PLESIOSAUR ANCESTORS FROM THE UPPER PERMIAN OF MADAGASCAR

By R. L. CARROLL

Redpath Museum, McGill University, 859 *Sherbrooke Street West,*
*Montreal, Quebec, Canada, H*3*A* 2*K*6

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(Plates 1 and 2; pullouts 1–4)

CONTENTS

Numerus well preserved fossils from the Upper Permian of Madagascar are structurally intermediate between primitive diapsid reptiles and nothosaurs and plesiosaurs. *Claudiosaurus germaini* (gen.nov., sp.nov.) is similar in its basic anatomy to eosuchian reptiles such as *Thadeosaurus colcanapi* (gen.nov., sp.nov.), but the absence of a lower temporal bar and the closure of the palate are characteristics of sauropterygian reptiles. *Claudiosaurus* shows the initiation of aquatic adaptations in the proportions and reduced ossification of the carpus and manus. A third pair of sacral ribs is partially incorporated. The small size of the skull, the nature of the palate and marginal dentition and the long neck are suggestive of aquatic feeding habits. *Claudiosaurus* does not, however, show the specific adaptations for aquatic locomotion seen in either nothosaurs or plesiosaurs. Even the most primitive known species of nothosaurs and plesiosaurs are too specialized in the postcranial skeleton for direct comparison with *Claudiosaurus*, although the similarities to the skull roof of primitive nothosaurs are very close. The configuration of the cheek in nothosaurs almost certainly resulted from the loss of the lower temporal bar from a pattern like that of *Youngina*, rather than from the ventral emargination of the cheek.

The nature of the Upper Permian sediments in Madagascar and the tectonic environment of their deposition indicate accumulation in deep rift valleys, some parts of which were open to the sea. The presence of oolites replaced with collophane suggests a rich phosphate source such as deep marine upwellings. Similar upwellings of phosphate have also been associated with the evolution of the marine iguanas on the Pacific coast of South America.

The concept of the derivation of nothosaurs from protorosaurs or araeosceloids may be traced to misunderstandings of the nature of the cheek in both *Nothosaurus* and *Protorosaurus*. *Araeoscelis*, despite the possession of a solid cheek, is closely related to *Petrolacosaurus*, an ancestral diapsid.

INTRODUCTION

Piveteau (1955*b*) referred briefly to two fossils from the Upper Permian of Madagascar as possible plesiosaur ancestors. Because of other obligations, he was unable to publish a more complete description of this material at that time. In 1975, he asked me to continue this study. The specimens cited by Piveteau had been presented to him by C. Germain, who was then employed by the Elf Oil Company in Madagascar. In all, Germain had collected more than twenty specimens of these aquatic reptiles, many of which were nearly complete skeletons. As indicated by Piveteau, this material provides the first substantial link between the marine plesiosaurs and nothosaurs of the Mesozoic and their terrestrial ancestors of the Palaeozoic (figure 1, plate 1).

Despite extensive knowledge of both nothosaurs and plesiosaurs, their ancestry is a question of continuing dispute. Romer (1933, 1945, 1956, 1966, 1971) and others have long maintained that plesiosaurs, nothosaurs and placodonts differed from the majority of Mesozoic reptiles in the configuration of the temporal region of the skull. They have a conspicuous dorsal temporal opening, but have been said to lack a lateral or lower temporal opening of the type seen in diapsids or synapsids. Comparison of nothosaurs and plesiosaurs (collectively termed sauropterygians) has been made with the small lizard-like reptile of the Lower Permian, *Araeoscelis*, in which there is a well developed upper temporal opening, but a solid cheek. *Araeoscelis* had been thought by Romer (1945, 1947, 1956, 1966) to be a representative of a modest radiation of terrestrial and semiaquatic reptiles of the Permian and Triassic termed the protorosaurs or araeosceloids. Although no direct links are known, it has been assumed that some early members of this group had given rise to nothosaurs. Romer (1971) admitted that there was little evidence for such an association, but suggested no other Palaeozoic reptiles that might have had such a role. Kuhn-Schnyder (1967) has argued that the skull pattern of nothosaurs and plesiosaurs might have evolved from that of primitive diapsid reptiles, such as those that had given rise to lizards and dinosaurs, by the loss of the lower temporal bar. Romer (1971), however, found no justification for this suggestion. In his last paper on this subject, Romer (1974) admitted that no adequately known Palaeozoic reptiles were probable ancestors for the specialized marine reptiles of the Mesozoic.

It is surprising that the ancestors of the Mesozoic marine reptiles have not been recognized, in view of the common bias in the fossil record for animals living in aquatic environments.

FIGURE 1. *Claudiosaurus germaini*, type specimen, Muséum National d'Histoire Naturelle, Paris (P.M.) 1978-6-1. Skeleton from the Upper Permian of Madagascar, primarily in dorsal view; mould of skull shows palate in ventral view.

(*Facing p.* 316)

FIGURE 2. Map of Madagascar showing in black the extent of surface exposures of the Lower Sakamena Formation, and indicating the principal localities from which fossil reptiles have been collected.

It is also surprising that no aquatic or terrestrial reptiles from the Palaeozoic, other than *Araeoscelis*, appears to have the type of temporal configuration described as characterizing nothosaurs and plesiosaurs.

A variety of Palaeozoic aquatic reptiles have been described, but none seem appropriate ancestors for nothosaurs. The position of the temporal opening in mesosaurs is subject to continuing dispute, but the specialization seen in the remainder of the skull, with a very long snout and extremely long, slender teeth, is not what would be expected in a nothosaur ancestor. Romer (1948) compared the skull of the semiaquatic pelycosaur *Ophiacodon* with ichthyosaurs, but admitted only the most general similarities. Haughton (1924) and Piveteau (1926) described a number of aquatic reptiles from east Africa and Madagascar, which have been included among the Eosuchia, but these have never been seriously considered as possible nothosaur ancestors because of the apparently diapsid nature of the skull.

In view of the previous lack of any definite information as to the origin of nothosaurs and plesiosaurs, it is a pleasure to be able to describe an extensive series of excellently preserved specimens that appear to be nearly ideal structural intermediates between ancestral terrestrial reptiles and Mesozoic nothosaurs and plesiosaurs.

This material is representative of a radiation of primitive, aquatic reptiles, almost certainly descended from the basic diapsid stock. They have already achieved the pattern of the temporal region seen in nothosaurs, as well as other cranial features suggesting a shift to aquatic feeding, but the limb structure is only beginning to be modified for aquatic locomotion. These newly discovered specimens may be related to the previously described aquatic eosuchians from Madagascar and east Africa, described by Piveteau and Haughton, but are much more similar to nothosaurs in their cranial anatomy.

All the Upper Permian vertebrates from Madagascar were preserved in rapidly filling linear basins, formed as rift valleys (Cliquet 1957). The manner of deposition resulted in the preservation of a fauna greatly different from that in South Africa, with a preponderance of diapsids, and only very fragmentary remains of therapsids. The Madagascar fauna includes a variety of terrestrial as well as aquatic diapsids and the oldest gliding reptiles (Carroll 1978). Similar animals may have lived in the nearby Karroo basin, but the specific environments in which they lived were apparently not preserved in the geological record. The aquatic animals, which are by far the most abundant elements of the Madagascar fauna, may have lived in streams, small rivers or shallow lakes which were only poorly represented in the sedimentary record of South Africa. At least some of the deposits may have accumulated in a near-shore marine environment. The unusually rapid and deep burial of the sediments and their included fauna in the rift basins in Madagascar may explain the absence of a similar fauna in other parts of the world.

All the specimens described in this paper were collected from the Upper Permian deposits in Madagascar, but from a series of distinct localities (figure 2). All material comes from the Lower Sakamena Formation, which is exposed in a linear belt just to the west of the crystalline massif that makes up much of the eastern side of the island. According to Cliquet (1957), seismic evidence shows that there were originally two narrow basins, both with north–south orientations, separated by a narrow arch which was later covered by sediments. The northern end of the more western trough has since been covered by younger deposits. The more eastern basin was open to the sea in the north. Tectonic activities spread from the east to the west in this area, suggesting that some of the deposits in the eastern basin are somewhat older than those to the west. There is also some evidence that deposition began in the south somewhat earlier than in the north. All these events, however, are apparently encompassed within the Upper Permian. The specimens described here come from three principal localities. All the specimens of the plesiosaur ancestor come from the more eastern basin. Most of the articulated material comes from near Leoposa. Considerable disarticulated material comes from near Benenitra. Most of the material previously described by Piveteau (1926) came from the Sakamena valley, running north–northeast from Mount Eliva. The sediments exposed there were deposited in the more western of the two rift valleys.

In view of the significance of the fauna, made up of many genera as yet known only from Madagascar, it is important to establish the age of the beds with as much assurance as possible. Piveteau (1926) attributed the reptilian fauna of Mount Eliva to the Upper Permian, primarily on the basis of assumed relationships to South African genera, and relative levels of evolution. Although concepts of the relationships of early diapsids have changed considerably since his determination, stratigraphic work and comparison of other fossils tend to support his estimate of the age of the beds. Stratigraphic work reported by Besaire (1972) placed the beds that contain these vertebrates in the Lower Sakamena Formation. Further north, this formation is overlain by beds containing the same genera as those of the extremely well known Eotriassic fish fauna in the north of the island, e.g. *Boreosomus* and *Birgeria* (Lehman *et al.* 1959).

Recent work by Goubin (1965) on spores and pollen from numerous localities in Madagascar divides the Lower Sakamena into three zones, all of which are indicated as Upper Permian. The terrestrial vertebrates occur in the uppermost of the three zones recognized by Goubin, and so at the very top of the Permian. Hart (1969) correlates the entire Lower Sakamena, typified by members of the Striatiti pollen zone, with the Russian Tatarian.

In addition to the terrestrial vertebrates of the Mount Eliva fauna, Priem (1924) described several fish specimens as members of a new species, *Atherstonia colcanapi*. According to recent study of this material by B. Gardner (personal communication) the fish agree well with other species of *Atherstonia* from the Upper Permian; members of this genus are not known in later horizons.

THADEOSAURUS gen. nov. (figures 2–8, 29)

Although the primary purpose of this paper is to describe animals that may be ancestral to the nothosaurs and/or plesiosaurs, it is necessary to provide first a basis of comparison with more primitive eosuchian reptiles. The recent description of *Youngina*, the type eosuchian, by Gow (1975) gives a general impression of the skeletal anatomy. Unfortunately, many elements of the skeleton were missing in the available material and others were incompletely ossified. Fortunately, excellently preserved postcranial material of a contemporary eosuchian is known from the Upper Permian in Madagascar.

Piveteau (1926) described several reptilian genera from the valley of the Sakamena River in southwestern Madagascar. Most of the specimens are of aquatic eosuchians assigned to the genera *Tangasaurus* and *Hovasaurus*.

Two specimens from the vicinity of Mount Eliva, near the headwaters of this river, were recognized by Piveteau as belonging to a distinct genus. He assigned them with some hesitation to the European genus *Dathesosaurus*, noting their affinities with 'saurian' or sauropsid reptiles. It is now recognized that the specimen to which the name *Datheosaurus* was originally applied is a member of the pelycosaur genus *Haptodus* (Currie 1979). The specimens from Madagascar are, in contrast, certainly eosuchian reptiles inasmuch as this can be accepted in the absence of significant cranial material. What comparable elements are preserved correspond to the pattern seen in *Youngina*.

Order Eosuchia

Family Younginidae

Thadeosaurus gen. nov.

Type species. *Thadeosaurus colcanapi*

Diagnosis. Eosuchian reptile of the family Younginidae. Differs from *Youngina* in the wider blade of the ilium and from *Galesphyrus* and *Kenyasaurus* by a greater mediolateral extent of the calcaneum. Distinguished from these genera by the relatively greater length of the neural spines of the trunk vertebrae in animals of comparable size. In contrast with *Youngina* and *Heleosaurus*, no dermal armour is associated with the neural spines. The entepicondyle of the humerus is expanded further than in *Youngina*, *Galesphyrus* or *Heleosuchus*. There is a large sternum. This bone is ossified in *Kenyasaurus* and *Tangasaurus*, but is not reported in *Youngina* or *Galesphyrus*. Known distribution: Upper Permian of Madagascar. Generic name is an anagram of *Datheosaurus*.

Thadeosaurus colcanapi sp. nov.

Specific diagnosis. Same as for genus. Specific name honours the collector of the type specimen.

Holotype. Skeleton, complete except for the head, approximately five cervical vertebrae, the lower portion of the right forelimb and the entirety of the right hindlimb, preserved as a natural cast in counterpart blocks, numbers P.M. 1908–11–13a and 1908–11–19a in the Muséum National d'Histoire Naturelle, Paris.

Referred specimens. Most of this description was based on the type and a second nearly complete specimen of a mature individual preserved in counterpart blocks, numbers P.M. 1908–11–8a and 1908–11–20a. The following specimens, probably from the same locality, are less complete, but apparently belong to the same taxon: 1908–5–1a, 1908–11–4a, 1908–11–4b, 1908–11–5b, 1908–11–6a, 1908–11–7a, 1908–11–15a and 1908–11–16a. They will be illustrated separately, as part of a paper discussing growth in this genus. Most of these specimens were attributed to the genus *Tangasaurus* by Piveteau (1926), but they do not pertain to that genus from Tanzania which has much expanded neural and haemal arches in the tail.

Horizon and locality. Upper part of Lower Sakamena Formation, Upper Permian. Sakamena River Valley in the vicinity of Mount Eliva, southwestern Madagascar. Evidence for the age of this locality is discussed in the introduction.

Description of material

The specimens were prepared by removing what little bone remained in the rock and casting with liquid latex or silicone rubber.

The individual elements of *Thadeosaurus* in general resemble material of *Youngina* figured by Broom (1922), Watson (1957) and Gow (1975). The reconstruction drawn by Gow, however, appears very different from that presented here. This may be attributed to the posture illustrated, and to the nature of the ribs. In his description, Gow states (1975, p. 95): 'There are several ribs.' Presumably this reflects their incomplete nature and poor preservation. In contrast, those of *Thadeosaurus* are well exposed, except for the cervical region. Other differences can be attributed to the incompleteness, and possibly the immaturity, of the material described by Gow.

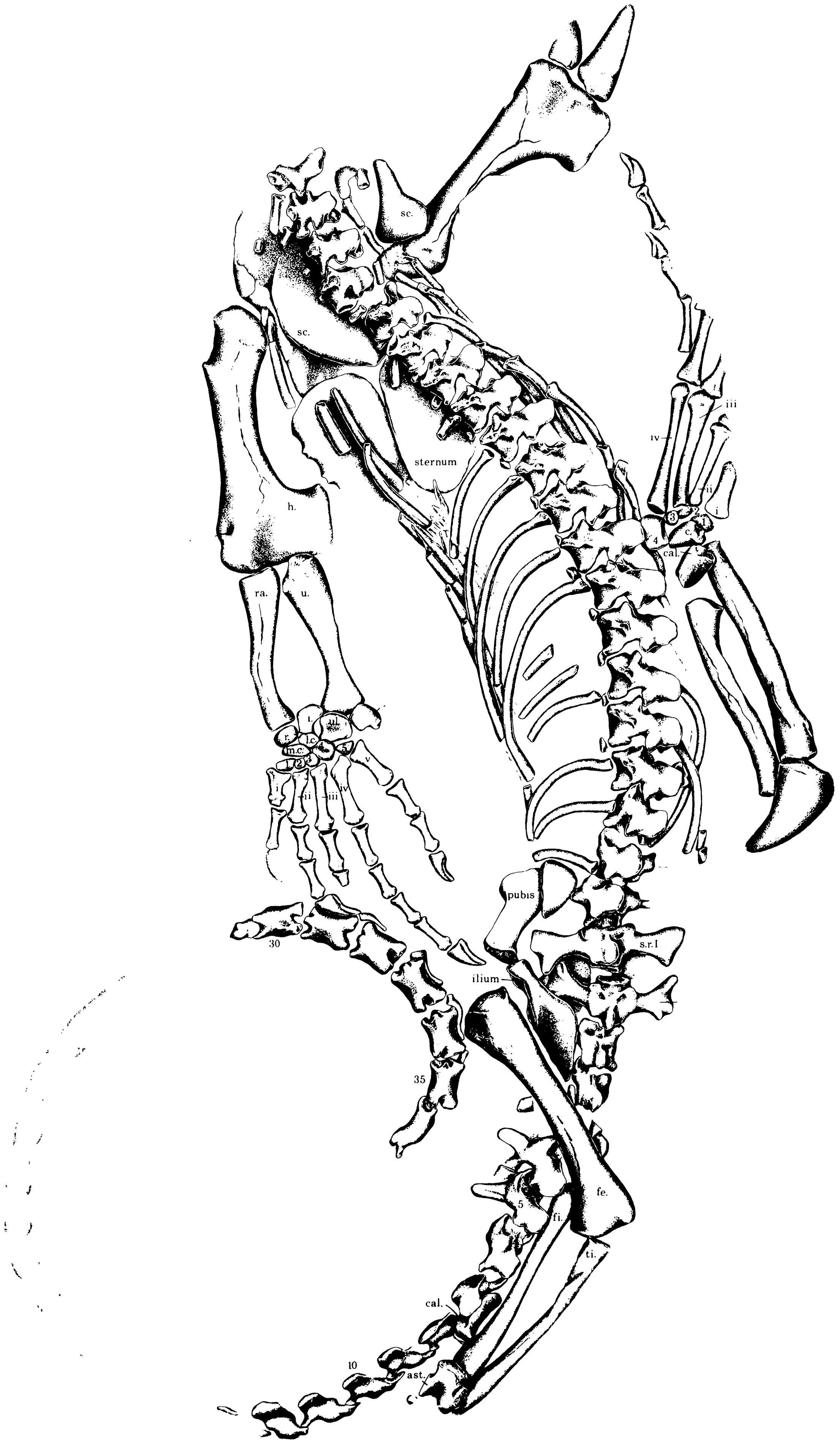


FIGURE 3. *Thadeosaurus colcanapi*, type specimen, P.M. 1908–11–13a. Abbre
figures are listed at end of paper.

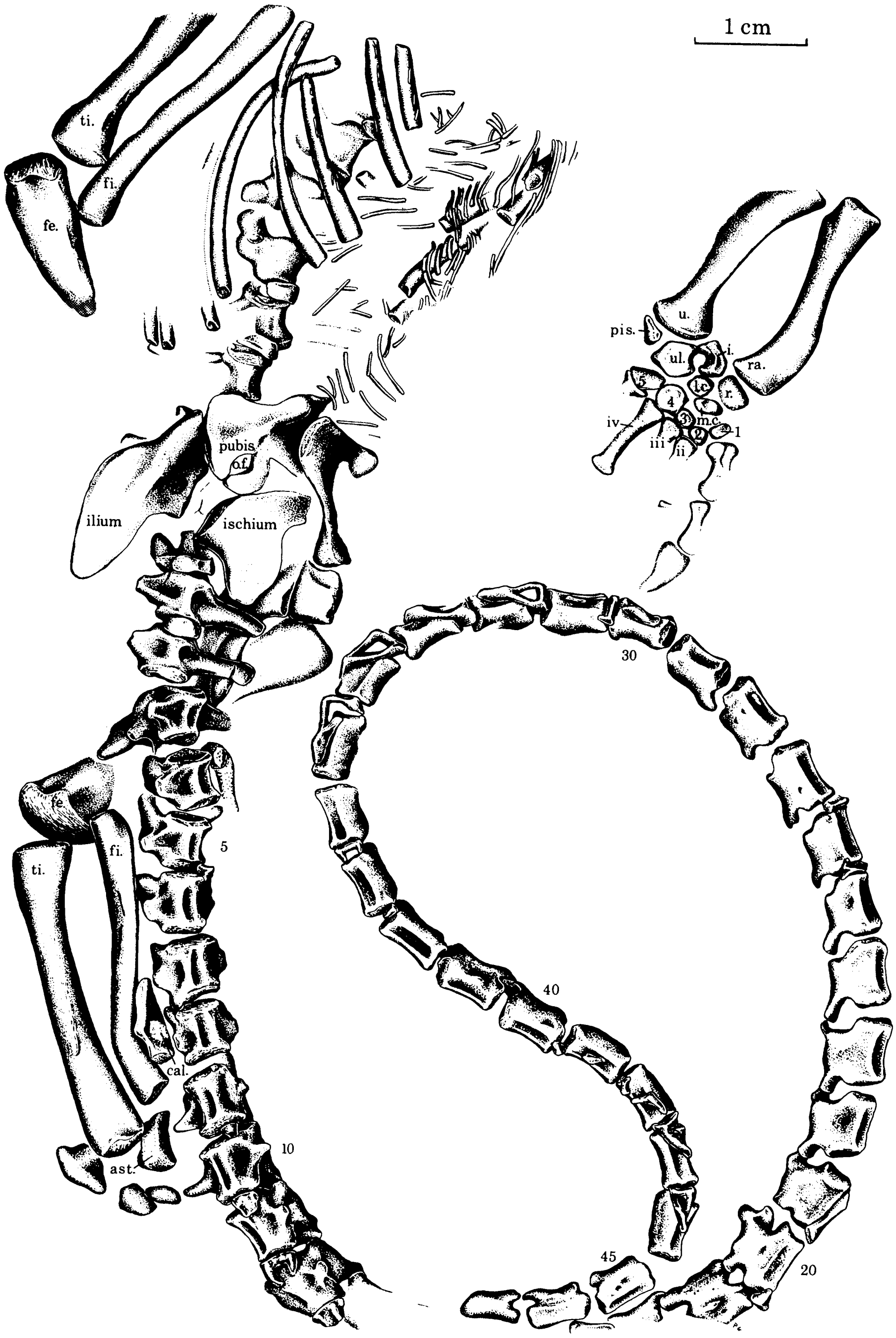


Figure 4. *Thadeosaurus colcanapi*, type specimen, P.M. 1908–11–19a (counterpart of P.M. 1908–11–13a).

Axial skeleton

The type lacks all trace of the skull. In the second specimen, elements of the palate and base of the braincase are visible adjacent to the left forelimb. They are attributable to an eosuchian reptile and may be presumed to belong with the body. The parts preserved include the posterior portion of the palatal ramus of the pterygoid, the adjacent basisphenoid, and the posterior plate of the parasphenoid. The pterygoid bears numerous short denticles arranged in what appears to be two rows, as in *Youngina* and *Heleosaurus*. There is apparently a distinct transverse flange on the pterygoid. The ventral surface of the anterior portion of the parasphenoidal plate is smooth, like that of *Youngina*, and lacks denticles. The basicranial processes are long, like those of *Youngina*, rather than short as in the aquatic genus from Madagascar. The length of the base of the parasphenoid is approximately twice as long as that of one of the specimens of the aquatic genus, although comparable postcranial elements of the aquatic genus are slightly longer than those of *Thadeosaurus*. It is probable that the entire skull of *Thadeosaurus* (if this fragment is correctly associated with the remainder of the skeleton) is of similar proportions to those of *Youngina* and *Heleosuchus*.

In the two most complete specimens of *Thadeosaurus*, the vertebral column is truncated at the level of the anterior margin of the endochondral shoulder girdle. It is thus impossible to give an accurate vertebral count. Among other primitive eosuchians, the number of vertebrae shows limited variability. The oldest known diapsid, *Petrolacosaurus* (Reisz 1981), has a well established count of 26. The long neck and epipodials of this genus appear to ally it most closely to a divergent line of eosuchians otherwise represented by *Protorosaurus* (Seeley 1888) from the Upper Permian of Europe, and *Prolacerta* (Gow 1975), from the Lower Triassic of South Africa. Both these genera also have 26 presacral vertebrae. This line culminates with *Macrocnemius* and *Tanystropheus* in the Middle Triassic of Europe and *Tanytrachelos* from the Upper Triassic of North America. *Macrocnemius* has 24 presacrals (Kuhn-Schnyder 1974). Wild (1973) figures *Tanystropheus* as having 26, but states in the summary of the text that there are only 25. *Tanytrachelos* has 25 (Olsen 1978). *Araeoscelis*, from the Lower Permian, resembles *Petrolacosaurus* in many features of the postcranial skeleton and may be related to ancestral diapsids, despite the absence of a lateral temporal opening. According to Vaughn (1955) *Araeoscelis* has 31 presacral vertebrae, far above the number in primitive eosuchians. Nine are cervicals. *Heleosaurus*, an eosuchian derivative with characteristics cited as suggesting affinities with archosaurs, has, with some chance of slight error, 25 (Carroll 1976*c*).

Gow restores *Youngina* with 23 presacral vertebrae, admitting that at least the atlas and axis were missing in the only articulated specimen that he studied. Another eosuchian from South Africa, but without horizon and locality data, *Heleosuchus griesbachii* (long ago figured by Owen (1876)), is clearly very similar to *Youngina*. This specimen can be restored as having 25 presacrals (figure 9). Finally, the aquatic genus to be described below has a well established count of 24.

Thadeosaurus is restored as having 25 presacral vertebrae. In the type, the most anterior ribs preserved are longer and more robust than would be expected in the first two or three cervicals. At least four, or more probably five, are missing in this specimen. In *Sphenodon*, in which the vertebrae are otherwise strikingly similar to those of *Thadeosaurus*, the first four vertebrae have notable small articulating surfaces on the transverse processes. The fifth has a length intermediate between those of the anterior cervicals and those in the remainder of the column. The most anterior preserved cervical in *Thadeosaurus* resembles the fifth or sixth in *Sphenodon*. The most anterior vertebrae present would be the sixth, if a count of 25 is accepted. The posterior trunk vertebrae closely resemble those of *Youngina* as illustrated by Watson (1957, fig. 20), and are generally similar to those of both primitive lizards and *Sphenodon*. The centra are deeply amphicoelous cylinders, approximately 70% as wide as long in the anterior trunk region. The length of the centra increases slightly posteriorly in the trunk, but is reduced again just anterior to the sacrum. The centra of the sacral vertebrae are again somewhat longer than those in the anterior trunk region, as are the first three caudals, after which the length is reduced and the remaining centra are of nearly constant length to the end of the tail. Foramina subcentralia are clearly visible in several trunk vertebrae and may have been present in all (figure 7).

Short crescentric intercentra comparable to those of *Sphenodon* are present throughout the trunk region. They do not bear facets for the articulation of the ribs, but end dorsally below the level of the area of capitular articulation.

The arches are attached without sign of suture in the mature specimens. They are low and slightly longer than broad. The anterior zygapophyses extend further laterally than the posterior. The neural spines are essentially rectangular in lateral view throughout the trunk region, angling slightly posterior from the vertical. The height of the spines is slightly greater relative to the length of the arch in the larger specimen.

As in *Youngina*, *Galesphyrus* and *Kenyasaurus*, the transverse processes are notable for being very short. Behind the fourth trunk vertebra they extend no further than the width of the zygapophyses. Anteriorly they are slightly more prominent. The transverse processes in the cervical region of *Youngina*, as illustrated by Gow, are considerably longer than those in the trunk. The shortness of the transverse processes is in marked contrast with those of the early archosaurs (Cruickshank 1972), and the ancestral diapsid *Petrolacosaurus* (Reisz 1981). *Prolacerta* (Gow 1975) also has much longer processes. The articulating surfaces for the capitular and tubercular heads of the ribs are contiguous, but demarcated by a posterior constriction. It may be significant that the basic pattern of the transverse processes and the nature of the rib articulation resemble those of lizards and sphenodontids, which have basically similar trunk and limb proportions and probably similar locomotor patterns.

The angle of the zygapophyses varies throughout the column in a manner resembling that of modern lizards such *Varanus* and *Iguana iguana*. In the anterior trunk region the angle is slight, approximately 5 to 10° from the horizontal. Just anterior to the sacrum the angle increases to about 30°. The anterior zygapophyses of the first sacral vertebra show an angle of approximately 45°; they open posteriorly so as to lock the posterior zygapophyses of the last trunk vertebra into place. They are considerably wider than the posterior zygapophyses of the same vertebra. All these features are matched in *Varanus* and *Iguana*. The zygapophyses of the 2nd sacral vertebra are flatter, as are those of the 1st caudal. More posteriorly, the angle suddenly increases to approximately 55°. This configuration is characteristic of the next six to eight vertebrae. More posteriorly the zygapophyses are only rarely clearly exposed, but the angle appears to be reduced to about 45° to the end of the tail. The variation in the angle of the zygapophyses in the caudal region is similar to those of *Iguana* and *Varanus*, but other lizards show a variety of slightly different patterns. In *Sphenodon*, the anterior zygapophyses of most of the caudal vertebrae wrap around the lateral surfaces of the posterior zygapophyses.

There may be a trace of zygosphenial joints, such as are present in both *Sphenodon* (Hoffstetter & Gasc 1969) and early lizards (Carroll 1977).

As in all terrestrial eosuchians, there are two sacral vertebrae to which ribs are fused without a trace of sutures.

In the type, 47 caudal vertebrate are preserved, in contrast to 56 in the related genus *Kenyasaurus* (Harris & Carroll 1977). The end of the tail is coiled within a larger loop and lies adjacent to the more proximal portion of the tail. It is unlikely that additional segments had been present, unless they were lost before burial.

The width of the centra and the neural arches decreases in a regular manner to the end of

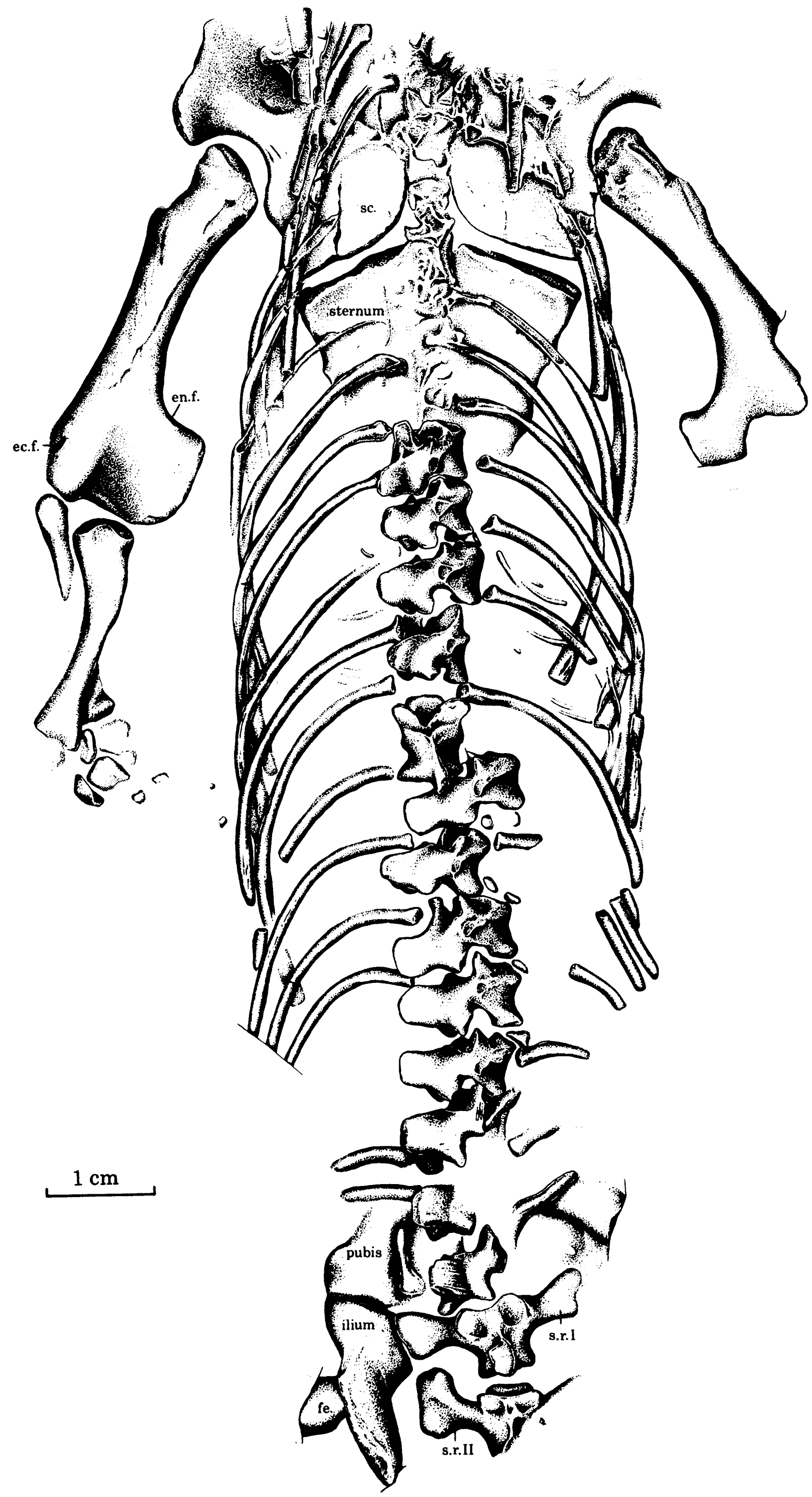


FIGURE 5. *Thadeosaurus colcanapi*, referred specimen, P.M. 1908-11-20a.

the tail as preserved. The first five caudal vertebrae bear ribs fused to the centra that are nearly as long as the sacral ribs. They extend directly laterally. The first shows no association with the ilium. The extremities of the caudal ribs 6 through 8 are lost, but the narrowing of the base suggests progressive shortening. From the 9th to the 19th they are short and pointed. More posteriorly, there is no trace of ribs.

The neural spines on the sacral and anterior caudal vertebrae continue the pattern of those in the posterior trunk region. They shorten gradually, but are still prominent to the level of the 12th caudal. By the 19th, the spine is much reduced and appears as a triangular process above the posterior zygapophyses. It gradually decreases in height, but is still recognizable as far as the very end of the tail. The neural arches progressively narrow, and the zygapophyses are still recognizable, but have little overlap at the very end of the column.

Intercentra are present anterior to caudal vertebrae 1 and 2. Haemal arches are present more posteriorly. The first two caudal centra have a single ventral ridge. From caudal 3 to the end of the tail, there are two ventral ridges, separated by a sharp groove. *Sphenodon* has three caudal intercentra. The pattern is extremely variable in lizards (Hoffstetter & Gasc 1969).

The cross pieces of the haemal arches are continuous, rather than paired, at least to the 44th caudal. The length of the haemal arches decreases gradually from a length equal to that of $1\frac{1}{2}$ centra at the base of the tail, to slightly less than the length of a single centrum in the 44th caudal.

Caudal autotomy has been reported among Permian captorhinomorphs (Price 1940), but neither *Thadeosaurus* nor other eosuchians shows any specialization of the caudal vertebrae to facilitate breakage.

All of the cervical ribs are lost with the head and neck in these specimens of *Thadeosaurus*. Apparently the most anterior to be preserved in both specimens is the 6th. It is clearly a long, ventrally directed rib like those in the remainder of the trunk region. The tuberculum is a well exposed, oval structure. There may not have been a clearly separable capitulum. Even more posteriorly, a clear division is not observed between the two heads. They are distinct in the angles at which they attach to the vertebrae, and the proximal end of all but the most posterior trunk ribs is grooved posteriorly. The articulating surfaces, however, are contiguous throughout the column.

In the trunk region, the length of the ribs remains more or less constant, approximately the length of five trunk centra, from those associated with the 6th or 7th to the 16th vertebra, after which the length gradually shortens toward the sacrum. The last two ribs are approximately the length of $1\frac{1}{2}$ centra. The last three are bluntly rounded at the tip. More anteriorly, the ends are flattened, and slightly recessed at the tip and were almost certainly continued in cartilage. Ribs 12 through 16 were probably attached to the sternum via a short section of intervening cartilage. The rib immediately anterior to the sacrum is fused to the transverse process (in common with *Kenyasaurus* and *Sphenodon*), as are the sacrals and caudals. The structure of the sacral ribs and the nature of their attachment to the ilium are essentially as in primitive living lizards. The ribs slope ventrally at an angle of approximately 30° from the horizontal. They are expanded distally to a width slightly exceeding the length of the posterior trunk centra. The expanded proximal ends of the ribs are grooved anteriorly; this may mark the position of the original division between capitular and tubercular heads. Both the 1st and 2nd sacral ribs are grooved dorsally toward the tip, giving a somewhat bifurcated

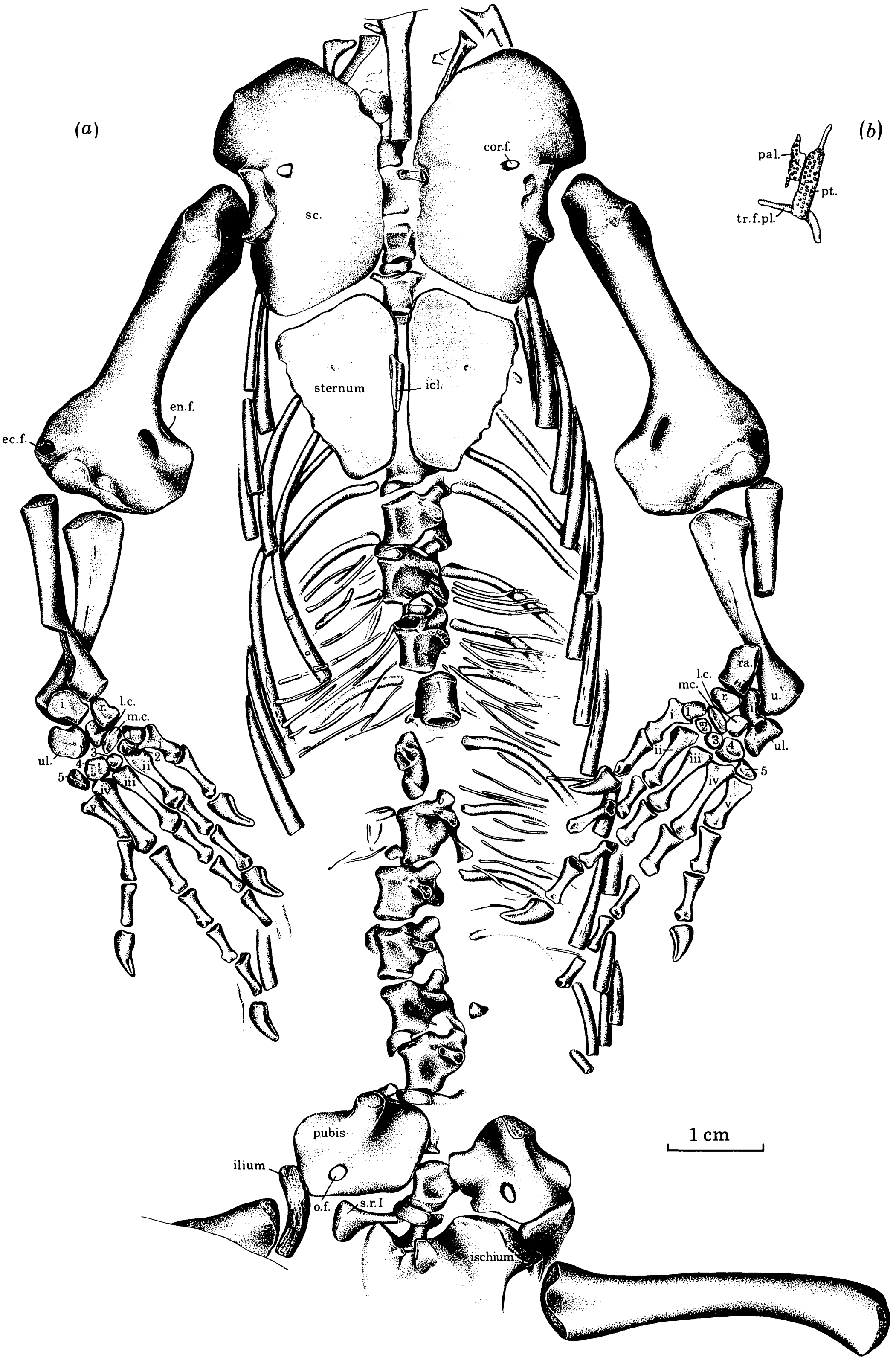


FIGURE 6. *Thadeosaurus colcanapi*, specimen, P.M. 1908–11–8a, counterpart of P.M. 1908–11–20a. (*a*) Ventral view of skeleton. (*b*) View of palate as exposed between two fragments that make up the block.

appearance as noted by Cruickshank (1972) in primitive archosaurs and rhynchosaurs. Except for the smaller size of the specimens, the entire area of sacral attachment in *Thadeosaurus* is very much like that of *Proterosuchus*. The anterior distal margin of the second sacral rib fits against the posteromedial surface of the blade of the first. Both show a clearly defined surface for attachment. Such a close association of the sacral ribs is common to many lizards, but the ends of the sacral ribs are not in contact in *Sphenodon*. The 2nd sacral is simple in *Sphenodon*, but bifurcates in Jurassic members of the family (Cocude-Michel 1963).

In the caudal region, the ribs are indistinguishably fused to the centra in adults. Immature specimens show that the ribs were initially distinct and became fused during growth. Both the sacral ribs and the anterior caudal ribs are initially separate during development in *Sphenodon* as well (Hoffstetter & Gasc 1969).

Appendicular skeleton

Little of the dermal shoulder girdle is preserved in these specimens. There is no evidence of a cleithrum, and little of the clavicle is preserved. The long stem of the interclavicle can be seen in P.M. 1908–11–8a; it is displaced somewhat anteriorly, but from the configuration of what remains of the anterior portion, the anterior border of the coracoid being matched, the distal end would have extended near to the end of the sternum. The specimens are exposed primarily in dorsal and ventral views so that the appearance of the scapulocoracoid in lateral view must be reconstructed and the height of the blade is difficult to establish exactly. It is certainly not very high, compared with other dimensions of the bone and may be presumed to have been completed dorsally in cartilage. The bone is ossified as a unit in the adult, but the scapula and coracoid are separate in an immature specimen. The lateral and ventral surfaces meet one another in a gentle curve. The general appearance of the bone is similar to that of Lower Permian captorhinomorphs. The anterior margin in smoothly rounded without the fenestration apparent in contemporary ancestral lizards (Carroll 1977). Gow (1975) reports an anterior notch in *Youngina*, but this is apparently a result of the incomplete ossification of the scapula and coracoid.

The glenoid retains its primitive screw-shaped articulating surface, as in *Captorhinus* (Holmes 1977) and presumably the humerus articulated with it in a basically similar manner. It is, however, considerably shorter, relative to the anteroposterior length of the scapulocoracoid. The length of the glenoid is 60% greater in *Captorhinus*. Such a short glenoid is also matched by *Araeoscelis*. The great width of the head of the humerus in *Thadeosaurus* presumably indicates considerable freedom of movement since it would have had an excursion far beyond the confines of the glenoid. The anterior, more or less vertical portion of the glenoid, which faces primarily posteriorly, is narrower (by almost half) than the posterior. The dorsal margin is constricted sharply where the surface curves toward the transverse plane. More posteriorly, the articulating surface is not as flat as in *Captorhinus*, but curves somewhat more ventrally, allowing the humerus to be moved more underneath the body in a posture approaching that of lizards. At the extreme medial margin, the articulating surface curves to face ventrally.

The posterior margin of the glenoid is sharply set off from the general bone surface. The posterior edge of the glenoid approaches the vertical in *Thadeosaurus*, in contrast with an approximately 45° angle from the vertical in *Captorhinus*. The stereotyped rigidity of forelimb locomotion in *Captorhinus* and *Petrolacosaurus* is probably lost, but the freedom of movement of lizards is not yet achieved. To judge from the configuration of the glenoid, motion was restricted

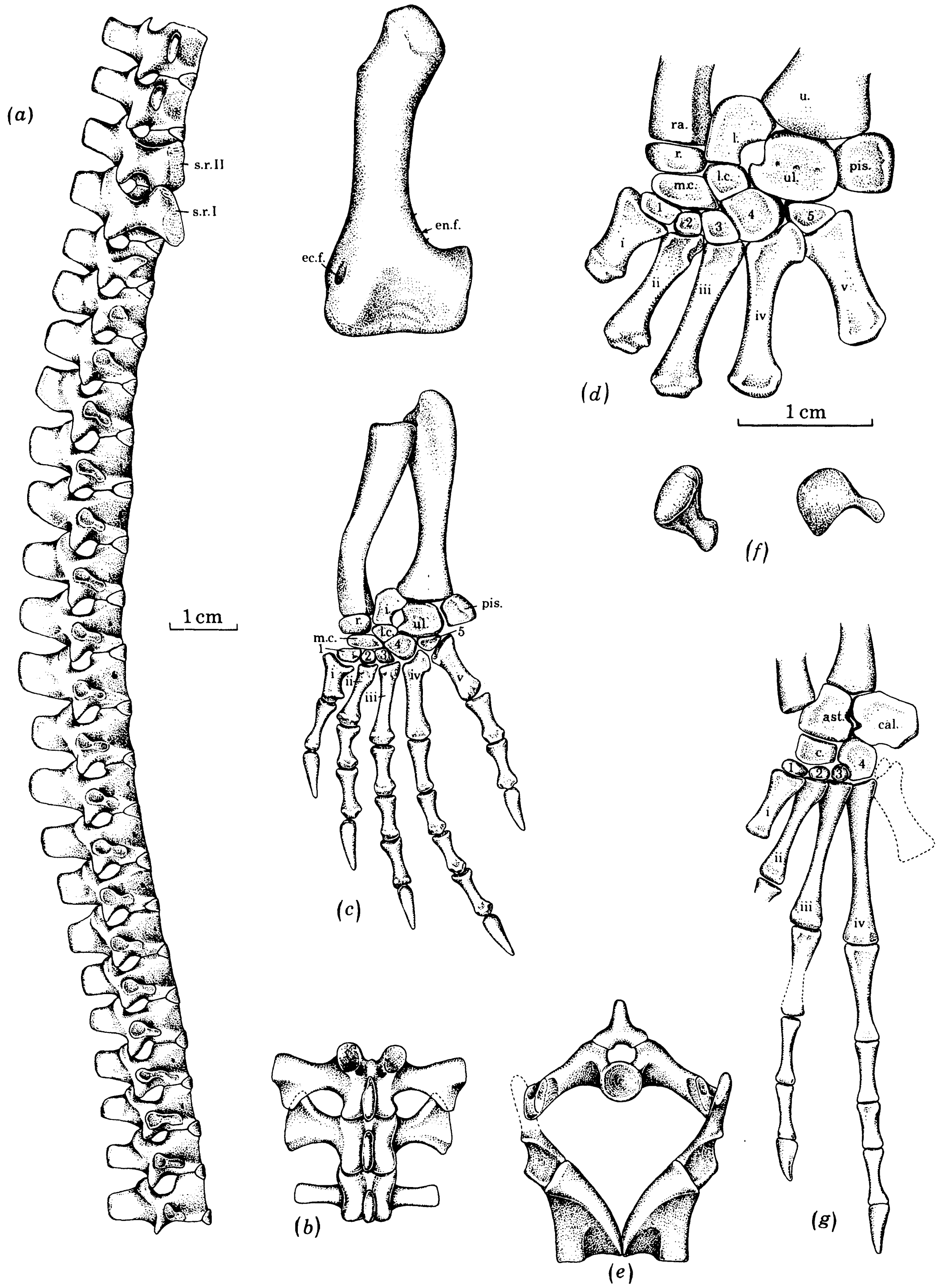


FIGURE 7. *Thadeosaurus colcanapi.* (*a*) Trunk, sacral and anterior caudal vertebrae in lateral view. Four or five cervical vertebra are missing. Based on P.M. 1908–11–13a (magn. × 2. (*b*) Sacral and first caudal vertebrae in dorsal view (magn. × 2). (*c*) Left forelimb in dorsal view, based primarily on P.M. 1908–11–13a, entepicondylar foramen not visible in directly dorsal view; radius, ulna, carpus and manus are unnaturally drawn in one plane; the distal articulating surface of the radiale is exposed anteriorly; metacarpals are slightly spread from their natural position, in which their proximal ends may have somewhat overlapped (magn. × 2). (*d*) Detail of carpus; elements in close articulation, pisiform angled posteriorly (magn. × 4). (*e*) Second sacral vertebra and pelvic girdle in posterior view (magn. × 2). (*f*) Proximal end of femur of *Thadeosaurus* (right) and *Iguana* (left) (magn. × 2). (*g*) Reconstruction of left tarsus and pes in dorsal view (magn. × 2).

anteriorly, but freer ventrally. Posteriorly, the humerus probably could have approached the body wall. Holmes suggests that the humerus of *Captorhinus* moved in a horizontal arc of only 60°. In *Thadeosaurus*, this would certainly have been exceeded by the addition of a further ventral component.

The general configuration of the glenoid shows few other features approaching the lacertoid pattern except for its decrease in relative size. The lacertoid pattern may be linked with the development of distinct areas of scapular and coracoid ossification, a feature that marks the successors of eosuchians in numerous lines. Within the Triassic the scapular and coracoid become distinct in lizards, rhynchosaurs, crocodilians and other archosaurs, and in nothosaurs. The potential for evolving separate areas of scapular and coracoid ossification is readily open to all primitive reptiles since these bones remain distinct in immature forms. Pelycosaurs and *Araeoscelis*, in contrast, retain the primitive configuration of the glenoid, while the scapular and coracoid areas remain distinct in the adult.

The coracoid foramen is present and in the same position as in captorhinomorphs and the primitive diapsid *Petrolacosaurus*. There is no tendency to enlarge the opening and, in fact, it is smaller than in comparable-sized specimens of *Captorhinus*. Above the front of the glenoid there is a small pit that may mark the entrance of the supraglenoid foramen. This is at the back of the area of origin of the subcoracoscapularis muscle, rather than above it as in *Captorhinus*. In *Thadeosaurus*, the area where this muscle originated is apparently much smaller, but no less well defined. The medial surface of the scapulocoracoid broadly resembles that of captorhinomorphs, with a clearly defined subcoracoscapular fossa, bordered posteriorly by a strong buttress supporting the glenoid and the margin of the scapula, and a longitudinal ridge extending anteriorly, essentially as in *Petrolacosaurus*. The coracoid and supraglenoid foramen, visible externally, should open into this area internally, but they are not evident. The tubercule for the coracoid head of the triceps is evident in medial view, behind the glenoid in P.M. 1908-11-20a, much as in pelycosaurs.

A small cartilaginous sternum is restored in *Captorhinus* (Holmes 1977), its proportions determined by the configuration of the coracoid margins, the extremity of the stem of the interclavicle and the anterior extent of the ventral scales. An ossified sternum is not known in any captorhinomorph, pelycosaur or the primitive diapsid *Petrolacosaurus*. It is present, however, in the apparently related, but technically non-diapsid genus *Araeoscelis* (Vaughn 1955). This structure apparently has an irregular distribution among the eosuchians. It is not reported in *Protorosaurus*, *Prolacerta* or *Youngina*, but is evident in the aquatic genera *Hovasaurus* and *Tangasaurus* and in *Kenyasaurus*. In the genus *Heleosaurus*, clearly an eosuchian derivative, but with teeth and dermal armour closely resembling those of thecodonts, there would be space for a short sternum between the coracoid and the anterior margin of the ventral scales. The interclavicle in that genus extends only a short distance beyond the posterior margin of the scapulocoracoid.

It is reasonable to suppose a small, unossified sternum as a heritage of eosuchians, with its ossification or extent posteriorly being related to the importance of the pectoralis musculature. Together, the paired halves of the sternum form a large triangular element closely approaching the posterior margin of the coracoids. It would appear that the coracoid fitted into slots at the anterior margin of the sterum. These elements are linked by connective tissue in lizards. The sternum thins distally. The lateral margins are marked by three pairs of processes for attachment of the ventral cartilagenous extensions of the ribs. The bone ends bluntly posteriorly.

It may, as in many lizards, have been continued in cartilage for connection with additional ribs. Although the sternum is paired in these specimens, the halves approach the midline and were almost certainly united in the adult, as they are in large specimens of the tangasaurids. Slightly anterior to the middle of the bones are small foramina opening ventrally. They may have accommodated blood vessels.

The configuration of the sternum and its relationship with adjacent structures are comparable in all respects with those in lizards as a group (Lecuru 1968) and particularly to the ancestral pattern (Carroll 1977). Presumably this is associated with the growing importance of the pectoralis as a muscle assisting in drawing the forelimbs under the body.

The humerus of *Thadeosaurus* is a stout bone, with widely expanded extremities. It appears heavily built by the standards of the early diapsid *Petrolacosaurus*, but that genus appears exceptional in the gracile nature of its limbs. The humerus of *Youngina* is not adequately known for detailed comparison. It appears poorly ossified, to judge by the figures of Broom (1922) and Gow (1975). The humerus of *Thadeosaurus* is in general comparable with those of pelycosaurus and captorhinids in its proportions, and also resembles that of the early lizard *Palaegama* (Carroll 1975). The proximal articulating surface resembles in general that of *Captorhinus* and *Petrolacosaurus*. As in other eosuchians, the ectepicondylar as well as the entepicondylar foramen is present; it is completely surrounded by bone in both specimens. Bone grows across the posterior border of this opening during ontogeny in tangasaurids. The entepicondyle appears large relative to that of other eosuchians, but not as extensive as that of *Captorhinus*. Anteriorly, the shaft of the bone bears a sharp crest, presumably separating the insertions for the brachialis inferior and the triceps musculature dorsally. The prominance for attachment of the pectoralis and the deltoid muscles are close to the articular surface.

A ridge proceeds proximally from the crest of bone enclosing the ectepicondylar foramen, giving the shaft a thicker appearance as seen in dorsal and ventral views, and reducing the appearance of the lateral expansion of the ectepicondyle. In *Captorhinus*, the entepicondyle serves as the origin for a host of muscles that flex the lower limb. This area is deeply pitted for tendinous attachment of muscles in *Thadeosaurus*, suggesting a similar function of the elbow joint to that proposed for captorhinids (Holmes 1977). The smaller size of the distal articulating surface, relative to that of captorhinids, suggests a somewhat greater flexibility at this joint, however. The low degree of ossification of the olecranon makes more exact analysis of possible movement difficult.

The ulna and particularly the radius are basically similar to those of *Captorhinus*, with relatively few distinguishing features for comparison. The proximal head of the radius is an oval, slightly concave surface, with the long axis, when articulated, parallel to the shaft of the humerus. A slight posterior lip extends over the end like a miniature olecranon. The shaft angles laterally toward the distal end. Here, the anterior and medial surfaces of the bones are sharply demarcated. The distal end of the radius is little expanded beyond the shaft and fits essentially flatly against the radiale.

In contrast with the generally high degree of ossification of the skeleton, especially of the carpus, the olecranon shows little ossification, although the base of the semilunar notch is recognizable anteriorly. Grossly, the proximal end of the bone gives the appearance of the ulna in lizards in which the proximal epiphysis has been lost. There is, however, no evidence from the remainder of the skeleton that epiphyses were developed in this genus, as has been claimed for contemporary lizards (Carroll 1977). Distally, the ulna ends in a broadly expanded arc which articulated closely with the proximal surface of the intermedium, the ulnare (which is grooved to receive it) and the pisiform. There is no specialized epiphysial surface such as is present at the end of the ulna in ancestral as well as modern lizards and in *Sphenodon*. On the anteroventral surface, a sharp ridge extends from the base of the semilunar notch toward the middle of the area of distal expansion. This might be identified as the line of separation between the epitrochleoanconaeus and the palmaris communis profundus, to judge from the suggested position of these muscles in *Captorhinus* (Holmes 1977).

The carpus and manus of *Thadeosaurus* are well shown in both specimens. The elements of the carpus are fully ossified, fitting together in a tight mosaic. Among modern genera, the pattern is similar to that of *Sphenodon* (Lecuru 1973), except for the proximodistal flattening of most of the elements in the living genus. As a result of this flattening, the medial centrale does not reach the radial margin in *Sphenodon*, but wedges out between the radiale and the 1st distal carpal. The perforating foramen is smaller in *Sphenodon*, but still clearly evident. The arrangement and relative size of the elements are readily derived from those of primitive captorhinomorphs. Comparison with *Youngina* is complicated by the apparent low degree of ossification and resulting poor definition of the elements. Gow (1975) does not figure the pisiform. Both *Captorhinus* and *Petrolacosaurus* have a relatively longer intermedium and ulnare, and a relatively small pisiform. The intermedium in *Thadeosaurus* is large as in *Sphenodon* and earlier Palaeozoic sauropsids, supporting the ulna proximally. It in turn is wholly supported by the lateral centrale. In *Sphenodon*, the ulnare reaches the medial centrale as well. The ulnare is the largest carpal, with the medial surface widely concave to form the margin of the perforating foramen.

The radiale appears anteriorly as a flattened oval. Proximally, it is slightly recessed to form a close union with the radius. Distally, the radiale has a convex surface that fits into a broad basin in the surface of the medial centrale. Laterally there is a less clearly defined articulation with the lateral centrale. The radiale does not reach this bone in *Sphenodon*, but it does in most lizards. The radiale is less well integrated with the remainder of the carpus; it appears to be freely movable relative to the intermedium. In contrast with *Captorhinus* and *Petrolacosaurus*, the lateral centrale of *Thadeosaurus* would be precluded from contact with distal carpal 3 by proximal contact of the medial centrale and distal carpal 4. Distal carpal 2 is the smallest, with 1 widened laterally. The 3rd distal carpal is closely integrated with the 4th, which is recessed for it on the mediodistal margin. As far as the distal surface of the 3rd distal carpal can be seen ventrally, it does not underlie the head of the third metacarpal as in *Captorhinus* and *Petrolacosaurus*. Mechanically, the carpus probably differed little in the relative mobility of the elements from that of *Captorhinus*.

Ventrally, the carpus is not quite as well exposed as dorsally, but several features should be noted. In general the areas of finished bone are smaller than dorsally, so that each element acts like a keystone to give stability to the mosaic of the carpus. There appears to be a small plate of bone underlying distal carpal 5 that might be interpreted as a sesamoid. Such elements have previously been reported in *Captorhinus* (Holmes 1977) and are common in lizards.

Each distal carpal supports primarily a single metacarpal, except for the 5th, which is in contact with a corner of the 4th metacarpal as well. All of the metacarpals have a concave surface for close association with their respective carpals. The proximal surface of metacarpals 3 and 4 are sharply angled laterally, so that the lateral corner reaches the next successive distal carpal.

There is little overlap seen in the specimens as preserved, but the proximal heads of the metacarpals are slightly twisted relative to the distal so that the lateral surface of each is above the medial side of the one adjacent on the lateral side. The proximal end of the 1st is expanded medially, proximal to the 2nd, with which it seems to articulate. The relative position of the elements is nearly identical with that seen in *Iguana* and *Sphenodon*, if the epiphyses of digits 2 through 5 in the living genera are considered as extensions of the metacarpals. The element usually termed an epiphysis of the 1st metacarpal in living lizards has the role of the 1st distal carpal in eosuchians.

As in most primitive reptiles, the metacarpals increase in length from the 1st to the 4th and the 5th is intermediate in length between the 1st and the 2nd. The digital count is the typical reptilian 2, 3, 4, 5, 3. Each digit ends with a long, sharp, recurved terminal phalanx. In all the digits, the penultimate phalanx is longer than the next most proximal element (the metacarpal for the 1st digit). Ostrom (1969) noted a similar pattern in *Deinonychus*, but it is also widespread in lizards. He also stressed the prevalence of this feature in birds of prey, but it also occurs in the herbivorous green iguana. The distal phalanges were presumably covered with horny claws. The flexor tubercles are not well demarcated, but extend below the surface of the penultimate phalanx to provide considerable leverage. The articulating surface between the last two phalanges would have permitted a wide arc of movement. The proximal articulating surface of the penultimate phalanx extends under the more proximal phalanx, somewhat restricting rotation at that joint. The joints of the distal surfaces are concave in both dimensions, providing considerable scope for controlled lateral movement. In all these features, the manus of *Thadeosaurus* resembles that of *Sphenodon* very closely. In the living genus, however, all the elements are shorter, relative to the proximal limb elements.

The three elements of the pelvic girdle are well exposed in the type with confirmation provided by the second specimen. The ilium, pubis and ischium are well ossified, but have separated from one another in both skeletons. The entire pelvis is shorter than that of primitive reptiles and approximates the proportions seen in primitive living lizards. It stretches the length of four trunk centra (as in *Iguana iguana* and *Varanus*). That of the primitive diapsid *Petrolacosaurus* and most romeriids (Carroll & Baird 1972) extends the length of more than five centra. Both the pubis and the ischium of *Thadeosaurus* are proportionately shorter. Of the eosuchians described by Gow (1975), the closer resemblance is to that of *Prolacerta* rather than *Youngina*, but the distinctive features of the latter may be due to immaturity. The blade is expanded anterodorsally from what may be the primitive condition represented by *Petrolacosaurus*, so that the dorsal margin of the ilium is nearly horizontal. Medially, the surface of the ilium is rugose for attachment of the two pairs of sacral ribs. The ilium extends posteriorly just beyond the level of the posterior margin of the ischium. The pubis appears ventrally as a roughly square bone, with a large obturator foramen near the posterior margin and a very prominent pubic tubercle extending anteroventrally. The pelvis may be restored according to the pattern common to primitive modern lizards with the lateral margin of the pubis in in a parasagittal plane, sloping anteroventrally at about a 45° angle. Medially the bone is thin in the area that develops as a thyroid fenestration in lizards. Gow notes a notching of the pubis and ischium in *Youngina* that he attributes to immaturity.

The femur is the length of six trunk centra, or approximately 40 % of the glenoid–acetabular distance. That of *Youngina* and *Galesphyrus* appears relatively stouter. The bone appears slim compared with the humerus and not as fully ossified. It is 4 % longer. The configuration is essentially like that in modern lizards such as *Iguana*, if the specialized epiphysial nature of the articulating surfaces in the modern forms is discounted. The distal end has recognizably, but not strongly separated, anterior and posterior condylar surfaces; the posterior is only slightly extended beyond the anterior. Proximally, the internal trochanter extends ventrally below the level of the shaft, forming the anterior margin of a clearly defined (and hence primitive) intertrochanteric fossa. The proximal articulating surface is in the form of an elongate condyle, the long axis of which is at an angle of about 10° anterior from the vertical axis when the distal condyles are horizontal. In *Iguana*, the major axis of the proximal condyle is about 40° posterior to the vertical axis.

The tibia and fibula are well exposed in the type. The tibia is 88 % the length of the femur, and the fibula 80 %. These bones are incompletely known in *Youngina* and much longer and thinner than their counterparts in *Galesphyrus* but relatively shorter than those in *Petrolacosaurus*. The tibia is a stout bone which, as in modern lepidosaurs, bears most of the weight of the limb. The ends are slightly convex and at right angles to the shaft. The distal end resembles that of lizards, if the epiphysis is not included. Several longitudinal ridges are evident. One extends from a short distance distal to the proximal articulating surface on the anterior face of the bone. It is short and narrow. Another thicker ridge is present on the medial surface at about the same distance from the proximal end of the bone. A third, on the lateral surface, is approximately two-thirds of the way down the shaft. It may be associated with attachment of the muscle sheet that bound the tibia to the fibula. Association of the other ridges with specific muscles recognized in modern lepidosaurs does not appear justified.

The fibula is long and thin; the shaft is more conspicuously sigmoidal than in modern lepidosaurs. The distal end appears like that in lizards, except that there is not a separate epiphysial element. It is expanded from the width of the shaft and forms an angle of approximately 55° medial to the long axis of the bone. It is broadly rounded with the areas for articulation with the astragalus and calcaneum not distinct. The proximal surface ends bluntly whereas a rounded epiphysis is developed in lizards.

In the two most complete specimens, the tarsus and pes are not fully exposed. Study is complicated by the fact that the division of the counterparts passes through both the astragalus and calcaneum, and so both elements must be studied by piecing together the two halves. In general, the pattern of these elements resembles that in other genera of eosuchians, *Galesphyrus*, *Kenyasaurus* and *Tangasaurus*, although the mediolateral extent of the calcaneum, (readily discernable both dorsally and ventrally) is unusually great. The articulating surface between the astragalus and the calcaneum suggests that the bones were essentially in a single plane, rather than having the extremity of the calcaneum extending posteriorly as a heel, as in crocodiles or pseudosuchians. In proportions, both the astragalus and the calcaneum resemble those of *Noteosuchus* (Carroll 1976*a*). The centrale is oblong and the fourth distal tarsal, next in size to the astragalus and calcaneum, is nearly circular and supports both the proximal elements. It is recessed on the medial side of the distal margin for the 3rd distal tarsal. The 2nd, 3rd and 4th distal tarsals are round to oval bones fitting into the concave proximal surfaces of the first three metatarsals. Less complete material that is attributed to *Thadeosaurus* shows that the 5th distal tarsal is still distinct and the 5th metatarsal shows no evidence of the hooking characteristic of most lizards and sphenodontids. The first four metatarsals increase sequentially in length. The 4th is 16 mm in length, 36 % of the length of the tibia. They overlap in sequence. The ends of the digits are lost or displaced in the better specimens. Two terminal series are visible that are attributed, with little probability of error, to digits 3 and 4. That attributed to the 3rd is the only one showing all the distal phalanges. The penultimate is slightly shorter than that more proximal to it. The terminal phalanges resemble those of the hand in being laterally compressed, sharply pointed and recurved.

Numerous ventral scales are present in both specimens. The individual elements are well preserved, but only in a few places can the number of units per segment and the number of scales in each row be determined. The condition described below for *Claudiosaurus* applies to *Thadeosaurus*, inasmuch as comparison is possible. None of the medial elements are well preserved in *Thadeosaurus*.

Taxonomic position

In the absence of adequate cranial remains, it is difficult to be specific in evaluating the taxonomic position of *Thadeosaurus*. On the basis of comparable postcranial remains, it appears close to *Youngina*. There is no evidence of a sternum in *Youngina*, but the element was probably present, but unossified. A further species that may be quite similar to *Thadeosaurus*, was originally described by Owen (1876) as *Saurosternon griesbachii*. It is from the Karroo series in South Africa, but no additional data are available. Broom (1913) later recognized major differences from the earlier named species, *Saurosternon bainii*, and made it the type of a new genus, *Heleosuchus*. The specimen, which was said to be in the Imperial Museum of Vienna, can no longer be located. The original drawing (figure 8) is quite clear and a cast in the collection of the South African Museum in Cape Town shows some additional detail. It is evidently an eosuchian and shows the body proportions quite clearly. Tentatively, *Thadeosaurus*, *Youngina* and *Heleosuchus* appear to make up a group of relatively conservative eosuchians with short necks of four or five vertebrae. *Galesphyrus* (Carroll 1967*b*) might belong to this group, but, in the absence of the skull, this is open to question. The limbs are much shorter and stouter than in the other genera and the foot appears somewhat more primitive. *Kenyasaurus*, from the Lower Triassic of Kenya, is another form that might be allied here, but it too lacks the skull.

SKULL OF *YOUNGINA*

Almost no cranial material of *Thadeosaurus* is known. The skull of the related genus *Youngina*, however, provides a very useful basis for comparison of the primitive eosuchian pattern (figure 9). The orbits are large and slightly posterior to the middle of the skull length. The external nares are near the anterior margin of the skull. The lateral temporal opening is nearly as large as the orbit and the upper opening is somewhat smaller. The lateral opening is completely surrounded by bone, with no evidence of streptostyly of the quadrate. The quadratojugal is limited to the ventral margin of the cheek, rather than extending dorsally along the posterior border of the lateral temporal opening as in archosaurs. The lacrimal is reduced from the primitive pattern and reaches no more than half the distance from the orbit to the naris. Traces of postparietal and tabular are present on the occipital surface, as well as a long supratemporal that helped to tie the skull table to the posterior margin of the cheek. Ridges on the lateral and posterior margin of the parietal may have served to strengthen the skull table. The quadrate is exposed laterally behind the squamosal. It is slightly emarginated posteriorly. The braincase is primitive in that the paroccipital processes only barely make contact with the cheek and the stapes is a massive rod, possibly still retaining a supporting function.

FIGURE 8. *Heleosuchus greisbachii* (from Owen 1876), type and only known specimen, cited as Vienna Museum, can no longer be located.

The internal nares are elongate slits, extending nearly one-third of the length of the skull. The suborbital fenestrae are large, with only narrow portions of the ectopterygoid and palatine reaching the margin of the palate on either side. The transverse flange of the pterygoid supports a row of large denticles and two other rows of denticles radiate from the area of the basicranial articulation. The interpterygoid vacuities are narrow, triangular slits. There are approximately 25 teeth in each side of the jaw, roughly conical in shape.

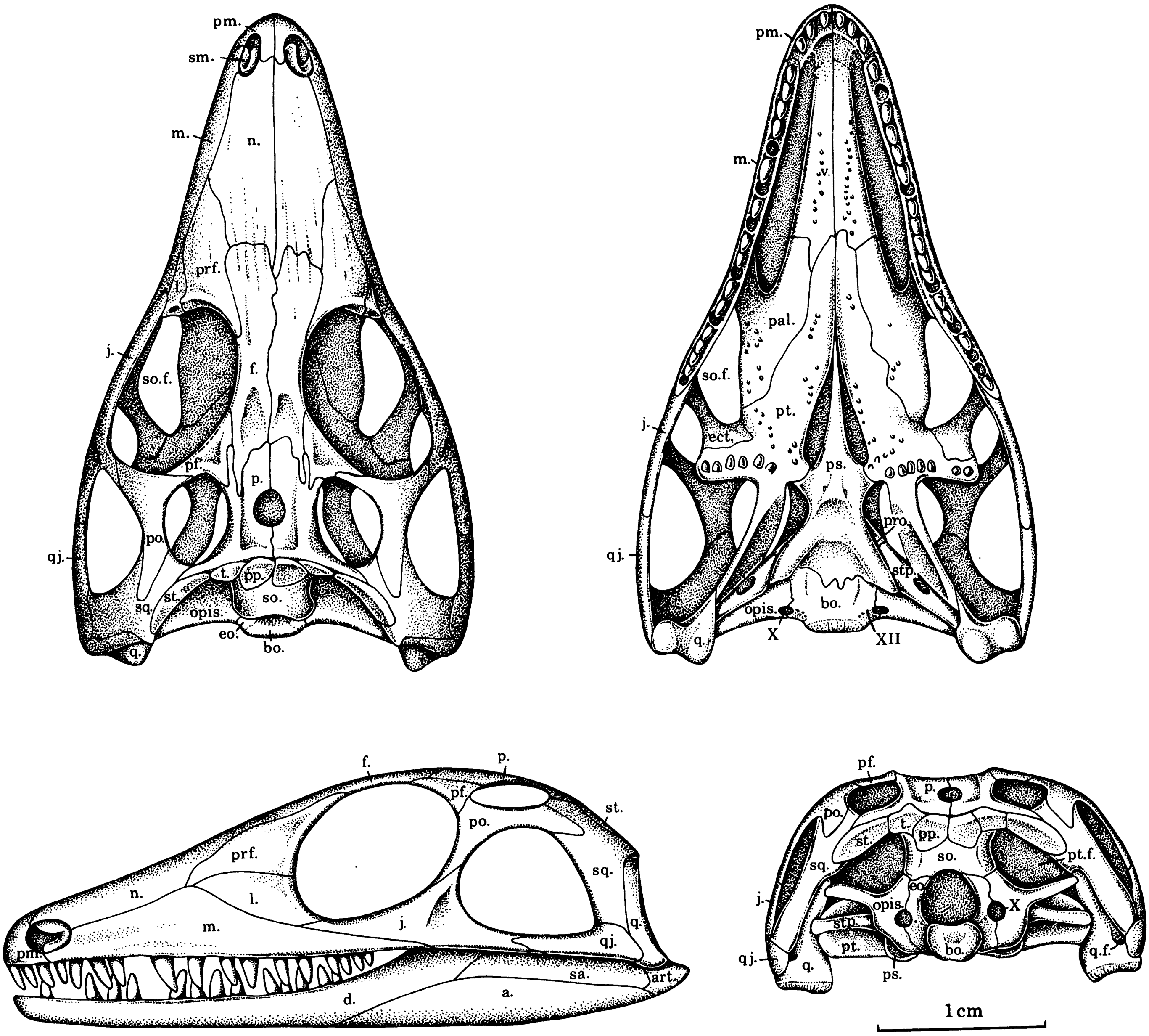


FIGURE 9. Skull of *Youngina capensis*, in dorsal, palatal, lateral and occipital views (magn. × 2.7)

The proportions of the skull, neck and body of *Youngina*, *Heleosuchus* and the tangasaurids of

Madagascar and Tanzania are similar to one another and can be taken as characteristic of conservative members of the Eosuchia.

Thadeosaurus (figure 28) is restored as having similar proportions. This general body pattern and the details of cranial and postcranial elements may be considered as ancestral to the pattern exhibited by the primitive sauropterygian *Claudiosaurus*.

CLAUDIOSAURUS gen. nov.

Subclass Synaptosauria

Order Sauropterygia

Claudiosauridae fam. nov.

Family diagnosis. Differs from all described nothosaurs and plesiosaurs in having the scapulocoracoid ossified as a unit. Coracoid foramen not enlarged, no thyroid fenestration. Substantial sternum present, but unossified. Eight cervical vertebrae. Two pairs of principal sacral ribs and partial incorporation of a third. Differs from eosuchians in loss of lower temporal bar and posterior process of the jugal. Area of transverse flange of pterygoid not differentiated in orientation from remainder of palate. Palatal bones covered with a continuous pattern of denticles rather than three discrete rows. Small but distinct suborbital fenestrae. Internal nares long and narrow. Large dorsal temporal openings. Skull not flattened. Differs from plesiosaurs in retaining large nasal. Numerous short, subpleurodont marginal teeth. Teeth of premaxillae not precumbent.

Claudiosaurus gen. nov.

Type species. Claudiosaurus germaini

Diagnosis. Same as for family. The name honours C. Germain, who collected most of the material on which the family is based.

Claudiosaurus germaini sp. nov.

Diagnosis. Same as for family.

Holotype. P.M. 1978–6–1 in the collection of the Muséum National d'Histoire Naturelle, Paris; a complete skeleton collected at Leoposa.

Referred material. P.M. 1978–6–2 a partial skeleton collected at Leoposa. Specimens in the private collection of C. Germain, Port Menach, France, all collected from Leoposa: C.G. 20/4, most of skeleton, minus skull, in counterpart blocks; C.G. 20/5, most of skeleton, minus skull and cervical vertebrate in counterpart blocks; C.G. 20/6, counterpart blocks showing most of skeleton, including skull in dorsal and ventral views; C.G. 20/7, counterpart blocks, most of skeleton minus skull and cervical vertebrae; C.G. 20/8, counterpart blocks, most of skeleton minus skull and cervical vertebrae; C.G. 20/9, counterpart blocks including vertebrae and left rear foot; C.G. 20/10, counterpart blocks containing entire skeleton; surface of blocks badly weathered, skull shows little more than weathered surface of internal bones; C.G. 20/11, counterpart blocks showing trunk region; C.G. 20/13, trunk region, some of both girdles, weathered; C.G. 20/16, counterpart blocks of juvenile, most of skeleton except skull and cervical vertebrae; C.G. 20/17, counterpart blocks showing rear limbs, vertebrae and pelvic girdle; C.G. 20/18, piece of nodule showing carpus of medium-sized individual and disarticulated skull bones; C.G. 20/19, four proximal caudal vertebrae. Material collected from Benenitra: P.M. 1925–5–102, humerus; P.M. 1909–3–25, vertebrae, scapulocoracoid; P.M. 1909–3–13, humerus; P.M. 1925–5–111, femur; P.M. 1925–5–90, humerus; P.M. 1909–3–43, humerus; P.M. 1925–5–120, tibia; P.M. 1925–5–85, ulna; P.M. 1909–3–37, pelvis, sacral rib, scapulocoracoid (many other disarticulated elements have been found at this locality). Sakamaniga (Ranohira): P.M. 1910–33–1a, skeleton, nearly complete except for skull, cervical vertebrae and most of tail. Specimen without locality data: P.M. 1911–18, foot.

Localities. The type and most of the articulated material has come from a single restricted locality near the village of Leoposa in southwestern Madagascar (figure 2). All were collected by C. Germain in 1953. A large amount of disarticulated vertebral, girdle and limb material was collected in 1909 by J. Colcanap and in 1925 by J. Piveteau from the vicinity of Benenitra.

Horizon. The most recent and detailed stratigraphic study has been carried out at the type locality by Elf Oil Company, under the direction of Cliquet (1957). This is one of the localities from which Goubin (1965) collected pollen and spore samples for correlation with Karroo-age deposits in other areas. Locally, the top of the Permian has been recognized by a prominent nodular layer, above which the nature of the sedimentary record is indicative of the Middle Sacamena Formation, dated throughout the island as Lower Triassic. According to Germain, the aquatic reptiles come from just below this horizon. The spore and pollen flora confirms the Upper Permian age for the beds containing the fossil reptiles. These beds are thought to be the same age as those that are exposed near Ranohira, 15 km further north, from which have come abundant remains of the reptile *Barasaurus* which Piveteau (1955*a*) has described as being very similar to the South African genus *Owenetta*. *Owenetta* occurs near the top of the Permian in South Africa (Kitching 1977). No specific stratigraphic information is available on the beds in the region of Benenitra, but they are typically assigned to the same formation as those further north.

Environment of deposition

One might expect that the transition between primitive terrestrial reptiles and the Mesozoic marine genera would have occurred via freshwater intermediates. The environment of the Madagascar localities unfortunately cannot be unequivocally established. There are no accompanying invertebrate fossils at Leoposa, which might be taken as evidence of a depauperate freshwater fauna. There are thin marine beds within the Lower Sakamena, but they are clearly distinct from those that contain the vertebrates. In other parts of the sequence there are dolomitized reefal structures, however, which suggest a marine environment in which diagenic conditions have destroyed the remains of any identifiable invertebrate fossils. The Lower Sakamena Formation also contains tar sands, which suggest large accumulations of microscopic marine organisms, although not necessarily associated with the vertebrates. Within the system of fault basins there is evidence for marine deposition to the north of the main fossil locality, and (mostly by default of fossils) stronger evidence of freshwater in the south (Cliquet 1957 and unpublished reports). Taking this as a whole, one can imagine a mixed environment that would have had a continuous transition from freshwater streams and lakes to brackish and shallow-water marine, seemingly ideal conditions for the evolution of marine reptiles. The complete absence of any trace of aquatic reptiles from the immediately overlying marine beds in northern Madagascar, otherwise extremely rich in amphibians, fish and ammonites, suggests that the ancestors of nothosaurs had not yet become adapted to truly marine conditions.

The specimens from Leoposa are all preserved in nodules of uniformly fine-grained sandy shale. They were found during preparation for drilling in the immediate subsurface sediments. Most of the specimens were uncovered by Germain as the result of systematic excavation by bulldozer. It is thanks to his diligence in collecting and care in preserving the specimens that this collection is available for study. The specimen collected from Sakamaniga is preserved in a similar manner. The Leoposa nodules are oval or round in outline and relatively thin. They clearly formed in response to the presence of the contained reptiles. Formation of the nodule may be associated with the central core of the animal, since heads and tails are only preserved when they are folded in toward the trunk. Several specimens have a posture expected in a swimming animal, following the pattern in modern crocodiles. This suggests rapid inundation, as if by an underwater landslide or turbidity currents carrying enough sediments to immediately immobilize the animals. Other specimens have the limbs and girdles somewhat distorted or disarticulated from the vertebral column, but all have the individual elements of the carpus, tarsus, manus and pes closely associated. The individual elements may be overturned or slightly displaced, but this might be accounted for by the action of decomposing organisms following burial. There is no evidence of the environment having been anaerobic, for there is little evidence of soft tissue accompanying the bones.

The specimens from the area of Benenitra are preserved in a much different manner. Almost all the bones are isolated from one another and jumbled in an apparently random manner in the samples collected. Some bones show wear, but most have very sharp edges as if they were buried without much transport following disintegration of the skeletons. The matrix is a course, dirty arkose, with large pieces of orthoclase as well as quartz, flakes of graphite and mica. The presence of feldspars, graphite and mica indicates relatively rapid burial of the sediments, without intense surface weathering. There are also many clay pebbles, suggestive of reworking partially indurated sediments. Such sediments may be derived from the weathering of granites such as the crystalline massif that makes up the core of the island. Garnet, zircon, tourmaline and one collophane grain were observed.

At both Benenitra and Leoposa, the bones represent substantial growth series. Some are clearly immature forms with the ends of the bones and the carpals and tarsals unossified and others are presumably from fully adult individuals. There is approximately a twofold difference in the linear dimensions of comparable bones, or a sixfold difference in total mass. Apparently a more or less equally complete sample of the community is present in both localities, despite the different mode of preservation. There is a very clearly biased sample in terms of skeletal elements from Benenitra, but it is not possible to know whether this is a result of preservational or collecting factors. Accompanying the multitude of bones of *Claudiosaurus* at Benenitra are a few worn and broken remains of therapsids: the symphysial region of a theriodont broken on all bone surfaces, and a very much worn tooth of a dicynodont. In contrast, relatively delicate metatarsals of the aquatic genus are preserved intact and without wear. Presumably the therapsid remains are from carcasses that weathered on the land and were swept into the water and carried some distance until they settled to the bottom in a place less disturbed by the current. The remains of *Claudiosaurus* were fully disarticulated before burial, but transport appears to have been very limited. Elements of both sides of the pelvic girdle and the scapulocoracoid appear together in a single block. To judge from the size distribution, the original environment of the animals may have been the same in both localities.

Most of the previously described vertebrates from the Upper Permian of Madagascar were

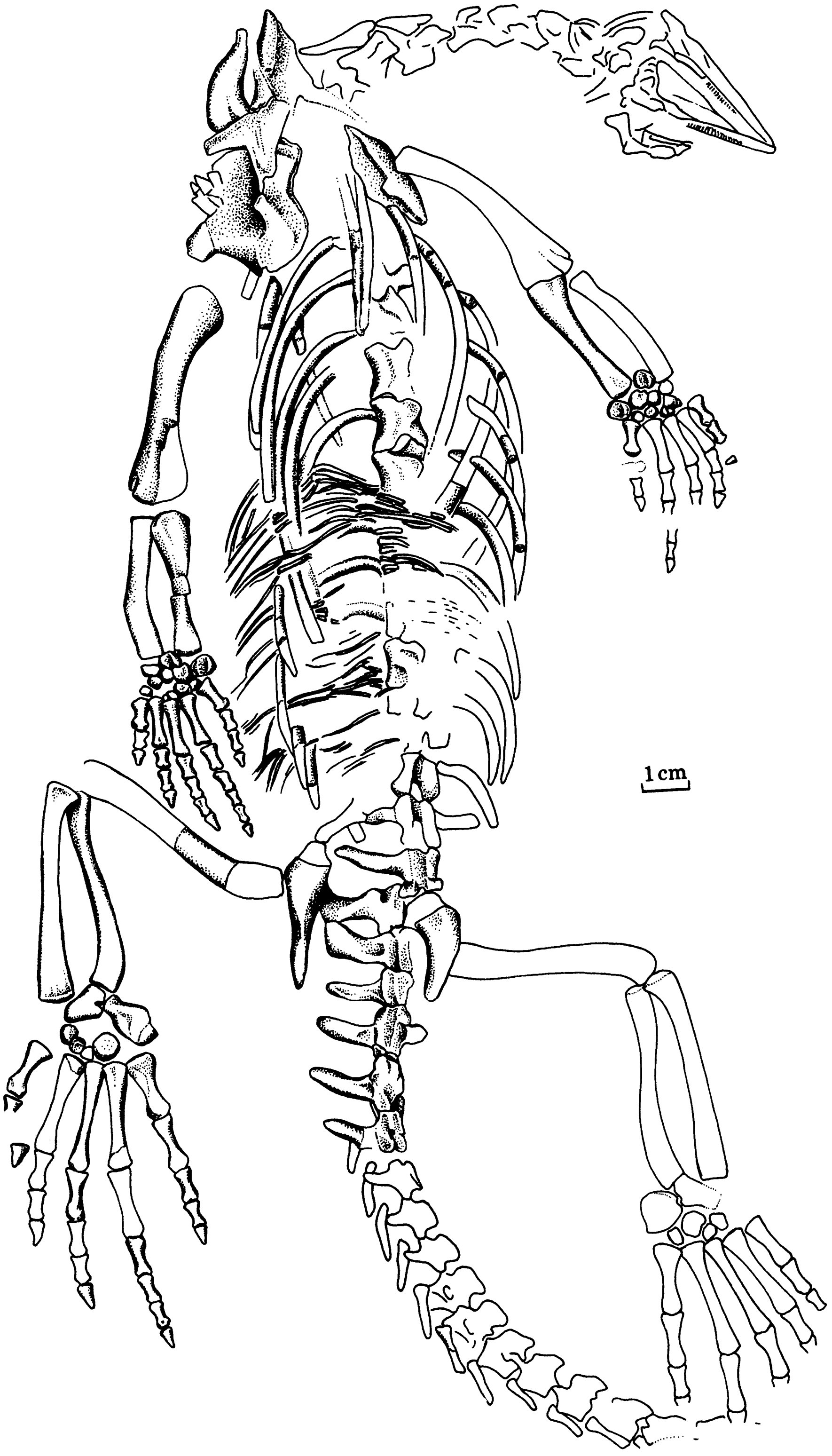


FIGURE 10. Type of *Claudiosaurus germaini*; drawing based on specimen with preserved bone shown in relief.

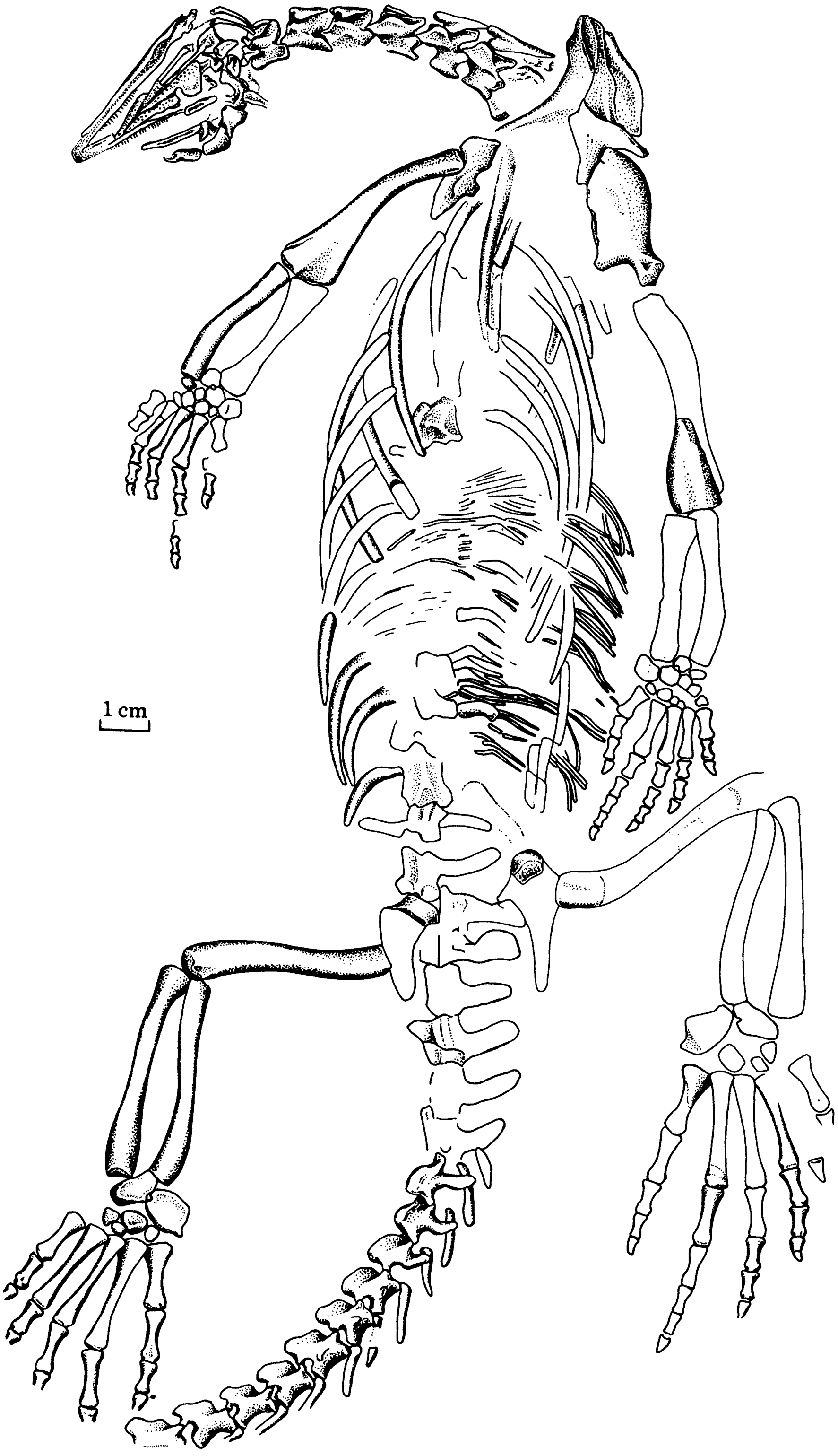


Figure 11. Type of *Claudiosaurus germaini*; drawing based on latex cast of specimen, with bones represented as natural moulds shown in relief.

from the valley of the Sakamena River, in the vicinity of Mount Eliva, some 50 km southwest of the Leoposa locality (Piveteau 1926; Carroll 1978). No remains from these areas can be assigned to *Claudiosaurus* and no other vertebrates accompany that genus at Leoposa. The single specimen attributed to *Claudiosaurus* collected from Sakamaniga has on the same block an elongate rib of the type characteristic of the gliding genus *Daedalosaurus* (Carroll 1978).

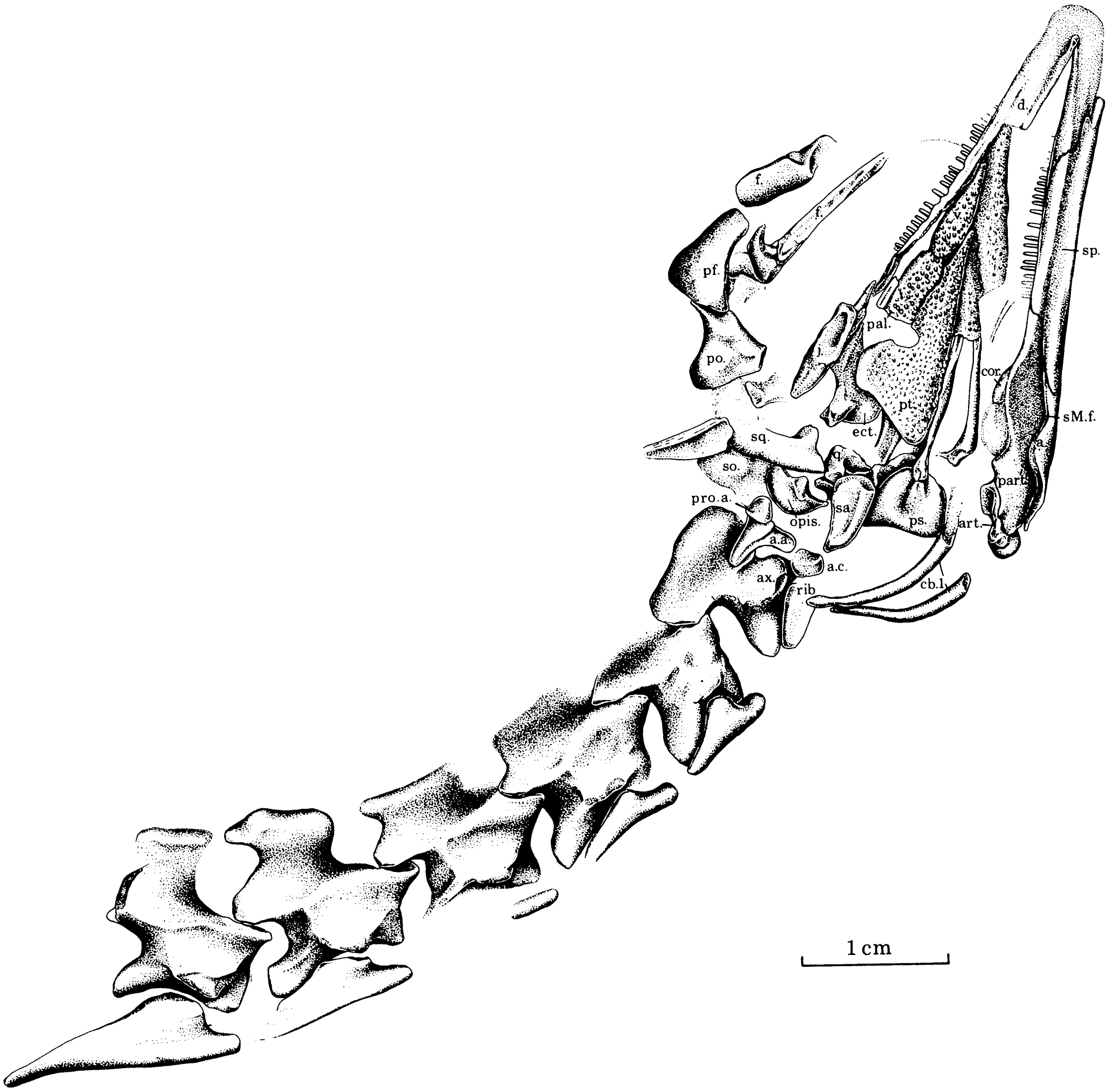
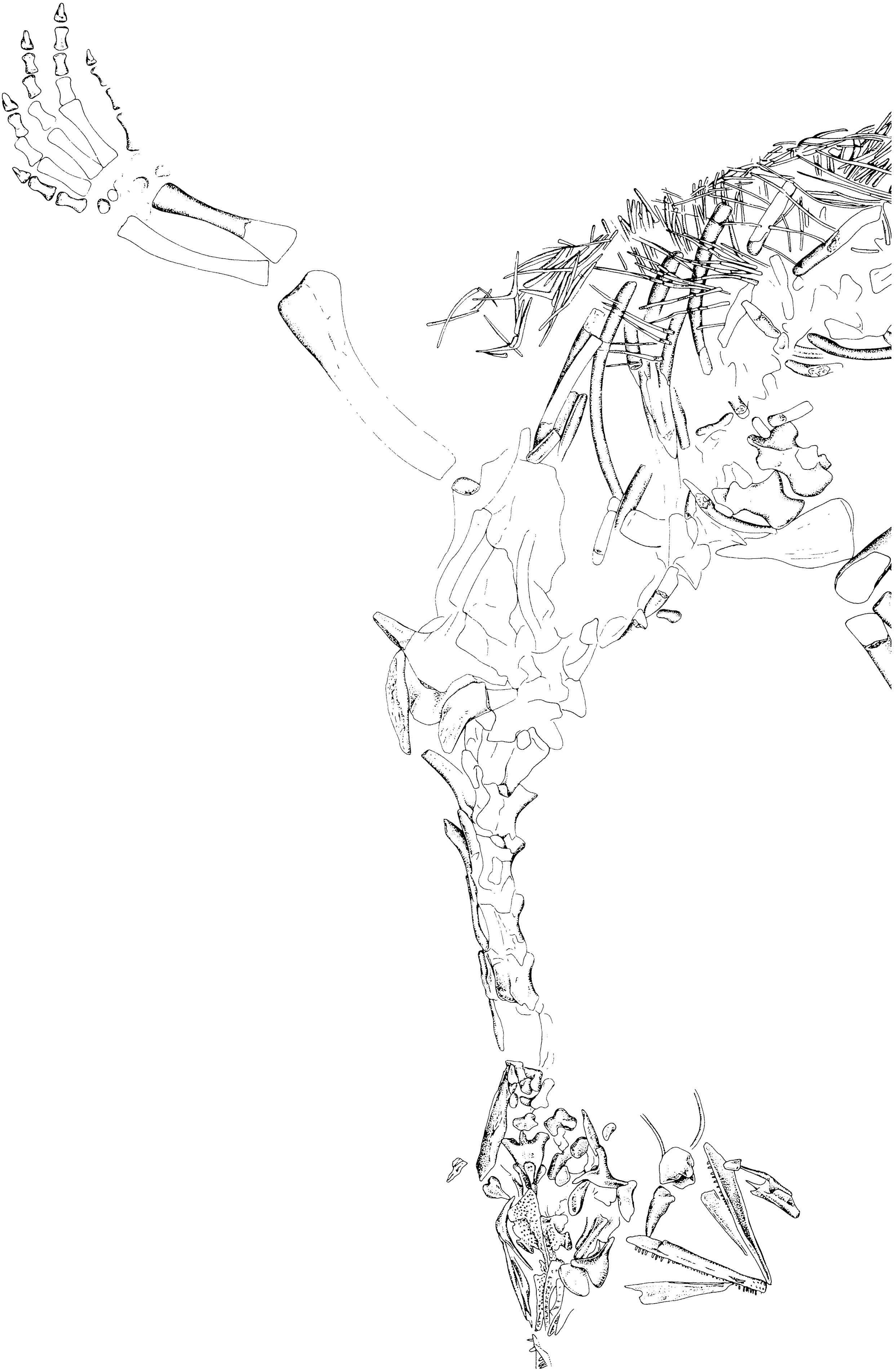


FIGURE 12. Type of *Claudiosaurus germaini*; skull, primarily shown in ventral view, drawn from latex cast (magn. × 2).

The specimens from Benenitra that are here identified as *Claudiosaurus* include elements that were previously attributed to *Tangasaurus* by Piveteau. His identification is understandable since the elements do resemble in a general way those that he recognized as *Tangasaurus* from near Mount Eliva. It is only with the discovery of complete, well preserved material of *Claudiosaurus* that these isolated bones can be identified.



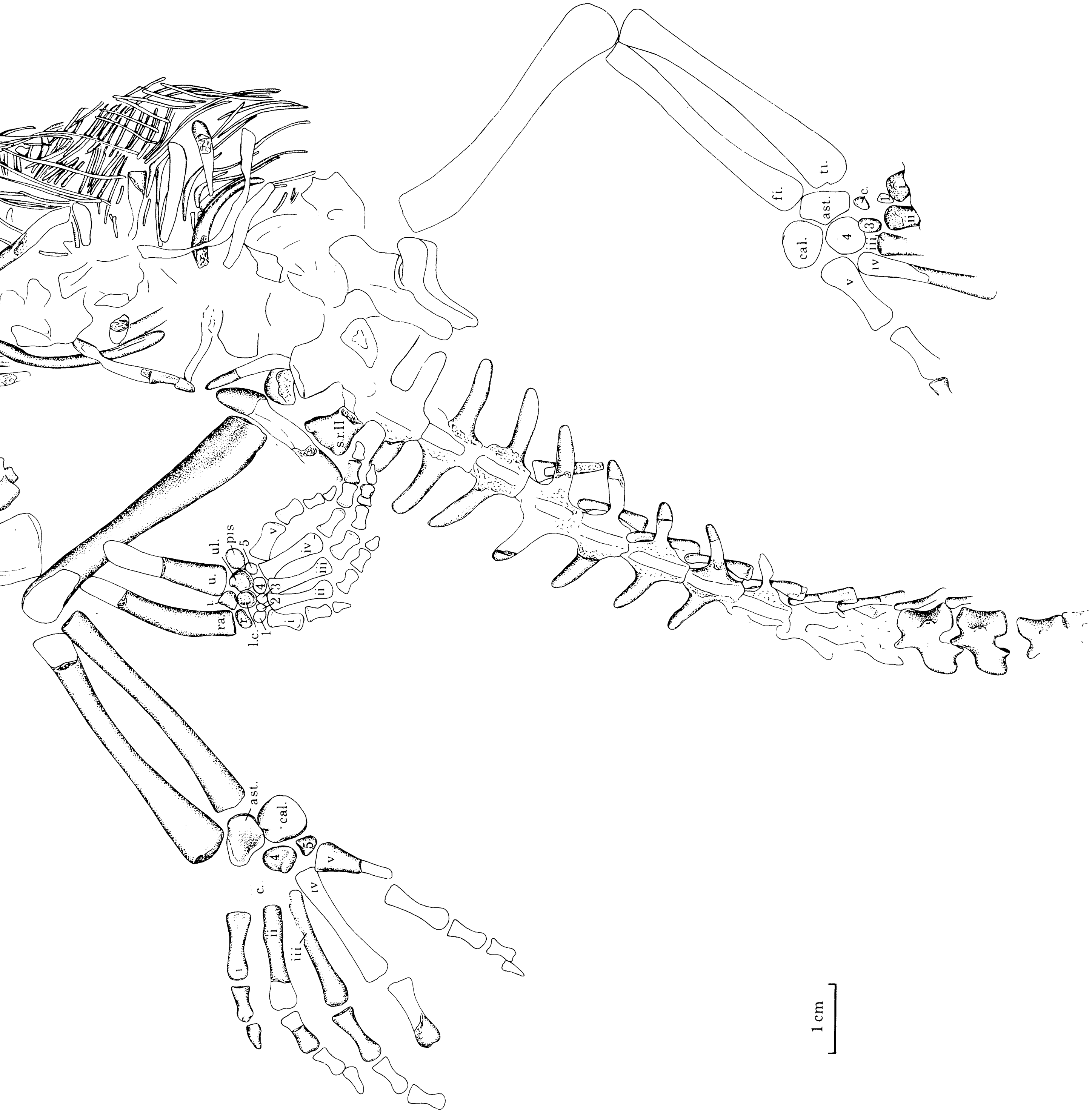
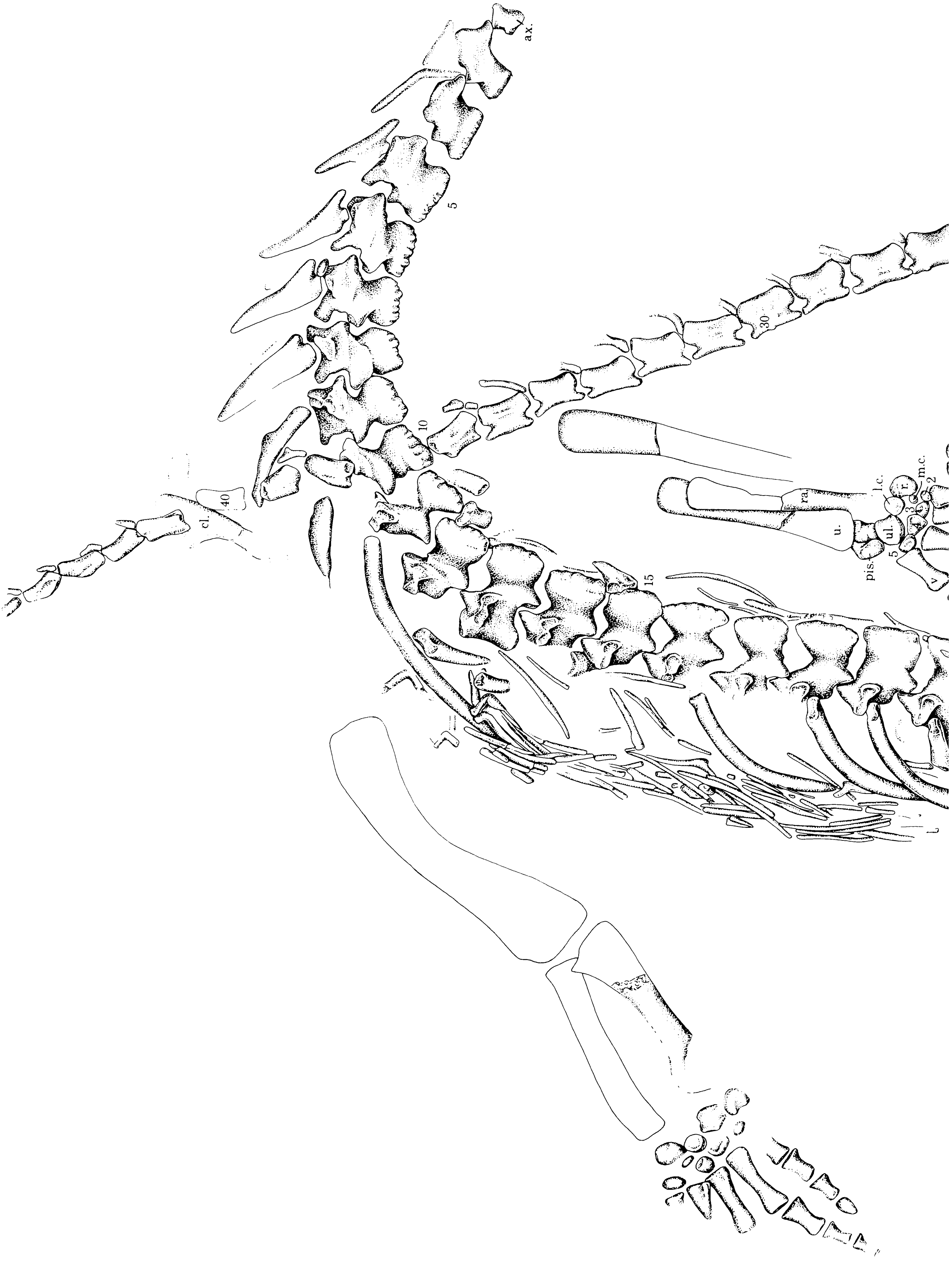


FIGURE 13. *Claudiosaurus germaini*; C.G. 20/6, drawing based on silicon cast.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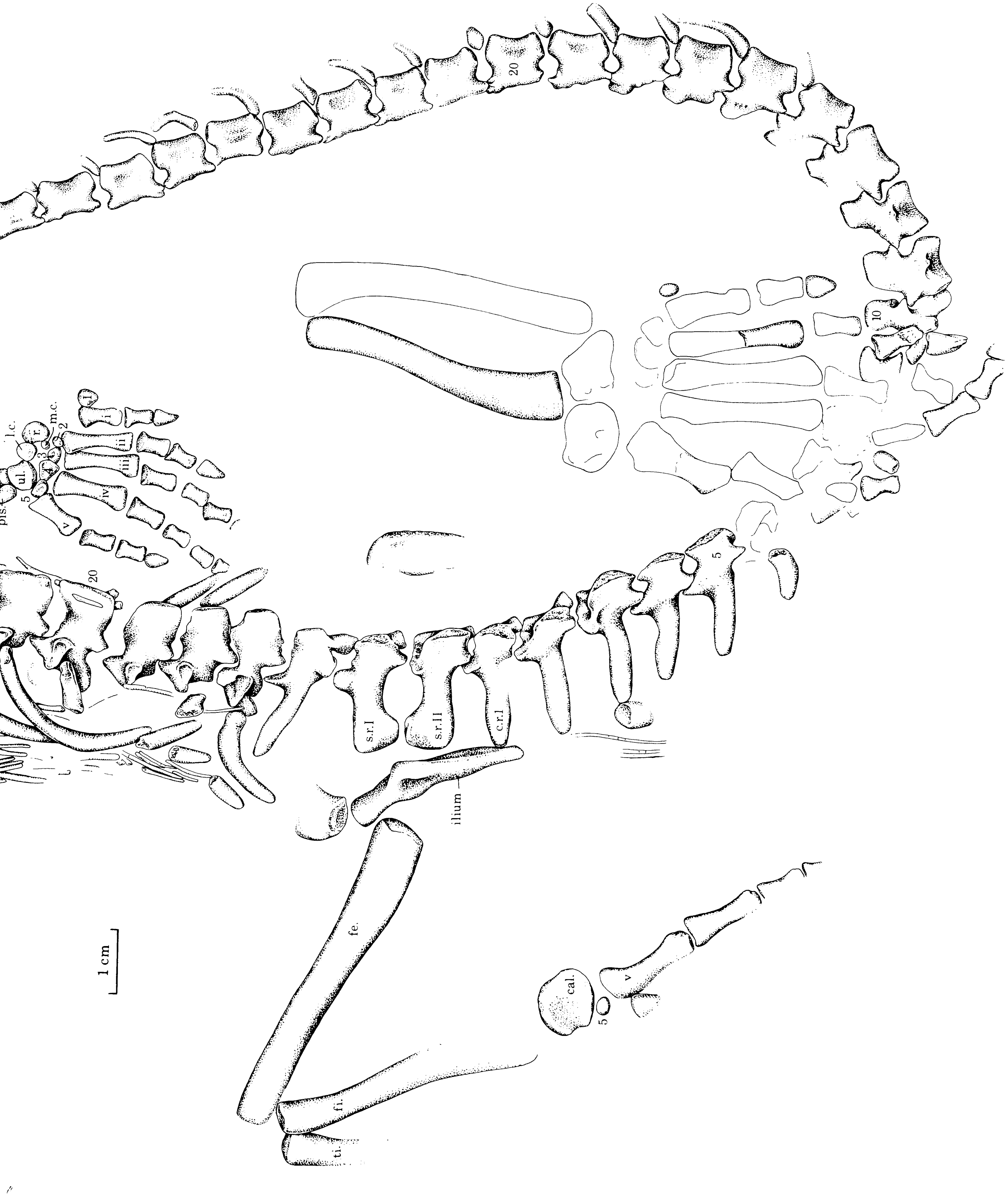


FIGURE 16. *Claudiosaurus germaini*; C.G. 20/4; nearly complete skeleton, lacking skull.

Description of material

The complete skeletons of *Claudiosaurus* show an essentially lizard-shaped body with a long neck and disproportionately small head. Compared with most small reptiles of this time the hands are short and broad.

Axial skeleton

Information on the cranial anatomy of *Claudiosaurus* is supplied from the following specimens: the type, showing the palate and some elements of the skull roof; C.G. 20/6, almost complete skull exposed in dorsal and ventral views in counterpart blocks; C.G. 20/10, extremely badly weathered skull, only the disarticulated premaxillae have been drawn; C.G. 20/18, scattered cranial elements associated with the manus.

In contrast with the generally closely integrated postcranial complexes, such as the carpals and tarsals, the skull is very badly disarticulated in the one specimen in which most of the elements are preserved. All have remained within a small area, but their orientation may be far from normal. The individual elements are generally well preserved and exposed, however, so that they can be reassembled with little likelihood of serious error. From the restoration, the skull dimensions are as follows: length, 33.5 mm; width at the quadrate, 25 mm; height from the base of the quadrate to the top of the skull, 13 mm. In dorsal view, the proportions of the skull roof resemble those of *Youngina* (figure 9). There are large upper temporal openings, a large parietal fenestra and large orbits. The antorbital region is somewhat shorter. Unlike the condition in *Youngina*, the parietal is deeply sculptured. The frontal, postfrontal and postorbital are also roughened and irregularly pitted. The remaining bones of the skull are generally smooth, except for the premaxilla, which bears a deep pit just lateral to the midline. Where seen in cross section, the bones of the skull table appear very thick. It is probable that the deep sculpturing indicates an intimate association with the dermus that would have assisted in holding the bones of the skull table together to provide additional stability in the absence of the lower temporal bar. As in *Youngina*, but in contrast with the primitive diapsids *Petrolacosaurus* and *Araeoscelis*, flanges of the parietal extend ventrally, medial to the temporal opening, to provide origin for the adductor jaw musculature.

The posterior, occipital margin of the parietal has recesses that may have accommodated postparietals and tabulars, although these bones cannot be specifically identified among the smaller elements visible behind the skull. The tip of the posterolateral extension of the parietal is recessed to receive the dorsal margin of the squamosal. By analogy with *Youngina*, the lateral portion of the occipital surface of the parietal may have been covered by a relatively large supratemporal. In view of the otherwise weak attachment of the squamosal with the skull roof, it would not be surprising for the supratemporal to have been retained as an overlapping unit. A bone of the appropriate size and shape is present at the back of the skull of C.G. 20/6.

The postfrontal is relatively larger than in *Youngina* and bulges upwards, as if to follow the contours of a very large eyeball. The postorbital is thick, presumably to help compensate for the absence of a lower temporal bar; it shows extensive but smooth areas of overlap with the postfrontal and jugal, but the area of overlap with the squamosal is short. The prefrontals are large and extend nearly to the area of the external nares.

The anterior end of the skull is not well known. The exact area of attachment of the frontals with the nasals is not shown, but the nasals appear to be shorter than in *Youngina*, to judge by the preserved extent of the frontals. The lateral margins of the nasal bones are not evident and so the posterior configuration of the external nares is speculative.

The premaxillae are present in C.G.20/10 but disarticulated from the remainder of the skull and incompletely exposed. The two bones have remained attached at the midline, although a suture between them is clearly visible. The most striking feature is the presence of a very long, narrow nasal process. The maxillary or palatal portion is also considerably longer than in contemporary eosuchians. Only a few teeth are exposed, but there is room for 14 or 15, to judge by the size of those visible. They are little if at all procumbent. The bones are marked by one large pit on either side of the midline. The extent of the maxillary ramus of the bone suggests an elongate external nares, but the opening remains essentially terminal, rather than showing evidence of the posterior migration common to secondarily aquatic tetrapods. Lacrimals are restored, but their exact configuration is difficult to establish. This area of the skull is preserved on both sides in the counterpart blocks, but the outlines of the bones are not consistent. The lacrimal appears very thin and there may have been considerable overlap with the prefrontal and maxilla. It probably did not enter the margin of the orbit.

Functionally and taxonomically, the cheek region is one of the most important parts of the skull. There is no evidence of a lower temporal bar. The jugal is well displayed in C.G. 20/6 and appears as a disarticulated element in C.G. 20/18; it is present but not well exposed in the type. It is a simple element in the shape of an open L, with no trace of a posterior process. The bone is thick and cylindrical in the area of the angle between the anterior and dorsal portions. It thins somewhat dorsally, where it is overlapped by the postorbital, and anteriorly, where it is extensively overlapped by the maxilla. Medially, the bone is marked by several linear grooves at the posteroventral angle, which may mark the point of attachment of a ligament extending to the region of the quadrate, such as the maxilloquadrate ligament of lizards. There is no evidence laterally of any area for attachment to the quadratojugal. The squamosal is present in both the type and C.G. 20/6, but disarticulated from its natural position. In C.G. 20/6, the right squamosal is visible in both external and internal views, between the rami of the lower jaws. The bone resembles that of *Youngina* in general, with a wide dorsal portion for attachment to both postorbital and parietal, together forming the posterior and lateral margin of the upper temporal opening. The bone tapers somewhat ventrally, where it is exposed in both occipital and lateral views. The lower portion of the lateral surface appears to extend anteriorly in a thin sheet over the surface of the quadrate. On the left side in C.G. 20/6, where the bone is more or less in its natural position, there appears to be a small, very thin overlapping element near the base of the squamosal, which, if truly a separate ossification, can be identified as the quadratojugal. This bone certainly does not extend anteriorly beyond the margin of the squamosal and could not be considered to form any part of the lower temporal bar.

Both quadrates, with at least portions of both the medial and lateral surfaces, are exposed in C.G. 20/6, the left more or less in its natural position and the right between the rami of the lower jaws. It is not greatly different from that of *Captorhinus* (Fox & Bowman 1966; fig. 13), with a thin dorsal process and an articulating surface expanded at right angles to it. The posterior margin is essentially vertical and strongly marked by grooves and ridges indicative of a solid zone of attachment to the squamosal. Presumably there was considerable intervening connective tissue or cartilage since the medial surface of the squamosal is essentially smooth. Laterally, this surface is indented to form the margin of the quadrate foramen. The

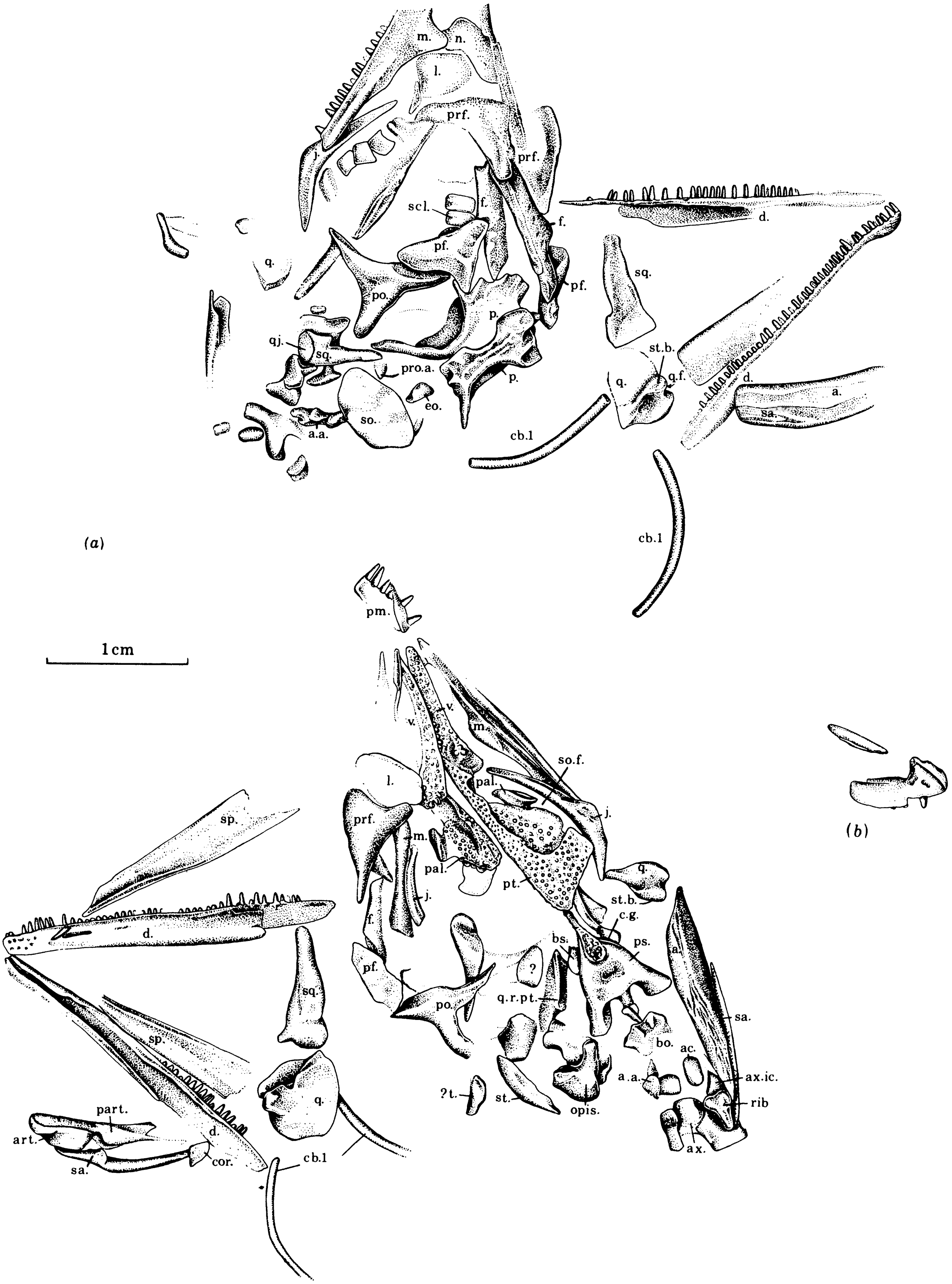


Figure 14. *Claudiosaurus germaini.* (*a*) C.G. 20/6; details of skull drawn from casts of counterpart. (*b*) C.G. 20/10 premaxillae.

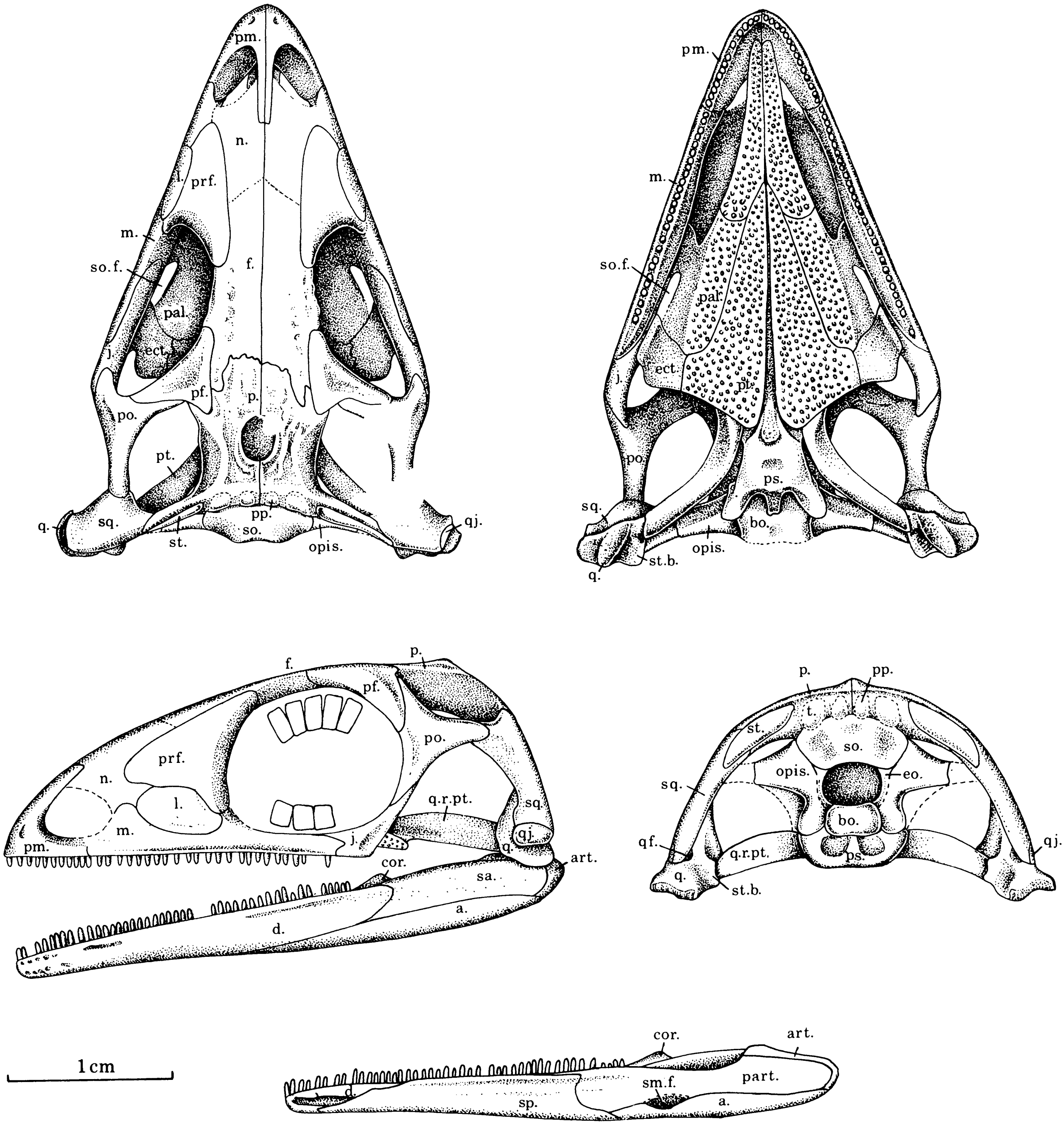


FIGURE 15. Reconstruction of the skull and lower jaw of *Claudiosaurus germaini*, based on the type and G.C. 20/6; skull in dorsal, ventral, lateral and occipital views; lower jaw in medial view (magn. × 2.7).

posterior surface of the squamosal differs from that of *Youngina*, in which the posterior margin of the quadrate is exposed, and from that in early lizards, in which it is embayed for the attachment of a tympanum. Dorsally and anteriorly, the margin of the quadrate is unfinished, suggesting extension in cartilage.

The articulating surface appears to have a configuration very similar to that of *Captorhinus*. (Comparison is made with that genus, although very distinct in time and taxonomic position, because of the availability of well preserved disarticulated elements. This is not to imply that it differs significantly from that of contemporary eosuchians.)

Medially, the quadrate differs from that of *Captorhinus* in lacking a stapedial recess. Instead, there is a raised area, ending bluntly, to which the stapes (otherwise unrepresented) or its cartilagenous extension might have articulated. Anteriorly, the boss is supported by a narrow buttress which extends down toward a narrow triangular area for attachment to the quadrate ramus of the pterygoid.

The palate is well exposed in the type and in C.G. 20/6. The only element whose outline is not quite definitely established is the ectopterygoid. Unlike the palate of eosuchians such as *Youngina* and eosuchian derivatives such as *Heleosaurus* and early lizards, the paired bones are covered by a nearly uniform shagreen of small denticles. There is no evidence of the pattern of radiating lines of denticles, as in other contemporary reptiles. The pterygoids extend nearly, if not completely, to the midline. The cultriform process of the parasphenoid, raised above the posterior portion of the bone, may be visible between them, but there are no open interpterygoid vacuities. The palatine has a narrow zone of contact with the maxilla, behind which is a narrow suborbital fenestra. In general, the plate has expanded to cover nearly all the space available to it between the tooth rows, except for the large internal nares and the adductor fossae. The vomers are narrow bones, posteriorly continuous with the palatines and separated medially by the pterygoids. Their entire surface is covered with denticles. The palatine is covered with denticles except on the lateral margins, including the process that articulated with the maxilla. In the type a poorly preserved bone partially covered by the back of the pterygoid may be identified as the ectopterygoid. It lacks denticles. The bone apparently articulated primarily, if not entirely, with the jugal laterally rather than with the maxilla. The pterygoid has a large triangular exposure on the palatal surface, completely uniformly covered with denticles. The margin bordering the adductor fenestra is not specialized as a ventrally directed transverse flange, but is in the same plane as the remainder of the palate. Unlike the condition in eosuchians or captorhinomorphs, the denticles on this margin are not enlarged. The quadrate ramus of the pterygoid extends posteriorly as a narrow strip of bone. The surface for articulation with the basicranial process of the braincase lies at the base of the quadrate ramus, above the medially extending palatal portion of the bone. It is unlikely that the epipterygoid (nowhere visible) contributed to this joint, as it did in more primitive reptiles. The premaxilla and maxilla form a broad margin to the palate. No specimen shows the dentition in its entirety, and so an exact tooth count is not possible, but there would have been room for approximately 35 in each maxilla.

The parasphenoid is most completely shown in C.G. 20/6. The long cultriform process is raised above the general palatal surface, to be almost, if not entirely, obscured by the pterygoids ventrally. The basipterygoid processes are directed anteriorly, ventrally and laterally, ending in a vertically oriented articulating surface fitting above the medial palatal extension of the pterygoid. It is doubtful whether there was much movement at this joint.

The bases of the processes are marked by deep grooves for the passage of the carotid arteries. Between the basipterygoid processes is a small raised rugose area of the parasphenoid. More posterior is a small hollow in the surface of the bone. The parasphenoid is strongly demarcated from the basioccipital, incompletely exposed in C.G. 20/6. The plate of the parasphenoid is below the level of the occipital condyle and its posterior surface is recessed to receive ventral occipital musculature.

Fragments of the opisthotic are present in both the type and C.G. 20/6. The base appears bulbous, narrowing to a short process distally which did not reach the cheek. An anterior groove may mark the position of the proötic, otherwise not represented in this material. There is a large plate-like supraoccipital, similar to that of *Youngina*. A bone that appears to be the dorsal end of the exoccipital is exposed in C.G. 20/6 between the parietal and supraoccipital. It has a broad dorsal surface for articulation with the supraoccipital, but forms a narrow margin to the foramen magnum. The ventral portion of the exoccipital is not exposed, and so neither the nature of its contribution to the occipital condyle, nor its specific relationship with the opisthotic, can be determined.

The lower jaw is well exposed both in the type and in C.G. 20/6. It is long and narrow, expanding only slightly in the area of the angular. The dentary forms a thin sheath around the Meckelian canal. Laterally, it is grooved beneath the tooth tow and pitted lateral to the symphysis. None of the jaws show the entire dentition, but there was space for approximately 50 narrow, sharply tipped teeth, most of which are in place. None are procumbent. They are slightly overlapped laterally by the dentary at their bases. The teeth are set in a shallow trough, but it cannot be said that the medial surface is covered with bone as might be expected in a group that develops a thecodont dentition. A few teeth show resorption pits, suggesting a replacement pattern as in most primitive reptiles. There is a long thin splenial extending dorsally to the base of the tooth row. The Meckelian canal is open anterior to it. The prearticular forms a broad covering on the medial surface of the Meckelian fossa. The angular, which extends more than half the length of the jaw, is indented for the sub-Meckelian fossa, but the margin of the opening formed by the prearticular is obscured. The posterior dorsal surface of the surangular is expanded as if the bone articulated with the lateral surface of the quadrate. The articular has a broad longitudinal trough for articulation with the quadrate. There is little, if any, area that could be termed a retroarticular process. Nothosaurs typically have a prominent retroarticular process, although it is not well developed in *Nothosaurus*. A small triangular coronoid extends above the margin of the jaw behind the tooth row. Limited propalineal movement might be possible.

From the articulated type and C.G. 20/4, a count of 24 presacral vertebrae can be established. From their position anterior to the shoulder girdle and the nature of their ribs, the first eight may be termed cervicals. There are two vertebrae bearing typical sacral ribs. The rib of the next succeeding vertebra extends laterally to the end of the ilium. It probably helped support the girdle on the column, in contrast with the condition in *Thadeosaurus* and other eosuchians. Otherwise, this vertebra resembles those more posterior in position and will be termed a caudal for the sake of enumerating the vertebrae. In C.G. 20/4, the tail continues across the margin of the block, with 45 vertebrae represented. This was presumably near the end of the tail, for the haemal arches are quite short, but it may have been somewhat longer. *Thadeosaurus* has at least 47 caudal vertebrae and another eosuchian, *Kenyasaurus*, has 56. As restored the tail is 39 cm in length, with a snout–vent length of approximately 26 cm. If only the 45 caudal vertebrae in common between *Thadeosaurus* and *Claudeosaurus* are counted, the relative length of the tail is just slightly shorter in the latter genus.

The type shows the atlas–axis complex in lateral view. The pattern resembles that of more primitive reptiles, with a small, oblong proatlas, presumably articulating with the exoccipital, paired atlas arch and a much larger axis arch, fully integrated with its centrum. The configuration of the atlas intercentrum and pleurocentrum is not clearly shown. Presumably they had a pattern similar to that of *Heleosaurus* (Carroll 1976*c*), with large intercentra anterior to both the atlas and the axis pleurocentra and a small, more or less cylindrical atlas pleuro-

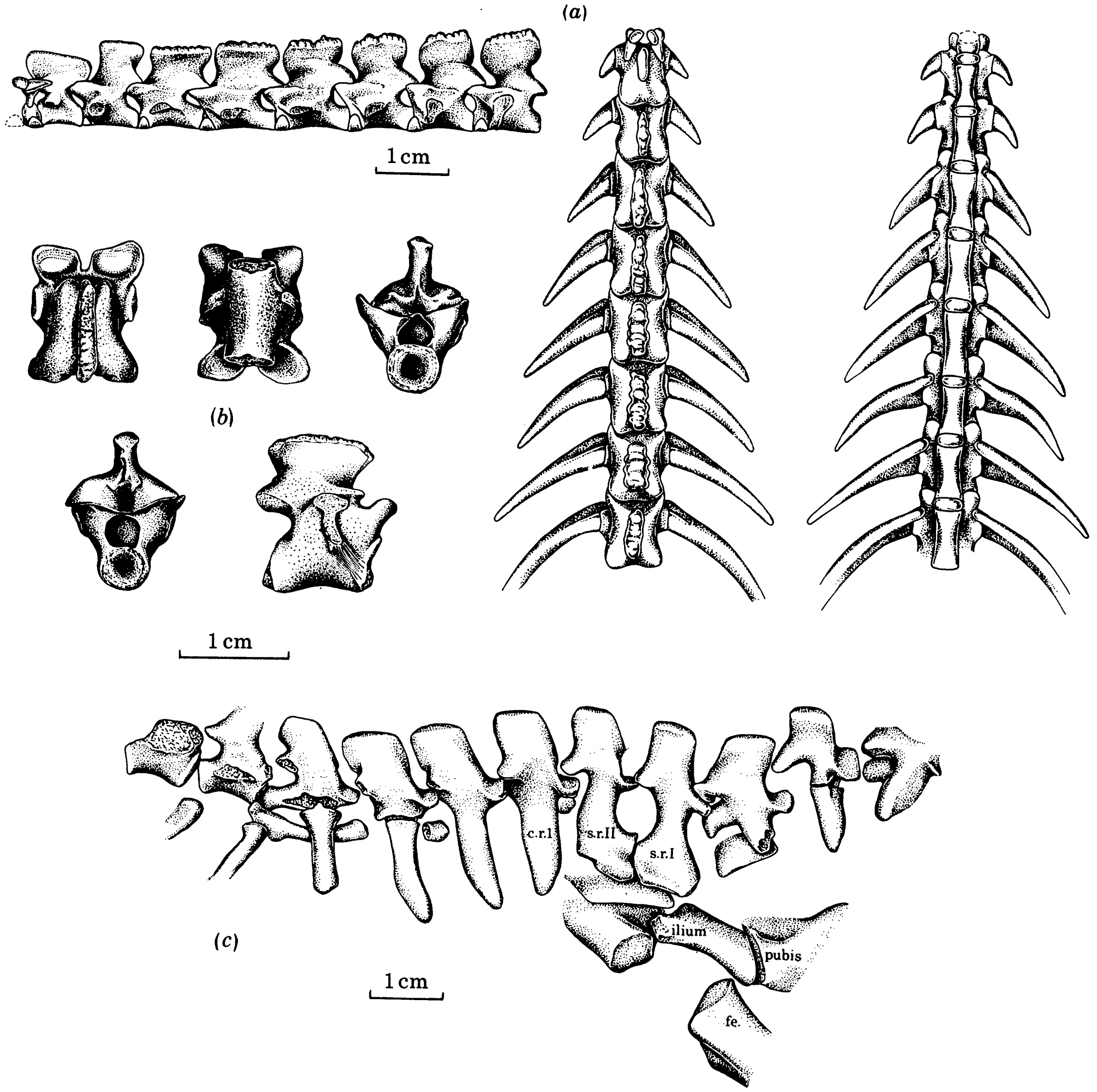


FIGURE 17. *Claudiosaurus germaini*. (*a*) Reconstruction of the cervical vertebrae and ribs in lateral, dorsal and ventral views, based on the type and C.G. 20/4 (natural size). (*b*) Trunk vertebra (approximately the 16th) P.M. 1909–3–26, in dorsal, ventral, anterior, posterior and lateral views; specimen from Benenitra; note growth rings on zygapophyses (magn. × 1.5). (*c*) Posterior trunk, sacral and proximal caudal vertebrae of one of the largest specimens, C.G. 20/9; note increase in the size of the transverse process of the first caudal vertebrae relative to that of the second, compared with the condition in C.G. 20/4, figure 16.

centrum loosely attached to the arch. The spine of the axis arch is distinctive in being, in lateral view, low and rounded, slightly higher anteriorly than posteriorly, in contrast to the expanded squarish pattern of the more posterior cervical vertebrae. It is this shape that allows one to recognize the first preserved cervical in C.G. 20/4 as the axis and so to establish the vertebral count. In the type, the length of the centrum increases from the axis to the 6th cervical, from 0.6 to 0.94 cm. The next is 0.91 cm in length. In C.G. 20/4, in which the more posterior cervicals and adjacent trunk centra are better exposed, the length remains more or less constant from the 7th to the 14th and, to judge by the configuration of the arches, to just anterior to the sacrum, with the last presacral being slightly shorter.

As in the cervical region, the centra of the trunk vertebrae are relatively long and narrow. The width is approximately 50% of the length, compared with approximately 70% in *Thadeosaurus*. The arch, nevertheless, gives a nearly square outline, as seen dorsally, just as in *Thadeosaurus*. The neural spines are strikingly developed in the cervical and trunk regions. Distally, they are expanded anteroposteriorly so that each is in contact with those adjacent to it. The dorsal surface of the spine is expanded laterally as well and marked by rough, irregular transversely oriented grooves and ridges. This may be served for attachment of interspinous ligaments. Such a structure would have made dorsoventral flexure of the trunk very limited in scope. Some spines show longitudinal ridges on their lateral surfaces. The neural spines of the last three presacral vertebrae are not expanded anteroposteriorly or laterally, nor are they rugose.

As in *Thadeosaurus*, the transverse processes of the trunk are short, hardly reaching the level of the zygapophyses, but are slightly longer in the posterior cervicals. From the 2nd to the 7th cervical, the transverse processes have narrow oval to triangular articulating surfaces for attachment of the tubercular heads of the ribs. At the 8th vertebra, the articulating surface begins to expand ventrally and includes a large surface for attachment of the capitulum in the 9th.

Intercentra are present throughout the trunk.

The centra of the two principal sacrals and the first four caudals are as long as the longest trunk centra, after which the length somewhat decreases. From the 11th to the 38th caudal the central length remains essentially constant at 0.81 cm, while the radius decreases from 0.41 to 0.24 cm. The last complete centrum is 0.60 cm in lengh. Posterior to the 38th caudal, the neural arches barely reach the level of the ends of the centra and apparently had no overlap. At the posterior end of the tail, the neural arch remains as a partial cover over the neural tube, but the zygapophyses are gone. Such reduction suggests that very few additional centra had been present. Tiny vestiges of the haemal arch continue to the very end. These are relatively much shorter than the last haemal arches in *Thadeosaurus* and are bent posteriorly rather than being straight. Their appearance closely resembles those of the living caiman.

In the sacral and anterior portion of the caudal region as far back as the 11th vertebra, the spines are long and rectangular, as in the posterior trunk. Subsequently they narrow and shorten. The last of this series that is well preserved is the 16th. From the 17th to the 25th they are not well exposed on any specimen and their shape and extent is not certain. By the 25th, the arch certainly does not extend above the level of the zygapophyses. Presumably the spines were progressively shorter between the 17th and the 24th.

In the anterior vertebrae, to about the level of the loss of the transverse processes, the zygapophyses are only slightly reduced from their length in the trunk region. In the cervical and trunk region the angle of the zygapophyses is between 15 and 20°. The zygapophyses in an isolated trunk vertebrae from Benenitra (figure 17) show clearly developed growth lines. The zygapophyses become increasingly sharply angled in the midcaudal region. By the 20th caudal, the anterior zygapophyses appear to be primarily lateral, rather than ventral to the posterior. By the 35th caudal, the arches no longer exceed the length of the centra so that no articulation of the zygapophyses can occur. The arch is further abbreviated posteriorly, so that much of the neural canal is exposed dorsally beyond the 41st caudal. This configuration is reached only at about the 54th caudal in *Kenyasaurus*.

Intercentra are present anterior to the 1st and 2nd caudals. Haemal arches are present from the 3rd caudal to the end of the series as preserved. The more anterior are $1\frac{1}{2}$ times the length of the centra, from about the 30th they are reduced to about one central length and at the very end of the tail they are approximately one-half the length of the centra. The centra are deeply notched ventrally to form a triangular gap for the cross piece of the haemal arch and adjacent areas for their articulation. In contrast with in *Thadeosaurus*, the caudal centra are rounded ventrally without a well defined ridge and with but a slight trace of a median groove on caudals 5, 6 and 7. There is no evidence of caudal autotomy.

The most anterior of the fused caudal ribs extends laterally to the ilium. It is not expanded distally, but probably gave some support to the girdle. Among eosuchians, the only group to show the incorporation of more than two pairs of sacral ribs are the champosaurs. In that group there are only two pairs in a juvenile specimen and a third pair is fully integrated into the sacrum in adults (Erickson 1972). In *Claudiosaurus*, the 'third sacral' increases in size, relative to the next transverse process, in larger individuals (figure 17). The transverse process on the second caudal is even longer than that of the first. Those more posterior in position show a gradual reduction in length. There is considerable variation in the position of the last caudal to bear a transverse process. It is the 11th in the type, the 12th in C.G. 20/4, and the 13th in the juvenile specimen. The last vertebra bearing a process in *Thadeosaurus* is the 19th.

Claudiosaurus shows no skeletal features of the tail that are obviously related to an aquatic way of life. Among small modern alligators, however, there is also no obvious skeletal features that indicate support of what has been demonstrated (Manter 1940) to be the primary element in aquatic propulsion. Although most sauropterygians have a short tail, a specimen of *Pachypleurosaurus* from Harvard, MCZ 1057, has 45 caudal vertebrae and the tail is 90% as long as the snout–vent length.

Ribs are present on all presacral vertebrae except, apparently, the atlas. The two heads are only clearly separate in the cervical region. More posteriorly, the two articulating surfaces are contiguous. The rib on the axis is a small triangular plate, lying alongside the centrum. Dorsally the rib articulates by a small facet to the transverse process and ventrally to the lower anterior margin of the centrum. The rib of the 3rd vertebra is approximately as long as the centrum, and the heads are more clearly separated, leaving between them a gap for the vertebral artery. The capitular head is slightly anterior to the tubercular. The shaft of the rib, still essentially triangular, extends primarily horizontally, at an uncertain angle from the vertebra. From the 4th to the 8th, the capitulum becomes further anterior in position, at the extremity of a strong ventral axis of the rib. Posteriorly, the ventral margin is sharply ridged. The tubercular and capitular articulating surfaces of the vertebrae are here separated by a sharp groove. The ribs curve posteriorly from a transverse plane and slightly ventral from the horizontal. The 8th rib is a little more than twice the length of the centrum.

The pattern shifts markedly with the rib on the 9th vertebra. The heads of the ribs, although still distinct in their angle with the end of the shaft, are now confluent. Probably the 9th and certainly the 10th are much longer than those more anterior in position, exceeding the length of four trunk centra. From the configuration of the proximal end of the shaft and their orientation in the specimens, these ribs appear to extend not ventrally like the other trunk ribs but posterolaterally in the manner of the posterior cervicals. If this was actually so, they must have passed beneath the more posterior ribs. Two pairs of ribs in the modern lizard *Varanus* (the 7th and 8th) have this orientation, but are not so long. The next nine ribs are of approximately the same length and oriented ventrally. The ends are flat and were presumably continued in cartilage, connecting them with the sternum. The lengths of the last five ribs rapidly shorten. The last two end bluntly. The last trunk rib, like that of *Thadeosaurus*, is fused, with only a trace of suture, to the vertebra. The shaft is straight and extends slightly anterior and ventrally. In the last three ribs, the dorsal margin of the articulating surface faces about 30° from the transverse plane.

The two pairs of principal sacral ribs are fused to the vertebrae and extend laterally at right angles to the trunk and ventrally at about a 35° angle from the horizontal. The distal end of the more anterior is expanded posteriorly and that of the 2nd anteriorly. Distally they are closely integrated, with the 2nd fitting into a depression on the posterior distal margin of the 1st. The ends are thickened, but not downturned. In general they fit the pattern common to lizards. There are no free ribs in the tail.

The ribs are not pachyostotic. All are long and slender except for the last three or four in the trunk. In 1910–33–1a, a number of ribs were broken across, both longitudinally and transversely, when the block was originally opened. They are hollow in the middle, filled with crystalline calcite. The cortex is heavy laminar bone. In these features the ribs resemble those of other terrestrial eosuchians, in contrast with those of both champosaurs and nothosaurs.

Appendicular skeleton

The dermal shoulder girdle of *Claudiosaurus* is basically similar to that of *Thadeosaurus* and somewhat better exposed in the available specimens. The interclavicle has a very long stem, but an abbreviated anterior plate, anteriorly in articulation with the narrow, faintly sculptured plates of the clavicles. The narrow, pointed clavicular stems are not fully exposed. They cover the anterior margin of the scapulocoracoid, but do not reach its top. The angle between the blade and the stem is a little more than 130°, as in primitive lizards, following the curvature of the endochondral units.

Basically, the scapulocoracoid resembles that of *Thadeosaurus*. The most significant difference is in the position of the glenoid relative to the anteroposterior extent of the bone. The anterior margin is anterior to the middle of the bone in *Thadeosaurus*, and well posterior to the middle in *Claudiosaurus*. The distance from the anterior margin of the glenoid to the posterior margin of the scapulocoracoid in *Thadeosaurus* is 55% of the total length; in *Claudiosaurus*, it is 40%. The length of the glenoid in the two genera is essentially the same: 23% of the total length of the bone in *Claudiosaurus* and 26% in *Thadeosaurus*.

The configuration of the glenoid resembles that of *Thadiosaurus*, including the possibility of considerable ventral movement of the humerus and narrowing of the glenoid anterior. The coracoid foramen is 2.7 mm in diameter in *Claudiosaurus*, compared with 1.75 mm in *Thadeosaurus*, relative to a length of the scapulocoracoid in the two genera of 35 and 27 mm respectively.

The coracoid foramen shows no evidence presaging the great size of this opening in nothosaurs and plesiosaurs. An excellently preserved scapulocoracoid from Benenitra is exposed in medial view (figure 18). It shows a large infrascapular fossa of primitive configuration, into which would have opened the coracoid foramen. Perhaps the most significant feature is the presence of growth lines along the anterior and dorsal margins of the scapula surface. These are cited by Ricqlès (1974) as a feature indicative of aquatic reptiles, and are conspicuous in *Mesosaurus*.

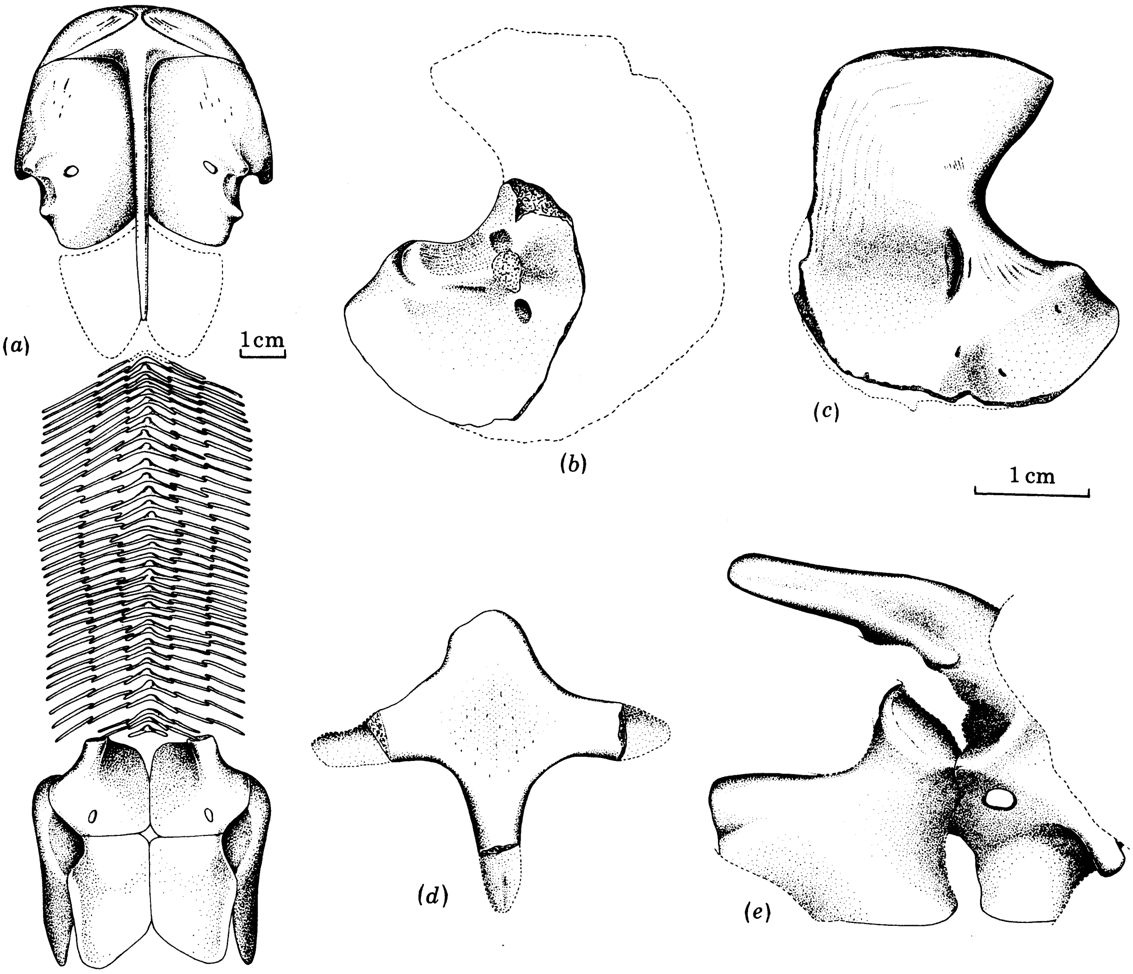


FIGURE 18. *Claudiosaurus germaini*. (*a*) Reconstruction of the girdles and ventral scales in ventral view, composite. (*b*) P.M. 1909–3–22 scapulocoracoid in lateral view. (*c*) P.M. 1909–3–26, scapulocoracoid in medial view, showing growth lines. (*d*) P.M. 1909–3–21, interclavicle in dorsal view, attribution to *Claudiosaurus* not certain. (*e*) P.M. 1909–3–37, right half of pelvic girdle in lateral view. Isolated elements from Benenitra (magn. × 1.5).

Numerous, well preserved specimens reveal no ossified sternum, but the position and extent of an unossified sternum can be readily determined from the anterior extent of the ventral scales which terminate, in all articulated specimens, the length of two trunk centra behind the posterior margin of the coracoid. A sternum of essentially the same proportions as that of *Thadeosaurus* can be restored in this position. A smooth area, suggestive of an impression of the sternum, can be seen in this area in 1910–33–1a. The absence of ossification of the sternum is somewhat surprising, considering its presence in the aquatic eosuchian *Hovasaurus*, also from Madagascar. The presence of a sternum, ossified or not, in possible relatives of the sauropterygians is unexpected. Both nothosaurs and plesiosaurs (figure 31) have a large coracoid, an ossification distinct from the scapula. The two ossifications together form the glenoid and the margin of an enormous coracoid foramen. One may assume that, whatever their specific ancestry, the line leading to nothosaurs and plesiosaurs delayed the coossification of the scapulocoracoid. The position of the suture moves anteriorly relative to its position in more primitive reptiles, so that it passes through the position of the coracoid foramen.

Functionally, one might think of the expanded coracoids, particularly in plesiosaurs, replacing the sternum of primitive eosuchians as an area for the origin of the pectoralis and ceratobranchialis muscles. The posterior shift of the glenoid in *Claudiosaurus* places it near the middle of the anterior–posterior length of the ventral portion of the shoulder girdle (if the unossified sternum is included), so that a symmetrical distribution of pectoral muscles, much as in plesiosaurs (Robinson, J. A. 1975), can be attained. The pattern in *Claudiosaurus*, compared with that of typical eosuchians, indicates a more symmetrical arrangement of pectoral musculature. The ventral length of the scapulocoracoid is roughly the same, relative to the glenoid–acetabular length, in *Thadeosaurus*.

There is no evidence of a cleithrum.

Humeri are in articulation with the skeletons and are also known from isolated elements from Benenitra. From that locality and from Leoposa a range of sizes are preserved from 25 to 52 mm in length. The configuration changes somewhat with growth, as the extremities become ossified. When well ossified, the bone appears somewhat longer and slimmer than that of *Thadiosaurus*, with the distal extremities much less expanded. The anterior margin of the bone is nearly straight. The articulating surfaces are fully ossified, with a clearly defined capitellum and trochlear notch. There is a large oval entepicondylar foramen. The ectepicondylar foramen is open as a dorsal groove except in the most mature specimens. The proximal and distal articulating surfaces are essentially at right angles to one another.

In the very immature specimen C.G. 20/16, neither the proximal nor distal articulating surfaces are ossified, although the entepicondylar foramen is closed distally. The ectepicondylar foramen is expressed as a slit on the anterior edge of the bone.

The ulna and radius resemble in general those of *Thadeosaurus*, although the ulna shows even less development of the olecranon.

The carpus and manus are well displayed in several specimens of *Claudiosaurus*, showing a series of growth stages. In the smallest individual, with the humerus 25 mm long, only five carpals are present: intermedium, radiale, ulnare, lateral centrale and 4th distal carpal. All the other specimens show a full complement of carpals. Although the maximum body size of *Claudiosaurus* is nearly twice that of *Thadeosaurus*, the carpals never achieve such a high degree of ossification. Their margins of contact are poorly defined and there must have retained a considerable amount of cartilage. In view of the high degree of ossification of the ends of the limb bones and other articulating surfaces, it may be assumed that the carpus remained incompletely ossified in mature individuals. This would provide a degree of flexibility that might be advantageous to an aquatic, but not to a fully terrestrial, animal. For the most part, the proportions and interrelationships of the elements are close to the pattern seen in *Thadeosaurus* although the pisiform is relatively larger in the larger individuals. The bone appears to increase its relative size with growth. The pisiform ossifies after the ulnare, inter-

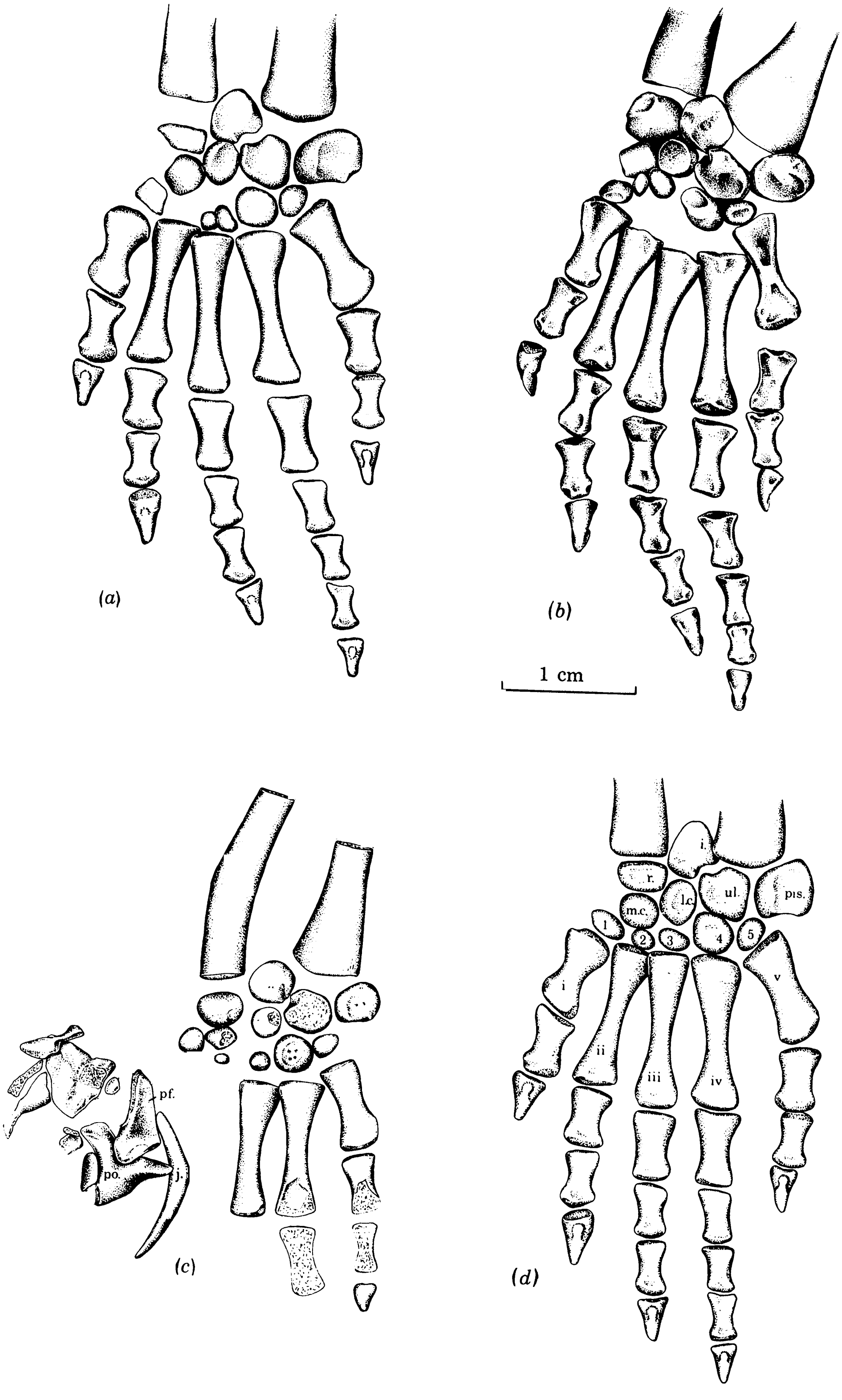


FIGURE 19. *Claudiosaurus germaini*. (*a*) Type, right carpus and manus in ventral view. (*b*) P.M. 1910–33–1a, left carpus and manus in dorsal view. (*c*) C.G. 20/18, right carpus and manus in ventral view and disarticulated skull elements. (*d*) Restoration of right carpus and manus in ventral view, based primarily on the type.

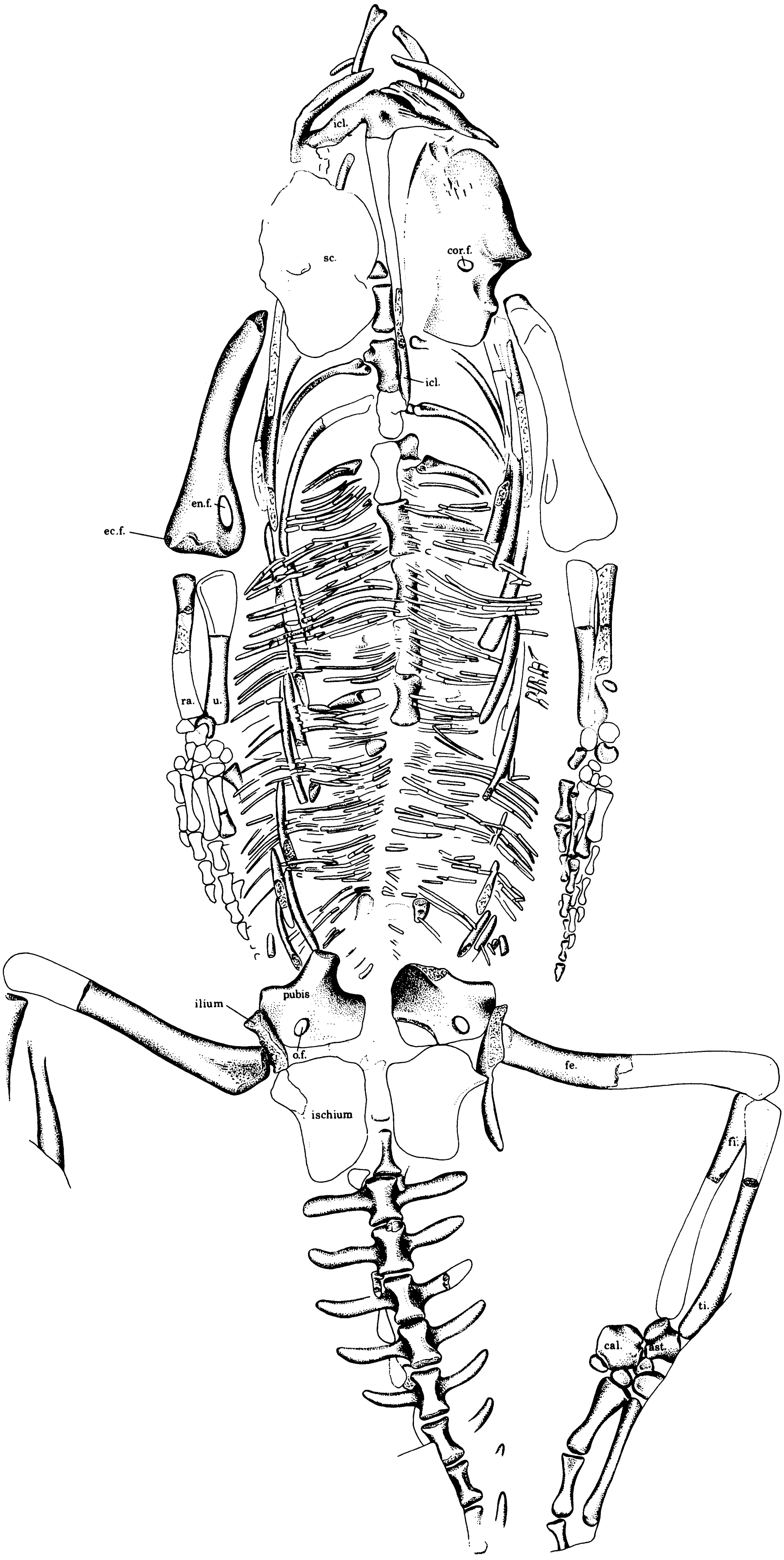


Figure 20. *Claudiosaurus germaini*: C.G. 20/7, ventral view of skeleton; the orientation of the limbs may reflect their position during swimming. (Drawing slightly less than natural size.)

medium and lateral centrale; it remains smaller than the ulnare in medium-sized animals and only exceeds it in the larger individuals.

The medial centrale is oval in shape, rather than being as elongate as in *Thadeosaurus* and, as in *Captorhinus*, is separated from the 4th distal carpal by the lateral centrale. The mature condition is well shown in the type, where the carpus is exposed in ventral view. The proximal ends of the metacarpals overlap in sequence from the 1st to the 5th.

The metacarpals appear to show more significant differences from the pattern of *Thadeosaurus*. In particular, they show a more symmetrical appearance. The 4th was unquestionably the longest and most robust in *Thadeosaurus*. In *Claudiosaurus*, the 3rd is equal to or greater than the 4th in length. The increase in relative size of the 3rd appears increasingly evident with maturity. The 2nd, although not as long as the 4th, approximates it much more closely than in *Thadeosaurus*.

In the juvenile specimen of *Claudiosaurus* exact measurements are impossible due to the large unossified portions of the bones, but measurements of the ossified elements indicate a less striking difference from *Thadeosaurus* than that encountered in the larger, more adult specimens. All the articulating surfaces are much less well defined than in *Thadeosaurus*, even when the bones are close together in the large specimens with little room for intervening cartilage. Movement would be neither enhanced nor specifically limited to a particular direction. Simple hinging seems most probable. It is easy to imagine the elements enclosed in a fleshy paddle, but no strong evidence for such a reconstruction is known.

A more symmetrical pattern of digital length is a feature of aquatic animals using the limbs as paddles (Robinson, J. A. 1975) and is expressed in crocodiles and nothosaurs. The shift in relative length of the metacarpals in *Claudiosaurus* should not be taken as a telling argument for its aquatic nature, however, since it is also observed in modern varanids and iguanids that are almost exclusively terrestrial. Even *Thadeosaurus* shows some incipient development of more symmetrical metacarpals, for, despite the greater overall length of the 4th, its proximal end is so integrated with the row of distal carpals that the distal articulating surface lies proximal to that of the 3rd.

In *Claudiosaurus*, the length of the phalanges decreases progressively from the proximal to distal, with one important exception. The penultimate phalanx of the 3rd (like all the penultimate phalanges in *Thadeosaurus*) is longer than the antepenultimate. Its greater length is particularly striking in comparison with that of the 4th digit. This may be associated with the general trend to increase the length of the 3rd digit relative to the 4th.

The terminal phalanges are much different from those of *Thadeosaurus* in their general configuration as well as their shorter length. Those of *Thadeosaurus* are the typically trenchant, recurved, laterally compressed claws associated with terrestrial carnivores. Those of *Claudiosaurus*, in contrast, are dorsoventrally flattened at the tip, the base forming flattened oval pads. They bear a prominent tubercle at their base for attachment of a flexor tendon.

Both metacarpals and digits are shorter than in *Thadeosaurus*. The 4th metacarpal and the 4th digit measure respectively 39 % and 74 % of the length of the radius in the type of *Claudiosaurus* and 47 % and 84 % in a juvenile. The latter measurements are minimized by the amount of cartilage since these measurements include measurements of the shaft alone. In *Thadeosaurus*, these measurements are 46 % and 120 % in the type. *Claudiosaurus* certainly shows negative allometry in these structures.

The most completely exposed pelvic girdle is P.M. 1909-3-37 from Benenitra (figure 18).

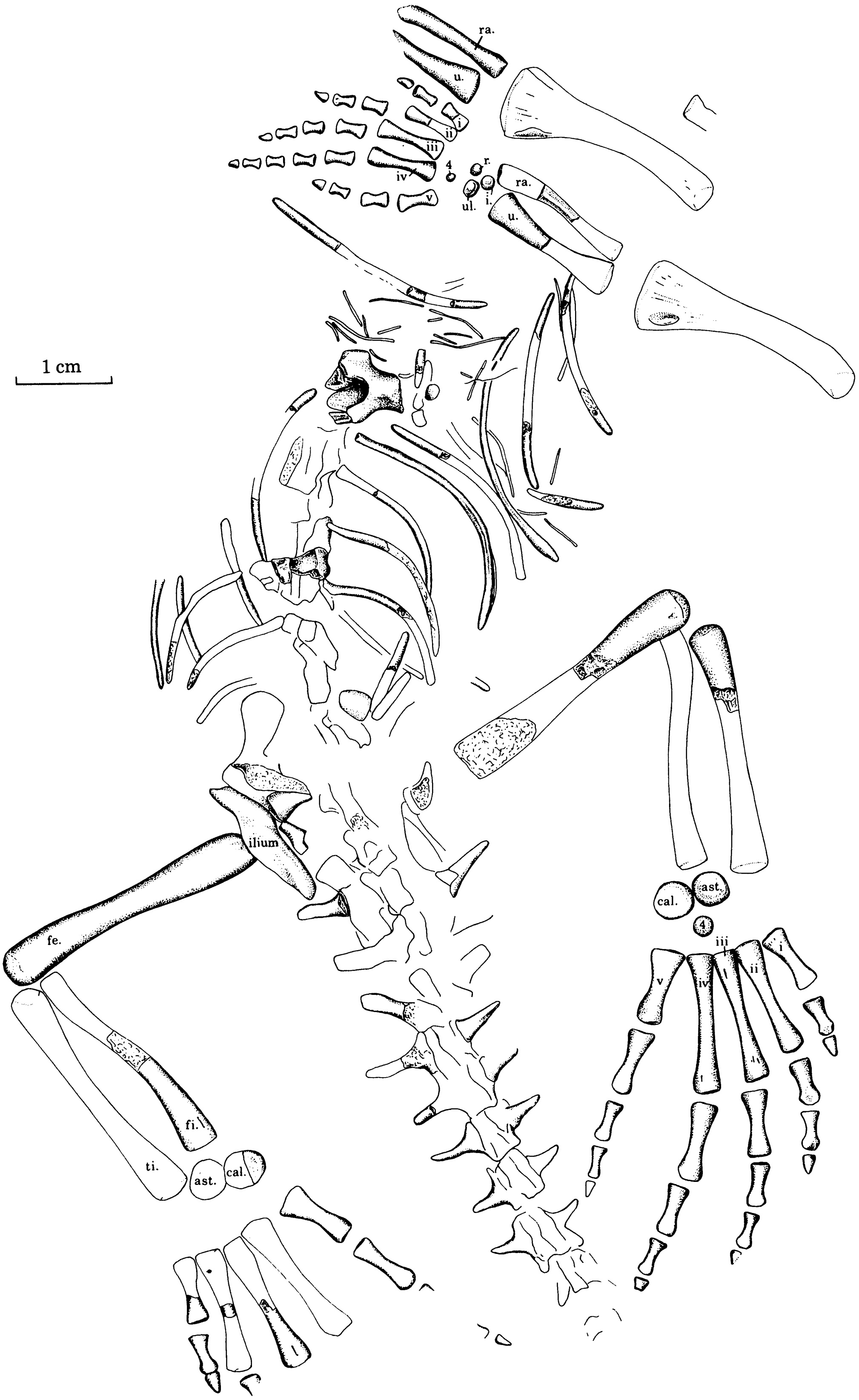


FIGURE 21. *Claudiosaurus germaini*; C.G. 20/16, skeleton of juvenile individual in dorsal view.

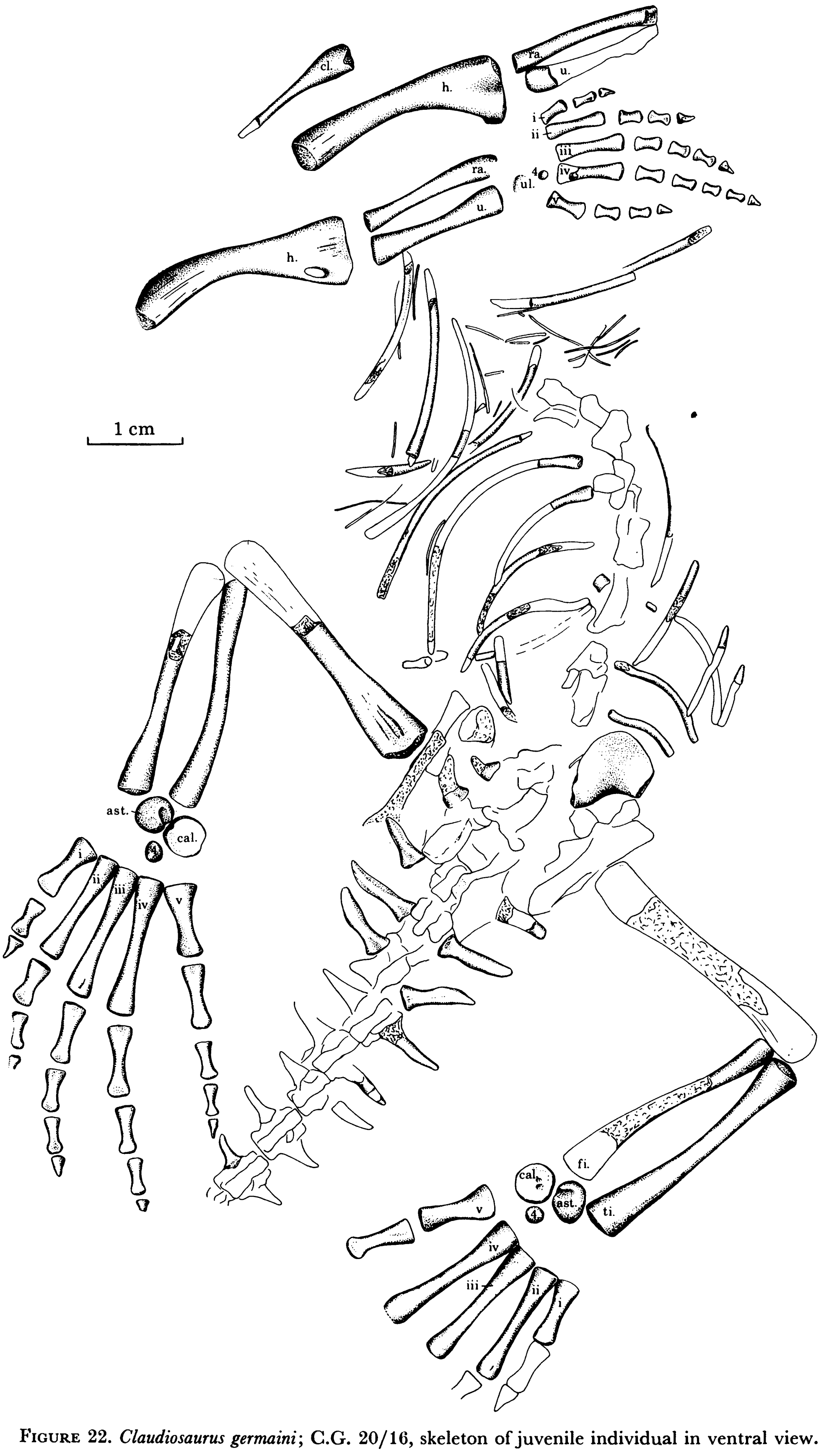


FIGURE 22. *Claudiosaurus germaini*; C.G. 20/16, skeleton of juvenile individual in ventral view.

Enough of the pelvis is exposed in the numerous articulated specimens from Leoposa to confirm the association. The ilium differs from that of *Thadeosaurus* in the long blade, whose dorsal margin is nearly horizontal. Its greater length can be associated with the initial stages in the incorporation of the 3rd pair of sacral ribs. There is definitely no thyroid fenestration. The public tubercle is very conspicuous. The orientation of the pelvis is like that of *Thadeosaurus* and primitive lizards, with the pubis and ischium meeting at an angle of approximately 80°.

There is almost nothing to distinguish the femora of *Claudiosaurus* from those of *Thadeosaurus*, except for the larger size and later achievement of adult features in the former genus. The tibia also appears basically similar, as does the fibula.

More or less complete feet are known in several specimens. From the smallest to the largest there is approximately a 70% increase in the length of the longest single element, the fourth metatarsal. In this series, the tibia increases by approximately 79%. The most striking change is in the ossification of the tarsals. In the smallest specimen, in which both feet are well exposed in both dorsal and ventral views, only three elements are ossified. They can unquestionably be identified as the astralagus, calcaneum and 4th distal tarsal. In C.G. 20/6, which shows a 33% increase in the length of the 4th metatarsal from that of the smallest specimen, seven tarsals are ossified: the centrale and distal tarsals, 1, 3 and 5, in addition to those present in the earlier stage. In C.G. 20/11, showing a further 5% increase in the length of the 4th metatarsal, the 2nd distal tarsal is ossified, completing the primitive reptilian complement. Other specimens of larger size show variability either in the rate of ossification or relative size of the distal tarsals. Specimen 1910–33–1a lacks the 2nd distal tarsal and the type lacks both the 1st and 2nd distal tarsals.

Even in the larger specimens there is considerable room for cartilage, compared with the tight mosaic seen in *Kenyasaurus* (Harris & Carroll 1977).

In the immature specimens, the calcaneum appears as a flat disc, thickened medially. The astralagus is nearly spherical dorsally; ventrally it is marked by a diagonal groove for the perforating artery. There is little more area of finished bone than that which lines this groove. The 4th distal tarsal is spherical. The mature specimens show a well ossified tarsus. Proximally, the surface of the astralagus for articulation with the tibia is more extensive ventrally than dorsally. Ventrally, there is a deep wide groove for the perforating artery, resembling that of *Tangasaurus* and *Kenyasaurus* (Harris & Carroll 1977). The articulation with the calcaneum indicates that the two bones are in essentially the same plane. They abut with a nearly flat surface. The astragalus takes most of the forces of the fibula. The 4th distal tarsal fits as a wedge in between the distal surfaces of the astragalus and calcaneum. Ventrally, the centrale can be seen to be grooved proximally, apparently for closer integration with the astragalus.

The calcaneum bears a conspicuous distolateral process. The gastrocnemius would be expected to cross over this area, but whether this unfinished surface served as a tie or actual insertion of the muscle cannot be determined.

The 3rd distal tarsal fits into a groove on the mediodistal surface of the 4th and probably did not move independently. The centrale and the distal tarsals probably moved as a unit relative to the astragalûs and calcaneum. The first digit and its distal tarsal may have been free to move somewhat independently. The extensive overlapping of the heads of the metatarsals probably linked them in the manner of modern lizards (Robinson, P. L. 1975). Only in the very immature specimens would a nothosaur-like flexibility of the limb be possible.

Ossification occurs more rapidly among the metatarsals and phalanges, which are essentially contiguous in all but the smallest two specimens. Measurements of the various elements were taken in an effort to determine what changes in proportions might occur with growth, but the number of comparable measurements was too limited for a truly quantitative analysis. There is slight evidence that the tibia grows more slowly than the femur, and the metatarsals and phalanges more slowly than the tibia but the digits faster than the metatarsals. The 5th metatarsal grows relatively faster than the 4th, and the proximal end expands considerably to differentiate it from the rest.

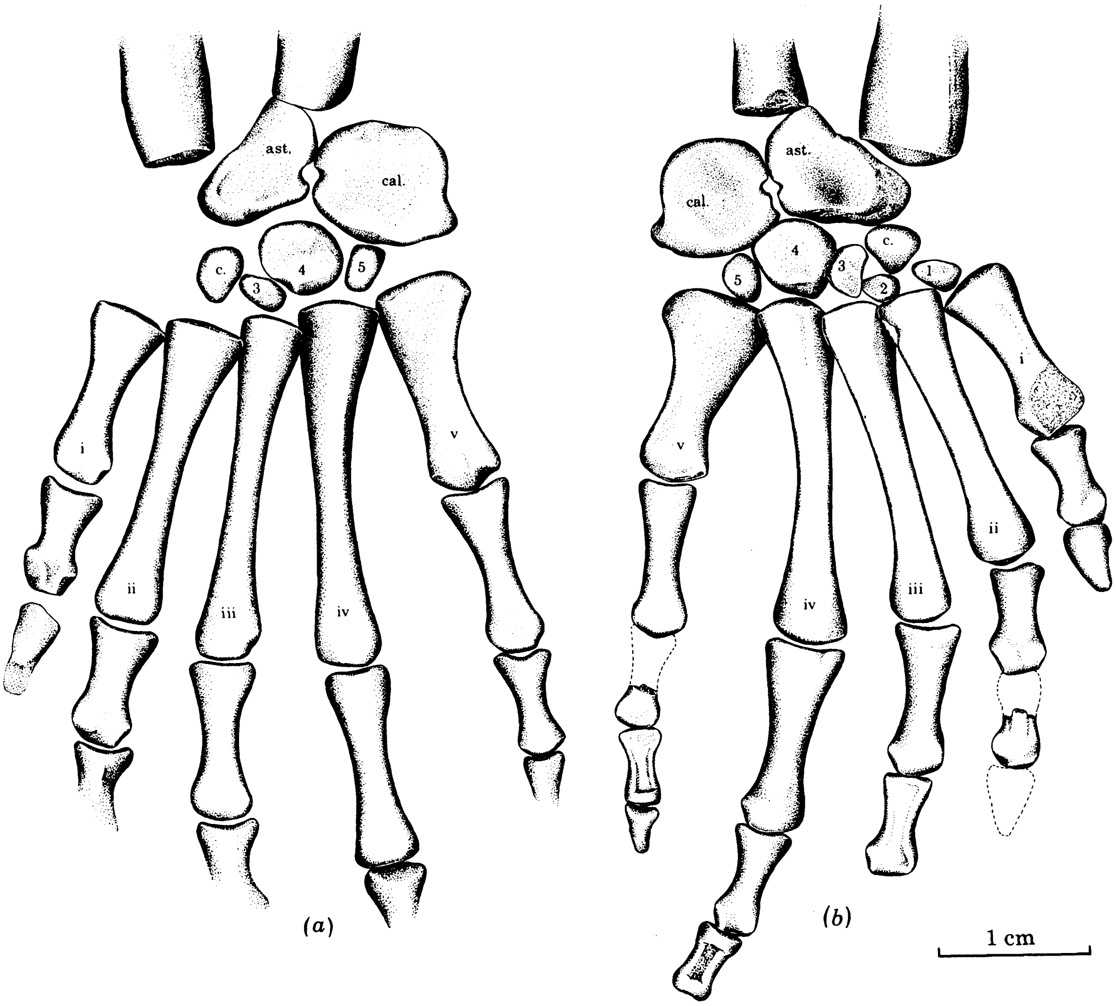


Figure 23. *Claudiosaurus germaini*: (*a*) right tarsus and pes of type in dorsal view; (*b*) P.M. 1978-6-2 left tarsus and pes in dorsal view. (Both magn. × 2.) Note differences in numbers of distal tarsals ossified.

The terminal digits, as in the hand, are quite unlike those of other contemporary reptiles. Their surface bone is not finished but rough and, ventrally, the distal surface is flat, rather than sharply pointed. In most primitive reptiles, the penultimate phalanx is longer than the antepenultimate (*Kenyasaurus Tangasaurus*, *Thadeosaurus* of similar size and age provide the closest comparison), presumably for the attachment of a large tendon to flex the terminal phalanx. In *Claudiosaurus* they may be slightly shorter than the antepenultimate. This may

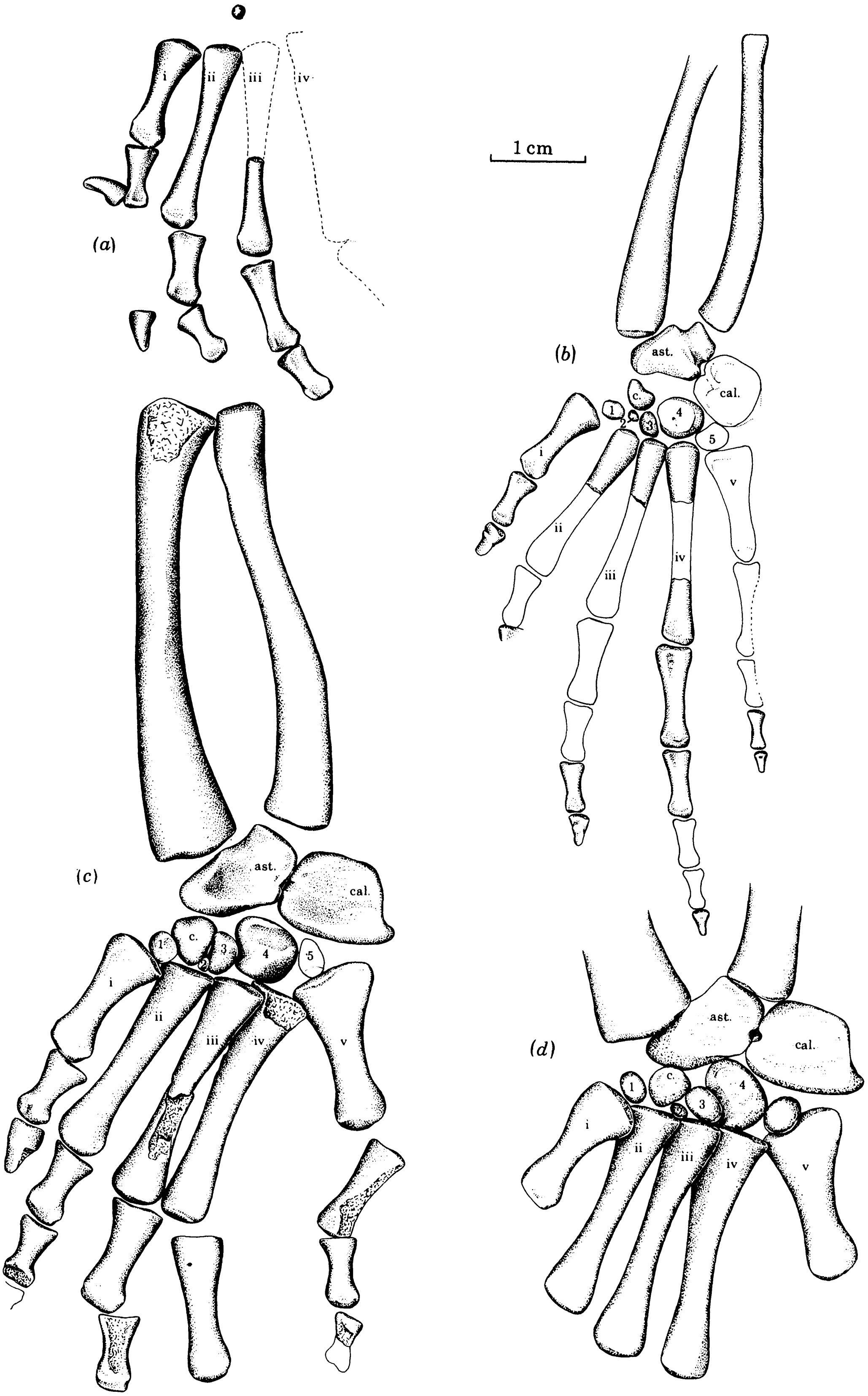


FIGURE 24. *Claudiosaurus germaini.* (*a*) P.M. 1911–18 (specimen without locality data), left pes in dorsal view. (*b*) C.G. 20/17, ventral view of right crus, tarsus and pes. (*c*) C.G. 20/9, dorsal view of left crus, tarsus and pes of largest individual; 5th distal tarsus is present as an impression in this view. (*d*) Reconstruction of tarsus and metatarsals of left foot in dorsal view. (All magn. × 1.5.)

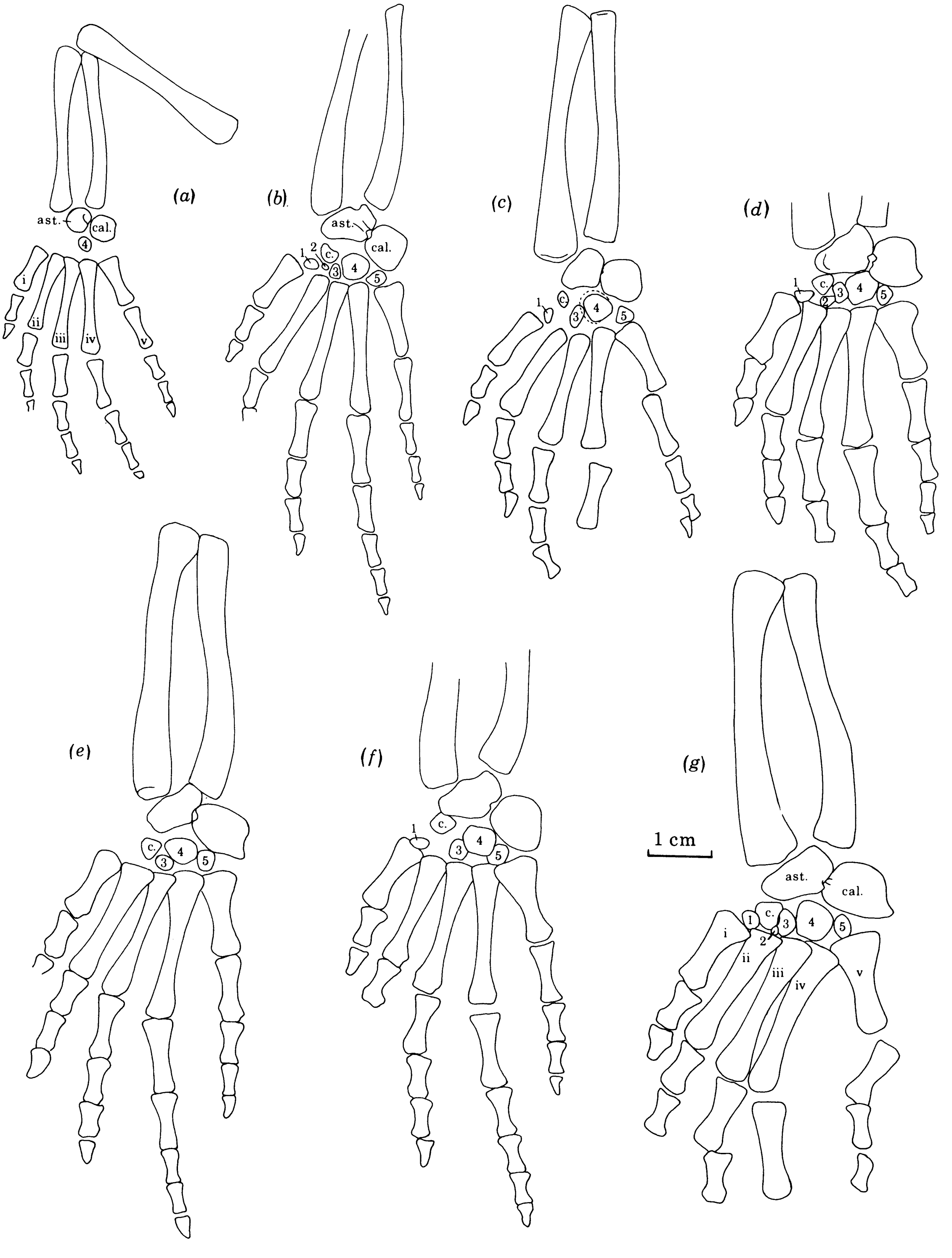


Figure 25. *Claudiosaurus germaini.* Tarsus and pes drawn to the same scale showing changes during growth. (*a*) C.G. 20/16; (*b*) C.G. 20/17; (*c*) C.G. 20/6; (*d*) P.M. 1978–6–2; (*e*) type (*f*), P.M. 1910–33–1a; (*g*) C.G. 20/9. (All magn. × 1.)

be interpreted as indicating less effective flexion of the ungual, or might presumably accord with a different use of the feet and might be associated with an aquatic rather than a terrestrial way of life. The terminal phalanges do, however, bear a prominent tubercle at their base for attachment of a flexor tendon. Otherwise, the structure and proportions of the tarsus and pes are not obviously specialized from the pattern of contemporary eosuchians. The 5th metatarsal is divergent, but not hooked; the 5th distal tarsal, although small and slow to ossify, is distinct.

The tarsus of numerous nothosaurs were illustrated by Arthaber (1924). The most common pattern seen in *Nothosaurus* shows three ossified tarsals, clearly comparable to the calcaneum, astragalus and 4th distal tarsal. Other genera have one or two additional distal tarsals. Some show no ossified distal tarsals. One could reasonably consider the specialized features of the rear limb in nothosaurs as resulting from the retention of immature features of an animal such as *Claudiosaurus*.

The ventral scales are superbly displayed in P.M. 1910–33–1a. They are slightly disarticulated, but almost every element can be accounted for. Unlike primitive reptiles, the median elements are fused into a rigid chevron, rather than simply overlapping as in pelycosaurs and captorhinomorphs. Except for the very first and last three rows each has two pairs of scales lateral to the middle element. Thirty-eight rows can be counted. The middle element of rows 22 and 23 are fused to one another. The scales span a distance of seven to eight vertebrae, giving about five rows of scales per segment. This pattern is essentially the same as that described for some nothosaurs such as *Paranthosaurus* (Saint-Seine 1961). The number of scale rows per segment is reduced in plesiosaurs, and each element becomes much larger. Primitive reptiles (Clark & Carroll 1973) have a similar number of scale rows per segment and scales in each scale row, but the medial elements overlap, rather than being fused.

PROPORTIONS OF *THADEOSAURUS* AND *CLAUDIOSAURUS*

The pattern of the vertebrae, girdles and limbs indicates that *Claudiosaurus* and *Thadeosaurus* share a close common ancestry. Although there may be some justification in classifying *Claudiosaurus* among the sauropterygians, it is almost certainly of eosuchian derivation. Despite the similarities of particular elements of the skeleton, *Thadeosaurus* and *Claudiosaurus* differ markedly in proportions.

Although there might be some question as to the exact position of the pectoral girdle since the column could have shifted either anteriorly or posteriorly as the skeleton was compacted, the consistency among several specimens of *Claudiosaurus*, as well as the configuration of the ribs, indicates the presence of at least eight vertebrae anterior to the margins of the clavicles. In *Thadeosaurus* and other similar younginids, there were apparently only four or five. There are 16 trunk vertebrae in *Claudiosaurus* and 21 in *Thadeosaurus*. The appearance of a long neck is further accentuated by the small size of the skull in *Claudiosaurus*, with the neck nearly twice the skull length. In *Youngina* and *Heleosuchus*, the neck is apparently shorter than the length of the skull. The elongate appearance of the neck of *Claudiosaurus* is also associated with the proportional differences in the individual vertebrae. The ratio of width to length of the anterior centra is approximately 45 to 50% in *Claudiosaurus*, but 65 to 70% in *Thadeosaurus*. Other proportional differences are more difficult to evaluate. Particularly in relation to possible patterns of aquatic locomotion it would be useful to know whether the limb proportions

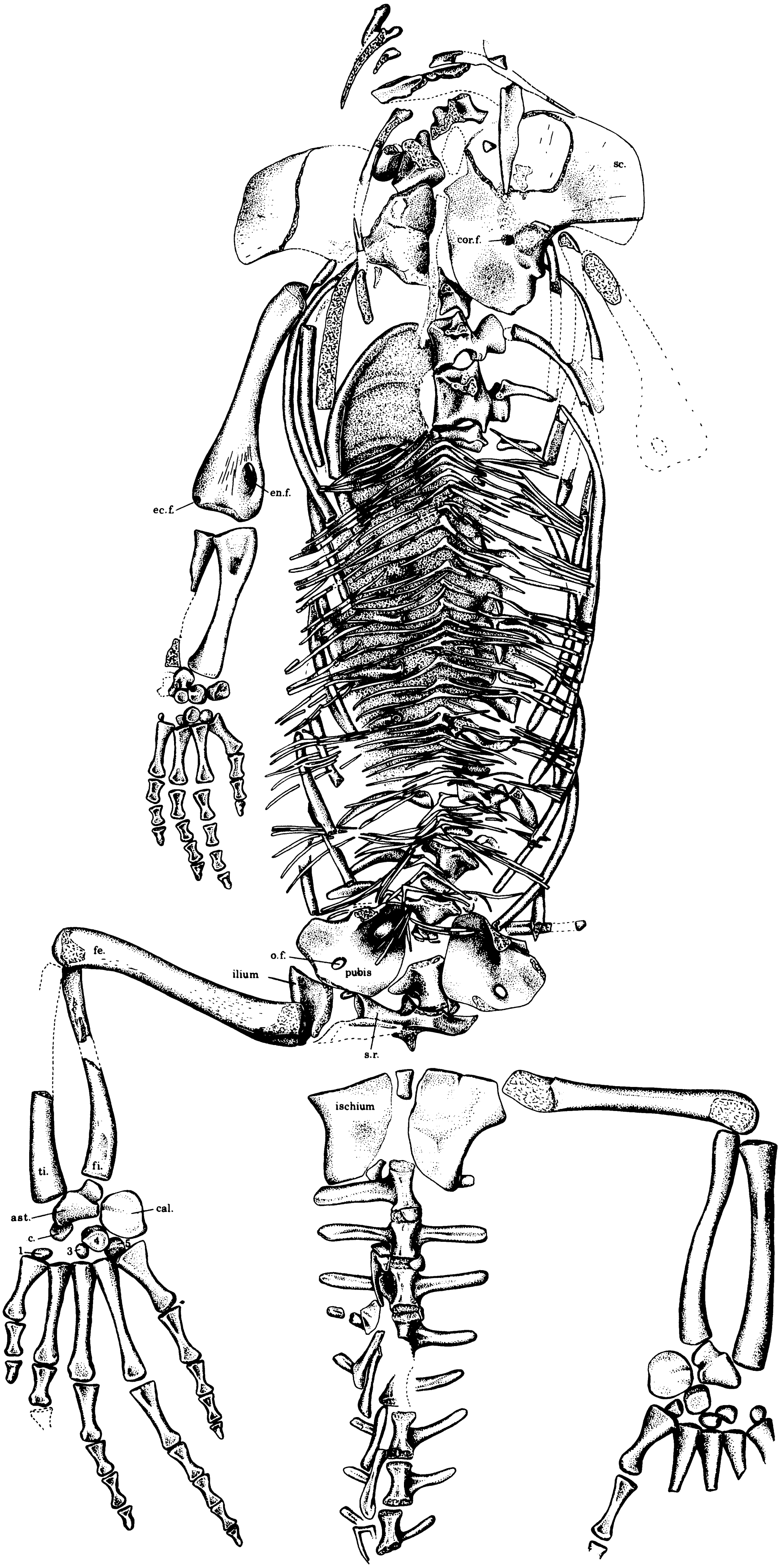


FIGURE 26. *Claudiosaurus germaini*; P.M. 1910–33–1a skeleton in ventral view. (Drawing slightly less than natural size.)

Table 1. Limb measurements in *Claudiosaurus* and *Thadeosaurus*

(All measurements are in centimetres.)

					metacarpals									metatarsals				
	hum.	rad.	uln.	carpus†	1	2	3	4	5	fem.	tib.	fib.	tarsus†	1	2	3	4	5
Claudiosaurus																		
20/16 juvenile	2.4	1.5	1.5	0.7	0.3	0.6	0.7	0.7	0.4	2.9	2.6	2.5	0.9	0.8	1.25	1.4	1.45	0.8
20/6	3.7	2.2	2.3	0.6	0.5	0.9	0.95	1.0	0.7	4.2	3.8	3.5	1.25	1.0	1.7	1.85	1.95	1.2
1910–33–1a	4.5	2.9	2.85	1.0	0.65	1.05	1.15	1.2	0.8	4.8	4.2	4.0	1.6	1.17	1.89	2.17	2.29	1.5
type	4.5	2.9	2.85	1.0	0.6	1.05	1.15	1.1	0.8	5.1	4.5	4.3	1.3	1.2	2.0	2.25	2.4	1.45
20/7	4.5	3.0	2.9	1.0	0.62	1.09	1.15	1.21	0.74	5.3	4.5	4.2	1.4	—	—	—	2.3	1.4
20/9 isolated rear limb	—	—	—	—	—	—	—	—	—	5.4?	4.7	4.3	1.65	1.4	2.15	2.4	2.5	1.6
Thadeosaurus																		
type	3.25	2.04	1.95	0.8	0.49	0.68	0.85	0.9	0.63	3.33	2.95	2.71	—	0.67	1.14	1.47	1.67	—
1908–11–13a	3.67	2.3	2.19	—	0.54	0.76	0.85	0.93	0.59	3.75	—	—	—	—	—	—	—	—

† Greatest proximodistal extent.

Table 2

	glenoid-acetabular distance, cm	H, cm	$\frac{H}{G-A}$(%)	R, cm	$\frac{R}{H}$(%)	$\frac{R}{G-A}$(%)	carpus and manus, cm	$\frac{C+M}{G-A}$(%)	F, cm	$\frac{F}{G-A}$(%)	T, cm	$\frac{T}{F}$(%)	$\frac{T}{G-A}$(%)	tarsus and pes, cm	$\frac{T+P}{G-A}$(%)	$\frac{C+M}{T+P}$(%)
Thadeosaurus – type	8.0	3.25	41	1.95	60	24	3.9	49	3.33	42	2.95	0.89	37	6.0	75	65
Cladiosaurus – type	11.7	4.5	38	2.85	63	24	4.4	38	5.1	44	4.5	0.88	38	7.6	65	58
Caiman	14.5	4.3	30	2.9	67	20	4.0	28	4.9	34	4.0	0.82	28	6.7	46	60

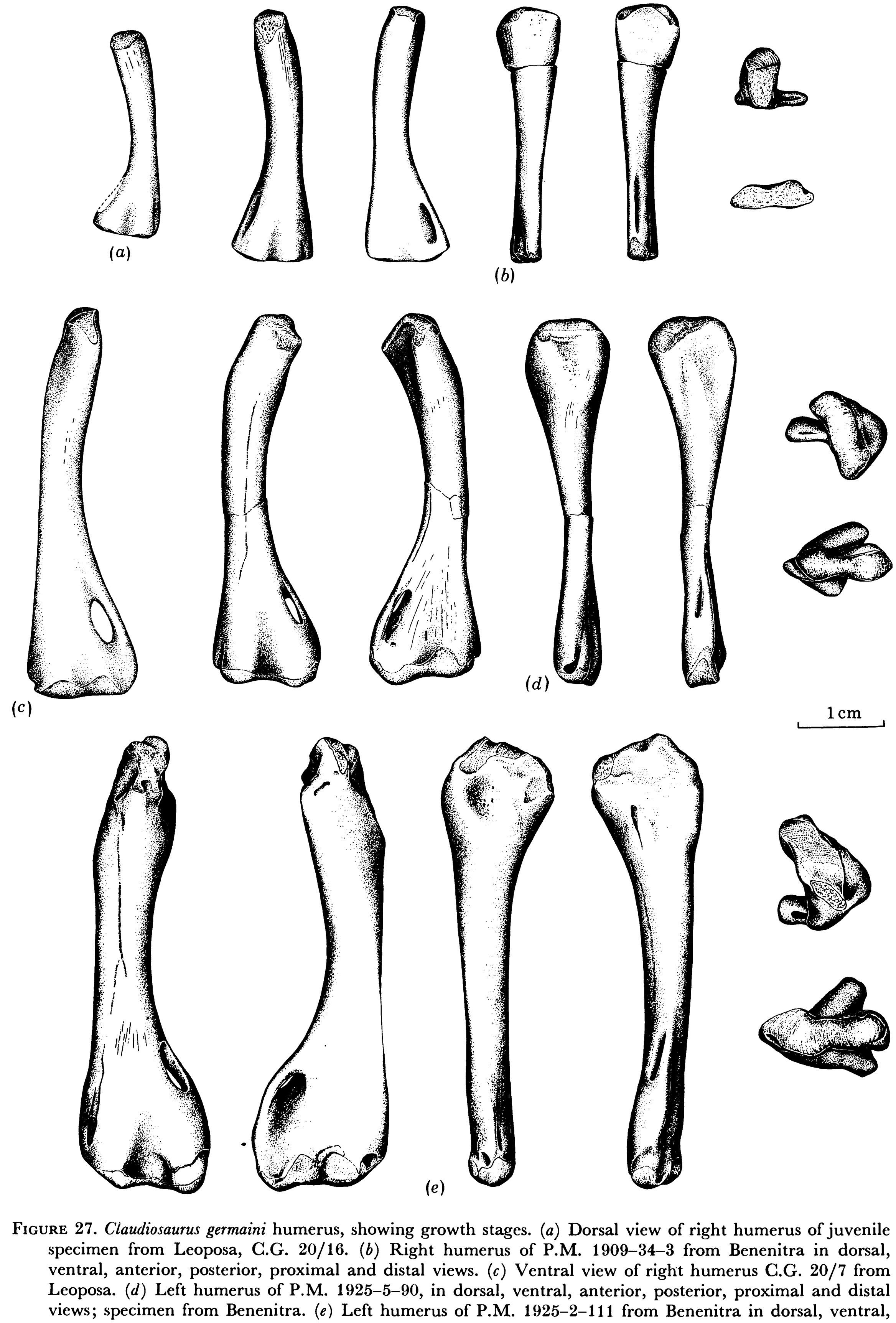


FIGURE 27. *Claudiosaurus germaini* humerus, showing growth stages. (*a*) Dorsal view of right humerus of juvenile specimen from Leoposa, C.G. 20/16. (*b*) Right humerus of P.M. 1909–34–3 from Benenitra in dorsal, ventral, anterior, posterior, proximal and distal views. (*c*) Ventral view of right humerus C.G. 20/7 from Leoposa. (*d*) Left humerus of P.M. 1925–5–90, in dorsal, ventral, anterior, posterior, proximal and distal views; specimen from Benenitra. (*e*) Left humerus of P.M. 1925–2–111 from Benenitra in dorsal, ventral, anterior, posterior, proximal and distal views. Proximal and distal views are drawn with the plane of distal expansion horizontal. Difference in apparent position of distal expansion as seen in proximal view are the result of slight differences in the orientation of the specimens when drawn. (All magn. × 1.5.)

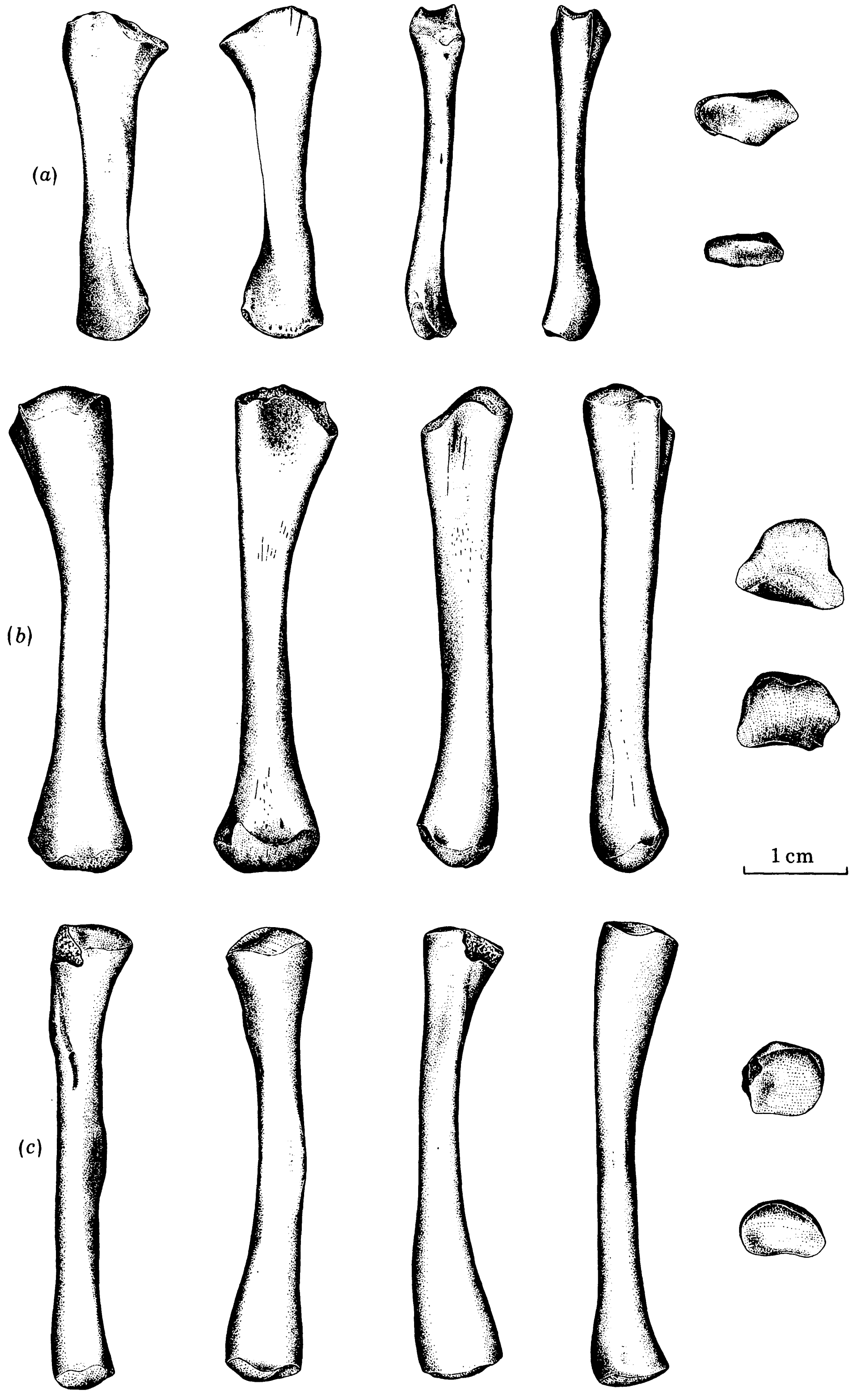


FIGURE 28. *Claudiosaurus germaini*; isolated elements from Benenitra. (*a*) Right ulna, P.M. 1925–2–85, anterior, posterior, medial, lateral, proximal and distal views. (*b*) Left femur, P.M. 1925–5–97 in dorsal, ventral, anterior, posterior, proximal and distal views. (*c*) Right tibia, P.M. 1925–5–106, in six views. (All magn. × 1.5).

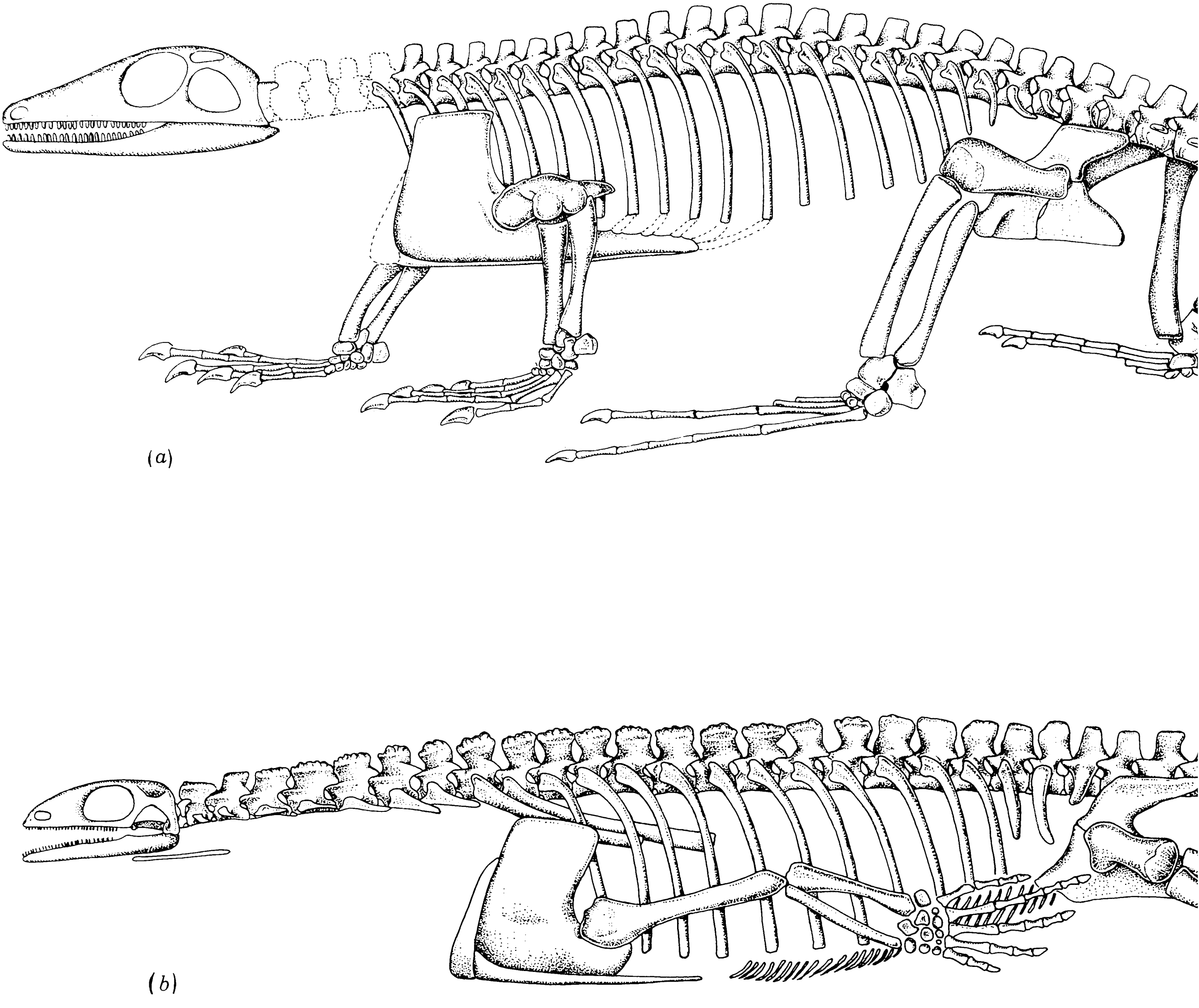
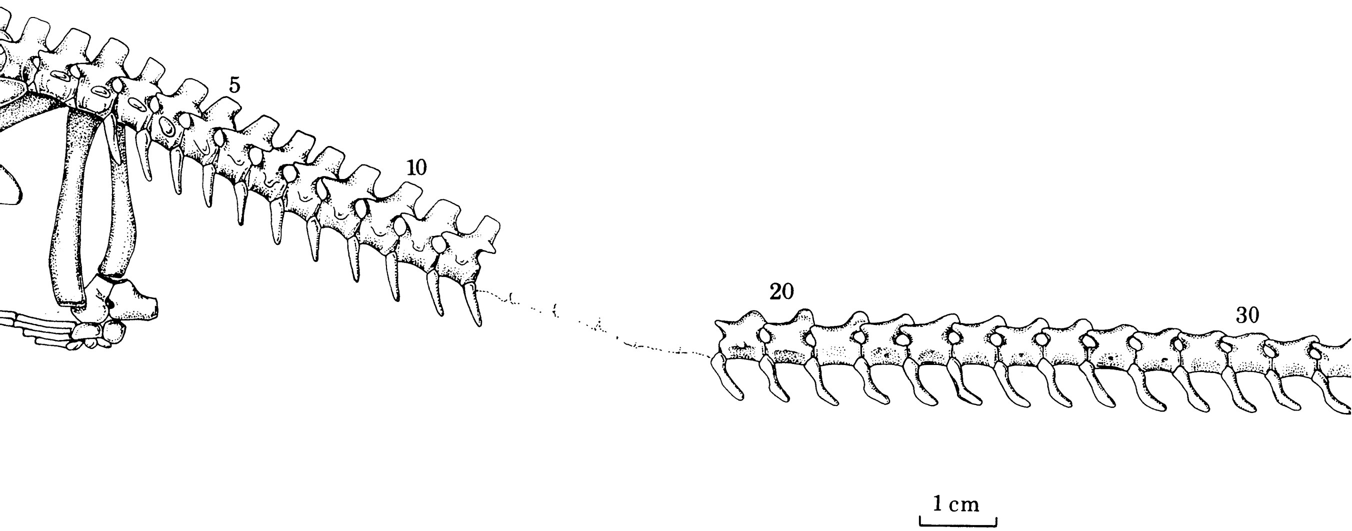
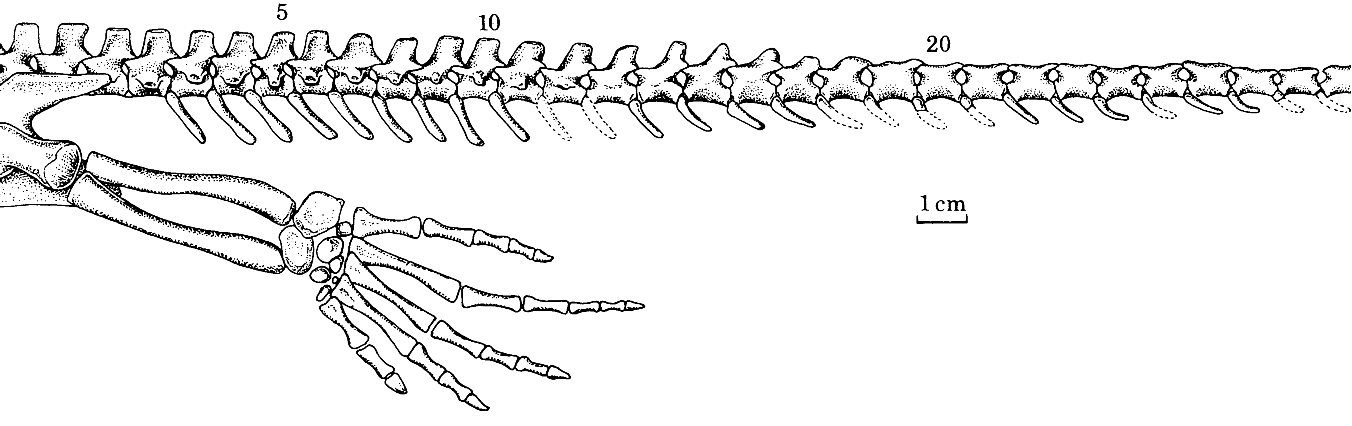


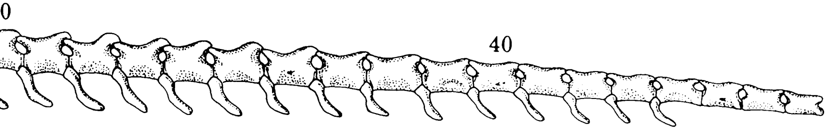
FIGURE 29. (*a*) *Thadeosaurus c*
(*b*) *Claudiosaurus germaini*

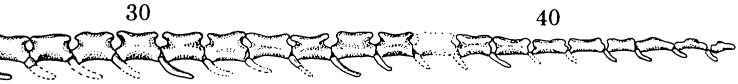




deosaurus colcanapi; restoration of skeleton in lateral view; skull from *Youngina*.
us germaini; restoration of skeleton in lateral view, showing a swimming pose.

Pullout 3





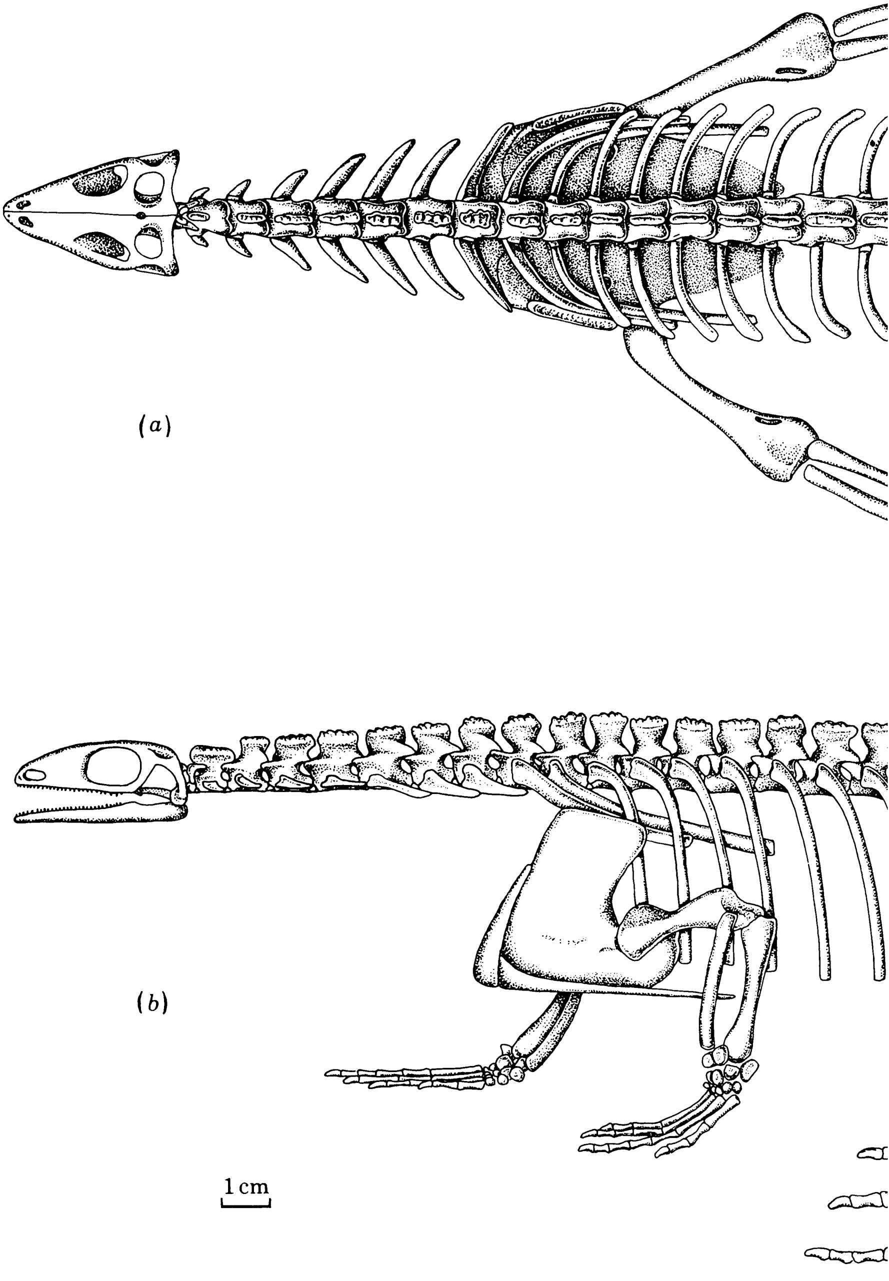
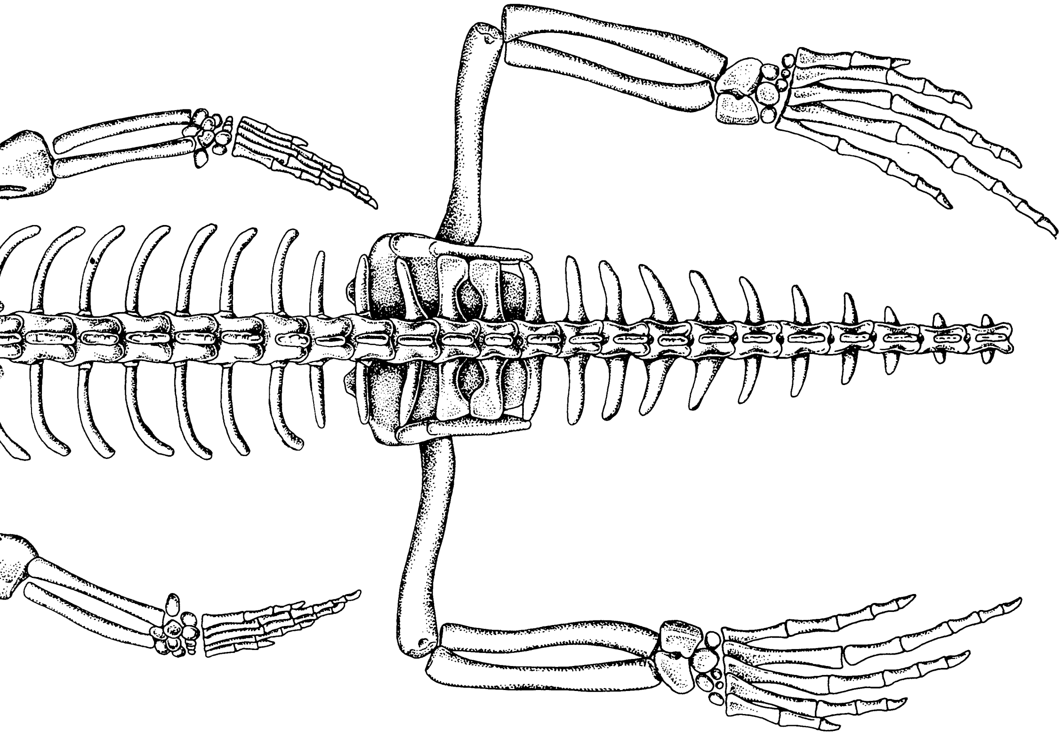
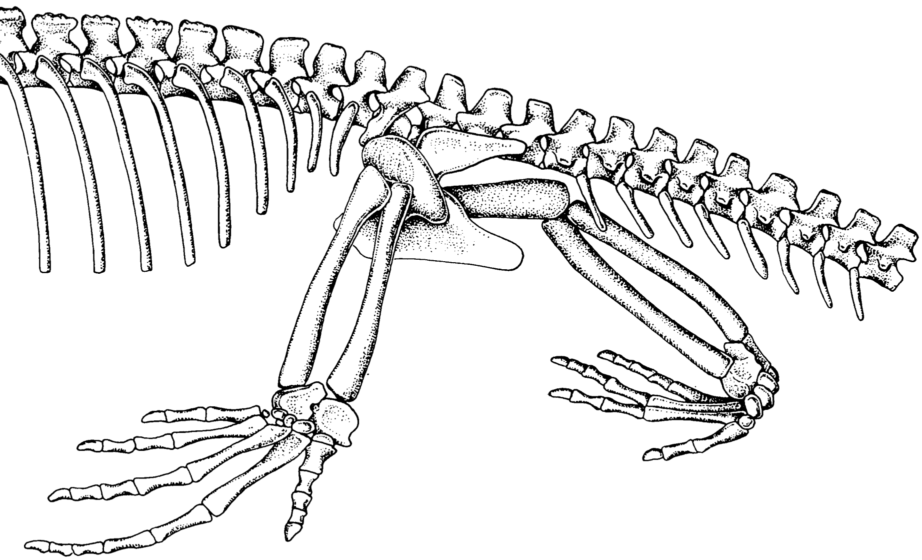


FIGURE 30. (*a*) *Claudiosaurus germaini*; restoration of skel
(*b*) *Claudiosaurus germaini*, restoration of skeleton





tion of skeleton in dorsal view, showing a swimming pose.
of skeleton in lateral view, showing a walking pose.

in *Claudiosaurus* could be considered specialized. The problem arises in establishing some justifiable unit for comparison.

The elongation of the individual vertebrae in the trunk region of *Claudiosaurus* tends to compensate for the relatively small number of vertebrae; so that the trunk region retains approximately the same proportions as in *Thadeosaurus*, relative to the girdles and proximal limb elements (see tables 1 and 2). The humerus and femur would appear shorter in *Claudiosaurus* if measured either against the length of individual vertebrae or total presacral length. Comparison was also made with the 'unit measure' devised by Romer & Price (1940) (see discussion by Currie (1978). There is some difficulty in measuring the vertebral diameter accurately in the two genera and there is some regional variation, but within this margin of uncertainty, the humerus and femur can be considered to be of essentially equivalent length in the two genera.

Use of the unit measure implies a certain uniformity of body support in the two groups. One might expect that the central diameter would be less in a permanently aquatic animal, since it would be supported by the buoyancy of the water. Unfortunately this assumption has not been tested in other groups; Romer considered ophiacodont pelycosaurs as somewhat aquatic in habit, but their vertebral diameter is comparable to that of other pelycosaurs. If the vertebrae of *Claudiosaurs* do have centra of smaller radius than expected in a terrestrial animal of the same mass, then the humerus and femur would also be smaller. Without other evidence, however, it will be assumed that both vertebral diameter and the length of the humerus and femur are roughly constant in the two genera and other comparisons will be made on this basis.

Whether or not the lengths of the humerus and femur in the two genera are considered comparable, it is apparent that the metacarpals and digits of the hand are markedly shorter in *Claudiosaurus* but that the radius is slightly longer, relative to the humerus. The length of the longest (4th) digit (including the metacarpal) is 70 to 74 % of the length of the humerus, while in *Thadeosaurus* it is 92 to 97 % of the length of the humerus. In the rear limb, in contrast, the difference is much less.

Aquatic adaptations of *Claudiosaurus*

Two lines of evidence suggest the initiation of aquatic adaptation in *Claudiosaurus*: (1) specific anatomical adaptations; (2) similarities to nothosaurs and/or plesiosaurs.

Relative to more primitive, presumably terrestrial, reptiles, *Claudiosaurus* has specialized the proportions of the hand in a manner similar to that seen in a variety of vertebrates that use the limbs as paddles (Robinson, J. A. 1975). Conspicuous growth lines are evident on the scapula and zygapophyses, as in a variety of aquatic forms discussed by Ricqlès (1974).

Comparison was made with a small caiman (from Carolina Biological Supply) with dimensions similar to those of an adult *Claudiosaurus* (table 2). The crocodilian has the 3rd, rather than the 4th digit of the manus the longest, and both the carpus and tarsus differ considerably in their components, but the proportions of the hands and feet in the caiman suggest a continuation of the trends observed between *Thadeosaurus* and *Claudiosaurus* toward an amphibious way of life. The position of the limbs in the several articulated specimens of *Claudiosaurus* approximate that of the alligator while swimming (Manter 1940).

Apart from limb proportions, there is little support for assuming an aquatic way of life for *Claudiosaurus*, although the palatal structure and the neck proportions can be interpreted as associated with aquatic feeding. As with modern alligators, one can imagine *Claudiosaurus* using the hindlimbs to kick off from the bank or for occasional strokes while swimming, but the tail for sustained locomotion. Small alligators, at least, show little specialization in the caudal vertebrae, nor does *Claudiosaurus*. The more lateral position of the zygapophyses in the tail, which differentiates *Claudiosaurus* from *Thadeosaurus*, also differentiates caimans from terrestrial lizards such as *Iguana* and *Varanus*. The addition of a potential 3rd pair of sacral ribs and the posterior elongation of the ischium and ilium accord with strong adduction of the femur. This would be of advantage in either terrestrial or aquatic locomotion. The relative simplicity and low degree of ossification of the tarsus and especially of the manus accord better with aquatic locomotion.

Despite these features, there is nothing in the osteology of *Claudiosaurus* that suggests that it was obligatorily aquatic. No features of the skeleton would definitely preclude it from terrestrial locomotion. The girdles, carpus and tarsus are not obviously distinct from those of terrestrial forms, although the carpus shows a lower degree of ossification than does that of mature eosuchians. The anatomy of the terminal phalanges is distinctive, but not necessarily related to an aquatic way of life.

The elongation of the neck is not in itself indicative of aquatic adaptation; a similarly elongate neck is evident in living monitor lizards, in the primitive diapsid *Petrolacosaurus* and in the possibly related genus *Araeoscelis*. Neck elongation is, however, also a characteristic of nothosaurs and most plesiosaurs and is presumably associated with aquatic specialization in these groups. It can reasonably be attributed to increased mobility of the head, compared with the remainder of the body, which is little suited for rapid manoeuverability in the water. The small size of the head may be a further adaptation for manoeuverability while feeding in the water.

Taken together, these features of the skeleton indicate a significant period of time during which selection was acting to increase aquatic specialization.

The general similarity of the skull of *Claudiosaurus* to that of *Youngina* and the remainder of the skeleton to that of other early terrestrial diapsids support the evolution of this genus from the same basic stock. Presumably, earlier in the Permian, the ancestors of *Claudiosaurus* were in a situation in which aquatic prey was available as an important food source. Competition with evolving archosaurs and lizards may have provided additional selection pressure to specialize for aquatic feeding.

It is noteworthy that a pellet of collophane was found in association with the bones of *Claudiosaurus* in the deposit near Benenitra. This mineral forms as replacement for calcitic or aragonitic oolites where a rich source of phosphates is available. Such conditions occur today where marine waters show upwelling from depth. This phenomena has been suggested by Dawson *et al.* (1977) to be an important factor in the evolution of the marine iguana on islands off the Pacific coast of South America. Similar conditions may have prevailed in marine waters developing off the west side of the crystalline massif, as Madagascar separated from east Africa in the Permian.

Most modern reptiles have the capacity for aquatic locomotion, and one can assume that a similar capacity was available to the early diapsids, without the need for any structural or physiological specialization. All that would be required is an intensification of behavioural patterns that were already present. Dawson *et al.* have demonstrated how little physiological or anatomical specialization has occurred in the marine iguana in relation to a quite extreme behavioural specialization of feeding on intertidal and subtidal marine macrophytic algae surrounding the Galapagos Islands.

The most important (or far reaching) changes occurred in the skull of *Claudiosaurus*. The presence of numerous small marginal teeth, a complete covering of denticles on the palate and the relative increase in palatal area suggest a shift to small prey, which might escape from the linearly arranged denticles and larger marginal teeth of younginids and other early diapsids. The smaller size of the head as a whole may also be correlated with small prey size. There is no evidence from the deposits of possible prey, but one might imagine invertebrates such as small crustaceans.

A particularly important similarity between *Claudiosaurus* and the subsequent nothosaurs is in the absence of the lower temporal bar. This is not a necessary adjunct to aquatic adaptation, since champsosaurs and marine crocodiles retain a diapsid configuration. However, the pleurosaurids, Jurassic derivatives of the sphenodontid stock, are generally considered to be aquatic and also show loss of the lower temporal bar (Cocude-Michael 1963). In *Claudiosaurus*, and probably in smaller nothosaurs as well, loss of the lower temporal bar may be related to the small size of the skull and relative expanse of the surface area of the palate that has occurred to some extent at the expense of the area of the adductor jaw musculature, particularly the pterygoideus. Loss of the lower temporal bar or emargination of the cheek would provide for some degree of lateral expansion of the adductor jaw musculature at this initial stage of synaptosaurian evolution. Such an open cheek is evident in all described nothosaurs and in some plesiosaurs but in other plesiosaurs the cheek has presumably redeveloped ventrally, much as did the temporal bar in some therapsids (e.g. *Cynognathus*). Such a re-expansion of the cheek may also have occurred in the ancestors of placodonts, if they had a similar ancestry. A solid cheek is associated in some sauropsid reptiles with a crushing dentition, for example in *Araeoscelis*, placodonts and *Trilophosaurus*. This does not indicate a close relationship among these forms, but suggests that a solid cheek is unlikely to have been present in the immediate ancestors of *Claudiosaurus* and nothosaurs, which show a primitive dentition of numerous piercing marginal teeth.

RELATIONSHIP OF *CLAUDIOSAURUS* TO EOSUCHIANS

It is obvious from these descriptions that *Claudiosaurus* is closely related to the eosuchians as characterized by *Thadeosaurus* and *Youngina*. It is more difficult to establish to which of the known eosuchian families *Claudiosaurus* might be most closely related. Before the relationships of *Claudiosaurus* with other well known eosuchians can be discussed, it is necessary to consider another Permian reptile, *Araeoscelis*, typically linked with the ancestry of nothosaurs and plesiosaurs. It has usually been considered to be very isolated from other primitive reptiles, belonging to a distinct order. Recent description of the ancestral diapsid *Petrolacosaurus* (Reisz 1981) demonstrates a host of similarities in the postcranial skeleton. Were it not for the cranial differences, this genus and *Araeoscelis* might well be placed in the same family, and they certainly share a close common ancestry. The configuration of the skull of *Araeoscelis* might represent the retention of the condition before cheek fenestration, or a secondary strengthening of the cheek from an ancestrally diapsid condition related to the development of a crushing dentition. At present there is no way to differentiate these two possibilities. *Araeoscelis* is currently the only known Palaeozoic genus with this configuration of the cheek.

For the origin of the cheek configuration seen in *Claudiosaurus*, there are two obvious choices: loss of the lower temporal bar from an ancestor like *Youngina*; and emargination of a solid cheek like that of *Araeoscelis*. The pattern of the remainder of the skull is much closer to that of *Youngina*. One would have to postulate a parallel evolution of most other cranial characteristics from the level of *Araeoscelis* in the ancestors of *Youngina* and *Claudiosaurus* to account for such an origin. For this there is no evidence. A much more parsimonious relationship is maintained by assumption of direct origin from an animal such as *Youngina*. *Youngina* itself is slightly advanced over the pattern seen in *Claudiosaurus* in the posterior exposure and slight emargination of the quadrate, but this would not preclude a slightly more primitive animal, otherwise resembling *Youngina*, from being ancestral to *Claudiosaurus*, at least as regards the cranial anatomy.

Postcranially, several of the specialized features of *Claudiosaurus* may be associated with an aquatic habit, and more primitive characteristics do not assist in establishing specific relationships. One prominent feature that might help to establish relationship is the long neck. Compared with *Youngina*, it appears as a specialization, but equally long necks have been described in the earliest known diapsid *Petrolacosaurus* and the closely related genus *Araeoscelis*. Hence the long neck might be used to support closer relationship to the earlier forms. The question is further complicated by the configuration of the neck in other early diapsids. *Prolacerta* (Camp 1947; Gow 1975) has a long neck, which is even further exaggerated in *Tanystropheus* (Wild 1973). Early lizards (Carroll 1977), in contrast, have short necks, as do the ancestral captorhinomorphs. The early archosaurs, such as *Euparkeria* (Ewer 1965), and the possibly ancestral *Heleosaurus* (Carroll 1976*c*) have long necks. As the oldest eosuchian, *Petrolacosaurus*, and many of the descendant stocks have long necks, it is simplest to suppose that this is an ancestral pattern, with short necks in lizards and younginids a derived character. The exceedingly close resemblance of the skull in *Claudiosaurus* to that of *Youngina* suggests closer relationship than between *Claudiosaurus* and any of the long-necked genera. On the scanty information available, it seems possible that the length of the neck may be a very labile characteristic at this stage in 'diapsid' evolution.

On the basis of overall cranial similarities, essentially typological criteria, *Claudiosaurus* might be included in the Eosuchia, as a member of a distinct family parallel to the Younginidae and Tangasauridae. When other late Palaeozoic and Mesozoic reptiles are taken into consideration, however, the relatively few differences from typical eosuchians must be given greater weight. These include particularly the features of the cheek and palate. The nature of the quadrate suspension and configuration of the boundary of the lower temporal area are almost exactly like those of a number of primitive nothosaurs. Structurally, this is in strong contrast to such diapsids as *Youngina*, typical sphenodonts and archosaurs, although the contrast of this particular feature with that of *Petrolacosaurus* is less striking for the lower temporal bar is not a strong structural element in that genus.

The problems of the Parapsida and Euryapsida

The material of *Claudiosaurus* demonstrates a combination of features seen otherwise in eosuchian reptiles and nothosaurs. Consideration of a variety of nothosaurs (figure 32) reinforces the impression that their skull structure could have derived from that seen in primitive diapsids. Such a derivation has been repeatedly suggested by Kuhn-Schnyder, but as often refuted by Romer. The extensive recent literature concerning a non-diapsid origin for nothosaurs requires some comment in order for *Claudiosaurus* to be considered as a possible nothosaur ancestor.

The problem has been centred primarily on the various conceptions of the nature of the temporal openings in plesiosaurs and nothosaurs. Williston (1907) compared the configuration of the temporal region of plesiosaurs (with which he was very familiar) to therocephalian reptiles among the therapsids. In both groups, the temporal opening faced dorsally, and was bounded medially by the parietal and laterally by the cheek formed from the squamosal, jugal and postorbital. In the *Osteology of the reptiles* (Williston 1925), he compared plesiosaurs with a variety of reptiles, including therapsids, but concluded that there was no strong evidence of their relationship with any other reptile groups.

Williston unwittingly contributed to the problem of establishing the affinities of nothosaurs and plesiosaurs by describing the genus *Araeoscelis* and pointing out the peculiar nature of the temporal region. This genus has an upper temporal opening and a solid cheek, a configuration for which Williston coined the name parapsid. He suggested that *Araeoscelis* might be ancestral to lizards and that the open cheek in the latter group had developed by a process of ventral emargination. As originally proposed, the term parapsid did not distinguish between the condition in which the cheek was entire (as in *Araeoscelis*), and that in which it was very open (as in lizards). Williston related *Araeoscelis* to the previously described genus *Protorosaurus*, from the Upper Permian of Europe, assigning it to the order Protorosauria, which he defined as 'with a single upper temporal opening between the parietal and the temporal arch, the quadrate fixed' (Williston 1925, p. 259).

Broom (1925) presented strong evidence (subsequently confirmed by other discoveries) that lizards had evolved from eosuchian ancestors by the loss of the lower temporal bar, rather than by emargination of the cheek. The ancestors of lizards were diapsids, not protorosaurs, or at least not animals with a skull configuration similar to that of *Araeoscelis*.

In 1933, Romer allied *Araeoscelis*, not with lizards, but with Williston's Synaptosauria: nothosaurs, plesiosaurs and placodonts. Such a derivation for nothosaurs assumed that they had a cheek region similar to that of *Araeoscelis*. In the third edition of *Vertebrate paleontology* (Romer 1966, p. 123) Romer stated that nothosaurs have a 'single upper temporal opening of euryapsid type, which, as in *Araeoscelis*, lay above a broad cheek plate formed by the squamosal'. Colbert (1955, 1969) gave illustrations of *Araeoscelis* and *Nothosaurus* to demonstrate this similarity.

In fact, neither *Nothosaurus* nor any other nothosaur that has been described has such a solid cheek. The source of Romer's and Colbert's error may be traced to von Meyer's description of *Nothosaurus*, published between 1847 and 1855. Von Meyer's specimen drawings were beautifully executed and show very clearly the presence of a narrow temporal bar, formed by the postorbital and squamosal, basically comparable with the temporal bar in lizards. Below this the cheek is widely open. Restoration of the skull in dorsal and ventral view shows the narrow configuration of this bar. The difficulty arose from von Meyer's attempt to restore the skull in lateral view. The bar is clearly evident, crossing the upper part of the cheek, but beneath it is an area that appears to represent a large plate of bone. This bone is not superficial, however, but represents more medial ossifications, including the dorsal portion of the quadrate ramus of the pterygoid, the lateral surface of the braincase and the epipterygoid. Zittel subsequently (1902) published a restoration based on that of von Meyer, but giving the impression that the cheek was covered with dermal bone, although a gap is shown at the anterior margin so that the mouth cavity is continuous with the cheek. Gregory (1951) and Colbert (1955, 1969) supplied the anterior margin and concluded that there was a solid cheek, occupied by a plate-like squamosal.

It is surprising that Zittel's restoration continued to be used, since an excellent reconstruction had been published by Schröder (1914) and was reproduced by Arthaber (1924). These illustrations show, as did von Meyer's specimen drawings, that there was a narrow temporal bar and a very open cheek. This is not a structure unique to *Nothosaurus* among the nothosaurs, but has been illustrated in numerous other genera and is almost certainly characteristic of the group as a whole. *Simosaurus*, *Cymaposaurus*, *Eurysaurus* and *Anarosaurus* were all illustrated by Arthaber (1924), either in lateral view or otherwise showing that there was a narrow temporal bar and an open cheek. Apart from the genus *Nothosaurus*, which was frequently shown as if it had a solid cheek, it is striking how often review articles show the skulls of nothosaurs in dorsal or ventral views, but not in lateral view. Of seven genera illustrated in the *Traité de Paléontologie*, vol. 5 (1955), only in *Nothosaurs* has the skull been illustrated in lateral view. This restoration does, however, illustrate the open nature of the cheek.

Only Kuhn-Schnyder among recent authors has made a point of illustrating the skulls of nothosaurs in lateral view and has recognized their fundamental diapsid structure. It seems very surprising that neither Colbert or Romer, writing general reviews after the publication of Kuhn-Schnyder's work, have accepted his conclusions as to the skull pattern. Colbert (1969) continued to use the modified Zittel reconstruction of *Nothosaurus*, although noting in the text that this genus had a narrow temporal bar. Romer (1971) argued that the configuration of the sauropterygian skull could have resulted from the emargination of the cheek in a genus such as *Araeoscelis* and denied any significant similarities between nothosaurs and diapsids. A concept of nothosaurs with a solid cheek appears to have taken precedence over the repeated observations that the cheek was widely open.

Comparison of the pattern of the skull roof and cheek region in such an unquestionable diapsid as *Youngina* and in small nothosaurs such as *Anarasaurus* and *Pachypleurosaurus* shows only a single fundamental difference: the loss of the lower temporal bar in the nothosaurs. Differences in the palate are striking but are largely bridged by *Claudiosaurus*.

Further light may be cast on this conceptualization of the ancestry of nothosaurs by considering the evolution of the cheek region of *Protorosaurus*, from its inception by Seeley (1882), to the third edition of Romer's *Vertebrate Paleontology* (Romer 1966). As one of the earliest known fossil reptiles. *Protorosaurus* has had an extremely varied taxonomic history. The only adequate study of the skull was published by Seeley (1882). It showed a clearly developed upper temporal opening and an open, lizard-like cheek. Williston (1914*b*) suggested that 'If it should be found that the side (of the cheek) was largely covered below the squamosal, leaving a vacuity above, the structure would be essentially like that of *Araeoscelis*'. First Williston (1913) and later von Huene (1944) restored the cheek with dotted lines, conforming with this suggestion. Von Huene's illustration was reproduced by Gregory (1951) and later by Romer (1966). In the latter publication, because of the great degree of reduction of the illustration and the nature of the printing process, the breaks in the dotted lines are almost obliterated, so that a very strong similarity with *Araeoscelis* is achieved. This has the effect of giving the cheek region the same configuration as that which we saw 'evolving' in *Nothosaurus*.

In fact, there seems no reason to deny Seeley's original reconstruction of the open cheek in *Protorosaurus*. Romer (1956) gives in the description of the family Protorosauridae, 'cheek appears to be deeply emarginated below postorbital bar'. Camp (1945) emphasized the overall similarities of *Prolacerta*, with an open, lizard-like cheek, and *Protorosaurus*. On comparing the superb illustration of the postcranial skeleton of *Protorosaurus* in von Meyer (1855) with the neck vertebrae of *Prolacerta* illustrated by Camp and other elements drawn by Gow (1975), it is difficult to deny very close relationship to these two genera. It is ironic that Williston thought that protorosaurus were closely related to lizards because they had a closed cheek and that Camp thought them closely related to lizards because they had an open cheek. As both Gow (1975) and Carroll (1975, 1977) have pointed out, neither *Prolacerta* nor any of the genera usually placed in the Protorosauria are close to the ancestry of lizards, regardless of the configuration of the cheek. And what of nothosaurs? If both nothosaurs and protorosaurs have an open rather than a closed cheek, are they then related? Again the answer is no. The cheek may be open in both groups, but the structure and attachment of the quadrate are fundamentally different. Although not closely related to lizards, *Prolacerta*, *Tanystropheus* and *Macrocnemius* have a loosely attached quadrate, which is recessed posteriorly and presumably housed a large tympanum. Seeley's restoration shows a similar pattern in *Protorosaurus*. The nothosaurs, in contrast, have the quadrate firmly attached, with the squamosal covering it both laterally and posteriorly except at the very base. Functionally, the situation is entirely different in the two groups.

Although not specifically called for in a paper on nothosaurs, it is nevertheless appropriate here to consider the taxonomic position of protorosaurs, as a group without either sauropterygian or squamate affinities. The closest affinity of *Protorosaurus* is clearly with *Prolacerta*, as indicated by Camp. As pointed out by Gow, *Prolacerta* can also be related very closely with *Tanystropheus* and *Macrocnemius*. These genera differ markedly from *Araeoscelis* in both the nature of the cheek region and the configuration of the dentition. The common presence of a long neck does not in itself seem sufficient to suggest close relationship in the face of other differences. It would be fairly simple to derive *Protorosaurus* from *Petrolacosaurus*, although the similarities are not sufficient to support inclusion in a single family. The name Protorosauria clearly has precedence over Araeosceloidea or Parathecodontia in referring to *Protorosaurus* and its close relatives. None of the included genera show any significant similarities to either squamates or archosaurs. Conservatively, they may be considered as a family, Protorosauridae, or a suborder within the Eosuchia.

The terms diapsid, synapsid and anapsid are clearly understood and defined, despite the presence of some variation within each structural pattern. These terms were originally coined to describe the configuration of the temporal region, but have been extended to taxonomic groups as well. The structural term synapsid coincides exactly with the subclass Synapsida, the mammal-like reptiles, including the two orders Pelycosauria and Therapsida. The subclass Anapsida includes both the turtles and the most primitive reptiles, although turtles as a group possess openings on the occipital surface to accommodate the temporal musculature and many genera have a ventral emargination of the cheek. The term Diapsida was used by H. F. Osborne and E. S. Goodrich to apply to all reptiles that either primitively possessed a diapsid condition or had evolved from genera that had possessed this condition. Such a classification encompasses such an enormous spectrum of reptilian types that most authors have followed Romer's suggestion of a division between two subclasses, Archosauria and Lepidosauria, for animals with a well established diapsid ancestry.

Two other terms have been used to describe the configuration of the temporal region, parapsid and euryapsid, but without the clear understanding that has been established for anapsid, diapsid and synapsid. Both have been used to refer to animals with an upper temporal opening, with either a solid or an emarginated cheek. They have always been intended as categories distinct from both diapsids and diapsid derivatives. That is, parapsids and euryapsids are presumed never to have had a proper lower temporal opening and bar.

The term parapsid was initially coined by Williston (1917, p. 416) to apply to squamates and the Ichthyosauria which he thought closely related to one another. He envisaged that the configuration of the temporal region in primitive lizards and ichthyosaurs resulted from the ventral emargination of the cheek region in descedents of an animal such as *Araeoscelis* which he assigned to the order Protorosauria. This order was originally named by von Meyer (1856) for the inclusion of *Protorosaurus* but the concept was switched by Williston to the genus *Araeoscelis*, in which the skull was better known. Romer (1966) extended this process further by renaming the group including *Protorosaurus* and *Araeoscelis* the order Araeoscelidia, which he included within the subclass Synaptosauria.

Colbert (1955) restricted the term Parapsida to the ichthyosaurs and coined the name Euryapsida for the nothosaurs, plesiosaurs, placodonts and their presumed araeoscelid ancestors, as a more euphonius alternative to Williston's Synaptosauria. This was accepted by Romer (1966). Both Romer and Colbert originally distinguished this group from the ichthyosaurs, because of their apparently distinctive pattern of the bones surrounding the upper temporal opening. It had long been accepted that the supratemporal formed the posterolateral border, in contrast with the condition in nothosaurs and plesiosaurs, in which this margin is formed by the squamosal. This difference suggested that the opening was not homologous in the two groups, but had arisen separately from ancestors without a dorsal temporal fenestration. Subsequently, Romer (1968*a*) described ichthyosaurs in which the bones at the back of the skull had been completely disarticulated by acid preparation. This material demonstrated that the bone in question was the squamosal, whose surface had been almost completely covered by the postorbital. The dorsal temporal opening could thus be considered comparable with that in nothosaurs and plesiosaurs. Colbert (1969) used this information as the basis for including the ichthyosaurs as well as the plesiosaurs and their kin in the sublcass Euryapsida. Romer (1968*b*) himself did not go this far and did not feel this one morphological similarity was sufficient to unite ichthyosaurs and plesiosaurs. In Romer's last paper on this subject (1974), published posthumously, he abandoned all thoughts of deriving either the ichthyosaurs or the plesiosaurs and their kin from any known groups of terrestrial reptiles.

The terms Parapsida and Euryapsida have both been used to cover a variety of structural conditions and taxonomic assemblages. Both suggest structural conditions that are unrelated to the diapsid pattern, but include animals that have either a solid or a completely open cheek. It does not appear advisable to continue the usage of either of these terms. The name Sauropterygia, used by Owen (1860) to include both nothosaurs and plesiosaurs, and by

Romer (1956, 1966), can continue to be used to designate these groups with little likelihood of misunderstanding. Sauropterygians may be considered derivatives of the main stock of diapsid reptiles without the application of any specific term to describe the configuration of their temporal region.

The specific position of the placodonts remains unresolved, but does not appear to affect our understanding of the relationships of nothosaurs and plesiosaurs. Ichthyosaurs, whatever their ancestry, are clearly not closely related to the other major groups of Mesozoic aquatic reptiles.

Comparisons with nothosaurs and plesiosaurs

Claudiosaurus expresses a mosaic of characteristics and character states that make classification difficult. The skull roof shows an essentially nothosaurian pattern, and the palate shows the initiation of the solid palate that characterizes that group. Postcranially, there are several features that might be accepted as indicating aquatic adaptations, but none that is developing strongly in the direction expected in the ancestors of nothosaurs or plesiosaurs.

Nothosaurs are known primarily from the Triassic of Europe. With the exception of the genus *Pistosaurus*, which has been variously classified as a nothosaur or a plesiosaur, and a number of incompletely known or inadequately described species, nothosaurs are readily recognized and fit into a single broad pattern. Within the order, there is no agreed classification of the approximately 20 genera. The group had obviously undergone a major radiation before its appearance in the fossil record, as well as considerable reorganization from an immediately ancestral pattern. None of the described genera is obviously ancestral to any of the others and none is an apparent relict of an ancestral structural stock. One may assume that in the origin of nothosaurs important modifications in the locomotor apparatus permitted the nothosaurs to enter a major adaptive zone that was previously not occupied. Subsequent radiation occurred rapidly, with the zone subdivided at the level of the family and genus. Many genera retain some primitive characteristics, but these seem to be distributed in a rather random manner throughout the suborder. Among features mentioned by Nopsca (1928), the long tail in *Pachypleurosaurus*, the suborbital vacuities of *Neusticosaurus* and *Lariosaurus*, the presence of only three pairs of sacral ribs in several genera and the shape and proportions of the skull roof in *Anarosaurus* and *Dactylosaurus* may be considered primitive when compared with known reptiles of the Permian. Such evidence is not very useful for evaluating the ancestry of the group, however, or for specific comparison with *Claudiosaurus*.

It is difficult to provide specific evidence that *Claudiosaurus* is an actual ancestor for either specific nothosaurs, or for nothosaurs as a group. It may have been, however, or at least it may have belonged to a group that did. Most importantly, the similar pattern of the skull roof in *Claudiosaurus* and numerous small, apparently primitive, nothosaurs can be readily derived from the general primitive diapsid pattern. The closest comparisons can be made with the genus *Anarosaurus*.

In possessing a closed palate and in the configuration of the coracoids, *Anarosaurus* (figure 32) follows the pattern of the other, better known nothosaurs. Locomotor and feeding patterns were evidently similar. As illustrated and described by Nopsca (1928) there are no features that would support a separate origin. As assumed for nothosaurs as a group, the specialized palatal structure presumably precludes close relationship with plesiosaurs, which are in any case represented by *Pistosaurus* as early as the middle Triassic. The humerus and femur of *Anarosaurus* are of the pattern typical to nothosaurs; the epipodials are only incompletely known, but it is extremely unlikely that they could have achieved the typical plesiosaur specialization in association with the primitive propodials. Despite the specialization of the palate, girdles and limbs, the skull roof of *Anarosaurus* retains a configuration that is primitive in retaining the proportions and bone configuration of such generalized reptiles as *Petrolacosaurus* and *Youngina*. The most striking feature of the skull of *Anarosaurus*, as seen from the casts and photographs, is that it is essentially that of a diapsid. There are small dorsal temporal openings and a very extensive emargination of the cheek. The latter, at first glance, resembles that of lizards, but it is functionally far different in that the quadrate is low and appears firmly braced by the squamosal and pterygoid, a hallmark of sauropterygians. In contrast with other, generally larger, nothosaurs, the postorbital bar is in the shape of a narrow arch. Such an obviously primitive pattern in the temporal region in otherwise relatively early, and unspecialized nothosaurs should have considerable weight in establishing the affinities of the group. It emphasizes Kuhn-Schnyder's suggestion of diapsid affinity of nothosaurs (1962, 1967), based on other, better known, material.

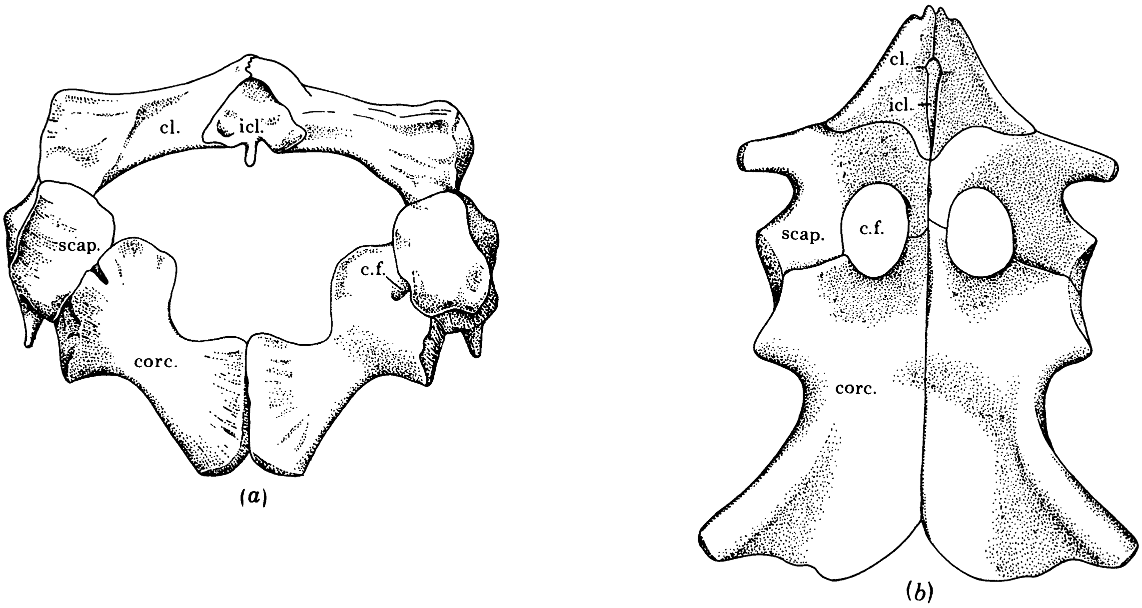


FIGURE 31. Pectoral girdles of (*a*) *Nothosaurus* and (*b*) the plesiosaur *Cryptocleidus*, redrawn from Romer (1956).

Plesiosaurs and nothosaurs have both evolved skeletal modifications than can be associated with aquatic locomotion, but both limbs and girdles are distinct in many important features, suggesting that their specific manner of use was different. The general body form also appears to be distinct, with nothosaurs exhibiting marked dorsoventral flattening. This is emphasized by the normal posture of preserved specimens and the almost universally dorsal or ventral views shown in restorations.

Plesiosaurs show a much higher degree of modification of the limbs into paddles with the epipodials as well as the tarsals and carpals typically represented by flattened polygonal

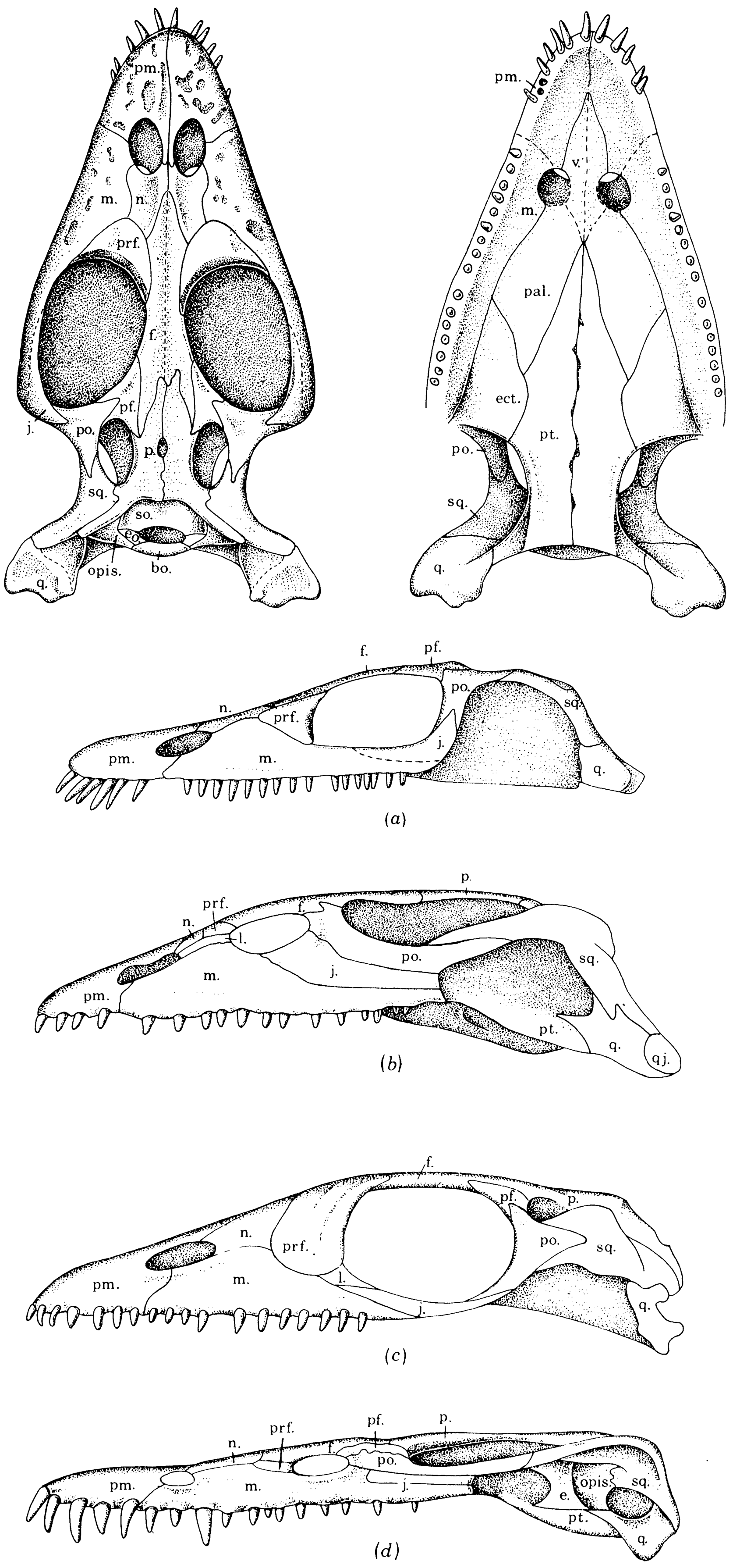


FIGURE 32. Skulls of nothosaurs. (*a*) *Anarosaurus*: dorsal, palatal and lateral views, drawn from casts and illustrations published by Nopsca (1928) (magn. × 2). Lateral views of the skulls of (*b*) *Simosaurus*, (*c*) *Pachypleurosaurus* and (*d*) *Nothosaurus*, redrawn from Kuhn-Schnyder (1967) and Romer (1956).

plates of bone. The outline of the paddle, according to J. A. Robinson (1975) would suggest flying through the water in the manner of a sea turtle or penguin, rather than rowing. Plesiosaurs commonly have high neural spines and relatively narrow arches, which may suggest limitations of the degree of sinuous locomotion possible in the spinal column between the limbs.

Most described nothosaurs, in contrast, have low neural spines and broad neural arches with broad, flat zygapophyses. In snakes and a variety of heavy-bodied primitive reptiles (Olson 1976), this configuration of the vertebrae may have been associated with a considerable degree of lateral undulation of the vertebral column. In general, the distinctiveness of these two patterns of vertebral, girdle and limb structure suggests that nothosaurs and plesiosaurs represent two distinct radiations, based on different, but equally specialized means of locomotion.

Two genera show a mixture of characteristics and so raise the possibility that the plesiosaur pattern might have evolved from that typical to nothosaurs. Both *Nothosaurus* and *Pistosaurus* have long neural spines and narrow arches, and are less conspicuously dorsoventrally flattened than most nothosaurs. Both genera have a typically nothosaurian pectorial girdle with the coracoids separate for most of their length and relatively long epipodials. *Pistosaurus* has been suggested, on the basis of both cranial and postcranial features, to be allied with plesiosaurs and to form a link between the two groups. *Pistosarus* is either the oldest known plesiosaur or the most plesiosaur-like of the nothosaurs. The features in which *Pistosaurus* resembles plesiosaurs might have been achieved separately, however. The nature of the relationship between nothosaurs and plesiosaurs naturally affects what characters one would expect in a common ancestor of the sauropterygians. If *Pistosaurus* is really a representative of a stock that evolved from nothosaurs to plesiosaurs, an ancestor of nothosaurs would not be expected to have any important features in common with plesiosaurs that were not also expressed in nothosaurs. If nothosaurs and ancestral plesiosaurs are sister groups, both of which diverged from a distinct ancestral stock, such a common ancestor might be expected to show as many features in common with plesiosaurs as with nothosaurs

Claudiosaurus shows some features that might be expected in any group beginning adaptation toward an aquatic way of life, but little that approaches the specifically nothosaurian pattern. In the presence of long, anteroposteriorly broadened neural spines and moderately narrow neural arches, the pattern approaches that of plesiosaurs and suggests a limitation of lateral flexure of the column. This is not actually very much modified from the pattern in other primitive diapsids, most of which have relatively high neural spines and narrow arches. This condition could readily give rise to that seen in nothosaurs (similar lowering of the neural spines and broadening of the arches are seen in the ancestry of captorhinids from primitive romeriid reptiles, and presumably in the ancestors of procolophonids and seymouriamorphs). What would be less likely is the change from tall neural spines in an ancestral group, to the short configuration seen in nothosaurs and back to the tall pattern of plesiosaurs. This, however, may well have occurred in the ancestors of both *Pistosaurus* and *Nothosaurus*.

More specific comparison of *Claudiosaurus* with nothosaurs and plesiosaurs awaits the description of more primitive members of these groups than are currently known.

Nearly all the specimens of *Claudiosaurus* described in this paper were carefully and diligently collected by Mr Claude Germain. I very much appreciate the opportunity to study many of them in his private museum in Brittany. Professor Piveteau was also most kind in inviting me to study two specimens that were in his collection. Professor Lehman was helpful in providing space and various facilities in the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, during my several visits. Dr Goujet was extremely helpful in locating specimens and arranging other facilities. The excellent photograph of the type specimen of *Claudiosaurus* was taken by R. Kandarown and D. Serrette in that Museum. Mr Germain and Mr Cliquet, both of whom did stratigraphic work on the Sakamena Formation in Madagascar, provided field notes, reports and other useful information on the geology of the beds containing fossil vertebrates. Dr Reinhart Hesse, Department of Geology at McGill University, studied thin sections of the matrix containing specimens from Benenitra. He identified the collophane and indicated the significance of its presence. I am especially grateful to Mrs Pamela Gaskill for the great care and attention taken in the numerous drawings. This work was supported by grants from the Merrill Foundation and the National Research Council of Canada.

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KEY TO ABBREVIATIONS USED IN FIGURES

a.	angular
a.a.	atlas arch
a.c.	atlas centrum
art.	articular
ast.	astragalus
ax.	axis
ax. ic.	axis intercentrum
bo.	basioccipital
bs.	basisphenoid
c.	centrale
cal.	calcaneum
cb. 1.	first ceratobranchial
c.f.	coracoid foramen
c.g.	groove for carotid artery
cl.	clavicle
cor.	coronoid
corc.	coracoid
c.r.1	first caudal rib
d.	dentary
e.	epipterygoid
ec. f.	ectepicondylar foramen
eo.	exoccipital
en. f.	entepicondylar foramen
f.	frontal
fe.	femur
fi.	fibula
h.	humerus
icl.	interclavicle
j.	jugal
l.	lacrimal
l.c.	lateral centrale
m.	maxilla
m.c.	medial centrale
n.	nasal
o.f.	obturator foramen
opis.	opisthotic
p.	parietal
pal.	palatine
part.	prearticular
pf.	postfrontal
pis.	pisiform
po.	postorbital
prf.	prefrontal
pro.	proötic
pro. a.	proatlas
ps.	parasphenoid
pt.	pterygoid
pt.f.	post-temporal fenestra
q.	quadrate
q.f.	quadrate foramen
qj.	quadratojugal
q. r. pt.	quadrate ramus of pterygoid
r.	radiale
ra.	radius
sa.	surangular
sc.	scapulacoracoid
scap.	scapula
sm.	septomaxilla
sM. f.	sub-Meckelian fossa
so. f.	suborbital fenestra
sp.	splenial
sq.	squamosal
s.r. I	first sacral rib
s.r. II	second sacral rib
st.	supratemporal
st. b.	stapedial boss
stp.	stapes
t.	tabular
ti.	tibia
tr. f. pt.	transverse flange of pterygoid
u.	ulna
ul.	ulnare
i–v	metacarpal and metatarsals
1–5	distal carpal and tarsals

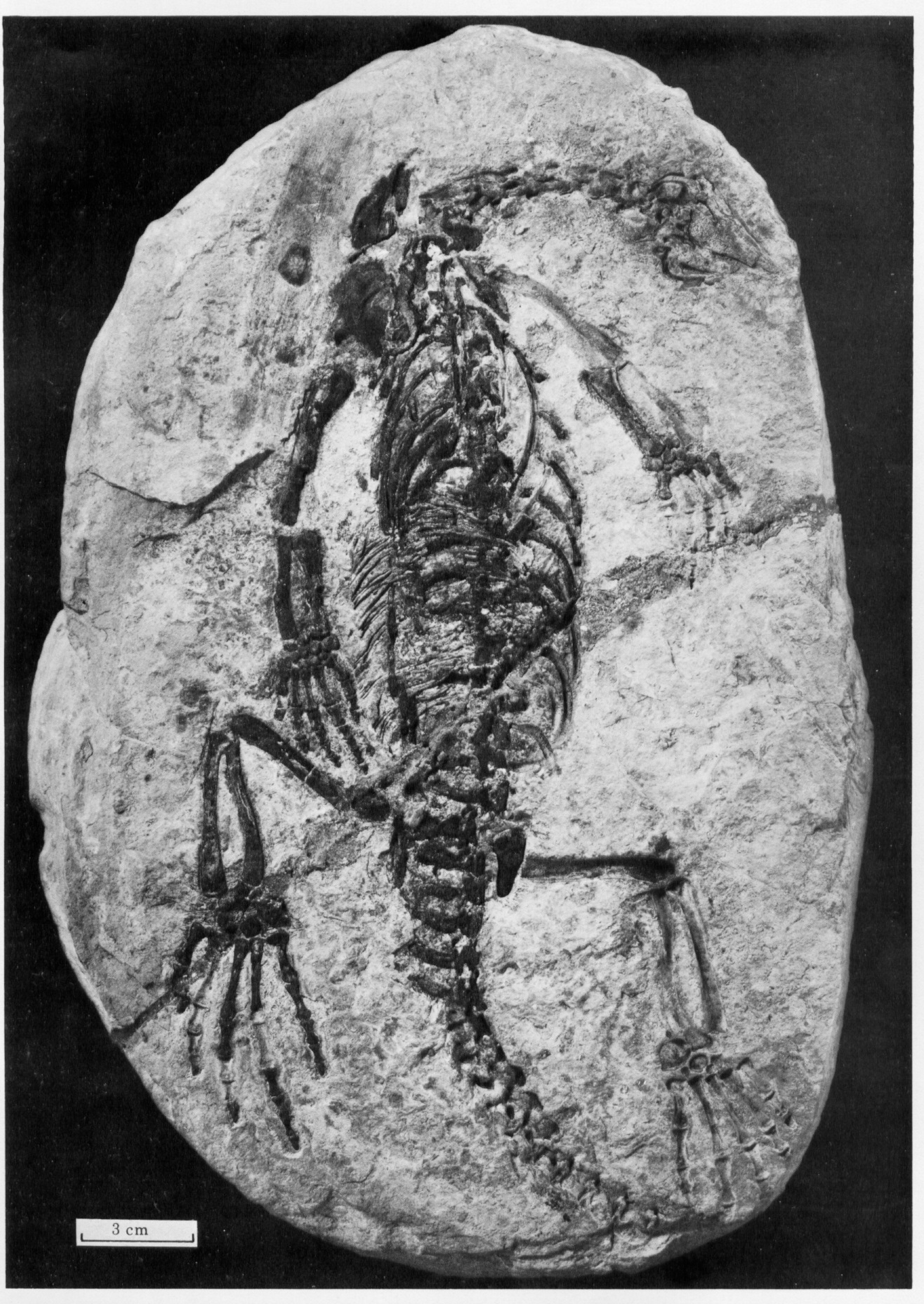

FIGURE 1. *Claudiosaurus germaini*, type specimen, Muséum National d'Histoire Naturelle, Paris (P.M.) 1978–6–1. Skeleton from the Upper Permian of Madagascar, primarily in dorsal view; mould of skull shows palate in ventral view.

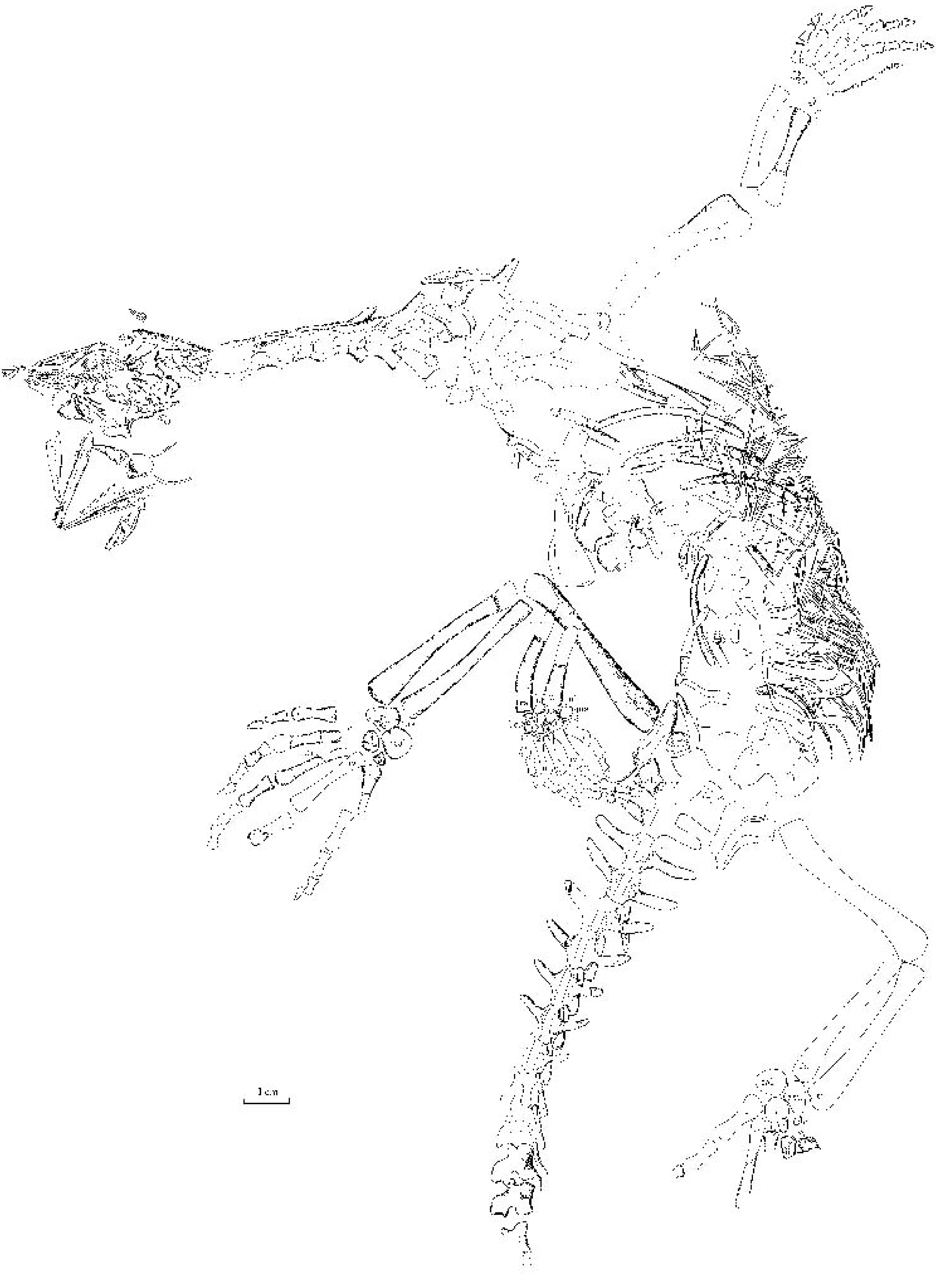

FIGURE 13. *Claudiosaurus germaini*: C.G. 20/8, drawing based on silicon cast.

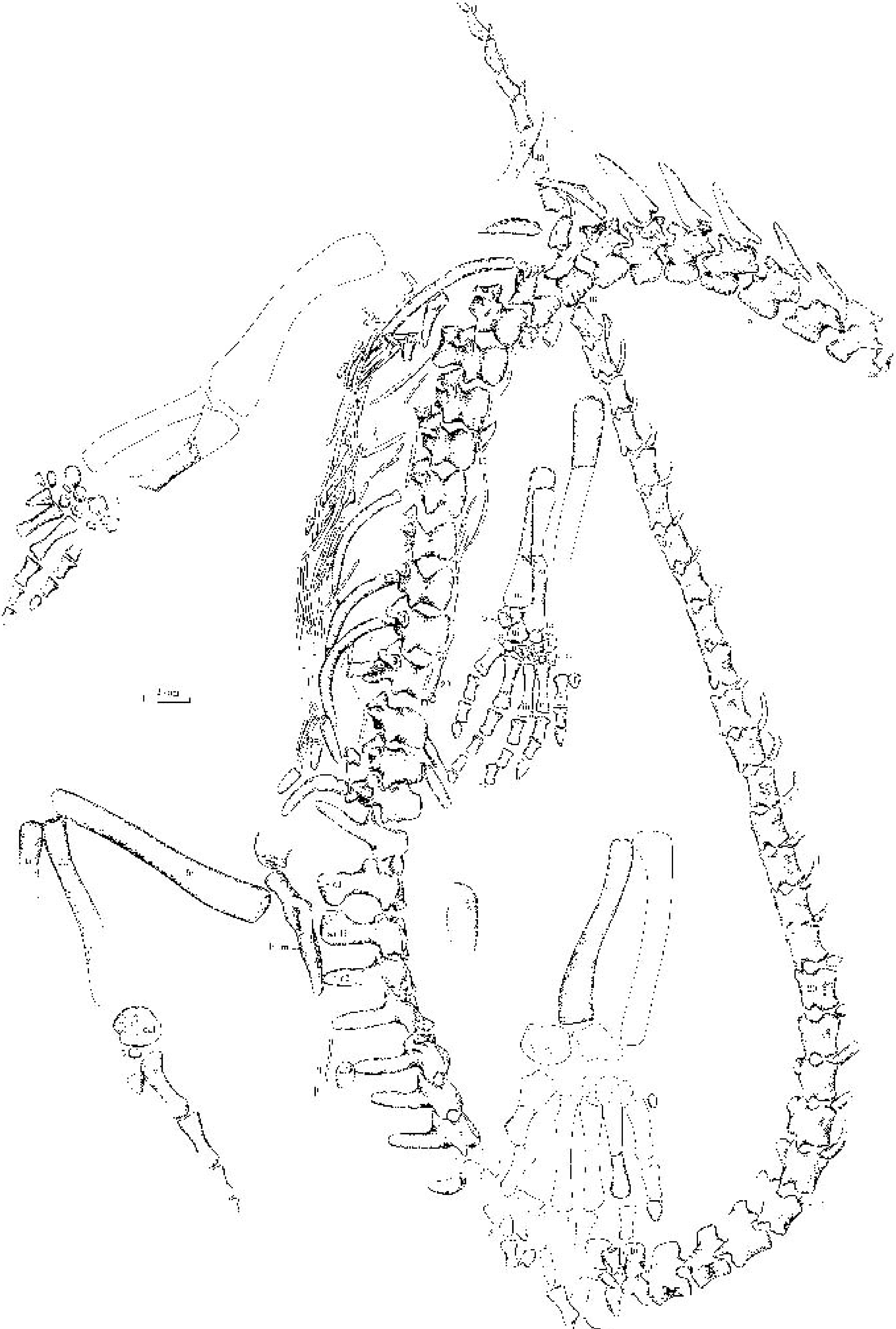

Figure 16. *Claudiosaurus germaini* C.G. 2074, nearly complete skeleton, lacking skull.

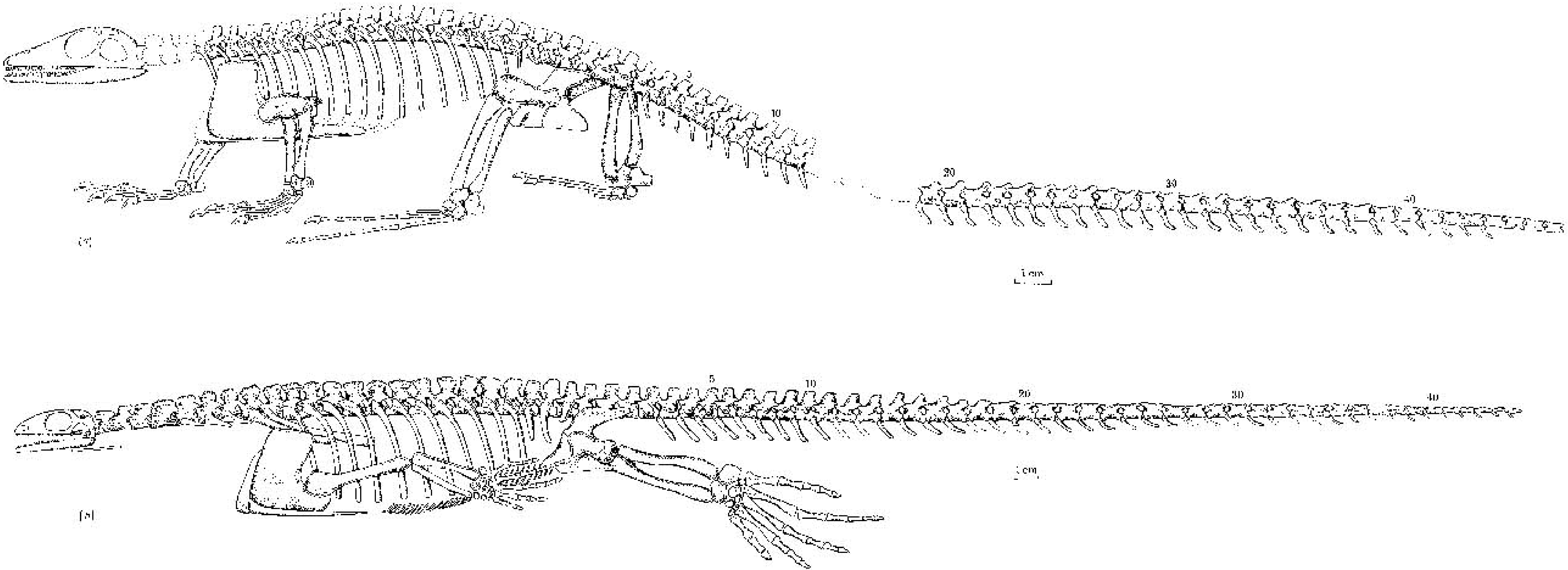

FIGURE 20. (*a*) *Thadeosaurus colcanapi*; restoration of skeleton in lateral view; skull from *Youngina*. (*b*) *Claudiosaurus germaini*: restoration of skeleton in lateral view, showing a swimming pose.

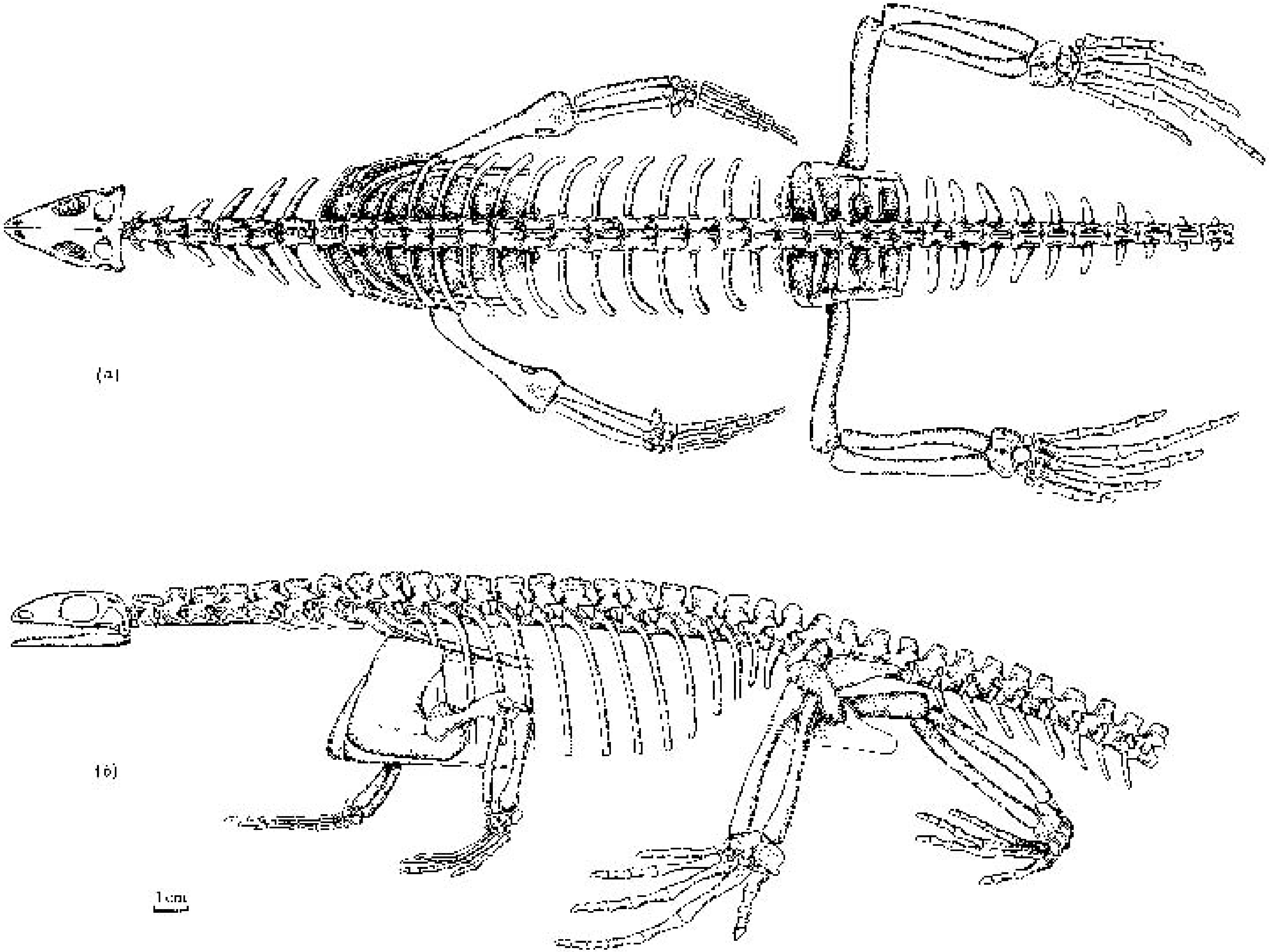

Figure 30. (a) *Claudiosaurus germaini*; restoration of skeleton in dorsal view, showing a swimming pose.
(b) *Claudiosaurus germaini*, restoration of skeleton in lateral view, showing a walking pose.