib in a juvenile (MNHN 1908-32-21) and 16% in an adult (MNHN 1908-32-67).

The distal ends of the sixth to 24th ribs are concave and probably continued in cartilage. It is possible that the cartilaginous extensions of the eleventh to fifteenth ribs attached directly to the sternum, while an unspecified number of pairs of more posterior ribs would have been connected to the sternum by cartilaginous mesosternal elements.

The sacral ribs have the same shape and orientation as most primitive reptiles. The proximal suture covers most of the lateral surface of the centrum and extends onto the neural arch. A small, anteroventral extension of the proximal sutural surface does not reach the intercentrum, but represents the primitive capitular head. The first sacral rib extends laterally, ventrally and anteriorly and meets the ilium in a broad contact. The distance between the first sacral vertebra and the ilium is 1.6x. The diameter of the shaft is .5x at its narrowest point, and anteroposteriorly longer than the centrum at the distal end. Most of the distal expansion is anteroventral to the longitudinal shaft of the sacral rib.

The orientation is almost the same in the second sacral (MNHN 1908-32-24), although it curves anteriorly to a lesser extent. The head of the second sacral is larger than that of the first sacral, and the measurement between the proximal and distal sutures is five to ten per cent greater than the shaft length of the first sacral rib (figs. 19, 24, MNHN R146). The distal expansion is flat and bladelike, and is anteroposteriorly shorter than the centrum. The nature of contact between the distal ends of the sacral ribs cannot be seen in any of the specimens examined. The distal end does not bifurcate as it does in Youngina (Gow, 1975).

The number of pairs of caudal ribs is variable in Hovasaurus. There are a minimum of ten pairs (MNHN 1908-32-29) and a maximum of twelve (MNHN 1908-21-5). Ten pairs of caudal ribs are preserved in MNHN 1908-32-73, but there are facets on the eleventh caudal vertebra for another caudal rib pair. In MNHN 1908-32-58, the tenth caudal rib is minute, and resembles a smaller projection of bone on the eleventh caudal vertebra. However, the eleventh is clearly an outgrowth of the vertebra, does not have a separate centre of ossification, and is therefore not a rib. Ten pairs of ribs are preserved with MNHN 1908-32-77 (fig. 21), but articular facets on the eleventh and twelfth caudal vertebrae show that the animal had twelve pairs of caudal ribs. There is a pronounced transverse process on each side of the thirteenth caudal vertebra, and a smaller process on the fourteenth.

It is difficult to distinguish fused caudal ribs from transverse processes in the mid caudal region of many primitive reptiles. The fact that all but one or two of the lateral processes of the caudal vertebrae of Hovasaurus are true caudal ribs suggests that the majority of such processes in the tails of other eosuchians are caudal ribs rather than transverse processes. For simplicity, all lateral processes of caudal vertebrae will be referred to as caudal ribs.

The anterior caudal ribs are constricted distal to the vertebral suture, but expand distally into horizontal plates of bone in Hovasaurus (figs. 19, 20, 21, 24). A distinct proximoventral groove divides the rib head into capitular and tubercular portions (figs. 20, 21). The distal ends of the first two caudals are concave regions of unfinished bone in all but the largest specimens. The remaining caudal ribs taper distally. The first four caudals extend 1.5x laterally, and the first has a maximum expansion of approximately .75x.

The proximal caudals of Thadeosaurus, Kenyasaurus and probably Tangasaurus have slender, tapering caudal ribs, as in all other eosuchians.

The first caudal rib of Hovasaurus is oriented slightly anteriorly as well as laterally (figs. 20, 21, 24), and seems to almost reach the ilium. The unfinished bone on the distal end suggests there was a cartilaginous or at least ligamentous attachment with the distal end of the ilium. It probably represents the first stage of incorporation of a third rib into the sacrum, and is present in Tangasaurus (figs. 17a, b) and Kenyasaurus (Harris and Carroll, 1977).

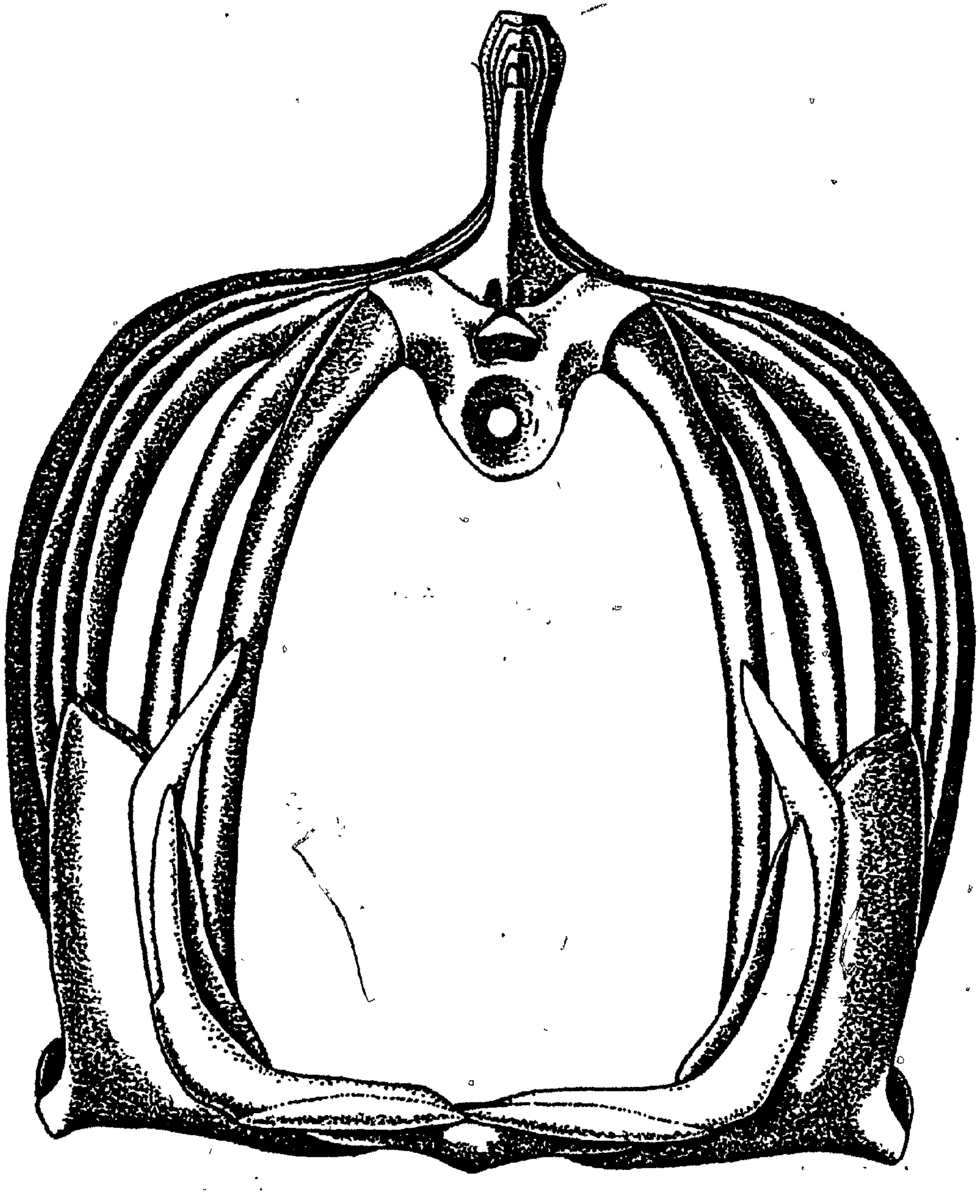
Pectoral Girdle and Limb

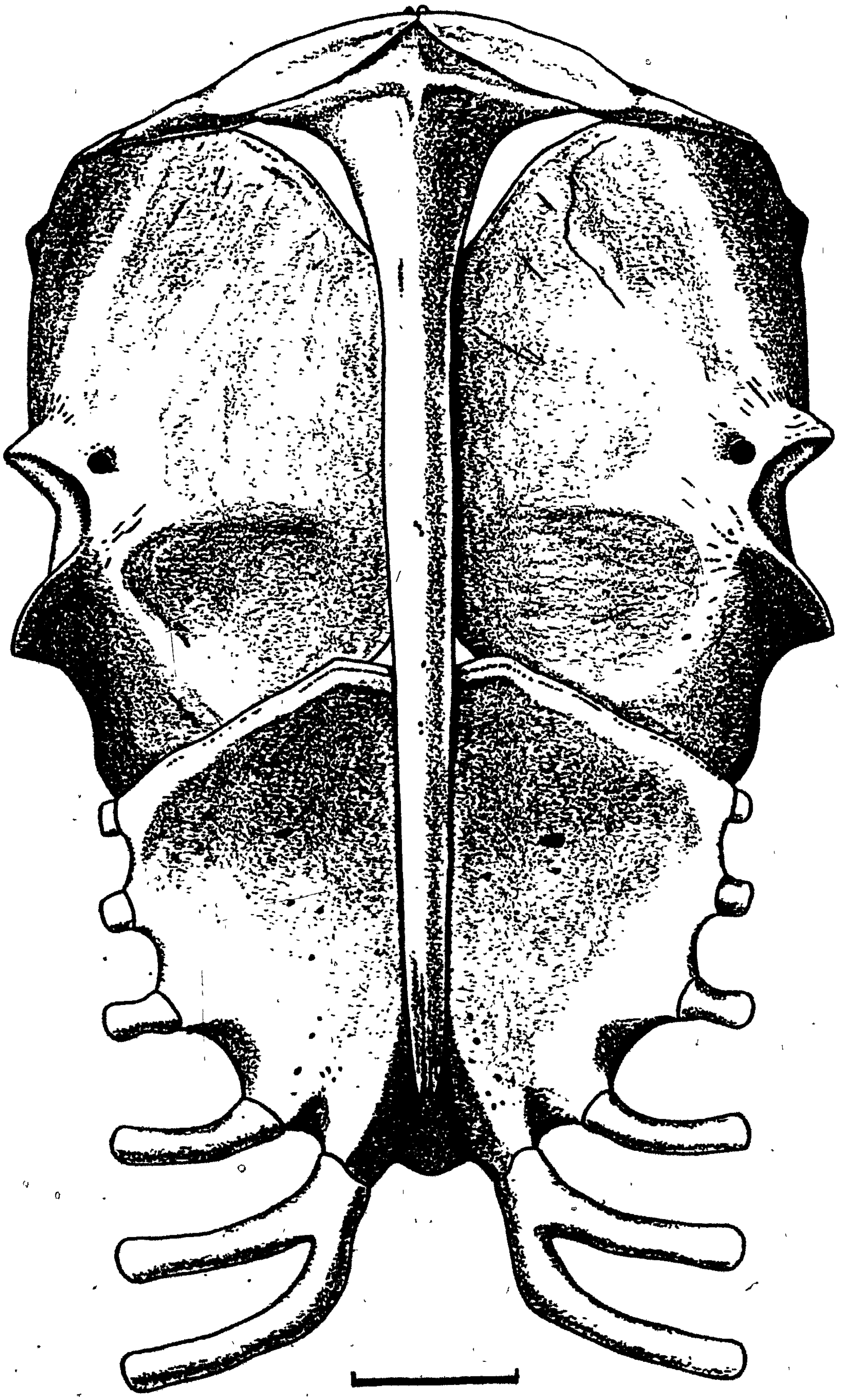
Scapulocoracoid. The scapula and a single coracoid fuse into a single element, the scapulocoracoid, in mature specimens. In contrast with most primitive reptiles, eosuchians have one rather than two coracoids. The coracoid foramen is found in the anterior coracoid of pelycosaurs (Romer and Price, 1940), and ossification of the posterior coracoid was often delayed. The presence of the coracoid foramen in Hovasaurus suggests that the single element is the same as the anterior coracoid of more primitive reptiles.

The scapular blade is extremely low (figs. 37b, c), even in mature animals, and the almost horizontal ventral plate is massive. The orientation of the scapulocoracoid can be reconstructed with little chance of serious error because of associated bones of the pectoral girdle. The posterior width across the paired scapulocoracoids would have been the same as the maximum width of the sternum, and the anterior width was delimited by the clavicles and interclavicle. As reconstructed (fig. 35a), the ossified scapular blade extends less than 50% up the side of the body. The clavicle and cleithrum extend slightly farther dorsally, but are still lower than expected. The posterior margin of the scapular blade lies above the glenoid, and is higher than the anterior margin. The anterodorsal rim of the scapula is longitudinally striated, indicating that there was a cartilaginous suprascapula. For maximum advantage of the serratus musculature (Holmes, 1977), the suprascapular blade would have been extensive.

The scapula and coracoid do not fuse into a single unit until stage E (fig. 36) as in Thadeosaurus. The ventral, horizontal portion of the scapula was apparently larger than the ossified scapular blade.

Figure 35. Hovasaurus boulei, reconstruction of pectoral region. a, anterior view. b, ventral view. Scale = 1 cm.



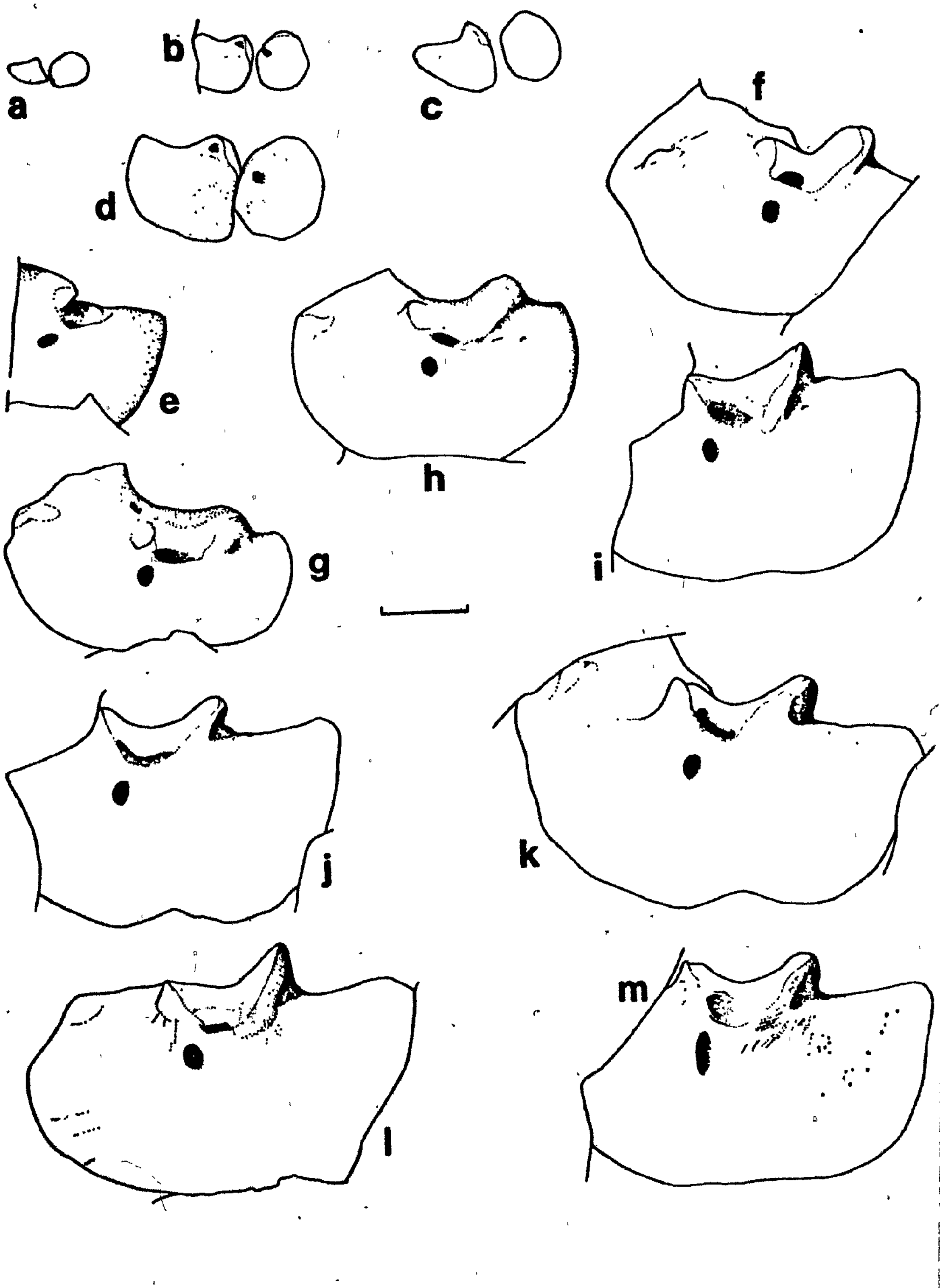


In contrast with most primitive reptiles, there is no supraglenoid ridge in Hovasaurus. The anterior facet of the glenoid is supported by an anteroventral ridge. The supraglenoid foramen has also been lost. In several specimens, there is a depression in the ridge anterior to the glenoid (figs. 36b, d). This depression has a more dorsal position in larger specimens (fig. 34g), where it is comparable to a similar pit in Champsosaurus (Sigogneau-Russell, 1979). Carroll noted the presence of a similar depression in Thadeosaurus and speculated that it may have been the opening for the supraglenoid foramen, although this is unlikely. The depression could have served as part of the origin of the subcoracoscapularis.

The vertical and horizontal plates of the scapula meet at almost right angles. Anteriorly there is a well-defined process along the inflection. The position of the process anterodorsal to the glenoid suggests that it served as the origin for the long head of the triceps lateralis. In living reptiles this muscle often originates from an area of the same relative size and position by means of a tendon.

The glenoid is formed by both scapula and coracoid (figs. 36a-e), and is the primitive "screw-shaped" type common to nearly all primitive reptiles. The anterior facet is strongly convex in transverse section, and faces more

Figure 36. Hovasaurus boulei, scapulocoracoid, ventral view. a, MNHN 1908-21-8; b, MNHN 1925-5-30; c, MNHN 1908-21-7; d, MNHN 1908-32-23; e, MNHN 1925-5-12; f, MNHN 1925-5-49, partially restored from right side; g, MNHN 1908-32-26; h, MNHN 1908-32-27; i, MNHN 1925-5-56; j, MNHN 1908-21-18; k, MNHN 1908-32-67, partially restored from right side; l, MNHN 1925-5-54, partially restored from right side; m, 1925-5-38, reversed image. Scale = 1 cm.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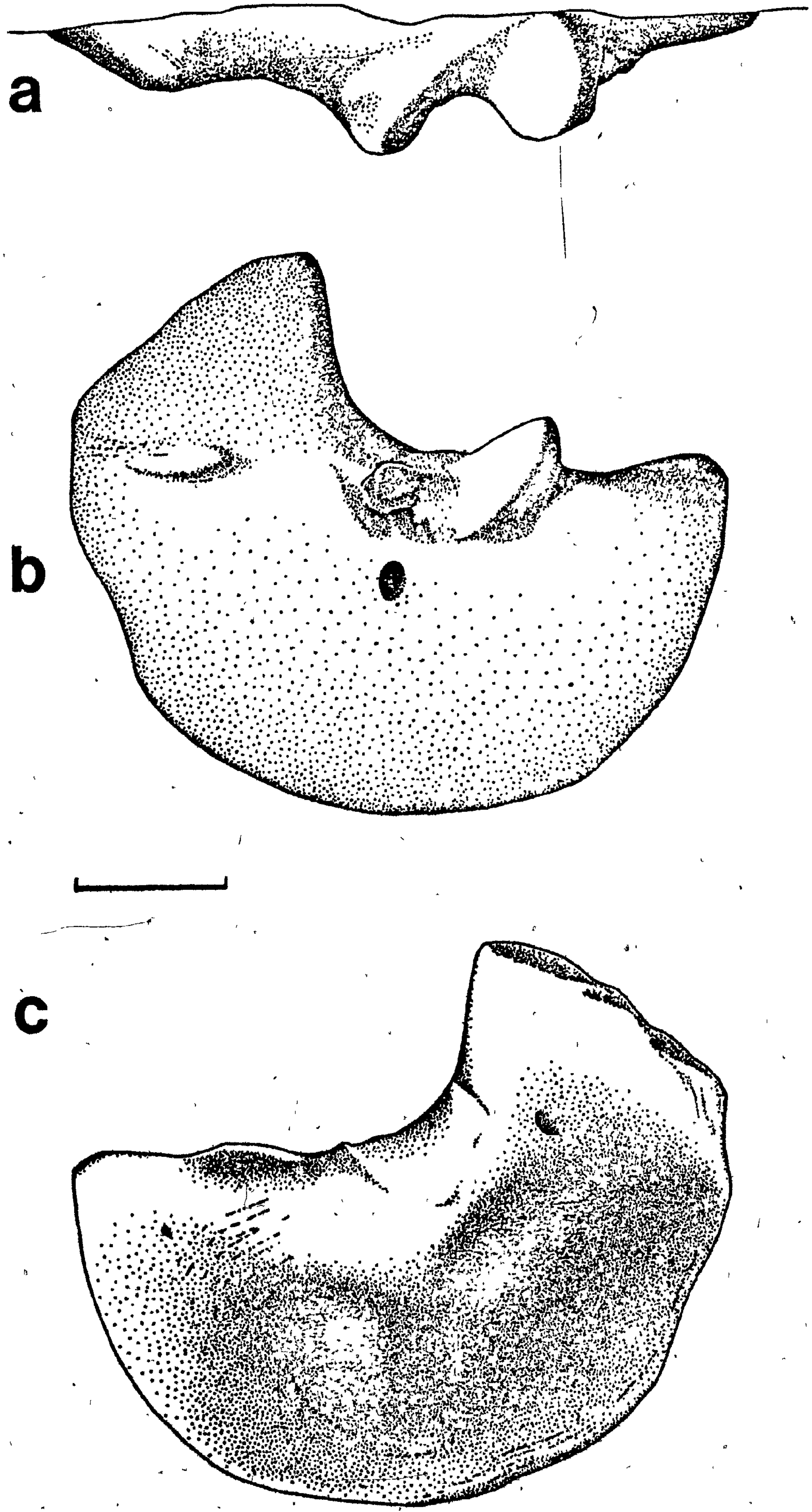
posteriorly than laterally. Centrally the glenoid is low, extending into a pit on the ventral surface of the coracoid. The posterior facet is broad and relatively flat. It extends as far laterally as the anterior facet, and faces anterolaterally and somewhat dorsally. The glenoid is indistinguishable from that of Thadeosaurus, the study of which suggested to Carroll (1981) that;

- Thadeosaurus could move its humerus more under the body than Captorhinus, and therefore could have had a more lizard-like posture;
- the humerus had greater freedom of motion than Captorhinus, especially ventrally, and was capable of moving in an arc greater than 60°;
- posteriorly, the humerus could approach the body wall.

The base of the strong, lateral ridge on the coracoid that supports the posterior glenoid facet is heavily scarred (fig. 36m), probably in part for the long head of the triceps, medialis, but mainly for the joint ligaments. The biceps and coracobrachialis muscles would have originated on the external surface of the coracoid medial to the glenoid. The coracoid foramen is represented by a notch in the coracoid at stage A (fig. 36b), but closes anteriorly early in life (fig. 36d).

The scapulocoracoid is preserved in internal view in MNHN R147 (fig. 37). The concave medial surface has some

Figure 37. Hovasaurus boulei, MNHN R147. Scapulocoracoid. a, lateral view; b, ventral view; c, dorsal view. Scale = 1 cm.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muscle scarring centrally for insertion of the sternocoracoideus and costosternocoracoideus musculature. Anteriorly the inner surface has been damaged and muscle scarring cannot be seen. A distinct ridge on the medial surface of the lateral edge of the coracoid posterior to the glenoid may be the origin of part of the subcoracoscapularis, which in lizards and Sphenodon inserts onto the proximal head of the humerus. The ridge extends ventromedially to strengthen the scapulocoracoid.

The scapulocoracoid of Thadeosaurus has the same features as that of Hovasaurus, including the limited dorsal extent of the scapular blade and an identical glenoid. Proportions are slightly different in mature specimens of Thadeosaurus and Hovasaurus. In the former genus, the distance from the anterior margin of the glenoid to the posterior margin of the coracoid is 55% the total length of the complex and the length of the glenoid is 25% the total length. The respective figures in Hovasaurus are 60% and 30%, suggesting that the glenoid is relatively larger.

The scapula is poorly preserved in Tangasaurus, but Haughton (1924) felt that the scapular blade was short.

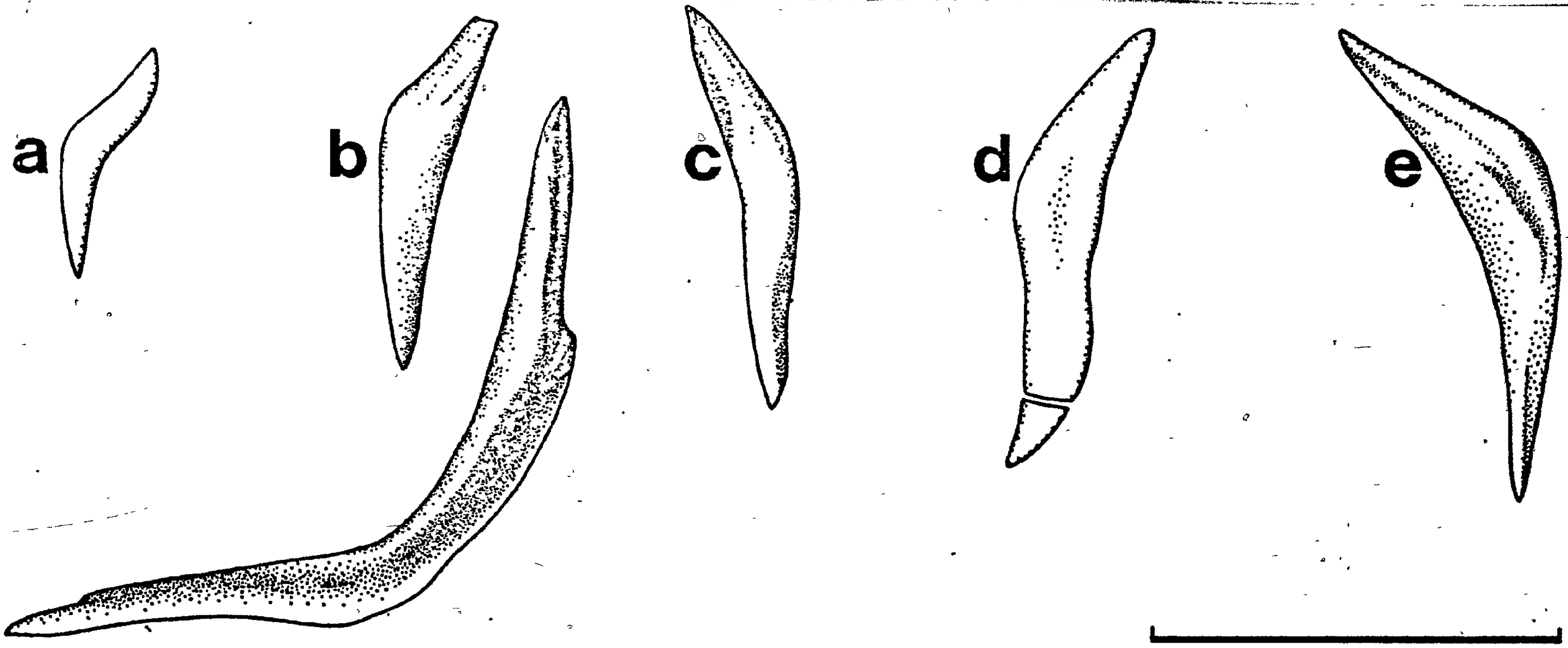
Youngina, despite its apparent immaturity of ossification in other parts of the skeleton, has a well developed scapular blade (fig. 56c).

Cleithrum. The cleithrum can be seen in six specimens (fig. 38, MNHN R147, MNHN 1908-32-1). It is a relatively small bone that is obscured by other elements in most specimens. It is thickest near its longitudinal centre, where the mediolateral width is about 20% the length of the bone, and tapers at both ends. The outer surface is divided into proximal and distal segments by a well-defined inflection close to the middle of the bone. The outer surface of the proximal section faces laterally, and the distal surface curves 50° medially to face dorsolaterally. The distal segment is situated dorsal to the ossified scapular blade, and the curvature suggests that the dorsal tip may have overlapped the anterior margin of the first dorsal rib (fig. 35a). The distinction between the proximal and distal sections of the cleithrum is not as evident along the mesial edge of the bone where the curvature is more gradual.

More than half of the anteromedial edge of the cleithrum articulates with the clavicle. The combined lengths and curvatures of the clavicles and cleithra, like the scapular blade, indicate that *Hovasaurus* had a broad, relatively low pectoral girdle.

Clavicle. Numerous specimens of *Hovasaurus* include clavicles (figs. 27, 38b, 39). The anteroposterior length of the ventral plate is approximately .5*x*, slightly less than the same dimension of the vertical shaft of the clavicle.

Figure 38. <u>Hovasaurus</u> <u>boulei</u>, cleithrum.
a, MNHN 1908-21-8, posterior view of left cleithrum; b, MNHN 1908-32-99, anterior view of right cleithrum and posterior view of right clavicle; c, MNHN 1908-32-99, anterior view of left cleithrum; d, MNHN 1908-32-23, Anterior view of right cleithrum; e, MNHN 1925-5-34, posterior view of right cleithrum. Scale = 1 cm.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The paired clavicles contact each other at the midline ventral to the proximal end of the interclavicle. In MNHN 1925-5-54 (fig. 39j) and other specimens, the proximal end of the left clavicle lies dorsal to the proximal tip of the right one. Sculpturing on the ventral surface of the clavicular blade suggests that the dermis was closely adhering in this region. The articular surface for the interclavicle is convex in section, fitting snuggly into the concave anterior articulations of the latter bone. Lateral to the interclavicle, the shaft of the clavicle curves sharply dorsad so that the lateral surface is at right angles to the ventral.

A groove in the posterior margin (fig. 38b) of the distal shaft probably nested the proximal edge of the scapula. About halfway up the vertical height of the clavicle, the lateral margin is emarginated (figs. 38b, 39f), and the medial margin becomes thicker anteroposteriorly. The lateral surface of this region is concave and striated for a firm contact with the cleithrum. The clavicle overlaps anteriorly, medially and laterally the proximal tip of the cleithrum. The vertical shaft of the clavicle of <u>Hovasaurus</u> is slightly longer than the horizontal portion.

The shape of the clavicle does not change significantly during growth, although the coefficient of allometry is less than 1.0 (Table 8).

Figure 39. _Hovasaurus_ _boulei_, dermal elements of pectoral girdle. a, MNHN 1925-5-30, interclavicle and clavicles; b, MNHN 1908-32-99, clavicles and cleithra; c, MNHN 1908-32-23, interclavicle and clavicles; d, MNHN 1925-5-38, interclavicle and clavicles; e, MNHN 1925-5-49, interclavicle and clavicles; f, MNHN 1925-5-34, interclavicle, clavicle; g, MNHN 1908-32-26, interclavicle, clavicles; h, MNHN 1908-21-24, interclavicle; i, MNHN R147, interclavicle, clavicle; j, MNHN 1925-5-54, interclavicle, clavicle; k, MNHN 1908-32-25, interclavicle; l, MNHN 1908-21-18, interclavicle; m, MNHN 1908-32-67, head of interclavicle. Scale = 1 cm.


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Interclavicle. The head of the interclavicle is t-shaped (fig. 39), and the articulation with the clavicle is primarily on the anterior surface of the cross bar. An anterior process on the midline is overlapped ventrally by the clavicles.

The width of the interclavicular head is more than twice the length of an average dorsal centrum (Tables 6,8) in mature animals, and is relatively larger in juveniles.

The shaft is variable in outline. It is broadest approximately halfway along its longitiudinal axis where it is 2/3x (1/3 the width of the head of the interclavicle). Behind this point, the shaft tapers rapidly in MNHN 1925-5-54 (fig. 39j), possible because of crushing, but tapers more gradually in most specimens. The ventral surface is convex in transverse section, and concave dorsally (MNHN 1908-32-1). The ventral surface is smooth with sparse pitting, and served as part of the origin of the pectoralis. The posterior end of the shaft lies in a groove on the ventral surface of the sternum and ends just anterior to the posterior margin of the sternum. The dorsal and ventral surfaces of the distal end are longitudinally striated, possibly for attachment of ligaments that extended to the gastralia. The anterior and posterior tips of the interclavicle tend to bifurcate.

The coefficient of allometry for the length of the interclavicle is less than 1.0 in Hovasaurus, and the bone is relatively longer in juveniles than adults. In an animal with a dorsal vertebra ten millimetres long, the expected length of the interclavicle is almost 6x (Table 8).

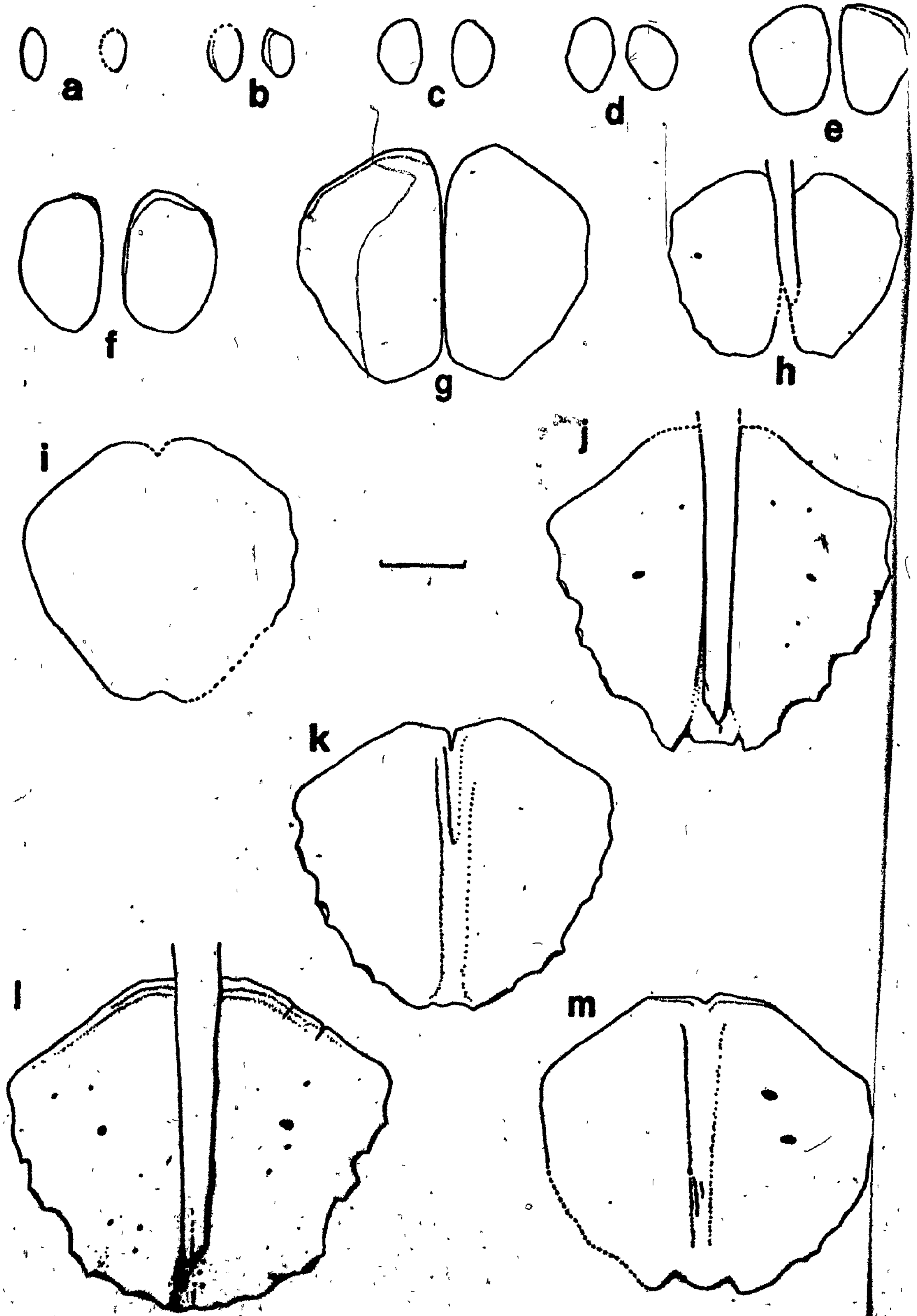
Sternum. The sternum appears first in juvenile specimens as a pair of widely separated oval ossifications (fig. 40). The intervening space was probably filled by cartilage. As the animal grew, the medial gap decreased until the sternal ossifications contact on the midline at stage D. They coossified into a single unit by stage F (fig. 40i), although the suture can still be seen on the dorsal surface of MNHN 1908-32-38 (fig. 41), one of the largest sterna.

The sterna of mature specimens show considerable variation in shape (fig. 40j, k, l, m). This diverseness is partially attributable to the age range represented, and partially to individual variation.

The ventral surface is grooved along the midline for the interclavicle. The surface slopes at a low angle from the horizontal lateral to the groove, and is smooth with small, irregular pits. Much of the fleshy origin of the pectoralis would have been from this region.

The anteroventral margin is notched on the midline. In ventral view, the anterior margin between the notch and the point where the sternum meets the inner edge of the coracoid faces anteriorly or anteromedially. The sternum is

Figure 40. Hovasaurus boulei, sternum, ventral view. a, MNHN 1908-21-8; b, MNHN 1908-32-29; c, MNHN 1925-5-30; d, MNHN 1908-21-7; e, MNHN 1908-32-77; f, MNHN 1908-32-23; g, MNHN 1925-5-12; h, MNHN 1925-5-29; i, MNHN 1908-32-26; j, MNHN 1908-21-24; k, MNHN R147; l, MNHN 1908-21-18; m, MNHN 1908-32-67. Scale = 1 cm.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dorsoventrally thin on the midline but becomes thicker laterally (fig. 41a). In this region the ventral surface of the sternum underlies a pair of anterodorsally oriented facets, one on each side of the midline, that are heavily scarred, finished bone. As the coracoids are separated from each other posteromedially, there is an open area anterior to the facets. The superficial layer of the sternocoracoideus would have originated from the scarred facets on the sternum and passed through this open area onto the internal surface of the scapulocoracoid as in *Sphenodon* and *Iguana* (Holmes, 1977).

Lateral to the origin of the sternocoracoideus superficialis is a laterally elongate, anterolaterally oriented trough with a surface of unfinished bone. The coracoid would have articulated with this surface of the sternum. The greatest thickness (fig. 41c) and width (fig. 41b) of the sternum is at the lateral edge of the articulation with the coracoid.

The sternum has four, possibly five costal connections on each side. There appears to be a dorsolaterally oriented facet immediately behind the lateral limit of the coracoid articulation (fig. 41b), to which the eleventh rib was probably connected via cartilage. Four concave facets of unfinished bone are found on short projections along each side of the sternum. The sternum is thicker anteriorly and would have been almost directly ventral to the distal end of the ribs. The first unquestionable costal facet therefore is dorsoventrally high and faces somewhat dorsally. The last facet is on the thin posterior edge of the sternum close to the midline (fig. 41c) and consequently is low with a horizontal orientation. The intervening two facets are intermediate in height and dorsolateral orientation. With the exception of the last facet, all points of attachment for the ribs are oriented primarily laterally when viewed from above (fig. 41b) and all have about the same anteroposterior length. It appears that only one rib would have attached to each of these facets by means of a cartilaginous extension (fig. 35b). The last facet is anteroposteriorly longer and is oriented more posteriorly than laterally. At least two ribs would have been connected to this facet via a mesosternal element (fig. 35b) of cartilage.

Posteriorly the sternum has an extension along the midline in most mature specimens (fig. 40), which is separated from the last facet for the ribs by a shallow emargination.

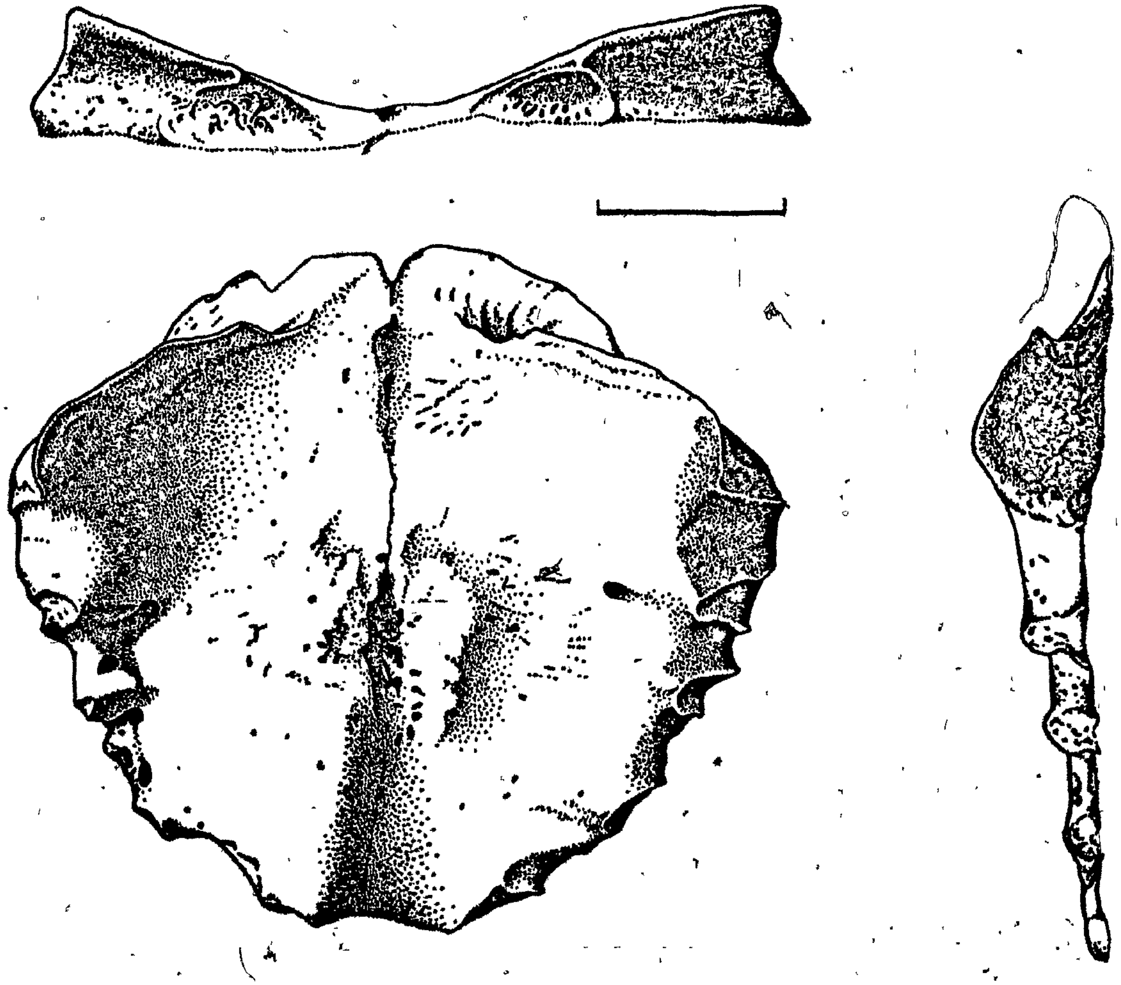
The dorsal surface of the sternum is more strongly concave in transverse section at the front (fig. 41a) than it is posteriorly. The centre of the dorsal surface is excavated along the midline, possibly representing a region where the two sternal plates have not yet coossified completely (fig. 41b). A low ridge lateral to this pit is scarred for the origin of the profundus layer of the sternocoracoideus.

The sternum of Tangasaurus falls within the range of variation seen in Hovasaurus. Thadeosaurus (Carroll, 1981) has a growth series of sternal ossifications that cannot be distinguished at equivalent ages from those of Hovasaurus. Paired sternal ossifications in Youngina (Broom, 1922), indicate that this specimen was immature. A single, central sternal plate is present in Kenyasaurus (Harris and Carroll, 1977), and shows the same characteristics as the sternum of Hovasaurus. Most other eosuchians had a cartilaginous sternum of smaller size.

An ossified sternum is present in one specimen of Araeoscelis (Vaughn, 1955), but it is not known whether it was a paired or single structure. As reconstructed (fig. 57b) it bears no resemblance to the paliguanid and tangasaurid type of sternum.

In general the sternum of Hovasaurus resembles those of Lacerta (Romer, 1956) and Sphenodon (Howes and Swinnerton, 1901). Although the sterna of modern lacertilians are cartilaginous, each forms ontogenetically from two centres of condensed mesoderm that are continuous anteriorly with the mesodermal rudiments of the coracoids (Gladstone and Wakely, 1932).

Figure 41. *Hovasaurus boulei*, MNHN 1908-32-38. Sternum in anterior, dorsal and right lateral views.



Limb proportions. In the smallest specimens of Hovasaurus the humerus is about 20% shorter than the femur (Table 6). However, the humerus grows at a higher rate than the femur, and in mature specimens can be 10% longer than the femur (Tables 6, 8). The coefficient of allometry of the humerus also exceeds that of the femur in Tangasaurus (Haughton, 1924) and Thadeosaurus (Table 3) and the length of the humerus exceeds that of the femur. This appears to be a characteristic of tangasaurids not found in most other types of reptiles. Compared to the femur, the humerus is relatively shorter in Youngina than it is at any life stage in Hovasaurus. There is no information available on growth of postcranial elements in Youngina, so although the humerus is 32% shorter than the femur in the immature specimens that have been found, the ratio of humerus to femur length could have been higher in larger specimens.

The length of the forearm of Hovasaurus is 77% the length of the humerus in immature specimens, and only 52% in large individuals. The ratio of radius to humerus length is slightly higher in the largest specimens of Thadeosaurus (.59) and Tangasaurus (.62). However, the lengths of the radii are not significantly different in any of the three genera.

The lower segments of the front and back limbs maintain approximately the same ratio throughout life in Hovasaurus (Table 6). The radius is 67% the length of the tibia, which is close to that of Thadeosaurus and Tangasaurus (73%).

In the smallest specimens of Hovasaurus, the expected mean length of the tibia is 88% that of the femur. The relative length decreases to 85% in mature specimens. These figures are comparable with Tangasaurus (85%), Thadeosaurus (90%) and Youngina (89%).

Limb proportions are often used as an indication of habitat preference. Osteological evidence shows that Hovasaurus and Tangasaurus were aquatic animals. There is nothing in the skeleton to indicate that Thadeosaurus preferred an aquatic habitat, yet its limb proportions are very similar to those of Hovasaurus. Perhaps Thadeosaurus spent a great deal of time in the water, but had not become specialized for an aquatic existence. Among living reptiles, marine iguanas and aquatic varanoids are excellent swimmers but do not show any special adaptations in the skeleton.

Champsosaurus and Askeptosaurus were Mesozoic eosuchians that unquestionably spent much of their life in the water. Their limb proportions are quite different from those of Hovasaurus however, which is a strong indication that the limbs were used in a different manner.

Of the non-eosuchian reptiles that are unquestionably aquatic, nothosaurs show the greatest similarity in limb proportions to tangasaurids. In Pachypleurosaurus (Zangerl, 1935), the humerus is only 80% the length of the femur in the smallest specimens, but is more than 115% in large animals. The forearm is about 50% the length of the humerus as in Hovasaurus. The significance of limb proportions will be discussed later.

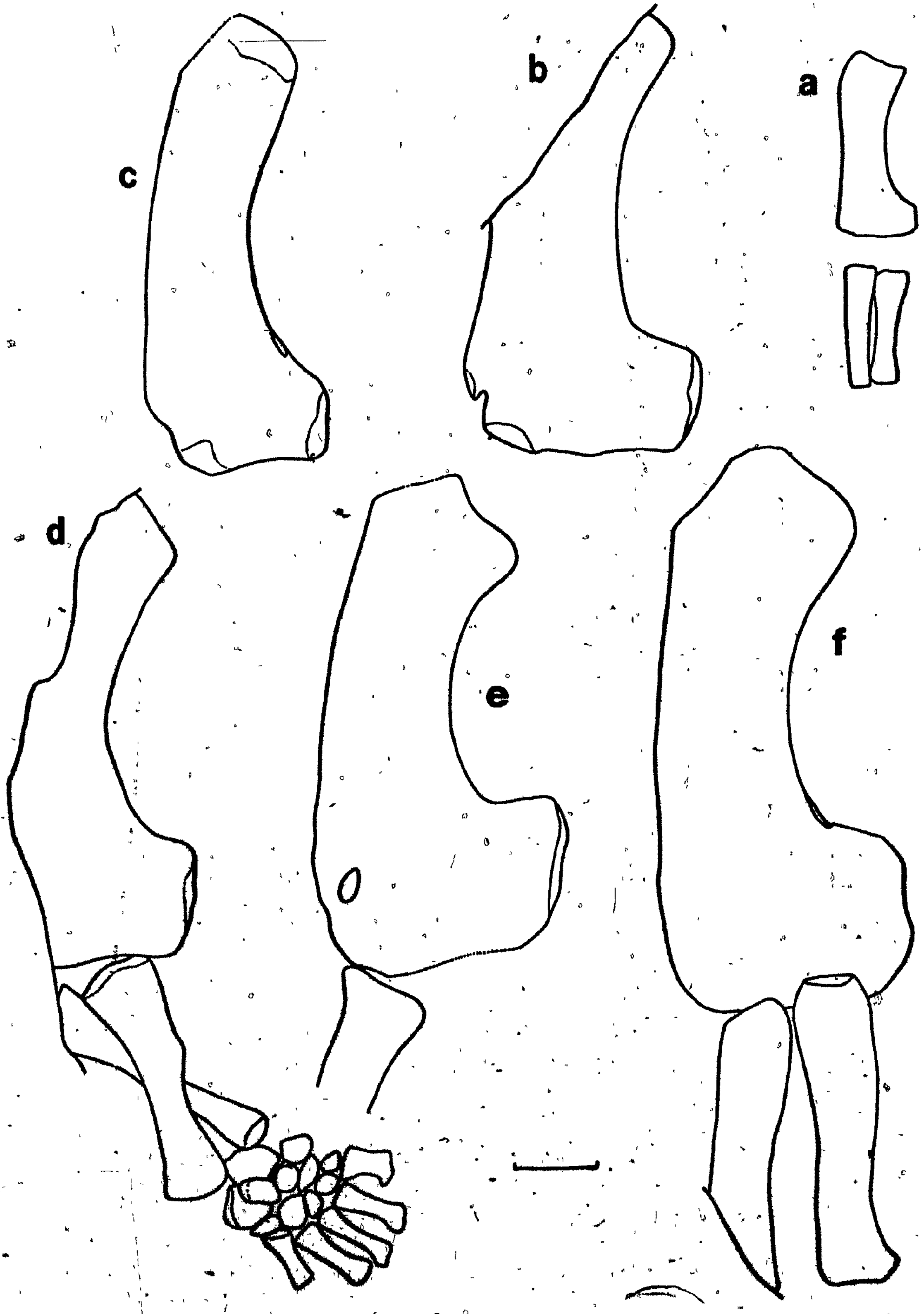
Humerus. In general configuration, the humerus of Hovasaurus is primitive for a reptile. The powerful development of the entepicondyle beyond the elbow joint increased the mechanical advantage of the flexor musculature, indicating that the animals were probably obligatory sprawlers.

The humerus grows with a high coefficient of allometry (1.6). The expected length of a humerus in an animal with a 10 mm long dorsal centrum is 72 mm (27.8 OLU, 7.2x). Hovasaurus has a relatively long humerus compared with other Permian reptiles. Palaeothyris has a humerus 19 OLU (5.0x) in length (Carroll, 1970). The humerus of the larger specimen of Tangasaurus falls close to the expected length of a Hovasaurus of similar size (Table 4). The humerus of Thadeosaurus is significantly shorter (25.8 OLU, 6.7x).

In juvenile specimens of Hovasaurus boulei (figs. 42a, 43a, b, c), little more than the cylindrical shaft of the humerus was ossified at the time of death. The width of the distal end of the bone is 47% the length of the bone. The plane of proximal expansion is almost perpendicular to that of the distal end. Consequently, the extent of the proximal expansion cannot be determined in the majority of the specimens because the expansion is directed into the matrix, and usually only half of the specimen is preserved. The measurements given in Tables 6 and 8 for proximal width of the humerus are maximum width in the same plane as the distal end. This amounts to 34% of the length of the humerus in juveniles. In juveniles the proximal articulation and the head of the deltopectoral crest form a continuous surface of unfinished bone. The entire distal end of the bone is unfinished with no evidence of the specialized articulations for the radius and ulna. Gaps between the bones of articulated specimens indicate that the ossified length of the bone may have been extended in cartilage by 16%. The entepicondylar foramen does not become enclosed in bone until the end of stage B when the animal is almost half of its full size, and the ectepicondylar foramen is closed much later in life.

In the largest specimens, the proximal articulation is restricted to the posterior half of the proximal expansion. Its surface remains unfinished bone with a cartilaginous cap,

Figure 42. Hovasaurus boulei, front limb, a, MNHN 1908-32-1, humerus (dorsal view), radius (anterior view), ulna (anterior view); b, MNHN 1925-5-50, humerus, reversed image; c, MNHN 1908-32-24, humerus, reversed; d, MNHN 1908-32-59, humerus, radius, ulna, carpus, reversed image; e, MNHN 1925-5-46, humerus; f. MNHN 1908-32-60, humerus, radius, ulna reversed. Scale = 1 cm.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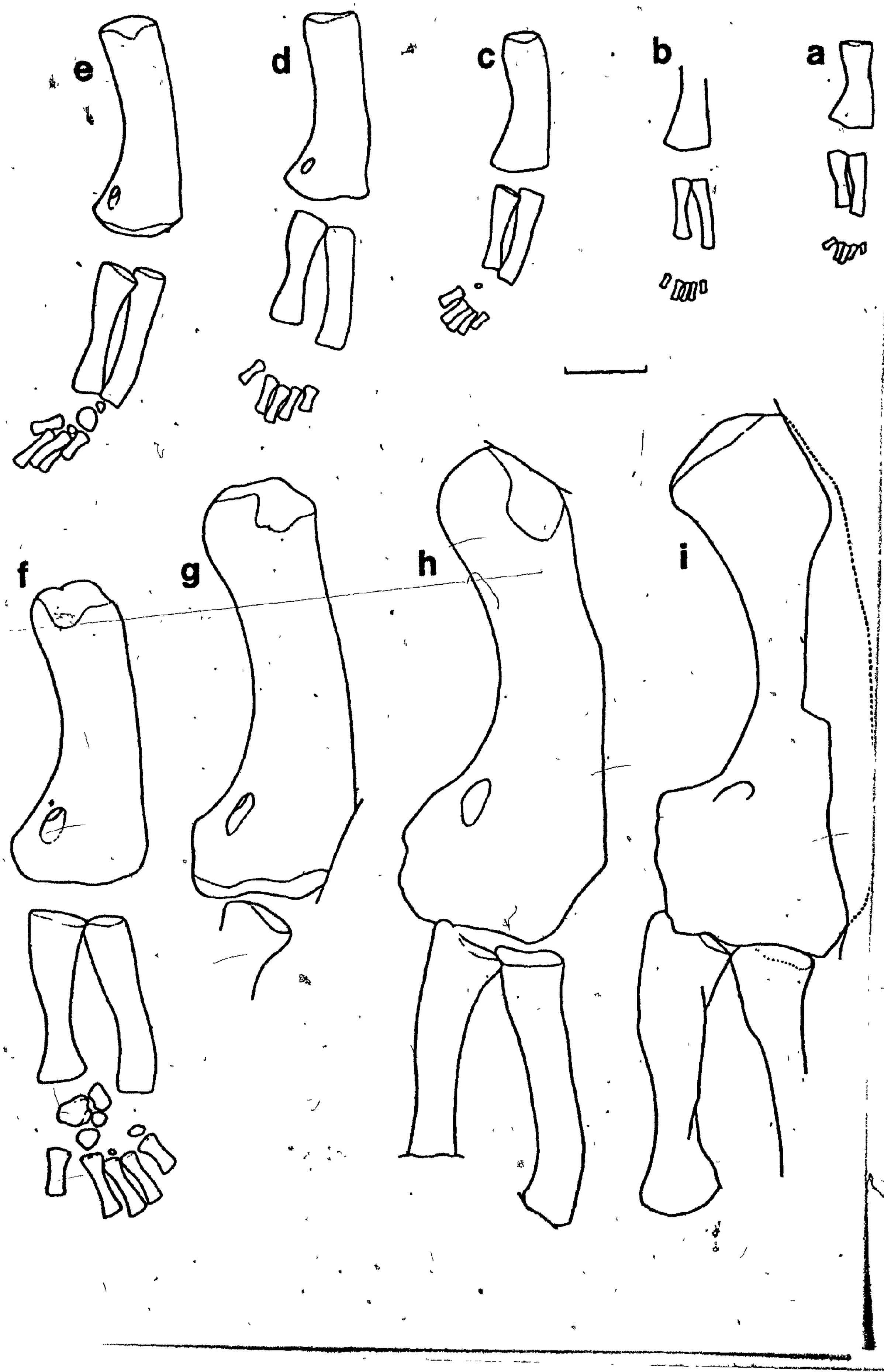
and is distinguishable from the deltopectoral crest, which becomes finished and muscle scarred. The ventral margin of the articular surface is almost straight, and the dorsal outline arched. The length of the proximal articular surface of the humerus is double its height, and about ten per cent greater than the length of the glenoid. As in Captorhinus (Holmes, 1977) and pelycosaurs (Jenkins, 1971), Hovasaurus has a humeral groove that runs from the anterodorsal corner of the articular surface to a midventral point, describing a small part of a helix. The longitudinal axis of the proximal articulation is twisted 60° from the plane of the distal head as in most eosuchians.

The deltopectoral crest is large. The crest extends ventrolaterally to the same degree as in Captorhinus, but the dorsoventral thickness is about 40% greater in Hovasaurus. The summit of the crest is formed by a ridge running from the anteroventral margin of the proximal articulation to the most ventral point on the crest. About halfway down the proximal surface of the deltopectoral crest, a second low ridge diverges from the first and extends to the anterior surface. This ridge separates the areas of insertion of the pectoralis and the deltoids (fig. 44d). The supracoracoideus would have inserted onto the concave region posterior to the summit of the proximal portion of the deltopectoral crest. The insertion

Figure 43. *Hovasaurus boulei*, anterior limb. a, MNHN 1908-21-8, humerus (ventral view), ulna (posterior), radius (medial aspect), metacarpus (ventral view), reversed image; b. MNHN 1908-32-29; c, MNHN 1908-21-7; d, MNHN 1908-32-77, partially restored from right side; e, MNHN 1908-32-23, reversed; f, MNHN 1925-5-12; g, MNHN 1908-32-25; h, MNHN 1925-5-56; i, MNHN 1908-32-67. Scale = 1 cm.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of this muscle is delimited posteriorly by a low ridge extending from the most ventral point of the proximal humeral articulation to the most ventral point of the deltopectoral crest. Scarring on the ventral surface of the proximal head of the humerus posterior to the supracoracoideus marks the insertion of the coracobrachialis brevis. The extent of fleshy attachment cannot be made out, but it probably would have extended down the shaft of the humerus as in living reptiles. A sharply defined ridge extends from the deltopectoral crest onto the anterior margin of the shaft of the humerus, and shows the anterior extent of the proximal portion of the brachialis inferior insertion. The distal extent of this muscle is defined by a tapering concavity near the ventroanterior margin of the distal head of the humerus.

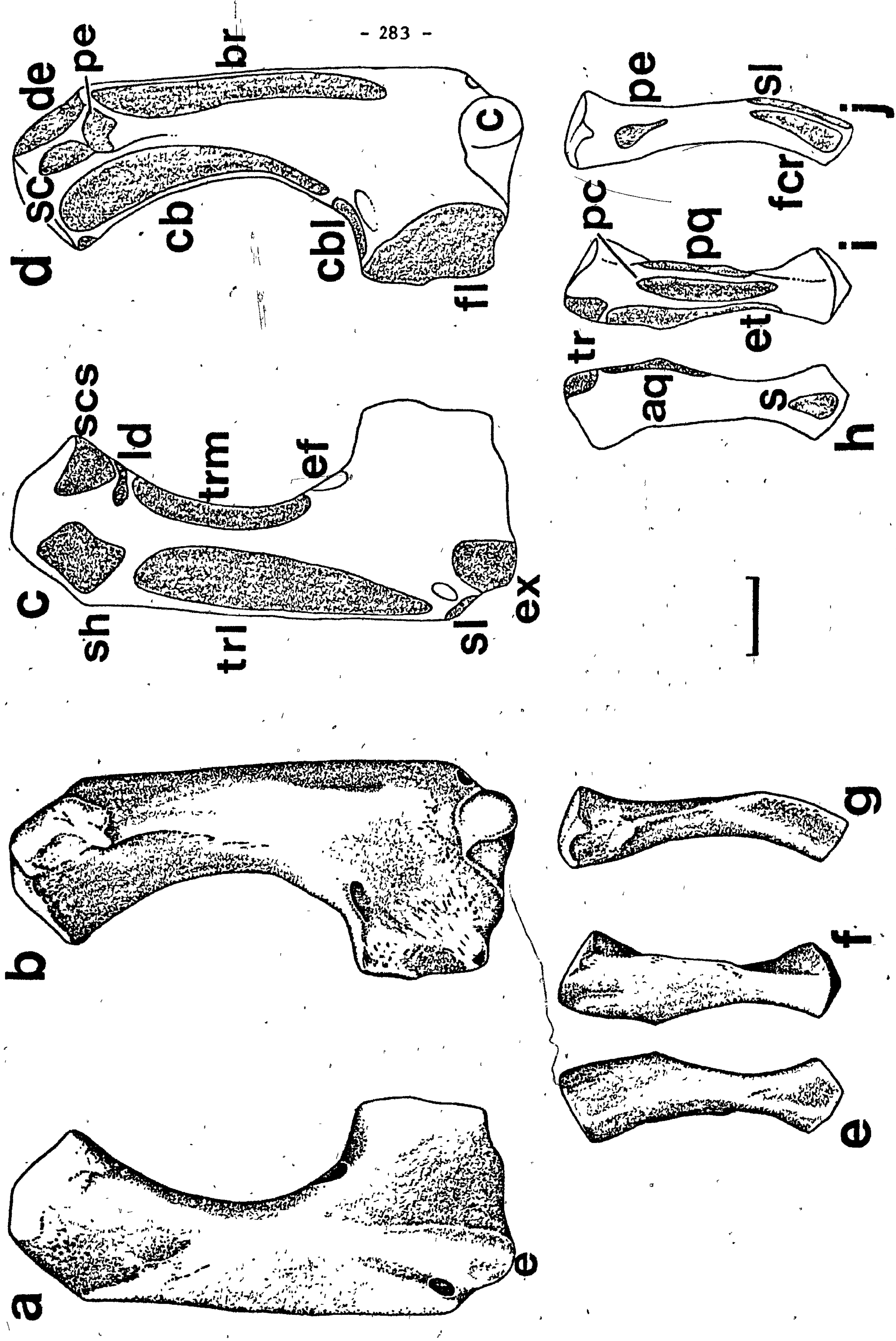
The posterior margin of the proximal head is scarred distal to the articulation for the subcoracoscapularis insertion, which extends onto a scarred region on the dorsal surface. A low ridge distal to the slightly concave, dorsal insertion of the subcoracoscapularis would have been the point of insertion of the latissimus dorsi.

The dorsal surface of the humerus is divided into posterodorsal and anterodorsal regions by a low ridge extending from the posterodorsal corner proximally to the ectepicondyle. The short head of the triceps medialis would have originated posterior to this ridge along the shaft of the humerus, but there is nothing on the humeri of Hovasaurus to indicate the extent of this muscle. The fleshy origin of the short head of the triceps lateralis would have been anterior to the longitudinal ridge. Its proximal limit is marked by a prominent, heavily scarred ridge near the anterior margin of the proximal head. Proximal to this ridge, the dorsal surface is excavated above the deltopectoral crest, and scarred for the insertion of the scapulohumeralis.

The proximal head of the humerus of Hovasaurus is different from the primitive condition exemplified by Captorhinus (Holmes, 1977) in several minor, but significant, respects. The proximal articulation has taken a more posterior orientation and position, which by itself would suggest more restricted capability of anterior motion of the distal end of the humerus. However this potential restriction has been compensated for by the lateral extension of the posterior facet of the glenoid. Similarly the proximal articulation has become more ventrally oriented in Hovasaurus than in Captorhinus, and cannot be seen in dorsal aspect. This would restrict the dorsoventral arc of movement of the humerus from that seen in Captorhinus, except that it has been compensated for by increased convexity of the glenoid, plus greater exposure of its ventral surface. The articulation between the glenoid and humerus indicates that Hovasaurus was better adapted for bringing the front limb under the body and was somewhat less sprawling than *Captorhinus*. The distal end of the humerus could not have been raised above the proximal end because the proximodorsal rim of the humerus would contact the dorsal margin of the glenoid. *Hovasaurus* would have been able to pull its humerus into a more vertical position than *Captorhinus*. But more importantly, when the humerus was brought under the body in *Hovasaurus* it would have been beneath the glenoid and not lateral to it. This means that the front limb was thrusting against the bony support of the scapulocoracoid when it was brought underneath the body, rather than against the tendons and ligaments holding it to the scapulocoracoid.

The separation between dorsal and ventral surfaces for muscle insertion is more pronounced in *Hovasaurus* and *Captorhinus*. The area of insertion of the scapulohumeralis has shifted anteriorly from the position in *Captorhinus* (Holmes, 1977) and increased in area. The increased ability of this muscle to pull the distal end of the humerus dorsoanteriorly is correlated with the increased ability of the ventral musculature to pull the humerus ventroposteriorly. The more ventral position of the deltopectoral crest and its increased size shows that more emphasis was placed on pulling the front limb under the body in *Hovasaurus* than in *Captorhinus* and

Figure 44. Hovasaurus boulei. Reconstruction of humerus, radius and ulna; a, humerus in dorsal aspect; b, humerus, ventral view; c, d, muscle origins and insertions on dorsal and ventral surfaces of humerus; e,f, ulna, anterior and posterior aspects; g, posteromedial view of radius; h, i, muscle origins and insertions on anterior and posterior surfaces of ulna; j, posteromedial areas of muscle origin and insertion of the radius. Scale = 1 cm.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protorothyridids (Reisz, 1980).

The distal end of the humerus is primitive in appearance. The entepicondyle is massive for an eosuchian, so that the distal expansion of the humerus is more than double the shaft diameter.

The dorsal opening of the entepicondylar foramen is located on the proximal surface of the entepicondyle rather than the more typical position on the dorsal surface. The ventral wall of the entepicondylar groove is more pronounced than the dorsal wall so that the dorsal groove and opening cannot be seen in anteroventral aspect. Because of its position, the foramen is often not seen in posterodorsal aspect either (figs. 42a, b, d, e). When this happens, the more prominent ventral margin of the entepicondylar groove is not showing and the inflection between the shaft of the humerus and the entepicondyle appears more pronounced.

The ectepicondylar ridge is powerful in mature specimens. It is rounded distally with a surface of finished bone in MNHN 1908-32-60 and AMNH 5333. The extensor musculature of the forearm would have originated here.

A distinct supinator process and ectepicondylar groove are present in MNHN 1925-5-50 (fig. 42b). The distal ends of the supinator and ectepicondyle in this specimen are unfinished bone, so the ectepicondylar foramen was probably closed distally by cartilage. In slightly larger specimens of Hovasaurus (MNHN 1925-5-46, fig. 42e; AMNH 5333) the ectepicondylar foramen for the radial nerve and associated blood vessels is enclosed entirely in bone. The ectepicondylar foramina of Youngina (Gow, 1975) is open distally and shows that specimens of this animal were immature when they died.

There is a shallow groove distolateral to the ectepicondylar foramen on the posterodorsal surface where the supinator process and the ectepicondyle are joined by a bridge of bone. The supinator musculature would have originated here as in modern lizards (Romer, 1944). The presence of this groove in MNHN 1908-32-60 (fig. 42e) indicates that the ectepicondylar foramen was completely encircled by bone in this specimen, even though the foramen itself cannot be seen because of damage.

There is a pronounced ridge of bone on the anteroventral surface of the humerus proximal to the entepicondylar foramen for the insertion of the coracobrachialis longus. The anteroventral surface of the entepicondyle is concave in longitudinal section, and heavily scarred for the origins of the flexor musculature of the forearm and hand. A distomedially oriented ridge bounds this region distolaterally, and has longitudinal muscle scarring along its surface. The ridge terminates where the posterior and distal surfaces of the entepicondyle meet and has a distoventrally oriented depression for muscle insertion. It appears that the ulnar flexors originated on this ridge and in the scarred region between the ridge and the humeroulnar articulation.

The ectepicondylar foramen emerges from the bone lateral to the capitellum on the distal surface of the humerus and cannot be seen in anteroventral aspect (fig. 43).

There is an almost circular capitellum for articulation with the radius on the anteroventral surface on the distal end. As in other primitive reptiles, the humeroulnar articulation is medial to the capitellum and includes a convex region posterior to a narrow concavity next to the capitellum.

Except for size, the humerus of *Hovasaurus* is indistinguishable from that of *Thadeosaurus* (fig. 58g). The prominent development of the entepicondyle is also evident in *Tangasaurus* (fig. 17). The humerus of *Youngina* is poorly ossified (fig. 58e) and only the base of the entepicondyle is preserved. However, as in tangasaurids it is sharply divergent from the shaft, and the entepicondylar foramen is located close to the proximal margin of the entepicondyle.

Radius. The radius shows moderate positive allometry in its growth. At maturity its length is approximately 14.4 OLU, or 3.7*x*. This is not significantly different from the length in Thadeosaurus (15.1 OLU, 3.9x). The length of the radius of Tangasaurus falls within the range of variation for this dimension in Hovasaurus (Table 4).

The radius is slightly longer than the ulna as in most eosuchians. In Acerosodontosaurus, the ulna (excluding the olecranon) is longer than the radius.

In general outline, the radius of Hovasaurus has a twisted outline similar to that of Acerosodontosaurus (fig. 12), Thadeosaurus (Carroll, 1981) and Champsosaurus (Erickson, 1972). The shaft is straight for the proximal two thirds of the bone, but curves posteriorly at the distal end (figs. 43b, c, d, e, f, h). The anterior and lateral surfaces of the radius are visible in only two juvenile specimens (figs. 19, 42a) where no details are preserved. The remaining specimens are exposed in posterior and medial aspect.

The proximal surface of the radius is concave for articulation with the capitellum. The outline of the articular surface is oblong with a mediolateral longitudinal axis, a flattened posterior margin and a strongly convex medial rim. A slight lip extends over the end of the humerus like a miniature olecranon. The humeroradial articulation is continuous posteriorly with a limited articular surface for the ulna. This posterior surface forms the dorsal and mediodorsal margins of a distinct concavity in the proximoposterior surface of the radius. Ventromedial to this hollow is a tubercle for insertion of a tendon of the biceps muscle. A ridge twists ventromedial from this process to a point about halfway along the longitudinal axis of the radius where it ends (MNHN 1925-5-56, 1908-32-67). This ridge probably served for insertion of the biceps also.

The distal end of the radius is exposed in medial view in MNHN 1925-5-12 (fig. 23) and posteromedial view in MNHN 1925-5-56 (fig. 43h). A sharp ridge separates the medial and anterior surfaces of the distal half of the radius as in *Thadeosaurus* (Carroll, 1981). The supinator longus would have inserted onto the ridge. The radius is flattened and scarred medial to the ridge, probably for the insertion of the flexor carpi radialis. The distal articulation is oval in outline with a convex surface.

Ulna. The olecranon process is not ossified in *Hovasaurus*. There is a series of longitudinal grooves and ridges on the lateral, anterolateral and posterolateral surfaces of the proximal end of the radius. A similar series on the olecranon of captorhinids suggested to Holmes (1977) that the triceps would have inserted broadly on this region via a tendinous sheet.

Approximately a third the length of the ulna from the proximal end there is a protuberance of bone on the lateral margin (fig. 42d) that was probably the centre of insertion of the anconaeus quartus as in Captorhinus (Holmes, 1977) and protorothyridids (Reisz, 1980). The distal end of the anterior surface of the ulna is shallowly concave over most of the surface. As in all living reptiles this region would have served as the origin of the supinator manus. It is bordered medially by a low but distinct ridge that runs along the medial edge of the radius in the distal half of the bone.

On the posterior surface of the ulna, the ridge of insertion for the triceps musculature is bounded medially by a shallow trough. There is a ridge along the rim of the articulation. The posteroventral surface of this narrow ridge is rugose, suggesting perhaps that the joint ligaments attached here. A longitudinal ridge originates distal to the proximal articulation on the posterior surface, and becomes prominent distally as the medial edge of the bone (figs. 43i, 44f). The same ridge is present in Acerosodontosaurus (fig. 12a) but is not as conspicuous. In Thadeosaurus the ridge is as well developed as in Hovasaurus. The central area of the ulna is flattened posterolateral to the ridge. One of the profundus heads of the palmaris communis muscle probably would have had its origin here. The pronator quadratus would have originated from the medial edge of the ridge. The ventral end of the ridge is relatively low and terminates posterodorsal to the articulation with the ulnare (fig. 45).

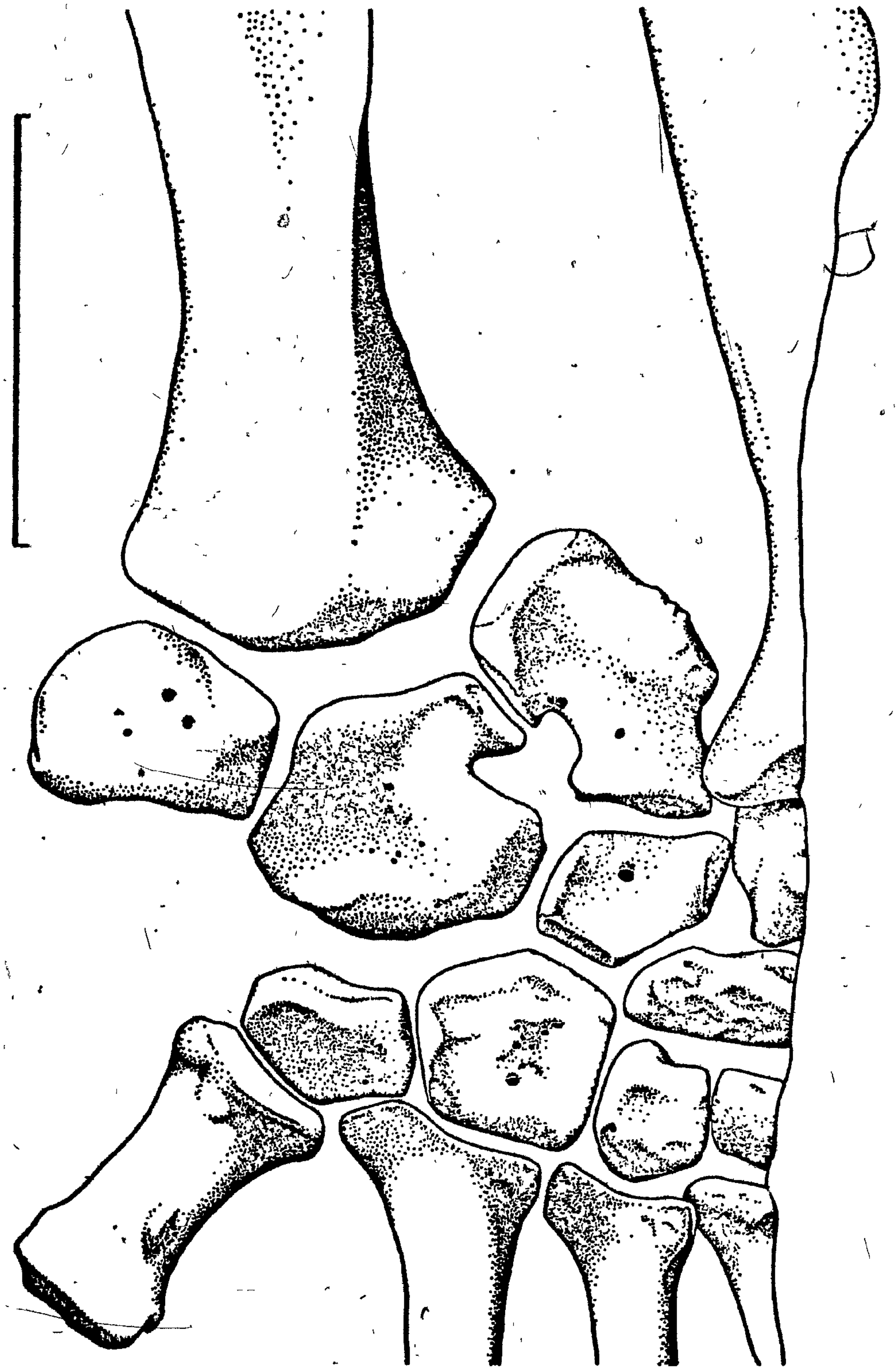
Manus. The carpus, like that of most primitive reptiles, has eleven elements (figs. 42d, 45, 60j). Each element tends to have a smaller surface area ventrally than it does dorsally. The elements key together to form a dorsally arched carpus.

The carpus is not fully ossified until at least stage D (fig. 43f). In at least one specimen, there is partial ossification of the ulnare at stage B (fig. 43c). Three ossifications can be seen at stage C (fig. 43e). In Claudiosaurus (Carroll, 1981), the ulnare, intermedium and radiale are the first three bones to have finished surfaces, which suggests that these three bones may have been the first to ossify in Hovasaurus.

The radiale is a relatively small element, approximately half the size of the ulnare. The articulation with the radius is broad and slightly concave. The lateral surface of the radiale articulated with the lateral centrale, but unlike Acerosodontosaurus (Currie, 1980) there is also a small proximolateral articular facet for the intermedium (fig. 60j).

The intermedium is at least 50% longer than its maximum width. The proximal articulation with the ulna is extensive and is delimited ventrally by a low ridge where the joint ligaments inserted. The surface of the articulation with the

Figure 45. Hovasaurus boulei, SAM 9457, manus. ventral aspect. Scale = 1 cm.



ulnare is flat, and has been expanded by a ridge on the ventral surface. It is doubtful that much movement was possible at this joint. A protuberance on the medial rim of the intermedium (fig. 45) is the most dorsolateral point of origin of the extensor digitorum communis brevis.

The ulnare is the most prominent bone of the carpus. It is wider than it is long as in Thadeosaurus (fig. 60i), Youngina (fig. 60g), Acerosodontosaurus (fig. 6) and most other eosuchians. The articulation below the perforating foramen with the lateral centrale is broadened ventrally by a ridge, and the articular surface is relatively flat and incapable of much movement. The distal articular surface with the fourth and fifth distal carpals is convex, and is broader than the concave joint surfaces on the distal carpals. Rotation was therefore possible between the proximal and distal carpals. The ventrolateral surface of the ulnare is concave where the digiti minimi inserted. The dorsal surface is flat and featureless (MNHN 1925-5-50).

The pisiform would have projected posterolaterally when articulated properly with the ulna and ulnare. The ventral medial face of the bone is concave for the insertion of the flexor carpi radialis.

The lateral centrale appears to separate the intermedium and ulnare at the base of the perforating foramen, and yet apparently formed little or none of the border of that foramen.

The medial centrale is a wide bone that, like Acerosodontosaurus (Currie, 1980), articulated with the first three distal tarsals. In all three specimens of Hovasaurus where this region shows, the medial centrale has extended laterally from the primitive position seen in most Permian reptiles, and contacts the fourth distal tarsal as well. This contact prevents the lateral centrale from articulating with the third distal carpal. This specialized character exists in Thadeosaurus (Carroll, 1981), and probably in Tangasaurus (Haughton, 1924, fig. 1).

The first distal carpal is relatively small and contacts only the first metacarpal distally. In several eosuchians, including Acerosodontosaurus (fig. 60h), the first distal carpal is large enough to articulate with the first two metacarpals. The second distal carpal of Hovasaurus is larger than the first, and contacts metacarpals I and II. The fourth distal carpal is large and contacts five of the ten other carpals plus the third and fourth metacarpals. As in Thadeosaurus, the fifth distal carpal articulates with the fourth and fifth metacarpals.

The metacarpals and phalanges are known from specimens of all ages (Table 7). The first and fifth metacarpals are approximately the same length, and are about 25% shorter than the subequal second, third and fourth metacarpals. These proportions are essentially the same in Claudiosaurus and Champsosaurus (fig. 60), but in Thadeosaurus and Tangasaurus the fourth metacarpal is clearly longer than the others. The increase in symmetry of the metacarpals of Hovasaurus could be related to the use of the manus as a paddle, which is apparently the case in nothosaurs and crocodiles (J. Robinson, 1975). With the exception of the first metacarpal, each metacarpal is overlapped dorsomedially by its neighbour in Hovasaurus and Thadeosaurus. Metacarpal IV grows with strong positive allometry (Table 8) and at maturity is 13.4 mm (1.3x, 5.2 OLU) in length. This bone is the same relative length in Tangasaurus (Table 4). In contrast growth in this element in Thadeosaurus is isometric, but the mature length is significantly greater (1.6x, 6.1 OLU).

The phalangial formula is 2.3.4.5.3 for the manus. The first digit, including the metacarpal, is 47% the length of the fourth digit, the second is 68%, the third is 85% and the fifth is 64%. On the average, the fifth digit is 75% the length of the third. These proportions are about the same at any life stage so all elements probably have approximately the same coefficient of allometry during growth. The coefficient for the phalanges of the fourth digit is 1.2, which is the lowest allometric growth rate in the front limb. At maturity the fourth digit is 93% the length of the radius, or 13.3 OLU (3.5x). The fourth digit of the manus grows with negative allometry in Thadeosaurus, but at maturity the relative length of the digit (15.0 OLU, 3.9x) is greater than that of Hovasaurus.

The ventral surface of each phalanx is flattened with a shallow longitudinal groove for one of the ligaments of the palmaris communis profundus.

The penultimate phalanx of each digit is as long as or longer than the antepenultimate phalanx (or metacarpal in the case of the first digit). This characteristic has been noted in many primitive and extant reptiles, but its significance is not understood at present.

The unguals are recurved and sharply pointed distally. The flexor tubercles are not strongly developed (figs. 19, 20, 21, 22, 23, 24), and the unguals are indistinguishable from those of most other eosuchians.

Pelvic Girdle and Limb

Ilium. The three pelvic bones are known from all life stages in Hovasaurus (fig. 46). In even the largest specimens the three elements are not coossified, although the sutures have small interfingering protuberances and pits for strength.

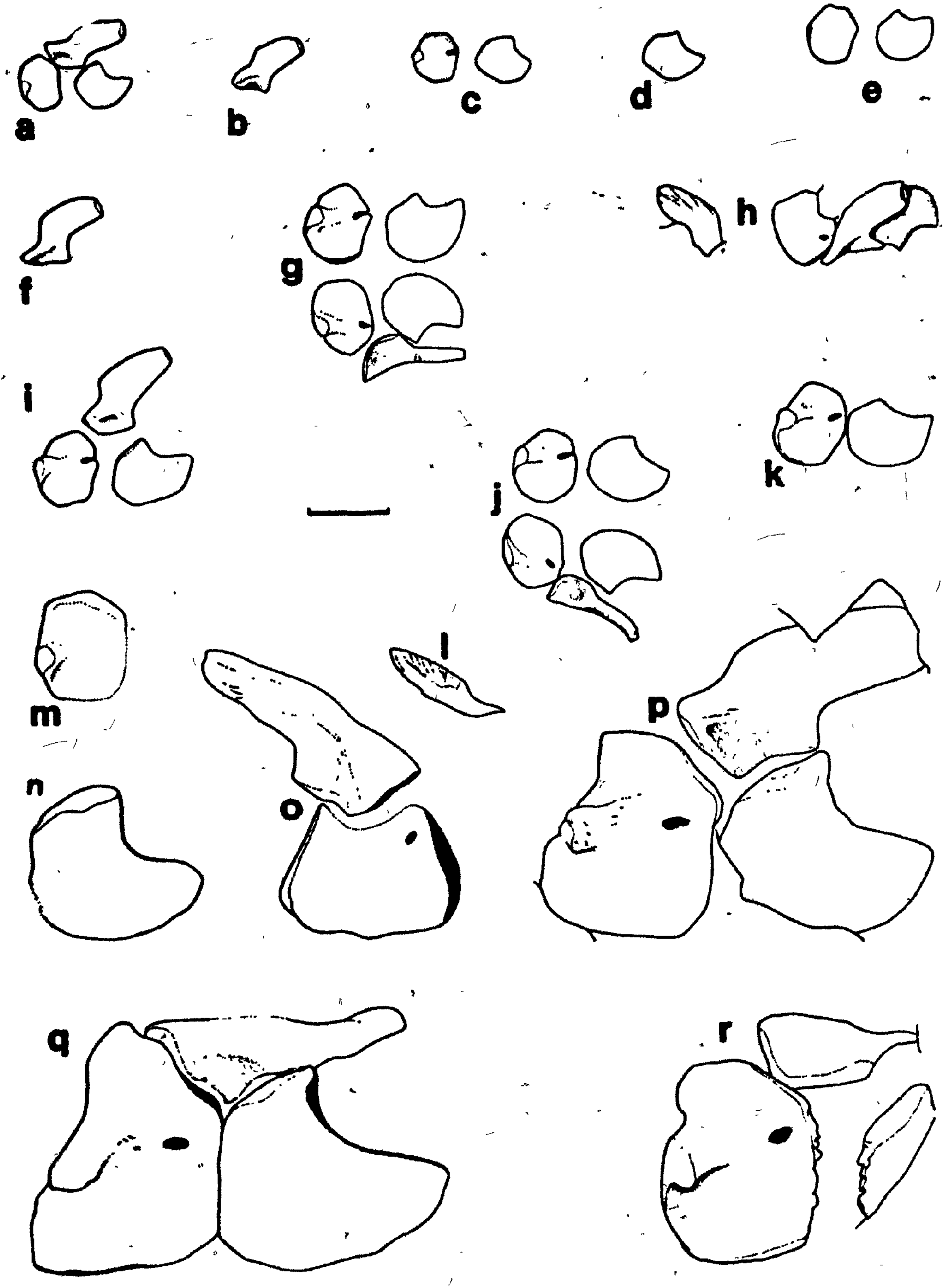
The distal end of the iliac blade has posteriorly facing, concave facet in juvenile animals (figs. 46a, b, f, h, i), which indicates that the bone was continued distally in cartilage. As an individual became more mature, the facet became relatively smaller. It has disappeared by stage F, and in the larger specimens the iliac blade terminates caudally in a point (MNHN 1908-32-24).

Two measurements were taken (Table 6) -- the length of the base (between the anterior limit of the iliopubic suture and the posterior of the ilioischiatic suture) and the length of the iliac blade (between the anterior limit of the iliopubic suture and the most caudad point of the blade). Both dimensions increase isometrically in size during growth (k_{yx}' is not significantly different from 1.0). At maturity the base is 7.3 OLU (1.9x) in length, and the blade is 13.2 OLU (3.4x). Growth is isometric in Thadeosaurus as well for these dimensions, and the base (6.6 OLU, 1.7x) and blade (13.1 OLU, 3.4x) are not significantly different from those of Hovasaurus. Compared with the average length of a dorsal centrum (x), the length of the iliac blade is the same in Acerosodontosaurus.

The ilium, as would be expected in any element where two of the major dimensions grow at almost the same rate, does not change much in outline through its life history (fig. 46).

As in most eosuchians, the acetabulum is formed mainly by the ilium in Hovasaurus. A strong ridge arches over the

Figure 46. Hovasaurus boulei, pelvic girdle. a, MNHN 1925-5-10, composite drawing from right and left sides; b, MNHN 1925-5-20, reversed image; c, MNHN 1925-5-25; d, MNHN 1908-21-8, reversed; e, MNHN 1908-32-29, composite; f, MNHN 1908-32-21, reversed; g, SAM 9460; h, MNHN 1908-32-4, ilium (medial view), ilium (lateral view, reversed image), pubis and ischium (dorsal view, reversed); i, MNHN 1908-21-2/7; j, MNHN 1908-32-22; k, MNHN 1908-21-5, composite; l, MNHN 1925-5-41, dorsomedial view of ilium; m, MNHN 1908-32-23, reversed; n, MNHN 1925-5-32, composite; o, MNHN R146, medial view of ilium, dorsal view of pubis, reversed; p, MNHN 1908-32-45, reversed; q, MNHN 1908-32-49, reversed; r, MNHN 1908-21-6. Scale = 1 cm.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acetabulum anteriorly and dorsally, and is confluent posteriorly with less prominent ridges from the ilioischiatic contact and the ventral margin of the iliac blade. This ridge system has replaced the supraacetabular buttress of protorothyridids, and permits a more powerful anterodorsal thrust of the hind limb against the pelvis for greater speed (Brinkman, 1979).

The iliac blade extends caudally far beyond the acetabulum at all life stages, and is much more extensive than that of Youngina (Gow, 1975). The external surface of the blade is concave and the internal is convex. Consequently the internal surface of the blade faces dorsomedially for attachment of the sacral ribs. This region is striated (figs. 46h, 1) by ridges and grooves for strong contacts. The length of the sutural surface on the ilium of MNHN R146 is equal to the sum of the lengths of the distal ends of the two sacral ribs, which shows that the first caudal rib did not have an osseous contact with the ilium despite its orientation.

Pubis. The pubis is a large, platelike bone that, judging from the vertical, well-ossified interpubic suture of MNHN 1908-21-16, must have been almost horizontal in the living animal.

In small specimens (fig. 46c), all pelvic elements were widely separated by cartilage. The immature pubis is oval in outline with the small protuberance to represent the "pectineal" tubercle and a posterolateral slit for the obturator foramen.

In contrast with the ilium, the allometric growth coefficients for both length (1.2) and width (1.3) of the pubis are significantly different (Table 8) from isometry. A mature pubis is wider (10.8 OLU, 2.8x) than long (8.6 OLU, 2.2x) in Hovasaurus. Growth in Thadeosaurus is isometric (Table 3), and the width (9.6 OLU, 2.5x) is not significantly different from Hovasaurus. The length (6.8 OLU, 1.7x) is relatively smaller than in the pubis of the more aquatic genus.

The proportions of the pubis show that Hovasaurus was broad in the pelvic region. The ratio of pubis width to anteroposterior length in the adult is 1.27 compared with 1.47 in Thadeosaurus and 1.22 in Acerosodontosaurus. In Youngina, the ratio is less than 1.00, but the pubis is not well ossified.

The pubis contributes only a small area (fig. 46p) to the acetabular surface.

There is a powerful "pectineal" tubercle that terminates anteroventrally in unfinished bone. It can extend as much as .7x below the main surface of the pubis. Longitudinal striations along the finished bone of the ventromedial surface of the tubercle would have served for strengthing the attachment of the ambiens and pubotibialis muscles.

The anterior margin of the pubis medial to the tubercle curves anteromedially and meets the other pubis at the midline in an acute angle. The rim is sharply offset from the shallowly concave ventral surface of the main body of the pubis.

The tubercle extends posteriorly as a ridge that decreases in height and ends a short distance anterolateral to the obturator foramen for the obturator nerve. The internal opening of the obturator foramen (fig. 46o) is lateral to the position of the external opening.

The suture with the ischium (fig. 46r) is strong and interfingering. There is no thyroid fenestra such as may have existed in Acerosodontosaurus. A notch in the back of the pubis (fig. 61f) of Youngina was attributed to incomplete ossification (Gow, 1975). However, a notch as pronounced as this does not appear in the posterior margin of the pubis of Hovasaurus or Thadeosaurus at any life stage. It is possible that Youngina did have an incipient thyroid fenestra.

Ischium. The appearance of the ischium does not change much with increased size in Hovasaurus (fig. 46), although the curvature of the medial margin tends to be greater in juveniles. The degree of positive allometric growth ($k_{yx}' = 1.2$) in the length and width of the ischium is about the same as that of the pubis. A large specimen would have an ischium 10.9 OLU (2.8x) long and 8.9 OLU (2.3x) wide.

Growth in Thadeosaurus is isometric, and the mature ischium is 9.7 OLU (2.5x) by 7.6 OLU (2.0x), which is significantly smaller than Hovasaurus.

An anterolaterally oriented facet on the ischium forms about a quarter of the area of the acetabulum. A ventral ridge borders the acetabular facet, and is scarred for attachment of joint ligaments.

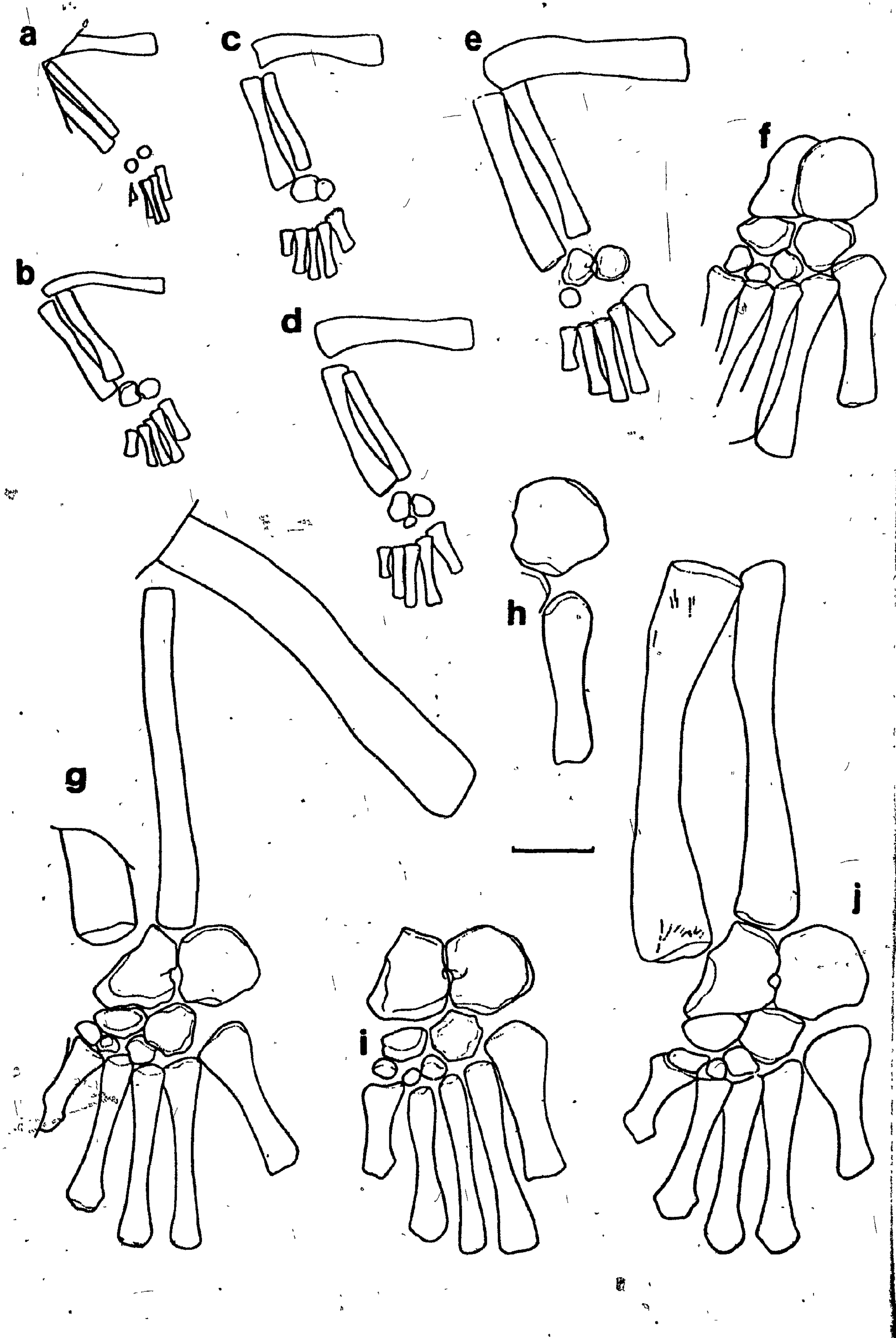
The ventral surface of the ischium is flat in most specimens, and slightly concave in others. The main part of the ischium would have faced more laterally than the pubis.

Femur. The femur (figs. 47, 48) is a more gracile bone than the humerus. In juveniles the ossified portion is longer than the humerus. Allometric growth of the femur is positive ($k_{yx}' = 1.3$), but not as much as the humerus. When full grown, the femur is 25.2 OLU (6.5x) long. The femur of Tangasaurus falls within the expected range of variation for Hovasaurus (Table 4). In Thadeosaurus, the femur increases isometrically in length to reach 23.2 OLU (6.0x) at maturity, which is not significantly different from the femur of Hovasaurus.

The entire proximal end of the femur is unfinished bone in immature specimens, and can be concave in the smallest ones. The proximal end of one mature specimen, MNHN 1908-32-49 (fig. 48j), is well exposed. As in other eosuchians, the articular head of Hovasaurus turns markedly dorsally, and is well differentiated from the internal trochanter. The articulation is oval, and its longitudinal axis slopes anterodorsally about 45° when the distal condyles are horizontal. This is fundamentally the same in Thadeosaurus. The long axis of the articular surface is about 40% longer than the greatest width of the surface measured perpendicular to the axis, and is equivalent to 1.2x. A cartilaginous head would have covered this slightly convex surface of unfinished bone. The acetabulum is about 40% longer than the ossified head of the femur, suggesting that there was either a great deal of cartilage involved in the joint, or that the head of the femur was capable of moving a great deal in the acetabulum.

The internal trochanter for the tendinous insertion of the puboischiofemoralis externus is well developed and makes up more than half of the dorsoventral height of the proximal head. It terminates in an oval facet with a ventromedial orientation. This is connected proximodorsally by a sharp ridge of finished bone to the proximal articulation. The femur is concave anterior to the internal trochanter with longitudinal scarring for the puboischiofemoralis internus muscle (fig. 48j), and bears a short ridge near the distal end of the trochanter. This process can be seen in Thadeosaurus (MNHN 1908-11-8) also, and probably marks the insertion of the caudifemoralis muscle.

Figure 47. *Hovasaurus boulei*. Femur (posterior view), tibia (posterior), fibula (anterior) and tarsus (dorsal). a, MNHN 1925-5-20, reversed image; b, MNHN 1925-5-18; c, 1908-32-21, reversed; d, MNHN 1908-21-2, reversed; e, MNHN 1925-5-41; f, MNHN 1925-8-14; g, MNHN 1908-32-24; h, MNHN 1908-21-6, calcaneum and metatarsal V, reversed; i, MNHN 1925-5-61; j, 1908-21-14, reversed. Scale = 1 cm.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The distal head of a mature femur is exposed only in SAM 9457. The femoral shaft curves posteroventrally at the distal end. The paired condyles are not greatly differentiated from each other, and face distally. The changes are correlated with the greater ability of eosuchians to bring their limbs under the body when moving quickly.

There is a relatively deep but narrow intercondylar fossa for the tendon of the quadriceps muscle on the dorsal surface of the distal end of the femur. Ventrally, the popliteal area of primitive reptiles is represented by a shallow depression, The distal end is scarred near the articular surface on the anterior and ventral surfaces for the joint ligaments.

Tibia. The coefficient of allometry for the tibia of Hovasaurus is 1.3, so the length of this bone is relatively greater in adults than juveniles. The length of this bone is 21.3 OLU (5.5x), approximately 10% longer than the fibula. The tibia of Tangasaurus falls within the range of variation for Hovasaurus. The tibia of Thadeosaurus attains almost the same length (20.9 OLU, 5.4x) by means of isometric growth.

The anteroposterior width of the proximal head is about 20% of the total length of the tibia, and is about the same absolute width as the distal end of the femur. The mediolateral width is only slightly less than the anteroposterior width, but the proximal head is flattened on the flexor surface. There is a pair of shallow concavities on the proximal articular surface for the femoral condyles.

The tibia is strongly arched so that the medial (flexor) side is longitudinally convex. The diameter of the shaft is about 80% that of the femur, and is equivalent to 12% of the total length of the tibia.

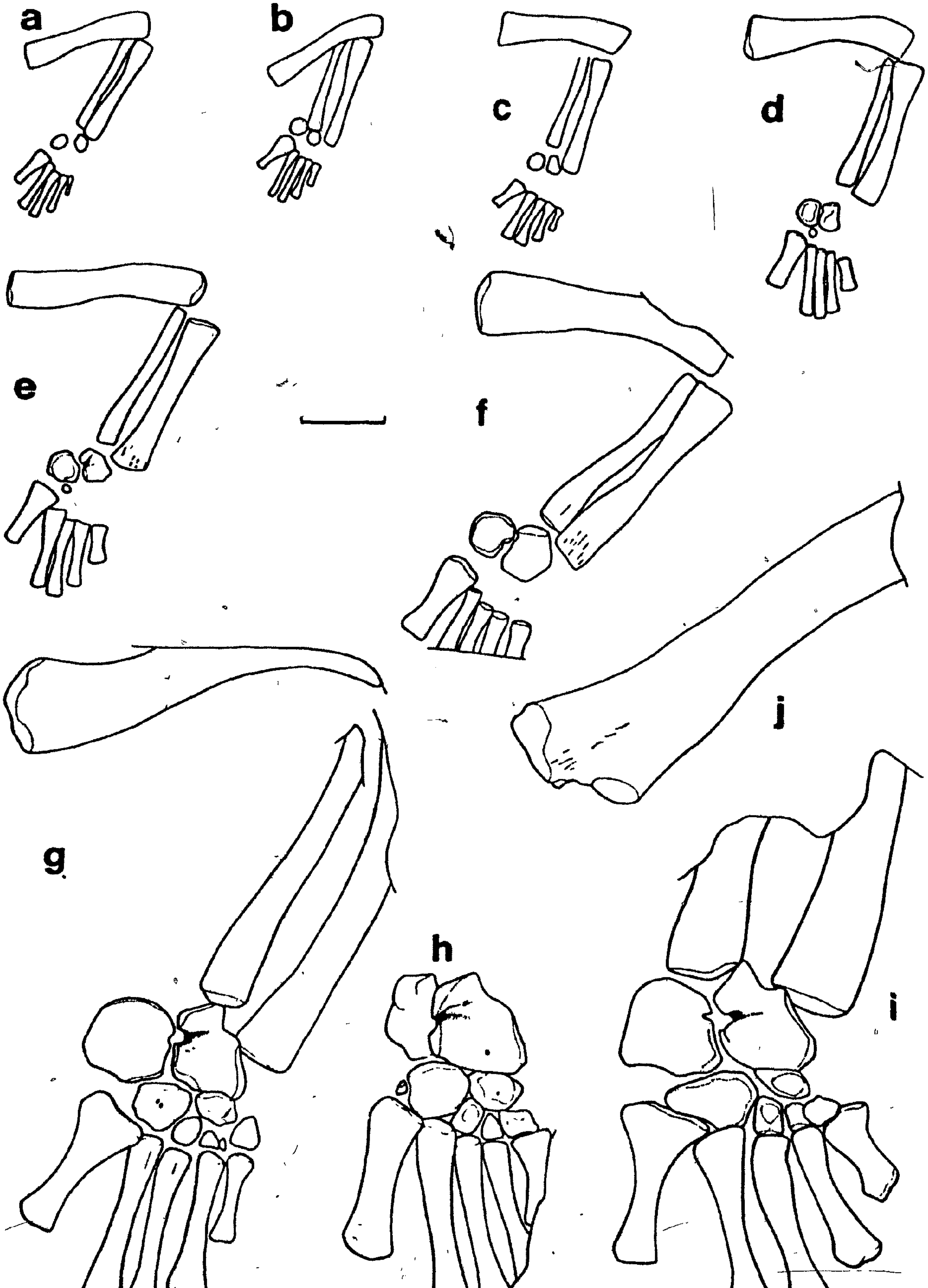
A well-developed ridge extends from the proximal articulation on the anterior surface, twists to the medial edge of the anterior surface, and continues to the distal end (fig. 21). The medial edge of the ridge is well defined, and often bears a pronounced tuberosity for the puboischiotibialis as in protorothyridids (Reisz, 1980), Acerosodontosaurus (fig. 12e) and Thadeosaurus.

A second ridge originates near the proximal head in the middle of the posterior face. It runs diagonally across the posterior surface to the medial edge (MNHN 1908-21-14) where it forms a ridgelike prominence just distal to the halfway point along the longitudinal axis of the bone. This feature is also found in protorothyridids (Reisz, 1980).

Fibula. Positive allometric growth occurs at approximately the same rate as that of the tibia, and at maturity the fibula is 19.2 OLU (5.0x) long.

The maximum diameter of the proximal head is 11% the length of the bone, and only 17% greater than the diameter

Figure 48. <u>Hovasaurus</u> <u>boulei</u>. Femur (anterior view), tibia (anterior view), fibula (posterior) and tarsus (ventral view). a, MNHN 1925-5-10; b, MNHN 1925-5-25; c, MNHN 1908-32-29; d, MNHN 1908-21-7; e, MNHN 1908-21-5; f, SAM 9459; g, MNHN 1925-5-32; h, MNHN 1908-32-68; i; MNHN 1908-21-10, reversed; k, MNHN 1908-32-49, reversed. Scale = 1 cm.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of the shaft. The distal end expands to 16% of the total length of the bone.

The proximal half of the bone is convex medially (figs. 47b, c, g, j, 48g), whereas the medial margin is concave distally when viewed in anterior or posterior aspect. The plane of the proximal head is twisted about 45° on the distal head. The distal articulation is mediolaterally elongate, has a convex surface at maturity, and tends to face more medially than laterally.

Pes. The pes of tangasaurids has been described recently by Brinkman (1979) as part of a study on the structural and functional evolution of the diapsid tarsus. Although some overlap is inevitable, the pes of Hovasaurus is being redescribed here from the viewpoint of growth and comparative anatomy.

The tarsus is composed of seven elements at maturity (figs. 47f, g, i, j, 48i), although an additional element may have fused into the fourth distal tarsal. As in the carpus, the elements tend to taper ventrally so that the tarsus would have been arched when properly articulated. A distinct intratarsal joint has developed between the proximal elements (astragalus, calcaneum, centrale) and the distal tarsals (Brinkman, 1979).

The tarsus is fully ossified by stage F in Hovasaurus, but stages D and E are not represented. In Thadeosaurus it is ossified at the equivalent of stage D. In even the most juvenile specimens of the aquatic genus the astragalus and calcaneum have started to ossify (figs. 47a, 48a). By stage B (figs. 47d, 48d) a third ossification has appeared. This one cannot be identified by its position, but may be the fourth distal tarsal as in *Claudiosaurus* (Carroll, 1981). The remaining tarsals appear in stages D, E or F.

One specimen, MNHN 1908-32-68 (fig. 48h), has the seven tarsals normally seen, plus a small bone in the position of the fifth distal tarsal in other reptiles. This bone is less than half the dorsoventral thickness of the other tarsals and cannot be seen in dorsal aspect (fig. 47f) of the same specimen. Harris and Carroll (1977) have suggested that the fifth fuses into the fourth distal tarsal in large specimens, and is in the process of doing so in this specimen.

The astragalus and calcaneum have been shortened proximodistally from the condition seen in primitive eosuchians (Carroll, 1976b; Reisz, 1981). The astragalus of *Hovasaurus* is about 1.5x long.

The astragalus has a relatively small dorsal facet for the fibula, and a more extensive, dorsomedially concave articulation for the tibia. A groove passes diagonally across the lateral face of the astragalus and forms the medial border of the perforating foramen. The extensor surface is shorter below the perforating foramen than the flexor surface in the same area. On the flexor surface, a pronounced ridge runs from the ventral margin of the perforating foramen to the dorsal edge of the articulation with the tibia. Dorsal to this ridge there is a deep transverse groove for the perforating artery. The distal surface of the astragalus is convex in longitudinal and transverse section, and articulates with both the centrale and fourth distal.

The calcaneum is almost flat medially with only a slight emargination for the perforating foramen. There is a low ridge of bone on the extensor surface to strengthen the articulation with the astragalus proximal to the perforating foramen. Most of the flexor surface is relatively flat, although there is a low protuberance of bone near the articulation with the astragalus below the perforating foramen. The medial half of the ventral (distal) edge articulates with the fourth distal tarsal, and this joint is strengthened by a ridge on the extensor surface. The calcaneum becomes very thin lateral to the distal articulation, and tends to be unfinished bone along the convex margin. There is no evidence of a pronounced "heel" as in Youngina (Broom, 1921), or a muscle scar as in Kenyasaurus (Brinkman, 1979) for the origin of the adductores digit five.

The lateral centrale is transversely elongate (figs. 47f, g, j) in dorsal (extensor) aspect. There is an elongate, troughlike depression on the proximal surface for articulation with the astragalus. Laterally the centrale broadly overlaps the fourth distal (figs. 48h, i). A convex articular surface on the distal end has distinct but continuous contacts for the first three distal tarsals.

The first two distal tarsals are relatively small but seem to have articulated with two metatarsals each (Brinkman, 1979). The third distal tarsal has double the proximodistal length of the first two, and has five facets (figs. 47f, g) around the extensor surface for articulation with the centrale, the second and fourth distal tarsals, and metatarsals III and IV.

The fourth distal tarsal articulates with all the tarsals except the first and second distals, and supports the fourth and fifth metatarsals. The lateral surface is unfinished bone in all specimens in which it can be seen, and there is a gap between the fifth metatarsal and calcaneum in most specimens. The possible fifth distal of MNHN 1908-32-68/1924-8-14 (fig. 48h) fills part of this space. In MNHN 1908-21-10 (fig. 48i) this area has been infilled on the flexor surface by a lateral extension of the fourth distal that may be the coossified fifth distal.

The metatarsals and phalanges are known from specimens of all ages (Table 7). The length of the metatarsals increase from I to IV, and V decreases to the length of III. In the smaller specimen of <u>Tangasaurus</u> (SAM 6231), metatarsals II and V are

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equal in length and III and IV are subequal. The larger specimen of *Tangasaurus* (SAM 6232) has an assymmetrical metatarsus like *Hovasaurus*.

With the exception of the first metatarsal, each element of the metatarsus is overlapped dorsomedially by its neighbour. The overlapping nature in *Hovasaurus* and other eosuchians probably indicates a consolidation of the metatarsus in response to an increase in the propulsive force passing through it (Brinkman, 1979). The head of the fifth metatarsal is greatly expanded from the primitive condition seen in *Galesphyrus* where the ratio of proximal width to shaft length is .33, compared with .53 in *Hovasaurus*, .53 in *Tangasaurus* and .63 in *Kenyasaurus*. The proximal end of metatarsal five is expanded in *Youngina* (Broom, 1921). The expansion of the proximal head may represent the initial change leading to the development of the hooked fifth metatarsal of prolacertids and later diapsids. The articulation between this element and the fourth distal tarsal is flat in tangasaurids and there would have been little movement possible here (Brinkman, 1979).

Metatarsal IV grows with the same rate of positive allometry as Metacarpal IV (Table 8), and at maturity is 10.9 OLU (2.8x). The fourth metatarsal of *Thadeosaurus* grows isometrically but is slightly longer (11.6 OLU, 3.0x) than that of Hovasaurus. The length of metatarsal IV in Tangasaurus falls within the range of variation of Hovasaurus.

The phalangeal formula is 2.3.4.5.4 for the pes. The proportional lengths of the digits are relatively constant throughout life (Table 7), and must have grown at approximately the same rate. The coefficient of allometry for digit IV, excluding the metatarsal, is high (1.4). The combined length of the fourth metatarsal and phalanges is equal to that of the tibia in large specimens, and amounts to 21.2 OLU (5.5x). The fourth digit of Thadeosaurus apparently grew isometrically to approximately 22 OLU in length. Tangasaurus (Table 4) has a fourth digit that is significantly shorter than that of Hovasaurus, and amounts to only 4.9x.

The first digit, including the metatarsal, is 40% the length of the fourth, the second is 64%, the third is 84% and the fifth is 83%. On the average, digit V is 99% the length of digit III. The proportions are very close to this in Tangasaurus, Thadeosaurus and Kenyasaurus.

In digit I of Hovasaurus, the first phalanx is as long as the first metatarsal in only one of fifteen specimens. In digit II, the penultimate phalanx is as long as or longer than the antepenultimate in 58% of the specimens, in digit III 91%, in digit IV 40% and in none of eleven specimens of digit V. This contrasts strongly with the manus where the penultimate phalanx exceeds the antepenultimate bone 90% of the time. This strongly suggests that there was a functional difference between the digits of the manus and pes. Possibly the manus was adapted better for grasping food. Whatever the reason for the difference, it also seems to be present in Thadeosaurus. The penultimate does not consistently exceed the antepenultimate in either the manus or pes of Tangasaurus (Table 7). It is apparent that the relative length of the penultimate phalanx cannot be correlated with aquatic lifestyles (Section VII).

In Hovasaurus and Tangasaurus the largest phalanx in the foot is the first one in digit V. The first phalanx in digit IV is the largest in the pes of Kenyasaurus. In Thadeosaurus (all ages), phalanges IV-1 and V-1 are subequal.

The unguals of the pes of Hovasaurus are similar to those of the manus, but tend to be longer in equivalent digits.

Integument of Hovasaurus

Piveteau (1926, Pl. X, fig. 3) described a small specimen of skin impression that he found with the remains of Hovasaurus at Mt. Eliva. The scale-like impressions are small, ranging from one to two millimetres in diameter. The smaller ones are round, and the larger tend to be penta- or octagonal because they are more closely packed. There is no consistent arrangement, and they could be osteoderms. The presence of granules of this size and shape in the caudal region of some specimens of Hovasaurus indicates that this specimen (MNHN 1925-5-33) could be from the tail of this genus.

Epidermal scales can be seen in MNHN 1908-21-24 on the ventral surface between the sternum and gastralia. The scales are oval, and are all about the same size. The anteroposterior length ranges between 2.5 and 3.0 mm, and the width between 2.0 and 2.5 mm. Each scale on the right side of the specimen overlaps the anteromedial and anterolateral portions of the two scales posterior to it. Saurosternon (Carroll, 1975, fig. 6) has scales in the sternal region that are approximately the same size and configuration as those of Hovasaurus.

Epidermal scales are present in the anterior caudal region of Kenyasaurus (Harris and Carroll, 1977). Dorsally they are rectangular and diverge from the midline posteriorly. On the ventral surface the scales are square and aligned parallel to the centra.

Epidermal scales near the tail region of Tangasaurus (SAM 6231) are elongate rhomboids in outline, eight millimetres by three (Haughton, 1924). Each scale has a low, longitudinal median ridge. The free posterior border of each scale overlaps the anterior edges of the two directly caudad.

There is no evidence in tangasaurids of dermal ossicles along the spine as in Youngina (Gow, 1975) and Heleosaurus (Carroll, 1976a).

Gastralia (ventral dermal scales) underlie the abdomen between the sternum and pubes (figs. 20, 22, 23). They are present in the smallest specimens (MNHN 1925-5-27). Gastralia increased in size as the animal grew, but the number per individual remained constant. Approximately forty segments can be counted along the midline of each of four specimens, which gives an average of four gastralia per vertebra. Each includes a median piece with an anteriorly oriented apex on the midline, and one or two pairs of long lateral segments. The first two have one lateral section per side (MNHN 1908-21-24), the last one has none (MNHN 1908-21-16), and four before the ultimate have one. There are two laterals on each side of every remaining median segment.

There is rostral process on the midline of this median section (fig. 23) that is often fused to the preceding ventral scale. The bone extends posterolaterally as much as 3.5x, and tapers to a needle-like point. The first lateral segment is closely appressed to the anterior surface of the median element, and sometimes reaches the midline proximally. The proximodistal length of this segment can be as much as 5x (MNHN 1908-21-2/7), although the maximum thickness is only .2x. It does not extend far beyond the posterolateral end of the median element before it picks up the proximal end of the second lateral section on its anterior surface. The more lateral segment is the longest of the three, up to 5.5x (MNHN 1908-21-2/7), and is slightly thicker (.3x) than the first lateral scale. The distal end does not taper as gradually as the proximal end.

Gastralia are poorly known in most eosuchians, but seem to have been universally present in the living animals. The ventral armature of Claudiosaurus is well preserved (Carroll, 1981), and is numerically and morphologically indistinguishable from that of Hovasaurus. The shape and size of the gastralia in Thadeosaurus, Kenyasaurus, Acerosodontosaurus and Heleosaurus all indicate that a similar pattern of ventral armature existed in these genera.

Considering the tendencies in the ventral bones of Hovasaurus towards lowering the centre of gravity, it is surprising that the gastralia are not pachyostotic as in Champsosaurus (Russell, 1956).

DISCUSSION

Hovasaurus was the most highly adapted for swimming of any known tangasaurid eosuchian. The most conspicuous anatomical adaptations are in the tail, which is at least double the snout-vent length. The caudal neural spines are taller than the spines in the dorsal region. They contact along the midline above the neural canal to restrict the dorsoventral flexure of the tail. The haemal spine mimics the shape and size of the associated neural spine, so the tail is dorsoventrally symmetrical. This suggests that the animal swam beneath the surface of the water. If it had been swimming primarily on the surface, the haemal spines probably would have been longer than the dorsals. Lateral undulations of the tail would have provided the necessary force to push the body through the water as it does in sea snakes (Hydrophiidae), semi-aquatic lizards (iguanids, agamids, varanids), crocodilians, caudate amphibians and many elongate fish.

Pachyostosis of the ribs is another indication of the aquatic habits of Hovasaurus. Enlargement of the rib shaft has occurred in mesosaurs, some nothosaurs and sirenian mammals as well, and serves to increase the specific gravity of the animal.

The scapular blade is very short, as it is in Mesosaurus, ichthyosaurs, nothosaurs and plesiosaurs. It should be pointed out that some terrestrial animals, such as varanid lizards, also have low scapular blades. More importantly, the ventral portion of the pectoral girdle is massive to lower the centre of gravity for stability underwater, to increase the specific gravity, and for muscle attachment. As in plesiosaurs, the scapulae of Hovasaurus meet at the midline to firmly brace the girdle during the power stroke.

The presence of a large mass of pebbles in the abdominal cavity is comparable with a similar mass in plesiosaurs. This would have increased the specific gravity of the animal by five to ten percent, shifted the centre of gravity posteroventrally and stabilized the animal in the water.

Delayed ossification is a characteristic of many aquatic tetrapods. For example, the carpal and tarsal elements of nothosaurs, placodonts, marine crocodiles and mosasaurs never fully ossified. This is not the case in Hovasaurus. The total lengths of the humeri of Thadeosaurus and Hovasaurus juveniles are composed of about 16% cartilage. The obturator foramen is surrounded by bone by stage B in both genera, the carpus is ossified by stage D, and the scapula and coracoid coalesce by stage E. The tarsals are all ossified in Thadeosaurus by stage D, but the tarsus of this life stage is not known in Hovasaurus. The ectepicondylar foramen is encircled by bone by stage F in Thadeosaurus, and not until stage G in its more aquatic relative. The sternal plates, which fuse into a single element by stage F in Hovasaurus, do not coossify until stage G in Thadeosaurus. Therefore, ossification is not delayed in Hovasaurus. At maturity this animal could have moved efficiently on land to lay eggs or extend its range.

Limb proportions are an indication of aquatic habits in Hovasaurus. This genus is similar to nothosaurs and plesiosauroids in that the humerus to femur ratio is less than 1.0 in juveniles, but greater than 1.0 in adults. The forearm is about half the length of the humerus in Hovasaurus, Mesosaurus and nothosaurs at maturity. The metacarpus is symmetrical, and digit IV is shorter relative to the first three digits of the manus than in Thadeosaurus.

Despite the presence of a powerful tail for swimming, Hovasaurus had powerful front limbs that, by analogy with other aquatic genera, were used when swimming. The manus, like that of Claudiosaurus, has become broader and more symmetrical distally than in Thadeosaurus. The similarity in shape of the manus to that of other aquatic genera (extinct and living) suggests that there could have been webbing between the digits. The front limb would have acted as an oar or paddle when swimming, rather than as an underwater "wing" (J. Robinson, 1975). Like a paddle, the distal end of the front limb is broad and flattened to maximize drag. The front limb could have been used in the same manner that a duck uses its webbed feet, and probably also behaved as a rudder for controlling direction. On land or the bottom of a body of water, the front limb was not so highly adapted that it couldn't be used for walking.

The pelvic girdle and limb do not show any aquatic adaptations. The tibia is about 85% the length of the femur, a normal ratio for a terrestrial animal, compared with 50% in Askeptosaurus (an aquatic eosuchian) and many nothosaurs. The relative lengths of the digits of the pes are not significantly different from those of Thadeosaurus. It would appear that the hind limb was used for walking on land or on the floor of a body of water. On the basis of the well developed limb with a large internal trochanter, the puboischitibialis insertion on the tibia and the perforating foramen in the tarsus, Brinkman (1979) concluded that tangasaurids were capable of terrestrial locomotion.

The coefficients of allometry were calculated for 41 common dimensions in Thadeosaurus and Hovasaurus (Tables 3, 8). Differences in the coefficients between the genera are only considered significant when the coefficients of Thadeosaurus fall outside the 95% confidence intervals of the corresponding coefficients of Hovasaurus. There is no significant difference in allometric growth rates for fifteen dimensions, but the coefficient is significantly higher in Hovasaurus for 22, and lower than Thadeosaurus for four. These figures were calculated on the basis of the preserved, ossified portions of the bones, and do not make allowance for cartilaginous extensions. As previously indicated, gaps between the bones of the articulated skeletons of juveniles are the same relative size in Thadeosaurus and Hovasaurus. This indicates that the same percentages of the total lengths of the limb bones in juveniles were formed by cartilage in specimens of the two genera. The percentage composition of cartilage therefore does not account for the higher coefficients of allometry in Hovasaurus. This can be confirmed by an alternate method. Even if the length of the humerus of one of the smallest specimens of Hovasaurus (MNHN 1908-21-8) is increased by 20% (the maximum possible percentage of cartilage that would have filled the gaps between the humerus and adjacent bones in articulated specimens), the total length would have been only 12.3 mm. The expected length of the ossified portion for this element in a specimen of Thadeosaurus the same size is 17.4 mm, and cartilage would have increased this length. It appears that the limb elements of immature specimens of the more terrestrial genus were significantly longer than in Hovasaurus even if cartilage is included, and that the differences in allometric coefficients are real.

If we exclude the limb elements of the two genera, there are thirteen dimensions in the vertebrae and limb girdles in which the growth coefficients are known for both genera. Of these, there is no significant difference in seven, and the coefficients are higher in three dimensions of Thadeosaurus and lower in three. This is another indication that the differences in allometric growth rates are biologically significant. If the coefficient was consistently higher in Hovasaurus for all dimensions, it would show that differences in the coefficients of the two genera are related to negative allometric growth of the dorsal centra (x) in Hovasaurus.

It is significant that the degree of allometry is generally higher in the larger animal, Hovasaurus. Usually, the opposite effect is discovered in closely related animals because allometric coefficients that differ markedly from 1.00 are strongly size-limiting (Dodson, 1975b).

In juveniles, the limb bones of Thadeosaurus are longer than those of Hovasaurus (figs. 4a, b), and the genera are distinguishable by measurement. This is a clear indication of functional differences in the use of the limbs in the two genera as juveniles. It is possible that a newborn Hovasaurus entered the water as sea turtles do, and seldom ventured onto land until mature. In adults, the higher allometric growth in Hovasaurus has resulted in relatively longer limb bones, and this genus could have been as mobile on land as Thadeosaurus. Dodson (1975b) suggested that increased relative length of limbs in Sceloporus adults is related to the increase in home range. Similarly, Hovasaurus adults could have spent more time on land for range dispersal, mating or laying eggs.

Differences in the relative lengths of the limb bones of Thadeosaurus and Hovasaurus are evident from the unit measurements based on x and the OLU. The two systems correlate well, although one is a linear comparison and the other is geometric. Even though most of the bones in Hovasaurus grow with positive allometry, comparison of unit measurements based on the orthometric linear unit has biological significance provided the interspecific size changes are isometric (Currie, 1978). Unit measurements of nineteen dimensions measured in both genera can be compared. Of these, there are no significant differences in thirteen cases. Five unit measurements (length of neural spine, length of humerus, length and width of pubis, width of ischium) are greater in Hovasaurus, whereas the length of the fourth metacarpal is significantly less than in Thadeosaurus.

Unit measurements based on OLU and x are not biologically significant for widths of limb bones, particularly if comparisons are being made between animals of different mature sizes (Currie, 1978). Bone widths are more closely related to the weight of the animal than to the function of the limb. Because Thadeosaurus and Hovasaurus have overlapping size ranges, it can be shown on scatter diagrams (fig. 4c) that differences in width measurements are insignificant.

VI

THE RELATIONSHIP OF THE TANGASAURIDAE TO OTHER PRIMITIVE DIAPSIDS

Figure 49. Skulls of primitive reptiles in lateral view. a, *Protorothyris*, after Heaton and Reisz, unpublished manuscript, 1979;

b, *Araeoscelis*, after Vaughn, 1955;

c, *Petrolacosaurus*, after Reisz, 1977;

d, *Palaeagama*, after Carroll, 1975a;

e, *Paliguana*, after Carroll, 1975a;

f, *Daedalosaurus*, after Carroll, 1978;

g, *Youngina*, after Carroll, 1977;

h, *Acerosodontosaurus*, after Currie, 1980;

i, *Heleosaurus*, after Carroll, 1976a;

j, *Claudiosaurus*, after Carroll, 1981;

k, *Askeptosaurus*, after Robinson, 1967;

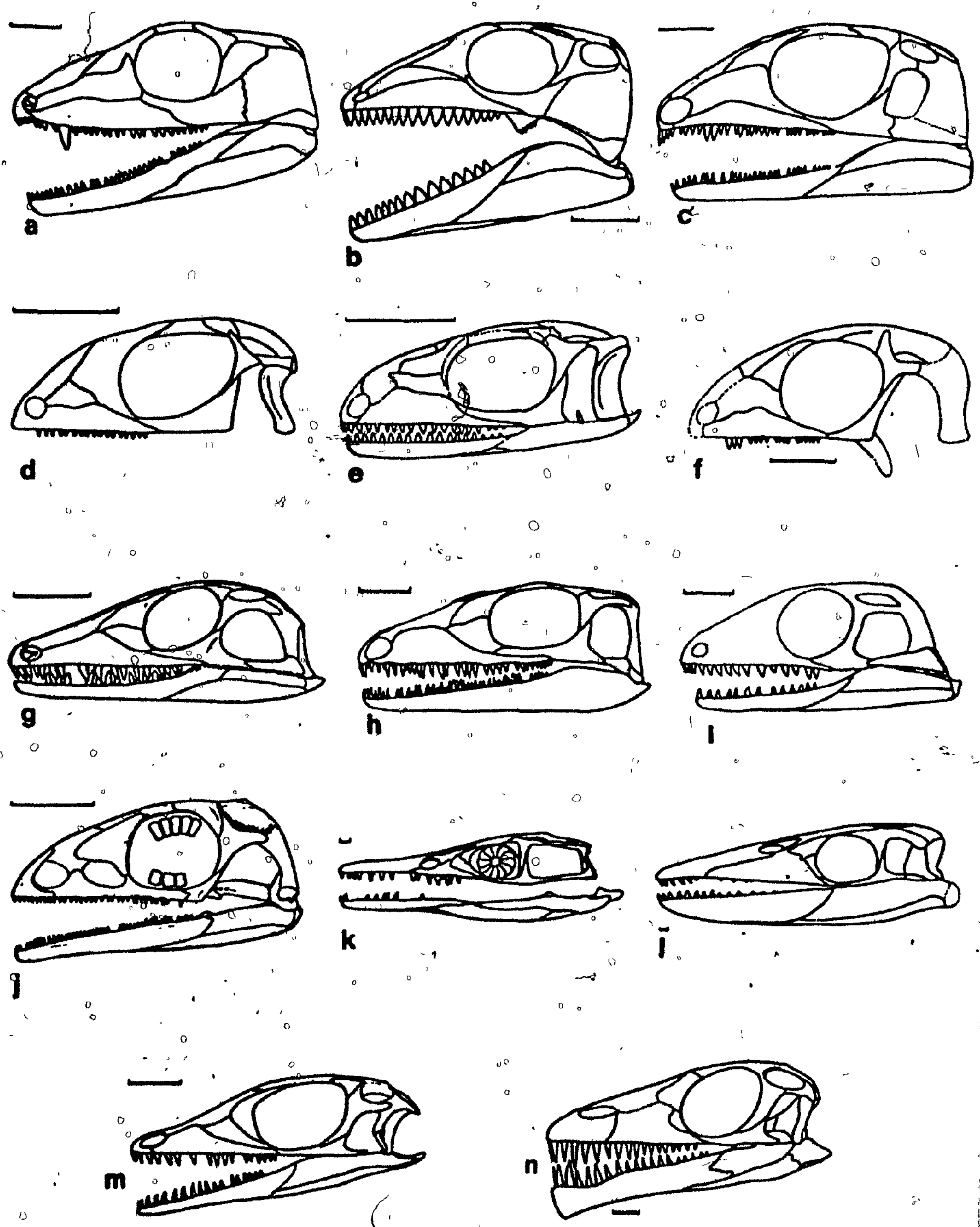
l, *Thalattosaurus*, after Merriam, 1905;

m, *Prolacerta*, after Robinson, 1967;

n, *Tanystropheus*, after Wild, 1973;

o, *Weigeltisaurus*, based on the plates of the original description (Weigelt, 1929).

Each scale = 1 cm.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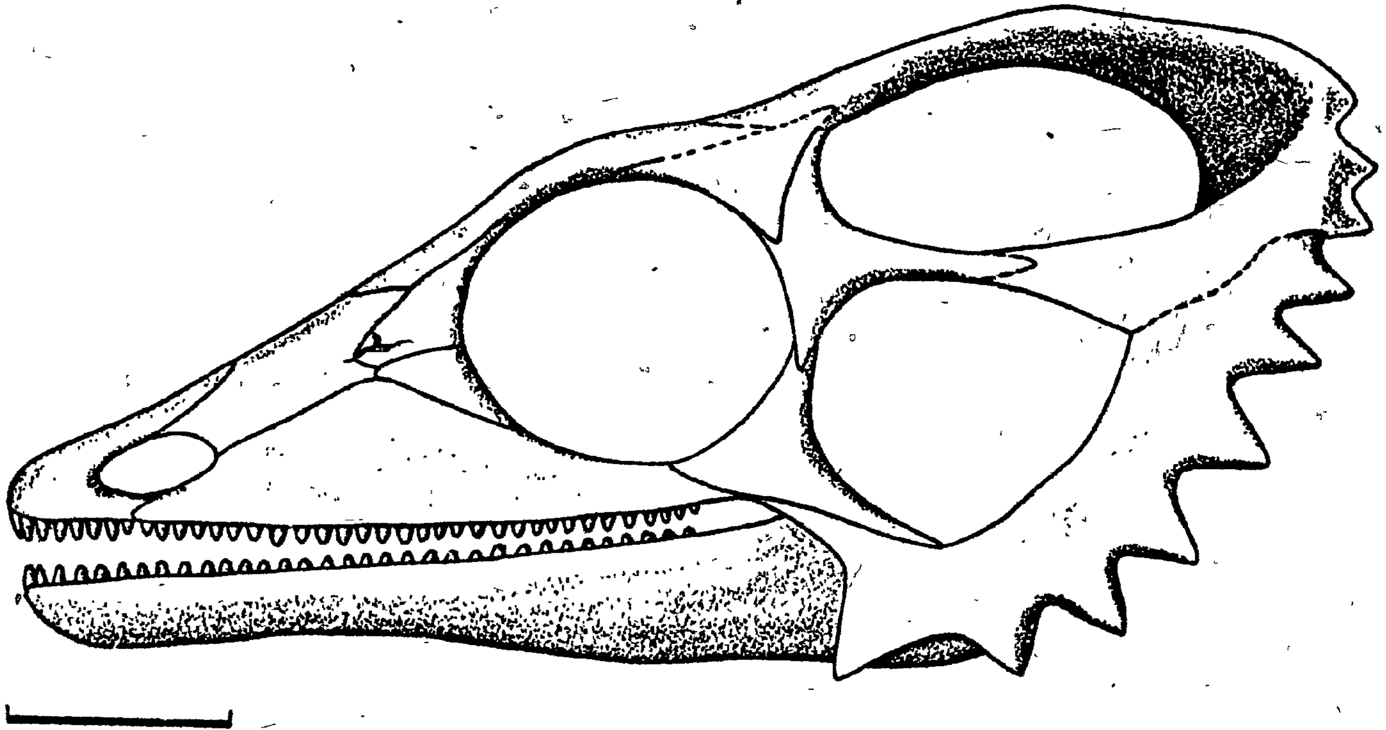

Figure 50. Skulls of primitive reptiles in dorsal view. a, Protorothyris, after Heaton and Reisz, in preparation; b, Araeoscelis, after Vaughn, 1955;
c, Petrolacosaurus, after Reisz, 1977;
d, Palaeagama, after Carroll, 1975a;
e, Paliguana, after Carroll, 1975a;
f, Youngina, after Carroll, 1977;
g, Acerosodontosaurus, after Currie, 1980;
h, Claudiosaurus, after Carroll, 1981;
i, Askeptosaurus, after Robinson, 1967;
j, Thalattosaurus, after Merriam, 1905;
k, Champsosaurus, Russell, 1956;
l, Prolacerta, after Robinson, in prep.;
m, Macrocnemus, after Kuhn-Schnyder, 1962;
n, Tanystropheus, after Wild, 1973.
Each scale = 1 cm.

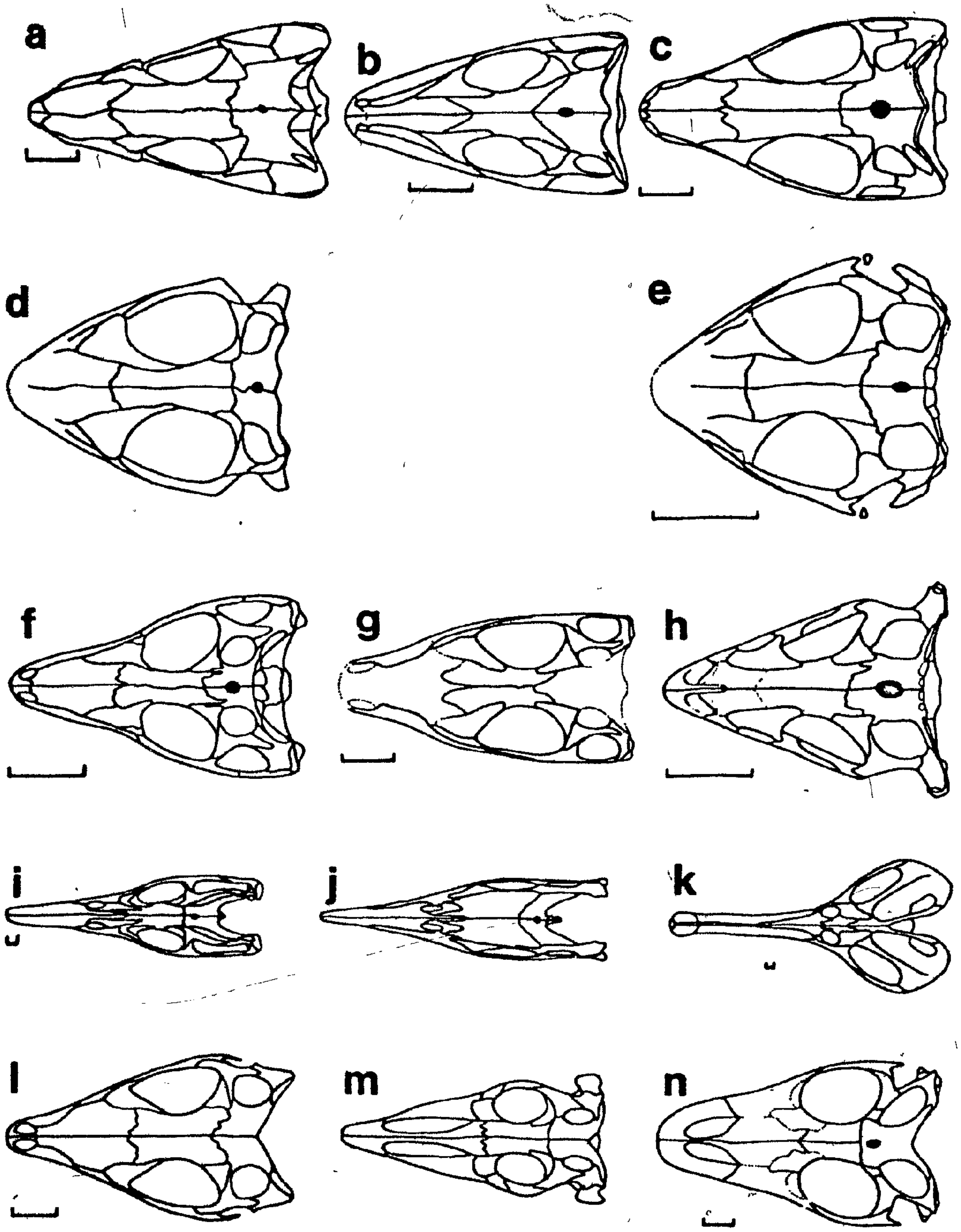
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Figure 51. Skulls of primitive reptiles in palatal view. a, <u>Protorothyris</u>, after Clark and Carroll, 1973; b, <u>Araeoscelis</u>, after Vaughn, 1955; c, <u>Petrolacosaurus</u>, after Reisz, 1977; d, <u>Youngina</u>, after Carroll, 1977; e, <u>Heleosaurus</u>, after Carroll, 1976a; f, <u>Claudiosaurus</u>, after Carroll, 1981; g, <u>Champsosaurus</u>, after Russell, 1956; h, <u>Prolacerta</u>, after Camp, 1945; i, <u>Tanystropheus</u>, after Wild, 1973. Scale = 1 cm.

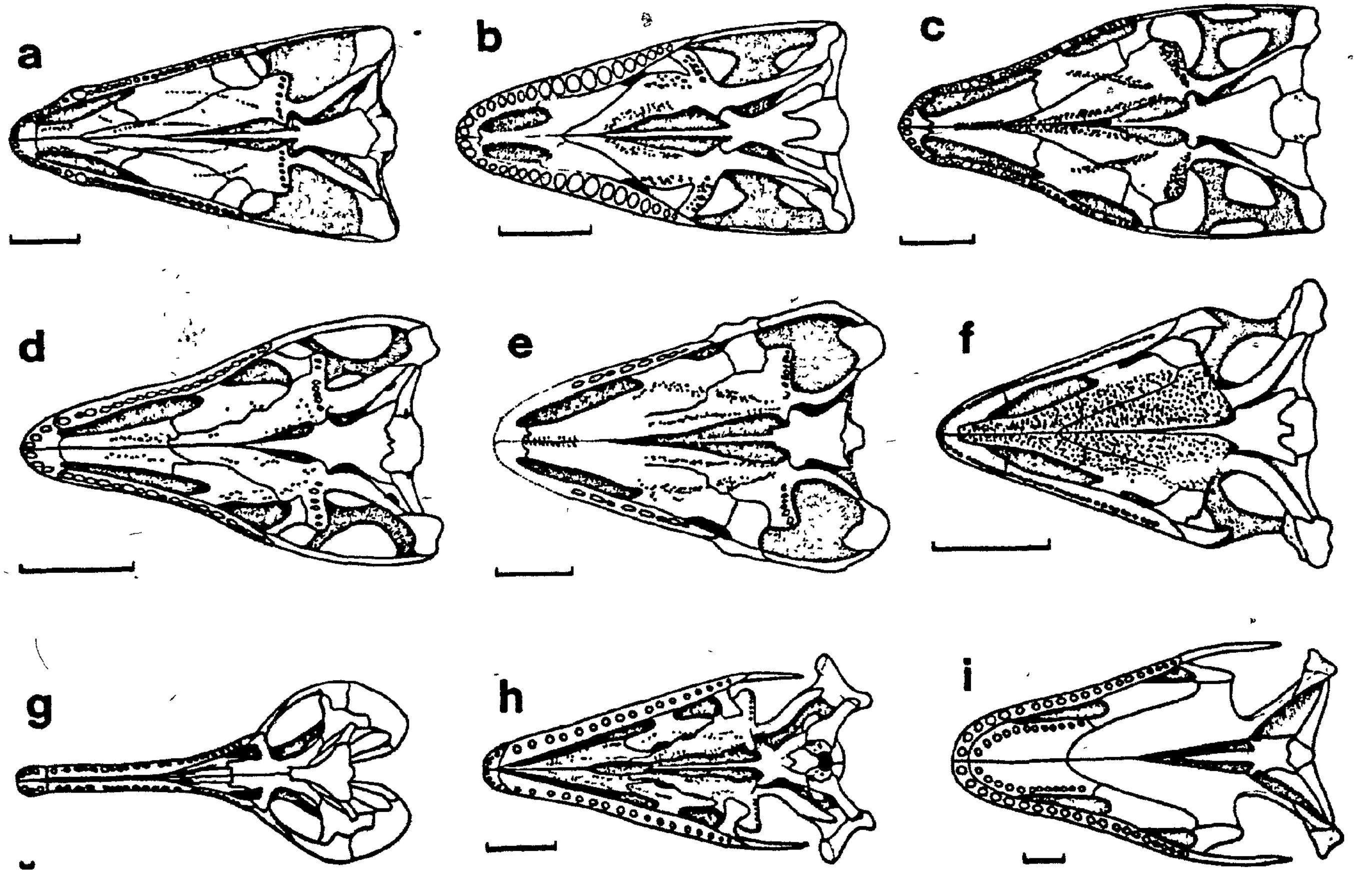
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Figure 52. Skulls of primitive reptiles in occipital view. a, Protorothyris, after Clark and Carroll, 1973; b, Araeoscelis, after Vaughn, 1955; c, Petrolacosaurus, after Reisz, 1977; d, Youngina, after Carroll, 1977; e, Claudiosaurus, after Carroll, 1981; f, Prolacerta, after Robinson, 1967; g, Tanystropheus, after Wild, 1973. Each scale = 1 cm.

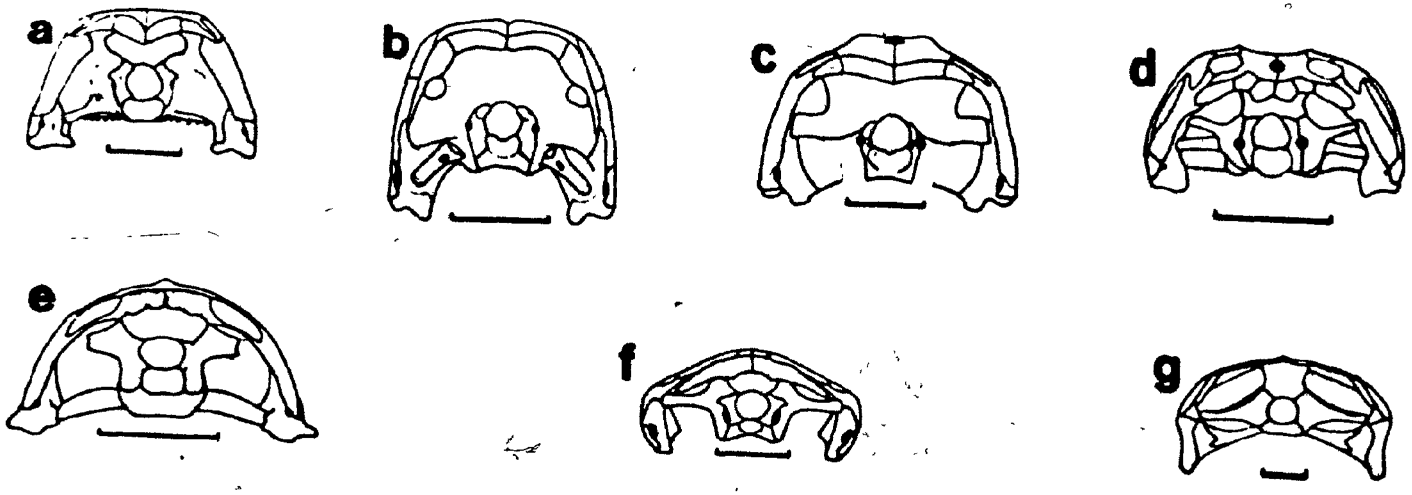
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Figure 53. Cervical vertebrae of primitive reptiles. a, Protocaptorhinus, 4th, after Clark and Carroll, 1973; b, Araeoscelis, 4th, after Vaughn, 1955; c, Petrolacosaurus, 4th, after Reisz, 1975; d, Coelurosauravus, 4th, after Carroll, 1978; e, Daedalosaurus, 4th, after Carroll, 1978; f, Youngina, after Gow, 1975; g, Acerosodontosaurus, after Currie, 1980; h, Heleosaurus, 4th, after Carroll, 1976a; i, Askeptosaurus, after Kuhn-Schnyder, 1952; j, Champsosaurus, 4th, after Russell, 1956; k, Prolacerta, 7th, after Gow, 1975; l, Tanystropheus, 9th, Wild, 1973.

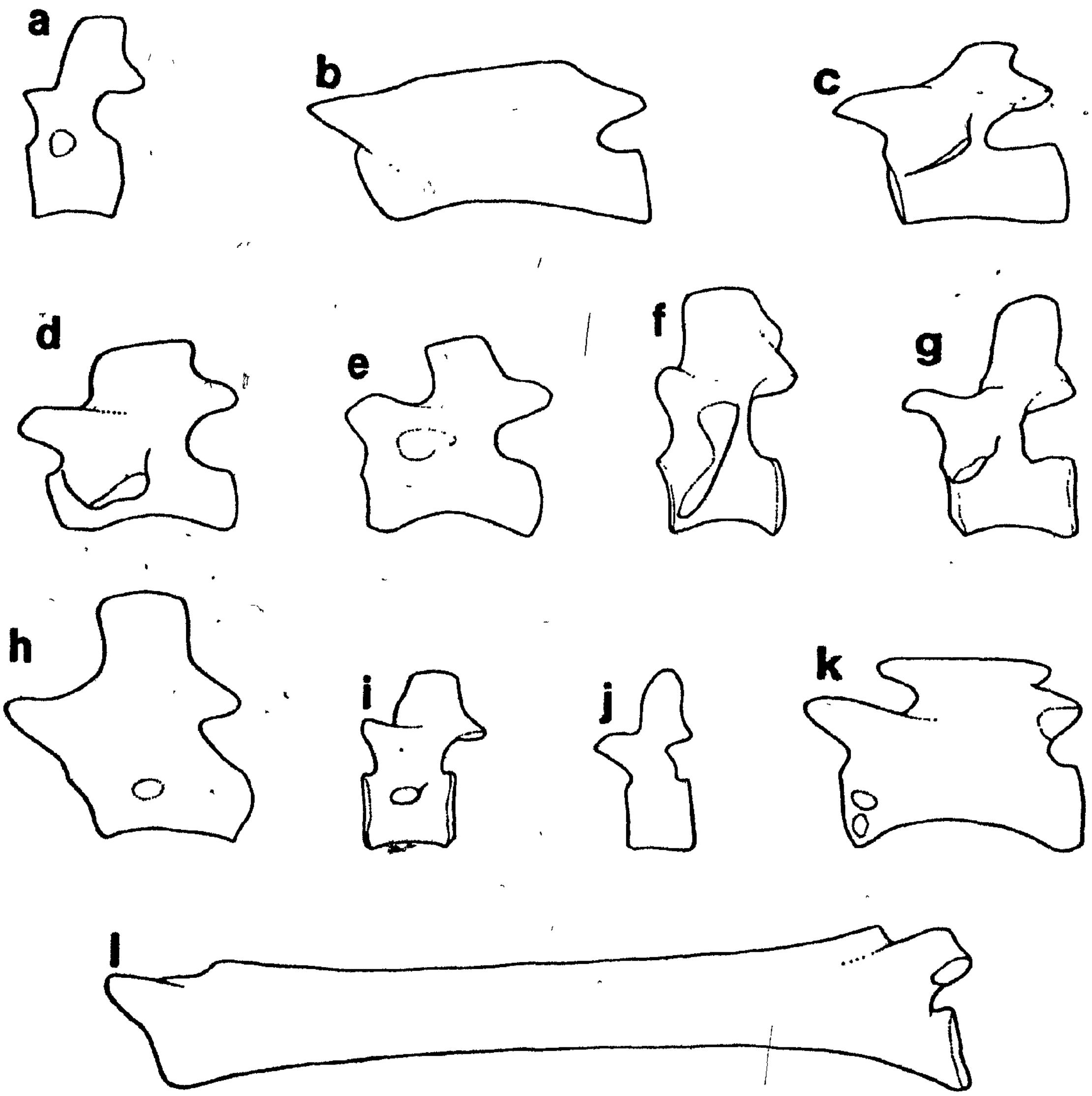
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Figure 54 . Thoracic vertebrae of primitive reptiles. a, <u>Protorothyris</u>, after Heaton and Reisz, in preparation; b, <u>Araeoscelis</u>, mid dorsal, after Vaughn, 1955; c, <u>Petrolacosaurus</u>, mid-dorsal, after Reisz, 1975; d, <u>Coelurosauravus</u>, 18th, after Carroll, 1978; e, <u>Youngina</u>, 22nd, AMNH 5561; f, <u>Acerosodontosaurus</u>, posterior dorsal, after Currie, 1980; g, <u>Heleosaurus</u>, 15th, after Carroll, 1976a; h, <u>Thadeosaurus</u>, after Carroll, 1981; i, <u>Kenyasaurus</u>, 18th, Harris and Carroll, 1977; j, <u>Hovasaurus</u>, 13th, SAM 9463; k, <u>Claudiosaurus</u>, 16th, after Carroll, 1981; l, <u>Askeptosaurus</u>, Kuhn-Schnyder, 1952; m, <u>Thalattosaurus</u>, anterior dorsal, after Merriam, 1905; n, <u>Champsosaurus</u>, 16th, after Russell, 1956; o, <u>Prolacerta</u>, 21st, after Gow, 1975; p, <u>Tanystropheus</u>, posterior thoracic, after Wild, 1973.

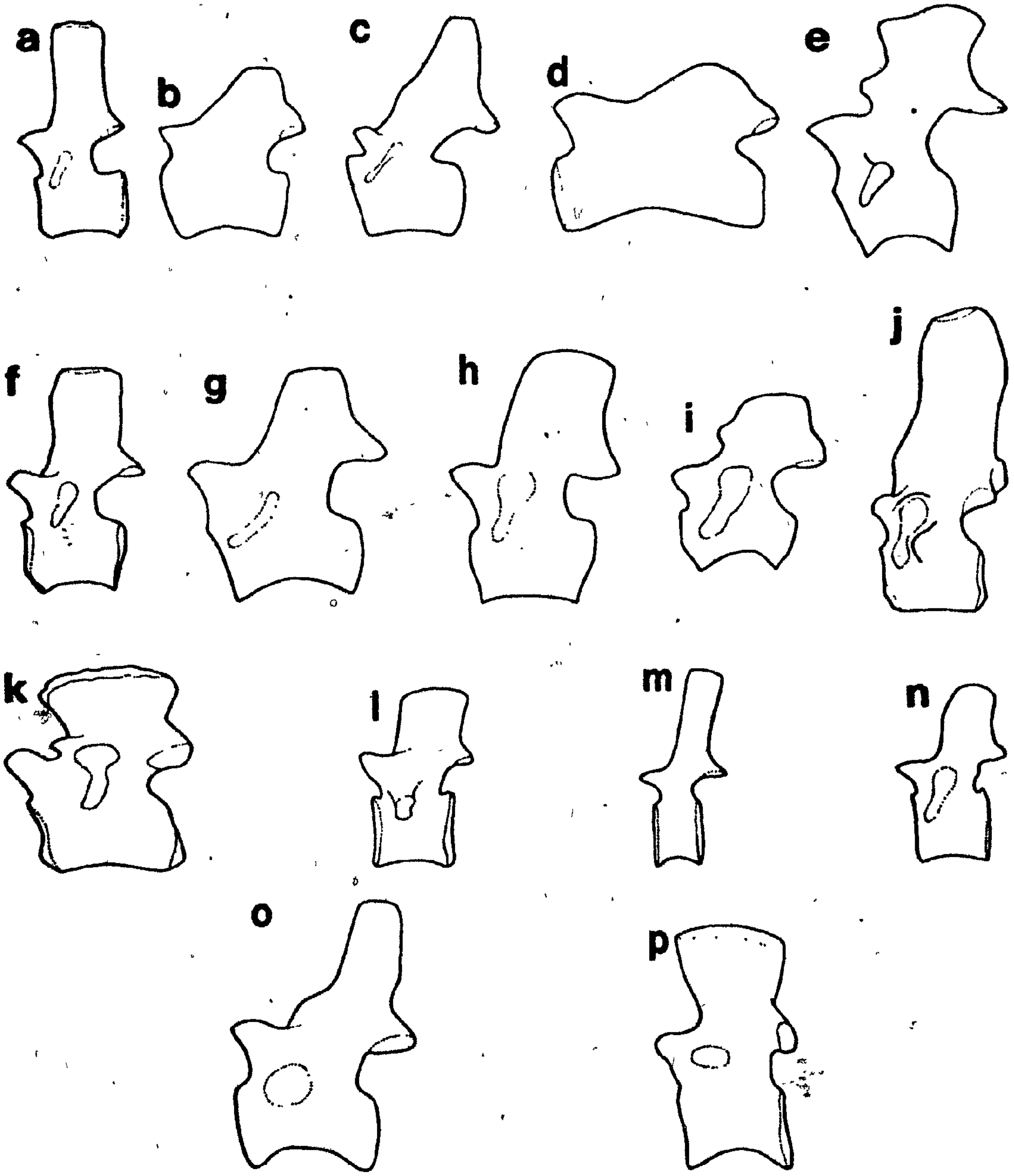
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Figure 55. Caudal vertebrae of primitive reptiles. a, Petrolacosaurus, anterior caudal, after Reisz, 1975; b, Youngina, 3rd caudal, AMNH 5561; c, Thadeosaurus, anterior caudal, MNHN 1908-5-1; d, Tangasaurus, reconstruction of 20th caudal; e, Hovasaurus, mid caudal region, MNHN 1908-21-11; f, Askeptosaurus, 10th caudal, after Kuhn-Schnyder, 1952; g, Thalattosaurus, anterior caudal, after Merriam, 1905; h, Champsosaurus, 2nd caudal, after Erickson, 1972; i, Prolacerta, 2nd caudal, after Gow, 1975; j, Tanystropheus, anterior caudal, after Wild, 1973.

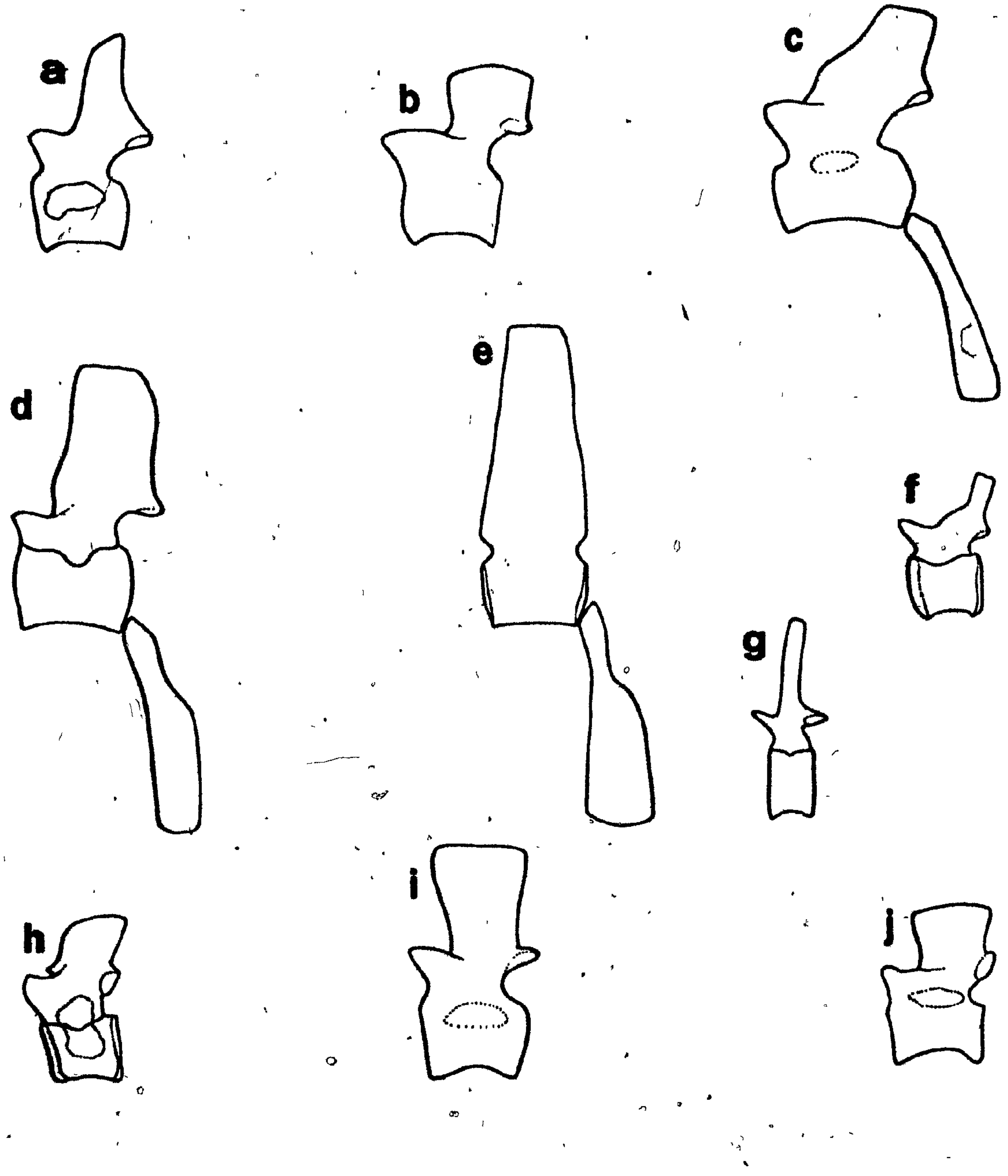
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Figure 56. Lateral view of pectoral girdle of primitive reptiles. a, Protorothyris, after Clark and Carroll, 1973; b, Araeoscelis, Vaughn, 1955; c, Youngina, after Gow, 1975; d, Hovasaurus; e, Claudiosaurus, after Carroll, 1981; f, Champsosaurus, after Russell, 1956; g, Thalattosaurus, after Merriam, 1905; h, Prolacerta, after Gow, 1975; i, Tanystropheus, after Wild, 1973.

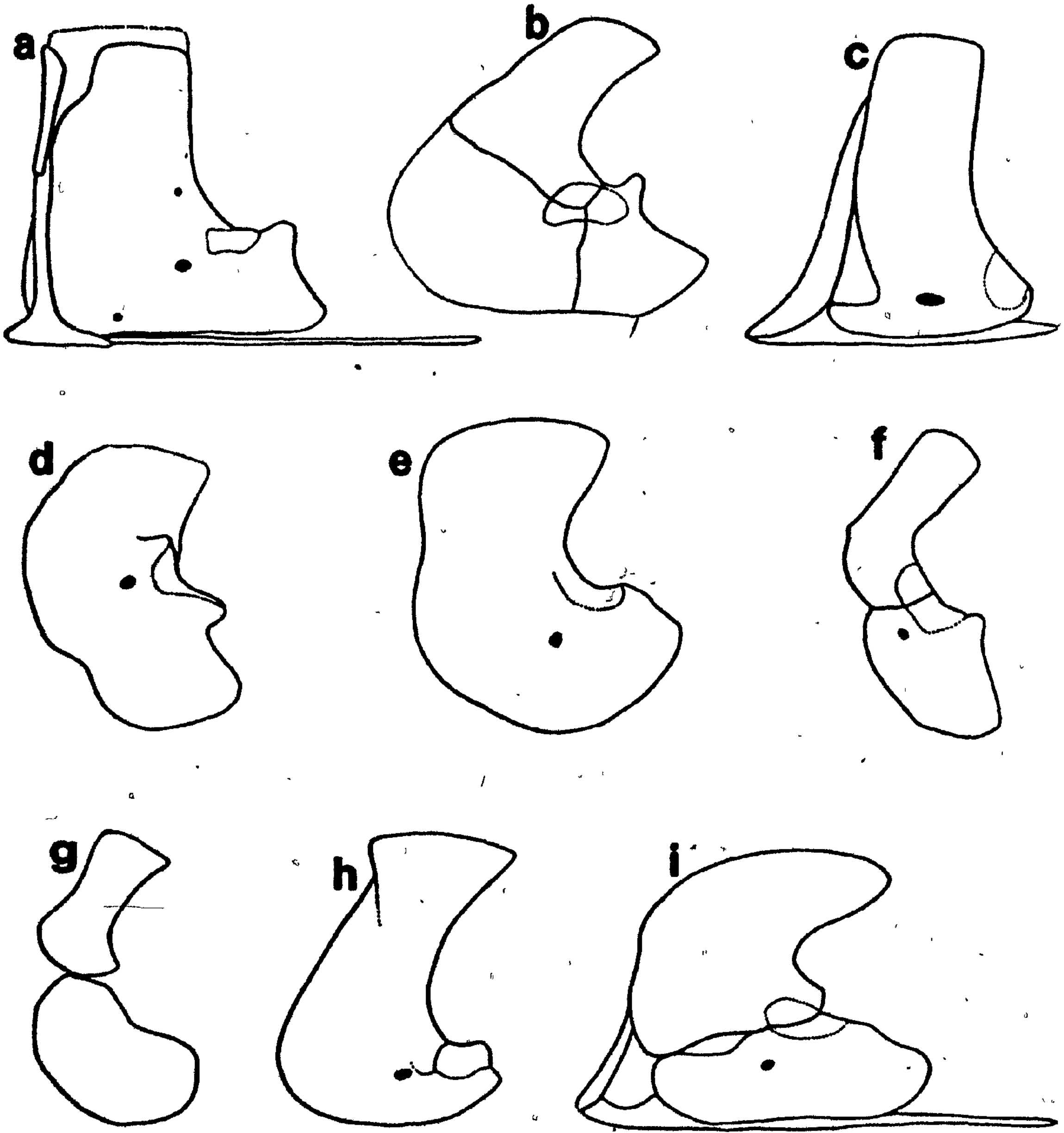
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Figure 57. Ventral view of pectoral girdle of primitive reptiles. a, *Protorothyris*, after Clark and Carroll, 1973; b, *Araeoscelis*, after Vaughn, 1955; c, *Saurosternon*, after Carroll, 1975a; d, paligua[illegible]id (Albany Museum 4133), after Carroll, 1975a; e, *Youngina*, fragments of right coracoid and right sternal plate, left sternal plate, after Broom, 1922; f, *Youngina*, interclavicle, after Gow, 1975; g, *Thadeosaurus*, after Carroll, 1981; h, *Tangasaurus*, specimen in Bulawayo Museum; i, *Hovasaurus*, MNHN 1908-21-24 (sternum); j, *Hovasaurus*, MNHN 1925-5-38 (clavicles and interclavicle); k, *Claudiosaurus*, after Carroll, 1981; l, *Askeptosaurus*, after Kuhn-Schnyder, 1960; m, *Champsosaurus*, interclavicle, after Erickson, 1972; n, *Tanystropheus*, after Wild, 1973. Each scale = 1 cm.

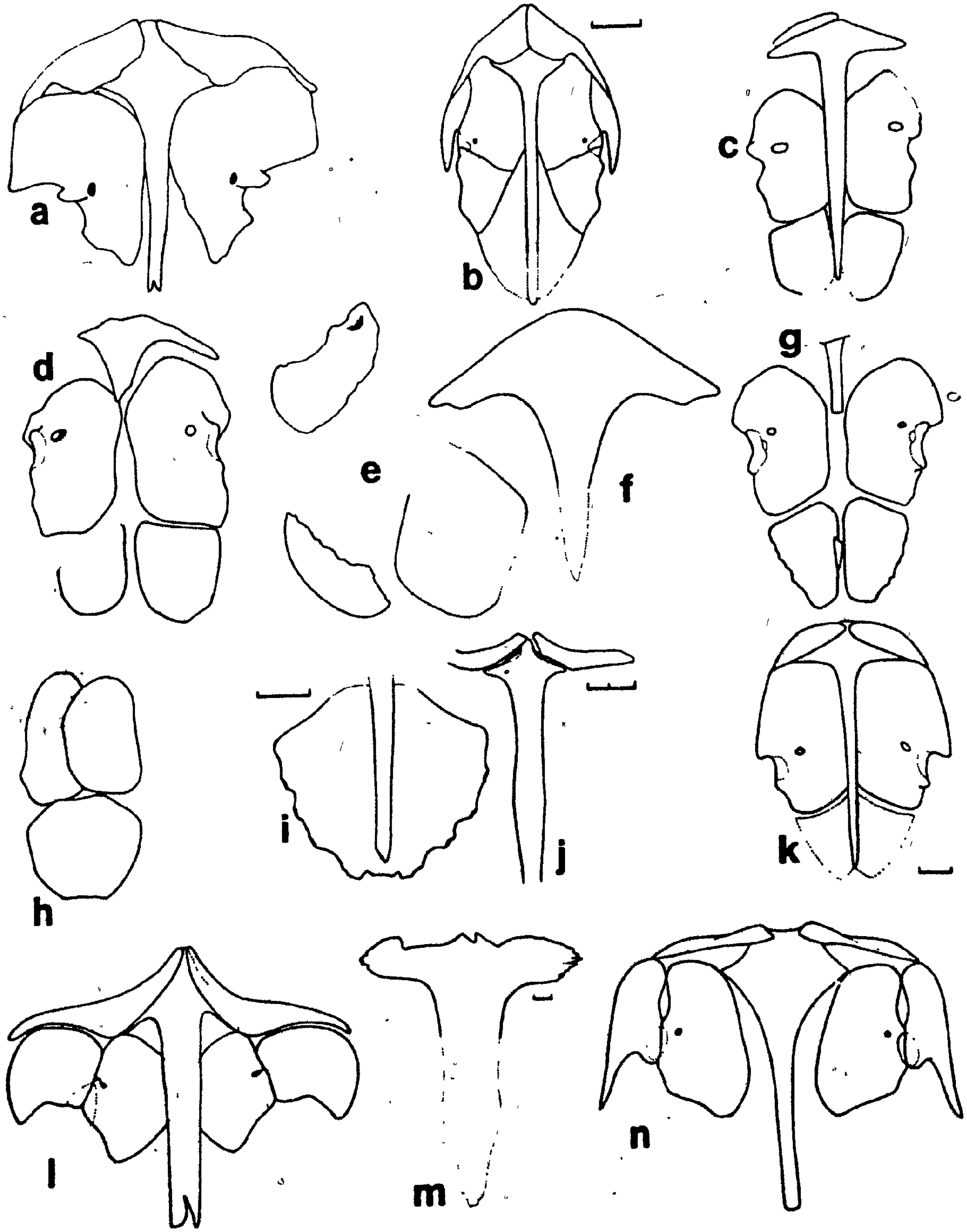
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Figure 58. Dorsal view of humeri of primitive reptiles. a, Paleothyris, Heaton and Reisz, in preparation; b, Petrolacosaurus, after Reisz, 1975; c, Araeoscelis, after Vaughn, 1955; d, Saurosternon, after Carroll, 1975a; e, Youngina, after Gow, 1975; f, Acerosodontosaurus, after Currie, 1980; g, Thadeosaurus, after Carroll, 1981; h, Hovasaurus; i, Claudiosaurus, after Carroll, 1981; j, Thalattosaurus, after Merriam, 1905; k, Champsosaurus, after Brown, 1905; l, Tanystropheus, after Wild, 1973. Each scale = 1 cm.

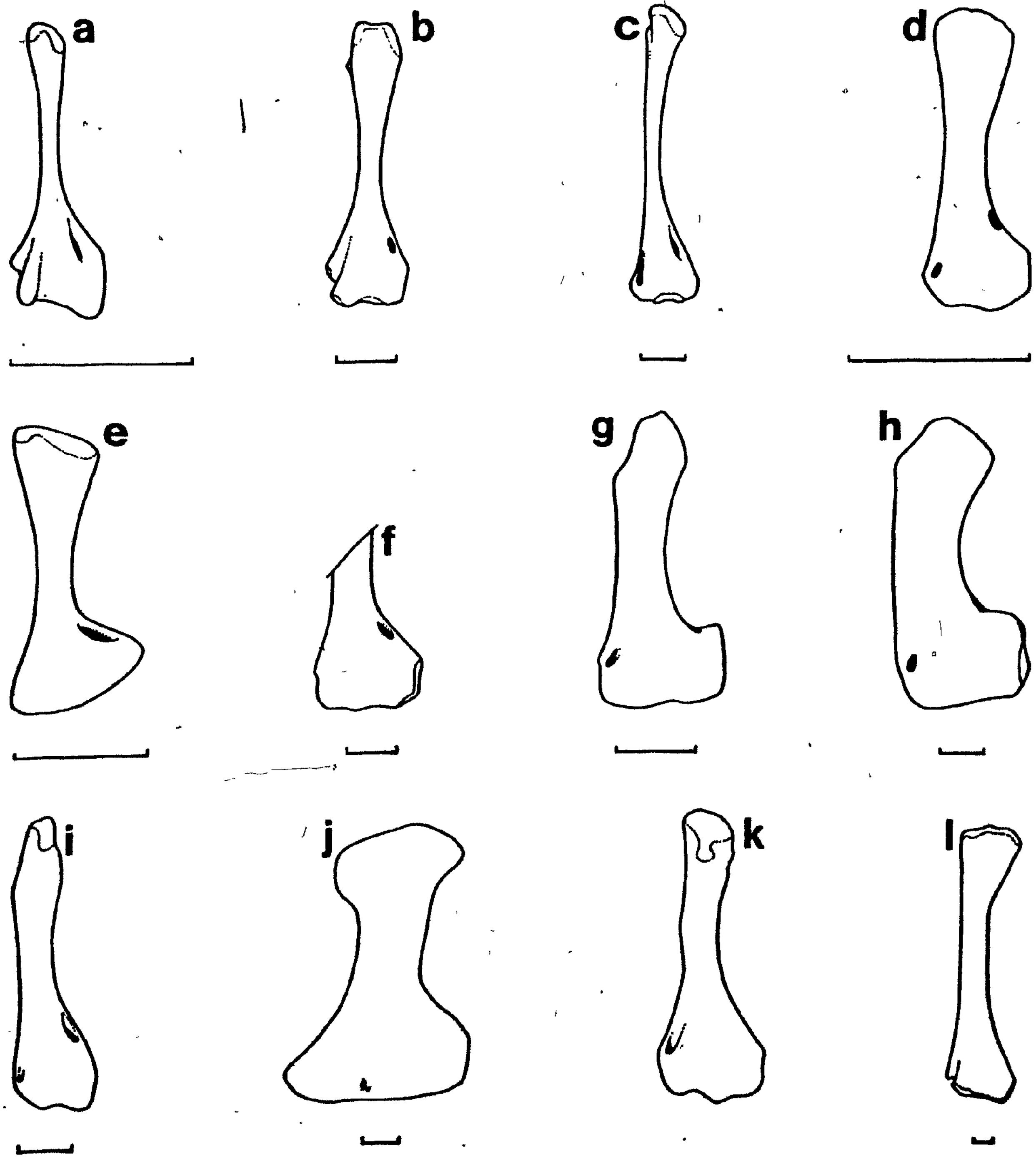
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Figure 59. Ventral view of humerus of primitive reptiles. a, Araeoscelis, after Vaughn, 1955; b, Petrolacosaurus, after Reisz, 1975; c, Palaeagama, after Carroll, 1975a; d, Saurosternon, after Carroll, 1975a; e, Albany Museum 4133, after Carroll, 1975a; f, Daedalosaurus, after Carroll, 1978; g, Acerosodontosaurus, after Currie, 1980; h, Thadeosaurus, after Carroll, 1981; i, Tangasaurus, specimen in Bulawayo Museum; j, Hovasaurus; k, Claudiosaurus, after Carroll, 1981; l, Prolacerta, after Gow, 1975; m, Thalattosaurus, after Merriam, 1905; n, Champsosaurus, after Brown, 1905; o, Tanystropheus, after Wild, 1973. Each scale = 1 cm.

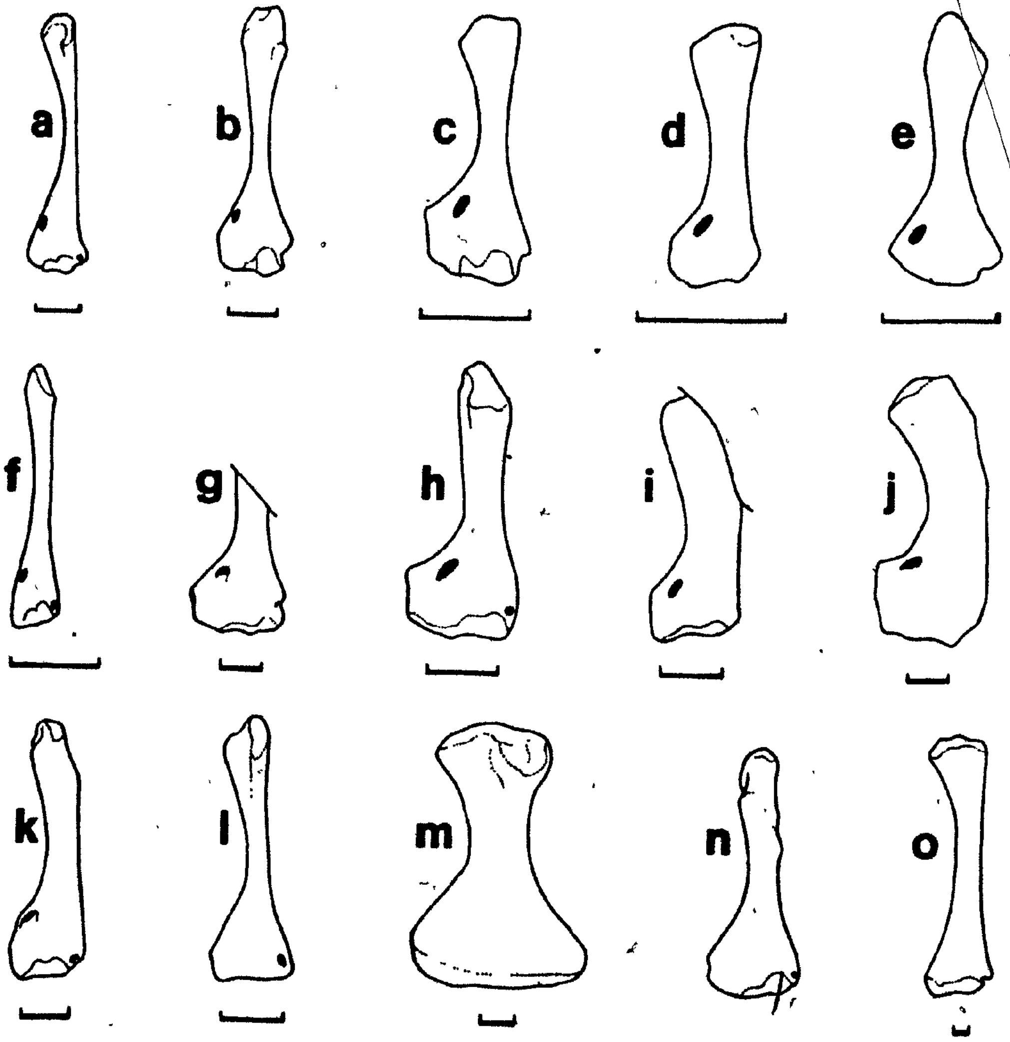
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Figure 60. Carpus of primitive reptiles. a, Palaeothyris, after Heaton and Reisz, in preparation; b, Petrolacosaurus, after Reisz, 1975; c, Araeoscelis, after Vaughn, 1955; d, Saurosternon, after Carroll, 1975a; e, Daedalosaurus, after Carroll, 1978; f, Galesphyrus, after Carroll, 1976b; g, Youngina, after Gow, 1975; h, Acerosodontosaurus, after Currie, 1980; i, Thadeosaurus, after Carroll, 1981; j, Hovasaurus, MNHN 1925-5-31; k, Claudiosaurus, after Carroll, 1981; l, Askeptosaurus, Kuhn-Schnyder, 1952; m, Champsosaurus, after Russell, 1956; n, Protorosaurus, after Williston; o, Tanystropheus, after Wild, 1973. Each scale = 1 cm.

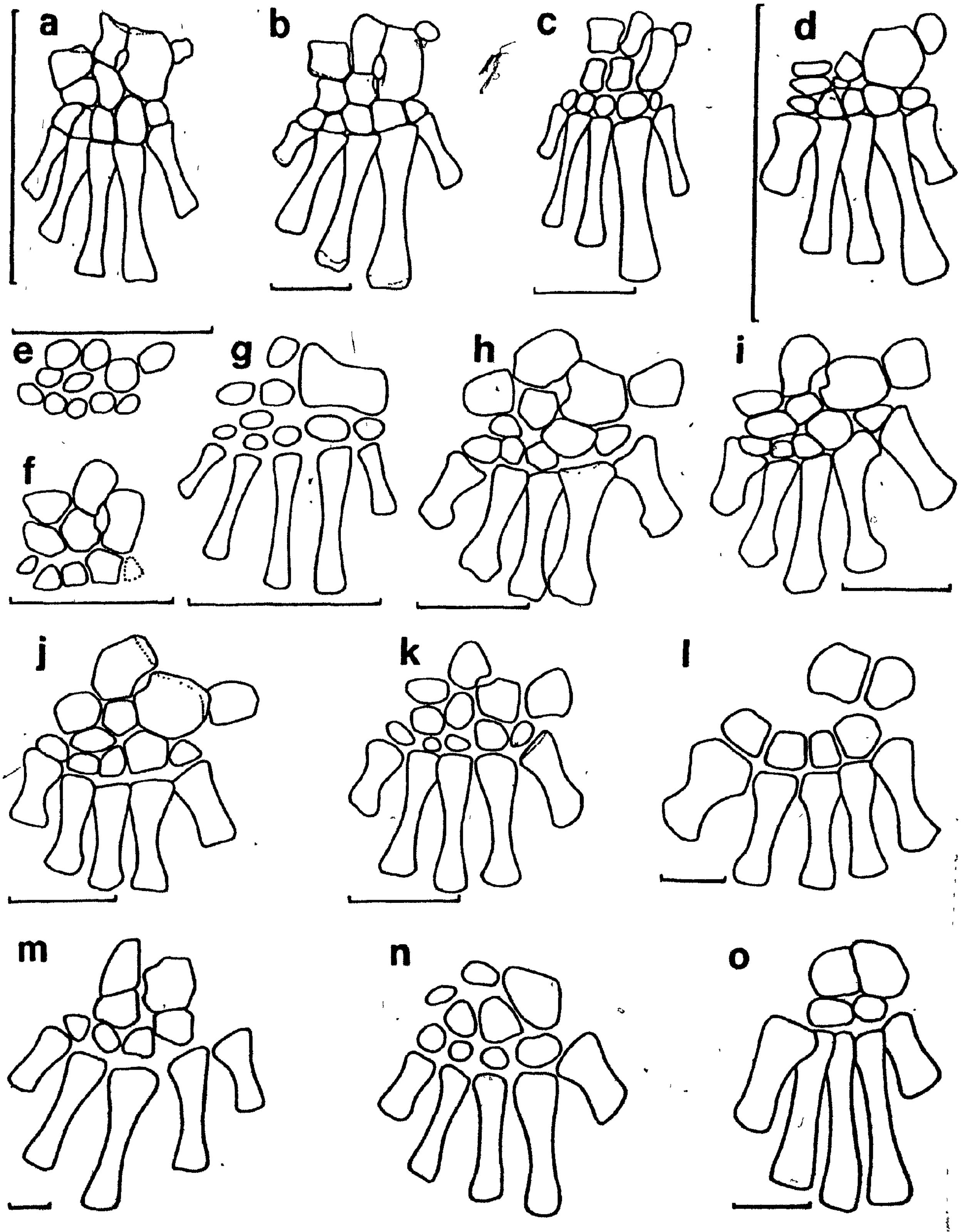
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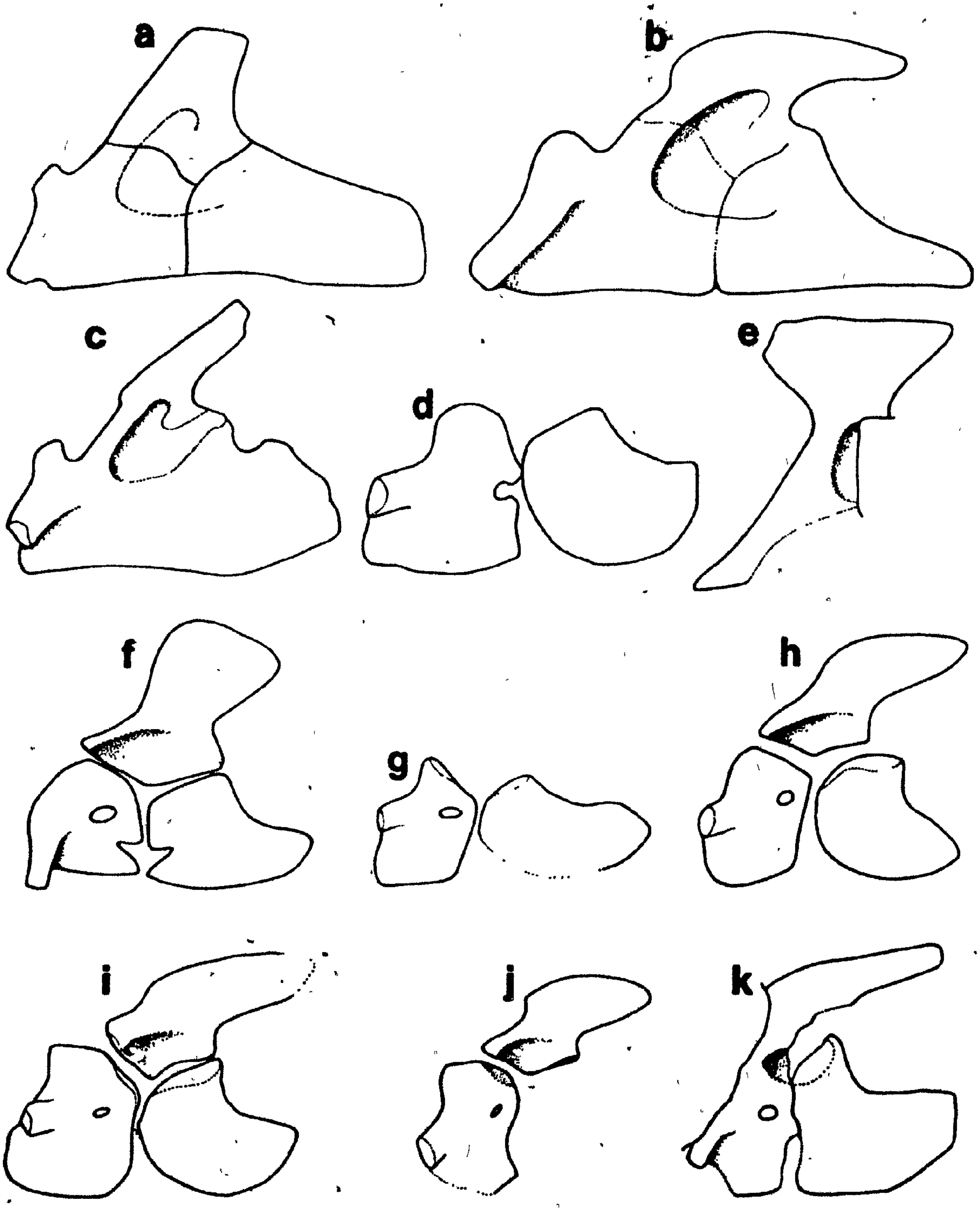
Figure 61. Pelvic girdle of primitive reptiles. a, Protorothyris, after Clark and Carroll, 1973; b, Araeoscelis, after Vaughn, 1955; c, Petrolacosaurus, after Reisz, 1975; d, Saurosternon, after Carroll, 1975a; e, Daedalosaurus, after Carroll, 1978; f, Youngina, after Gow, 1975; g, Heleosaurus, after Carroll, 1976a; h, Thadeosaurus, after Carroll, 1981; i, Hovasaurus, MNHN 1908-32-45; j, Acerosodontosaurus, after Currie, 1980; k, Claudiosaurus, after Carroll, 1981; l, Champsosaurus, ilium after Parks, 1933, pubis and ischium after Erickson, 1972; m, Askeptosaurus, after Kuhn-Schnyder, 1952; n, Thalattosaurus, pubis and ?ischium, after Merriam, 1905; o, Prolacerta, after Gow, 1975; p, Tanystropheus, after Wild, 1973.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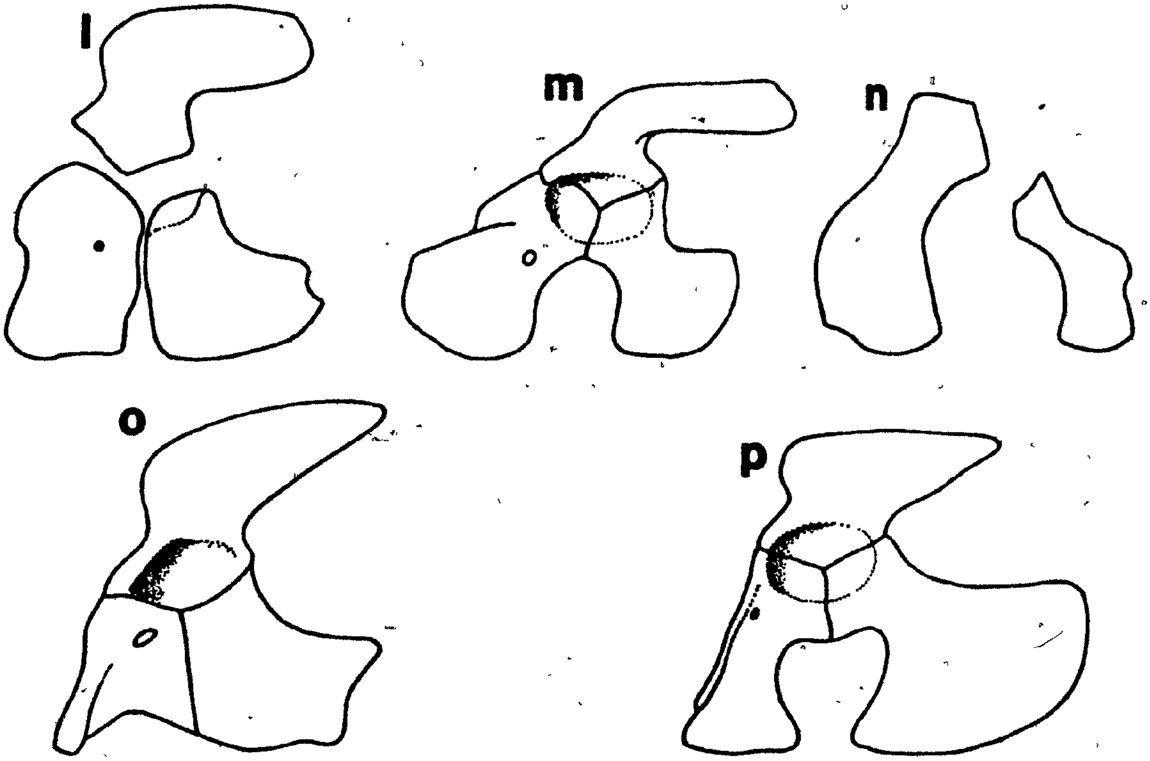
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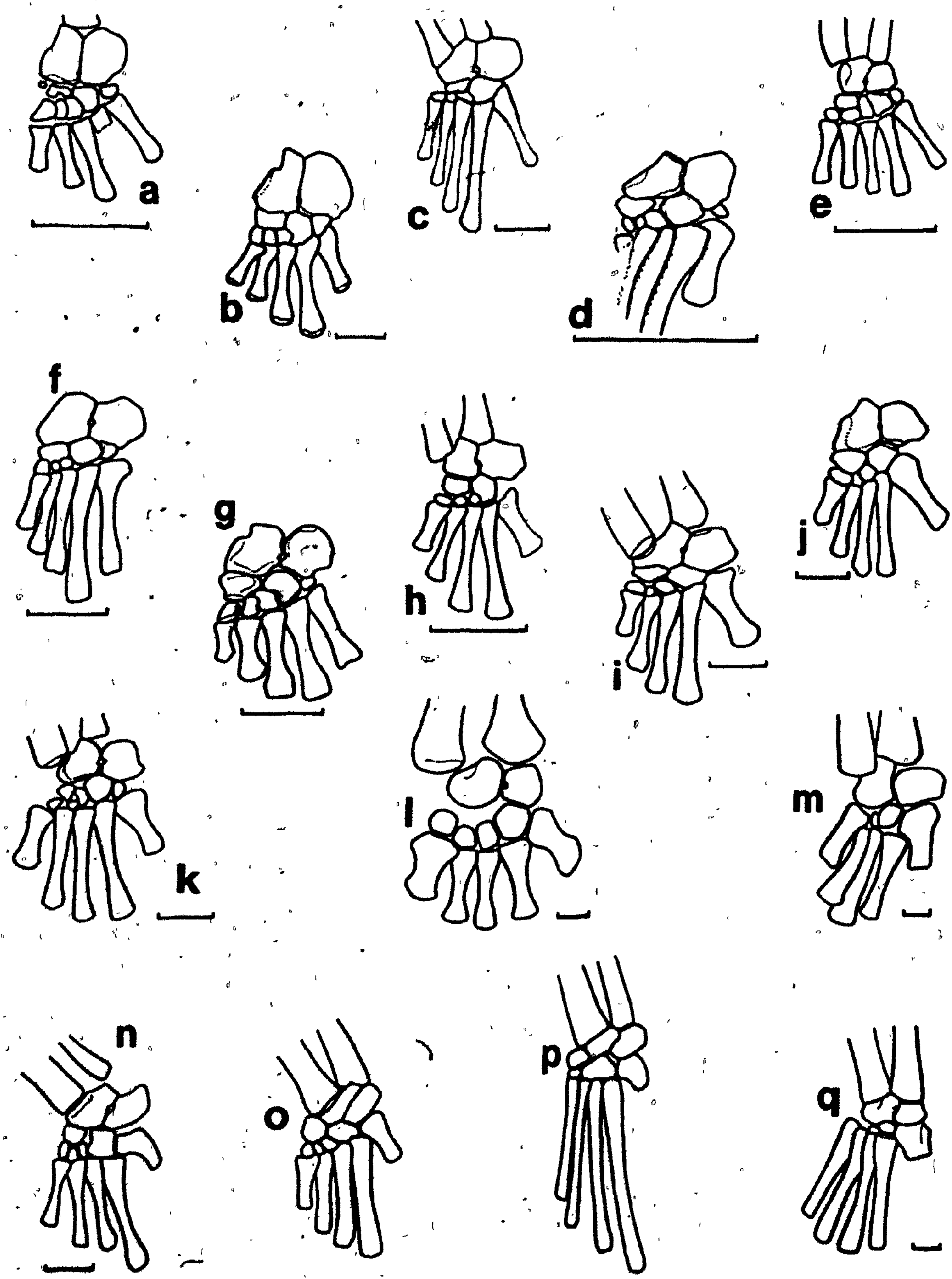
Figure 62. Tarsi of primitive reptiles.

a, *Palaeothyris*, after Brinkman, 1979;
b, *Petrolacosaurus*, after Reisz, 1975;
c, *Araeoscelis*, after Vaughn, 1955;
d, *Saurosternon*, after Brinkman, 1979;
e, *Coelurosauravus*, after Carroll, 1978;
f, *Youngina*, after Broom, 1921;
g, *Galesphyrus*, after Carroll, 1976b;
h, *Thadeosaurus*, after Carroll, 1981;
i, *Kenyasaurus*, after Brinkman, 1979;
j, *Hovasaurus*, after Brinkman, 1979;
k, *Claudiosaurus*, after Carroll, 1981;
l, *Askeptosaurus*, after Kuhn-Schnyder, 1952;
m, *Champsosaurus*, after Parks, 1933;
n, *Prolacerta*, after Gow, 1975;
o, *Protorosaurus*, after Wild, 1973;
p, *Macrocnemus*, after Wild, 1973;
q, *Tanystropheus*, after Wild, 1973.
Each scale = 1 cm.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In light of the improved knowledge of eosuchian anatomy, it is worthwhile to consider the interrelationships within the Tangasauridae, and the relationship of the family to other reptiles.

It has become widely accepted in recent years that a proper taxonomic diagnosis should emphasize derived or advanced character states (synapomorphies) rather than shared primitive character states (symplesiomorphies of Hennig, 1966). Although a cladogram is used to show the interrelationships of tangasaurids and younginids, the approach is phylistic (Holmes, 1980), not cladistic.

The Origin of Eosuchians

Protothyridid captorhinomorphs are probably ancestral to all eosuchians. At least, this family does not have any universal, derived characters that would bar them from ancestry of diapsid reptiles. Reisz (1981) has already used shared derived characters to test the hypotheses of relationship between *Paleothyris* and *Petrolacosaurus*, and between *Petrolacosaurus* and *Youngina*. As it is necessary to know what characters are primitive to appreciate synapomorphic changes in eosuchian genera, the osteology of protorothyridid captorhinomorphs (Carroll, 1964, 1969, 1970; Carroll and Baird, 1972; Clark and Carroll, 1973) will be reviewed here.

The skull of protorothyridids (figs. 49a, 50a, 51a, 52a) lacks temporal openings and suborbital fenestra, and has a pineal foramen. The lacrimal extends from the orbit to the external naris. The posterior end of the frontal and posterodorsal corner of the postfrontal are clasped in some genera by rostral processes of the parietal. These distinctive contacts are retained by Youngina and the tangasaurids. The postorbital contacts the parietal in the Protorothyridae, and the squamosal forms the posterolateral margin of the skull. The quadratojugal, supratemporal, tabular and postparietal bones are present. The palate is movably attached to the braincase. There is a massive footplate on the stapes, and a stapedial foramen and ossified dorsal process are present. There are four to six premaxillary teeth, fifteen to 35 maxillary (one or two of which are caniniform), and teeth on all of the palatal bones. The denticles on the pterygoid are usually arranged in two rows on the palatal ramus, and are enlarged on the transverse flange. Generally two coronoid bones are present, and there is no retroarticular process on the articular.

There are 29 to 32 presacral vertebrae. The neck is short, composed of five or six cervical vertebrae that are shorter than the dorsal centra. There are one or two sacral vertebrae, and more than fifty caudals. The centra are amphicoelous and notochordal. Neural arches are narrow in relation to central width, and have relatively low, triangular neural spines in Hylonomus and Paleothyris, and high, rectangular spines in Protorothyris (fig. 54a). The axial intercentrum is distinct from the atlas centrum in Hylonomus but fused (an advanced character) in most other genera. In mature animals, the tubercular and capitular articular surfaces on the transverse process are separated by a groove for the segmental artery, as are the two rib heads. Cervical ribs are flattened rods of bone. There are six to eight pairs of long, slim, posteriorly curved caudal ribs that are not fused to the centra. The cleithrum is present (fig. 56a). The clavicle is broadly expanded (fig. 57a) where it overlaps ventrally the broad, platelike head of the interclavicle. The scapular blade is relatively high (fig. 56a) and has a well-developed supraglenoid buttress and foramen. Both anterior and posterior coracoids are present, but fuse into a single unit with the scapula at maturity. The glenoid articulation is screw-shaped. The sternum was present, but not ossified. The humerus is slightly shorter than the femur (Table 9), and the epipodials are about two thirds the length of the propodials. Total lengths of manus and pes are greater than sums of the corresponding propodials and epipodials. There is an entepicondylar foramen and an entepicondyle of moderate size (fig. 58a) in the humerus. At least some genera have an ossified supinator process, but there is always an ectepicondylar groove and strong ectepicondylar ridge. The ulna has a well developed olecranon and subterminal sigmoidal notch, and the shaft exceeds the length of the radius. There are eleven carpals (fig. 60a), most of which are proximodistally longer than their maximum widths. The lateral centrale contacts the third distal carpal. The phalangeal formula of the manus is 2,3,4,5,3. The penultimate phalanx is longer than the antepenultimate bone. No anterodorsal expansion of the lateral surface of the ilium (fig. 61a) is evident, and the supraacetabular buttress of this bone is distinct. A lateral pubic tubercle, a pectineal tubercle and an obturator foramen are present, and the pubis forms at least a quarter of the acetabular surface. There is never any evidence of a thyroid fenestra. A terminal, anterior articulation, the

Y-shaped adductor ridge system, a well-defined intertrochanteric fossa, the more lateral extension of the posterior distal condyle in comparison with the anterior distal condyle, a distinct intercondylar fossa and articulating surfaces that extend onto the ventral surfaces of the distal condyles are all primitive characteristics of the femur that indicate a sprawling gait of the hind limb. The tibia has a well developed triceps tubercle on the cnemial crest. The tarsus is a flexible mosaic of bones with four axes of rotation. The astragalus has a condyloid process distally, and the lateral centrale is hourglass shaped. Carroll (1969) reconstructed the pes of *Paleothyris* with a small medial centrale. Reisz (1981) suggested that this was an artifact and that the larger centrale with the hourglass shape represents fusion of the lateral and medial centrale of pelycosaurs. It should be pointed out that in at least one pelycosaur, *Haptodus garnettensis* (Currie, 1977), the lateral centrale seems to be formed ontogenetically from two centres of ossification. As pelycosaurs retain a medial centrale, the hourglass shape of the lateral centrale could represent fusion of the second and third centralia of amphibians. Therefore the shape of the larger centrale in *Paleothyris* cannot be used to prove that the smaller element is not the medial centrale. The metatarsals of protorothyridids do not overlap proximally, and the phalangeal formula of the pes is 2,3,4,5,4. The skin is pebbly but does not seem to have any discrete epidermal scales. The ventral scales are short, broad and "wheat-shaped," are arranged in rows with up to five ranks per side, and do not articulate with a chevron-shaped scale on the midline.

The Earliest Diapsids

Primitive reptiles of the late Paleozoic include pareiasaurs, procolophonians, millerosaurs, mesosaurs, pelycosaurs, captorhinomorphs and lepidosaurs. *Araeoscelis*, *Petrolacosaurus* and eosuchians have the shared, derived characters of an upper temporal opening, and suborbital fenestra. A foramen is found in the position of the suborbital fenestra in pareiasaurs and captorhinomorphs, but is only large enough to permit passage of the lateral palatal ramus of the facial nerve and possibly a branch of the inferior orbital artery (Heaton, 1979). The enlargement of this foramen into a fenestra in even the earliest lepidosaurs could indicate that the pterygoid vein also passed through it as in *Sphenodon* and lizards. Most lepidosaurs have a lateral temporal opening, but so do millerosaurs, mesosaurs and pelycosaurs. Although the number of derived characters uniting the Lepidosauria is few, there are no strong synapomorphies evident at this time that would unite any of the lepidosaur components more closely to any other groups of Paleozoic reptiles.

The order Araeoscelidia (Williston, 1913) is the most primitive level of lepidosaur known, and includes Araeoscelis (Vaughn, 1955), Kadaliosaurus (Credner, 1889) and Petrolacosaurus (Reisz, 1981). There are a number of derived characters in the members of this order that indicate they have a common ancestor that had already diverged from the line leading to the eosuchia. The supratemporal extends anteriorly to the upper temporal fenestra (figs. 49b, c, 50b, c), the postemporal fenestrae are small, the axial intercentrum is fused to the atlantal centrum, there is an increased number of cervical vertebrae, the cervical vertebrae are longer than the dorsals, there is alternation of neural spine height in the anterior dorsals, mammilary processes are present on the anterior neural spines, a conspicuous lateral fossa excavates the neural arch, the limb bones are slender and hollow and the epipodials are elongate. Araeoscelidians are similar to protorosaurids in the elongation of the neck and the epipodials. These are probably features that can be correlated with similar life styles, because araeoscelidians are very primitive and have none of the fifteen derived characters shared by younginiform and prolacertiform eosuchians.

Some of the significant primitive characters retained by the Araeoscelidia include: lacrimal extends to the external naris (figs. 49b,c); the postorbital contacts the parietal (figs. 50b,c); caniniform teeth in Petrolacosaurus and some specimens of Araeoscelis; dichocephalous ribs in the dorsal region; hook-shaped anterior caudal ribs; three scapulocoracoid ossifications (fig. 56b); supraglenoid ridge and foramen; expanded clavicular blade where it covers diamond-shaped head of interclavicle (fig. 57b); entepicondylar and ectepicondylar **foramin,** and supinator process (figs. 58b, c, 59a, b) retained; 11 carpal elements (figs. 60b, c); supraacetabular ridge, lateral pubic tubercle (figs. 61b, c) present; terminal proximal articulation on femur, Y-shaped adductor ridge system, assymetrical distal condyles; condyloid process on astragalus, dumbell-shaped centrale (figs. 62b, c); 7 tarsal elements, each of which is longer than broad; tarsals form a flexible mosaic without a mesotarsal joint.

Eosuchian Reptiles

There are a large number of shared, derived characters that unite the order Eosuchia. Even though the order is extremely diverse, the suite of derived characters is not found in captorhinomorphs, pareiasaurs, procolophonians, millerosaurs, mesosaurs, pelycosaurs or araeoscelidians. Many of the synapomorphies are correlated with improved limb mechanics, but the presence of so many shared derived characters in the skull, vertebrae, ribs, limb girdles and limbs is a strong indication that the Eosuchia is paraphyletic.

Tangasaurids share the following characteristics with all eosuchians. Lateral temporal fenestra are present in the skull. The quadrate forms the posterior margin of the skull rather than the squamosal None of the teeth are caniniform, and the parasphenoid never has teeth. Between 24 and 26 presacral vertebrae and two or three sacral vertebrae are generally present. The atlantal rib is lost in all but the coelurosauravids. Cervical ribs taper to a point distally. The articular facets of the capitulum and tuberculum of a dorsal rib are continuous but distinct. Rather than being hook-shaped, the caudal ribs are straight. The supraglenoid buttress and foramen are lost along with the prominent process behind the glenoid for the coracoid head of the triceps. The head of the interclavicle is t-shaped, and the ventral head of the clavicle is narrow. The limb elements are generally longer than those of protorothyridid captorhinomorphs. The ulna has a reduced olecranon, and the shaft is shorter than the radius in most genera. The external surface of the ilium has expanded anterodorsally. The supraacetabular buttress of more primitive reptiles has been replaced by a strong ridge that bounds the oval-shaped acetabulum anteriorly and dorsally. With increased development of the "pectineal" tubercle, the lateral pubic tubercle was lost. The head of the femur is strongly turned posterodorsally and there is a prominent internal trochanter correlated with reduction of the Y-shaped ventral ridge system and fourth trochanter. The distal condyles of the femur are subequal, and the articular surface is restricted to the distal surface. There is no knob-like process on the cnemial crest of the tibia. Unlike protorothyridids and araeoscelidians, there is no condyloid process on the astragalus and the centrale is not hour-glass shaped. A mesotarsal joint has developed in all eosuchians except <u>Galesphyrus</u>. The ventral dermal scales are chevron-shaped on the midline, and needle-like laterally.

Taxonomic Relationships of *Acerosodontosaurus*, *Youngina* and the Tangasauridae

In light of the improved knowledge of the morphology of the tangasaurids and related genera, it is worthwhile to refine the classification of these forms. Numbers in brackets refer to significant character traits noted on figure 63.

Class REPTILIA Linnaeus 1758

Subclass LEPIDOSAURIA Duméril and Bibron 1839

Order EOSUCHIA Broom 1914

Suborder YOUNGINIFORMES Romer 1945

Family ACEROSODONTOSAURIDAE

Genus. — *Acerosodontosaurus* Currie 1980

Diagnosis. — Skull wider in antorbital region than *Youngina* (fig. 50g; 1); more than 30 maxillary teeth, a count higher than any known eosuchian. Ulna longer than radius (2), in contrast with most eosuchians. Thyroid fenestra (3) not a small notch as in *Youngina*.

Discussion. — There are no accessory articulations on the neural spines (fig. 54f) such as are found in younginids and tangesaurids. Nevertheless, a derived character in the carpus, whereby the lateral centrale has lost contact with the third distal carpal, is found in these three families. The lengths of two bones, the radius and the femur, are known, and these are close to the relative lengths of the same elements in tangasaurids.

Superfamily YOUNGINOIDEA

Diagnosis — Additional intervertebral articulations found on the midline near the base of the neural spine (#4). A pair of ossified sternal plates coossify into a single unit in mature animals (#5). Entepicondyle strongly developed at maturity (#6). Proximal head of 5th metatarsal expanded (#7).

Discussion. — Ossified sterna are found in Araeoscelis (fig. 57b) and paliguanid lacertilians (figs. 57c, d). The nature of the sternum in Araeoscelis is not clear, although it is quite different in appearance. The ossified sterna of paliguanids may indicate shared ancestry with younginoid eosuchians. This hypothesis is supported by the presence of accessory intervertebral articulations in Saurosternon (Carroll, 1975) and a well developed entepicondyle. Younginoid eosuchians lack the specialized characters of the skull (figs. 49d, e, 50d, e) and skeleton, scapulocoracoid and tarsus of paliguanids.

Family YOUNGINIDAE Broom 1914

Genus. — Youngina Broom 1914.

Diagnosis. — Zygapophyses of anterior dorsal vertebrae extend laterally beyond the centra and are inclined at low angle from horizontal (#8). Iliac blade short and almost vertical (fig. 61f) (#9); small thyroid fenestra present (10). Humerus relatively short (11).

Discussion. — Numerous specimens are known, but all show a degree of ossification that suggests immaturity and prevents a full understanding of many features. The skull is relatively long (10x) and has about 3 premaxillary, 15-23 maxillary and 20 dentary teeth. The neural spines are low and rectangular (figs. 53f, 54e). The humerus is about the same length as that of *Paleothyris*, but the remaining limb bones are about what is expected in younginiform eosuchians. The humerus is only 70% the length of the femur, compared with 75% in immature *Hovasaurus* and 110% in mature *Hovasaurus*.

Family TANGASAURIDAE Camp 1945

Diagnosis. — Frontals narrow between orbits (12); posteromedial corner of prefrontal separated from orbital rim by anterolateral process of frontal (13); jaw articulation anterior to occipital condyle (14); quadrate almost as wide as it is high (15). Ossified scapular blade extends less than 50% of the way up the body wall (16); coracoid larger than scapular blade (17); cleithrum curved (18). Relative length of humerus is high so that this bone is as long as or longer than the femur in mature animals (19). Fifth distal tarsal lost as a discrete element (figs. 62h, i, j) (20).

Discussion. — This family includes terrestrial and aquatic forms. The greater proportional length of the humerus is attained through elongation of this element and not shortening of the other long limb bones. The fifth distal tarsal has apparently fused into the fourth (Harris and Carroll, 1977). The proximal head of metatarsal V is expanded to at least .5 of the total length of the bone.

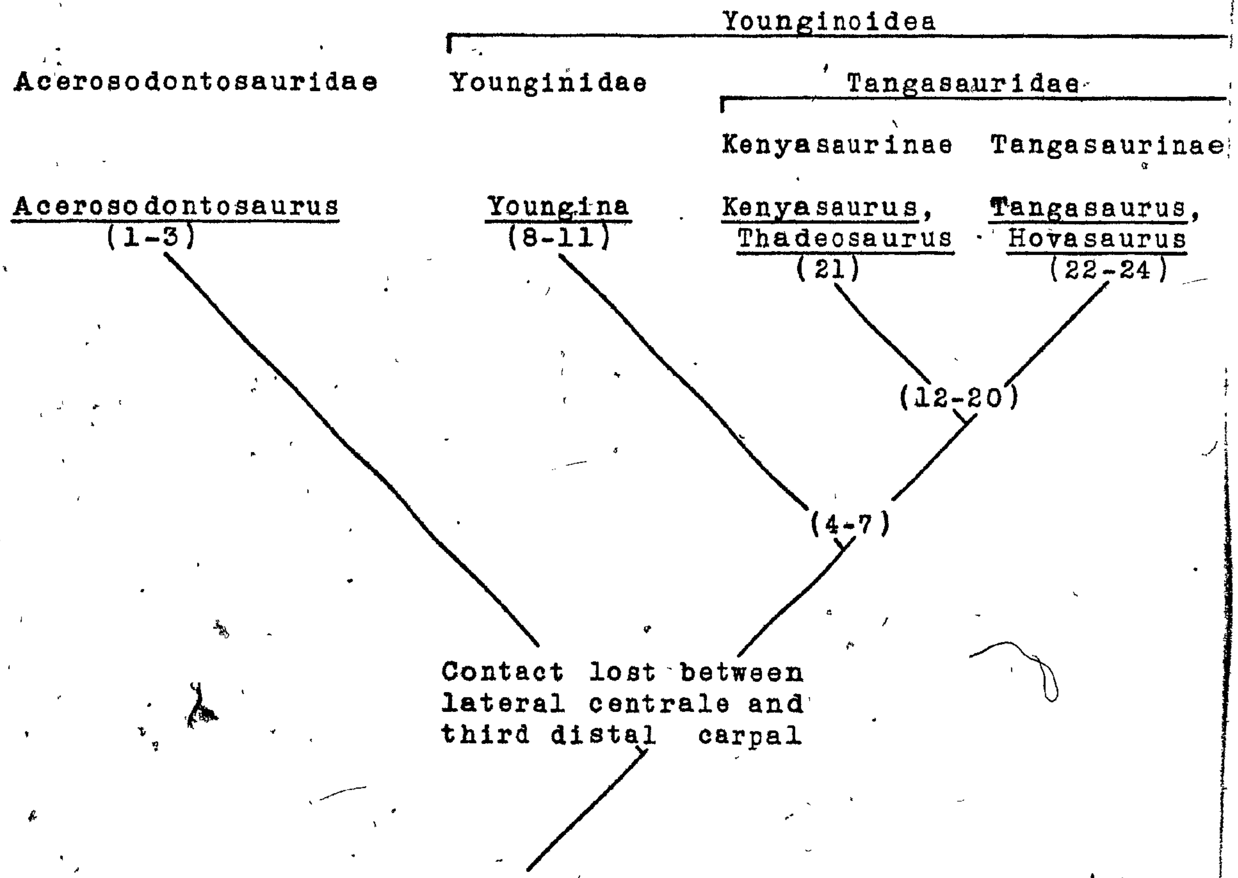
Subfamily KENYASAURINAE

Genera. — Kenyasaurus Harris and Carroll 1977
Thadeosaurus Carroll 1981

Diagnosis. — 19-28 pairs of caudal ribs and transverse processes, all of which taper distally (21).

Discussion. — Kenyasaurine tangasaurids do not have the aquatic specializations seen in tangasaurine genera, and were probably terrestrial animals. The tail is composed of fewer than 56 vertebrae. Only the paliguarid Saurosternon has such a high number of caudal ribs and transverse processes as the kenyasaurines. Most eosuchians have twelve or fewer. The lateral margin of the basioccipital is separated from the opisthotic by the basisphenoid-parasphenoid complex, but it is not known how widespread this trait is among the Younginiformes.

Figure 63. Cladogram showing the possible relationships between *Acerosodontosaurus*, *Youngina* and the Tangasauridae. Numbers in brackets represent significant derived characters and are explained in the text.



Subfamily TANGASAURINAE Piveteau 1926

Genera. — Tangasaurus Haughton 1924
Hovasaurus Piveteau 1926.

Diagnosis. — Neural spines high in dorsal region but even higher in the proximal and mid caudal vertebrae (figs. 55d, e) (22). 12 pairs of caudal ribs; anterior caudal ribs expanded distally (23). Haemal spines expanded into platelike structures (24).

Discussion. — There are 5 cervical, 20 dorsal and at least 70 caudal vertebrae. The height of the neural spines in the caudal vertebrae is 1.35x in Tangasaurus and 2.25x in Hovasaurus. Hovasaurus is more specialized in that there are mammilary processes on the neural spines of the anterior dorsals, and the ribs are slightly pachyostotic. The distal end of the second sacral rib does not bifurcate as it does in Youngina and Prolacerta (Gow, 1975). The clavicle overlaps the ventral tip of the cleithrum anteriorly, whereas in protorothyridid captorhinomorphs the cleithrum fits into a well defined groove on the anteromedial margin of the clavicular stem (Clark and Carroll, 1973). The primitive arrangement is retained by Petrolacosaurus (Reisz, 1981), but the situation in other eosuchians is unknown. Large numbers of ingested pebbles in

Hovasaurus were probably used for ballast.

Relationship between Coelurosauravids and Tangasaurids

In many features, coelurosauravids are the most primitive of eosuchians. There are 29 presacral vertebrae as in protorothyridids, and the atlas rib is apparently retained. Limb elements are the same relative lengths (Table 9) as those of protorothyridids. In other characteristics, these animals are highly specialized. The maxilla enters the orbital margin (figs. 49f, o). The quadratojugal of *Weigeltisaurus* is relatively large with distinctive toothlike projections (fig. 49o), and there is some evidence to suggest that those of *Coelurosauravus* and *Daedalosaurus* (Carroll, 1978) may have been the same. The ribs of *Daedalosaurus* and *Weigeltisaurus* are elongate (up to 30 times the length of a dorsal centrum) presumably to support a gliding membrane, whereas those *Coelurosauravus* are only 3*x* in length. The ribs of tangasaurids and most other Permian eosuchians are about 7*x* long. Coelurosauravids are clearly not closely related to the Tangasauridae.

Relationship of *Galesphyrus* to the Tangasauridae

Only two partial skeletons have been identified as *Galesphyrus* (Carroll, 1976b). The presence of holocephalous ribs, straight caudal ribs, a single centrale in the tarsus and an advanced type of femur clearly indicate that this animal is an eosuchian. Carroll (1976b) assigned the genus to the Younginidae, but Galesphyrus is more primitive than any younginiform or prolacertiform eosuchian. The carpal and tarsal elements are as elongate as those of protorothyridids and araeoscelidians. A mesotarsal joint has not developed, and the proximal heads of the metatarsals do not overlap (Brinkman, 1979). The head of metatarsal V is narrow; its width is about a third the total length of the bone. The humerus is relatively shorter than that of Paleothyris, the radius and femur are the same relative lengths as those of the captorhinomorph, and the tibia is intermediate in length to those of Paleothyris and more advanced eosuchians (Table 9). There are no derived characters known that can prove that Galesphyrus is not the ancestral morphotype of both younginiform and prolacertiform eosuchians.

Relationship of Heleosaurus to Tangasaurids

The bladelike teeth with cutting edges along the anterior and posterior surfaces, the loss of the coronoid, the presence of a sixth cervical vertebra and elongation of the cervicals to the same length as the dorsals are derived characters that are not found in younginids or tangasaurids. Carroll (1976a) has suggested that this genus is close to the ancestry of archosaurs. It does not appear to be closely related to younginids and tangasaurids.

Relationship of Tangasaurids to the Prolacertiformes

Members of the suborder Prolacertiformes have become highly specialized in many respects. The lower temporal bar is lost (figs. 49m, n), the squamosal is tetraradiate (sickle-shaped in *Tanystropheus*), the quadrate is streptostylic with an offset pterygoid flange, there is no stapedial foramen, the teeth are implanted in sockets, the vertebrae are amphicoelous, the cervicals are longer than the dorsal vertebrae (figs. 53k, l) and number more than seven, and the entepicondylar foramen is lost. In at least one respect, the retention of contact between the postorbital and parietal, the prolacertiform eosuchians are less specialized than the Younginiformes. Clearly these two suborders have diverged considerably.

Relationship of Tangasaurids to other Aquatic Eosuchians

Askeptosaurus and *Thalattosaurus* are highly specialized marine reptiles that have elongate premaxillae (figs. 49k, l), external nares placed far back from the anterior margin of the skull, nasals separated by premaxillae and frontals (figs. 50i, j) and upper temporal fenestra that are reduced to a slit. *Askeptosaurus* has 14 cervical vertebrae and 25 dorsals. The humerus, radius and tibia are relatively shorter than in any other eosuchians. There is a large thyroid fenestra. The presence of thecodont teeth, amphicoelous vertebrae and an elongate neck, and the loss of the fifth distal carpal and the entepicondylar foramen suggests that thalattosaurs are more closely related to prolacertiform eosuchians than to the Younginiformes.

Champsosaurs have many derived characters not found in other eosuchians. The posterolateral margin of the skull is greatly expanded, and the confluent external nares are located at the end of the elongate snout (fig. 50k). The prefrontals contact each other on the midline, and the posttemporal fenestra is lost. As in tangasaurids~~, the ribs~~ are pachyostotic, and the epipodials are relatively shorter than the propodials (Table 9). These are characters developed in response to an aquatic life style however, and do not indicate relationship. The postorbital-parietal contact, loss of the entepicondylar foramen, the presence of a hooked fifth metatarsal (fig. 62m) and other similarities suggest that champsosaurs are more closely related to the Prolacertiformes than to tangasaurids.

Figure 64. Phylogenetic chart showing the interrelationships of eosuchians and their descendants.

1, Protorothyrididae;

2, Araeoscelidia;

3, Coelurosauravidae;

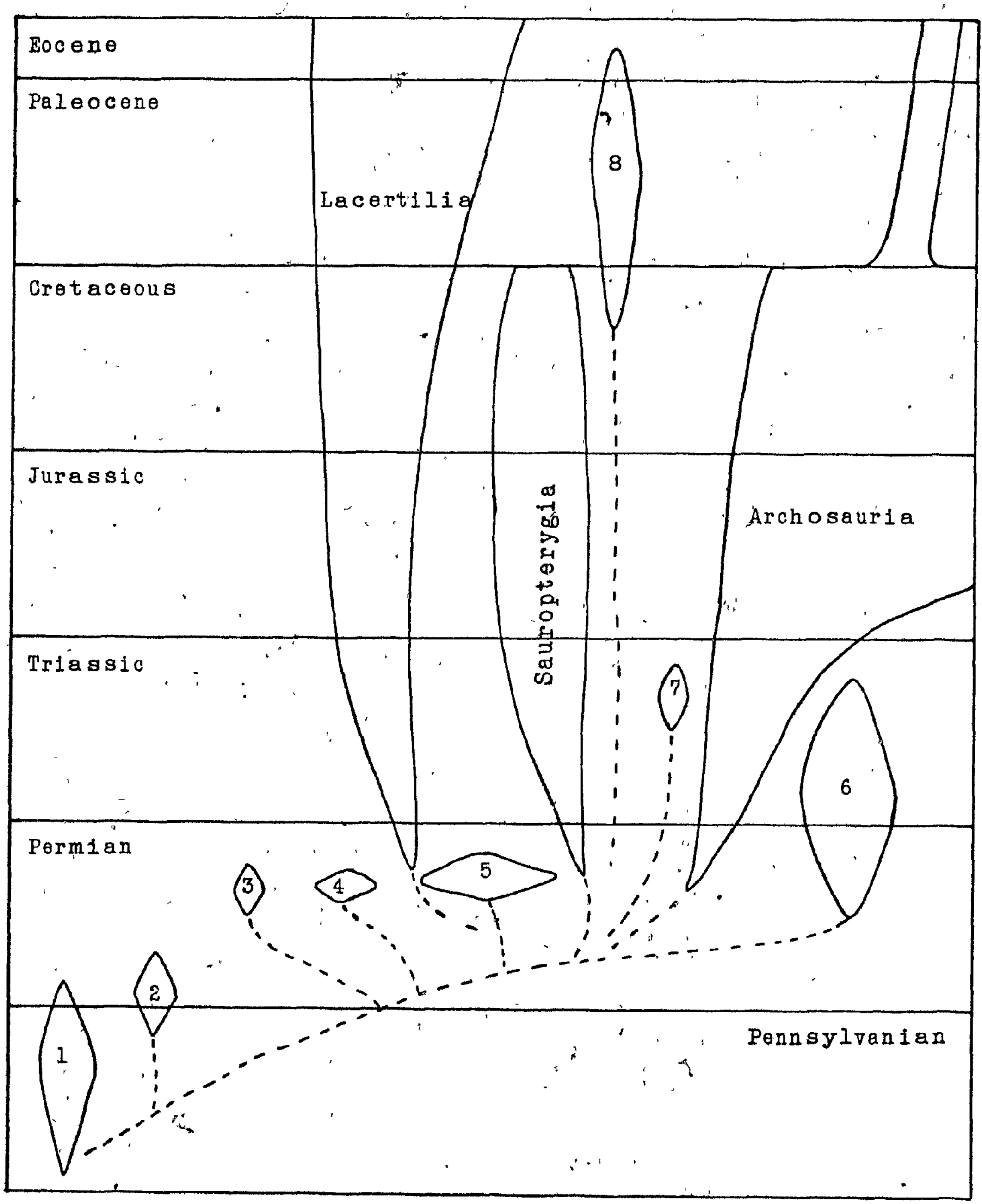
4, _Galesphyrus_;

5, _Acerosodontosaurus_, _Youngina_, Tangasauridae;

6, Prolacertiformes;

7, Thalattosauria;

8, Champsosauridae.


Eocene
Paleocene
Cretaceous
Jurassic
Triassic
Permian
Pennsylvanian
Lacertilia
Sauropterygia
Archosauria
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8

EOSUCHIAN DESCENDANTS

Eosuchians have been considered as the ancestral stock of both archosaurs and lizards ever since the discovery of Youngina (Broom, 1914). The origin of these and other diapsid lineages have proven to be complex problems that are not within the scope of this investigation. However, it is worthwhile to determine if tangasaurids could have given rise to any other groups of reptiles.

The Origin of Lizards. — Carroll (1975a, b; 1977) has proposed that the Permo-Triassic paliguanids of South Africa are ancestral to the Lacertilia. He has provisionally placed the Paliguanidae, long considered as eosuchians, into the infraorder Eolacertilia. There are many derived characters, such as a streptostylic quadrate, shared by paliguanids and more recent lacertilians that are not found in eosuchians. These have been discussed in detail by Carroll (1975a, 1977) and will not be reiterated here because they shed no light on the origin of the paliguanidae.

Palaeagama, Paliguana and Saurosternon are the three known genera of paliguanids. A specimen from South Africa that was originally described as Saurosternon (Owen, 1876) was renamed Heleosuchus by Broom (1913). The original specimen has been misplaced, but on the basis of a cast Carroll (1981) has suggested that this animal is a younginid. In contrast with paliguanids, the lower temporal bar is apparently complete (Carroll, pers. comm., 1981). However, the skull of this animal is broad, about 85% of its length and about seven times the length of a dorsal centrum. This is very close to the estimated skull proportions (width/length = .85) and width (6x) of Palaeagama (Carroll, 1975a). In contrast, the skulls of Youngina, Heleosaurus, Acerosodontosaurus and other eosuchians are more elongate and narrower (3x-5x). The neural spines are low and triangular, whereas those of younginids and tangasaurids are relatively taller and rectangular in outline. The absolute sizes and proportions of the vertebrae and limbs are very close to those of Palaeagama (Table 9). Because of the poor preservation of the only known specimen of Heleosuchus, it is not possible to determine with certainty whether this genus is a paliguanid or an eosuchian. If the latter identification is correct, this animal must have been close to the ancestral stock of paliguanids.

The parietal does not contact the postorbital in paliguanids, which suggests (but does not prove) relationship with younginiform eosuchians. In contrast with prolacertiform eosuchians, the entepicondylar foramen, the fifth distal carpal and the fifth distal tarsal have been retained, and the vertebrae are notochordal. The neck is short. There are only five cervical vertebrae and all are shorter than the dorsal centra as in younginids, tangasaurids and the ancestral protorothyridids.

Paliguanids share a number of apparent synapomorphies with younginids and tangasaurids. As in Hovasaurus, the jaw articulation is anterior to the posterior margin of the skull (figs. 49d, e, 50d, e). The interorbital to intertemporal width ratio (.6) is close to that of tangasaurids, whereas most eosuchians have a higher ratio. Accessory articulating processes are found on the midline of the neural arch in Saurosternon (Carroll, 1975a), but because the neural spine is so low in paliguanids, these processes do not look like those of Youngina and the tangasaurids. The scapular blade of Saurosternon is very low like that of tangasaurids, but in contrast with Youngina. The sternum (fig. 57c) is ossified in paliguanids, and fuses into a single unit at maturity as in tangasaurids. The humerus is relatively longer than those of Youngina and more primitive eosuchians (Table 9), but shorter than any tangasaurid humerus. The paliguanid specimens are relatively mature, but the humerus of each is at least 15% shorter than the femur. The radius and tibia are more elongate than those of younginids and tangasaurids, and the femur is relatively longer than in any eosuchian. Limb proportions and size suggest that paliguanids were more efficient as terrestrial animals than younginid and tangasaurid eosuchians, but do not disprove relationship.

The possible retention of two primitive characters could falsify the hypothesis that paliguanids are more closely related to the Younginoidea than to any other eosuchians. In Palaeagama (fig. 49d), the lacrimal is shown as extending to the external naris. This region of the specimen is poorly preserved (Carroll, 1975a) however. Because the lacrimal extends to the external naris in only the most primitive eosuchians, it is possible that this detail of the reconstruction is incorrect. As reconstructed (fig. 60d), the lateral centrale of Saurosternon contacts the third distal carpal. In Acerosodontosaurus and the tangasaurids, these bones are separated by the medial centrale and fourth distal carpal. However, the carpus of Saurosternon does not show the relationship of the various elements, so it is possible that the same arrangement existed in paliguanids and tangasaurids. This hypothesis is supported by the fact that the medial centrale of Saurosternon is almost double the size of the lateral centrale.

It appears highly probable that the earliest known lizards, the Paliguanidae, were closely related to younginids and tangasaurids.

The Origin of Archosaurs. — In his redescription of Heleosaurus, Carroll (1976a) suggested that this animal may be closer to the ancestry of archosaurs than any other eosuchian known. The bladelike, finely serrated teeth are set in sockets and are not distinguishable from those of the archosaur Euparkeria. Both Heleosaurus and archosaurs have lost both coronoid bones, and other less significant similarities exist. Existing evidence suggests that Heleosaurus is a younginiform eosuchian. However, characteristics of the skull roof and tarsus that are used to distinguish the two major eosuchian lineages are not preserved in the only known specimen, so it is possible that Heleosaurus is a prolacertiform eosuchian. In either case, this animal is not closely related to tangasaurids.

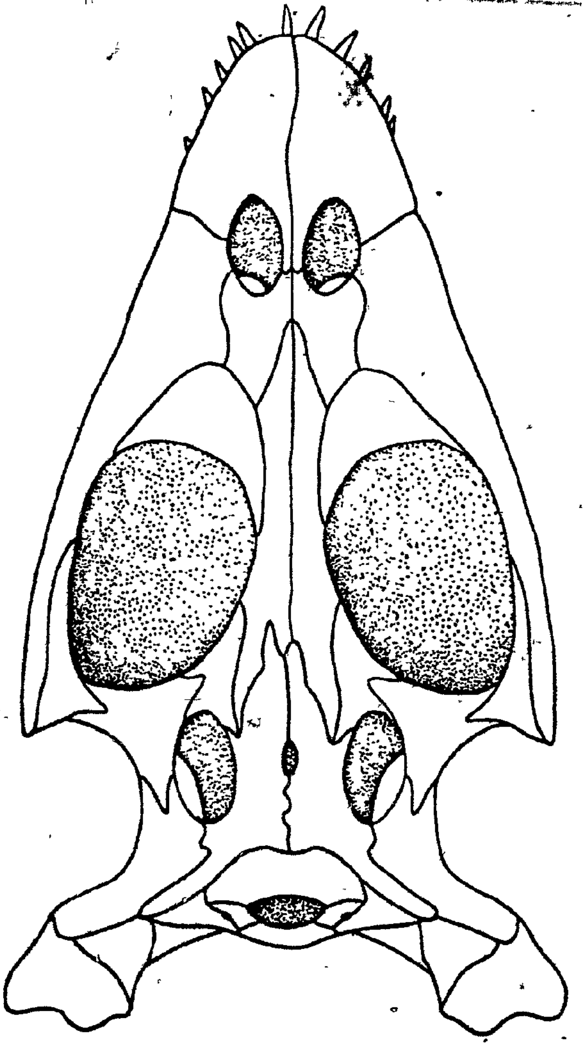
There are alternate theories on the origin of archosaurs. Gow (1975), like many earlier authors, has noted the similarities between prolacertiform eosuchians and primitive archosaurs. Brinkman (1979) concluded that the tarsi of prolacertiform eosuchians, primitive rhynchosaurs and primitive archosaurs are structurally the same.

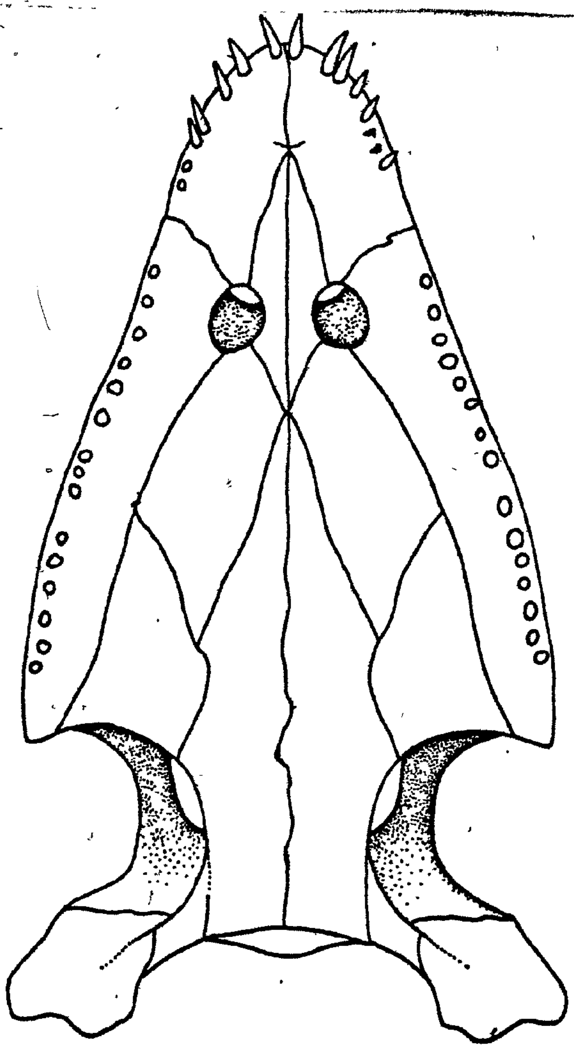
No characters are known to suggest that tangasaurids are close to the ancestry of archosaurs or rhynchosaurs.

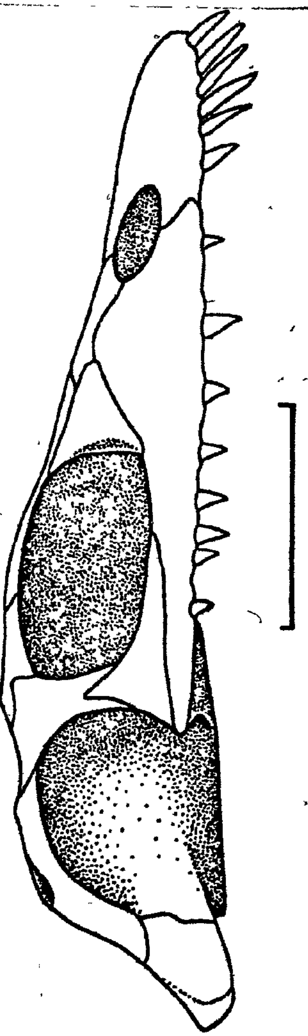
<u>The Origin of Sauropterygians</u>. — Examination of the skull of the nothosaur <u>Anarosaurus pumilio</u> (fig. 65) led Jaekel (1910) to the conclusion that sauropterygians were descendants of diapsid reptiles. Kuhn-Schnyder (1962, 1967) has also stated that diapsids were the precursors of nothosaurs and plesiosaurs. For reasons discussed by Carroll (1981), most palaeontologists have looked elsewhere for the ancestry of sauropterygians.

In 1955, J. Piveteau announced the discovery of two specimens from the Upper Permian of Madagascar representing a very primitive level of sauropterygian evolution. <u>Claudiosaurus</u> (Carroll, 1981) is clearly derived from eosuchian reptiles. The sauropterygian characteristics of this genus have been described in detail (Carroll, 1981). Consequently, only the

Figure 65. Anarosaurus pumilio. Reconstruction of the skull in dorsal, ventral and lateral views, based on Nopcsa, 1928 and specimen drawings by Carroll (unpublished).



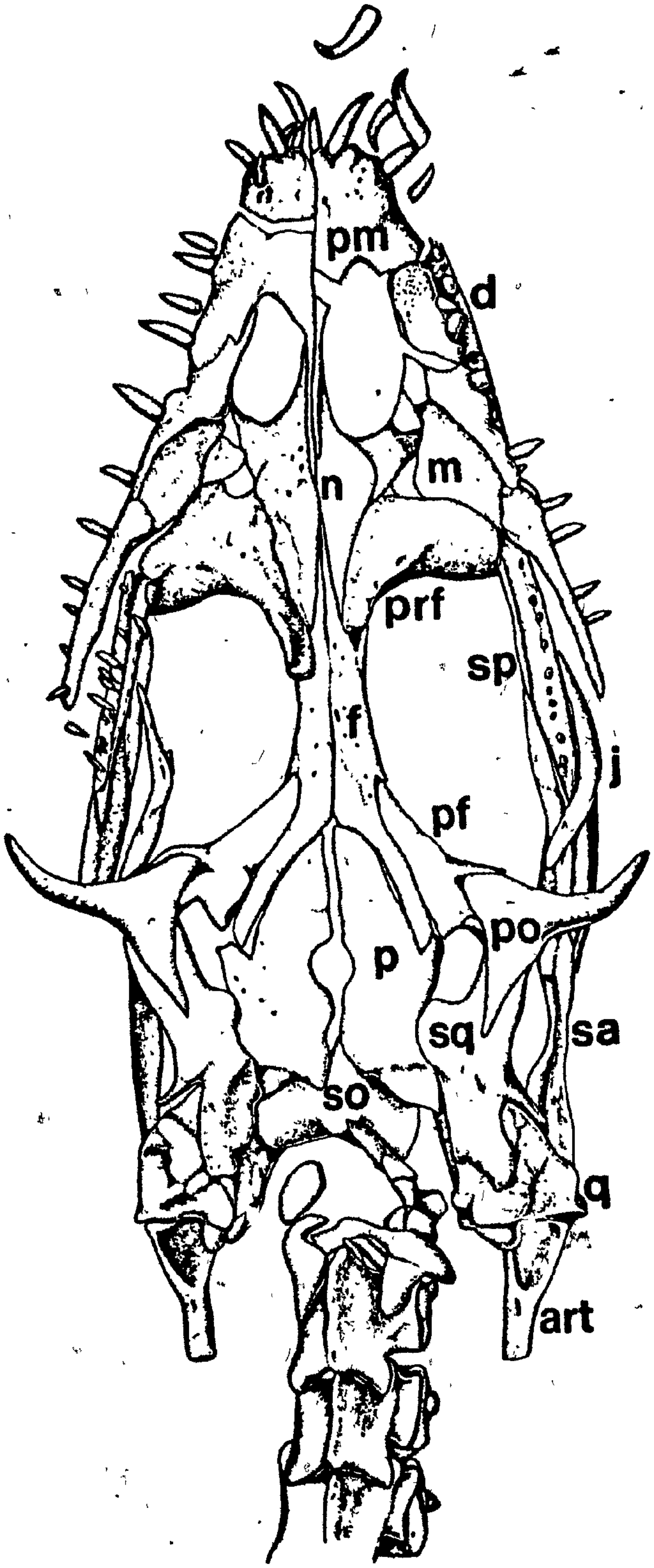




eosuchian affinities will be considered here.

Claudiosaurus (fig. 50h), primitive nothosaurs (figs. 65, 66) and plesiosaurs resemble younginiform eosuchians in the loss of contact between the parietal and postorbital. The configurations of the circumorbital bones, particularly the frontal, are similar to those in younginid and tangasaurid eosuchians. There are no accessory articulations at the base of the neural spine, and the sternum is not ossified (fig. 57k). The humerus is shorter and more gracile than the tangasaurid humerus, but the other long limb bones are comparable in length. The primitive articulation between the lateral centrale and third distal carpal is persistent (fig. 60k). The mesotarsal joint (Brinkman, 1971) is similar to that of Hovasaurus, although there are some minor differences that suggest divergence since the development of the joint. The fifth metatarsal is not hooked, but has a wide proximal head as in younginids and tangasaurids. Claudiosaurus may be more closely related to younginiform eosuchians than to the Prolacertiformes, but is not derived from tangasaurid stock.

Figure 66. Pachypleurosaurus edwardsi, specimen drawing of skull (MCZ).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VII

CONCLUSIONS

CONCLUSIONS

1. Four genera of tangasaurid eosuchians are known from the Permo-Triassic strata of Africa and Madagascar. Specimens from Madagascar that were originally identified as Tangasaurus and Datheosaurus are now assigned to Thadeosaurus. Thadeosaurus and Kenyasaurus are not specialized for swimming to the degree that the other two known tangasaurids, Tangasaurus and Hovasaurus, are.

2. Tangasaurid specimens from Madagascar are found in the Lower Sakamena formation. Pollen, spores, macro plants, corals, bivalves, ammonites and fish fossils have been used to show that this formation is equivalent to the Dzulfian Standard Stage of the Upper Permian. The Tangasaurus bearing beds of Africa are considered to be equivalent in age on the basis of lithological similarities and plant fossils. The strata from which Kenyasaurus was recovered is considered to be Lower Triassic by most authors.

3. Tangasaurus, Kenyasaurus and Thadeosaurus are each known from a single site. Hovasaurus is known from at least three localities, and is the most common vertebrate in the Lower Sakamena formation.

4. Faunal association data suggests that there were at least four distinct palaeoenvironments. Thadeosaurus

and Hovasaurus were apparently contemporaries living in the same general region, but lived in different environments.

4. Comparative measurements can be used to identify individual, partial skeletons of Thadeosaurus and Hovasaurus that lack diagnostic characters in the preserved sections.

Two systems of relative measurement, based on the orthometric linear unit and the average length of a dorsal centrum, were found to be useful for making comparisons between mature specimens of different genera. The two systems correlate well, although neither has biological significance for dimensions controlled by the animals' weight such as the shaft widths of limb bones. Regression analysis had to be used for comparison of immature specimens.

The ratio of adult length to hatchling length was analysed for 38 extant species of lizards and crocodylians and was found to be equivaltent to

$$2.70 + .003(\text{adult length in mm})\ \text{mm}^{-1}.$$

From this formula it was determined that the smallest known specimens of Thadeosaurus and Hovasaurus were not hatchlings, but probably were less than a year old when they died.

The presence of long growth series for these genera presents a unique opportunity to study differences in growth strategies in two closely related Permian genera, one that was essentially terrestrial and the other aquatic.

The growth rates calculated might better be referred to as ossification rates. The amount of cartilage in the majority of endochondral bones cannot be measured, but a rough estimate of cartilaginous composition was calculated for the humerus of each genus. Humeri of immature specimens of Thadeosaurus and Hovasaurus had cartilaginous ends making up to 16% of the total length of the bones. Because the amount of cartilage in the limb bones of both genera seems to be equivalent, differences in the growth rates of the ossified portions of the same bones of Thadeosaurus and Hovasaurus are biologically significant.

5. A new genus and species of eosuchian, Acerosodontosaurus piveteaui, is described. This animal is not a tangasaurid, but is a relatively unspecialized younginiform eosuchian. A derived character, loss of contact between the lateral centrale and third distal carpal, is found in Acerosodontosaurus and the Tangasauridae. This probably indicates common ancestry. Acerosodontosaurus is anatomically primitive enough to be close to the

ancestral form of younginids and tangasaurids, although the presence of several specialized characters indicate that it was not the ancestor itself.

6. The type specimen of Youngina shows that this genus is not as primitive as is generally thought. Accessory intervertebral articulations are found at the bases of the neural spines, and their presence allies this animal with the tangasaurids. Youngina is close to the ancestry of tangasaurids and possibly paliguanid lepidosaurs, but is not directly ancestral to any known taxa.

7. Specimens from Madagascar that had been identified as Tangasaurus have been reassigned to three other genera. The majority are juveniles of Thadeosaurus, and indicate that this animal was a tangasaurid. Anatomical characteristics not seen in the specimens described by Carroll (1981) are described here. There are significant differences in the allometric growth patterns of Thadeosaurus and the closely related but more specialized Hovasaurus.

8. The type specimens of Tangasaurus are redescribed. The tail of this animal is specialized as a swimming appendage, but not to the degree seen in Hovasaurus. Regression analysis shows that the limb elements of

both genera are the same relative lengths except that the fourth digit of the pes is relatively shorter in Tangasaurus.

9. Hovasaurus is represented by hundreds of specimens, both juveniles and adults, and therefore should be the best known Paleozoic reptile. The original description (Piveteau, 1926), although well illustrated with photographic plates, was based on only seven, immature specimens however. This paper, the first detailed description of Hovasaurus, reveals that this genus is more interesting than previously suspected. It is the most highly adapted of the known tangasaurids for swimming. The skull is only partially known, but is more specialized than Youngina in that the jaw suspension slopes anteroventrally. The palatal teeth are long, slender and recurved distally, showing that Hovasaurus was carnivorous. The neck is short, and the tail is at least double the snout-vent length of the body. Accessory intervertebral articulations are present throughout the vertebral column as in Youngina and other tangasaurids, but are more complicated. The neural spines in the presacrum are taller than in other known eosuchians, and bear mammilary processes in the anterior dorsals. The caudal neural spines are taller than the presacral

ones, and are platelike and laterally compressed. The haemal spines mimic the associated neural spines in size and shape. There is no doubt that the tail was a powerful swimming appendage. The ribs, like those of some aquatic reptiles and mammals, are pachyostotic at maturity. The dorsal portions of the pectoral girdle are reduced, and the ventral bones are relatively large and platelike. This would serve to lower the centre of gravity for increased stability in the water, and to increase the areas of attachment for muscles associated with the power stroke of the front limb. The humerus is longer than those of other eosuchians, and exceeds the length of the femur. It superficially appears primitive, but analysis of the morphology and muscle insertions indicates that the front limb was mechanically more efficient than that of captorhinomorphs. The radius is almost half the length of the humerus and the manus is more symmetrical than in terrestrial eosuchians. The front limb is paddle-like in shape, and would have been used for swimming and for direction control when swimming. The hind limb is mechanically as efficient for terrestrial locomotion as most eosuchians and has no characters to indicate that it was used for swimming. The abdominal cavity of most specimens includes enough ingested pebbles to have raised the specific gravity of individuals by five to ten percent. The pebble mass is positioned to shift the centre of gravity posteroventrally for greater stability when swimming.

10. Anatomical evidence suggests that Thadeosaurus was primarily a terrestrial animal, and Hovasaurus was mainly aquatic. Unlike most aquatic genera, the replacement of cartilage with bone did not occur at a slower rate in Hovasaurus than in its terrestrial relative. Nevertheless, the limbs of Hovasaurus are relatively shorter than those of Thadeosaurus at birth. Allometric growth rates are similar in vertebrae and limb girdles, but are significantly higher in the limb bones of Hovasaurus. Usually if there are differences in allometric growth rates in two closely related animals, the smaller form will have the higher rates because allometric coefficients that differ markedly from 1.0 are strongly size limiting. In mature specimens, the limb elements of Hovasaurus are relatively longer than those of Thadeosaurus and could have functioned as efficiently on land. It is possible that a newborn Hovasaurus entered the water as sea turtles do, and seldom ventured onto land until mature. Adults may have spent more time on land for mating, laying eggs and/or range dispersal.

11. The improved knowledge of tangasaurids makes it worthwhile to consider the relationship of this family to other eosuchians. The most significant synapomorphy of lepidosaurian reptiles is the presence of both upper temporal and suborbital fenestra. The Eosuchia is defined by a suite of at least fifteen shared derived characters, and is probably monophyletic. Tangasaurids are younginiform eosuchians, and are united with the Younginidae into the superfamily Younginoidea. Only one other eosuchian, Acerosodontosaurus, seems to be closely related to the tangasaurids.

Two subfamilies are recognized in the Tangasauridae. The Kenyasaurinae, which includes Thadeosaurus and Kenyasaurus, are essentially terrestrial animals. Tangasaurus and Hovasaurus are united as the Tangasaurinae on the basis of the specialization of the tail as a swimming appendage.

Among eosuchian descendants, only paliguanid lacertilians might have come from reptiles closely related to tangasaurids.

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Table 1. Vertebral measurements of the holotype of <u>Youngina capensis</u> (AMNH 5561). It has been assumed that there was a typical presacral vertebral count of 25. C = caudal, S = sacral. Measurements in mm.

#	Centrum (maximum length)	Centrum (height)	Neural spine (height)	Neural spine (length)	Total vertebral height
14	5.7	—	5.2	—	10.0
15	5.8	—	5.4	5.8	10.5
16	5.3	4.3	5.6	—	11.0
17	5.5	4.2	—	—	—
18	5.3	4.6	—	—	—
19	5.4	4.0	—	—	—
20	5.4	—	5.3	5.3	11.9
21	5.3	—	5.6	4.9	11.1
22	5.4	4.0	5.9	4.9	11.3
23	5.4	—	5.9	4.9	11.3
24	4.9	—	5.8	—	10.8
25	5.7	—	5.2	—	—
S1	—	—	—	—	—
S2	—	—	—	—	—
C1	—	—	—	—	—
C2	—	4.4	5.0	4.3	10.7
C3	4.9	3.8	4.1	4.3	10.0
C4	5.1	—	—	—	—
C5	5.8	—	—	—	—
C6	—	—	—	—	—

Table 2. Figured specimens of Tangasauridae.

Identification (this paper)	Specimen number	Previous identification
Thadeosaurus	MNHN 1908-5-1	*Tangasaurus menelli* (Piveteau, 1926, Pl. XII, Fig. 1)
Thadeosaurus	MNHN 1908-11-4	*T. menelli* (Piveteau, 1926, Pl. X, Fig. 2)
Thadeosaurus	MNHN 1908-11-5	*T. menelli* (Piveteau, 1926, Pl. XI, Fig. 2, Text-Figs. 17, 18; Piveteau, 1955, Fig. 9; Gladstone & Wakely, 1932 Fig. 2; Kuhn, 1969, Fig. 18-6, 18-8)
Thadeosaurus	MNHN 1908-11-6	*T. menelli* (Piveteau, 1926, Pl. XVI, Fig. 2)
Thadeosaurus	MNHN 1908-11-7	*T. menelli* (Piveteau, 1926, Pl. X, Fig. 1)
Thadeosaurus	MNHN 1908-11-19	?*Datheosaurus* sp. (Piveteau, 1926, Pl. XVII, Fig. 2)

Identification (this paper)	Specimen number	Previous identification
Hovasaurus boulei	MNHN 1908-21-2	*Hovasaurus boulei* (Piveteau, 1926, Pl. VIII, Fig. 2)
H. boulei	MNHN 1908-21-7	*H. boulei* (Piveteau, 1926, Pl. VIII, Fig. 1; Haughton, 1930, Fig. 3C)
H. boulei	MNHN 1908-21-8	*H. boulei* (Piveteau, 1926, Pl. VII, Fig. 1)
H. boulei	MNHN 1908-21-10	*T. mennelli* (Harris and Carroll, 1977, Text-Fig. 5B)
H. boulei	MNHN 1908-21-11	Indeterminate reptile (Piveteau, 1926, Pl. X, Fig. 4)
H. boulei	MNHN 1908-21-16	*T. mennelli* (Piveteau, 1926, Pl. XV, Fig. 5, Text-fig. 20; Gladstone and Wakely, 1932, Text-fig. 2)
H. boulei	MNHN 1908-32-22	*H. boulei* (Piveteau, 1926, Pl. IX, Fig. 4, Text-fig. 14)
H. boulei	MNHN 1908-32-23	*H. boulei* (Piveteau, 1926, Pl. IX, Figs. 1, 2, Text-fig. 16)

Identification (this paper)	Specimen number	Previous identification
H. boulei	MNHN 1908-32-24	*T. mennelli* (Piveteau, 1926, Pl. XIII, Fig. 1; Harris and Carroll, 1977, Text-fig. 5A)
H. boulei	MNHN 1908-32-25	*T. mennelli* (Piveteau, 1926, Pl. XIV, Fig. 3)
H. boulei	MNHN 1908-32-26	*T. mennelli* (Piveteau, 1926, Pl. XV, Fig. 1)
H. boulei	MNHN 1908-32-29	*H. boulei* (Piveteau, 1926, Pl. VII, Fig. 2)
H. boulei	MNHN 1925-5-30	*H. boulei* (Piveteau, 1926, Pl. IX, Fig. 3, Text-fig. 12)
H. boulei	MNHN 1925-5-31	*T. mennelli* (Piveteau, 1926, Pl. XV, Fig. 4, Text-fig. 22; Piveteau, 1955, Text-fig. 10)
H. boulei	MNHN 1925-5-32	*T. mennelli* (Piveteau, 1926, Pl. XVI, Fig. 1, Text-fig. 23; Haughton, 1930, Text-fig. 4C; Piveteau, 1955, Text-fig. 11; Kuhn, 1969, Text-fig. 18-7; Harris and Carroll, 1977, Text-fig. 5C)

Identification (this paper)	Specimen number	Previous identification
H. boulei	MNHN 1925-5-33	*T. mennelli* (Piveteau, 1926, Pl. X, Fig. 3)
H. boulei	MNHN 1925-5-34	*T. mennelli* (Piveteau, 1926, Pl. XIV, Fig. 2; Camp, 1945, Text-fig. 10)
H. boulei	MNHN, number unknown	*H. boulei* (Piveteau, 1926, Pl. VII, Fig. 3; Haughton, 1930, Text-fig. 1A)
?*H. boulei*	MNHN, number unknown	*T. mennelli* (Piveteau, 1926, Pl. XIII, Fig. 5 , Pl. XIV, Fig. 1)
Kenyasaurus mariakaniensis	KNM-MA1	*Kenyasaurus mariakaniensis* (Harris and Carroll, 1977, Text-figs. 1, 2, 3, 4)
Tangasaurus mennelli	SAM 6231	*Tangasaurus mennelli* (Haughton, 1924, Pl. II, Text-figs. 1, 2, 3; von Huene, 1926, Text-fig. 33; Romer, 1956, Text-fig. 186E; Orlov, 1964, Text-fig. 468; Kuhn, 1969, Text-fig. 17-12; Harris and Carroll, 1977, Text-fig. 6)

Identification (this paper)	Specimen number	Previous identification
T. mennelli	SAM 6232	T. mennelli (Haughton, 1924, Plate I)
Not a tangasaurid	MNHN 1909-3-30	T. mennelli (Piveteau, 1926, Pl. XV, Figs. 2,3)
Not a tangasaurid	MNHN, number unknown	T. mennelli (Piveteau, 1926, Pl. XIII, Figs. 2, 2A)
Not a tangasaurid	MNHN, number unknown	T. mennelli (Piveteau, 1926, Pl. XIII, Fig. 3)
Not a tangasaurid	MNHN, number unknown	T. mennelli (Piveteau, 1926, Pl. XIII, Figs. 4, 4A)

Table 3. Postcranial measurements (in mm) and growth in Thadeosaurus. Lengths are measured between perpendiculars to the longitudinal axes and widths between lines parallel to the axis. When sternal plates are paired, the average width of one plate of the pair is given. When the sternal plates are fused, one half of the total width is given. The lengths of digits IV of the manus and pes do not include the lengths of the metacarpal and metatarsal. The constants b' and k_{yx}' of the power equation $y = b'x^{k_{yx}'}$ have been solved using the least squares method. Growth is isometric when $k_{yx} = 1.00$. Abbreviations: dw, distal width; h, height; l, length; Metac., metacarpal; Metat., metatarsal; N, size of sample; pw, proximal width; R, correlation coefficient; sw, shaft width; x, average length of centra of posterior dorsal vertebrae.

Table 3 (continued)

	Vertebrae		Interclavicle		Sternum		Scapula	
	x	Neural spine height	l	Head width	l	Width ($x\frac{1}{2}$)	l	h
MNHN 1908-5-1	6.4	7.2	—	—	—	—	—	—
MNHN 1908-11-4	3.0	1.8	—	—	4.0	2.8	—	—
MNHN 1908-11-5	4.2	—	33.0	—	11.0	7.0	11.0	8.0
MNHN 1908-11-6	6e	—	—	—	—	—	—	—
MNHN 1908-11-7	2.3	—	—	—	—	—	—	—
MNHN 1908-11-8/20	6.0	6.8	—	—	20.0	13.1	27.0	16.0
MNHN 1908-11-13/19	5.5	4.8	—	—	17.8	11.0	—	—
MNHN 1908-11-15	4.5	3.9	—	—	—	—	—	—
MNHN 1908-11-16	3.2	—	—	—	—	—	—	—
N	9	5	—	—	4	4	2	2
R	—	.991	—	—	.989	.993	1.00	1.00
k_{yx}'	—	1.78	—	—	2.32	2.20	2.52	1.71
b'	—	.26	—	—	.34	.27	.30	.69

Table 3 (continued)

	Coracoid l	h	Humerus l	pw	sw	dw
MNHN 1908-5-1	—	—	—	—	—	—
MNHN 1908-11-4	5.8	5.6	15.0	3.5	2.5	5.5
MNHN 1908-11-5	13.0	9.0	21.5	5.5	4.0	9.5
MNHN 1908-11-6	—	—	—	—	—	—
MNHN 1908-11-7	—	—	10.5	2.0	1.7	3.8
MNHN 1908-11-8/20	26.8	18.0	36.4	—	5.6	14.9
MNHN 1908-11-13/19	—	—	32.6	9.0	5.3	14.0
MNHN 1908-11-15	—	—	—	—	4.0	9.5
MNHN 1908-11-16	—	—	15e	—	—	—
N	3	3	6	4	6	6
R	.999	.996	.997	.996	.996	.997
k_{yx}'	2.21	1.69	1.30	1.68	1.25	1.46
b'	.52	.85	3.84	.51	.62	1.12

Table 3 (continued)

	Radius				Ulna			
	l	pw	sw	dw	l	pw	sw	dw
MNHN 1908-5-1	—	—	—	—	23.2	—	—	7e
MNHN 1908-11-4	10.5	2.5	1.3	2.0	10.0	2.5	1.3	2.5
MNHN 1908-11-5	14.0	3.3	2.1	2.8	13.3	3.6	2.0	3.4
MNHN 1908-11-6	—	—	—	—	—	—	—	—
MNHN 1908-11-7	7.4	1.8	1.0	1.5	7.2	1.7	1.0	1.6
MNHN 1908-11-8/20	22.4	—	—	—	21.9	5.7	2.4	5.4
MNHN 1908-11-13/19	21.0	4.9	2.5	4.0	20.5	5.3	2.5	5.3
MNHN 1908-11-15	17.0	3.5	2.2	2.7e	16.2	—	1.9	4.0
MNHN 1908-11-16	11.2	2.5	1.5	2.0	10.5	2.5	1.3	2.3
N	7	6	6	6	8	6	7	8
R	.995	.990	.991	.983	.996	.998	.979	.990
k_{yx}'	1.10	1.08	1.11	1.06	1.16	1.27	.97	1.36
b'	3.04	.72	.40	.60	2.72	.59	.45	.51

Table 3 (continued)

	Metac. IV	Digit IV	Ilium		Pubis		Ischium	
			blade l	base l	l	h	l	h
MNHN 1908-5-1	10.8	25.2	—	—	—	16.2	17.0	12.6
MNHN 1908-11-4	4.7	14.2	8.0	5.7	5.6	7.3	7.2	6.0
MNHN 1908-11-5	6.7	18.3	13.2	—	7.0	9.5	9.8	8.5
MNHN 1908-11-6	—	—	—	—	—	—	—	—
MNHN 1908-11-7	3.5	—	7.6	3.8	—	—	5.8	4.7
MNHN 1908-11-8/20	8.7	22.4	17.5	9.5	11.0	14.0	—	—
MNHN 1908-11-13/19	8.2	22.6	19.0	10.0	—	—	—	—
MNHN 1908-11-15	7.8	21.1	15.0	—	—	—	—	—
MNHN 1908-11-16	5.3	—	9.6	—	6.0	—	7.1	—
N	8	6	7	4	4	4	5	4
R	.986	.972	.971	.984	.985	.991	.988	1.000
k_{yx}'	1.00	.71	1.05	.97	.95	1.03	1.07	.97
b'	1.58	6.72	2.91	1.80	1.94	2.28	2.21	2.09

Table 3 (continued)

	Femur l	pw	sw	dw	Tibia l	pw	sw	dw
MNHN 1908-5-1	37e	8.0	4.9	—	35e	—	—	—
MNHN 1908-11-4	20.0	4.3	2.3	3.2	17.5	2.7	1.9	2.7
MNHN 1908-11-5	26.0	5.7	3.0	4.7	22.5	4.1	2.5	3.3
MNHN 1908-11-6	—	—	—	—	—	—	—	—
MNHN 1908-11-7	14.2	2.8	1.6	2.1	12.4	2.1	1.5	2.0
MNHN 1908-11-8/20	37.4	7.3	4.2	5.4	—	—	—	—
MNHN 1908-11-13/19	33.2	6.9	3.7	—	29.3	4.4	3.0	4.4
MNHN 1908-11-15	—	5.3	3.6	—	—	—	—	—
MNHN 1908-11-16	20.5	—	2.5	3.2	19.0	2.8	1.8	2.5
N	7	7	8	5	6	5	5	5
R	.995	.983	.984	.966	.993	.977	.987	.986
k_{yx}'	.93	.95	.98	.99	.96	.91	.82	.88
b'	6.85	1.37	.75	1.01	5.89	1.00	.75	.96

Table 3 (continued)

	Fibula l	pw	sw	dw	Metat. IV	Digit IV (Pes)
MNHN 1908-5-1	—	—	—	4.8	19.8	—
MNHN 1908-11-4	16.5	2.0	1.3	2.5	10.0	20.5
MNHN 1908-11-5	21.5	—	2.0	3.0	12.9	—
MNHN 1908-11-6	—	—	—	—	—	—
MNHN 1908-11-7	11.9	—	1.0	1.6	7.2	14.4
MNHN 1908-11-8/20	—	—	—	—	—	—
MNHN 1908-11-13/19	26.8	3.3	2.3	4.2	16.1	—
MNHN 1908-11-15	—	—	1.8	—	—	—
MNHN 1908-11-16	—	—	—	—	—	—
N	4	2	5	5	5	2
R	.995	—	.983	.987	.995	—
k_{yx}'	.91	.83	.96	1.02	.94	1.34
b'	5.75	.80	.45	.73	3.38	4.71

Table 4. Comparisons of the lengths of postcranial elements of Hovasaurus boulei and Tangasaurus mennelli. The constants b' and k_{yx}' of the power equation $y = b'x^{k_{yx}'}$ have been solved to describe a growth series of H. boulei. From this information, the expected mean lengths (in mm) of each element have been computed for H. boulei specimens the same size as the co-types of T. mennelli ($x = 6.6$ mm for SAM 6231, 8.0 mm for SAM 6232). Lengths of the metacarpals and metatarsals are not included in the lengths of the digits of the manus and pes. Abbreviations: N, size of sample; R, correlation coefficient.

Table 4 (continued)

y = length of;	N	R	kyx'	b'	x	Estimated Mean Value of y for *H. boulei*		Measured value of y for *T. mennelli*
						y	95% confidence interval	
Coracoid	9	.981	2.229	.360	6.6	24.1	20.7 - 28.0	25.3
					8.0	37.0	30.8 - 44.6	31.7
Sternum	15	.987	1.780	.739	6.6	22.1	20.7 - 23.7	21.8
					8.0	29.9	27.4 - 32.7	30.3
Humerus	20	.993	1.638	1.674	6.6	36.8	35.6 - 38.1	36.0
					8.0	50.5	48.4 - 52.7	48.5
Radius	13	.994	1.306	1.893	6.6	22.2	21.2 - 23.3	21.6
					8.0	28.6	26.9 - 30.3	28.0
Metacarpal IV	12	.991	1.354	.599	6.6	7.7	7.2 - 8.2	8.0
Digit IV (manus)	12	.983	1.236	2.035	6.6	20.9	19.2 - 22.7	21.0
Ilium	14	.996	1.067	2.952	6.6	22.1	21.1 - 23.1	23.0
Femur	16	.990	1.334	3.146	6.6	39.0	36.9 - 41.2	39.0
					8.0	50.4	47.1 - 54.0	47.2

Table 4 (continued)

y = length of;	N	R	k_{yx}'	b'	x	Estimated Mean Value of y for *H. boulei*		Measured value of y for *T. mennelli*
						y	95% confidence interval	
Tibia	15	.991	1.298	2.872	6.6	33.2	31.3 - 35.1	34.0
					8.0	42.6	39.6 - 46.0	40.0
Metatarsal IV	14	.995	1.340	1.310	6.6	16.4	15.6 - 17.2	17.4
					8.0	21.2	20.0 - 22.6	20.5
Digit IV (Pes)	9	.991	1.493	1.996	6.6	33.3	30.8 - 36.2	32.2
					8.0	44.5	39.9 - 49.5	39.1

Table 5. Hovasaurus boulei. Vertebral measurements (in mm) and growth. 1, maximum length of centrum; 2, width of centrum; 3, height of centrum; 4, width of vertebra across transverse processes; 5, height of neural spine; 6, anteroposterior length of neural spine; 7, width of neural spine; 8, total height of vertebra; 9, length of haemal spine (excluding haemal arch).

Note: allometric growth of neural spine of caudals and haemal spine calculated by comparison with the maximum length of the associated caudal centra and not with x.

Table 5 (continued)

Specimen number.	x	Anterior dorsal		15th - 18th						19th to 22nd
		6	7	1	2	3	4	5	6	5
MNHN R146	8.7	-	-	-	-	-	-	-	-	14.0
MNHN 1908-21-2/7	4.2	-	-	4.2	-	-	-	5.2	-	5.7
MNHN 1908-21-5	4.4	-	-	5.0	-	-	-	-	-	-
MNHN 1908-21-6	9.2	-	-	-	-	-	-	-	-	-
MNHN 1908-21-8	3.2e	-	-	-	-	-	-	-	-	-
MNHN 1908-21-11	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-12	8.0e	-	-	-	-	-	-	-	-	-
MNHN 1908-21-14	9.3e	-	-	-	-	-	-	-	-	-
MNHN 1908-21-16	8.2	-	-	7.9	-	-	-	12.3	-	-
MNHN 1908-21-18	8.6	-	-	8.6	-	-	-	-	-	-
MNHN 1908-21-19	9.6e	-	4.0	-	-	-	-	-	-	14.8
MNHN 1908-32-1	4.8	-	-	4.8	-	-	-	-	-	7.8
MNHN 1908-32-4	4.0	-	-	4.3	-	-	-	4.7	-	-

Table 5 (continued)

Specimen number	x	Anterior dorsal		15th - 18th						19th to 22nd
		6	7	1	2	3	4	5	6	5
MNHN 1908-32-21	3.7	-	-	3.6	-	-	-	4.4	-	4.6
MNHN 1908-32-22	4.2	-	-	4.1	-	-	-	-	-	5.6
MNHN 1908-32-23	5.5	-	-	5.4	-	-	-	-	-	-
MNHN 1908-32-24	8.7	4.9	3.8	8.9	-	-	11.7	14.0	6.1	14.8
MNHN 1908-32-25	8.5	-	-	-	-	-	-	-	-	-
MNHN 1908-32-29	3.3	-	-	3.3	-	-	-	4.0	-	-
MNHN 1908-32-45	9.2	-	-	9.2	-	-	-	13.4	-	14.7
MNHN 1908-32-49	9.5e	-	-	-	-	-	-	-	-	-
MNHN 1908-32-58	8.8	-	-	-	-	-	-	-	-	-
MNHN 1908-32-59	8.2	6.1	4.5	8.2	-	-	10.6	13.2	6.9	12.3
MNHN 1908-32-60	9.3	7.0	4.0	9.3	-	-	12.6	13.0	7.9	-
MNHN 1908-32-64/73	4.9e	-	-	-	-	-	-	-	-	-
MNHN 1908-32-67	9.0	-	-	9.0	-	-	-	13.9	-	-

Table 5 (continued)

Specimen number	x	Anterior dorsal		15th - 18th						19th to 22nd
		6	7	1	2	3	4	5	6	5
MNHN 1908-32-75	-	-	-	-	-	-	-	-	-	-
MNHN 1908-32-77	4.9	-	-	4.9	-	-	-	-	-	-
MNHN 1908-32-99	4.8	-	-	4.8	4.1	2.8	6.6	5.8	-	-
MNHN 1925-5-10	3.0	-	-	2.9	-	-	-	-	-	-
MNHN 1925-5-12	6.7	-	-	6.7	-	-	-	-	-	-
MNHN 1925-5-18	3.5	-	-	3.9	-	-	-	-	-	-
MNHN 1925-5-20	3.1	-	-	-	-	-	-	-	-	4.0
MNHN 1925-5-25	3.2	-	-	3.2	-	2.0	5.0	3.4	-	-
MNHN 1925-5-27	3.1c	-	-	-	-	-	-	-	-	-
MNHN 1925-5-28	5.0	-	-	4.8	-	-	-	6.9	-	6.7
MNHN 1925-5-29	6.9	-	-	6.8	-	4.6	-	-	-	-
MNHN 1925-5-30	3.8	-	-	-	-	-	-	-	-	-
MNHN 1925-5-34	6.4	-	-	6.4	-	-	-	-	-	-

Table 5 (continued)

Specimen number	x	Anterior dorsal		15th - 18th						19th to 22nd
		6	7	1	2	3	4	5	6	5
MNHN 1925-5-41	5.0	-	-	5.0	-	-	-	-	-	-
MNHN 1925-5-60	5.4	-	-	5.4	-	-	-	-	-	-
SAM 9456	-	-	-	-	-	-	-	-	-	-
SAM 9461	9.3	6.7	-	9.3	7.8	6.0	-	16.5	7.8	-
SAM 9462	-	-	-	-	-	-	-	-	-	-
SAM 9463	-	6.1	3.5	7.0	5.6	4.6	10.7	14.3	6.2	-
N	-	-	-	-	-	-	-	15	-	11
R	-	-	-	-	-	-	-	.98	-	.99
k_{yx}	-	-	-	-	-	-	-	1.34	-	1.20
b'	-	-	-	-	-	-	-	.89	-	1.03

Table 5 (continued)

Specimen number	20th - 25th							S1	S2
	1	2	3	4	5	6	7	5	5
MNHN R146	8.7	7.2	5.1	14.4	14.3	7.6	2.3	-	-
MNHN 1908-21-2/7	4.4	-	-	-	5.3	-	-	5.4	-
MNHN 1908-21-5	-	-	-	-	-	-	-	-	-
MNHN 1908-21-6	9.9	-	-	-	-	-	-	-	-
MNHN 1908-21-8	-	-	-	-	-	-	-	-	-
MNHN 1908-21-11	-	-	-	-	-	-	-	-	-
MNHN 1908-21-12	-	-	-	-	-	-	-	-	-
MNHN 1908-21-14	-	-	-	-	-	-	-	-	-
MNHN 1908-21-16	-	-	-	-	-	-	-	-	-
MNHN 1908-21-18	-	-	-	-	-	-	-	-	-
MNHN 1908-21-19	9.7	-	-	14.4	13.9	7.3	2.9	12.5	-
MNHN 1908-32-1	5.0	-	-	-	5.8	-	-	-	-
MNHN 1908-32[illegible]	-	-	-	-	-	-	-	4.0	4.0

Table 5 (continued)

Specimen number	20th - 25th							S1	S2
	1	2	3	4	5	6	7	5	5
MNHN 1908-32-21	3.8	-	-	-	4.2	-	-	3.7	4.0
MNHN 1908-32-22	4.3	-	3.1	-	4.8	-	-	5.1	-
MNHN 1908-32-23	5.6	-	-	-	-	-	-	-	-
MNHN 1908-32-24	9.0	-	-	-	15.4	7.5	2.9	12.0	-
MNHN 1908-32-25	8.3	-	-	-	-	-	-	-	-
MNHN 1908-32-29	3.6	-	-	-	-	-	-	-	-
MNHN 1908-32-45	-	-	-	-	-	8.3	-	-	-
MNHN 1908-32-49	9.2	-	-	-	-	-	-	-	-
MNHN 1908-32-58	-	-	-	-	-	-	-	-	-
MNHN 1908-32-59	-	-	-	-	11.0	-	2.8	-	-
MNHN 1908-32-60	-	-	-	-	-	-	-	-	-
MNHN 1908-32-64/73	-	-	-	-	-	-	-	-	-
MNHN 1908-32-67	-	-	-	-	-	-	-	-	-

Table 5 (continued)

Specimen number			20th - 25th					S1	S2
	1	2	3	4	5	6	7	5	5
MNHN 1908-32-75	-	-	-	-	-	-	-	-	-
MNHN 1908-32-77	5.0	-	3.3	-	-	-	-	-	-
MNHN 1908-32-99	-	-	-	-	-	-	-	-	-
MNHN 1925-5-10	3.0	-	-	-	-	-	-	-	-
MNHN 1925-5-12	-	-	-	-	-	-	-	-	-
MNHN 1925-5-18	-	-	-	-	-	-	-	-	-
MNHN 1925-5-20	3.0	-	-	-	3.3	-	-	3.1	3.3
MNHN 1925-5-25	-	-	-	-	-	-	-	-	-
MNHN 1925-5-27	3.1	-	-	-	-	-	-	-	-
MNHN 1925-5-28	-	-	-	-	-	-	-	-	-
MNHN 1925-5-29	-	-	-	-	-	-	-	-	-
MNHN 1925-5-30	3.8	-	-	-	-	-	-	-	-
MNHN 1925-5-34	-	-	-	-	-	-	-	-	-

Table 5 (continued)

Specimen number			20th - 25th					S1	S2
	1	2	3	4	5	6	7	5	5
MNHN 1925-5-41	-	-	-	-	-	-	-	-	-
MNHN 1925-5-60	5.4	-	-	-	-	-	-	-	-
SAM 9456	-	-	-	-	-	-	-	-	-
SAM 9461	-	-	-	-	-	-	-	-	-
SAM 9462	-	-	-	-	-	-	-	-	-
SAM 9463	-	-	-	-	-	-	-	-	-
N	-	-	-	-	9	-	-	-	-
R	-	-	-	-	.99	-	-	-	-
k_{yx}	-	-	-	-	1.33	-	-	-	-
b'	-	-	-	-	.74	-	-	-	-

Table 5 (continued)

Specimen number	10th - 15th caudal 1	5	8	9
MNHN R146	-	-	-	-
MNHN 1908-21-2/7	-	-	-	-
MNHN 1908-21-5	4.0	6.0	13.0	9.0
MNHN 1908-21-6	-	-	-	-
MNHN 1908-21-8	-	-	-	-
MNHN 1908-21-11	-	-	-	-
MNHN 1908-21-12	8.0	16.0	24.0	-
MNHN 1908-21-14	8.2	17.0	27.0	21.0
MNHN 1908-21-16	-	-	-	-
MNHN 1908-21-18	-	-	-	-
MNHN 1908-21-19	-	-	-	-
MNHN 1908-32-1	-	-	-	-
MNHN 1908-32-4	-	-	-	-

Table 5 (continued)

Specimen number	10th - 15th caudal 1	5	8	9
MNHN 1908-32-21	3.3	5.0	11.0	7.5
MNHN 1908-32-22	-	-	-	-
MNHN 1908-32-23	-	-	-	-
MNHN 1908-32-24	-	-	-	-
MNHN 1908-32-25	-	-	-	-
MNHN 1908-32-29	3.1	4.0	9.0	6.5
MNHN 1908-32-45	-	-	-	-
MNHN 1908-32-49	-	-	-	-
MNHN 1908-32-53	8.8	18.0	26.0	-
MNHN 1908-32-59	-	-	-	-
MNHN 1908-32-60	-	-	-	-
MNHN 1908-32-64/73	4.9	10.0	-	10.5
MNHN 1908-32-67	-	-	-	-

Table 5 (continued)

Specimen number	10th - 15th caudals 1	5	8	9
MNHN 1908-32-75	-	-	-	-
MNHN 1908-32-77	4.9	8.5	15.5	10.7
MNHN 1908-32-99	-	-	-	-
MNHN 1925-5-10	3.0	-	-	6.3
MNHN 1925-5-12	-	-	-	-
MNHN 1925-5-18	-	-	-	-
MNHN 1925-5-20	3.2	4.0	8.0	6.5
MNHN 1925-5-25	-	-	-	-
MNHN 1925-5-27	-	-	-	-
MNHN 1925-5-28	-	-	-	-
MNHN 1925-5-29	-	-	-	-
MNHN 1925-5-30	-	-	-	-
MNHN 1925-5-34	-	-	-	-

Specimen number	10th - 15th caudals			
	1	5	8	9
MNHN 1925-5-41	4.9	9.8	-	11.2
MNHN 1925-5-60	-	-	-	-
SAM 9456	-	-	-	-
SAM 9461	-	-	-	-
SAM 9462	-	-	-	-
SAM 9463	-	-	-	-
N	-	10	-	9
R	-	.98	-	.99
k_{yx}	-	1.43	-	1.18
b'	-	.86	-	1.73

Table 6. Postcranial measurements (in mm) of tangasaurids Lengths are measured between perpendiculars to the longitudinal axes and widths between lines parallel to the axis. When sternal plates are paired, the average width of one plate of the pair is given. When the sternal plates are fused, one half of the total width is given. The lengths of digits IV of the manus and pes do not include the lengths of the metacarpal and metatarsal. Abbreviations: A, shortest distance between the extremeties of the clavicle; B, Besakoa; c, calculated; dw, distal width; E, Mount Eliva; e, estimated (measurement may be slightly more or less than recorded); fem, femur; h, height; hs, length of haemal spine and arch; hum, humerus; l, length; Metac., metacarpal; Metat., metatarsal; ns, height of neural spine; pw, proximal width; rad, radius; sw, shaft width; T, Tanzania; tib, tibia; V, Vohibory; x, average length of centra of dorsal vertebrae. Size range; $A \leqslant 3.9 < B \leqslant 4.9 < C \leqslant 5.9 < D \leqslant 6.9 < E \leqslant 7.9 < F \leqslant 8.9 < G$ (according to x).

Table 6 (continued)

	Local.	Size range	Vertebrae x	Dorsal ns	Caudal l	ns	hs
MNHN 1925-5-10	—	A	3.0	—	3.0	—	6.3
MNHN 1925-5-20	E	A	3.1	4.0	3.2	4.0	6.5
MNHN 1925-5-27	E	A	3.1c	—	—	—	—
MNHN 1908-21-8	—	A	3.2e	—	—	—	—
MNHN 1925-5-25	E	A	3.2	—	—	—	—
MNHN 1908-32-29	—	A	3.3	—	3.1	4.0	6.5
MNHN 1925-5-18	—	A	3.5	—	—	—	—
MNHN 1908-32-21	—	A	3.7	4.6	3.3	5.0	7.5
MNHN 1925-5-30	—	A	3.8	—	—	—	—
MNHN 1908-32-4	—	B	4.0	—	3.9	—	8.3
SAM 9460	E	B	4.0	—	—	—	—
MNHN 1908-32-22	—	B	4.2	5.6	—	—	—

Table 6 (continued)

	Local.	Size range	Vertebrae				
			x	Dorsal	Caudal		
				ns	l	ns	hs
MNHN 1908-21-2/7	—	B	4.2	5.7	—	—	—
MNHN 1908-21-5	—	B	4.4	—	4.0	6.0	9.0
MNHN 1908-32-99	—	B	4.8	—	—	—	—
MNHN 1908-32-1	—	B	4.8	7.8	—	—	—
MNHN 1908-32-64/73	—	B	4.9e	—	4.9	10.0	10.5
MNHN 1908-32-77	—	B	4.9	—	4.9	8.5	10.7
MNHN 1925-5-28	E	C	5.0	6.7	—	—	—
MNHN 1925-5-41	E	C	5.0	—	4.9	9.8	11.2
MNHN 1925-5-60	E	C	5.4	—	—	—	—
MNHN 1908-32-23	—	C	5.5	—	—	—	—
SAM 9459	E	C	5.9c	—	—	—	—
MNHN 1925-5-34	—	D	6.4	—	—	—	—

Table 6 (continued)

	Local.	Size range	Vertebrae				
			x	Dorsal	Caudal		
				ns	l	ns	hs
MNHN 1925-5-12	E	D	6.7	—	—	—	—
MNHN 1925-5-29	E	D	6.9	—	—	—	—
SAM 6231	T	E	6.6	—	—	—	—
MNHN 1925-5-38	B	E	7.5	—	—	—	—
MNHN 1925-5-49	E	E	7.6e	—	—	—	—
MNHN 1908-32-26	—	E	7.7e	—	—	—	—
MNHN 1908-21-12	—	F	8.0e	—	8.0	16.0	—
SAM 6232	T	F	8.0	—	—	—	—
MNHN 1925-5-32	—	F	7.9+	—	—	—	—
MNHN R147	—	F	8.1e	—	—	—	—
MNHN 1908-21-16	—	F	8.2	—	—	—	—
MNHN 1908-32-59	—	F	8.2	12.3	—	—	—

Table 6 (continued)

	Local.	Size range	Vertebrae x	Dorsal ns	Caudal l	ns	hs
MNHN 1925-5-31	—	F	8.5c	—	—	—	—
MNHN 1908-32-25	—	F	8.5	—	—	—	—
MNHN 1908-21-18	—	F	8.6	—	—	—	—
MNHN 1908-32-68/ 1925-8-14	—	F	8.6c	—	—	—	—
MNHN R146	—	F	8.7	14.0	—	—	—
MNHN 1908-32-24	—	F	8.7	14.8	—	—	—
MNHN 1908-21-24	—	F	8.8c	—	—	—	—
MNHN 1908-32-58	—	F	8.8	—	8.8	18.0	—
MNHN 1925-5-50	B	G	9.0c	—	—	—	—
MNHN 1925-5-56	B	G	9.0	—	—	—	—
MNHN 1908-32-67	—	G	9.0	—	—	—	—

Table 6 (continued)

	Local.	Size range	Vertebrae x	Dorsal ns	Caudal l	ns	hs
SAM 9457	E	G	9.1c	—	—	—	—
MNHN 1925-5-54	—	G	9.1c	—	—	—	—
MNHN 1908-32-38	—	G	9.1c	—	—	—	—
MNHN 1908-21-6	—	G	9.2	—	—	—	—
MNHN 1908-32-45	—	G	9.2	14.7	—	—	—
MNHN 1925-5-46	V	G	9.2c	—	—	—	—
SAM 9461	E	G	9.3	—	—	—	—
MNHN 1908-21-14	—	G	9.3e	—	8.2	17.0	21.0
MNHN 1908-32-60	—	G	9.3	—	—	—	—
MNHN 1908-32-49	—	G	9.5e	—	—	—	—
MNHN 1908-21-19	—	G	9.6e	14.8	—	—	—
MNHN 1925-5-36	V	G	10.5c	—	—	—	—

Table 6 (continued)

	Clavicle			Interclavicle		Sternum	
	h	w	A	l	Head width	l	Width (x½)
MNHN 1925-5-10	—	—	—	—	—	—	—
MNHN 1925-5-20	—	—	—	—	—	—	—
MNHN 1925-5-27	—	—	—	—	—	—	—
MNHN 1908-21-8	10.0	7.0	12.0	—	—	5.8	3.3
MNHN 1925-5-25	—	—	—	—	—	—	—
MNHN 1908-32-29	—	—	—	—	—	5.5	4.0
MNHN 1925-5-18	—	—	—	—	—	—	—
MNHN 1908-32-21	—	—	—	—	—	—	—
MNHN 1925-5-30	—	—	—	—	—	7.5	5.1
MNHN 1908-32-4	—	—	—	—	—	10.3	7.4
SAM 9460	—	—	—	—	—	—	—
MNHN 1908-32-22	—	—	—	—	—	—	—

Table 6 (continued)

	Clavicle			Interclavicle		Sternum	
	h	w	A	l	Head width	l	Width (x½)
MNHN 1908-21-2/7	—	—	—	—	—	8.0	6.0
MNHN 1908-21-5	—	—	—	—	—	—	—
MNHN 1908-32-99	14.0	13.0	18.0	—	—	—	—
MNHN 1908-32-1	14e	—	16e	39.5	12.3	—	—
MNHN 1908-32-64/73	—	—	—	—	—	—	—
MNHN 1908-32-77	—	—	—	—	—	12.5	8.8
MNHN 1925-5-28	—	—	—	—	—	—	—
MNHN 1925-5-41	—	—	—	—	—	—	—
MNHN 1925-5-60	—	—	—	—	—	—	—
MNHN 1908-32-23	17.0	17.5	20.0	41.0	15.0	16.3	11.2
SAM 9459	—	—	—	—	—	—	—
MNHN 1925-5-34	20.5	16.0	23.5	—	—	—	—

Table 6 (continued).

	Clavicle			Interclavicle		Sternum	
	h	w	A	l	Head width	l	Width (x$\frac{1}{2}$)
MNHN 1925-5-12	—	—	—	—	—	25.0	19.5
MNHN 1925-5-29	—	—	—	—	—	21.0	14.0
SAM 6231	—	—	—	49.0	14-	21.8	12.6
MNHN 1925-5-38	—	—	—	50.0	19.4	—	21.0
MNHN 1925-5-49	—	18.0	—	—	—	—	—
MNHN 1908-32-26	—	16.0	—	52e	17.0	29.0	16.5
MNHN 1908-21-12	—	—	—	—	—	—	—
SAM 6232	—	—	—	—	—	30.3	14.6
MNHN 1925-5-32	—	—	—	—	—	—	—
MNHN R147	18.5	—	—	54e	20.0	34.1	20.0
MNHN 1908-21-16	—	—	—	—	—	—	—
MNHN 1908-32-59	—	—	—	—	—	31.0	20.0

Table 6 (continued)

	Clavicle			Interclavicle		Sternum	
	h	w	A	l	Head width	l	Width (x½)
MNHN 1925-5-31	—	—	—	—	—	—	—
MNHN 1908-32-25	—	—	—	—	—	28.5	18.0
MNHN 1908-21-18	—	—	—	—	—	37.5	23.0
MNHN 1908-32-68/ 1925-8-14	—	—	—	—	—	—	—
MNHN R146	—	—	—	—	—	—	—
MNHN 1908-32-24	—	—	—	—	—	—	18.0
MNHN 1908-21-24	—	—	—	—	—	—	21.0
MNHN 1908-32-58	—	—	—	—	—	—	—
MNHN 1925-5-50	—	—	—	—	—	—	—
MNHN 1925-5-56	—	—	—	—	—	—	—
MNHN 1908-32-67	—	—	—	—	21e	33.5	21.0

Table 6 (continued)

	Clavicle			Interclavicle		Sternum	
	h	w	A	l	Head width	l	Width (x½)
SAM 9457	—	—	—	—	—	—	—
MNHN 1925-5-54	—	21-	—	59.5	21.5	—	20.0
MNHN 1908-32-38	—	—	—	—	—	41.0	21.0
MNHN 1908-21-6	—	—	—	—	—	—	—
MNHN 1908-32-45	—	—	—	—	—	—	—
MNHN 1925-5-46	—	—	—	—	—	—	—
SAM 9461	—	—	—	—	—	—	27.0
MNHN 1908-21-14	—	—	—	—	—	—	—
MNHN 1908-32-60	—	—	—	—	—	32.5-	—
MNHN 1908-32-49	—	—	—	—	—	—	—
MNHN 1908-21-19	—	—	—	—	—	—	—
MNHN 1925-5-36	—	—	—	—	—	—	—

Table 6 (continued)

	Scapula		Coracoid		Humerus			
	l	h	l	h	l	pw	sw	dw
MNHN 1925-5-10	—	—	—	—	—	—	—	—
MNHN 1925-5-20	—	—	—	—	—	—	—	—
MNHN 1925-5-27	—	—	—	—	—	—	—	—
MNHN 1908-21-8	—	—	4.7	3.6	11.0	4.2	3.2	5.9
MNHN 1925-5-25	—	—	—	—	—	—	—	—
MNHN 1908-32-29	—	—	—	—	—	—	3.2	6.0
MNHN 1925-5-18	—	—	—	—	—	—	—	—
MNHN 1908-32-21	—	—	—	—	—	—	—	—
MNHN 1925-5-30	7.2	7.0	7.1	6.6	16.0	4.5	4.5	6.5
MNHN 1908-32-4	—	—	—	—	15.6	4.9	3.5	6.8
SAM 9460	—	—	—	—	—	—	—	—
MNHN 1908-32-22	—	—	—	—	—	—	—	—

Table 6 (continued)

	Scapula		Coracoid		Humerus			
	l	h	l	h	l	pw	sw	dw
MNHN 1908-21-2/7	8.5	9.0	8.0	6.9	17.5	5.0	4.6	7.3
MNHN 1908-21-5	—	—	—	—	—	—	—	—
MNHN 1908-32-99	10,8	10.5	—	—	20.0	—	4.2	8.6
MNHN 1908-32-1	13.0	—	—	—	21.5	7.0	6.0	9.2
MNHN 1908-32-64/73	—	—	—	—	—	—	—	—
MNHN 1908-32-77	—	—	—	—	24.0	7.4	6.5	11.0
MNHN 1925-5-28	—	—	—	—	22.5	7.5	5.5	8.5
MNHN 1925-5-41	—	—	—	—	—	—	—	—
MNHN 1925-5-60	—	—	—	—	—	—	—	10.5
MNHN 1908-32-23	12.5	14.5	12.5	10.0	25.3	8.0	6.9	11.5
SAM 9459	—	—	—	—	—	—	—	—
MNHN 1925-5-34	—	—	—	—	—	—	—	18.6

Table 6 (continued)

	Scapula		Coracoid		Humerus			
	l	h	l	h	l	pw	sw	dw
MNHN 1925-5-12	—	—	—	—	35.5	10.5	9.2	17.0
MNHN 1925-5-29	—	—	—	—	36.0	8.7	7.5	16.5
SAM 6231	—	—	25.3	—	36.0	—	8.3	15.8
MNHN 1925-5-38	—	—	45.0	23.0	—	—	—	—
MNHN 1925-5-49	—	—	—	24.0	—	12.2	8.0	—
MNHN 1908-32-26	—	—	33.5	18.0	45.0	13.5	10.0	18.5
MNHN 1908-21-12	—	—	—	—	—	—	—	—
SAM 6232	—	—	31.7	17.8	48.5	—	12.0	20.3
MNHN 1925-5-32	—	—	—	—	—	—	—	—
MNHN R147	32.0	45.0	42.0	24.5	60.0	14.0	—	23.0
MNHN 1908-21-16	—	—	—	—	—	—	—	—
MNHN 1908-32-59	—	—	—	—	55.0	—	12.0	—

Table 6 (continued)

	Scapula		Coracoid		Humerus			
	l	h	l	h	l	pw	sw	dw
MNHN 1925-5-51	—	—	—	—	—	—	—	—
MNHN 1908-32-25	—	—	35.0	19.8	54.0	13.7	11.5	20.5
MNHN 1908-21-18	—	—	—	27.0	62.0	19.5	—	—
MNHN 1908-32-68/ 1925-8-14	—	—	—	—	—	—	—	22.0
MNHN R146	—	—	—	—	—	—	—	—
MNHN 1908-32-24	—	—	—	—	54.0	13.5	11.0	21.8
MNHN 1908-21-24	—	—	—	—	—	—	—	—
MNHN 1908-32-58	—	—	—	—	—	—	—	—
MNHN 1925-5-50	—	—	—	—	55-	—	14.0	28.0
MNHN 1925-5-56	—	—	—	26.0	61.0	—	13.2	26.2
MNHN 1908-32-67	—	—	47.5	26.0	66.0	20.7	9.5	26.2

Table 6 (continued)

	Scapula		Coracoid		Humerus			
	l	h	l	h	l	pw	sw	dw
SAM 9457	—	—	—	—	—	—	—	—
MNHN 1925-5-54	—	—	45.0	25-	—	—	—	—
MNHN 1908-32-38	—	—	—	—	—	—	—	—
MNHN 1908-21-6	—	—	—	—	—	—	—	—
MNHN 1908-32-45	—	—	—	—	—	—	—	—
MNHN 1925-5-46	—	—	—	—	55?	18?	14.5	30.0
SAM 9461	—	—	—	—	—	—	—	—
MNHN 1908-21-14	—	—	—	—	—	—	—	—
MNHN 1908-32-60	—	—	—	—	64.0	20.0	15.5	29.5
MNHN 1908-32-49	—	—	—	—	—	—	—	—
MNHN 1908-21-19	—	—	—	—	—	—	—	—
MNHN 1925-5-36	—	—	—	—	—	—	14.8	—

Table 6 (continued)

	Radius				Ulna			
	l	pw	sw	dw	l	pw	sw	dw
MNHN 1925-5-10	8.5	—	1.1	1.4	7.6	2.4	1.2	1.8
MNHN 1925-5-20	—	—	—	—	—	—	—	—
MNHN 1925-5-27	—	—	—	—	—	—	—	1.8
MNHN 1908-21-8	7.9	2.4	1.4	1.9	7.2	2.5	1.4	2.0
MNHN 1925-5-25	—	—	—	—	—	—	—	—
MNHN 1908-32-29	8.5	2.0	1.4	2.0	7.5	2.2	1.4	2.0
MNHN 1925-5-18	—	—	—	—	—	—	—	—
MNHN 1908-32-21	—	—	—	1.9	—	—	—	2.0
MNHN 1925-5-30	—	—	—	—	—	—	—	—
MNHN 1908-32-4	10.9	2.7	1.8	2.5	10.0	3.0	1.8	2.9
SAM 9460	—	—	—	—	—	—	—	—
MNHN 1908-32-22	—	—	—	—	—	—	—	—

Table 6 (continued)

	Radius				Ulna			
	l	pw	sw	dw	l	pw	sw	dw
MNHN 1908-21-2/7	11.6	3.0	1.9	2.3	10.5	3.0	1.9	2.4
MNHN 1908-21-5	—	—	—	—	—	—	—	—
MNHN 1908-32-99	—	3.3	2.1	—	13.5	3.5	2.0	—
MNHN 1908-32-1	14.5	4.2	2.7	3.0	13.5	3.8	2.6	3.7
MNHN 1908-32-64/73	—	—	—	—	—	—	—	—
MNHN 1908-32-77	15.5	4.4	2.5	3.6	14.1	4.3	2.5	4.0
MNHN 1925-5-28	—	—	—	—	—	—	—	—
MNHN 1925-5-41	—	—	—	—	—	—	—	—
MNHN 1925-5-60	18.5	4.2	2.2	2.9	—	—	—	—
MNHN 1908-32-23	17.0	4.1	3.0	3.2	16.0	4.9	2.7	3.9
SAM 9459	—	—	—	—	—	—	—	—
MNHN 1925-5-34	—	—	—	—	—	—	—	—

Table 6 (continued)

	Radius				Ulna			
	l	pw	sw	dw	l	pw	sw	dw
MNHN 1925-5-12	22.0	5.3	3.7	4.6	20.0	6.8	3.2	6.5
MNHN 1925-5-29	23,5	6.0	3.8	4.0	21.3	6.0	3.4	5.0
SAM 6231	21.6	5.7	3.4	5.1	21.0	5.8	3.1	4.9
MNHN 1925-5-38	—	—	—	—	—	—	—	—
MNHN 1925-5-49	—	—	—	—	—	—	—	—
MNHN 1908-32-26	—	—	—	—	—	—	—	—
MNHN 1908-21-12	—	—	—	—	—	—	—	—
SAM 6232	29.0	8.0	4.6	5.9	28.0	7.4	4.6	—
MNHN 1925-5-32	—	—	—	—	—	—	—	—
MNHN R147	—	—	—	—	—	—	—	—
MNHN 1908-21-16	—	—	—	—	—	—	—	—
MNHN 1908-32-59	31e	—	—	5.0	29.1	9.3	4.0	8.0

Table 6 (continued)

	Radius l	pw	sw	dw	Ulna l	pw	sw	dw
MNHN 1925-5-31	31.0	6.8	5.5	6.5	31.0	9.5	4.2	7.3
MNHN 1908-32-25	—	—	—	—	—	9.0	—	—
MNHN 1908-21-18	—	—	—	—	—	—	—	—
MNHN 1908-32-68/ 1925-8-14	—	—	—	—	—	—	—	—
MNHN R146	—	—	—	—	—	—	—	—
MNHN 1908-32-24	—	—	—	—	31.0	8.5	4.7	—
MNHN 1908-21-24	—	—	—	—	—	—	—	—
MNHN 1908-32-58	—	—	—	—	—	—	—	—
MNHN 1925-5-50	28.5	8.9	—	—	29.0	9.8	5.6	8.2
MNHN 1925-5-56	32.0	9.5	6.0	7.0	—	10.0	6.2	—
MNHN 1908-32-67	—	10.2	6.0	—	33.0	11.5	5.2	10.1

Table 6 (continued)

	Radius l	pw	sw	dw	Ulna l	pw	sw	dw
SAM 9457	—	—	—	—	—	—	4.2	8.9
MNHN 1925-5-54	—	—	—	—	—	—	—	—
MNHN 1908-32-38	—	—	—	—	—	—	—	—
MNHN 1908-21-6	—	—	—	—	—	—	—	—
MNHN 1908-32-45	—	—	—	—	—	—	—	—
MNHN 1925-5-46	—	—	6.5	—	—	—	4.0	—
SAM 9461	—	—	—	—	—	—	—	—
MNHN 1908-21-14	—	—	—	—	—	—	—	—
MNHN 1908-32-60	—	—	6.2	—	35.5	9.0	6.0	10.0
MNHN 1908-32-49	—	—	—	—	—	—	—	—
MNHN 1908-21-18	—	—	—	—	—	—	—	—
MNHN 1925-5-36	—	—	—	—	—	—	—	—

Table 6 (continued)

	Metac. IV	Digit IV	Ilium		Pubis		Ischium	
			blade l	base l	l	h	l	h
MNHN 1925-5-10	2.8	—	9.6	5.5	5.2	6.5	6.9	6.0
MNHN 1925-5-20	—	—	9.9	5.0	—	—	—	—
MNHN 1925-5-27	3.2	8.8	—	—	—	—	—	—
MNHN 1908-21-8	2.5	7.0	—	5.4	5.0	7.0	7.3	6.2
MNHN 1925-5-25	—	—	—	—	5.5	6.0	6.7	6.0
MNHN 1908-32-29	2.9	8e	—	—	6.5	6.8	7.2	6.2
MNHN 1925-5-18	—	—	—	—	—	—	—	—
MNHN 1908-32-21	3.2	9.9	12.0	6.3	—	—	—	—
MNHN 1925-5-30	—	—	—	—	—	—	—	—
MNHN 1908-32-4	3.9	12.0	13.3	—	6.9	8.7	8.9	7.7
SAM 9460	—	—	14.0	7.3	7.8	9.2	9.5	8.4
MNHN 1908-32-22	—	—	12.3	6.3	7.9	9.0	10.0	7.9

Table 6 (continued)

	Metac.	Digit	Ilium		Pubis		Ischium	
	IV	IV	blade l	base. l	l	h	l	h
MNHN 1908-21-2/7	4.0	12.3	13.2	7.0	7.9	9.0	10.5	8.0
MNHN 1908-21-5	—	—	14.0	7.0	8.7	10.0	10.3	8.3
MNHN 1908-32-99	—	—	—	—	—	—	—	—
MNHN 1908-32-1	—	—	—	—	—	—	—	—
MNHN 1908-32-64/73	—	—	—	—	—	—	—	—
MNHN 1908-32-77	5.0	—	16.5	8.9	9.6	10.6	12.4	10.2
MNHN 1925-5-28	—	—	—	—	—	—	—	—
MNHN 1925-5-41	—	—	16.5	—	—	—	—	—
MNHN 1925-5-60	—	19.6	—	—	—	—	—	—
MNHN 1908-32-23	6.1	17.2	—	—	—	—	—	—
SAM 9459	—	—	—	—	—	—	—	—
MNHN 1925-5-34	—	—	—	—	—	—	—	—

Table 6 (continued)

	Metac. IV	Digit IV	Ilium blade l	Ilium base l	Pubis l	Pubis h	Ischium l	Ischium h
MNHN 1925-5-12	8.2	—	—	—	—	—	—	—
MNHN 1925-5-29	8.5	22.3	—	—	—	—	—	—
SAM 6231	8.0	21.0	23.0	—	—	—	—	—
MNHN 1925-5-38	—	—	—	—	—	—	—	—
MNHN 1925-5-49	—	—	—	—	—	—	—	—
MNHN 1908-32-26	—	—	—	—	—	—	—	—
MNHN 1908-21-12	—	—	—	—	—	—	—	—
SAM 6232	—	—	—	—	14.7	—	19.6	—
MNHN 1925-5-32	—	—	—	—	—	—	—	—
MNHN R147	—	—	—	—	—	—	—	—
MNHN 1908-21-16	—	—	—	—	20.7	26.0	—	—
MNHN 1908-32-59	10.1	28.9	—	—	—	—	—	—

Table 6 (continued)

	Metac. IV	Digit IV	Ilium blade l	base l	Pubis l	h	Ischium l	h
MNHN 1925-5-31	10.5	30.3	—	—	—	—	—	—
MNHN 1908-32-25	—	29.2e	—	—	—	—	—	—
MNHN 1908-21-18	—	—	—	—	—	—	—	—
MNHN 1908-32-68/ 1925-8-14	—	—	—	—	—	—	—	—
MNHN R146	—	—	30.5	16.2	—	—	—	—
MNHN 1908-32-24	—	—	30.5	—	—	—	—	—
MNHN 1908-21-24	—	—	—	—	—	—	—	—
MNHN 1908-32-58	—	—	—	—	—	—	—	—
MNHN 1925-5-50	—	—	—	—	—	—	—	—
MNHN 1925-5-56	—	—	—	—	—	—	—	—
MNHN 1908-32-67	—	—	—	—	—	—	—	—

Table 6 (continued)

	Metac. IV	Digit IV	Ilium blade l	base l	Pubis l	h	Ischium l	h
SAM 9457	10.5	—	—	—	—	—	—	—
MNHN 1925-5-54	—	—	—	—	—	—	—	—
MNHN 1908-32-38	—	—	—	—	—	—	—	—
MNHN 1908-21-6	—	29e	—	—	20.0	23.0	—	—
MNHN 1908-32-45	—	—	31.0	18.5	20.5	25.5	27.0	22.0
MNHN 1925-5-46	—	—	—	—	—	—	—	—
SAM 9461	—	—	—	—	—	—	—	—
MNHN 1908-21-14	—	—	—	—	—	—	—	—
MNHN 1908-32-60	—	—	—	—	—	—	—	—
MNHN 1908-32-49	—	—	32.0	—	22.5	29.0	28.0	24.0
MNHN 1908-21-19	—	—	—	—	—	—	—	—
MNHN 1925-5-36	—	—	—	—	—	—	—	—

Table 6 (continued)

	Femur l	pw	sw	dw	Tibia l	pw	sw	dw
MNHN 1925-5-10	15.0	3.2	2.2	2.8	13.1	2.2	1.7	2.1
MNHN 1925-5-20	—	3.0	2.0	—	—	—	1.2	2.0
MNHN 1925-5-27	—	—	—	—	—	—	—	—
MNHN 1908-21-8	13.5	4.0	2.3	3.5	11.3	2.6	1.7	2.5
MNHN 1925-5-25	14.5	2.8	2.0	3.3	12.6	2.4	1.5	2.0
MNHN 1908-32-29	15.5	4.0	2.5	3.2	13.5	—	1.8	2.3
MNHN 1925-5-18	17.0	3.9	2.3	3.0	14.1	2.6	1.7	3.0
MNHN 1908-32-21	17.5	4.1	2.5	4.0	15.1	3.2	2.0	3.2
MNHN 1925-5-30	—	—	—	—	—	—	—	—
MNHN 1908-32-4	17.7	4.7	2.8	4.0	15.9	3.4	1.8	2.7
SAM 9460	20.8	4.6	2.8	4.0	19.0	2.4	2.4	3.5
MNHN 1908-32-22	19.5	4.6	2.3	3.7	—	3.2	1.7	—

Table 6 (continued)

	Femur l	pw	sw	dw	Tibia l	pw	sw	dw
MNHN 1908-21-2/7	20.7	5.0	3.0	3.8	17.3	3.9	2.0	3.3
MNHN 1908-21-5	23.3	4.5	3.2	4.5	20.6	4.0	2.6	4.0
MNHN 1908-32-99	—	—	—	—	—	—	—	—
MNHN 1908-32-1	—	—	—	—	—	—	—	—
MNHN 1908-32-64/73	—	—	—	—	—	—	—	—
MNHN 1908-32-77	27.0	6.0	4.0	5.0	23.9	5e	3.0	4.2
MNHN 1925-5-28	—	—	—	—	—	—	—	—
MNHN 1925-5-41	26.5	5.5	4.2	4.5	23.0	4.7	3.2	4.8
MNHN 1925-5-60	33.0	7.5	3.5	5.2	27.8	7.0	2.8	4.0
MNHN 1908-32-23	—	—	—	—	—	—	—	—
SAM 9459	30.5	7.8	4.5	—	26.0	6.0	3.0	4.7
MNHN 1925-5-34	—	—	—	—	—	—	—	—

Table 6 (continued)

	Femur l	pw	sw	dw	Tibia l	pw	sw	dw
MNHN 1925-5-12	—	—	—	—	—	—	—	—
MNHN 1925-5.29	—	—	—	—	—	—	—	—
SAM 6231	39.0	8.0	5.9	7.3	34.0	6.0	4.5	5.4
MNHN 1925-5-38	—	—	—	—	—	—	—	—
MNHN 1925-5-49	—	—	—	—	—	—	—	—
MNHN 1908-32-26	—	—	—	—	—	—	—	—
MNHN 1908-21-12	50.0	11.5	6.0	(13.0)	—	—	—	—
SAM 6232	47.2	11.0	6.2	8.5	40.0	7.5e	5.2	6.9
MNHN 1925-5-32	—	12.0	6.2	—	—	—	4.9	7.0
MNHN R147	—	—	—	—	—	—	—	—
MNHN 1908-21-16	—	—	—	—	—	—	—	—
MNHN 1908-32-59	—	—	—	—	—	—	—	—

Table 6 (continued)

	Femur l	pw	sw	dw	Tibia l	pw	sw	dw
MNHN 1925-5-31	—	—	—	—	—	—	—	—
MNHN 1908-32-25	—	—	—	—	—	—	—	—
MNHN 1908-21-18	—	—	—	—	—	—	—	—
MNHN 1908-32-68/ 1925-9-14	—	—	—	—	—	—	—	—
MNHN R146	—	—	—	—	—	—	—	—
MNHN 1908-32-24	—	9.7	6.8	8.0	46.0	—	—	7.8
MNHN 1908-21-24	—	—	—	—	—	—	—	—
MNHN 1908-32-58	—	—	—	—	—	—	—	—
MNHN 1925-5-50	-	—	—	—	—	—	—	—
MNHN 1925-5-56	—	—	—	—	—	—	—	—
MNHN 1908-32-67	—	—	—	—	—	—	—	—

Table 6 (continued)

	Femur				Tibia			
	l	pw	sw	dw	l	pw	sw	dw
SAM 9457	—	—	7.3	10.0	—	10.5	—	—
MNHN 1925-5-54	—	—	—	—	—	—	—	—
MNHN 1908-32-38	—	—	—	—	—	—	—	—
MNHN 1908-21-6	—	—	—	—	—	—	—	—
MNHN 1908-32-45	—	—	—	—	—	—	—	—
MNHN 1925-5-46	—	—	—	—	—	—	—	—
SAM 9461	—	—	—	—	—	—	—	—
MNHN 1908-21-14	—	—	—	—	51.0	10.0	5.4	10.0
MNHN 1908-32-60	—	—	—	—	—	—	—	—
MNHN 1908-32-49	60e	15.5	8.5	—	—	—	—	—
MNHN 1908-21-19	—	—	—	—	—	—	—	—
MNHN 1925-5-36	—	—	—	—	—	—	—	—

Table 6 (continued)

	Fibula l	pw	sw	dw	Metat. IV	Digit IV (Pes)
MNHN 1925-5-10	12.0	—	1.2	1.6	6.4	—
MNHN 1925-5-20	12.5	—	1.2	1.6	6.2	11.2
MNHN 1925-5-27	—	—	—	—	—	—
MNHN 1908-21-8	10.5	—	1.2	1.7	5.1	10.4
MNHN 1925-5-25	—	—	1.1	1.7	6.4	—
MNHN 1908-32-29	13.0	1.3	1.2	1.7	6.1	10.8
MNHN 1925-5-18	13.2	—	1.3	—	7.2	—
MNHN 1908-32-21	13.1	1.7	1.4	2.1	7.3	13.3
MNHN 1925-5-30	—	—	—	—	—	—
MNHN 1908-32-4	14.6	—	1.4	2.3	—	—
SAM 9460	—	—	—	—	—	—
MNHN 1908-32-22	—	1.9	1.6	—	—	—

Table 6 (continued)

	Fibula l	pw	sw	dw	Metat. IV	Digit IV (Pes)
MNHN 1908-21-2/7	15.7	—	1.6	2.7	8.6	17.2
MNHN 1908-21-5	18.5	2.3	1.9	2.9	9.6	20.2
MNHN 1908-32-99	—	—	—	—	—	—
MNHN 1908-32-1	—	—	—	—	—	—
MNHN 1908-32-64/73	—	—	—	—	—	—
MNHN 1908-32-77	21.5	—	1.8	3.4	11.3	21.7
MNHN 1925-5-28	—	—	—	—	—	—
MNHN 1925-5-41	21.5	2.9	2.2	3.6	11.5	22.4
MNHN 1925-5-60	—	—	2.1	—	—	—
MNHN 1908-32-23	—	—	—	—	—	—
SAM 9459	—	—	2.1	3.6	—	—
MNHN 1925-5-34	—	—	—	—	—	—

Table 6 (continued)

	Fibula l	pw	sw	dw	Metat. IV	Digit IV (Pes)
MNHN 1925-5-12	—	—	—	—	—	—
MNHN 1925-5-29	—	—	—	—	—	—
SAM 6231	31.0	—	3.2	4.3	17.4	32.2
MNHN 1925-5-38	—	—	—	—	—	—
MNHN 1925-5-49	—	—	—	—	—	—
MNHN 1908-32-26	—	—	—	—	—	—
MNHN 1908-21-12	—	—	—	—	—	—
SAM 6232	37.0	—	3.7	5.5e	20.5	37.1
MNHN 1925-5-32	—	—	3.5	6.5	21.2	42.1e
MNHN R147	—	—	—	—	—	—
MNHN 1908-21-16	—	—	—	—	—	—
MNHN 1908-32-59	—	—	—	—	—	—

Table 6 (continued)

	Fibula				Metat.	Digit
	l	pw	sw	dw	IV	IV (Pes)
MNHN 1925-5-31	—	—	—	—	—	—
MNHN 1908-32-25	—	—	—	—	—	—
MNHN 1908-21-18	—	—	—	—	—	—
MNHN 1908-32-68/ 1925-8-14	—	—	—	—	24.0	—
MNHN R146	—	—	—	—	—	—
MNHN 1908-32-24	44.0	4.0	4.0	5.7	24.7	—
MNHN 1908-21-24	—	—	—	—	—	—
MNHN 1908-32-58	—	—	—	—	—	—
MNHN 1925-5-50	—	—	—	—	—	—
MNHN 1925-5-56	—	—	—	—	—	—
MNHN 1908-32-67	—	—	—	—	—	—

Table 6 7 (continued)

	Fibula l	pw	sw	dw	Metat. IV	Digit IV (Pes)
SAM 9457	42.0	—	3.8	8.5	—	—
MNHN 1925-5-54	—	—	—	—	—	—
MNHN 1908-32-38	—	—	—	—	—	—
MNHN 1908-21-6	—	—	—	—	—	—
MNHN 1908-32-45	—	—	—	—	—	—
MNHN 1925-5-46	—	—	—	—	—	—
SAM 9461	—	—	—	—	—	—
MNHN 1908-21-14	—	—	—	—	—	—
MNHN 1908-32-60	—	—	—	—	—	—
MNHN 1908-32-49	—	—	—	—	—	—
MNHN 1908-21-19	—	—	—	—	—	—
MNHN 1925-5-36	—	—	—	—	—	—

Table 6 (continued)

	Proportions hum/fem	rad/hum	tib/fem	rad/tib
MNHN 1925-5-10	—	—	.87	.65
MNHN 1925-5-20	—	—	—	—
MNHN 1925-5-27	—	—	—	—
MNHN 1908-21-8	.81	.72	.84	.70
MNHN 1925-5-25	—	—	.87	—
MNHN 1908-32-29	—	—	.87	.63
MNHN 1925-5-18	—	—	.83	—
MNHN 1908-32-21	—	—	.86	—
MNHN 1925-5-30	—	—	—	—
MNHN 1908-32-4	.88	.70	.90	.69
SAM 9460	—	—	.91	—
MNHN 1908-32-22	—	—	—	—

Table 6 (continued)

	Proportions			
	hum/fem	rad/hum	tib/fem	rad/tib
MNHN 1908-21-2/7	.85	.66	.84	.67
MNHN 1908-21-5	—	—	.88	—
MNHN 1908-32-99	—	—	—	—
MNHN 1908-32-1	—	.67	—	—
MNHN 1908-32-64/73	—	—	—	—
MNHN 1908-32-77	.89	.65	.89	.65
MNHN 1925-5-28	—	—	—	—
MNHN 1925-5-41	—	—	.87	—
MNHN 1925-5-60	—	—	.84	.67
MNHN 1908-32-23	—	.67	—	—
SAM 9459	—	—	.85	—
MNHN 1925-5-34	—	—	—	—

Table 6 (continued)

	Proportions			
	hum/fem	rad/hum	tib/fem	rad/tib
MNHN 1925-5-12	—	.62	—	—
MNHN 1925-5-29	—	.65	—	—
SAM 6231	.92	.60	.87	.64
MNHN 1925-5-38	—	—	—	—
MNHN 1925-5-49	—	—	—	—
MNHN 1908-32-26	—	—	—	—
MNHN 1908-21-12	—	—	—	—
SAM 6232	1.00	.62	.85	.73
MNHN 1925-5-32	—	—	—	—
MNHN R147	—	—	—	—
MNHN 1908-21-16	—	—	—	—
MNHN 1908-32-59	—	.56	—	—

Table 6 (continued)

	Proportions			
	hum/fem	rad/hum	tib/fem	rad/tib
MNHN 1925-5-31	—	—	—	—
MNHN 1908-32-25	—	—	—	—
MNHN 1908-21-18	—	—	—	—
MNHN 1908-32-68/ 1925-8-14	—	—	—	—
MNHN R146	—	—	—	—
MNHN 1908-32-24	—	—	—	—
MNHN 1908-21-24	—	—	—	—
MNHN 1908-32-58	—	—	—	—
MNHN 1925-5-50	—	.52	—	—
MNHN 1925-5-56	—	.52	—	—
MNHN 1908-32-67	—	—	—	—

Table 6 (continued)

	Proportions hum/fem	rad/hum	tib/fem	rad/tib
SAM 9457	—	—	—	—
MNHN 1925-5-54	—	—	—	—
MNHN 1908-32-38	—	—	—	—
MNHN 1908-21-6	—	—	—	—
MNHN 1908-32-45	—	—	—	—
MNHN 1925-5-46	—	—	—	—
SAM 9461	—	—	—	—
MNHN 1908-21-14	—	—	—	—
MNHN 1908-32-60	—	—	—	—
MNHN 1908-32-49	—	—	—	—
MNHN 1908-21-19	—	—	—	—
MNHN 1925-5-36	—	—	—	—

Table 7. Manus and pes measurements (in mm) of <u>Tangasaurus</u> and <u>Hovasaurus</u>. a, sum of lengths of phalanges; b, sum of length of metapodial and phalanges; mp, metapodial. Proportions were calculated from b.

Table 7 (continued)

Specimen number	Manus Pes	I mp	1	2	a	b	II mp	1	2	3	a	b
MNHN 1925-5-10	M	1.8	2.0	-	-	-	2.8	1.8	-	-	-	-
MNHN 1925-5-27	M	2.1	2.1	1.6	3.7	5.8	2.9	1.8	2.0	1.6	5.4	8.3
MNHN 1908-21-8	M	1.5	1.4	1.1	2.5	4.0	2.1	1.3	1.5	1.4	4.2	6.3
MNHN 1908-32-29	M	1.8	1.9	1.3	3.2	5.0	2.5	1.7	1.9	1.2	4.8	7.3
MNHN 1908-32-21	M	2.2	2.3	1.6	3.9	6.1	3.0	2.0	2.3	1.6	5.9	8.9
MNHN 1908-32-4	M	2.6	3.0	2.0e	5.0e	7.6e	3.3	2.5	2.8	2.1e	7.4e	10.7e
MNHN 1908-32-22	M	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-2/7	M	2.5	2.7	2.0	4.7	7.2	3.7	2.5	2.8	2.2	7.5	11.2
MNHN 1908-32-77	M	3.4	-	-	-	-	4.6	3.2	3.5	2.3	9.0	13.6
MNHN 1925-5-60	M	-	-	3.0	-	-	-	4.0	4.1	3.1	-	-
MNHN 1908-32-23	M	4.3	4.3	2.6	6.9	11.2	5.7	3.7	4.1	2.5e	10.3e	16.0e

Table 7 (continued)

Specimen number	III mp	1	2	3	4	a	b	IV mp	1	2	3
MNHN 1925-5-10	2.8	1.7	1.6	-	-	-	-	2.8	1.8	-	-
MNHN. 1925-5-27	3.1	2.0	1.8	2.0	1.5	7.3	10.4	3.2	2.0	1.8	1.7
MNHN 1908-21-8	2.3	1.5	1.3	1.3	1.1	5.2	7.5	2.5	1.6	1.3	1.4
MNHN 1908-32-29	2.6	1.7	1.5	1.7	1.4	6.3	8.9	2.9	1.8	1.6	1.5
MNHN 1908-32-21	3.3	2.2	2.0	2.1	1.3	7.6	10.9	3.2	2.3	2.0	1.9
MNHN 1908-32-4	4.0	2.8	2.3	2.8	2.1	10.0	14.0	3.9	2.4	2.2	2.3
MNHN 1908-32-22	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-2/7	4.0	2.5	2.3	2.6	1.9	9.3	13.3	4.0	2.6	2.8	2.5
MNHN 1908-32-77	5.0	-	-	-	2.2	-	-	5.0	-	-	-
MNHN 1925-5-60	7.7	4.5	3.9	-	-	-	-	-	5.0	4.0	3.9
MNHN 1908-32-23	6.1	3.6	3.5	4.0	2.6	13.7	19.8	6.1	4.1	3.4	3.4

Table 7 (continued)

Specimen number	IV				V						
	4	5	a	b	mp	1	2	3	4	a	b
MNHN 1925-5-10	-	1.1	-	-	1.8	-	-	-	-	-	-
MNHN 1925-5-27	1.8	1.5	8.8	12.0	2.1	2.0	2.1	1.5	-	5.6	7.7
MNHN 1908-21-8	1.4	1.3	7.0	9.5	1.8	1.5	-	-	-	-	-
MNHN 1908-32-29	1.7	1.4e	8.0e	10.9e	1.9	1.7	1.8	1.1	-	4.6	6.5
MNHN 1908-32-21	2.2	1.5	9.9	13.1	2.2	2.2	2.4	1.5	-	6.1	8.3
MNHN 1908-32-4	2.6	2.5	12.0	15.9	2.9	2.3	2.9	1.8	-	7.0	9.9
MNHN 1908-32-22	2.5	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-2/7	2.4	2.0	12.3	16.3	3.0	2.7	2.6	1.7	-	7.0	10.0
MNHN 1908-32-77	3.1	2.1	-	-	3.8	-	-	-	-	-	-
MNHN 1925-5-60	4.0	2.7	19.6	-	-	-	4.4	2.8	-	-	-
MNHN 1908-32-23	3.8	2.5	17.2	23.3	4.6	3.7	3.9	2.5	-	10.1	14.7

Table 7 (continued)

Specimen number	I/IV	II/IV	III/IV	V/IV	V/III	IV/x
MNHN 1925-5-10	-	-	-	-	-	-
MNHN 1925-5-27	.48	.69	.87	.64	.74	3.87
MNHN 1908-21-8	.42	.66	.79	-	-	2.97
MNHN 1908-32-29	.46	.67	.82	.60	.73	3.30
MNHN 1908-32-21	.47	.68	.83	.63	.76	3.54
MNHN 1908-32-4	.48	.67	.88	.62	.71	3.98
MNHN 1908-32-22	-	-	-	-	-	-
MNHN 1908-21-2/7	.44	.69	.82	.61	.75	3.88
MNHN 1908-32-77	-	-	-	-	-	-
MNHN 1925-5-60	-	-	-	-	-	-
MNHN 1908-32-23	.48	.69	.85	.63	.74	4.24

Table 7 (continued)

Specimen number	Manus Pes	I					II					
		mp	1	2	a	b	mp	1	2	3	a	b
MNHN 1925-5-12	M	5.3	5.5	4.0	9.5	14.8	7.2	4.7	5.1	4.0	13.8	21.0
MNHN 1925-5-29	M	5.9	5.9	3.5	9.4	15.3	7.5	5.3	5.6e	3.6	14.5e	22.0e
SAM 6231	M	5.0	5.0	4.0	9.0	14.0	7.0	5.5	4.5	4.0	14.0	21.0
MNHN 1908-21-16	M	-	-	-	-	-	9.5	7.0	7.0	5.1	19.1	28.6
MNHN 1908-32-59	M	6.0	6.7	4.5	11.2	17.2	9.0	6.2	6.5	4.5e	17.2e	26.2e
MNHN 1925-5-31	M	6.8	7.1	5.5	12.6	19.4	9.5	5.5	6.7	6.0	18.2	27.7
MNHN 1908-32-25	M	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-32-24	M	-	-	-	-	-	-	-	-	-	-	-
SAM 9457	M	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-6	M	-	-	4.8	-	-	-	6.3	6.7	4.8e	-	-

Table 7 (continued)

Specimen number	III mp	1	2	3	4	a	b	IV mp	1	2	3
MNHN 1925-5-12	8.0	5.0	4.3	4.6	3.6	17.5	25.5	8.2	5.0	4.5	-
MNHN 1925-5-29	8.3	5.2	4.8	4.7	3.5	18.2	26.5	8.5	5.1	4.5	4.4
SAM 6231	7.5	5.0	5.5	5.0	4.0	19.5	27.0	8.0	5.0	4.0	4.5
MNHN 1908-21-16	-	-	-	-	5.0	-	-	-	-	-	-
MNHN 1908-32-59	10.0	6.2	5.4	5.7	4.5e	21.8e	31.8e	10.1	6.0	6.3	5.6
MNHN 1925-5-31	10.3	6.4	6.5	6.0	5.7	24.6	34.9	10.5	6.5	5.8	5.7
MNHN 1908-32-25	-	6.2	-	-	-	-	-	10.3	6.6	5.7	5.6
MNHN 1908-32-24	-	-	-	-	-	-	-	-	6.7	-	-
SAM 9457	9.8	6.1	6.4	-	-	-	-	10.5	6.5	6.0	-
MNHN 1908-21-6	-	6.6	6.3	6.6	5.5	25.0	-	-	6.6e	5.7	5.7

Table 7 (continued)

Specimen number	IV 4	5	a	b	V mp	1	2	3	4	a	b
MNHN 1925-5-12	-	-	-	-	5.9	5.0	5.0	-	-	-	-
MNHN 1925-5-29	4.7	3.6	22.3	30.8	6.2	5.5	5.6	3.5	-	14.6	20.8
SAM 6231	4.0	3.5	21.0	29.0	5.0	5.0	5.5	4.0	-	14.5	19.5
MNHN 1908-21-16	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-32-59	6.0e	5.0e	28.9e	39.0e	8.0	6.2	6.3	5.0	-	17.5	25.5
MNHN 1925-5-31	6.5	5.8e	30.3e	40.8e	8.0	6.3	6.5	5.3	-	18.1	26.1
MNHN 1908-32-25	6.2	5.1e	29.2e	39.5e	-	6.1	7.0	5.1	-	18.2	-
MNHN 1908-32-24	-	-	-	-	9.0	7.2	7.0	4.6	-	18.8	27.8
SAM 9457	-	5.0	-	-	7.5	6.5	-	5.5	-	-	-
MNHN 1908-21-6	6.2	4.8e	29.0	-	-	-	-	-	-	-	-

Table 7 (continued)

Specimen number	$\frac{\text{I}}{\text{IV}}$	$\frac{\text{II}}{\text{IV}}$	$\frac{\text{III}}{\text{IV}}$	$\frac{\text{V}}{\text{IV}}$	$\frac{\text{V}}{\text{III}}$	$\frac{\text{IV}}{\text{x}}$
MNHN 1926-5-12	-	-	-	-	-	-
MNHN 1925-5-29	.50	.71	.86	.68	.78	4.46
SAM 6231	.48	.72	.93	.67	.72	4.39
MNHN 1908-21-16	-	-	-	-	-	-
MNHN 1908-32-59	.44	.67	.82	.65	.80	4.76
MNHN 1925-5-31	.48	.68	.86	.64	.75	4.80
MNHN 1908-32-25	-	-	-	-	-	4.65
MNHN 1908-32-24	-	-	-	-	-	-
SAM 9457	-	-	-	-	-	-
MNHN 1908-21-6	-	-	-	-	-	-

Table 7 (continued)

Specimen number	Manus Pes	I mp	1	2	a	b	II mp	1	2	3	a	b
MNHN 1925-5-10	P	3.0	-	-	-	-	5.0	-	-	-	-	-
MNHN 1925-5-20	P	3.0	-	2.6	-	-	4.6	2.5	-	-	-	-
MNHN 1908-21-8	P	2.4	2.0	1.6	3.6	6.0	4.2	2.2	2.0	1.5	5.7	9.9
MNHN 1925-5-25	P	2.8	2.4	-	-	-	5.0	2.5	-	-	-	-
MNHN 1908-32-29	P	2.9	2.5	1.6	4.1	7.0	5.0	2.3	2.5	1.5	6.3	11.3
MNHN 1925-5-18	P	3.3	-	-	-	-	5.5	-	-	-	-	-
MNHN 1908-32-21	P	3.4	3.2	2.0	5.2	8.6	5.6	3.0	3.0	2.3	8.3	13.9
MNHN 1908-21-2/7	P	4.0	3.8	2.4	6.2	10.2	6.9	3.3	3.3	2.5	9.1	16.0
MNHN 1908-21-5	P	4.5	4.5	3.0	7.5	12.0	7.9	4.2	4.4	3.0	11.6	19.5
MNHN 1908-32-77	P	5.8	4.9	3.1	8.0	13.8	9.0	4.3	4.5	3.0	11.8	20.8

Table 7 (continued)

Specimen number	III mp	1	2	3	4	a	b	IV mp	1	2	3
MNHN 1925-5-10	6.3	-	-	-	-	-	-	6.4	-	-	-
MNHN 1925-5-20	5.8	2.7	2.0	-	-	-	-	6.2	3.3	2.3	2.1
MNHN 1908-21-8	5.1	2.2	2.0	2.0	1.6	7.8	12.9	5.1	2.7	2.1	2.0
MNHN 1925-5[illegible]5	6.0	-	-	-	-	-	-	6.4	3.2	-	-
MNHN 1908-32-29	6.0	2.6	2.1	2.2	1.5	8.4	14.4	6.1	3.0	2.3	1.9
MNHN 1925-5-18	-	-	-	-	-	-	-	7.2	3.8	-	-
MNHN 1908-32-21	6.8	3.2	2.7	2.8	1.9	10.6	17.4	7.3	3.9	2.7	2.4
MNHN 1908-21-2/7	8.0	4.0	3.2	3.4	2.4	13.0	21.0	8.6	4.9	4.0	3.0
MNHN 1908-21-5	9.6	4.8	3.8	4.0	3.1	15.7	25.3	9.6	5.5	5.0	3.5
MNHN 1908-32-77	11.0	5.2	4.0	4.1	3.0e	16.3e	27.3e	11.3	6.2	4.5	4.0

Table 7 (continued)

Specimen number	IV				V						
	4	5	a	b	mp	1	2	3	4	a	b
MNHN 1925-5-10	-	-	-	-	4.6	-	-	-	-	-	-
MNHN 1925-5-20	2.0	1.5e	11.2e	17.4e	4.5	3.9	2.6	2.3	1.2	10.0	14.5
MNHN 1908-21-8	1.9	1.7	10.4	15.5	4.1	3.4	-	-	1.7	-	-
MNHN 1925-5-25	-	-	-	-	5.0	3.9	-	-	-	-	-
MNHN 1908-32-29	2.1	1.5e	10.8	16.9	4.5	3.6	2.3	2.2	1.4	9.5	14.0
MNHN 1925-5-18	-	-	-	-	5.5	4.4	-	-	-	-	-
MNHN 1908-32-21	2.3	2.0	13.3	20.6	5.5	4.6	3.1	3.0	2.0e	12.7e	18.2e
MNHN 1908-21-2/7	3.0	2.3	17.2	25.8	6.9	5.5	3.5	3.2	2.2	14.4	21.3
MNHN 1908-21-5	3.7	2.5	20.2	29.8	7.6	6.3	4.1	3.8	2.1	16.3	23.9
MNHN 1908-32-77	4.0	3.0e	21.7e	33.0e	8.4	7.0	4.8	4.2	2.4	18.4	26.8

Table 7 (continued)

Specimen number	I/IV	II/IV	III/IV	V/IV	V/III	IV/x
MNHN 1925-5-10	-	-	-	-	-	-
MNHN 1925-5-20	-	-	-	.83	-	5.61
MNHN 1908-21-8	.39	.64	.83	-	-	4.84
MNHN 1925-5-25	-	-	-	-	-	-
MNHN 1908-32-29	.41	.67	.85	.83	.97	5.12
MNHN 1925-5-18	-	-	-	-	-	-
MNHN 1908-32-21	.42	.67	.84	.88	1.05	5.57
MNHN 1908-21-2/7	.40	.62	.81	.83	1.01	6.14
MNHN 1908-21-5	.40	.65	.85	.80	.94	6.77
MNHN 1908-32-77	.42	.63	.83	.81	.98	6.73

Table 7 (continued)

Specimen number	Manus Pes	I mp	1	2	a	b	II mp	1	2	3	a	b
MNHN 1925-5-41	P	5.7	5.0	3.2	8.2	13.9	9.5	4.9	4.8	3.1	12.8	22.3
SAM 6231	P	8.0	6.5	5.0	11.5	19.5	14.0	6.5	6.5	5.0	18.0	32.0
SAM 6232	P	8.0	7.5	7.0	14.5	22.5	15.5	7.5	7.0	5.0	19.5	35.0
MNHN 1925-5-32	P	10.6	9.9	7.0	16.9	27.5	17.5	8.6	8.6	7.5	24.7	42.2
MNHN 1908-21-10	P	11.0	10.0	8.0e	18.0e	29.0e	18.2	9.6	9.0	8.0e	26.6e	44.8e
MNHN 1908-32-68 1925-8-14	P	11.0e	-	-	-	-	-	-	-	-	-	-
MNHN 1925-5-61	P	12.1	9.2	-	-	-	19.9	-	-	-	-	-
MNHN 1908-32-24	P	12.5	9.2	-	-	-	20.0	9.5	8.5	-	-	-
MNHN 1908-21-6	P	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-14	P	12.0	9.5e	-	-	-	19.5	-	-	-	-	-

Table 7 (continued)

Specimen number	III mp	1	2	3	4	a	b	IV mp	1	2	3
MNHN 1925-5-41	11.0	5.5	4.5	4.7	3.0	17.7	28.7	11.5	6.5	4.7	4.0
SAM 6231	17.0	7.5	6.5	6.0	5.5	25.5	42.5	17.4	10.0	6.5	5.5
SAM 6232	18.5	9.0	7.0	7.0	5.0	28.0	46.5	20.5	11.5	7.4	7.5
MNHN 1925-5-32	20.3	10.1	7.6	8.0	7.5e	33.2e	53.5e	21.2	11.5	8.5	7.3
MNHN 1908-21-10	21.3	10.6	8.0	8.0	7.5e	34.1e	55.4e	22.6	12.9	8.8	-
MNHN 1908-32-68/ 1925-8-14	22.1	-	-	-	-	-	-	24.0	12.8	8.5	-
MNHN 1925-5-61	23.0	-	-	-	-	-	-	25.5	-	-	-
MNHN 1908-32-24	23.1	10.5	7.5	-	-	-	-	24.7	12.5	-	-
MNHN 1908-21-6	-	-	-	-	-	-	-	-	-	-	-
MNHN 1908-21-14	23.0	-	-	-	-	-	-	24.8	-	-	-

Table 7 (continued)

Specimen number	IV				V						
	4	5	a	b	mp	1	2	3	4	a	b
MNHN 1925-5-41	4.1	3.1e	22.4e	33.9e	8.7	7.3	5.0	4.6	2.5	19.4	28.1
SAM 6231	5.7	4.5	32.2	49.6	14.0	11.0	7.5	6.0	4.0	28.5	42.5
SAM 6232	6.8	5.9	39.1	59.6	16.5	12.0	8.0	7.0	5.0	32.0	48.5
MNHN 1925-5-32	7.3e	7.5e	42.1e	63.3e	17.5	13.3	8.6	7.9	5.2	35.0	52.5
MNHN 1908-21-10	-	-	-	-	18.5	14.2	9.5	-	-	-	-
MNHN 1908-32-68/ 1925-8-14	-	-	-	-	18.6	15.0	9.4	8.6	-	-	-
MNHN 1925-5-61	-	-	-	-	20.6	-	-	-	-	-	-
MNHN 1908-32-24	-	-	-	-	20.0	-	-	-	-	-	-
MNHN 1908-21-5	-	-	-	-	21.0	15.4	10.0	-	-	-	-
MNHN 1908-21-14	-	-	-	-	20.0	-	-	-	-	-	-

Table 7 (continued)

Specimen number	I/IV	II/IV	III/IV	V/IV	V/III	IV/X
MNHN 1925-5-41	.41	.66	.85	.83	.98	6.78
SAM 6231	.39	.65	.86	.86	1.00	7.52
SAM 6232	.38	.59	.78	.81	1.04	7.45
MNHN 1925-5-32	.43	.67	.85	.83	.98	8.01-
MNHN 1908-21-10	-	-	-	-	-	-
MNHN 1908-32-68/ 1925-8-14	-	-	-	-	-	-
MNHN 1925-5-61	-	-	-	-	-	-
MNHN 1908-32-24	-	-	-	-	-	-
MNHN 1908-21-6	-	-	-	-	-	-
MNHN 1908-21-14	-	-	-	-	-	-

Table 8. Growth in tangasaurids. The constants b' and k_{yx}' of the power equation $y = b'x^{k_{yx}'}$ have been solved using the least squares method. Growth is isometric when $k_{yx}' = 1.000$. From this information, the expected measurements (in mm and, where applicable, in unit measurement) of each dimension has been computed for an adult specimen of *Hovasaurus* by substituting x = 10 mm into the power equation. N = size of sample. R = correlation coefficient.

	N	R	k_{yx}'	95% confidence interval	b'	95% confidence interval
Neural spine height	11	.992	1.197	1.081-1.311	1.03	.84-1.26
Clavicle						
a, height	6	.932	.708	.469-.893	4.79	2.94-7.82
b	5	.993	.883	.626-1.140	4.46	2.97-6.71
c, width	6	.915	.921	.381-1.461	2.87	1.12-7.33
Interclavicle						
length	6	.979	.548	.387-.709	16.87	12.42-22.91
head, width	7	.878	.734	.234-1.234	4.06	1.54-10.72
Sternum						
length	17	.987	1.775	1.662-1.888	.74	.60-.91
½ width	21	.968	1.660	1.444-1.876	.60	.40-.90
Scapula						
height	5	.991	2.448	1.528-3.368	.25	.05-1.16
length	6	.963	1.874	1.360-2.388	.60	.26-1.37
Coracoid						
length	11	.981	2.194	1.786-2.602	.38	.17-.81
height	13	.978	1.666	1.487-1.845	.67	.48-.94
Humerus						
length	22	.991	1.612	1.520-1.704	1.75	1.47-2.08
prox. width	18	.981	1.421	1.246-1.596	.73	.54-1.01
shaft width	22	.957	1.282	1.103-1.461	.73	.52-1.01
dist. width	23	.979	1.488	1.390-1.586	.94	.79-1.27

	N	R	k_{yx}'	95% confidence interval	b'	95% confidence interval
Radius						
length	15	.993	1.285	1.183-1.387	1.94	1.63-2.31
prox. width	15	.970	1.378	1.149-1.607	.43	.29-.64
shaft width	17	.979	1.387	1.234-1.540	.27	.20-.35
dist. width	15	.969	1.263	1.102-1.424	.41	.31-.53
Ulna						
length	17	.995	1.387	1.311-1.463	1.53	1.34-1.74
prox. width	19	.981	1.345	1.194-1.496	.49	.37-.64
shaft width	18	.978	1.270	1.123-1.417	.31	.24-.41
dist. width	15	.974	1.479	1.268-1.690	.34	.24-.49
Metacarpal IV						
length	13	.992	1.342	1.229-1.455	.61	.51-.73
Manus; digit IV sum of lengths of phalanges	13	.983	1.225	1.062-1.388	2.06	1.57-2.72
Ilium						
blade length	15	.996	1.064	.955-1.173	2.96	2.47-3.56
base length	11	.986	1.107	.987-1.227	1.49	1.24-1.79
Pubis						
length	15	.989	1.200	1.149-1.251	1.41	1.30-1.54
width	14	.986	1.260	1.110-1.410	1.54	1.21-1.98
Ischium						
length	14	.994	1.200	1.123-1.277	1.79	1.58-2.02
width	14	.988	1.172	1.082-1.262	1.56	1.35-1.81

	N	R	k_{yx}'	95% confidence interval	b'	95% confidence interval
Femur						
length	18	.991	1.300	1.182-1.418	3.28	2.73-3.95
prox. width	21	.972	1.256	1.132-1.380	.80	.66-.97
shaft width	21	.969	1.185	1.038-1.332	.55	.43-.69
dist. width	17	.969	.987	.836-1.138	1.00	.80-1.26
Tibia						
length	17	.993	1.272	1.166-1.378	2.96	2.51-3.50
prox. width	15	.982	1.243	1.092-1.394	.60	.48-.76
shaft width	19	.958	1.236	1.028-1.444	.38	.27-.52
dist. width	19	.972	1.226	1.091-1.361	.57	.46-.71
Fibula						
length	15	.993	1.256	1.131-1.381	2.78	2.28-3.39
prox. width	7	.975	1.221	.877-1.565	.34	.19-.60
shaft width	19	.991	1.203	1.137-1.269	.29	.26-.33
dist. width	16	.986	1.326	1.239-1.413	.38	.33-.44
Metatarsal IV						
length	16	.995	1.330	1.256-1.404	1.33	1.18-1.50
Pes; digit IV						
sum of lengths of phalanges	11	.990	1.378	1.195-1.561	2.31	1.73-3.10

	Estimated mean value of y when x = 10 mm			
	y (mm)	95% confidence interval	y (unit measurement)	95% confidence interval
Neural spine				
height	16.18	14.96-17.50	6.22	5.75-6.73
Clavicle				
a, height	24.49	16.85-35.56	9.42	6.48-13.68
b	34.12	27.73-41.98	13.12	10.67-16.15
c, width	23.93	16.69-34.36	9.21	6.42-13.22
Interclavicle				
length	59.60	55.21-64.25	22.92	21.23-24.71
head, width	21.98	17.66-27.35	8.45	6.79-10.52
Sternum				
length	44.26	41.21-47.51	17.02	15.85-18.27
½ width	27.23	24.03-30.83	10.47	9.24-11.86
Scapula				
height	70.15	35.73-137.7	26.98	13.74-53.0
length	45.29	31.19-65.77	17.42	12.00-25.30
Coracoid				
length	58.61	45.92-74.82	22.54	17.66-28.78
height	31.12	26.03-37.24	11.97	10.01-14.32
Humerus				
length	71.61	67.92-75.49	27.54	26.12-29.03
prox. width	19.63	17.46-21.49	-	-
shaft width	13.90	12.45-15.52	-	-
dist. width	28.97	27.23-30.84	-	-

	Estimated mean value of y when x = 10 mm			
	y (mm)	95% confidence interval	y (unit measurement)	95% confidence interval
Radius				
length	37.41	34.67-40.36	14.39	13.33-15.52
prox. width	10.35	8.83-12.13	-	-
shaft width	6.49	5.37-7.83	-	-
dist. width	7.48	6.61-8.47	-	-
Ulna				
length	37.24	35.32-39.26	14.32	13.57-15.10
prox. width	10.79	9.76-11.94	-	-
shaft width	5.83	5.28-6.46	-	-
distal width	10.35	7.67-13.96	-	-
Metacarpal IV				
length	13.40	12.17-14.76	5.15	4.68-5.68
Manus; digit IV				
sum of lengths of phalanges	34.67	30.57-39.36	13.33	11.76-15.14
Ilium				
blade length	34.36	31.55-37.38	13.22	12.13-14.38
base length	19.01	17.08-21.18	7.31	6.57-8.15
Pubis				
length	22.39	21.48-23.34	8.61	8.26-8.98
height	28.12	24.77-31.92	10.82	9.53-12.28
Ischium				
length	28.31	25.50-31.40	10.89	9.81-12.08
height	23.23	21.53-25.06	8.93	8.28-9.64

	Estimated mean value of y when x = 10 mm			
	y (mm)	95% confidence interval	y (unit measurement)	95% confidence interval
Femur				
length	65.46	59.16-72.44	25.18	22.75-27.86
prox. width	14.39	13.23-15.67	-	-
shaft width	8.36	7.41-9.43	-	-
distal width	9.73	8.53-11.09	-	-
Tibia				
length	55.46	50.70-60.60	21.33	19.50-23.31
prox. width	10.49	9.18-12.00	-	-
shaft width	6.50	5.42-7.80	-	-
distal width	9.62	8.82-10.50	-	-
Fibula				
length	50.12	44.98-55.85	19.28	17.30-21.48
prox. width	5.64	4.32-7.35	-	-
shaft width	4.69	4.44-4.95	-	-
distal width	8.00	7.43-8.61	-	-
Metatarsal IV				
length	28.44	26.70-30.27	10.94	10.27-11.64
Pes; digit IV sum of lengths of phalanges	55.21	47.32-64.42	21.23	18.20-24.78

Table 9. Comparison of relative lengths of cranial and limb elements of protorothyridids, araeoscelidians, eosuchians, paliguanids and claudiosaurids. The average length of a dorsal centrum is represented by x, and the average width at the posterior end of the centrum is equivalent to 2r. Some measurements were taken from immature specimens, so a weight related factor had to be built into the orthometric linear unit ($r^{2/3}$ = OLU). A postscript "c" identifies those figures that have been adjusted. The ratio io/it represents the interorbital width divided by the intertemporal width. The length (y) of each element is divided by either x or OLU to produce a unitless relative measurement. The length and width of the skull and x are in millimetres.

Table 9 (continued)

	x	$r^{2/3}$	Skull l	 w	 io/it	Humerus y/x	 y/OLU	Radius y/x	 y/OLU
Paleothyris	3.0	.8	23	14	—	5.0	19	3.0	11
Petrolacosaurus	6.5	2.0	64		.7	5.4	18	6.5	21
Araeoscelis	8.3	2.0	42	24	.5	6.6	28	6.0	25
Kadaliosaurus	9.5	-	-	-	-	5.7	-	5.3	-
Coelurosauravus	6.7	-	-	-	-	4.3	-	-	-
	7.5	-	-	-	-	4.2	-	2.7	-
Daedalosaurus	5.2e	-	-	-	-	5.7e	-	3.8e	-
Weigeltisaurus	8.1	1.7	60	-	-	4.3	20	3.1	14
Galesphyrus	5.5	1.5	-	-	-	3.8	14	3.1	12
Heleosaurus	6.5	1.8	51	27	-	-	-	-	-
Acerosodontosaurus	9.0	2.1c	55	28	1.0	-	-	3.8	16c
Youngina	5.2	1.4c	55	30	1.1	4.4	17c	3.5	13c
Thadeosaurus	6.4	1.7	-	-	-	6.7	26	3.9	15
Kenyasaurus	6.3	1.6	-	-	-	-	-	-	-
Tangasaurus	8.0	-	-	-	-	6.1	-	3.5	-
Hovasaurus	10.0	2.6	-	-	.4	7.2	28	3.7	14

Table 9 (continued)

			Skull			Humerus		Radius	
	x	$r^{2/3}$	l	w	io/it	y/x	y/OLU	y/x	y/OLU
Thalattosaurus	16	5.1	350	94	1.1	4.7	15	2.5	8
Askeptosaurus	22	4.7	285	105	1.2	3.2	15	1.7	8
Champsosaurus	28	6.1	430	195	.4-1.4	5.1	23	2.9	13
Protorosaurus	-	-	-	-	-	-	-	-	-
Prolacerta	9.0	1.9	69	31	.8	4.7	22	4.1	19
Macrocnemus	9.0	2.3c	86	-	.9	6.1	24c	5.2	20c
Tanystropheus	42	-	147	-	1.1	4.7	-	3.1	-
Tanytrachelos	7.7	-	-	-	-	4.3	-	2.0	-
Palaeagama	3.7	1.0c	26	22	.7	6.3	23c	4.2	15c
Saurosternon	2.8	.8c	-	-	-	6.2	23c	4.2	15c
Heleosuchus	3.5	-	28	23	-	-	-	-	-
Claudiosaurus	9.2	2.2c	35e	25e	.9	4.9	20c	3.1	13c

Table 9 (continued)

	Femur		Tibia					
	y/x	y/OLU	y/x	y/OLU	H/F	R/H	T/F	R/T
Paleothyris	5.2	20	3.3	13	.97	.60	.65	.90
Petrolacosaurus	6.0	20	6.9	22	.90	1.10	1.20	.89
Araeoscelis	7.7	32	8.0	33	.86	.98	1.03	.82
Kadaliosaurus	5.7	-	5.3	-	1.00	.93	.93	1.00
Coelurosauravus	4.6	-	3.0	-	.93	-	.65	-
	4.5	-	3.0	-	.93	.63	.64	.92
Daedalosaurus	6.0e	-	3.8c	-	.95	.66	.65	.98
Weigeltisaurus	4.7	22	3.4	16	.92	.71	.72	.91
Galesphyrus	4.9	18	4.5	17	.78	.81	.93	.68
Heleosaurus	7.0	26	-	-	-	-	-	-
Acerosodontosaurus	6.1	26c	-	-	-	-	-	-
Youngina	6.5	25c	5.8	22c	.68	.78	.89	.59
Thadeosaurus	6.0	23	5.4	21	1.11	.59	.90	.73
Kenyasaurus	7.5	29c	5.7	22c	-	-	.77	-
Tangasaurus	5.9	-	5.0	-	1.00	.62	.85	.73
Hovasaurus	6.5	25	5.5	21	1.09	.52	.85	.67

Table 9 (continued).

	Femur		Tibia					
	y/x	y/OLU	y/x	y/OLU	H/F	R/H	T/F	R/T
<u>Thalattosaurus</u>	-	-	-	-	-	.53	-	-
<u>Askeptosaurus</u>	4.1	19	2.3	11	.77	.53	.55	.74
<u>Champsosaurus</u>	6.4	29	4.4	20	.80	.58	.69	.67
<u>Protorosaurus</u>	-	-	-	-	.74	.81	.95	.62
<u>Prolacerta</u>	6.0	28	6.5	30	.78	.88	1.07	.64
<u>Macrocnemus</u>	8.0	31	7,9	31	.73	.93	1.06	.64
<u>Tanystropheus</u>	7.0	-	5.2	-	.68	.65	.74	.60
<u>Tanytrachelos</u>	5.2	-	3.5	-	.84	.46	.68	.57
<u>Palaeagama</u>	8.1	30c	7.6	28	.78	.66	.93	.55
<u>Saurosternon</u>	8.4	30c	7.5	27	.72	.71	.89	.57
<u>Heleosuchus</u>	8.6	-	8.0	-	-	-	.93	-
<u>Claudiosaurus</u>	5.4	22c	5.0	21c	.91	.63	.91	.64

APPENDIX I
LOWER SAKAMENA FORMATION: KNOWN FOSSIL LOCALITIES

X	Y	Locality	Fossils
235	195	Mt. Eliva	Equisetes, *Atherstonia colcanapi*, *Hovasaurus boulei* (Piveteau, 1926)
235-280	193-215	Sakamena R.	*Glossopteris* cf. *indica* (Haughton, 1930), *Atherstonia colcanapi* (Boule, 1910; Priem, 1924), *Acerosodontosaurus piveteaui* (Currie, 1980), *Coelurosauravus elivensis*, *Daedalosaurus madagascariensis* (Carroll, 1978), *Hovasaurus boulei* (Piveteau, 1926), *Thadeosaurus colcanapi* (Carroll, 1981)
238-277	200-225	Vohipanana-Ambatokapika limestones	*Syringopora*, *Cladochonus* (Besairie, 1930)
255	206	Irangotsy-Sakamena confluence	*Estheria*, *Estheriella* (Besairie, 1971)
284	253	Soaserana	Amphibian jaw incorrectly identified as *Hovasaurus* (Tortochaux, 1950)
286	254	Ianapera Onilahy confluence	Isolated reptile bones (Tortochaux, 1949, 1950)
288	344	Ambohitra	*Cladochonus* (Tortochaux, 1950)
295	260	Benenitra region	*Acerosodontosaurus piveteaui* (Currie, 1980), *Claudiosaurus germaini* (Carroll, 1981), Dicynodontia *inc*. *sed*., Theriodontia *inc*. *sed*., isolated amphibian and reptile bones.
297	268	Ankotika Hills	Isolated reptile bones incorrectly assigned to *Tangasaurus* (Tortochaux, 1950)
304	277	Ampasindrasoa	Isolated reptile bones

317	274	Antsokaky	*Cladochonus* (Tortochaux, 1950)
323	283	Soaravy	Equisetes (Tortochaux, 1950)
334	281	Anteteza R.	Isolated reptile bones (Tortochaux, 1950)
335	287	Benaha Imaloto confluence	Actinostromides (Briere, 1924), Small coral reefs (Cliquet, 1950), *Cladochonus* (Basse, 1934), *Gervillia elianae*, *Modiolopsis stockleyi* (Basse, 1934, Cox, 1936)
373	288	Ilakaka R.	Isolated reptile bones, incorrectly identified as *Hovasaurus* (Tortochaux, 1950)
382	290	Leoposa	*Claudiosaurus germaini* (Carroll, 1981)
390	292	Ianakandrereza R.	Estheriids (Basse, 1934, Cliquet, 1950)
395	296	Ranohira	*Glossopteris* (Besairie, 1971), equisetes (Tortochaux, 1950), estheriids (Basse, 1934), Lower Triassic palaeoniscoid (B. Gardiner, pers. comm.), isolated amphibian bones (Basse, 1934), *Hovasaurus* (Tortochaux, 1950), *Barasaurus besairei* (Piveteau, 1955a), isolated reptile bones (Tortochaux, 1950)
397	302	Sakamanigy River	Equisetes (Zeiller, 1911), *Claudiosaurus germaini* (Carroll, 1981)
402	298	Tanambao	Fish and reptile skeletons in nodules (Besairie, 1971)
419	293	Menamaty R.	Jaw referred to *Rhinesuchus* cf. *senekalensis* (Piveteau, 1926)
497	270	Bevilo	Unidentified reptile bones (Tortochaux, 1949)
510	299	Bekinana	Isolated reptile bones identified incorrectly as *Hovasaurus* (Tortochaux, 1950)
552	321	Mandronarivo	Isolated reptile bones incorrectly identified as *Tangasaurus* (Tortochaux, 1950)

570	322	Sakeny R.	*Edmondia* cf. *amabilis*, *Posidonia* cf. *becheri* (Tortochaux, 1950)
590	327	Manambaeo	*Estheria minuta* (Besairie, 1971)
628	326	Tambohazo	*Glossopteris* cf. *indica* (Carpentier, 1935), *Baiera* sp. (Anderson and Anderson, 1970), *Voltziopsis africana* (Townrow, 1967).
695	—	Ankoriky	*Thinnfeldia callipteroides* (Townrow, 1967), *Lepidopteris madagascariensis* (Townrow, 1966), *Taenipteris* sp., *Baiera* sp., possible ginkgophyte (Anderson and Anderson, 1970), *Rissikia media* (Townrow, 1967), *Voltziopsis africana* (Townrow, 1967), *V. wolganensis* (Townrow, 1967) *Estheria minuta* (Besairie, 1971).
842	277	Saloka	*Glossopteris* cf. *indica*, *Estheria minuta* (Besairie, 1971)
—	—	Kalivari	*Hovasaurus boulei*

APPENDIX 2
FLORA AND FAUNA OF THE LOWER SAKAMENA FORMATION

PROTISTA
THALLOPHYTA
DINOPHYCEAE dinoflagellates
PERIDINIALES
acritarchs
FORAMINIFERA

PLANTAE
TRACHEOPHYTA
SPHENOPSIDA
EQUISETALES
SCHIZONEURACEAE
Schizoneura gondwanensis
CYCADOPSIDA
PTERIDOSPERMALES
Thinnfeldia callipteroides
Taeniopteris sp.
CAYTONIACEAE
?*Vitreisporites pallidus*
?*Alisporites papilio*
?*Pityosporites insularis*
?*Falcisporites enodis*
PELTASPERMACEAE
Lepidopteris madagascarensis
GLOSSOPTERIDALES
Glossopteris cf. *indica*
CONIFEROPSIDA
Rissikia media
Voltziopsis africana
Voltziopsis wolganensis
GINKGOALES
Baiera sp.
VOLTZIALES
?*Lueckispo ites virrkiae*
CORDAITALES
Dadoxylon
CONIFERALES
?*Araucariacites australis*
PODOCARPACEAE
?*Podocarpites* cf. *elipticus*
GNETOPSIDA
GNETALES
?*Vittatina striata*
TRACHEOPHYTA *incertae sedis*
Taeniaesporites noviaulensis
Protohaploxypinus pellucidus
Strotersporites panti
Platysaccus cf. *leschiki*

- TRACHEOPHYTA *incertae sedis*
  - *Platysaccus fuscus*
  - *Platysaccus praevius*
  - *Sulcatisporites prolatus*
  - *Guttulapollenites hannonicus*
  - *Guttulapollenites gondwanensis*
  - *Inaperturopollenites* cf. *orbicularis*

- ANAMALIA
  - COELENTERATA
    - STROMATOPOROIDEA
      - STROMATOPORIDEA
        - ACTINOSTROMIDAE
    - ANTHOZOA
      - TABULATA
        - AULOPORIDAE
          - *Syringopora* sp.
          - *Cladochonus* sp.
  - MOLLUSCA
    - BIVALVIA
      - PTERIOIDA
        - BAKEVELUIDAE
          - *Gervillia elianae*
        - POSIDONIIDAE
          - *Posidonia* cf. *becheri*
      - MODIOMORPHOIDA
        - MODIOMORPHIDAE
          - *Modiolopsis stockleyi*
      - PHOLADOMYOIDA
        - EDMONDIIDAE
          - *Edmondia* cf *amabilis*
    - CEPHALOPODA
      - GONIATITIDA
        - POPANOCERATIDAE
          - *Popanoceras* sp.
        - CYCLOLOBIDAE
          - *Cyclolobus walkeri*
      - PROLECANITIDA
        - MEDLICOTTIIDAE
          - *Propinacoceras* sp.
        - EPISAGECERATIDAE
          - *Episagecerus* sp.
      - CERATITIDA
        - XENODISCIDAE
          - *Xenaspis* sp.
  - ARTHROPODA
    - CRUSTACEA
      - CONCHOSTRACA
        - ?ASMUSSIIDAE
          - *Estheria minuta*
        - ESTHERIELLIDAE
          - *Estheriella* sp.
  - CHORDATA
    - OSTEICHTHYES
      - CHONDROSTEI

PALAEONISCIFORMES
Atherstonia colcanapi
AMPHIBIA
TEMNOSPONDYLI
RHINESUCHIDAE
cf. *Rhinesuchus* sp.
REPTILIA
COTYLOSAURIA
PROCOLOPHONIA
PROCOLOPHONIDAE
Barasaurus besairei
EOSUCHIA
YOUNGINIFORMES
YOUNGINOIDEA
Acerosodontosaurus piveteaui
TANGASAURIDAE
KENYASAURINAE
Thadeosaurus colcanapi
TANGASAURINAE
Hovasaurus boulei
EOSUCHIA *incertae sedis*
COELUROSAURAVIDAE
Coelurosauravus elivensis
Daedalosaurus madagascariensis
SAUROPTERYGIA
CLAUDIOSAURIDAE
Claudiosaurus germaini
THERAPSIDA
DICYNODONTIA *incertae sedis*
THERIODONTIA *incertae sedis*

ABBREVIATIONS

a	astragalus
AMNH	American Museum of Natural History
ag	angular
aq	anconaeus quartus
ar	articular
ATL-c	atlantal centrum
ATL-na	atlantal neural arch
AX	axial intercentrum
b	biceps
bo	basioccipital
bps	combined basisphenoid and parasphenoid
br	brachialis inferior
C	clavicle
c	capitellum
cal	calcaneum
cb	coracobrachialis brevis
cbl	coracobrachialis longus
CL	cleithrum
co	coronoid
COR	coracoid
cr	cervical rib
d	dentary
de	deltoids
e	ectepicondyle

ef	entepicondylar foramen
eo	exoccipital
ep	epipterygoid
et	epitrochleoanconaeus
ex	extensors
F	femur
f	frontal
fcr	flexor carpi radialis
FIB	fibula
fl	flexors
H	humerus
h	hyoid
ha	haemal arch
i	intermedium
IC	interclavicle
ic	intercentrum
IL	ilium
IS	ischium
j	jugal
l	lacrimal
lc	lateral centrale
ld	latissimus dorsi
m	maxilla
mc	medial centrale

MNHN	Museum National d'Histoire Naturelle, Paris
n	nasal
op	opisthotic
p	parietal
pal	palatine
pc	palmaris communis profundus
pe	pectoralis
pf	postfrontal
pi	pisiform
po	postorbital
pq	pronator quadratus
pr	prearticular
prf	prefrontal
pro	prootic
pt	pterygoid
ptf	transverse flange of the pterygoid
PU	pubis
q	quadrate
qj	quadratojugal
R	radius
r	radiale
S	scapula
s	supinator manus
sa	surangular
SAM	South African Museum
sc	supracoracoideus
scs	subcoracoscapularis

sh	scapulohumeralis
sl	supinator longus
sp	splenial
sq	squamosal
sr	sacral rib
ST	sternum
st	supratemporal
sta	stapes
T	tibia
tr	triceps
trl	triceps lateralis (short head)
trm	triceps medialis (short head)
U	ulna
u	ulnare
1-5	distal carpals, distal tarsals
I-V	metacarpals, metatarsals