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Comparative osteology of *Mastodonsaurus giganteus* (JAEGER, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen)

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With 4 plates and 54 textfigures

Abstract

Mastodonsaurus giganteus, the most abundant and giant amphibian of the German Lettenkeuper, is revised. The study is based on the excellently preserved and very rich material which was excavated during road construction in 1977 near Kupferzell, Northern Baden-Württemberg. It is shown that there exists only one diagnosable species of *Mastodonsaurus*, to which all Lettenkeuper material can be attributed. All finds from other horizons must be referred to as Mastodonsauridae gen. et sp. indet. because of their fragmentary status. A second, definitely diagnostic genus of this family is *Heptasaurus* from the higher Middle and Upper Buntsandstein. Finally a diagnosis of the family Mastodonsauridae is provided.

A detailed osteological description of *Mastodonsaurus giganteus* reveals numerous unknown or formerly inadequately understood features, yielding data on various hitherto poorly known regions of the skeleton. The sutures of the skull roof, which could be studied in detail, are significantly different from the schemes presented by previous authors. The endocranium and mandible are further points of particular interest. The palatoquadrate contributes a significant part to the formation of the endocranium by an extensive and complicated epipterygoid. The neurocranium is dominated by the exoccipital, otic, and several portions of the sphenethmoid. For the first time the stapes is found in articulation and uncompressed. The mandible is slender and bears a massive postglenoid area, and the symphyseal area is extended to accommodate giant tusks. The prearticular forms a pronounced process anterior to the glenoid facet.

The axial skeleton is strongly ossified. It consists of massive, cylindrical intercentra that tend to be lower towards the tail and which have a dorsal incisure for the chorda, further it contains paired pleurocentra which are set in facets of the neural arch and intercentrum, and finally it bears low neural arches possessing posteriorly inclined, short and unfinished processus spinosi and broad, laterally extended transverse processes. The costal apparatus is wide, bearing broadened ribs in the anterior and middle part of the trunk which are strengthened by two different uncinate processes. While in the trunk these processes disappear tailwards, the tail base and anterior tail proper again bear wide ribs with marked processes.

Doctoral dissertation Univ. Tübingen 1998.

The girdles and appendages are well represented in the Kupferzell material, with the exception of the pes; because of their disarticulated state their original arrangement has to be reconstructed. The dermal bones of the pectoral girdle consist of broad and flattened claviculae and a wide, rhomboidal interclavicle which has, as is typical of capitosaurs, a stilette-like anterior process with a broadened tip. The ontogeny of the cleithrum and scapulocoracoid is documented in detail. Scapula and coracoid are separate at first, but later in development fuse to give a compound ossification, whose coracoid portion tends to increase in area. In addition the geometry and surface of the glenoid facet changes during ontogeny. The humerus is relatively slender and long, yet poorly differentiated with respect to most other temnospondyls. Only in the largest specimens are there definite epicondyles and a faint supinator process. Radius and ulna are well differentiated and elongate, and the manus consists mainly of slender metacarpals and phalanges. In the pelvic girdle the ilium is slender and low, with an acetabulum that enlarged during later development. The ischium is small and remains poorly differentiated. In larger specimens it appears to fuse with the pubis which is still unknown as isolated element. The femur is slender, elongate, and differentiated, whereas the lower leg gains less than half the length of the upper leg and has a rudimentary structure.

Finally open questions and problems regarding the reconstruction of the whole skeleton are discussed. This involves a clarification of the methods used and a discussion of the lines of evidence. A complete yet still partially provisional restoration of the skeleton of *Mastodonsaurus giganteus* gives an animal similar to a gigantic salamander. *Mastodonsaurus* was most similar to cryptobranchid salamanders in its bodily proportions such as the relative length of the trunk and tail, as well as the considerable breadth and flattness of the rib cage.

Zusammenfassung

Mastodonsaurus giganteus, das häufigste und größte Amphib der europäischen Mitteltrias, wird eingehend revidiert. Die Untersuchung geht aus von dem hervorragend erhaltenen und sehr umfangreichen Material, das beim Autobahnbau 1977 bei Kupferzell geborgen wurde. Im Lettenkeuper existiert nur eine diagnostizierbare Art von *Mastodonsaurus*, während die fragmentarischen Funde aus anderen Formationen lediglich der Familie Mastodonsauridae zugeordnet werden können. Die zweite, gegenwärtig faßbare Gattung dieser Familie ist *Heptasaurus*, die auf den höheren Mittleren und Oberen Buntsandstein beschränkt bleibt. Die taxonomische Revision schließt mit einer Diagnose der Mastodonsauridae.

Im Rahmen einer detaillierten osteologischen Untersuchung von *Mastodonsaurus giganteus* werden zahlreiche neue Merkmale beschrieben und viele, bisher unzureichend verstandene Regionen des Skeletts vorgestellt und rekonstruiert. Die Suturen im Schädeldach können dank der guten Erhaltung der Kupferzeller Funde erstmals genau erfaßt werden; sie weichen in einigen Punkten erheblich von den Schemata früherer Bearbeiter ab. Das Endocranium und die Mandibel von *Mastodonsaurus* bilden weitere Schwerpunkte. Das Palatoquadratum ist mit einem ausgedehnten und kompliziert gebauten Epipterygoid wesentlich an der Gestaltung des Endocranium beteiligt. Im knöchernen Neurocranium dominieren das Exoccipitale, das Oticum sowie verschiedene Portionen des Sphenethmoid; der Stapes wird erstmals unverdrückt und in Artikulation vorgefunden und vorgestellt. Im Unterkiefer, der sehr niedrig ist und eine massive, langgestreckte Postglenoid-Region besitzt, dominieren riesige Fangzähne in der verbreiterten Symphyse. Ein hoher, allometrisch positiv wachsender Fortsatz des Praearticulare bildet eine knöcherne Sperre unmittelbar vor dem Unterkiefergelenk.

Das Axialskelett ist stark verknöchert. Es besteht aus massiven, kurz-zylindrischen Intercentra, die zur Cauda hin niedriger werden und eine Inzisur für die Chorda aufweisen, weiterhin enthält es paarige Pleurocentra, die in Facetten des Neuralbogens und des Intercentrum eingelassen sind, und schließlich die Bögen selbst, die niedrig sind, mit nach hinten geneigten Dornfortsätzen und breit nach lateral vorgreifenden Transversalfortsätzen. Der Rippenkorb ist breit, im vorderen und mittleren Rumpf aus kräftigen Rippen bestehend, die mehrere Uncinat-Fortsätze tragen können. Diese werden im hinteren Rumpfabschnitt kürzer und verschwinden schließlich ganz, während im Schwanzskelett die Rippen erneut größer sind und auch dort blatt- bis stilettförmige Uncinat-Fortsätze tragen.

Die Gürtel und Extremitäten sind bis auf das Fußskelett gut dokumentiert, müssen jedoch weitgehend anhand disartikulierter Reste rekonstruiert werden. Der hautknöcherne Schultergürtel besteht aus breiten, großflächigen Claviculae und einer breitrhombischen Interclavicula, die den für Capitosaurier typischen, vorne verbreiterten anterioren Fortsatz trägt. Die Ontogenese des Cleithrum sowie der ersatzknöchernen Elemente läßt sich im Detail verfolgen. Die Scapula und das Coracoid sind anfangs getrennt und verschmelzen später suturlos, wobei sich der Coracoid-Anteil stark medial ausdehnt. Auch die Glenoidfacette erweitert und verkompliziert sich im Zuge der späteren Ontogenese. Der Humerus ist anfangs verhältnismäßig schlank, insgesamt relativ lang und bis in das hohe Alter von rudimentärer Gestalt verglichen mit den meisten anderen Temnospondylen; erst bei den größten Individuen bilden sich die Condyli an seinem Distalende sowie ein schwacher Supinatorfortsatz. Radius und Ulna sind lang und differenziert, und das Handskelett besteht aus überwiegend schlanken Metacarpalia und Phalangen. Im Beckengürtel findet sich ein niedriges und schlankes Ilium, dessen Anteil am Acetabulum sich im Alter vergrößert. Das Ischium ist klein und bleibt zeitlebens wenig differenziert; bei größeren Tieren scheint es mit dem Pubis, das bisher isoliert nicht bekannt ist, verschmolzen zu sein. Das Femur ist schlank, langgestreckt und differenziert, während Tibia und Fibula weniger als halb so lang werden und rudimentär bleiben.

Die Untersuchung schließt mit der Besprechung offener Fragen und Probleme bei der Rekonstruktion des Gesamtskeletts. Dabei werden getrennt nach einzelnen Regionen die wesentlichen Schritte bei der Rekonstruktion des Rumpfes und der Extremitäten behandelt. Eine in Abschnitten sicherlich noch vorläufige Gesamtrekonstruktion ergibt für *Mastodonsaurus giganteus* die Gestalt eines Salamander-artig langgestreckten Tieres, die in einigen Punkten – etwa der relativen Länge von Rumpf und Schwanz, der Breite des Brustkorbes und dem hohen Grad der Abflachung – dem Habitus rezenter Asiatischer Riesensalamander (Cryptobranchiden) am nächsten kommt.

Contents

1. Introduction

In 1824, G. F. JAEGER was the first to mention finds of giant bones from Triassic strata resembling those of salamanders. These were collected in an alum mine at Gaildorf near Schwäbisch Hall in northern Baden-Württemberg. JAEGER's brief note – written in Latin – was succeeded by a more informative and illustrated account on the material (JAEGER 1828), and basing on a tooth and a piece of a large occiput he erected two genera – *Mastodonsaurus* and *Salamandroides*. The first name, a greek translation for 'wart-toothed lizard', referred to the worn-off tip of a giant tooth from Gaildorf, while the second pointed at the resemblance to extant amphibians, notably salamanders, which have similar-shaped occipital condyles.

Several publications, most of them being brief notes, followed (for details see synonymy list), among them the first diagnostic characterization of this species which is now called *Mastodonsaurus giganteus*. OWEN (1841) compared the Gaildorf material with teeth encountered in the Upper Triassic Warwick Sandstone of Southern England. His studies of dental fine structure were an important contribution to the understanding of early tetrapod teeth, as he was the first to publish on the labyrinthic infolding of the dentine and enamel. This culminated in the birth of the name 'Labyrinthodontes', giving rise to a long-used, though nowadays somewhat outdated expression for certain large early tetrapods (labyrinthodonts). MEYER in MEYER & PLIENINGER (1844) replied to OWEN by emphasizing his earlier yet unpublished discovery of the labyrinthic infolding in *Mastodonsaurus*, and he believed the animal to be a reptile ('Saurus') rather than an amphibian ('Batrachus'). MEYER therefore supported the name *Mastodonsaurus* in favour of *Salamandroides* (cf. JAEGER 1828; ALBERTI 1834), *Batrachosaurus* (MUENSTER 1834), or *Labyrinthodon* (OWEN 1841). Even though MEYER was wrong in his understanding of *Mastodonsaurus* as an amniote (as we may translate his concept into modern terms), he and PLIENINGER (1844) gave a first detailed overview on the morphology of the skull and certain presacral bones. MEYER in particular added an interesting discussion in which he compared the cranial anatomy of *Mastodonsaurus* with many Recent forms; these investigations doubtlessly stand as a masterpiece of early comparative anatomy until the present day, and they are unparalleled by all subsequent authors.

QUENSTEDT (1850), following earlier arguments of JAEGER (1828) and others, finally explicitly argued for the amphibian nature of the labyrinthodont finds. It remains unclear whether the weight of QUENSTEDT's and OWEN's authorities, or the strength of their arguments at the end resulted in the broad consensus on this question recognised after 1870.

E. FRAAS (1889), F. v. HUENE (1922), WEPFER (1922a, b, 1923 a), and finally PFANNENSTIEL (1932) successively added new and more detailed information on cranial

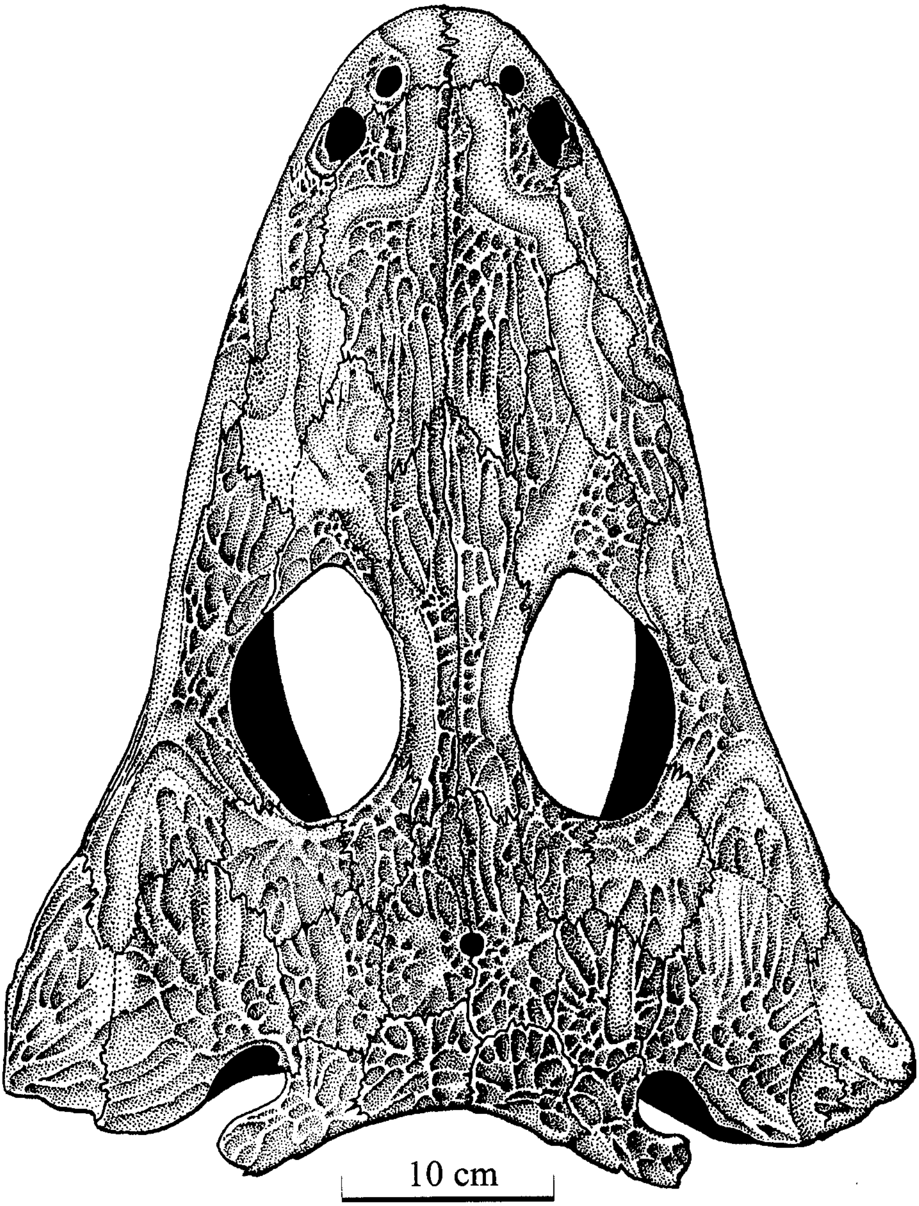


Fig. 1. Skull of *Mastodonsaurus giganteus* (JAEGER, 1828) in dorsal view (SMNS 54675; see also plate 2). Note the pronounced sculpturing of the dermal bones, the asymmetrical sutures, and the characteristic shape and large size of the orbits. The small openings anterior to the nares accommodated large tusks located on the mandibular symphysis.

and postcranial anatomy of the genus *Mastodonsaurus* (sensu lato), referring to material from Gaildorf and other Lettenkeuper localities (*M. giganteus*), as well as new material from the Upper Buntsandstein (*M. cappelensis* WEPFER, 1923), which was later assigned to the new genus *Heptasaurus* (SÄVE-SÖDERBERGH 1935).

Quite recently, rich and exceptionally well preserved material of *Mastodonsaurus giganteus* was discovered near the small town Kupferzell in Hohenlohe, northern Württemberg, during road works (Bundesautobahn 6, Heilbronn-Nürnberg) which transsected fossiliferous Lettenkeuper strata in spring, 1977. However, without the trained eyes of the engaged amateur collector JOHANN G. WEGELE, as well as the skilled and determined acting of the curator Dr. RUPERT WILD (and many other individuals then employed at the Staatliches Museum für Naturkunde Stuttgart) the finds would not have been recovered in this quantity and completeness. The excavation yielded more than twenty good skulls and thousands of single bones from all parts of the body. The quality of this material is optimally suited not only for a redescription of *Mastodonsaurus*, but also for detailed studies on the structure of the skeleton of large temnospondyls in general. It is fortunate that this historically so important species can be the focus of a detailed reinvestigation of stereospondyl amphibians, which form an important yet still little understood element in Triassic terrestrial ecosystems.

1.1. Outline of study

This study has three main interests: (1) a taxonomic clarification of all Middle European finds attributed to *Mastodonsaurus giganteus*, with particular emphasis on the taxonomy of the Kupferzell finds, (2) a detailed analysis of the osteology of *Mastodonsaurus giganteus* regarding all regions of the skeleton, with comments on taphonomy, preservation, and the problems related to disarticulation, and (3) a reconstruction of the skeleton, based on direct anatomical evidence, taphonomic evidence, and indirect evidence from the nearest fossil relatives of *Mastodonsaurus*.

The three sections are ordered as follows: the taxonomy section first clarifies the status of *Mastodonsaurus giganteus* and the Mastodonsauridae, thereby establishing a basis on which the succeeding sections operate. The osteological study forms the main part; it is subdivided into an introductive part which discusses the general structure of a particular structural unit, then continues with a detailed treatment of the anatomy of its components, and finally reviews the subject by focussing on some of the most conspicuous general structures, by which the single elements are integrated into the architectural frame. Finally a 3-d reconstruction of the skeleton is attempted, based on the osteological description and drawings, whereby single bones are successively added to the reconstructed region.

1.2. Stratigraphical range and geographical occurrence

The discovery of *Mastodonsaurus giganteus* dates back to a time of an awaking and intensive interest in the geology of Württemberg and neighbouring regions. Numerous practising geologists, miners, and not least various well-educated laymen began to work in the field (see reviews by WEBER 1990, 1992 a, b). Württemberg became particularly famous at the beginning of the last century as a fossil-bearing region, but only by the activity of the aforementioned people it became what HUENE later termed a "classical saurian country" (WILD 1980a).

The horizons rich in vertebrate fossils range from the Lower Triassic (Buntsandstein) up to the Upper Jurassic (Malm), and the peculiar southwest German geomorphology permits broad outcropping of all stratigraphic units (fig. 2). There is a general dip to the southeast. The main lithological units form slightly tilted plains each of which ends in an escarpment to the northwest. The landscape thus morphologically differentiated by erosional steps is therefore aptly called Schichtstufenland in German.

The Buntsandstein has its most extended outcrop in the northern Schwarzwald mountains; farther to the south it is restricted to the eastern margin of this mountain range.The Buntsandstein forms the lowermost unit of the Schichtstufenland which develops to the east and southeast. The following two steps in the landscape are formed by the escarpments of Muschelkalk and Keuper which overlay the Buntsandstein. The sequence of steps is continued by the escarpments of Lower and Middle Jurassic further southeast. The most spectacular step is then formed by the high and steep escarpment of the Upper Jurassic limestones of the Schwäbische Alb.

The main localities at which remains of the giant amphibian family Mastodonsauridae have been found are distributed on the outcroppings of two particularly fossiliferous stratigraphical units, the Upper Buntsandstein (Olenekian/Anisian boundary) and the Lettenkeuper (Upper Ladinian: Longobardian). The localities of the former are aligned along the margins of the Vosges, Schwarzwald, Odenwald, and Spessart mountains, whereas the localities of the latter (and only these are concerned by the present study) are situated especially in the vast outcrop in Hohenlohe, a region in northern Württemberg.

The Mastodonsauridae first appear in the Upper Buntsandstein at the eastern margin of the Schwarzwald mountain range (figs. 2, 3), as summarised recently by Kamphausen & Ortlam (1993). Even small bone fragments of mastodonsaurids are easily identified by their great thickness and the peculiar type of sculpturing; in larger fragments the advanced morphology, especially of the skull, is an unequivocal sign. To date, the family Mastodonsauridae encompasses two genera, *Heptasaurus* and *Mastodonsaurus*, which are separated by a considerable stratigraphical interval. *Heptasaurus* is abundant in the Pflanzensandstein topping the Violetter Horizont (VH) 5, below the Röttone (so4, Uppermost Buntsandstein), and most probably also occurs in equivalent horizons of the Prims Mulde, north of the Hunsrück mountains (Schmidt 1960; Jux & Pflug 1958; Jux 1962, 1966; Sander & Gee 1994). As far as can be said at this preliminary stage, all of these finds are attributable to *Heptasaurus cappelensis*, which was first described by Wepfer (1923 a) as a second species of *Mastodonsaurus*. An assemblage of almost fourty specimens, recovered between the villages Kappel and Niedereschach, between Villingen-Schwenningen and Rottweil, became famous (Wepfer 1922a, b).

Through the marine Muschelkalk sequence mastodonsaurid bones are found sporadically, particularly in the topmost part of the sequence, the Obere Terebratelbank (mo3). The finds designated as *Mastodonsaurus silesiacus* (Kunisch 1885) from the Lower Muschelkalk of Southern Poland are, as Schroeder (1913) noted, more reasonably attributed to *Parotosuchus (Capitosaurus)* sp. (Zittel 1887–90).

Definite mastodonsaurid fragments from the Oberer Muschelkalk consist of large labyrinthodont teeth, dermal skull roof fragments, vertebrae, and ribs. In theory, the enormous size of the tusks is diagnostic for the genus, although a similar capitosaur genus (*Eryosuchus*) with comparably large tusks appears in the Ural Forelands

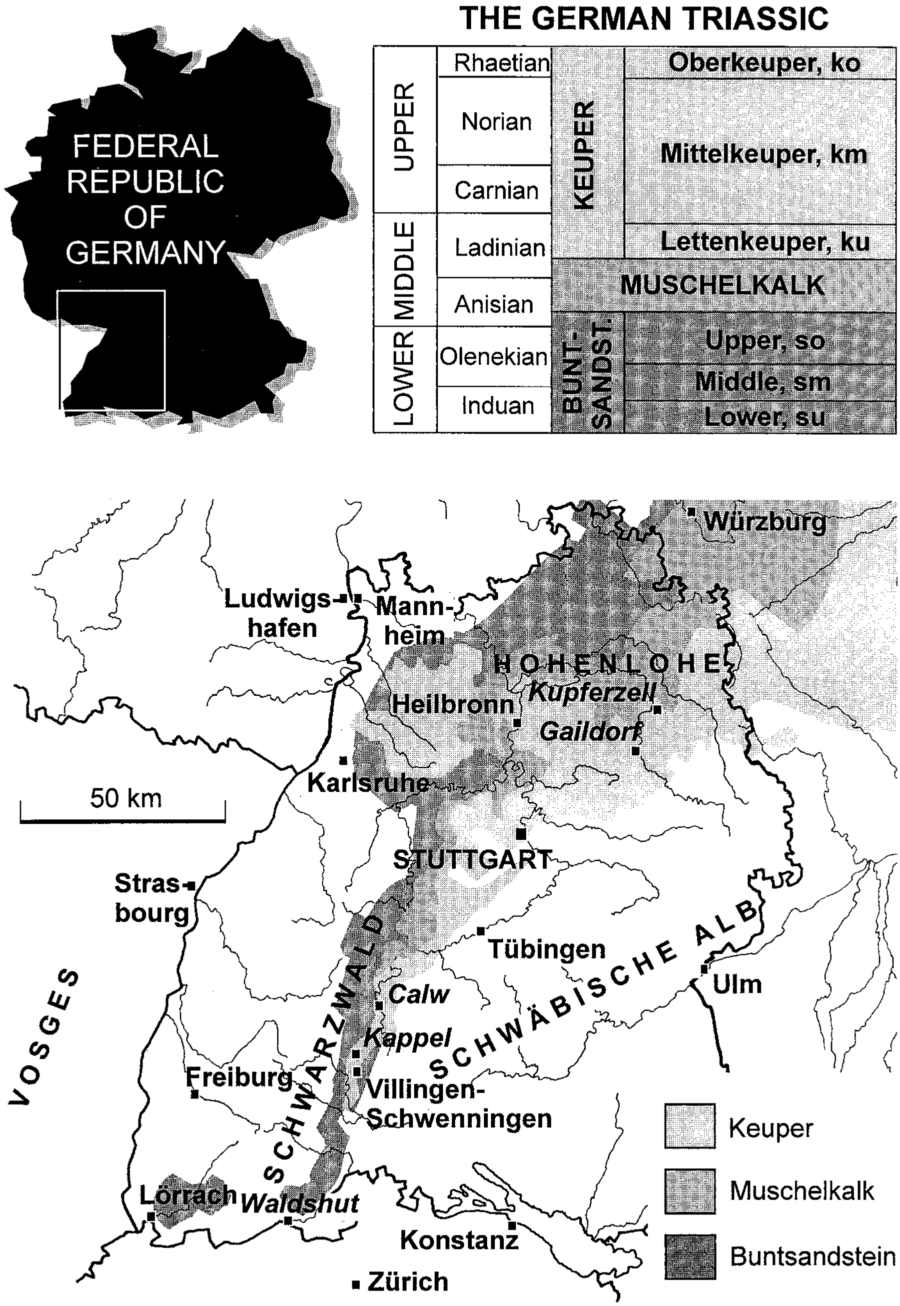


Fig. 2. Geographical occurrences of the Mastodonsauridae in southern Germany, and stratigraphical position of finds. Famous localities mapped onto geological setting.

(OCHEV 1972). However, by means of the above listed features, most of the larger finds are rather safely assigned to the Mastodonsauridae. The fragmentary nature of all these finds does not permit a clear assignment to *Mastodonsaurus giganteus*, the abundant and only Lettenkeuper mastodonsaurid species, but the very large size and high degree of ossification speaks in favour of *Mastodonsaurus* rather than *Heptasaurus*.

The Grenzbonebed usually bears many remains of *Mastodonsaurus*, which often stem from animals of the size exclusively gained by the species *M. giganteus* (i.e. a skull length of more than 60 cm). REIF (1971) and HAGDORN & REIF (1988) studied the composition and formation of these bonebeds and showed that they may contain very different faunal components. Remains of *Mastodonsaurus* thus appear therein in concert with marine, lacustrine, and terrestrial forms (HAGDORN & SIMON 1985).

Almost throughout the Lettenkeuper sequence (representing the deeper upper Ladinian stage), *Mastodonsaurus giganteus* occurs abundantly, and complete skulls were found in several stratigraphical horizons (fig. 4). HAGDORN & REIF (1988) compiled data on the occurrence of *Mastodonsaurus* in the Lettenkeuper, adding to earlier studies of PLIENINGER in MEYER & PLIENINGER (1844) and FRAAS (1889). The Lettenkeuper sediments of Württemberg and Franken and aspects of their palaeontology were studied by ZELLER (1908), WAGNER (1913), PROSI (1922), PATZELT (1964), BRUNNER (1973, 1977), URLICHS (1982), HAGDORN (1980 a, b, 1988), and WEBER (1992 a, b, 1996).

The Grenzbonebed is followed by the Vitriolschiefer, which consists of dark grey marls occasionally enriched in alum. It was mined in the 18th century, after the metal salts had long been used for colouring clothes in the vicinity of the outcrops (HAGDORN & SIMON 1985). There is a dissensus about the proper stratigraphical belonging of the mined sequence at Gaildorf (WEBER 1992a; HAGDORN 1988), where the first spectacular finds of *Mastodonsaurus* were made between 1820 and 1860.

In the following section light grey marls and dolomites alternate (Estherien-Schichten). Both sediments sporadically contain teeth, but *Mastodonsaurus* particularly occurs in a bonebed situated within the Estherien-Schichten, which otherwise contains many shark teeth and remains of rauisuchians (REIF 1974; HAGDORN & SIMON 1985). WEBER (1992a) argued for the Gaildorf Fossil-Lagerstätte to belong to this horizon, referring to sections studied by KURR (1852) and QUENSTEDT (1880). HAGDORN (1988) instead pointed out the lack of coal (which occurs in Gaildorf) in the Lower Lettenkeuper, and concluded that the famous mine was rather built in the Untere Graue Mergel (see below).

The Gaildorf Fossil-Lagerstätte [see FRAAS (1889), HAGDORN (1988), and WEBER (1992 a) for details] is peculiar in the presence of articulated specimens, which usually are very rare in other Lettenkeuper horizons. Hence the Gaildorf specimens constitute an important source of anatomical information. The preservation of vertebrates in this horizon is very variable, but usually distortion is strong exceeding that of localities such as Kupferzell-Bauersbach and Vellberg-Eschenau (see below).

The Hauptsandstein is the major gross-fraction unit in the Lettenkeuper sequence. Its thickness varies considerably, as its base is erosional, and in certain regions it directly overlies the Oberer Muschelkalk, although in reworking horizons indicating the former presence of the Vitriolschiefer, Blaubank, dolomites, and Estherien-Schichten. In many other regions the Hauptsandstein however is represented by argillaceous shales. The base of larger sandstone bodies frequently contains a bonebed enriched in labyrinthodont teeth, suggesting the presence of *Mastodonsaurus*.

The top of the Hauptsandstein may be locally overlain by grey to black shales, which in the Rothenacker Wald (Markgröningen) yielded a near-complete skull of *Mastodonsaurus giganteus* in 1867 (SMNS 4774). A field excursion performed by T. AIGNER (Tübingen) and A. ETZOLD (Freiburg) recently discovered a disarticulated partial skeleton of *Mastodonsaurus* in a grey shale equivalent to the Hauptsandstein (Baresel quarry, Vaihingen an der Enz), now also housed in Stuttgart (SMNS 80479).

The next horizon is a locally dark, rigid carbonate layer (Alberti-Bank) bearing scales of actinopterygian fishes, dipnoan teeth, thecodont teeth, and bones of *Mastodonsaurus* (especially in the *Serrolepis*-Bank, see HAGDORN & REIF 1988).

Further above, the Sandige Pflanzenschiefer, a variably argillaceous shale enriched in plant fragments, may be locally rich in vertebrate fossils. At Michelbach an der Bilz, south of Schwäbisch Hall, several partially articulated amphibian skeletons, among them one partial skeleton of *Mastodonsaurus*, a plagiosaurid, and two trematosaurid specimens were found (HAGDORN 1980 a; unpublished data).

The Upper Lettenkeuper starts with a calcareous to dolomitic section, the Anthrakonitbank, whose top often bears a bonebed. The following, much thicker unit is however richer in large and well-preserved vertebrate remains: the Untere Graue Mergel near a thickness of 2 m, and are mainly brown to green marls and clays, interrupted by thin carbonate layers. Since the last century especially finds of *Mastodonsaurus* and plagiosaurs have been made, most of them being housed in the collections at Stuttgart and Tübingen. During the ongoing construction of the Autobahn Heilbronn-Nürnberg the Untere Graue Mergel were cut at several sites in Hohenlohe. Two of them, one close to the village Bauersbach (Gemeinde Kupferzell), and one near to the Heidehöfe (Wolpertshausen), revealed particularly rich vertebrate faunas.

A large excavation at the Kupferzell site, carried out by the SMNS and with the help of amateur collectors (J. G. WEGELE, R. MUNDLOS, and J. TÖPFER) gave numerous specimens of *Mastodonsaurus giganteus*, and about 30,000 disarticulated bones, teeth, and coprolithes (WILD 1978 a-c, 1980 a-b, 1981; SCHOCH & WILD 1999 a; and section 1.3 herein) (fig. 5). H. HAGDORN collected a range of valuable specimens at the Wolpertshausen locality, now housed in the Muschelkalk Museum Ingelfingen. An additional site where Untere Graue Mergel are particularly fossiliferous is the Schumann quarry near Vellberg-Eschenau, where also well-preserved skulls and partially articulated skeletons of *Mastodonsaurus* have been found in the last decades (KUGLER & BARTHOLOMÄ 1985; R. WILD, pers. comm.). The Untere Graue Mergel were studied in detail by URLICHS (1982) who compared various sections, especially in the area of Kupferzell, including those at the excavation site.

The Hohenecker Kalk, confined to the Ludwigsburg region and famous for the occurrence of *Neusticosaurus pusillus*, also yielded the two large specimens of *Mastodonsaurus acuminatus* FRAAS, 1889, which are shown to be junior synonyms of *M. giganteus* here. The finds in this horizon are usually strongly flattened and distorted. Equivalent horizons in the Lettenkeuper of eastern Thüringen (Molsdorf near Arnstadt) have also yielded a suite of cranial and postcranial remains of *Mastodonsaurus giganteus* (SCHMIDT 1931).

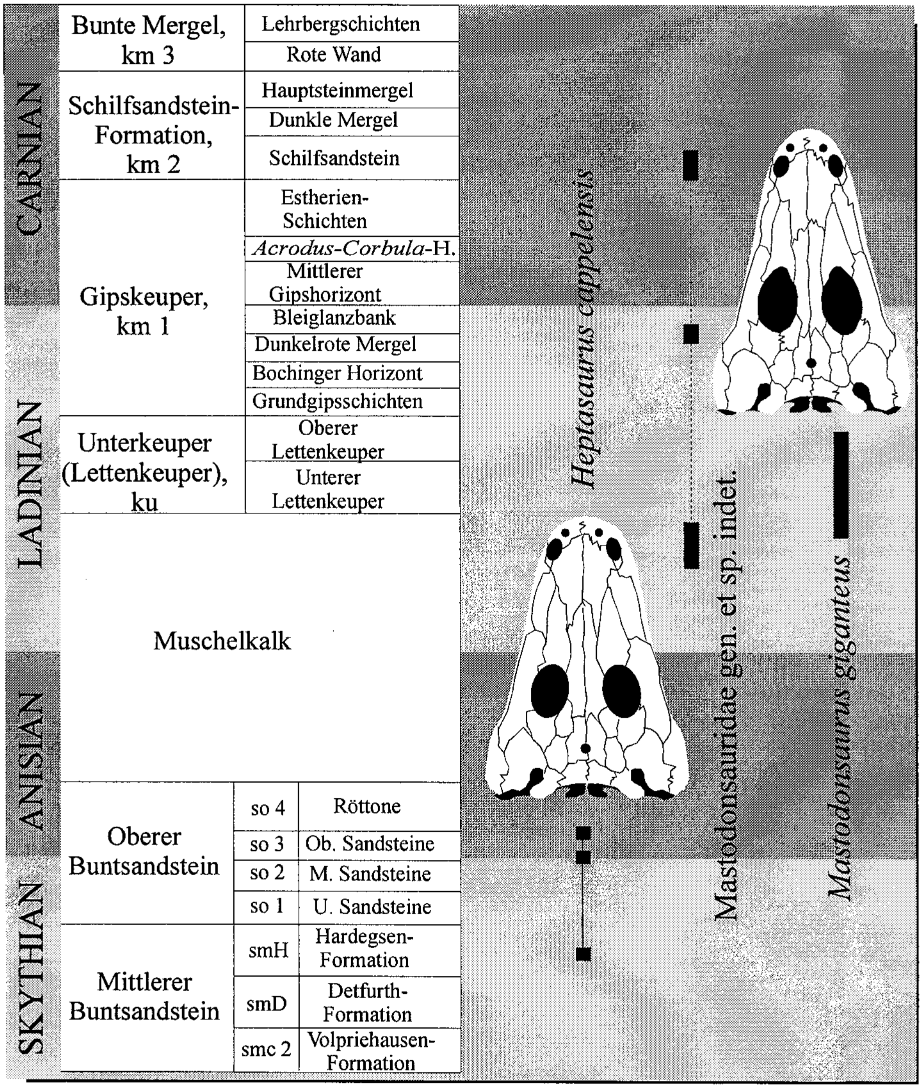


Fig. 3. Stratigraphical range of the Mastodonsauridae in the German Triassic, based on a recent survey of available material and information. Modified from Brunner (1973).

A locality close to this site, between the villages Molsdorf and Thörey, which has been recently opened by road works, gave numerous bones of *Mastodonsaurus*, plagiosaurs, and nothosaurs in several horizons. One of them appears to be an equivalent of the Lingula-Dolomit, as already presumed by Schmidt (1931). In Bedheim (Hildburghausen, southern Thüringen), Rühle von Lilienstern (1935) reported a find of *Mastodonsaurus acuminatus* from a sandstone in the uppermost Lettenkeuper sequence, slightly below the Grenzdolomit. Werneburg has recently (1994) reviewed the faunistic and stratigraphical data on this site.

The subsequent entire Gipskeuper sequence (lower Mittelkeuper, km$_1$), is poor in mastodonsaurid finds except for labyrinthodont teeth, such as those found in Gaildorf (HAGDORN & SIMON 1985). Recently, C. KLUG (Tübingen) collected vertebral intercentra of a mastodonsaurid from the Quarzitbank, at the top of the Dunkle Mergel (Ladinian/Carnian boundary).

The Schilfsandstein section (higher Mittelkeuper, km$_2$) again is particularly rich in temnospondyl amphibians, especially the stereospondyls *Cyclotosaurus* and *Metoposaurus* (MEYER & PLIENINGER 1844; QUENSTEDT 1850; FRAAS 1913). Besides the last definite trematosaurid find worldwide (*Hyperokynodon keuperinus*, see HELLRUNG 1987 and SCHOCH, MILNER & HELLRUNG in preparation), the Schilfsandstein has also revealed a snout fragment of a mastodonsaurid (FRAAS 1913). Although a clear assignment of this find is at this stage not possible, a stratigraphical range of the genus *Mastodonsaurus* well into the Mittelkeuper cannot be ruled out.

1.3. Lithology and fauna of the Kupferzell Fossil-Lagerstätte

URLICHS (1982) described the local lithology and commented on aspects of invertebrate palaeontology and palaeobotany at Kupferzell. According to his findings, lithology and fossil content vary considerably within the excavated area. The richest samples were found in the southern part of the area, and there also the vertebrate-bearing strata reached their maximal thickness (figs. 4, 5).

The Untere Graue Mergel form a horizon of variable thickness, which is largely grey to brown in colour, with a rather limited content of vertebrate fossils in general. Only in its topmost part, immediately below the Anoplophora-Dolomite, an enrichment in vertebrate bones, sometimes even articulated skeletons, is recorded. A similar situation is known in the Schumann quarry near Vellberg-Eschenau, differing in that preservation is generally better in Kupferzell, and the result of compaction less pronounced. In both localities, three different fossil-bearing horizons have been recorded (from bottom to top): (1) greenish-grey clay, (2) brown clay or marl, whose base sometimes attains the appearance of a bonebed, and (3) yellow carbonates (fig. 5).

The greenish layer in Kupferzell contains a large number of well-preserved yet often isolated bones. The majority of finds was made in this horizon. Although disarticulated, the bones are generally not worn-off or damaged. In addition, numerous complete skulls of *Mastodonsaurus* have been found in this layer, including some disarticulated specimens such as the giant specimen (SMNS 81310) or the medium-sized, partially articulated specimen (SMNS 80913). In Vellberg-Eschenau the greenish layer is thinner and less rich in fossils; in addition most of the bones are isolated and some suggest wearing from a longer transport, which has only rarely been observed among the Kupferzell finds.

The brown clay is characterized by a lower concentration of finds, which are however more clearly articulated or only partially disarticulated as compared with those in the greenish layer. This is most obvious in the case of completely articulated plagiosaurid skeletons. In Vellberg-Eschenau the single bones are frequently fragmented, though still being partially articulated.

The carbonates, which form the basal layer of the Anoplophora-Dolomite, only rarely bear fossils in Kupferzell, such as a partial skeleton of *Nothosaurus mirabilis*. In the Schumann quarry instead, this horizon may locally contain articulated

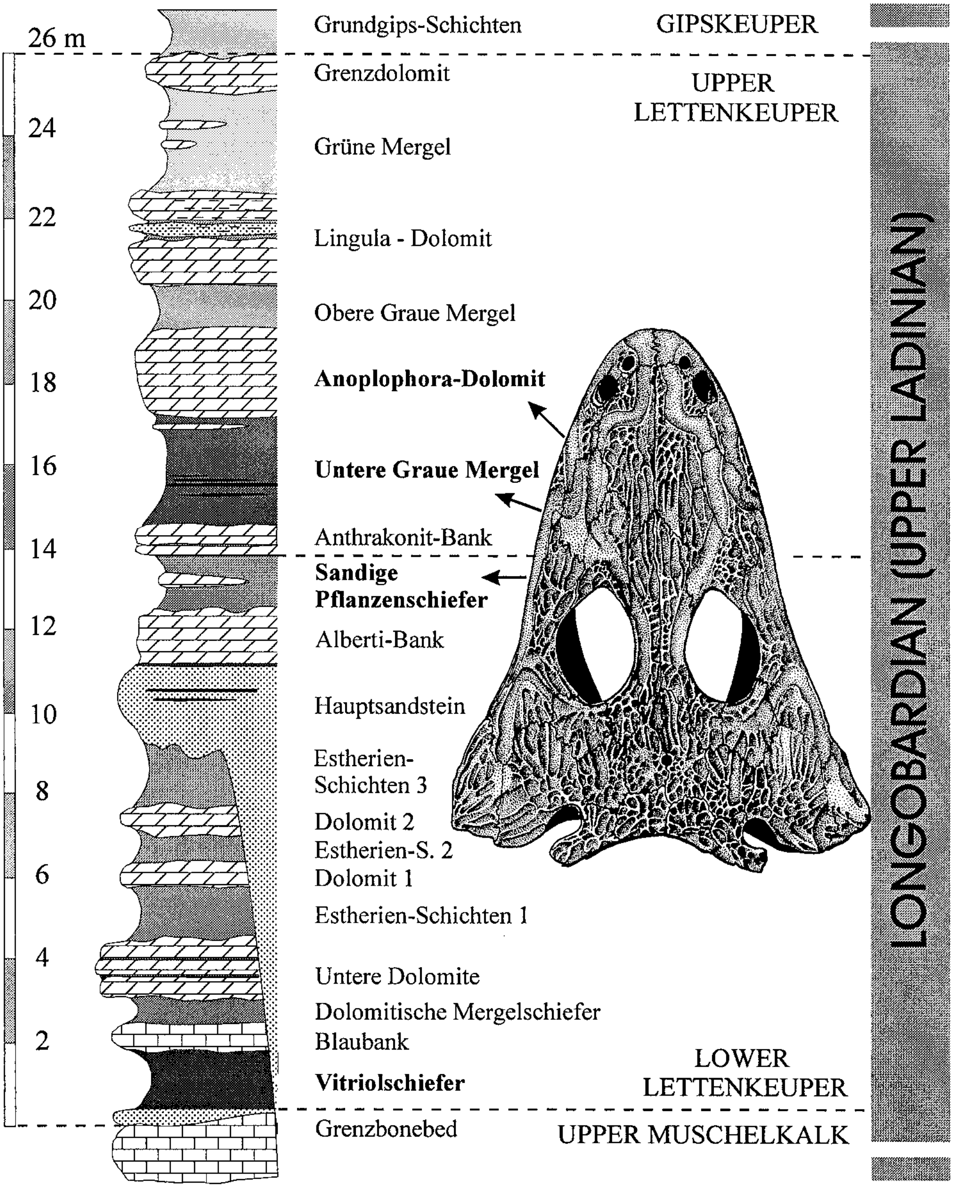


Fig. 4. Lithological section through the Lettenkeuper (Unterkeuper, Erfurt Formation) in the Hohenlohe region, northern Baden-Württemberg (modified after Brunner 1973). High concentration of mastodonsaurid bones in horizons indicated by bold letters.

skeletons of *Mastodonsaurus*, and also one rauisuchian was found (R. Wild pers. comm.).

Ongoing studies reveal that the following vertebrates definitely occur at Kupferzell; most of them have meanwhile been identified from other Lettenkeuper localities as well (fig. 6). Most amphibians belong to the Stereospondyli; an overview on the current systematic concept of this group is given in fig. 7.

1. Pisces

– Chondrichthyes:	*Hybodus* sp., *Acrodus* sp., etc. (R. Böttcher and D. Seegis, pers. comm.);
– Actinopterygii:	*Serrolepis* sp., *Gyrolepis* sp. (Wild 1980a);
– Actinistia:	gen. et sp. indet. (R. Böttcher and D. Seegis, pers. comm.);
– Dipnoi:	*Ptychoceratodus serratus* (Schultze 1981).

2. Amphibia

– Plagiosauridae:	*Plagiosuchus pustuliferus* (Wild 1980a; Hellrung, in prep.) *Gerrothorax* n. sp. (Hellrung, in prep.);
– Capitosauridae:	*Kupferzellia wildi* (Wild 1980a; Schoch 1997a);
– Mastodonsauridae:	*Mastodonsaurus giganteus* (Wild 1980a; Schoch 1997a);
– Trematosauridae:	*Bukobaja* cf. *enigmatica* (SMNS 56252, 57003, 80968, 84122–84126) (see Ochev 1972);
– Almasauridae:	n. g. n. sp. (SMNS 55385);
– Chroniosuchia:	n. g. n. sp. (SMNS 81698).

3. Reptilia

– Prolacertilia:	*Tanystropheus* cf. *conspicuus* (Wild 1980a);
– Lepidosauria:	gen. et sp. indet. (Wild, pers. comm.);
– Sauropterygia:	*Nothosaurus* n. sp. (Wild 1980a; pers. comm.); *Neusticosaurus* cf. *pusillus* (Wild 1980a);
– Rauisuchia:	n. g. n. sp. (Wild 1980a-c; Gower, in press).

4. Synapsida

– Cynodontia:	Gomphodontidae indet. (Wild 1980; Sues & Hopson, in prep.).

1.4. Material examined

All studied material was found in the Lettenkeuper of southern Germany. The examined specimens were for the largest part excavated during spring 1977 at Kupferzell, and they were prepared in the time since by employees of the SMNS, particularly by Dr. R. Wild and Mrs. B. Wild, J. Ginder, Th. Rathgeber, N. Adorf, as well as J. G. Wegele (Waldenburg). The specimens were almost throughout catalogued by R. Wild and the author, with the assistance of D. Metzger, M. Rücklin, F. Grossmann, and B. Greenwood, then practical students at the SMNS.

A small part of the material was collected and catalogued in the last century and early part of this century; these specimens are almost throughout from the Gaildorf mine, the Rothenacker Wald near Markgröningen, or from Hoheneck near Ludwigsburg. Of these, several finds from Gaildorf are lost, while certain others suffered considerable damage and had to be restored in the erly 1970s (see below).

1.4.1. *Mastodonsaurus giganteus*

1. SMNS 4698. Complete skull with mandibles (60 cm). Locality: Locus typicus. Horizon: Stratum typicum. References: Meyer & Plieninger (1844: 11, pl. 6fig. 1, pl. 7 fig. 1), Fraas (1889: Schädel I), Huene (1922).

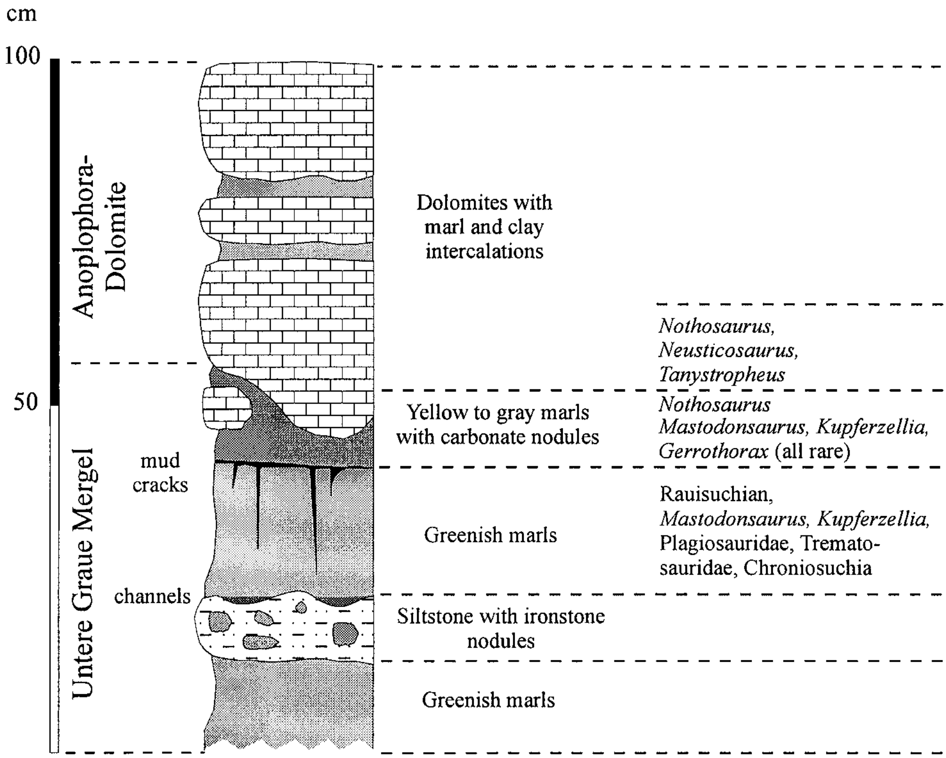


Fig. 5. Lithology of the fossiliferous horizons at the Kupferzell excavation site. Based on a recent compilation of unpublished stratigraphical data, some of them provided by courtesy of R. WILD and M. URLICHS. See WILD (1980a), URLICHS (1982), and SCHOCH & WILD (1999a) for further information.

2. SMNS 54679. Complete skull with mandibles (60 cm), damaged and restored in many regions. Locality: Locus typicus. Horizon: Stratum typicum. References: MEYER & PLIENINGER (1844: 11), FRAAS (1889: Schädel II).

3. SMNS 4707. Large, complete skull with mandibles (74 cm) and anterior part of vertebral column (9 intercentra). Condition rather poor, most sutures are invisible and dermal bone surface worn off. Locality: Locus typicus. Horizon: Stratum typicum. References: MEYER & PLIENINGER (1844: first specimen, p. 11), FRAAS (1889: Schädel III).

4. SMNS 4938. Tip of snout (estimated length 65 cm), poor condition. Locality: Locus typicus. Horizon: Stratum typicum.

5. SMNS 4774. A near-complete skull (75 cm), partially restored, with particularly coarse sculpturing. Locality: Rothenacker Wald near Markgröningen, Baden-Württemberg. Horizon: Hauptsandstein. References: FRAAS (1889: Schädel IV)

6. SMNS 740. Medium-sized palate (52 cm) exposed in ventral view. Locality: Hoheneck near Ludwigsburg, Baden-Württemberg. Horizon: Hohenecker Kalk. References: FRAAS (1889: 105, pl. 7: *M. acuminatus*).

7. SMNS 4194. Large skull roof (66 cm) in ventral view. Locality: Hoheneck near Ludwigsburg, Baden-Württemberg. Horizon: Hohenecker Kalk. References: FRAAS (1889: 105, pl. 8, fig. 1: *M. acuminatus*).

8. SMNS 54675. Complete skull (60,5 cm), almost undistorted, with perfectly preserved braincase. Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer. References: WILD (1978, 1981: figs. 4, 5).

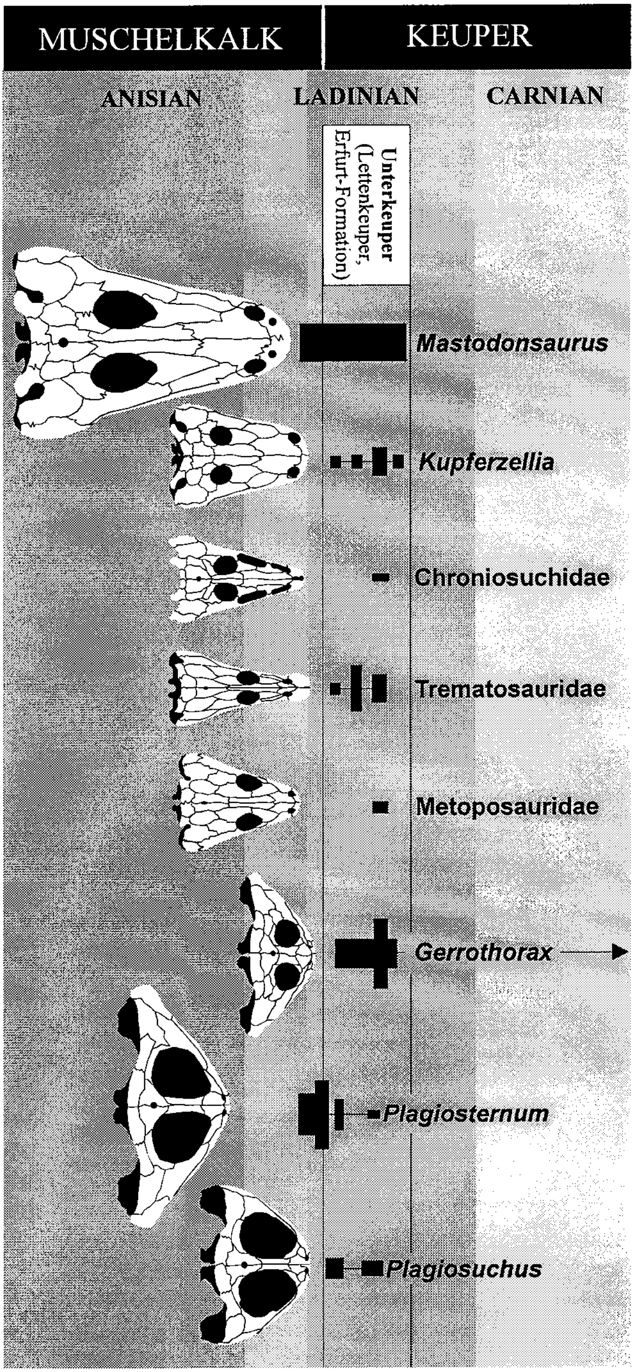


Fig. 6. Synopsis of the temnospondyl amphibian fauna in the Lettenkeuper. Based largely on new finds. Occurrence and relative frequency in different Lettenkeuper horizons are mapped; broad bars indicate high frequency of diagnostic finds. The differences in frequency among plagiosaurids is especially notable. Further details are provided by SCHOCH & WILD (1999a).

9. SMNS 54677. Complete skull (51 cm) with mandible in articulation (figs. 8, 17). Locality: Kupferzell. Horizon: Untere Graue Mergel, brown layer. References: Wild (1980).

10. SMNS 54678. Complete skull (54,5 cm) (figs. 12, 13). Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer. References: Ziegler (1986: fig. 150).

11. SMNS 80249. Posterior rim of skull (? 70 cm) with well-preserved braincase . (Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

12. SMNS 80704. Complete skull (55 cm) with mandible. Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

13. SMNS 80878. Near-complete skull (about 65 cm) with parts of mandible. Locality: Kupferzell. Horizon: Untere Graue Mergel, brown layer.

14. SMNS 80887. Snout fragment (? 60 cm). Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

15. SMNS 80889. Complete skull (59 cm) with mandible, partly dislocated right side. Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

16. SMNS 80890. Postorbital part of skull (about 40 cm skull length). Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

17. SMNS 80905. Partial, disarticulated skull (about 45 cm skull length). Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

18. SMNS 80913. Fragmentary skull (75 cm total length) with 28 presacral vertebrae. Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

19. SMNS 81310. Catalogued and frequently referred to as "Riesenexemplar von Kupferzell". Complete mandible (145 cm) with few remnants of the palate and a total of 28 presacral and 6 caudal vertebrae, 6–8 neural arches, 20 pleurocentra, and about 40, largely complete ribs from all regions in the axial skeleton. All elements were found in close proximity, and in association with a much smaller specimen of *Mastodonsaurus giganteus*, as well as several isolated, giant teeth of *Mastodonsaurus*. Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

20. SMNS 81368. Posterior part of palate, with attachment sites for braincase elements. Locality: Kupferzell. Horizon: Untere Graue Mergel, green layer.

Isolated cranial material consists of the following, rich body of specimens: 7 premaxillae, 3 maxillae, 4 jugals, 3 quadratojugals, 4 squamosals, 10 tabulars, 7 postparietals, 6 supratemporals, 5 postorbitals, 5 postfrontals, 5 parietals, 3 frontals, 5 nasals, 3 lacrimals, 3 prefrontals, 20 quadrata, 31 exoccipitals, 14 pterygoids, 10 parasphenoids (often fragmentary), 12 stapes, 15 epipterygoids, 2 palatines, and 2 ectopterygoids. There are several entirely unprepared skulls, and a large number of unprepared disarticulated cranial elements in the Stuttgart collection.

Further, 9 complete and prepared mandible halves are housed in the SMNS (54675, 56634, 80871, 80872, 80874, 80879, 80880, 80881, 80882). About 40 further fragments from all regions of the lower jaw have been investigated for this study.

Postcranial material. 1. Gaildorf (Locus typicus, stratum typicum): SMNS 4698 [20 vertebrae, mentioned by Plieninger in Meyer & Plieninger (1844) and Fraas (1889)], SMNS 56630 [the one figured in part by Meyer & Plieninger 1844, and referred to by Fraas (1889) and Huene (1922)], SMNS 4706 [left clavicle with ulna and part of manus, figured by Fraas (1889), right clavicle with badly preserved phalanges and carpal elements, fragmentary interclavicle, both scapulocoracoids, 1 radius, and about 10 presacral vertebrae]. In addition the Gaildorf material of the SMNS encompasses 10 ribs, 3 ilia, 1 fibula, 2 interclavicles, and one large clavicle. The GPIT possesses additional specimens: (1) three intercentra, neural arches, and rib fragments in articulation, and (2) various isolated presacral intercentra.

2. 1977 Kupferzell excavation (Untere Graue Mergel, almost throughout green layer, information by courtesy of R. Wild and M. Urlichs): About 120 prepared and catalogued, isolated presacral intercentra are housed in the SMNS. In addition there are at least 25 caudal intercentra prepared, 20 pleurocentra, 30 mostly very fragmentary neural arches, and 114 isolated ribs from all regions of the body. The appendicular skeleton is also well-represented: 13 cleithra, 25 claviculae, 29 interclaviculae (the numerous fragments not counted), 12 scapulocoracoids, 12 humeri, 5 radii, 3 ulnae, 10 phalanges, 19 ilia, 10 ischia, 8 femora, 1 tibia, and 1 fibula.

3. 1989 excavation at Vellberg-Eschenau (Untere Graue Mergel): 20 giant intercentra of a specimen of which the skull is in the private collection of Mr. Berner (Heilbronn).

1.4.2. Temnospondyl material studied for comparative purposes

A large suite of temnospondyl taxa housed in different institutions was examined, the number of studied specimens given in brackets.

AMNH: *Edops craigi* (cast of holotype), *Trimerorhachis insignis* (15), *Isodectes* sp. (1), *Isodectes (Saurerpeton) obtusus* (3), *Eryops megacephalus* (12), *Stanocephalosaurus birdi* (1).

BPI: *Rhinesuchus* sp. (5), *Rhineceps nyasaensis* (1), *Uranocentrodon senekalensis* (2), *Broomistega* sp. (1), *Lydekkerina huxleyi* (2), *Eolydekkerina magna* (1), *Kestrosaurus dreyeri* (2), *Parotosuchus africanus* (1).

GPIT: *Dvinosaurus* sp., cast (1), *Trimerorhachis* sp. (5), *Eryops* sp. (4), *Sclerocephalus* sp. (5), *Cheliderpeton latirostre* (2), *Archegosaurus decheni* (2), *Parotosuchus nasutus*, cast (1), *Heptasaurus cappelensis* (1 original, 1 cast),

IGWH: *Trematosaurus brauni* (38), *Parotosuchus nasutus* (23).

PIN: *Dvinosaurus primus* (2), *Thoosuchus jakovlevi* (6), *Prothoosuchus samariensis* (2), *Angusaurus dentatus* (1), *Benthosuchus sushkini* (5), *B. uralensis* (1), *Wetlugasaurus angustifrons* (2), *W. samaransis* (1), *Parotosuchus orientalis* (1), *P. orenburgensis* (1), *Eryosuchus antiquus* (1), *E. tverdochlebovi* (1), *E. garjainovi* (8), giant *Eryosuchus* sp. from the Bukobay Formation of Kazakhstan (1), *Mastodonsaurus torvus* (1), *Cyclotosaurus* sp. (1), "*Cyclotosaurus*" sp. from Arizona, cast (1), *Bukobaja enigmatica* (1).

SAM: *Lydekkerina huxleyi* (3), *Rhinesuchus* sp. (1), *Phrynosuchus whaitsi* (1), *Cyclotosaurus albertyni* (1).

SMF: *Parotosuchus nasutus* (2), *P. helgolandiae* (cast), *Lyrocephaliscus euri* (2), *Benthosuchus sushkini* (1).

SMNK: *Sclerocephalus haeuseri* (1), *Heptasaurus cappelensis* (remains of about 12 specimens), *Eocyclotosaurus* sp. (1).

SMNS: *Sclerocephalus haeuseri* (12), *Cheliderpeton latirostre* (2), *Archegosaurus decheni* (2), *Lydekkerina* sp. (1), *Benthosuchus* sp. (1), *Thoosuchus jakovlevi* (1), *Trematosaurus brauni* (4), *Hyperokynodon keuperinus* (2), *Parotosuchus nasutus* (3), *Heptasaurus cappelensis* (5), *Eocyclotosaurus woschmidti* (1), *E. lehmani*, cast (1), *Eocyclotosaurus* n. sp. from Arizona, cast (1), *Stenotosaurus semiclausus* (1), *Meyerosuchus fuerstenberganus*, cast (1), *Odenwaldia heidelbergensis*, cast (1), *Kupferzellia wildi* (18), *Cyclotosaurus robustus* (3), *C. posthumus* (1), *C. mordax* (6).

UCMP: *Trimerorhachis insignis* (13), *Zatrachys serratus* (11), *Eryops* sp. (2), *Wellesaurus peabodyi* (12), *Eocyclotosaurus* n. sp. (6).

1.5. Institutional abbreviations

AMNH: American Museum of Natural History, New York
BPI: Bernard Price Institute of Palaeontology, Johannesburg
GPIT: Institut und Museum für Geologie und Paläontologie, Tübingen
IGWH: Institut für Geologische Wissenschaften und Geiseltalmuseum, Halle
MMI: Muschelkalk Museum, Ingelfingen
PIN: Paleontological Institut of the Russian Academy of Sciences, Moscow
SAM: South African Museum, Cape Town
SMF: Naturkundemuseum Senckenberg, Frankfurt
SMNK: Staatliches Museum für Naturkunde in Karlsruhe, Karlsruhe
SMNS: Staatliches Museum für Naturkunde in Stuttgart, Stuttgart
UCMP: University of California Museum of Paleontology, Berkeley.

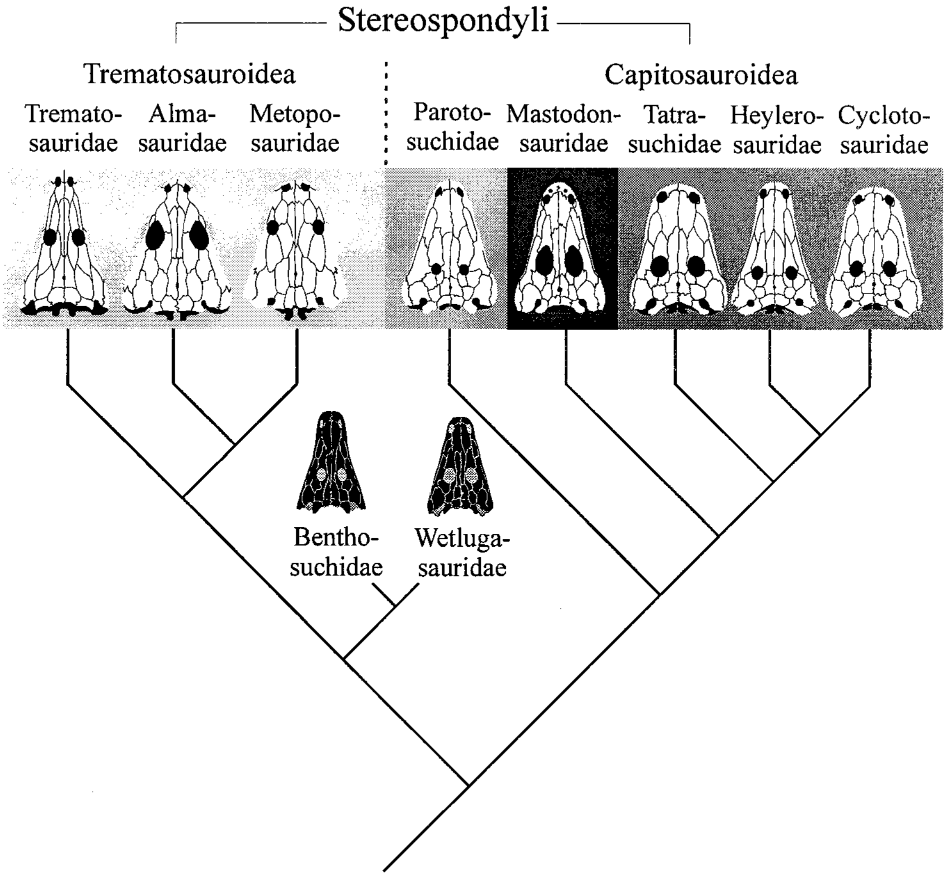


Fig. 7. Systematic position of the family Mastodonsauridae within the suborder Stereospondyli (Tetrapoda: Temnospondyli). Trematosaurids were dominant freshwater to marine dwellers in the Lower Triassic, while capitosauroids managed to become the most frequent and widespread stereospondyls by the Middle Triassic. The Cyclotosauridae and Metoposauridae are the last stereospondyls to be found in Europe, both being known by the Schilfsandstein (Middle Carnian).

2. Taxonomy of *Mastodonsaurus giganteus* (Jaeger, 1828)

2.1. Discovery and first assignment of *Mastodonsaurus*

In the early 1820s, two particular finds supposed to have come from the alum mine at Gaildorf attracted the attention of Professor Georg Friedrich Jaeger, later curator of the Königlich-Württembergisches Naturaliencabinet, the forerunner of the Staatliches Museum für Naturkunde in Stuttgart. According to his own words, the two specimens had been found almost side by side ("os occipitis … communis cum dente simul allato situs"). In 1828 he specified, that the tooth was brought to him by Mr. Zobel, the occiput by Prof. Schübler (who then taught Geology at the Eberhard-Karls University of Tübingen), and additional material, which now also is assigned to *Mastodonsaurus*, found by Mr. Hehl and Mr. Dietrich respectively, the latter was the owner of the alum mine at Gaildorf.

It is somewhat obscure whether all material was found in the same mine and at the same time, as JAEGER's note in 1824 suggests, or if the names he cites mean that the specimens where found at different times by different people. KURR (1850) and recently WEBER (1992 a) noted that the Gaildorf mine was the only site from which definitive finds of *Mastodonsaurus* had become known in these early days; this is the most convincing evidence in favour of JAEGER's (1824) original statement.

Concerning the taxonomic assignment of the finds, JAEGER (1824) further wrote: "Maxime distinguitur condylis ad modum prominentibus, quales nulli, quantum equidem scio, reptilium generi, excepto forte Proteo mexicano competunt". Obviously he had made comparisons with various extant reptiles and thereby had hooked at one particular feature, the double occipital condyle of *Mastodonsaurus*. By this character it differed from all reptiles known to him, but brought the 'Mexican Proteus' to his mind, by which he probably referred to the ambystomatid salamander *Ambystoma mexicanum*. He therewith pre-dated the findings of OWEN (1841, 1842) and QUENSTEDT (1850) on the amphibian nature of *Mastodonsaurus*, only that he used a different argumentation and based his comparison on a different extant taxon. (In fact, by comparing *Mastodonsaurus* with an aquatic salamander he came much closer to the current concept than any of his successors, although we cannot be sure about his reasons.) This explains his choice of *Salamandroides* as generic name for the occiput, which later became a junior synonym of *Mastodonsaurus*.

JAEGER (1824) concludes: "Pro certo itaque habere licet, ... vero Monitoribus forte affinis strato profundiori peculiaria esse, quod ….. etiam reliquias foveret, si os occipitis, quod utique probabile est, non ejusdem [sic] animalis esset". [JAEGER herein stresses the resemblance of the giant Gaildorf tooth with those of large Recent varanids (e.g. the monitor). Finally, he argues, the occiput might turn out to be from a different animal than the tooth, an alternative "which is particularly probable".]

2.2. Identification of the Kupferzell specimens

The only two capitosauroid species definitely present at the Kupferzell excavation site are the small-growing capitosaurid *Kupferzellia* and the large to giant mastodonsaurid *Mastodonsaurus*. The anatomy of these two forms differs conspicuously in the skull and mandible so even minor fragments may be readily distinguished (for details see SCHOCH 1997a). A well-defined yet only fragmentarily known form has clear trematosaurid affinities, and is also represented by numerous characteristic intercentra (see section 1.3). Finally the find of a small almasaurid-like temnospondyl in the Untere Graue Mergel of the Schumann quarry in Vellberg-Eschenau (MORALES 1988) demonstrates that additional stereospondyls might still be hidden in the large unprepared sample from Kupferzell. Both the trematosaurid and almasaurid cannot be confused with either *Mastodonsaurus* or *Kupferzellia*, because their cranial morphology is too distinct. This involves major differences in dermal sculpturing, proportions of skull roof bones in nearly all regions, and the structure of the palate; hence even small skull fragments are readily distinguished by that way.

The mastodonsaurid is identified by the enormous size of most finds, and generally the large extent of ossification. The dermal sculpturing is coarse in the sense that the ridges are broad and well-defined, applying even and in particular to the smallest specimens. Furthermore, even small finds are recognised by means of their peculiar cranial morphology: the skull forms a narrow, isoceles triangle with large orbits at midlevel, the symphyseal tusks penetrate the tip of the snout, the parasphenoid and pterygoid are massive ossifications meeting in a long suture much different from that of *Kupferzellia*, and the large size and shape of the interpterygoid vacuities. There are also numerous differences in the mandible (long postglenoid area, large and anteriorly extended Meckelian window, symphyseal region: postsymphyseal teeth) between *Mastodonsaurus* and *Kupferzellia* (SCHOCH 1997a).

The following valid species attributable to the Mastodonsauridae have been erected and described :

1. *Mastodonsaurus giganteus* (JAEGER, 1828) (MEYER & PLIENINGER 1844; FRAAS 1889; HUENE 1922): Lettenkeuper of northern Württemberg (Land Baden-Württemberg), Mainfranken (Freistaat Bayern), and north of the Thüringer Wald (Freistaat Thüringen). A junior synonym is *M. acuminatus* FRAAS 1889from the Lettenkeuper of Hoheneck in Baden-Württemberg and Molsdorf in Thüringen (SCHMIDT 1931; RÜHLE VON LILIENSTERN 1935; WERNEBURG 1994). See fig. 3 for stratigraphical range.

2. *Heptasaurus cappelensis* (WEPFER, 1923) (see WEPFER 1922 a, b; PFANNENSTIEL 1932; SÄVE-SÖDERBERGH 1935): Oberer Buntsandstein (Lower Anisian) of Vosges, Schwarzwald, and Mainfranken. Synonyms are possibly *Mastodonsaurus vaslenensis* MEYER, 1847–55 and *M. ingens* TRUSHEIM, 1937. See fig. 3 for stratigraphical range.

3. *Mastodonsaurus torvus* KONZHUKOVA, 1955 from the Orenburgskaya Oblast and Bashkirstan (Bashkortostan) in the Russian Federation and northern Kazakhstan. This form is in some aspects similar to *Heptasaurus cappelensis* (e.g., width of jugals), but has orbital windows of similar shape as in *M. giganteus* and attains the size of large specimens of this species (M.A. SHISHKIN, pers. comm.; pers.exam. of various specimens in the PIN). The available finds are throughout very fragmentary, so that a reasonable comparison with the two German genera is impossible thus far; a provisional assignment to *Mastodonsaurus*, paying tribute to the closer resemblance of the East European mastodonsaurid to this giant form, may be sufficient.

The Kupferzell mastodonsaurid material is throughout similar to *Mastodonsaurus giganteus* from Gaildorf and Markgröningen. The range of morphological variation in the Kupferzell specimens is fairly broad and continuous, strongly suggesting the presence of only one species. Re-examination of the type material of *M. acuminatus* revealed that the differences to the Gaildorf material mentioned by FRAAS are the result of extreme compaction in the latter. The variability in the Kupferzell skulls ranges from narrow-cheeked forms similar to *M. acuminatus* to very broad-cheeked specimens. The material from Molsdorf, attributed to *M. acuminatus* by SCHMIDT (1931) for stratigraphical rea-sons, is likewise throughout assigned here to *M. giganteus*.

Heptasaurus cappelensis, the only other valid German mastodonsaurid species to date, differs from all mentioned specimens by smaller orbits and a markedly broader snout tip. Correlated with the smaller size of the orbit is the greater width of the jugal and the frontal. An unequivocal assignment of all mastodonsaurid material from Kupferzell to *Mastodonsaurus giganteus* (JAEGER, 1828) is thus possible.

2.3. Taxonomic status of *Mastodonsaurus giganteus* (Jaeger, 1828)

Amphibia Linnaeus, 1758
Temnospondyli Zittel, 1890 [emend. Milner, 1993]
Stereospondyli Milner, 1994 [non Watson, 1919]
Capitosauroidea Säve-Söderbergh, 1935 [lapsus: -“oidae”]
Mastodonsauridae Watson, 1919 [non Lydekker, 1885]

Mastodonsaurus giganteus (Jaeger, 1828)

p. 38, tab. 5, figs. 1–2

v	1824	animal ignotus	Jaeger, p. 11–12
v	1828	*Mastodonsaurus*	Jaeger, p. 35; nomen imperfectum
v*	1828	*Salamandroides giganteus*	Jaeger, p. 38
	1832	*Mastodonsaurus jaegeri*	Meyer, p. 208
v	1833	*Mastodonotsaurus* [sic]	Jaeger, p. 86; printing mistake
v	1833	*Salamandroides*	Jaeger, p. 86
v	1834	*Salamandroides jaegeri*	Alberti, p. 120; first revisor
v	1838	*Mastodonsaurus salamandroides*	Jaeger, p. 547
	1841	*Labyrinthodon jaegeri*	Owen, p. 227
	1842	*Labyrinthodon salamandroides*	Owen, p. 512
	1842	*Mastodonsaurus salamandroides*	Roemer, p. 96
v	1844	*Mastodonsaurus jaegeri*	Meyer, p.11, plts. 6–7
v	1844	*Mastodonsaurus jaegeri*	Plieninger, p. 57, plts. 3–7
	1845	*Labyrinthodon jaegeri*	Owen, p.195
?	1847–55	*Xestorrhytias perrini*	Meyer, p. 81, pl. 62, fig. 5 (partim !)
v	1847–55	*Mastodonsaurus jaegeri*	Meyer, p. 89
v	1850	*Mastodonsaurus giganteus*	Quenstedt, p. 2
v	1864	*Mastodonsaurus jaegeri*	Alberti, p. 255
	1874 a	*Mastodonsaurus giganteus*	Miall, p. 151
	1874 b	*Mastodonsaurus giganteus*	Miall, p. 433
v	1889	*Mastodonsaurus giganteus*	Fraas, p. 32, pls. 1–5
v	1889	*Mastodonsaurus acuminatus*	Fraas, p. 104, pls. 7, 8
	1890	*Mastodonsaurus jaegeri*	Lydekker, p. 142
v	1919	*Mastodonsaurus giganteus*	Watson, p. 36, fig. 22
v	1922	*Mastodonsaurus giganteus*	Huene, p. 400, figs. 1–12
v	1928	*Mastodonsaurus giganteus*	Schmidt, p. 371, figs. 1047–1049
v	1928	*Mastodonsaurus acuminatus*	Schmidt, p. 373, fig. 1050 a
	1931	*Mastodonsaurus acuminatus*	Schmidt, p. 237, figs. 1–5, pls. 1–3
	1932	*Mastodonsaurus giganteus*	Pfannenstiel, p. 1
	1935	*Mastodonsaurus acuminatus*	Rühle von Lilienstern, p. 177
	1935	*Mastodonsaurus giganteus*	Säve Söderbergh, p. 81
	1942	*Mastodonsaurus giganteus*	Nilsson, p. 95
	1944	*Mastodonsaurus giganteus*	Nilsson, p. 5, fig. 2
	1947	*Mastodonsaurus giganteus*	Romer, p. 230, figs. 12, 13, 38, 39
	1955	*Mastodonsaurus giganteus*	Piveteau & Dechaseaux, p. 151
	1955	*Mastodonsaurus giganteus*	Konzhukova, p. 62
	1956	*Mastodonsaurus giganteus*	Huene, p. 94, figs. 130, 131
	1958 a	*Mastodonsaurus giganteus*	Ochev, p. 100
	1958 b	*Mastodonsaurus giganteus*	Ochev, p. 487
	1964	*Mastodonsaurus giganteus*	Shishkin, p. 95
v	1965	*Mastodonsaurus jaegeri*	Welles & Cosgriff, p. 12
	1966	*Mastodonsaurus giganteus*	Ochev, p.159
	1972	*Mastodonsaurus jaegeri*	Ochev, p.176
v	1974	*Mastodonsaurus jaegeri*	Paton, p. 281, fig. 18
v	1980	*Mastodonsaurus* sp.	Wild, p. 16, fig. 3
v	1981	*Mastodonsaurus* sp.	Wild, p. 49, fig. 4, 5

	1994	*Mastodonsaurus acuminatus*	Werneburg, p. 128, fig. 8
v	1997	*Mastodonsaurus jaegeri*	Schoch, p. 245
v	1999a	*Mastodonsaurus giganteus*	Schoch & Wild, p. 2, figs. 3–4, 6
v	1999b	*Mastodonsaurus giganteus*	Schoch & Wild, p. 3

Holotype: GPIT 1824, an occiput of a large specimen.

Remarks: 1. The nomenclatural situation of this species, its valid name, and the state of all objective synonyms are to be reviewed and discussed elsewhere. The binomen *Mastodonsaurus giganteus* (Jaeger, 1828) is used throughout the present study.

2. GPIT 1824 is clearly diagnostic of *Mastodonsaurus giganteus* (cf. Welles & Cosgriff 1965!). I came to this conclusion by personal examination of nearly all known large stereospondyl species (see list of material investigated). GPIT 1824 comprises the posteriormost part of the parasphenoid and large parts of the exoccipitals including the occipital condyles. The skull length of this specimen is estimated to approximately 75 cm. The large condylar facets, their shape, and the posterior region of the parasphenoid are particularly diagnostic of *Mastodonsaurus giganteus*. The presence of a tripartite fossa parasphenoidalis (Schoch 1997a) is unique to this species. In addition, the mode of contact between the pterygoid and exoccipital is characteristic of the Lettenkeuper mastodonsaurid. By these features, the occiput differs from all studied specimens of *Heptasaurus*, *Eryosuchus*, and *Parotosuchus* – i.e., those forms, which are structurally closest to *Mastodonsaurus*. SMNS 55911, the giant tooth, is probably from the same species as the occiput, although clearly from a much larger specimen. This is evident from complete finds (e.g. SMNS 80878, 80913) in which specimens matching the size of the occiput have teeth reaching only half the length of that in SMNS 55911. Jaeger's giant tooth is certainly not diagnostic, as large labyrinthodont teeth are common to all capitosauroids; in addition, the Kazakhian form *Eryosuchus garjainovi*, which is known to reach a skull length of one metre, may bear even larger teeth (pers. exam.).

The aforementioned arguments are based on careful re-examination of the original material and invalidate the remarks of Welles & Cosgriff (1965) who considered the occiput undiagnostic. Unfortunately they did neither examine this specimen, nor study mastodonsaurid morphology on the basis of any of then available Gaildorf specimens housed in Stuttgart, Tübingen, and Yale.

Locus typicus: Alum mine at Gaildorf in Hohenlohe, northern Baden-Württemberg, southwestern Germany. Kurr (1852), Quenstedt (1880), Hagdorn (1988), and Weber (1992a) have commented on the geological setting of this site. This mine was exploited between 1763 and 1895 (Weber 1996). Its owner Mr. Dietrich, a trader at Gaildorf, repeatedly sent specimens (SMNS 4698, 4707, 4938, and 54679) to the collections in Stuttgart and Tübingen, following Jaeger (1828) and Meyer & Plieninger (1844).

Stratum typicum: The "Gaildorfer Alaunschiefer", a black, pyrite-bearing horizon of some 25 cm magnitude (Kurr 1852). Several authors have commented and discussed on this particular site and stratum (op. cit.), but no agreement has been achieved on the exact stratigraphic position of this bed. A recent review is given by Weber (1996), who suggests a belonging to the Estherien-Schichten 3 (higher Lower Lettenkeuper). Alternative views are held by R. Wild (pers. comm.: Vitriolschiefer) and H. Hagdorn (1988: Untere Graue Mergel); see fig. 4.

Geographical occurrence: In many localities throughout Baden-Württemberg, Bayern (Rothenburg o. d. T., see Muenster 1834), and in Thüringen (Schmidt 1931; Rühle von Lilienstern 1935); see fig. 2.

Stratigraphical range: Fairly complete, diagnostic skull fragments are known from the Grenzbonebed (from quarries in the Crailsheim region) through the Hohenecker Kalk (Ludwigsburg, Molsdorf), which covers nearly the whole Lettenkeuper sequence (figs. 3, 4).

Isolated, large postcranial and lower jaw bones are occasionally found in the Obere Terebratelbank, Uppermost Muschelkalk (e.g. in Crailsheim). These specimens are conspicuously larger than those of *Heptasaurus* from the Oberer Buntsandstein (Wepfer 1922a, 1923a), and are therefore attributable to *Mastodonsaurus*. However, the find of *Mastodonsaurus ingens* Trusheim, 1937, which is by its stratigraphical position usually suggestive of *Heptasaurus*, demonstrates that giant mastodonsaurids were present in the Middle European Basin already by Anisian time.

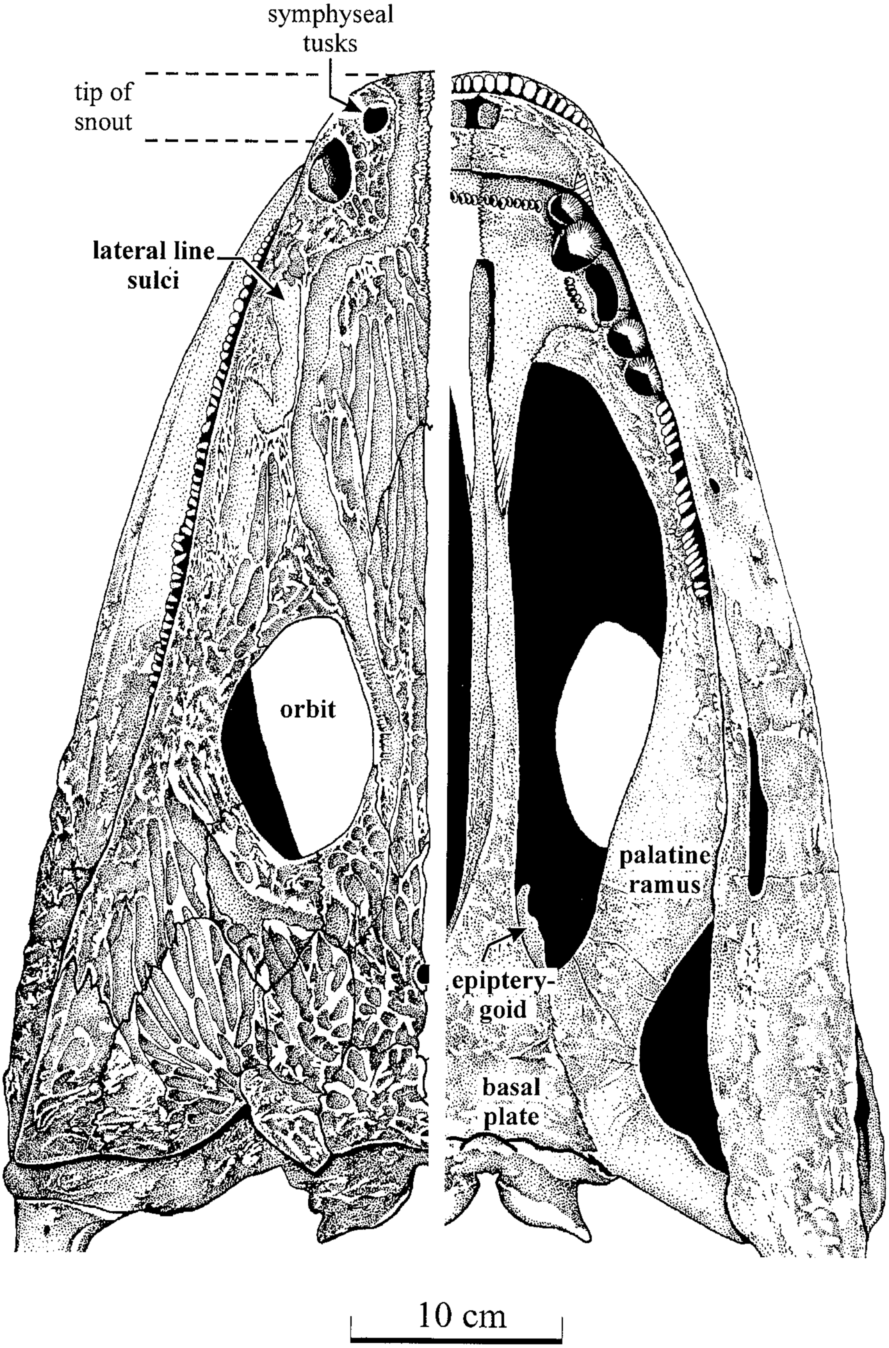


Fig. 8. Diagnostic features of the Mastodonsauridae (normal letters) and the genus *Mastodonsaurus* (bold letters) mapped onto a drawing of the skull roof and palate of *Mastodonsaurus giganteus*. Figure based on SMNS 54677.

Diagnosis

Mastodonsaurus giganteus (JAEGER, 1828) is characterized by the following unique features (fig. 8):

1. Orbits are very large (orbit length/ skull length = 0.24), the interorbital width is much narrower than the width of orbit, and the anterior end of the orbit is pointed.
2. Tripartite posterior rim of the basal plate (fossa parasphenoidalis).
3. Palatine ramus (pterygoid) stout and thickened by medial ridge and constricting interpterygoid vacuities laterally; quadrate ramus short and directed completely transversely; basal plate of parasphenoid broadened in its most posterolateral part.
4. Epipterygoid large and stout, with long anterior portion and a prominent processus lamellosus, and in contact to six cranial elements; in large specimens confluent with other regions of the palatoquadrate.
5. Processus hamatus (prearticular) very high and massive, forming an extended facet continuous with the glenoid area of the articular.

The following features are characteristic of, but not unique to *M. giganteus*:

6. The thoracal intercentra 3–26 form complete, nearly equally thick disks. This feature is however variable, as a broad study of individual variation in *Mastodonsaurus giganteus* revealed (this paper).
7. Anterior trunk ribs with stout processus uncinati and an additional proximal processus each (*Sclerocephalus, Cheliderpeton, Eryosuchus*).

Status of the Mastodonsauridae

The family name was introduced by LYDEKKER (1885) and later confined to the type genus *Mastodonsaurus* by WATSON (1919). LYDEKKER had summarized various temnospondyl genera under this heading, which are from our present knowledge only distantly related, e.g. the classical Keuper forms *Mastodonsaurus*, *Capitosaurus* (*Cyclotosaurus*), and *Metopias* (*Metoposaurus*). WATSON instead, who studied the Gaildorf specimens personally, already recognised some unique features of *Mastodonsaurus*, wherein he was principally followed by SÄVE-SÖDERBERGH (1935), ROMER (1947), and HUENE (1956). This concept has been upheld ever since (ROMER 1966; SHISHKIN 1964; OCHEV 1966, 1972; PATON 1974; CARROLL 1988; KAMPHAUSEN 1989).

SÄVE-SÖDERBERGH (1935: 79) regarded *Mastodonsaurus cappelensis* WEPFER, 1923 more closely related to *Capitosaurus* than to *Mastodonsaurus* and consequently erected an own genus *Heptasaurus*. ROMER (1947) and HUENE (1956) instead favoured *Mastodonsaurus cappelensis*, but this finally became obsolete (CARROLL 1988; KAMPHAUSEN 1989).

The Mastodonsauridae, conceived here to encompass the genera *Mastodonsaurus* and *Heptasaurus* only, are characterized by several unique features. These render the taxon a monophyletic group in traditional as well as the Hennigian sense.

The following unique characters are shared by *Mastodonsaurus giganteus* and *Heptasaurus cappelensis* (fig. 8):

1. Skull forms isoceles triangle, snout and median series very narrow.
2. Tip of snout elongated anterior to the nares.
3. Premaxillae pierced by large symphyseal tusks, anterior but not medial to the

nares and distinctly lateral to the lyrae; in the palate there is a paired apertura praemaxillaris, separated by a broad contact between premaxillae and vomers.

4. Orbits large, reaching more than 1/5 the lenght of the skull. Their shape is sagittally oval, and the anterior and lateral margins are frequently irregular and strongly convex.
5. Postorbital, prefrontal, and parietal much elongated anterior to the pineal foramen; this gives a particularly large postorbital, which is unparalleled by other stereospondyls.
   The parietal is much longer anterior to the pineal foramen than posterior to it. [This feature was regarded by SHISHKIN (1973) as characteristic of the Colosteiformes, a group supposed to enclose only brachyopids, trimerorhachids, and colosteids.]

Characters typical of, but not unique to the Mastodonsauridae are:

6. The degree of ossification is very high (a feature also found in *Buettneria perfecta*, *Parotosuchus orenburgensis*, and *Eryosuchus garjainovi* (all pers. exam.).
7. The parasphenoid-pterygoid suture is very long, giving a roughly triangular basicranial region, and posteriorly constricted interpterygoid vacuities (similar morphologies are present in *Eryosuchus*, *Cyclotosaurus*, and *Eocyclotosaurus* (all pers. exam.).
8. The cultriform process (parasphenoid) is strongly keeled (also present in *Cyclotosaurus*, *Eocyclotosaurus*, and the Trematosauridae; all pers. exam.).
9. The large tusks in the palate and symphysis reach giant size; this feature is only paralleled by *Eryosuchus garjainovi* OCHEV, 1972 (pers. exam.).
10. Lateral line sulci are very wide, especially in the anterior portion of the snout (this feature is also expressed in large specimens of *Eryosuchus* and the brachyopoid *Batrachosuchus*; all pers. exam.).
11. Fenestra Meckeli long and slender, 1/5 mandibular length (also in *Eocyclotosaurus* sp. from the Moenkopi Formation, Arizona, and *Cyclotosaurus posthumus* from the Middle Stubensandstein of Germany).

Assignment of other finds referred to *Mastodonsaurus*

The following species and fragmentary specimens have been originally or at some stage assigned to *Mastodonsaurus*, but thereafter turned out to be either synonyms of other species, or nomina dubia.

Mastodonsauridae [non *Mastodonsaurus*]:

- *Mastodonsaurus vaslenensis* MEYER, 1847–55 is clearly a mastodonsaurid and probably conspecific with *Heptasaurus cappelensis* (WEPFER, 1923). However, as this find is lost since World War II, and moreover lacks definite diagnostic features of *Heptasaurus cappelensis*, it cannot be taken as senior synonym of the latter, which thus retains validity.
- *Mastodonsaurus keuperinus* FRAAS, 1889 is clearly a mastodonsaurid. This applies, however, only to the snout fragment, which differs markedly from all co-occuring stereospondyl amphibians (*Cyclotosaurus*, *Metoposaurus*, *Hyperokynodon*) in the presence and position of the tusk holes in the premaxilla, the position of the naris, as well as the breadth and position of the lateral line sulci.

- *Mastodonsaurus ingens* TRUSHEIM, 1937 is probably also a junior synonym of *Heptasaurus cappelensis* (WEPFER, 1923), but this must await re-investigation of WEPFER's original material (SCHOCH in preparation).
- *Parotosuchus mechernichensis* (JUX & PFLUG, 1958) is clearly not a *Cyclotosaurus*, as its first describers thought, but a mastodonsaurid. It comprises a posterior skull table, with the orbits partially visible and the squamosal embayment partially preserved. According to all observed diagnostic features, definite mastodonsaurid characters are present (size of the orbits, proportion of frontals and jugals, and length of the parietal and supratemporal). It bears greatest similarities with *Heptasaurus*, and I herewith suggest to provisionally classify it as *Heptasaurus* cf. *cappelensis*.
- *Mentosaurus waltheri* ROEPKE, 1930 is quite probably a mastodonsaurid. The interclavicle is very large, but undiagnostic, whereas the sculpturing and proportions of the mandible are typical of the family. The missing hamate process and postglenoid area, however, render a definite assignment difficult.

Capitosauridae:
- *Mastodonsaurus robustus* QUENSTEDT, 1850 is a synonym of *Cyclotosaurus robustus* (QUENSTEDT, 1850).
- *Mastodonsaurus cyclotis* QUENSTEDT, 1850 (implicitly) is a synonym of *Cyclotosaurus robustus* (QUENSTEDT, 1850), referring to the same material as *M. robustus*.

Nomina dubia are:
- *Mastodonsaurus meyeri* MUENSTER, 1834 is clearly a nomen dubium. It consists of a single labyrinthodont tooth that might stem from any of the larger stereospondyl taxa occurring in the Mittelkeuper.
- *Mastodonsaurus andriani* MUENSTER, 1843 bears the same problems as the aforementioned taxon.
- *Mastodonsaurus durus* COPE, 1866 is clearly a nomen dubium. It might belong to a metoposaurid rather than a capitosauroid, as WELLES & COSGRIFF (1965) point out, although this is only inferred from its stratigraphical and geographical position.
- *Mastodonsaurus silesiacus* KUNISCH, 1885 is a nomen dubium. It bears resemblance to advanced capitosaurids, such as *Tatrasuchus kulczyckii* or *Kupferzellia wildi*, might however as well stem from a more primitive capitosauroid form such as *Parotosuchus nasutus*.
- *Mastodonsaurus fuerstenberganus* (MEYER, 1847–55) (spelled *M. fürstenbergensis* by ZITTEL 1890, but referred to the same specimen) was assigned to a new genus erected for it, *Meyerosuchus*, by KAMPHAUSEN 1989). I consider this to be a nomen dubium, as it lacks any definitely diagnostic features; an assignment to *Stenotosaurus* or *Eocyclotosaurus* would be equally plausible by the structure of the anterior palate, although these two genera are regarded as only distant relatives by KAMPHAUSEN (1989).
- *Mastodonsaurus lavisi* (SEELEY, 1876) is a nomen dubium, based on indeterminate material. The associated, very fragmentary specimens, however, bear close resemblance to *M. giganteus*, especially the circum-orbital elements (PATON 1974: figs. 5, 7b).

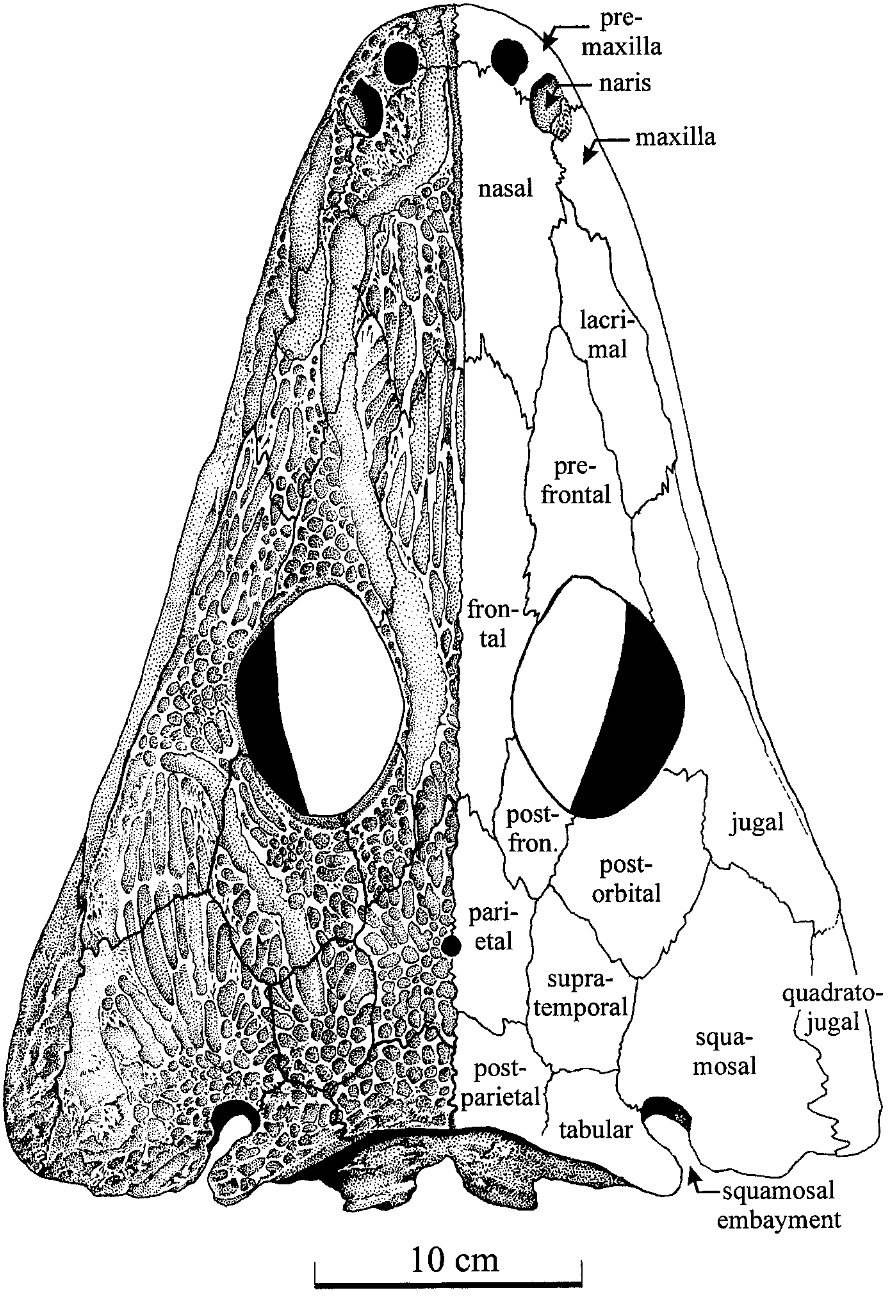


Fig. 9. Skull roof of *Mastodonsaurus giganteus* with anatomical terms mapped. Note the differences in the geometry of sutures, such as the failure of the supratemporal to contact the postfrontal on the right side. Figure based on SMNS 54678 (see also plate 3).

Capitosauroidea:

- *Mastodonsaurus weigelti* WAGNER, 1935 is considered a junior synonym of *Parotosuchus nasutus* (MEYER, 1858) (see WELLES & COSGRIFF 1956: 65).
- *Mastodonsaurus* sp. (SCHMIDT 1928) is an undiagnostic mandible fragment from the Middle Buntsandstein of Altensteig. It does not bear any definite mastodonsaurid features, but instead possesses additional teeth posterior to the symphyseal tusks, which is entirely untypical of the Mastodonsauridae.

3. Comparative osteology

3.1. Cranial anatomy

3.1.1. General structure

The skull of *Mastodonsaurus giganteus* is one of the most attractive exhibition items of any Triassic fossil collection. It strikes by its flatness, the elongated snout with the threehundred teeth, and the very large orbits which suggest enormous eyes. The skeleton reminds of a crocodile yet the structure is too different even to misguid a layman.

Mastodonsaurus is different in many aspects from all Recent tetrapods, which is especially apparent in the cranium. Instead, it is much closer to the primitive condition of tetrapods (HENNIG 1983; SCHULTZE & ARSENAULT 1985; PANCHEN & SMITHSON 1987; JANVIER 1997; CLACK 1998). The main differences are found in the palate, which characterizes the genus as an advanced temnospondyl, having wide interpterygoid vacuities.

The composition of the skull roof is readily compared to that of *Ichthyostega* sp. (JARVIK 1996), with minor differences in the proportions of elements (figs. 9, 10). The mandible is slightly more distinct from that of the earliest tetrapods, especially in possessing a large Meckelian window on its lingual side, and in the presence of a conspicuous retroarticular process. The palate and occiput of *Mastodonsaurus* clearly deviate in several aspects from the plesiomorphic pattern: the pterygoids and parasphenoid are anteriorly separated by extensive interpterygoid vacuities, the basipterygoid articulation is lost and, instead, extensive sutures exist in this region between pterygoids, parasphenoid, and the exoccipitals. In the occiput the exoccipitals are the only enchondral bones, making up widely separate, paired condyles of enormous size. The sculpturing of the dermal bones in *Mastodonsaurus* is also very characteristic. This particular type of bone surface, consisting of polygonally arranged ridges, is found almost as a rule in basal tetrapods and clearly is a groundplan feature. Among Recent groups it occurs only in large, hyperossified anurans and, moreover, rather frequently in crocodiles.

The skull of *Mastodonsaurus* has immediately apparent unique features (figs. 8, 9). The outline of the head forms an elongated, isoceles triangle. Its margins taper fairly continuously towards the narrow, bluntly ending snout. Irrespective of the gigantic size of the skull, the orbital fenestrae are very large, nearing 1/4 of the skull length. Moreover, the outline of the orbit is ir-regular in forming an elongated oval which is markedly pointed anteriorly (MEYER & PLIENINGER 1844; FRAAS 1889). A similar orbit shape occurs only in distant taxa such as baphetids (BEAUMONT 1977) and procolophonids (IVACHNENKO 1987). Consequently the jugals, postfrontals, and prefrontals cover much smaller areas than in related taxa. *Mastodonsaurus* is further peculiar in the large extent of skeletal ossification. This concerns most regions of the cranium, including the braincase. The neurocranium of Kupferzell *Mastodonsaurus* is beautifully preserved and thanks to the attentive treatment by the preparators at Stuttgart it offers a unique possibility to study the complete cranial osteology.

The threedimensional structure of the skull is very characteristic. In contrast to most other capitosaurs, the orbits are not raised above the flat skull table. The height of the skull increases continually but only very slightly from the snout to the occiput. Squamosals and tabulars comprise the most elevated regions of the head. On top of the skull table proper there is almost no relief, with the exception of the anterior part of the supratemporals where a weak depression may be found in some specimens. Besides sculpturing, the only relief is produced by the wide supraorbital sulci of the lateralis system.

3.1.2. Skull roof

The skull roof is throughout made up of very thick dermal ossifications which contact one another by means of complex, serrated sutures. The sculpturing is intense and frequently overprints these sutures, although co-ossification remains the exception (figs. 9, 11). Overprinting by sculpturing is the main reason for the difficulty to find most sutures in the Gaildorf specimens, a fact which had long precluded a comparison of *Mastodonsaurus giganteus* to other labyrinthodonts. MEYER (1847–55) and FRAAS (1889) gave provisional images of the proportion of the skull roofing elements which they probably gathered from irregularities in sculpturing. MEYER's illustration is fairly diagrammatic yet generally sound (1847–55: pl. 61, fig. 4), whereas FRAAS' (1889: fig. 1) interpretation of the posterior skull table departs clearly from the situation found in the originals. In the Kupferzell material practically all sutures can be studied in great detail. The cranial anatomy of *Mastodonsaurus giganteus* provided here therefore relies predominantly on material from this locality.

Transsection reveals that the dermal bones of *Mastodonsaurus* contain countless tiny pores and channels. BYSTROW (1935) studied sections of *Benthosuchus* bones and carefully described a similar situation in that comparatively small capitosaur. Characteristically the pores occur in the lower two thirds of the element, whereas the upper, most shallow portion consists of numerous parallel sheets of bone. These uppermost layers produce the prominent sculpturing ridges by means of intensified growth at discrete points. Following BYSTROW, the pores are arranged in a complexly internested channel system. He distinguished several types of channels which are also observable in the various specimens from Kupferzell. The arrangement of the pores is most characteristic as it corresponds with the sculpturing pattern: foramina occur in the pits and grooves mainly. The deepest part of each of these grooves usually contains a large pore, and in elongated grooves there is a whole series of pores of different size.

Preservation

The skull roofing elements are throughout very well preserved in the Kupferzell material. The sculpturing is uncrushed and not affected by wearing such as some exposed palate elements were. Only in one specimen the skull roofing bones have a surface apparently affected by dissolution. This specimen was found "palate-up" in the grey marl with the skull roof sticking to the bottom and the occiput being un-

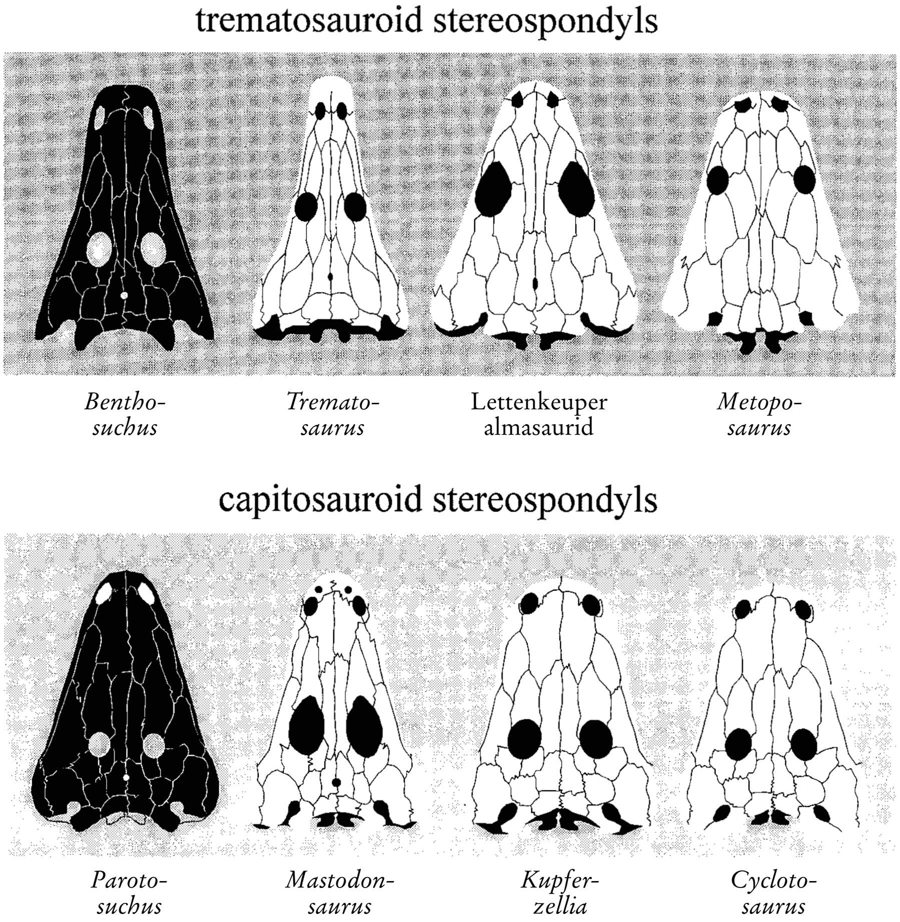


Fig. 10. The skull roof in selected temnospondyl amphibians, not to scale. Throughout the group, the number of dermal bones and the general pattern of sutures is remarkably conservative, although there is a wide range of proportions. All diagrams are based on personal observations.

crushed. Among the occipital dermal bones, compaction has resulted in a displacement of tabulars and postparietals against the exoccipitals. Sometimes the columnae verticales and the paroccipital processes are also entirely mashed, leaving a completely fragmented, anatomically unresolvable fabric. Three major types of mechanical destruction are observed in skull roofing bones.

1. Major fractures with large-scale displacement of fragments but preservation of most anatomical details:
   - transverse fractures in the long elements of the snout (frontal, nasal, lacrimal);
   - squamosal and tabular with radial fractures whose origin being in the most exposed areas;
   - displacement along sutures occurs only in the most exposed areas (tabular, postparietal, or in marginal elements which connect skull roof to palate (jugal, maxilla, quadratojugal).

2. Fine fractures:
   - oblique fractures arranged in various systems that overcross one another affect most dermal bones.
3. Distortion of dermal bones:
   - tabular and squamosal (surrounding squamosal embayment);
   - vertically oriented parts of dermal elements (lamina ascendens pterygoidei, lamina descendens squamosi);
   - well-ossified ventral parts of tabular and postparietal contacting processes of exoccipital (columna verticalis, paroccipital process);
   - dorsal process of jugal rotated into a steeper angle with the palatal plane.

Taphonomy

Taphonomic evidence is mainly gathered from finds of isolated skull roof bones and the record of partially disarticulated specimens (e.g. SMNS 80913). The collecting of taphonomic data at the excavation site was constrained by the short time interval in which excavation was possible. The amount of excellent material recovered and the possibility to collect numerous taphonomic data from the finds themselves, however, are nevertheless a most lucky and highly exceptional situation.

The most likely areas to fall apart in the skull roof of *Mastodonsaurus* are accordingly the cheek and tooth-bearing margin. On the contrary, the posterior skull table appears to be the most stable region. This is not clearly apparent from the topography of sutures, but was controlled by the binding effect of the braincase which is attached at several points to the median roofing series and the supratemporal. In the snout region the median series also is the most stable region. The premaxillae, nasals, and frontals are often found in concert, whereas lacrimal plus maxilla and prefrontal more easily disintegrate. Lacrimal, maxilla, and palatine together make up another fairly stable unit, whereas the jugal and postorbital very often are dislocated. These data are preliminary conclusions from ongoing studies on the body of taphonomic evidence available from the Kupferzell excavation. I am indebted to Dr. R. Wild for his comments on the settings of certain specimens, and his generous donation of numerous slides which he photographed on his own during the excavation.

Premaxilla

The tip of the snout is especially well ossified. Strong tooth arcades and the olfactory passage are located in close proximity to each other. The premaxilla supports the median roofing series by a broad suture with the nasal. Its three main branches are: (1) the dental ramus (dental shelf) which forms the tooth-bearing anterior margin of the skull, (2) the alary process that connects the skull roof with its margin, and (3) the processus vomeralis which connects the dental shelf to the vomer (figs. 12, 15).

The dental shelf is ventrally entirely flat and widens medially, and on top of it the labyrinthodont teeth are borne in acrodont fashion. The dentition is heterogenous but generally stronger than that of other capitosaurs. The four medialmost teeth which are arranged in a transverse row are the largest. Further posterolaterally, towards the maxilla, tooth size decreases markedly. Altogether 18 to 19 teeth are present. Their bases are elongated perpendicular to the longitudinal axis of the arcade. Throughout the smaller teeth are arranged equidistantly, with the tooth bases almost in contact. These laterally extended tooth bases cover the dental shelf almost completely. The surface of the shelf itself is concave transversely, a feature typical of all marginal tooth arcades (premaxilla, maxilla, dentary). All tooth crowns are bent lingually, irrespective of their size.

The processus vomeralis is a posteromedian outgrowth of the dental shelf which separates the symphysial tusks. It firmly connects the medially broadened dental shelf to the vomer; the suture may disappear in large specimens. The width of the processus vomeralis is solely determined by the position of the symphyseal fangs, as exemplified by comparison to other capitosaurs. The general structure of the snout is not influenced by these particular differences and thus rather uniform throughout the group. The premaxillar symphysis is sometimes co-ossified. The processus vomeralis is ventrally convex and cylindrical in transverse section. Its surface is smooth and covered only by very fine striations which supposedly trace connective fibre orientation.

The symphyseal tusks of *Mastodonsaurus* are extraordinarily large and always penetrate the skull roof. The position of these rather unusual fenestrations is different among the capitosaurs possessing them. In *Mastodonsaurus* and *Eocyclotosaurus* they sit anterior to the nares, tunnelling the alary processes, whereas in *Cyclotosaurus* they penetrate the nasals medial to the nares (FRAAS 1889; KAMPHAUSEN 1989). However, the size and proper position of these fenestrae is variable in the Kupferzell specimens. Their size is not strictly correlated with skull size.

Sculpturing covers the whole alary process as well as the dorsomedial wall of the dental shelf. It consists of a network of ill-defined, broad and rounded ridges. The depressions increase in size towards the posterodorsal portion of the alary process. There is a clear size difference between the sulcus supraorbitalis and the depressions in its proximity, a feature not found in smaller capitosaurs, where a distinction between the actual lateral line sulci and mere ornamentation is sometimes difficult (SCHOCH 1997a).

Nasal

The nasal of capitosaurs is a very conservative element, and in *Mastodonsaurus* it is only striking by its narrowness (fig. 9). The length of the nasal and frontal is generally relatively greater in capitosaurs as compared to plesiomorphic taxa such as *Sclerocephalus* or *Eryops* (SAWIN 1941; BOY 1988) and more similar to that of the actinodontid-grade *Cheliderpeton* and *Intasuchus*, and the very *Rhinesuchus*-like "archegosaurs" *Melosaurus* and *Konzhukovia* (KONZHUKOVA 1955; GUBIN 1984; BOY 1993; WERNEBURG & SCHNEIDER 1996). The tendency in capitosaurs to form a conservative naso-frontal suture type is further very conspicuous: the frontals are medially wedged between the nasals and converge towards a point in the midline. The nasals in turn are set in between the prefrontals and frontals posteriorly. Laterally they contact the lacrimals, anterolaterally the maxillae, and anteriorly the premaxillae. Rather unusual in capitosaurs is the long nasomaxillar suture, resulting from the relatively short lacrimal.

The shape of the nasal is that of an elongated rectangle which widens in its middle third. The sculpturing of the element is very characteristic. It is divided into two unequally large areas by the wide sulcus supraorbitalis. Throughout the radially arranged ridges have their centre at the margin of the sulcus.

The anterolateral, sculptured region bears a network of small, polygonal ridges which are arranged radially, the centre being at the edge of the flexura medialis of the sulcus. The sulcus supraorbitalis forms a very broad, shallow groove which has a largely smooth surface. Only sporadically there occur small foramina, situated in slight depressions within the sulcus. The margin of the sulcus is bordered by sculpturing ridges, and there is a zone immediately next to the first ridges which is covered by very fine, short stripes. Ventrally the nasal is attached to the anteriormost ethmoid region of the neurocranium. This may eventually ossify completely, being attached with its roof laterally to the planar inner surface of the nasal.

Frontal

The frontals of *Mastodonsaurus giganteus* are especially slender elements, and clearly differ from those of all other capitosaurs by this feature (figs. 9, 10). Laterally they form the intermediate part of the orbital rim, separating the prefrontal and postfrontal to an extent untypical even of capitosaurs. Because of the enormous size of the orbits the frontals are laterally slightly constricted. In their median extension they are markedly longer than the nasals and thereby the longest bones of the medial series. Their shape is that of elongated rectangles, the sutures with prefrontals being largely serrated and irregular though. In many specimens the frontal reaches well double the length of the parietal, by which the species differs clearly from *Heptasaurus*. The frontal contacts the nasal anteriorly, the prefrontal along its anterolateral margin, the postfrontal posterolaterally, and the parietal posteriorly. Typically, the anterior frontal sutures converge towards the midline, where their anteriormost extension is reached. This converging is, however, subject to variation, interestingly to a larger degree than it is in other capitosaurs.

Sculpturing on the frontal is dominated by long and slender ridges, as well as the very impressive supraorbital canal of the lateral sense. The latter is relatively very wide, about half the breadth of the frontal itself, and slightly increase in width anteriorly. Its course parallels the medial rim of the orbit, therefore bending anterolaterally in the posterior third of the frontal.

The ventral surface of the frontals forms a plane and is nearly smooth, with the exception of faint traces left by the attachment site of the braincase. This contact is sutural in most specimens and maximally continuous along the entire width and length of the sphenethmoid. There are no descending processes formed by the frontals, such as typical of the parietals throughout capitosaurs, or on the frontals such as in *Cyclotosaurus robustus* (Fraas 1913). The sphenethmoid always expands over almost the entire width of the elements in the interorbital region. Anteriorly, the extension of sphenethmoid ossification varies considerably, but roughened ventral surface of the frontals suggests a tight contact to the braincase irrespective of its state of mineralization.

Parietal

Mastodonsaurus is characterized by an elongate parietal which exceeds the length of the postparietal and prefrontal by far. This is most uncommon among capitosaurs, but an abundant feature in plesiomorphic temnospondyls (figs. 8–10). In contrast to all these, the frontal and nasal of *Mastodonsaurus* are still distinctly longer than the parietal. In most specimens it contacts the following bones: the frontal anteriorly, the postfrontal anterolaterally, the supratemporal laterally, and the postparietal posteriorly. In addition, a common suture with the postorbital may eventually be established in cases where the postfrontal is posteriorly small.

The position of the pineal foramen is in the posterior third of the parietal which is an unusual feature for capitosaurs, and advanced temnospondyls in general (SHISHKIN 1973). This posterior position results from the relative elongation of otic, laterosphenoid, and epipterygoid regions in the endocranium. By this, *Mastodonsaurus giganteus* differs from other basal tetrapods with a similarly elongated parietal, such as the Colosteidae, Trimerorhachidae, and Brachyopidae (WATSON 1956; SHISHKIN 1973; SMITHSON 1982).

Like in other medial elements, the sutures with the lateral neighbours and the medial counterpart are generally smoother than those with the anterior or posterior elements. Ventrally, the parietal is attached to the middle part of the roof of the sphenethmoid. This is accomplished by means of elongated sagittal crests that are borne by the otherwise smooth ventral side of parietal.

Postparietal

The postparietal is one of the morphologically most invariable elements in capitosaurs. It differs largely in its relative size, but hardly varies in morphology (fig. 10). It forms the posteromedial edge of the skull roof, connecting to the exoccipital by means of a slender descending outgrowth, the lamina supraoccipitalis. The roofing part is roughly quadrangular in outline and exceeds only slightly the width of the parietal to which it connects by an externally variably shaped suture line. The supratemporal also shares a variable, but in general rather short suture with it which is straight, and finally the relatively large tabular connects to it by means of a serrate suture posterolaterally. Finally the posterior margin of the skull roof is clearly concave in dorsal view, which is a widespread feature among temnospondyls.

Ventrally, the columna verticalis (exoccipital) firmly connects to the rather short descending process of the postparietal. The occipital part of the postparietal is very well ossified and slopes posteroventrally, being markedly thickened in medially. The whole occipital area is very much roughened, suggesting fleshy insertion of epaxial musculature. The dermal sculpturing consists of equally-sized, quadrangular polygons, which fail to connect to those of the neighbouring elements. The internal side of the bone is smooth except for the ventral suture surface of the processus supraoccipitalis.

Lacrimal

The lacrimal bridges the long space between the jugal and the anterior part of the snout, connecting the maxilla with the nasal and the prefrontal. It bears the supraorbital and infraorbital canals of the lateralis system, which are of huge size in this region (figs. 8, 9). Most of the dorsal surface of the lacrimal is in fact dominated by the impressions of these canals, so that only a small area in the posterior corner is sculptured in the typical way. The lacrimal does neither border the orbit nor the naris. It connects, however, to the palatine by means of a short and stout column, which tightly connects the palatine tusk region to the roof. This column has not been reported in other capitosaurs and may be a particular device of this genus or species, whose snout region is among the most flattened in temnospondyls.

Unlike the prefrontal, this bone does not differ in morphology or size as compared to other capitosaurs. It is about as long as the prefrontal, and only slightly narrower than the nasal. The contact to the latter comprises about , of the entire length of the bone. The lateralis canals occupy each about half of the width of the bone, whereby the supraorbital canal is straight though widens anteriorly, and the infraorbital canal curves in sigmoid fashion to give the flexura lacrimalis.

Prefrontal

The huge size and anterior extension of the orbital fenestra affects the posterior morphology of the prefrontal, whereas the anterior portion does not differ from the general structure of other, narrow-snouted capitosaurs (figs. 9–10). The element is however, most different in proportion from that of typical capitosaurids and benthosuchids. As pointed out before, the preorbital region of *Mastodonsaurus* is much abbreviated with respect to other genera, and this is most obvious in the prefrontal. The peculiar shape of the mastodonsaur skull is particularly due to the unique structure of the prefrontal region: moderately wide mid-level, very large orbits, and a narrow yet rather short snout.

The prefrontal wedges in between the medial and marginal series of the skull roof, and in *Mastodonsaurus giganteus* is basically a triangular element with a pronounced posterior indentation. The latter has the shape of an isoceles, wide triangle, making up 1/3 of the orbital window. In particular the posterior margin is much thickened and the area immediately anterior to this is the most elevated and clearly sculptured region. The supraorbital canal passes right through the imaginal centre of the bone. Thereby the canal widens conspicuously and carves into the otherwise markedly sculptured, planar dorsal surface of the bone. The canal leaves the prefrontal in its anterior third laterally to run through the lacrimal, and the suture between these elements abruptly curves in medial direction at this point. The internal side of the prefrontal is smooth with the exception of the rim of the orbital window that may be cevered by fine stripes in some specimens. In addition in the posterior third of the element, there is a deep groove which runs and deepens anteriorly, finally terminating in a large foramen.

Postfrontal

The postfrontal is widely separated from the prefrontal (which it contacts in all plesiomorphic capitosaurs and temnospondyls in general), and this to an extent unparalleled among capitosaurs (fig. 10). The element forms part of the posteromedial border of the orbit, and it wedges in between the postorbital, supratemporal, and parietal. In few cases a failure to contact the supratemporal is observed, and the parietal then has a moderately long suture with the generally large postorbital. The shape of the postfrontal is constrained by the narrow skull, the large orbit, and the rather long postorbital skull table to which it contributes only a minor component though. It forms an elongate oval or rectangle, does not constrict the parietal anteriorly, and forms at best half of the concave posterior border of the orbital window. The sculpturing is overprinted rather than interrupted by the supraorbital canal which is very weak and frequently terminates before it leaves the bone posteriorly. It consists of asymmetrical polygons which open posterolaterally and converge towards the orbital rim. The internal face of the bone is smooth, but may carry a weakly developed depression in the posterior part.

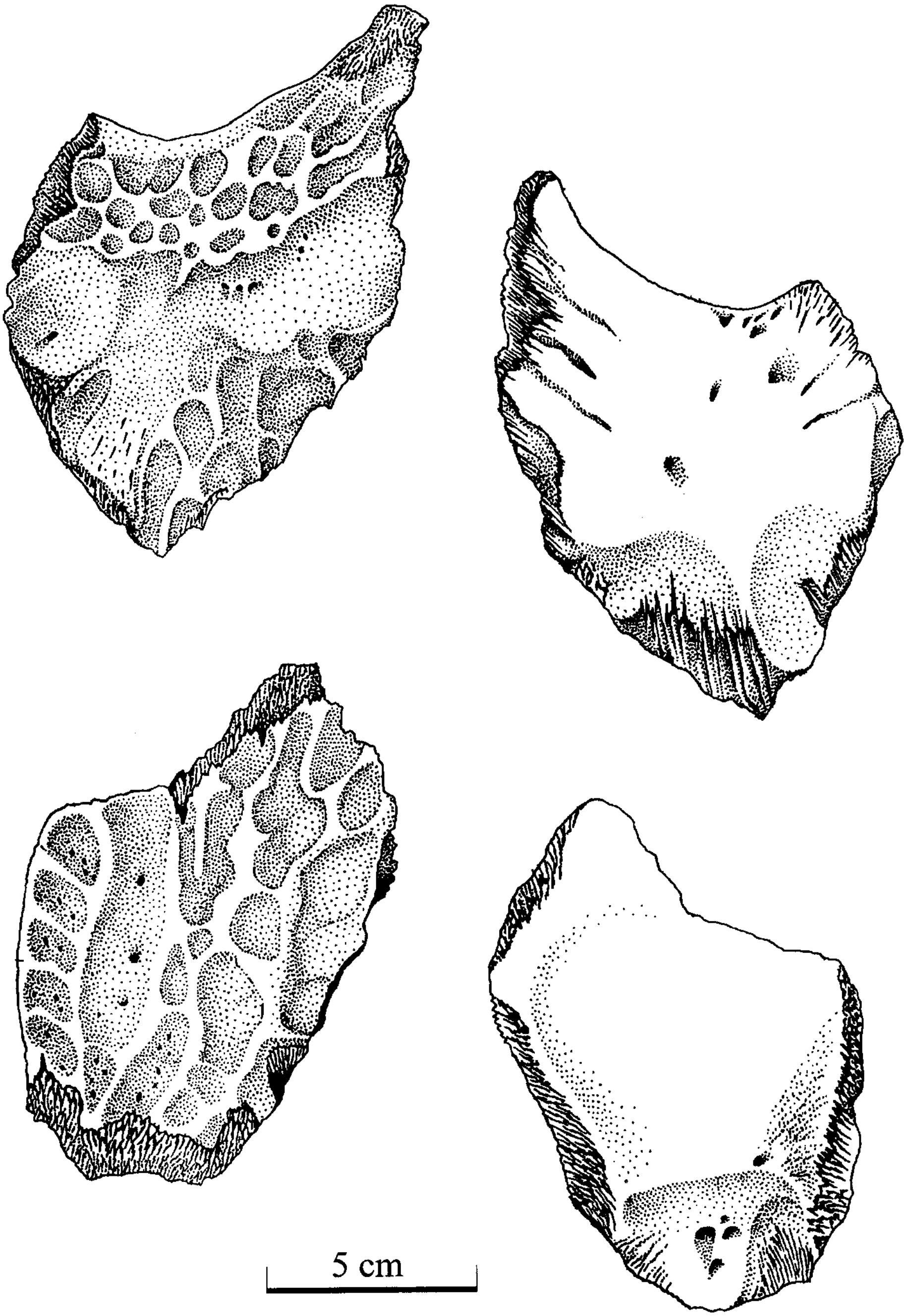


Fig. 11. Two dermal skull roofing elements of *Mastodonsaurus giganteus*, the postorbital (above) and supratemporal (below). The pronounced ornamentation on the dorsal surface (left side) is typical of bones and osteoderms growing in a relatively shallow position within the dermis. The inner or ventral surface is smooth with the exception of muscle scars and foramina for nutritive vessels, nerves, and tendons.

Postorbital

This is the dominant element in the postorbital region (figs. 8, 9). It is much longer than in many other capitosaurs, and its structure differs significantly from that figured by FRAAS (1889), to which most authors referred. The shape of the bone is more like in *Eryosuchus* or *Benthosuchus* than in most *Parotosuchus* species or *Cyclotosaurus*. It attains the outline of a nearly symmetrical pentagon with the symmetry axis orientated roughly sagittally.

Unique for *Mastodonsaurus giganteus* though is the length of the postorbital; it deeply wedges in between the supratemporal and squamosal. SHISHKIN (1980) was mistaken in assuming that there was no anterolateral process of the postorbital, which may indeed be very pronounced in this species; his interpretation relied on the false illustration of FRAAS (1889).

The sculpturing is arranged radially, consisting of distally widening and enlarging polygons. Instead the orbital rim is thickened and has a marked slope towards inside the orbit. The internal side of the bone is mostly smooth.

Supratemporal

The supratemoporal covers one of the most variable regions in the temnospondyl skull roof, but unlike more plesiomorphic genera [e.g. *Sclerocephalus*, see BOY (1972, 1988)] there is never an additional element (intertemporal) present. However, the bone may eventually fail to contact the postfrontal (fig. 9), a situation sometimes found in temnospondyls for which individual variation is known (BOY 1972). The supratemporal is peculiar in being remarkably narrow and proportionately small in *Mastodonsaurus*. Generally it has an asymmetric-hexagonal shape, with straight and unserrated sutures. The dermal sculpturing is well-defined. It consists of radially arranged polygons that tend to be elongated anteriorly, and which are strongly developed at the suture with the postorbital, overprinting the latter frequently. The temporal canal of the lateral sense is variably expressed, but in any case terminates slightly posterior to the central point of the bone. On the ventral side, the supratemporal bears a transverse ridge in its posterior third, and in addition to this several pores or larger foramina may be present. The anterior part of the bone has sometimes a weak depression on the internal side.

Tabular

This element forms the well-ossified posterolateral cornerpiece of the skull table, and it holds a key position regarding the architecture of this region. It contacts the squamosal anteromedial to the otic notch by means of a broad and serrated suture (fig. 9). The contact with the supratemporal is straight, whereas that with the postparietal varies but often is markedly curved and serrated. The tabular never contacts the squamosal posterior to the otic notch (as it does in *Cyclotosaurus*, *Eocyclotosaurus,* and various other capitosaurs), largely because of the poorly developed crista falciformis. The distal end of the tabular is, however, very strongly ossified and of stout appearance, and in contrast to most plesiomorphic capitosaurs is directed laterally rather than posteriorly (cf. *Benthosuchus*, *Wetlugasaurus*, *Parotosuchus nasutus*, *P. orenburgensis*, etc). It resembles closest the tabular in *Parotosuchus pronus* and *Eryosuchus garjainovi*, but in *Mastodonsaurus* may be highly variable in shape.

The ventral side of the bone bears a ventromedially directed process, the processus paroticus, which is blade-like, with widened anterior and posterior surfaces. It meets the exoccipital in a broad, serrated suture, thereby binding the occipital condyle to the lateral corner of the roof. Medially the parotic process frames the supraoccipital fenestra, which in *Mastodonsaurus* is very high and roughly triangular. The ventral surface of the tabular is complicated, being roughened especially in the area posterolateral to the base of the parotic process. Anterior to this base, which terminates in a sharp crest (crista tabularis externa), there is a large muscle impression.

Maxilla

The maxilla forms a large, completely dentigerous shelf bearing in between 85 and 100 throughout uniform teeth. For most of its length it is narrow and rather thin, with a convex dorsolateral surface and a flattened dentate shelf. The suture to the ectopterygoid and palatine is set in a marked and broad furrow that corresponds with the tooth arcade of the dentary. The tooth shelf in particular is remarkably thin, and posteriorly forms a sheet borne by the jugal ventral process and the quadratojugal (fig. 13).

The maxilla makes a well-defined contribution to the skull roof, especially anterior to the lacrimal, where it contacts the nasal. Further it borders the naris posterolaterally, although this part is overgrown by the dermal portion of the septomaxilla. There the maxilla contacts both the palatine and vomer, in the choanal region slightly broadening medially on the palatal side. For most of its length it forms the lateral rim of the skull, and by its structure and sculpturing (fine ridges only) it is distinct from all other roofing elements. It contacts the quadratojugal posteriorly, but often the immediate contact zone is broken.

The teeth are for most of its length of almost similar size and morphology. The tooth bases are characteristically anteroposteriorly compressed, giving flattened anterior and posterior surfaces. Obviously this is a device to gain a very dense tooth arcade. The tooth crowns are only very slightly bent medially, and are of conical shape. Carinae, such as described for *Cyclotosaurus hemprichi* (KUHN 1941), are not observed.

Jugal

A most characteristic element in the skull roof of *Mastodonsaurus giganteus* is the jugal, which has a concavely curved lateral margin, where it slopes towards the maxilla. It medially borders the large, oval orbital window (fig. 9). In transverse section the bone is convex towards the lateral side, with the dorsal and roofing part being a laterally slightly sloping plate. The jugal wedges in between the maxilla and palatine (and ectopterygoid, respectively) on the ventral side, and further forms the posterior edge of the marginal tooth arcade (fig. 13). The dentigerous, rather thin-walled elements are framed by this ventral process of the bone, and it has even a well-defined, ventrally triangular face on the palatal side.

Squamosal

The cheek is amongst the most elevated and strongly ossified regions in the head, a part which is largely formed by the squamosal. This element gives the posterior skull its characteristic shape (fig. 9). It connects the skull table to the margin, forms the largest part of the roof of the upper adductor chamber, and its posterior slope helps supporting the musculature of the neck and/or the depressor mandibulae. Its most elevated region is the posterior margin and the squamosal embayment (otic notch), of which it forms about one half. The posterior rim bears a pronounced crest, the crista falciformis. This is most similar to *Parotosuchus nasutus* and *Eryosuchus garjainovi* in not being posteriorly much extended and therefore far separate from the tabular. However, this is a condition which underlies particular developmental change, and the otic notch may near closure in large specimens. The resulting morphology is, however, quite different from that of *Cyclotosaurus* or similar forms.

The sculpturing of the squamosal is arranged radial from the frame of the otic notch, and the polygons tend to increase in length thereby. In addition, the ridges tend to become thinner yet higher distally, and are confluent with similar such ridges on the jugal, quadratojugal, and postorbital. In the whole anterior cheek region it is often difficult to identify the sutures because of this strong overprinting. On the ventral side the roofing part of the squamosal is roughened in several areas, especially posteriorly near the apex of the strongly convex, elevated region. The posteriorly sloping occipital portion is formed by the lamina ascendens of the squamosal, which is thin-walled and overlaps the pterygoid and quadratojugal ventrally.

Quadratojugal

The subtemporal window is laterally framed by the quadratojugal, which forms the posterolateral corner of the skull roof and integrates the quadrate trochlea into the framework of the palate, cheek, and occiput (figs. 9, 13). The quadratojugal is very massive and quite tightly set in a frame made by the jugal, squamosal, and pterygoid. It has only a minor occipital component that is significantly overlapped by the squamosal, but forms out a stout ventral process that abuts laterally against the quadrate. This process thins anteriorly where it curves to parallel the skull margin and finally merges into the main plane of the element anteriorly. Posteriorly, on the occipital face, the quadratojugal is pierced by a large paraquadrate foramen, and there again the lateral margin bears a prominent crest.

The sculpturing is of a similar type as that of the squamosal and jugal, and the centre of divergence is at the lateral margin of the roofing portion of the bone. The internal side reveals the large degree of overlapping by the squamosal, but is otherwise rather smooth. The subtemporal window is bordered laterally completely by this bone, which tends to curve convexely, especially in the largest specimens. The quadratojugal transsects the palatal plane, and terminates in a bulge lateral to the subtemporal fenestra. There is no contact to the maxilla, a feature found among most capitosaurs and paralleled in several other, more distant basal tetrapod clades.

Orbital windows

The orbits of *Mastodonsaurus giganteus* have long been known to be of peculiar size, morphology, and structure (Meyer & Plieninger 1844; Fraas 1889). The length of these windows is about , skull length, and their shape is long-oval with a pronounced anterior, triangular extension (figs. 1, 8, 9). Paton (1974) was mistaken in stating that this anterior extension was an artifact of preparation in the Gaildorf specimens, a fact proved by the Kupferzell material.

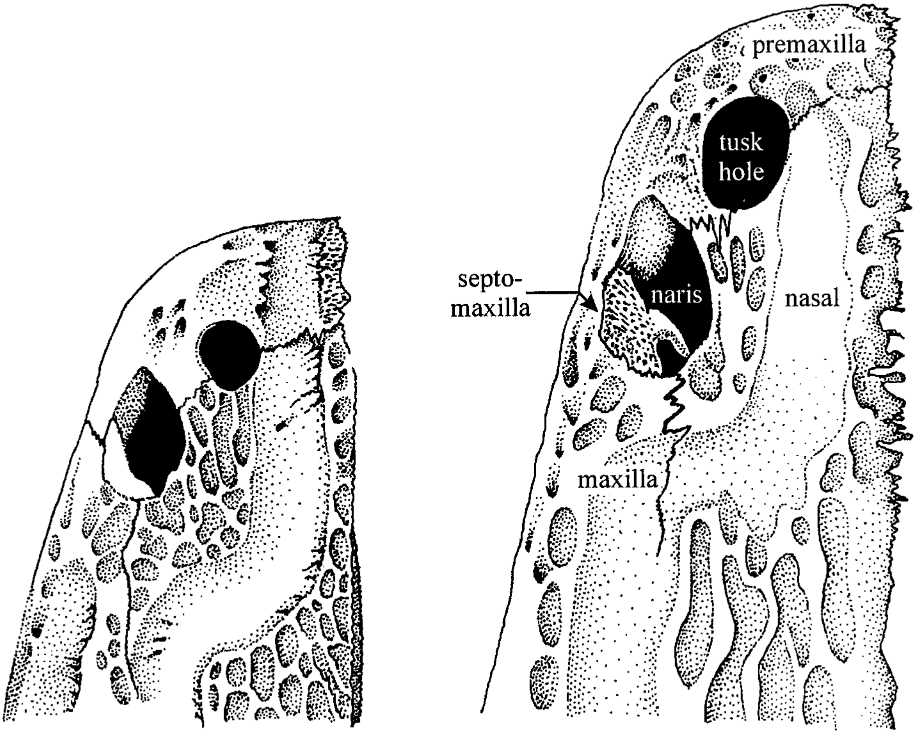


Fig. 12. Two growth stages of the preorbital region in *Mastodonsaurus giganteus.* The septomaxilla has two portions, a lateral one which participates in the bordering of the naris, and a medial and internal one, which supported the narial duct as in Recent salamanders.

Because of the huge size of these windows, the morphology of the bones anterior, lateral, and medial to the orbits is partially significantly different from that of other capitosaurs. In particular, the prefrontals are much shorter posteriorly, the jugals and frontals are very narrow. The rim of the window is unsculptured and thickened. It may be entirely smooth or covered by numerous fine stripes.

The paradox that the cranial morphology of *Mastodonsaurus* appears immature though the species is larger than any other temnospondyl has often struck scientists. The notion of such an immature morphology (e.g., large eyes in small skulls, which make surrounding elements appear rudimentary and juvenile) is sometimes transferred to large animals which have a similar morphology for entirely different reasons.

Naris and septomaxilla

The nares of *Mastodonsaurus giganteus* are proportionately relatively small, which is expectable from the large size of the skull. They are widely separated, sitting close to the margin of the skull, but slightly more posterior in position as compared to most other capitosaurids (fig. 12). The outline of the naris is very characteristic in being longitudinally oval with slightly pointed anterior and posterior ends.

The posterolateral portion may be slightly extended in most specimens, a feature found in *Wellesaurus*, *Kupferzellia*, and *Cyclotosaurus*, as well (WELLES & COSGRIFF 1965; SCHOCH 1997a).

As the snout is very much flattened, the naris forms only a slit (in transverse section) which leads into the very narrow and straight narial ductus. This passage is medially and ventrally constricted by the thickened roof for the vomerine tusk sockets. The ductus consequently narrows to one half of its anterior diameter and curves markedly laterally to end in the small, rounded choana proprieta, which then opens ventrally towards the reniform choana palatalis. There is no trace of an ossified nasal capsule, and also no attachment site for parts of the cartilaginous capsule are found. In any case the whole structure of the narial region suggests that the nasal capsules were underdeveloped with respect to most temnospondyls, and especially if compared with apparently terrestrial and lung-breathing forms as *Eryops* (SAWIN 1941), *Zatrachys* (BOY 1989; SCHOCH 1997a).

Surprisingly though, a definite septomaxilla is present in the naris of *Mastodonsaurus giganteus*. It is integrated into the dermal skull roof at the posterolateral rim of the naris, where it forms a concave-convexe stripe of well-sculptured bone (fig. 12). This element has a posteromedial process which points into the narial passage. This process is very thin and narrows medially, and is only present in larger specimens. It is unclear whether it actually floored the passage (which is suggested by preservation) or pointed, in half upright posture, into the otherwise unossified part of the narial duct.

Review on the structure of the skull roof

The skull of *Mastodonsaurus* is composed of extraordinarily massive, planar elements which differ considerably in size but are throughout similar in thickness. There is only one temnospondyl genus with a comparable amount of ossification at nearly the same size, namely *Eryosuchus* from Kazakhstan (OCHEV 1966, 1972; pers. exam).

The arrangement of sutures partially matches the topography of the endocranium (figs. 19–20). In addition, the proportions of the medial and temporal series are correlated with those of the otic, epipterygoid, and sphenethmoid ossifications. This is important for comparing the cranium with those of other capitosaurs in which the braincases are sufficiently known. The posterior rim, formed by postparietals and tabulars, is thickened and forms a descending occipital lamella.

The sutures are tight due to a pronounced serration along all spatial axes: the superficially visible suture is continued into the depth to interfingering bone layers of both elements (fig. 11). The result is an entirely akinetic cranium, a condition which is clearly derived among early tetrapods.

Mastodonsaurus has an overall very flat skull which lacks a pronounced slope anterior to the orbits. It is most similar to the capitosaurids *Wellesaurus peabodyi* (WELLES & COSGRIFF 1965), *Eryosuchus garjainovi* (OCHEV 1972), and *Parotosuchus pronus* (HOWIE 1970) in this respect, and it differs clearly from that of *Cyclotosaurus*, all other *Parotosuchus* species, *Eocyclotosaurus*, and *Benthosuchus* (BYSTROW & EFREMOV 1940).

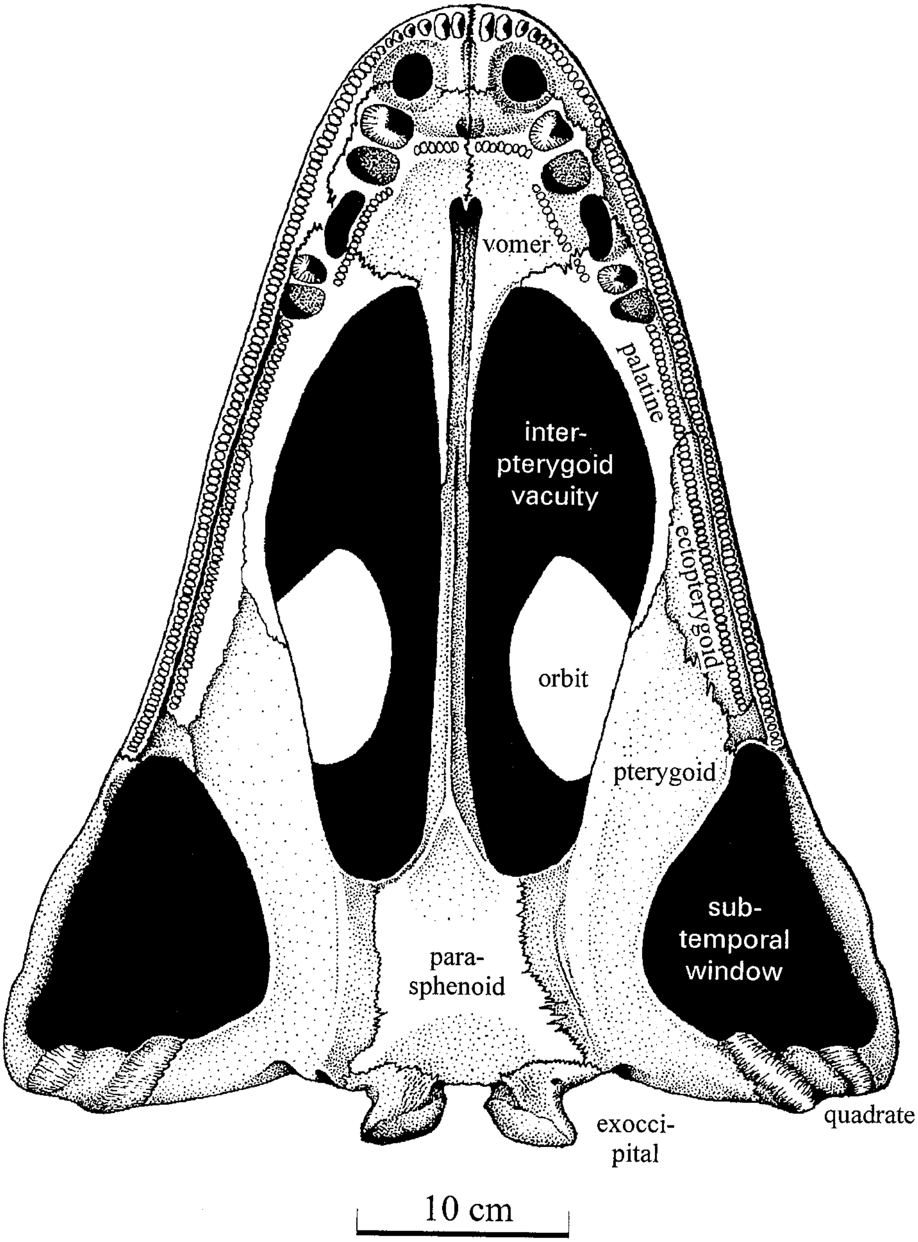


Fig. 13. The skull of *Mastodonsaurus giganteus* in ventral view (SMNS 54675). Characteristic are the two dental arcades, the large tusks in the anterior palate, and the strongly sutured and elongated basicranium.

3.1.3. Palatal dermal elements

The structure of the palate of *Mastodonsaurus* is in all aspects that of what has been conceived an advanced capitosaur (Romer 1947; Watson 1951, 1962). The interpterygoid vacuities are very large, having more than half the skull length and together two thirds the skull width (figs. 13–14). They do not completely match the position of the orbits, because they are constricted by the stout palatine rami of the pterygoids posterolaterally. The cultriform process of the parasphenoid is narrow and rather weakly ossified.

Jaw articulation, occipital condyles, braincase, and marginal tooth arcade are to be firmly integrated by the palatal dermal bones. A predominant role in this context play the parasphenoid and pterygoids (fig. 13). As the occipital and quadrate condyles are extraordinarily massive in larger capitosaurs, the pterygoids and parasphenoids tend to be very stout in these.

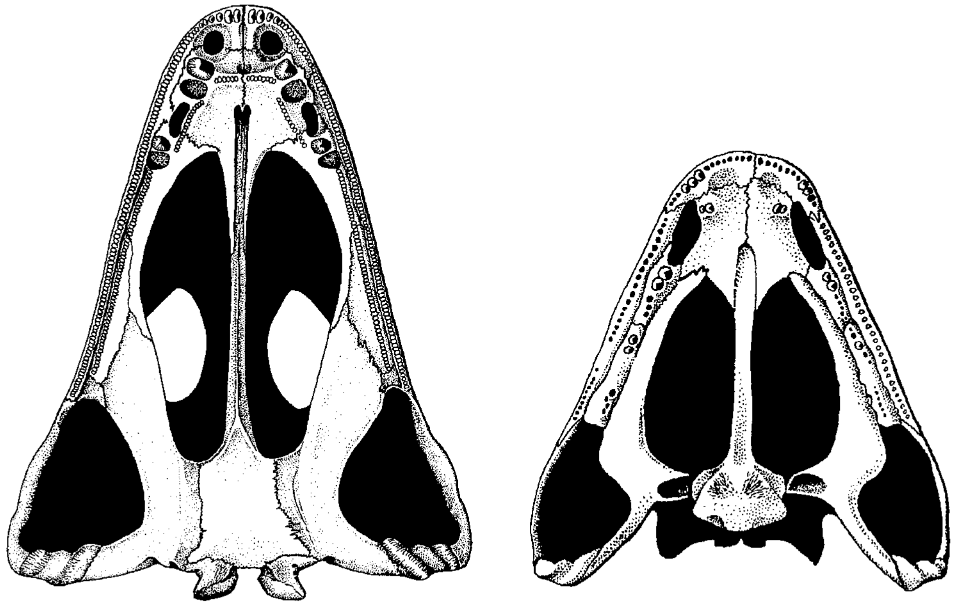
The dentition of the mastodonsaur palate is especially generalised and uniform. It consists largely of two parallel rows which roughly indicate the gape of the animal. The outer row is formed by the teeth of the maxilla and premaxilla and contours the outline of the snout. It is separated from the inner row by a narrow groove posteriorly and by the choana and the symphyseal tusks anteriorly. In two regions a specialised tooth pair of the inner row grows to large size to form palatal fangs. These are situated posterior and anterior to the choana. Besides the described tooth arcades there are no tooth-bearing regions. The ventral surfaces of the pterygoids and parasphenoid which in many basal tetrapods are vaulted and dentigerous, are instead smooth and flattened in *Mastodonsaurus*.

Preservation

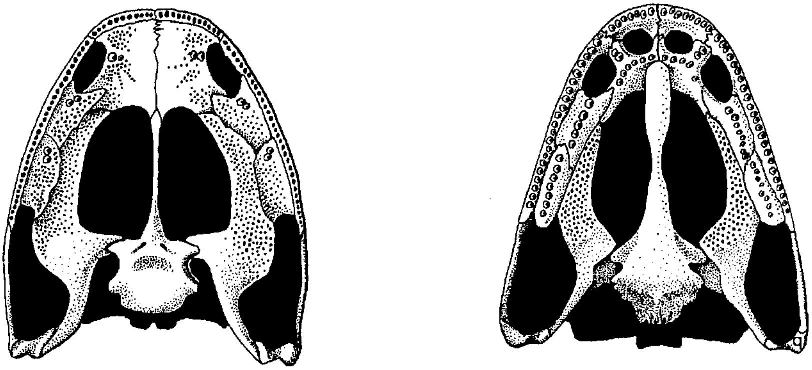
The palate is usually somewhat more affected by compaction than the skull roof. This does however not concern the teeth which generally are neatly preserved in situ in upright position and without major fractures. Empty tooth sockets are obviously not the result of taphonomic decay. There are basically two types of significant preservational bias affecting the palate of *Mastodonsaurus* in the Kupferzell material:

1. Major fractures have lead in certain well-defined regions to slight displacements of structural units. Such fractures occur in the following regions:
– transversely in the posterior third of the basal plate of the parasphenoid (and sometimes the quadrate ramus of the pterygoid);
– obliquely in the palatine ramus of the pterygoid (close to or along its suture with the ectopterygoid);
– transversely in the cultriform process (in various regions, but most frequently transversely along its contact with the basal plate);
– obliquely along the sutures of the quadrate trochlea, tending to isolate this structure;
– transversely in the narrowest regions of the palatine;
– along the suture between maxilla and palatine and ectopterygoid.

2. Dissolution is rare and confined to the most exposed regions such as the sagittal crest of the parasphenoid. This crest frequently appears to have been “worn off” for still unclear reasons. As the preparation was carried out throughout very cautiously, an early diagenetic partial dissolution of bone seems to be more probable.



Mastodonsaurus *Sclerocephalus*



Balanerpeton *Trimerorhachis*

Fig. 14. Palates of selected temnospondyls, exemplifying the proportion of the pterygoid, parasphenoid, and interpterygoid vacuities. Not to scale. *Balanerpeton* and *Trimerorhachis* are primitive forms, which have large pterygoids and extensive tooth patches on the palatal elements. *Sclerocephalus* is a stem-stereospondyl, representing a moderately advanced temnospondyl condition. *Mastodonsaurus* is an extreme variation of the latter, with a strongly ossified and akinetic skull.

Except for one skull, all crania were found in roof-up position, with the palate sticking in a slightly more finegrained layer. The preservation of fine structures such as sutural surfaces, attachment sites for cartilage and musculature, and nutritive foramina is nevertheless throughout excellent.

Vomer

The ventral snout region is dominated by large tusk pairs of vomer and dentary, an almost continuous row of small "circum-vomerine" teeth, and the palatine tusks (figs. 13, 15). This is the typical condition throughout capitosaurs; somewhat similar situations are found in *Ichthyostega* (JARVIK 1996: fig. 25) and *Trimerorhachis* (CASE 1935); see fig. 14. *Mastodonsaurus* is peculiar among capitosaurs in having extremely large fangs whose bases occupy a considerable area. Generally the tooth sockets have about twice the size of those in other large capitosaurs. The only exception is a still undescribed giant *Eryosuchus*-like form from Kazakhstan (M.A. SHISHKIN, pers. comm).

The vomer is the main supporting structure of the snout floor, firmly connecting the tooth-bearing margins of the skull to the ossified floor of the braincase (parasphenoid). The choana, a small, slit-like internal opening of the olfactory passage, is wedged in between the giant fangs of palatine and vomer sagittally and between the maxillar and vomerine tooth arcades transversely. The vomer is a long-rectangular plate which increases in thickness anteriorly. It contacts the following elements: the premaxilla anteriorly, the maxilla laterally, the palatine posterolaterally, and the cultriform process (parasphenoid) posteriorly. The latter contact is established by broad posteromedial processes (pr. parasphenoidales) that form a frame into which the parasphenoid is set in firmly. In *Mastodonsaurus* the processus parasphenoidales do not unite in the midline, so that the cultriform process is exposed ventrally. This is the condition found throughout true capitosaurids (sensu ROMER 1947), i.e. excluding *Benthosuchus*, *Wetlugasaurus*, and the Trematosauridae (BYSTROW & EFREMOV 1940). The parasphenoid hence separates the vomers in the midline up to the dentigerous region at their anterior rim where they meet in a tight suture. The exposed area of the cultriform process characteristically forms a countersunk, anteriorly deepening drain (fodina vomeralis). This drain bifurcates as it enters the canal formed by the vomers. It is bordered by a thickened margin of the vomers that may eventually form a shallow bulge. Further, the canal ends shortly anterior to the transverse vomerine tooth row in a single exit foramen. The median suture between the vomers, which is established along only 1/3 the whole length of the vomers, is serrated and sometimes even co-ossified. The parasphenoid process is thick at its base and compressed-oval in cross-section, but narrows posteriorly to form a thin sheet which moves into a more steep angle relative to the palatal plane as it nears its posterior end.

The symphysial tusks of the dentary are framed by an anteromedial and an anterolateral process of the vomer. The former (pr. fenestralis) contacts the posteromedial process of the premaxilla (pr. vomeralis), whereas the latter (pr. subnarialis) binds the vomer tightly to the medial wall of the premaxillar dental shelf (fig. 15). The aperturae praemaxillares are entirely separated by vomer and premaxilla whose suture is longer than the diameter of each of the aperturae. The anterior rim of the vomers is massive and declines gradually from the base of the transverse tooth row towards the apertural region. The latter is most similar to those of capitosaurids (*Parotosuchus, Eryosuchus, Cyclotosaurus*) in the morphology of the transversely elongated depression in which the aperturae proper are situated.

The ventral surface of the bone is flat and covered with numerous pores occurring in a broad string that runs medial to the circumvomerine tooth arcade. These pores

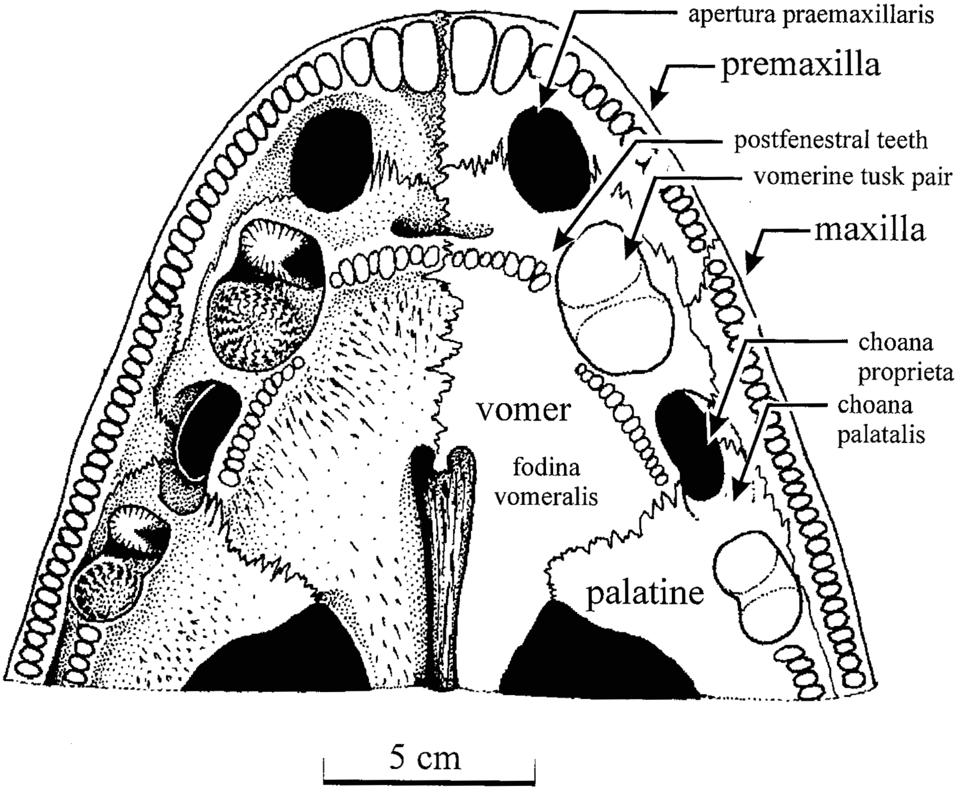


Fig. 15. Anterior portion of the palate in *Mastodonsaurus giganteus* (SMNS 54678). The large symphyseal tusks penetrated the premaxillae through paired openings anterior to the vomerine tusks. A second row of teeth, internal to the premaxillar-maxillar dental arcade, is a characteristic feature of most stereospondyls. In *Mastodonsaurus* the contrast between the tiny marginal teeth and the giant tusks is conspicuous.

open posteriorly, suggesting an intense vascularization of the base of the tooth arcade. The cultriform process further overlaps the vomer dorsally, reaching almost up to the fenestral process. It sits in a depression on the dorsal side of the vomer such as known in *Benthosuchus sushkini* (Bystrow & Efremov 1940: fig. 8). The dorsal surface of the vomer is otherwise smooth and without clear relief.

The vomerine tusk pair is situated at the anterolateral corner of the ventral side of the vomer, next to the region where vomer, premaxilla, and maxilla meet. The long axes of the tusk bases are oriented perpendicular to the long axis of the vomerine tooth arcade. This suggests that the large fangs are developmentally a derivate of the proper vomerine tooth arcade and have just greatly become enlarged. The vomerine tusks are larger than those of the palatine and only slightly smaller than the dentary symphyseal tusks. They occupy half the anterior width of the vomer. The rims of their empty sockets are slightly elevated, and the vomer is dorsally fused to the lacrimal in this region.

The circumvomerine tooth arcade consists of (1) a transverse row of 10–11 small teeth (dentes postfenestrales), (2) the tusk pair, (3) a sagittal row of 15–17 small teeth (dentes parachoanales). The postfenestral and parachoanal tooth rows bear the smallest teeth in the jaws of *Mastodonsaurus*. They are uniform, equidistant, and have medially and posteriorly bent crowns. Their tooth sockets are slightly raised above the vomerine surface, and the postfenestral tooth row has a straight, well-defined base raised above the flat surface of the vomer.

The sutures with the premaxilla and maxilla run lateral to the vomerine tusks, where the latter two bones contact at about midlength. The vomero-maxillar suture converges posteromedially towards the rim of the choana. Finally the suture with the palatine is curved and relatively longer than in the more plesiomorphic capitosaurids, separating the palatine from the vomerine parachoanal tooth rows, it first runs posteriorly and then bends medially where the palatine forms the entire anterolateral rim of the interpterygoid vacuity, finally abutting against the parasphenoid process of the vomer medially.

Choanal region

In plesiomorphic genera such as *Lydekkerina*, *Benthosuchus*, or *Wetlugasaurus* the choana forms an elongate oval, situated between the vomerine and palatine tusks and bordered by parasagittal tooth rows on both sides. In *Parotosuchus* the choana is merely a narrow and long slit, whereas in *Cyclotosaurus* it is instead very short and round to subcircular. Intermediate choanal shapes are possessed by *Eryosuchus*, *Wellesaurus*, and *Mastodonsaurus*.

The choanal region of *Mastodonsaurus giganteus* is reniform with its long axis aligned parallel to the maxillar tooth row. It is bordered by the vomer medially and anteromedially, the maxilla laterally, and the palatine posteriorly (fig. 15). The anterior end is rounded and broader than the posterior one which is constricted laterally. At least in *Mastodonsaurus*, two different openings have to be distinguished: (1) the reniform rim outlined by the palatal elements at the level of their plane ventral surfaces (choana palatalis, chpa), and (2) the proper opening of the olfactory passage towards the dorsal portion of the snout (choana proprieta, chpr). The former is 1/3 longer than the latter and constitutes the structure usually referred to as choana in temnospondyls. Further, the choana palatalis lies in the same plane as the ventral surface of the vomer, whereas the choana proprieta is aligned with a plane clearly inclined towards the palatal plane. The medial frame of the choanal region is straight vertical, thus both palatal and proprietal openings end exactly at the same medial level. Instead, the lateral and posterior walls of the choana palatalis are curved and incline rather shallowly to finally form in the rim of the choana proprieta which is distinctly further anteromedial.

The morphology of the choana proprieta is similar to that in the figure MEYER (1847–55) gave of the giant, now lost *Mastodonsaurus* skull from Gaildorf. The choana palatalis is most similar to that of *Eryosuchus*, *Wellesaurus* in being only moderately long, and it differs conspicuously from the broad choana of *Kupferzellia* and *Cyclotosaurus*. In small forms such as *Kupferzellia* or *Eocyclotosaurus*, there is no internal opening (choana proprieta) because of the low extent of ossification.

Parasphenoid

The parasphenoid is the longest and most differentiated component of the dermal palatal ossifications. It differs markedly in thickness and structure in its various regions. By its structure it can be readily divided into two architecturally different components: the basal plate and the cultriform process. The former is an elongated trapezoidal plate which floors the hindbrain and auditory capsules and firmly connects the pterygoids and exoccipitals (fig. 13). Its thickness increases markedly towards the extensive sutures with the latter two bone pairs. The cultriform process instead is a slender and rather delicate structure, strut-like in ventral view and roughly U-shaped in transverse cross-section. It connects the basal plate, of which it appears to form an anterior outgrowth, with the vomer. There is, however, developmental evidence according to which a separate origin of the two parasphenoidal units can be assumed (LEBEDKINA 1979; SCHOCH 1992).

The basal plate forms a well-ossified block in which the pterygoids and exoccipitals meet; it therefore constitutes the main integrating unit in the posterior palate. The resistance against forces from the quadrate and occipital condyles is certainly as important as the tight contact to the floor of the braincase cartilages and bones. As in basal tetrapods in general, the parasphenoid is almost the exclusive bearer of the endocranium. Also primitive for tetrapods is a basicranial articulation of which the basal plate forms part (ROMER 1947; WATSON 1962; BEAUMONT 1977; PANCHEN 1980; JARVIK 1996). In the plesiomorphic state there is no suture, but instead an elaborate joint between pterygoid and parasphenoid. This condition is found in plesiomorphic temnospondyls like *Edops* and *Trimerorhachis* (ROMER & WITTER 1942; WATSON 1956), and may even be present in advanced forms such as *Platyoposaurus* (KONZHUKOVA 1955). Capitosaurs instead are characterised by a completely flattend basal plate which contacts the pterygoids along extended sutures. In large genera like *Mastodonsaurus* or *Cyclotosaurus* this suture is extremely long and the morphology of the palatal elements strongly altered with respect to other capitosaurs. ROMER (1947), amongst numerous others, stressed this and took the morphology of the basicranial region as main guide in his phylogenetic reasoning. Others (OCHEV 1966; SHISHKIN 1980) on the contrary emphasised this region because they believed it be subject to manifold convergences. Any of these ways, the basal plate is a predominant structure that merits special attention. Its dorsal surface is, after the study of the braincase itself, most significant for the reconstruction of the position of endocranial elements.

Mastodonsaurus giganteus possesses a particularly extended basal plate which has elongated and very tightly fitting, partially co-ossified sutures with the pterygoids (fig. 13). These sutures run posterolaterally, giving the basal plate a roughly trapezoidal outline. In the posterior fourth of its length, the basal plate extends laterally to give an extended contact to the exoccipital. The pterygoid instead has only a short suture with the latter. There are clear differences to *Cyclotosaurus* or *Eocyclotosaurus* which have superficially similar, elongated basal plates. These genera lack the described posterolateral extension of the basal plate and instead the pterygoid contacts the exoccipital there by means of a pronounced posterior process.

The ventral surface of the basal plate is entirely smooth and forms a marked longitudinal bowl that continues for a short distance onto the base of the cultriform process. Such a depression is present in all capitosaurs, but is more clearly established in plesiomorphic forms such as *Parotosuchus orenburgensis*. The continuation of the depression onto the basal plate is instead confined to large genera such as *Cyclotosaurus* and *Mastodonsaurus*, among the advanced capitosaurs. The narrow anteriormost portion of the basal plate continues gradually into the base of the cultriform process, its lateral margins curving faintly. The suture with the pterygoid constitutes a plane that slopes weakly in lateral direction. The surface of this plane is roughened, with numerous small interfingering processes alternating from both sides. The large area and structure of this suture suggests a tight fitting, the result is an entirely akinetic basicranial region. Along the posterior margin the basal plate is firmly connected to the exoccipitals; its medialmost part slightly projects behind the level of this suture and separates the exoccipitals. Such a posterior portion is usually covered by paired 'muscular pockets' (WATSON 1962) supposed to form origin sites for hypaxial musculature. In *Mastodonsaurus* these fossae are very variable in size, position, and expression. In any case they are not as predominant as in most other capitosaurs, and especially their length is minimal as compared to *Parotosuchus*, *Lydekkerina*, and *Rhinesuchus* (SCHROEDER 1913; BROILI & SCHRÖDER 1937a, b; WATSON 1962). A definite crista muscularis, that is a sharp-cut transverse edge bordering the posterior sunk area (termed by BYSTROW & EFREMOV 1940) is not throughout present.

The dorsal side of the basal plate has a rugose surface and is attached to several ossified units of the endocranium (fig. 18). These are, from anterior backwards, (1) the laterosphenoid portion, (2) the basisphenoid region, (3) the otics, (4) the exoccipitals, and (5) the basioccipital ossification. All of these leave well-defined attachment areas, between which the surface is markedly smoother. The basal plate itself bears a complex system of crests and depressions, which are from posterior to anterior: (a) the medial crista basioccipitalis, (b) the paired cristae paroccipitales, (c) the paired cristae parapterygoideae, and (d) the paired cristae laterosphenoidales at the base of the cultriform process. Cristae paroccipitales and parapterygoideae converge towards a common point where they form a slightly raised point. This point is almost exactly at midlength of the basal plate in *Mastodonsaurus*.

The well-ossified laterosphenoid region of the braincase is tightly set in the region between the cristae laterosphenoidales, as transverse section revealed. The crests become higher but thin anteriorly, keeping their width roughly. Anteriorly they bear the sphenethmoid proper, which is not separable from the laterosphenoid ossification. The unpaired laterosphenoid unit is easily distinguished from its ventral supportings by the finer structure, the lighter colour, and the larger extent of compaction. This portion of the basal plate is fairly smooth and was probably not directly covered by cartilage. There are two pairs of foramina situated lateral to the cristae laterosphenoidales. BYSTROW & EFREMOV (1940: fig. 10) homologised these foramina as palatine ramus (the outer) and internal carotid ramus proper (the inner) of the carotid artery. The single entrance foramen was supposed to be at the posterolateral corner of the basal plate, anterior to the suture with the exoccipital. SHISHKIN (1968) and BOY (1988) agreed with this concept by homologizing similar foramina in other eryopoid species. In *Mastodonsaurus* the position of the exit foramina is very similar to that in *Benthosuchus sushkini*, whereas the proper entrance foramen is more difficult to localise, and perhaps may be variable in position. The basal plate of *Mastodonsaurus* differs from that of plesiomorphic capitosaurs by its anterior extension particularly. This is most evident by the relative position of markers, such as (1) the crista parapterygoidea, (2) the conical recess, and (3) the internal carotid foramen. Whereas in *Benthosuchus*, *Wetlugasaurus*, *Parotosuchus,* and *Kupferzellia* they are arranged sagittally very close to each other, in *Wellesaurus* and particularly *Mastodonsaurus* there is a long distance between the former two and the lattermost of these points. The epipterygoid, basisphenoid, and laterosphenoid regions are consequently longer. The floor of the laterosphenoid region (the dorsum sellae region) ends medial to the attachment of the basisphenoid. Whereas the former is an entirely unpaired element, the latter is separated partially by it and its attachment areas on the basal plate are far distanced. These areas are roughly triangular, and have about 2/3 the extension of the epipterygoid cross-section at this level. The epipterygoid does only have a very narrow attachment site on the basal plate, otherwise expanding on top of the basipterygoid ramus of the pterygoid exclusively. Medial to the epipterygoid, and slightly posterolateral to the basisphenoid, there is a short crest which attaches to the otic ossification (the crista basipterygoidea of the otic). Thus the epipterygoid, otic, and sphenethmoid-laterosphenoid ossifications are closely packed in this region; whether this situation is unique for *Mastodonsaurus* or simply an expanded yet topographically otherwise primitive state is yet to be elucidated.

The floor of the auditory capsule was apparently entirely cartilaginous and attached only at certain points to the basal plate. Such a contact is evident from rough markers on the bottom of a depression bordered by the parapterygoid crest, the epipterygoid, and the basisphenoid. This bowl-shaped depression is exactly medial to the conical recess, forming the apex of the floor of the auditory capsule. The parapterygoid crests are almost straight transverse, such as in *Kupferzellia* and *Wellesaurus*, but unlike in *Benthosuchus*. In *Mastodonsaurus* they meet in the midline where they form a slightly elevated medial crest, into which the paroccipital crests converge, as well. The cristae parapterygoideae have a rather complex surface: strictly speaking they bifurcate laterally by splitting into an anterior and posterior portion. The anterior part runs strictly transverse and continues into the gradually widening base of the epipterygoid. That means that parasphenoid and pterygoid are indeed co-ossified in this region. The posterior part runs slightly posterolateral, forming the posterior wall of the chamber of the stapes. Anterior and posterior parts of the crest are separated by a laterally widening groove, out of which a prominent boss rises close to the point of bifurcation. This is the site to which the ventral process of the stapes is attached, as cross-section clearly shows. The crista paroccipitalis rises from the posterior portion of the crista parapterygoidea. It widens posterolaterally to give a large suture for the attachment of the subtympanic process of the exoccipital.

The posterior part of the basal plate is demarcated by the prominent, anteromedially curved cristae paroccipitales which together outline a semicircle. The height of these crests increases posterolaterally, where they form stout attachment areas for the otics and exoccipitals. Inside this semicircle the surface of the plate forms a depression (fossa basioccipitalis of BYSTROW & EFREMOV 1940) which is sagittally elongate and ends bluntly at the transverse posterior margin. In *Mastodonsaurus* this bowl is partially subdivided by a crest that originates at the midpoint of the posterior margin (where it is highest) and runs about half the length of the bowl, continually shallowing towards there. The entire surface of these crests and the bowl contains grooves and ridges which converge towards the apex of the semicircle formed by the paroccipital crests. Well-preserved specimens suggest that the entire surface of the fossa basioccipitalis was covered by cartilage. The ossification of this cartilage follows a pattern already known from other capitosaur genera (e.g. *Eryosuchus tverdochlebovi*, OCHEV 1972). According to the topography of this cartilage a homologization with the basioccipital is rather straightforward (SAWIN 1941). The first portions to ossify are the regions lateral to the crista basioccipitalis, and they may eventually attach to the submedullar processes of the exoccipitals. Only in some specimens the extent of ossification is larger, comprising a large part of the fossa basioccipitalis. Characteristically, ossification of this region is recognised as a fine cover by a granular substance which easily disintegrates. Only the paired anlagen lateral to the crista basioccipitalis reach a bodily structure, rising markedly above the surface of the bowl. These paired anlagen are very similar in shape and position to the lateral portions of the basioccipital in *Eryops* (Sawin 1941: pl. 7, fig. B).

The cultriform process comprises more than 2/3 the length of the skull. It forms the largest part of the medial border of the interpterygoid vacuities. The sphenethmoid element, which is variable in its extent of ossification, is completely floored by the cultriform process. This contact is established by the cristae sphenethmoidales which are outgrowths of the dorsolateral margins of the element. The sphenethmoid is set in the space delimited by these cristae, and its side walls connect to these almost without a visible suture.

Ventrally, the cultriform process bears a ridge which rises from the converging lateral margins at about the posterior third of the length of the orbits, and persists up to the level of their anterior end. The height and surface structure of this ridge is variable, it is however clearly different from the sagittal crests present in various other capitosaurs (*Thoosuchus, Parotosuchus oreburgensis, Eocyclotosaurus, Cyclotosaurus*). Rather it resembles the more cylindrical rod-like cultriform process typical of *Parotosuchus nasutus* (Schroeder 1913). The base of the process is ventrally markedly depressed. Instead, the anterior third of the element is slightly convex posteriorly and gradually becomes concave, as the process is framed laterally by the vomers. The transverse cross-section of the element is U-shaped posteriorly, V-shaped about at midlength, and finally transversely oval to flat in the anterior third.

Palatine

The interpterygoid vacuities are laterally framed and separated from the marginal tooth arcades by the palatine and ectopterygoid. In *Mastodonsaurus* these bones are comparatively slender and thin (fig. 13). Posteriorly the palatine tooth row is separated from the vacuity by only a narrow stripe of planar and smooth bone. There the interpterygoid vacuities reach their widest measure. The palatine is an intercalated strut which (1) connects the vomer posterolaterally to the skull margin, (2) borders the choana posteriorly, (3) bears a pair of prominent tusks, and (4) forms part in the supporting of the continuous inner tooth arcade. It connects to four bones: to the maxilla laterally, the vomer anteromedially, the pterygoid posteromedially, and the ectopterygoid posteriorly. Among those the contact to the pterygoid is typical of capitosaurs, in which the palatine ramus of the pterygoid is reduced anteriorly. The proper contact is established by means of an elongated and slender posteromedial process of the palatine; the ectopterygoid is thereby completely excluded from the bordering of the interpterygoid vacuities.

The palatine tooth arcade altogether comprises in between 25 and 30 teeth of different size. Basically three regions can be arbitrarily distinguished (from posterior forewards): (1) a posterior row of 20–25 similar-sized and equidistant, (2) a pair of large tusks, and (3) three to six tiny teeth of the parachoanal tooth row. The teeth of the first and third groups are set in almost without a clear base, but instead rise directly from the flat plane of the ventral surface. Only the lateral and medial margins of the tooth sockets are slightly raised above this surface. The latter is otherwise entirely smooth. The medial margin of the palatine is in its middle part rounded but otherwise forms a rather thin sheet of bone. The anteriormost tooth pair is very large, forming the posteriormost of the palatal tusk pairs. It is situated well posterior to the choana palatalis, whose posterior part is formed entirely by the palatine.

Medial to the tusk pair the palatine is very wide, forming almost the complete anterior rim of the interpterygoid vacuities by means of a medial protuberance which is sutured to the vomer in serrated fashion. The anteriormost part of the interpterygoid vacuity is very narrow because of the broadening of the palatine in this region which is at the level of the posterior tusk. The suture with the maxilla runs anteromedially, at about midlength of the choana palatalis towards which it converges.

Dorsally the palatine contacts the lacrimal by a posteriorly directed spine which it meets in a horizontal, flat suture, a contact which was first observed and named in *Benthosuchus sushkini* (BYSTROW & EFREMOV 1940).

Ectopterygoid

This element is almost of the same length as the palatine, but clearly forms the larger part of the continuous tooth arcade borne by these bones. The ectopterygoid contacts the maxilla laterally, the palatine anteriorly, the pterygoid posterolaterally, and the jugal posterodorsally (fig. 13). It is excluded from the rim of the subtemporal window by a large ventral process of the jugal. The ectopterygoid is along most of its length equally wide, throughout being narrower than the palatine. It bears in between 39 and 43 teeth of similar size and morphology. The tooth sockets are characteristically laterally expanded and sagittally compressed.

The ectopterygoid is among the palatal elements the thinnest and least stabilised bone, basically it forms a sheet which largely overgrows other, more firmly integrated components of the palate and skull roof. The suture with the pterygoid is long and slightly serrate. The anterior half of the element overlaps the pterygoid, which is reversed posteriorly. The ectopterygoid itself overlaps the ventral process of the jugal extensively, leaving only a small triangular area of the latter exposed ventrally (insula jugalis). Most of the dorsal side of the ectopterygoid is, moreover, attached to the medial margin of the fissura maxillaris of the jugal. The suture with the maxilla is the longest contact and along the entire length the maxilla provides the underlapping base for the ectopterygoid. The furrow separating the ectopterygoid and maxillary tooth rows is entirely made up by the maxilla.

Pterygoid

In the primitive condition of the Tetrapoda the pterygoid (= entopterygoid + dermometapterygoid?) is a tooth-bearing element among others (ectopterygoid, palatine, vomer) which serves both the purposes of stabilisation and mobility (basicranial articulation). In capitosaurs the pterygoid has lost both the tooth arcades and the movable basipterygoid joint. Instead, it appears to predominantly guarantee maximum stability there. It has lost contact to the vomer entirely and the suture with the palatine is largely modified with respect to the plesiomorphic condition: only the posteriormost part of the palatine is reached. As a result of this anterior reduction, the interpterygoid vacuities are very large in capitosaurs.

By its architecture the pterygoid is basically a four-rayed strut which connects the upper jaws with the quadrate condyles, the cheek region, the occipital condyles, and the floor of the braincase (fig. 13). It therewith contacts all major ossified units of the posterior skull. These four rays are (from anterior backwards, in clockwise rotation): (1) the palatine ramus, (2) the basipterygoid ramus, (3) the quadrate ramus, and (4) the lamina ascendens, which actually is a dorsal, sheet-like prolongation of the latter (fig. 17).

The largest and most strengthened ramus is the palatine branch that connects the basal plate with the palatine, jugal, and ectopterygoid. It is stout and markedly widened in *Mastodonsaurus* (figs. 8, 13), by its extent differing from all other capitosaurs, even the closely related *Heptasaurus*. The column of the palatine ramus is formed by a broad, cylindrical rod which runs parasagittally, close to the medial margin of this unit. This rod continues anteriorly, by slightly bending into a more lateral direction, to form the margin of the interpterygoid vacuities. Posteriorly the column reaches towards the base of the quadrate branch near to the suture with the basal plate. The lateral parts of the palatine process form a flat yet well-ossified sheet which is covered by only minor striations. Anterolaterally, the branch becomes markedly wider, which culminates in a small posterolateral lappet, until the process bends medially again to align with the anterior embayment of the subtemporal window.

The basipterygoid branch is – even compared to the state found in most capitosaurs – relatively short. It is plesiomorphically the bearer of the basicranial articulation, but in capitosaurs connects by means of a long suture to the basal plate. On the dorsal side the basipterygoid branch bears the large attachment facet for the epipterygoid footplate. It rises anterior to a rounded hollow, the conical recess. In most other capitosaurs the epipterygoid facet is restricted to the region anterior to this recess. In *Mastodonsaurus* and *Eryosuchus*, however, the attachment area is greatly expanded (SCHOCH 1997a) and even extends lateral to the conical recess, connecting to the base of the lamina ascendens. Medial to the base of the epipterygoid a narrow bony sheet is borne which connects the pterygoid to the otic. The suture with the basal plate is an almost horizontal plane, with the basal plate overlapping the pterygoid ventrally. The quadrate ramus is relatively short but stout in *Mastodonsaurus*, by which this form is again similar to *Eryosuchus* and *Cyclotosaurus*. It connects the quadrate trochlea with both the exoccipital and basal plate. Unlike in plesiomorphic capitosaurs such as *Wetlugasaurus* and *Rhinesuchus* it is oriented nearly transversely. Typically the quadrate ramus forms a curved bony sheet that slopes posterodorsally where it forms a marked edge, then bending anterodorsally to contact the quadrate and quadratojugal in the occiput. The suture with the quadrate is large and apparently very tight. The surface of this suture is curved concavely, and the contact is tightened by the already described complex alternate indentation.

The lamina ascendens is an extended dorsal outgrowth of the quadrate ramus. Usually forming a rather thin bony sheet, in *Mastodonsaurus* it is a highly elaborate structure of remarkable thickness. It rises posterolateral to the conical recess and curves in anti-sigmoid fashion posteriorly. Dorsally it unites by complete fusion with the descendent flange of the squamosal, hence entirely closing the occipital surface anterior to the supposed columellar cavity. Its medial part is thickened, particularly firmly connected to the descendent lamella of the squamosal, and anteriorly bears an array of vertical ridges. Parts of this surface are covered by a thin sheet of apparently replacement bone, which is interpreted as ossification of the palatoquadrate.

Subtemporal windows

The subtemporal windows are especially wide in advanced capitosaurs such as in the genera *Cyclotosaurus*, *Eocyclotosaurus*, and *Mastodonsaurus*. Their relative transverse expansion results laterally from a convexly curved quadratojugal and medially is produced by a shortened basipterygoid ramus (fig. 13). With respect to more plesiomorphic capitosaurs, such as *Rhineceps nyasaensis* (WATSON 1962) or *Parotosuchus nasutus* (SCHROEDER 1913) their posterior extension is smaller, which results from the relative more anterior position of the quadrate condyles. In addition, both the depth of this upper adductor chamber and the depth of the window-framing elements is much smaller in *Mastodonsaurus* than in most other capitosaurs, again with the exception of *Eocyclotosaurus* and *Cyclotosaurus* (SCHOCH submitted 1). The medial rim is formed by the entirely flat palatine ramus of the pterygoid, the lateral rim by the largely thickened ventral process of the quadratojugal, the posterior rim by the qudrate trochlea, and the anterior rim by the ventral process of the jugal. There are complete walls on only two sides: laterally formed by the quadratojugal, and posteriorly built of the quadrate and lamina ascendens pterygoidei. Both of these are slightly curved in convex fashion. Anteriorly, the chamber opens into the circumorbital space which in the living animal most probably housed the eye, orbital musculature, and perhaps some jaw muscle portion. Medially, the adductor chamber is demarcated by the lamina ascendens pterygoidei, the otic process, the cornu oticalis, and the ascending portion of the epipterygoid. Because of the unexpected richness of endocranial ossifications, we are considerably well informed about the size of the adductor chamber in *Mastodonsaurus giganteus*, and with it about the (maximal) amount of the musculature, at least in the posterior corners of the cavity.

Interpterygoid vacuities

In the plesiomorphic condition, tetrapods possess narrow slits or small oval openings between the parasphenoid and the pterygoid anterior to the basicranial articulation (JARVIK 1996). These slits are enlarged in many basal tetrapods to small fenestrae (interpterygoid vacuities), largely as a result of the reduced medial growth of the palatine ramus of the pterygoid. In temnospodyls this reduction is most characteristic and gains a maximum in several, among which capitosaurs are the most spectacular example (fig. 14). In the latter group the pterygoid fails to reach the vomer and is, moreover, only connected to the posteriormost part of the palatine, which results in especially wide vacuities. The palatal elements lateral to the parasphenoid are reduced to mere struts, and except for a single, marginally placed tooth row they have completely lost the usual denticle fields (fig. 13). Whereas in plesiomorphic capitosaurs the interpterygoid vacuities keep a fairly constant length for most of their longitudinal measure, certain advanced genera have posteriorly constricted vacuities. This is a consequence of the stout palatine ramus mainly. In *Mastodonsaurus giganteus* this phenomenon has reached a maximum because of the very broad development of the palatine pterygoid branch. It may be interesting to note that – beyond their posterior end – the interpterygoid vacuities appear to be continued by paired depressions on the anterolateral parts of the basal plate. These are well-established in some specimens and clearly demarcated by the rod-like pterygoid columns.

Review on the structure of the palate

The palate of *Mastodonsaurus giganteus* is arranged in a single plane, with the flat surface of the bones having almost no relief. The extent of ossification varies markedly: the vomers, pterygoids, and the posterior basal plate are very strong and thick-walled elements. In addition, the vomer and palatine come so close to the skull roof that they form processes abutting to it. This is especially the case in the regions dorsal to the giant tusks. The vomer is further very firmly bound to the premaxilla, which results from the very lateral position of the symphyseal tusks. Consequently the apertura praemaxillaris is subdivided by a broad medial bridge that tends to co-ossify, and also almost reaches the alary processes of the premaxilla.

The most delicate structure is the cultriform process, which is filled by the sphenethmoid, by which it is almost completely connected to the medial skull roof series. Only the anterior integration of the parasphenoid into the palate is established by large posteromedial processes of the vomer. Apparent is furthermore that the relative weakness of the parasphenoid is contrasted by the large extent of bone in the braincase. This is a fact contradictory to the long-held opinion that capitosaurs – such as advanced temnospondyls in general – ‘tended’ to ‘progressively chondrify’ (Case 1911; Pfannenstiel 1932; Romer 1947; Watson 1958, 1962). Examination of other capitosaur finds instead suggests that at least some capitosaurs possessed among the most well-ossified braincases among temnospondyls.

The most conspicuous peculiarities of the palate in *Mastodonsaurus* are: (1) the extraordinary size of the tusks on palatine and vomer, (2) the stout basicranial region with the extreme elongation of the basal plate and its contact to the giant occipital condyles, (3) the broad and massive separation of the aperturae praemaxillares, and (4) the rather small, reniform (palatal) choana.

3.1.4. Occiput

General structure

The skull roof of *Mastodonsaurus* shallows continuously from the occiput forewards. By that it can be distinguished readily from all other capitosaurs, in which the entire posterior skull table is usually well raised, with the orbits sitting at the anterior slope towards the largely flattened snout. In contrast *Mastodonsaurus* is not characterised by particularly elevated orbits; they instead follow the slope of the preorbital region.

The occiput of *Mastodonsaurus* is clearly higher than in *Cyclotosaurus* and allied forms, but bears some resemblance in its general organization (fig. 16). The occipital condyles are situated at the same level as the quadrate condyles, and there is practically no relief within the palatal elements. The slope of the flanks of the occiput is similar to the condition in *Parotosuchus nasutus* and *Eryosuchus garjainovi* and differs by that from *Cyclotosaurus* and *Eocyclotosaurus*.

The foramen magnum is large and high, with keyhole-shaped outline. It is bordered laterally by strong yet slender columnae verticales (exoccipital), roofed by the postparietal and – in large specimens – the posteriormost extension of the otic ossifi-

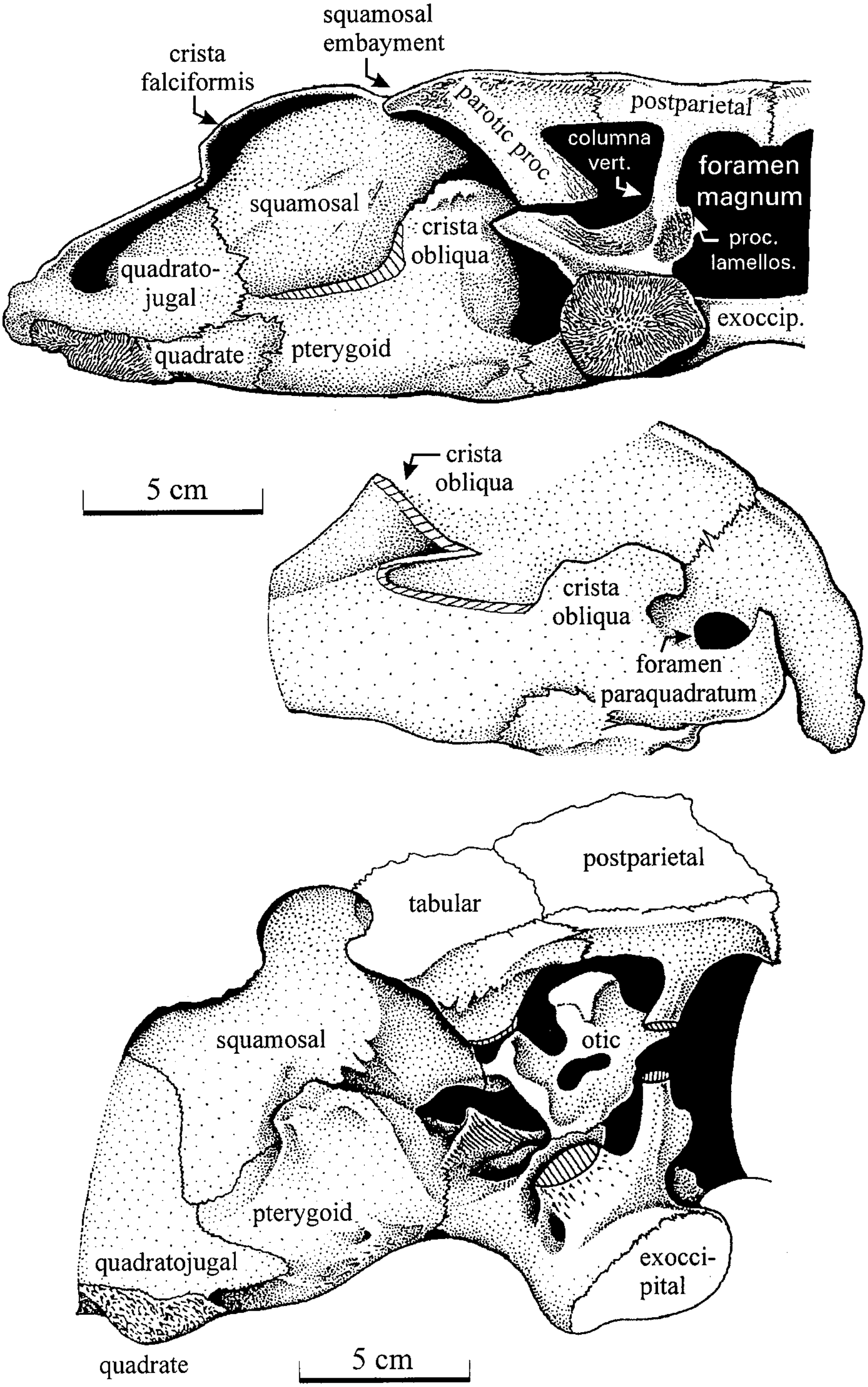


Fig. 16. The occiput of *Mastodonsaurus giganteus* (SMNS 54675). Above, left side of occiput in posterior view; middle, right side with details of the pterygoid and quadratojugal; below, oblique posterolateral view of left side, with parts of exoccipital removed and the fenestra vestibuli and otic depicted.

cation. There is no trace of a separate supraoccipital bone, although in large specimens the presence of a continuously ossified neurocranial roof is observed, whose posteriormost portion encompasses the region in which in basal tetrapods the supraoccipital exists.

The broad cheek regions are formed by mostly thin-walled dermal ossifications, in particular the quadratojugal, squamosal and pterygoid.

Preservation

Most Kupferzell specimens are badly crushed which has most seriously affected the occiput. The most heavily affected regions are the lamellae of the squamosal and pterygoid, and the processes by which the exoccipital connects to the skull roof. In most cases compaction has crushed the occipiti to such an extent that the supraoccipital fenestrae have disappeared and the foramen magnum is but a narrow slit.

Lamina ascendens of pterygoid

Nearly 1/3 of the occipital face of the cheek is formed by the pterygoid, and this is accomplished exclusively by the lamina ascendens. It forms a rather weak (and often fragmented) sheet of bone that wedges in between the squamosal, quadrate, and exoccipital, and which contacts the quadratojugal only faintly by its most lateral portion (figs. 16, 17). In horizontal section the lamina is roughly sigmoidally curved, thereby bending from a nearly sagittal into a completely transverse orientation.

The most prominent external structure borne by the lamina ascendens is the crista obliqua. This is a subvertical, well-ossified wall which is aligned transversely at an angle of 15–20° towards the anterodorsally sloping occipital face proper of the pterygoid and squamosal (fig. 16, below). It is grown out of the topmost portion of the lamina ascendens, slightly below the suture with the squamosal. The crista obliqua is very variable both individually and if compared among different species. It has so far been only reported for capitosaurs, and is an especially frequent phenomenon in either large or hyper-ossified species. Warren & Schroeder (1995) have recently reviewed some of the knowledge on this structure. In *Mastodonsaurus* the posterior face of this crest is prominently sculptured, and the topmost margin sometimes much roughened. It may reach laterally close to the paraquadrate foramen, but usually is affected by compaction or worn off. Medially it nears the paroccipital process, a feature also occuring in large *Uranocentrodon* specimens (pers. exam.), where it almost contacts the process, tending to form a nearly closed bony channel in which the middle ear was housed.

The sutures, especially those with the squamosal and quadratojugal, are squamate with an extensive extent of overlap. The suture shared with the quadrate trochlea is broader and the surface much more roughened, making up a complex and firm interfingering. There are several well-established roughened areas in this part of the lamina, as well.

Lamina descendens of squamosal

The squamosal forms the largest portion of the occipital face of the cheek. It occupies almost 40 % of this area, and forms a practically smooth, posteroventrally sloping wall (fig. 16). It meets the lamina ascendens of the pterygoid in a long suture where it overlaps the latter. The squamosal is so thin in the whole occipital region that it is frequently fragmented. Laterally it overlaps the quadratojugal by a convex suture, but ventrally fails to reach the trochlea quadrati by only a small distance.

Dorsally the lamina is connected to the anteroventrally sloping roof portion of the squamosal. The posterior rim of this part is formed by a moderately developed crista falciformis, which continues onto the quadratojugal laterally. The surface of the whole lamina is entirely smooth. Throughout the known developmental stages, the occipital portion of the cheek is completely closed by bone, such as is typical of ontogeny in capitosaurs.

Quadratojugal

The occipital portion of the quadratojugal is markedly concave and possesses in its apex a large paraquadrate foramen (fig. 16). The latter is transversely oval and sits close to the lateral margin of the element, where the lateralmost part of the crista falciformis runs. The bone is thinnest in the region immediately surrounding the foramen. The crista falciformis contours the posterior margin of the flat, roofing part of the bone, and in the posterolateral corner bends medially to merge into the upper bulge of the quadrate trochlea. In some specimens this area is roughened, whereas the rest of this face remains rather smooth. The processus ventralis of the quadratojugal abuts against the lateral edge of the quadrate trochlea and is tightly connected to this by means of a widened medial head.

3.1.5. Palatoquadrate ossifications

In gnathostomes the endocranium is basically composed of the neurocranial and palatoquadrate portions (Hennig 1983; Janvier 1997). They originally rise from rather different embryonic primordia, and in many basal tetrapods finally the basicranial articulation is their most important interface. The loss of a definite basicranial joint is apparent in all capitosaurs from the elongated suture between parasphenoid and pterygoid which floor the neurocranium and palatoquadrate respectively. Palatoquadrate ossifications are generally unossified, unpreserved, or badly crushed in basal tetrapods. In *Mastodonsaurus giganteus* at least three palatoquadrate regions are ossified, all of which are situated in the posterior part of the skull. These are the epipterygoid, the otic process, and the quadrate. Each of them in the ground-plan constitute either true joints or elements involved in the formation of articulations: the epipterygoid and otic process each connect the pterygoid to particular regions of the braincase while the quadrate forms the massive trochlea for the jaw articulation.

Preservation

The epipterygoid and otic process of the palatoquadrate are in most specimens seriously affected by compaction. In the former element, which is extensive in dimension yet lightly built, compaction has resulted in minor distortions and a fracturing of the anterior process. This may be due to its rather shallow position within the endocranium. In strongly compacted skulls, however, the epipterygoid is badly crushed. Late ontogenetic palatoquadrate ossifications (pterygoid process) are found as a thin cover on the dorsal surface of the pterygoid, and therefore are rather well preserved if present.

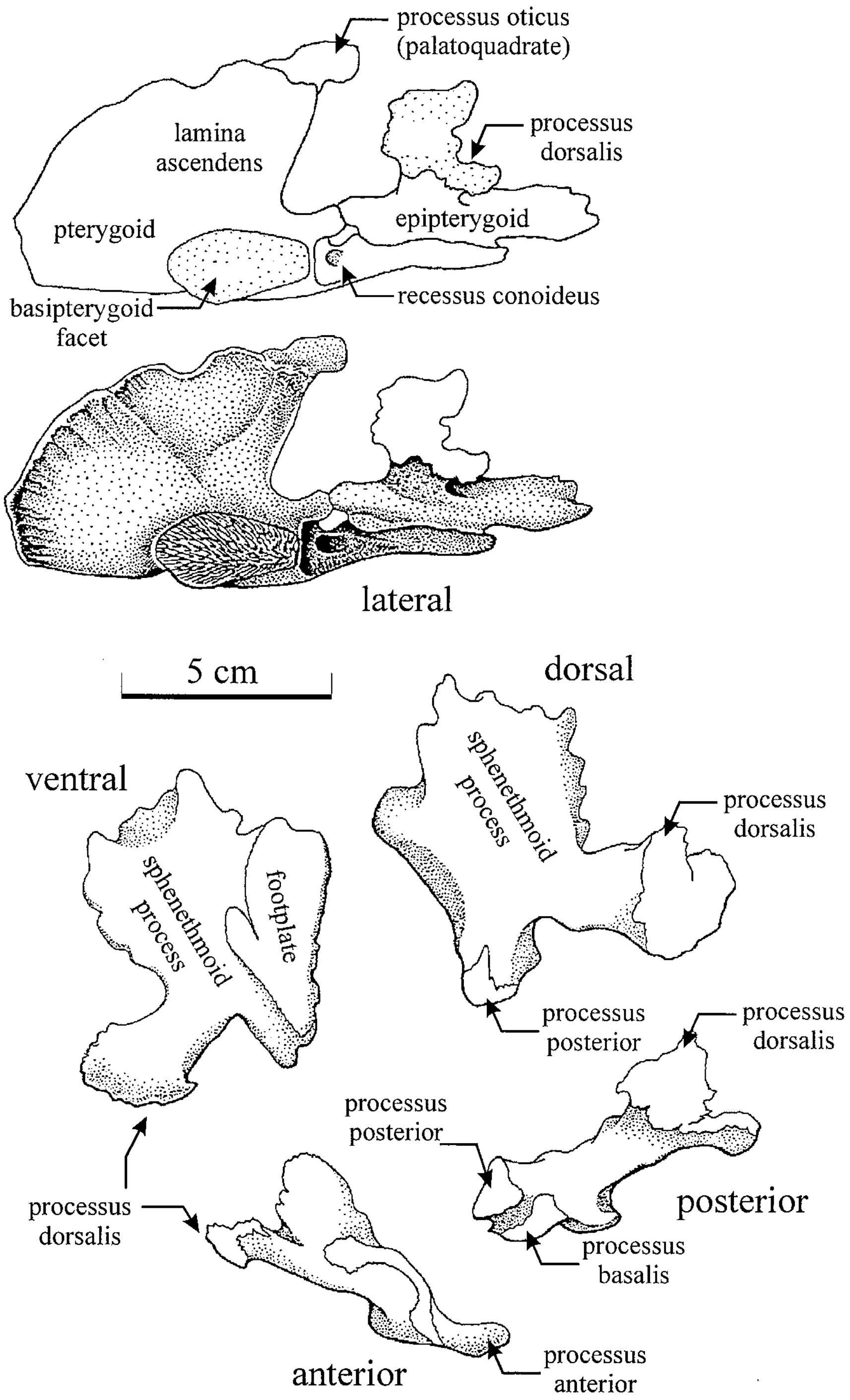


Fig. 17. Palatoquadrate ossifications in *Mastodonsaurus giganteus*. Above, epipterygoid in articulation with pterygoid, medial view (SMNS 81323); below, epipterygoid from different perspectives (SMNS 80977).

The otic process is absent in most specimens, supposedly according to large-scale fracturing of the lamina ascendens pterygoidei. Its proper extent is much more difficult to ascertain than that of the former element. The usually preserved part is raised very high in the column of the posteriormost cranium where considerable compaction is the rule in the Lettenkeuper material.

The quadrate trochlea is almost unaffected by compaction, though the thin occipital portions of the quadrate ossification are frequently only fragmentarily present.

Epipterygoid

The ascending process of the palatoquadrate primitively forms the anteriormost articulation of the palatoquadrate with the neurocranium (GOODRICH 1930; DEBEER 1937). In larvae of urodeles, which probably have retained a condition similar to that of the larval tetrapod ground-plan, it is a cartilaginous rod or strut growing dorsally out of the pterygoid process of the palatoquadrate. The pterygoid process forms the endocranial associate of the dermal pterygoid bone, and has so far been conceived entirely unossified in most basal tetrapods. The study of large *Mastodonsaurus giganteus* skulls from Kupferzell revealed, however, that a considerable portion of the palatoquadrate ossified in this species. This mostly very thin sheet of bone encompasses 2/3 of the palatoquadrate pterygoid process !

The epipterygoid such as defined by STADTMÜLLER (1936) is exclusively an ossification of the processus ascendens; it does neither have a contact to the lamina ascendens pterygoidei (contra PANCHEN 1970; SMITHSON 1982) nor the true otic process of the palatoquadrate (see below). Plesiomorphically, and probably in larval crania throughout, the ascending process of the palatoquadrate forms a joint which permits certain amounts of movement of the cheek relative to the skull table. Urodele larvae most clearly demonstrate and probably have retained this mechanism. The processus ascendens palatoquadrati is usually only partially ossified in temnospondyls. Especially in capitosaurs, there is much variation in the relative size and shape of this unit.

Mastodonsaurus has an extensive epipterygoid ossification (figs. 17, 18, 20). It differs from that of most other capitosaurs in being inclined more obliquely towards the sphenethmoid. It is often difficult to localise the proper suture with the dorsal and medial surfaces of the pterygoid, so that sometimes the elements appear to be co-ossified. This is however unprobable, as all disarticulated specimens have very elaborate suture surfaces between the pterygoid and epipterygoid. The extent of ossification is most similar to that in *Eryosuchus garjainovi* (OCHEV 1972) and *Parotosuchus pronus* (HOWIE 1970). *Parotosuchus orenburgensis* also has a well-ossified, stout epipterygoid, but this differs considerably in its morphology from both genera, especially in lacking a dorsomedial process.

The epipterygoid of *Mastodonsaurus* bears the following six unequal processes (fig. 17):

(1) a large footplate, which attaches to a particular facet on the anterodorsal surface of the basipterygoid ramus (pterygoid),

(2) a huge blade-like processus anterior that points straight anteriorly, thereby paralleling the lateral wall of the sphenethmoid (HOWIE 1970),

(3) an elongate processus sphenethmoidalis which is orientated obliquely dorsomedially and is suturally connected to the posteriormost portion of the sphenethmoid.

(4) a short, boss-like processus posterior which abuts against a protuberance at the anterior end of the lamina ascendens,

(5) a rudimentary processus basalis, forming a facet which nears the hypothetical basisphenoid cartilage, and

(6) an extensive processus dorsalis which contacts the skull roof as well as the laterosphenoid roof, with one specialised facet each.

As mentioned, the epipterygoid is aligned within one oblique plane mainly, so that the element has large medial and a lateral sides, in addition to the dorsomedial face of the processus dorsalis.

The footplate is a flat, extended portion attaching shallowly to the anterodorsal margin of the basipterygoid ramus. Its sutural surface is of longitudinally oval outline and runs sagittally. The suture itself lies within the horizontal plane, the main plane along which the epipterygoid is aligned is obliquely to this, pointing at an angle of about 30° dorsomedially. The footplate is moreover rather thin and almost completely flat.

The anterior process is much longer than in any other capitosaur. It forms a dorsomedially aligned plate whose anterior portion is curved in sigmoid fashion, if viewed transversely. The dorsal side of this blade bears several ridges, and the regions between these are markedly pitted. This process reaches forward up to about two thirds of the length of the sphenethmoid.

The sphenethmoid process forms an irregularly curved blade which is sutured along a broad area with a descending flange of the lateral wall of the sphenethmoid. This portion is likely to be homologous with the ascending process proper of the palatoquadrate, which by definition forms an articulation with the braincase in the region of the orbitosphenoid or sphenethmoid in larval lissamphibians as well as amniote embryos. The situation in *Mastodonsaurus* is nevertheless highly derived, as this process is much extended and flattened to give an extensive, secondary wall firmly attached to the neurocranium. In fact, no other capitosaur is known in which such a construction is established.

The posterior process is a fairly short yet well-defined rod which firmly attaches to a similar such, but somewhat longer process of the pterygoid. The latter is an outgrowth of the lamina ascendens. This contact encloses a large, sagittally oval foramen which lies dorsal to the conical recess, posterior to the footplate of the epipterygoid, and anterior to the basipterygoid process and suture proper. In addition, the posterior process takes part in forming the floor of a large unossified space into which the prootic foramen of the prootic opens anterolaterally.

The basal process is an outgrowth of the anterodorsal margin of the footplate and it faces medially as if to contact an unossified portion of the basisphenoid; its proper destination is unknown.

The dorsal process lies in the same plane as the anterior process, although it is raised well above the former. This portion is rod-like, with a widening dorsal end whose end surface is two-headed. By means of this structure a solid contact to the neurocranium, in extent unparalleled in temnospondyls, is established. This contact is established with the laterosphenoid roof by means of the lateral facet. The medial facet contacts a ventral flange of the parietal lateral to the pineal foramen.

Pterygoid process

In large specimens the basis epipterygoidei expands by covering a large part of the dorsal side of the pterygoid. According to its position and morphology there can be no doubt that this structure constitutes a partial ossification of the pterygoid palatoquadrate process. It reaches laterally up to the crista medialis of the pterygoid, covering the depression medial to this with a very delicate sheet of porous bone. Posteriorly the mineralization may continue at least towards the base of the quadrate ramus. Fragments of very thin bony sheets are, however, found even further posterolaterally, close to the suture between the pterygoid and quadrate. Medially, the pterygoid process overlaps the base of the lamina ascendens. This implies that the whole posterior portion of the palatoquadrate tends to ossify during late development in *Mastodonsaurus*, which to the present date appears to be a unique situation among basal tetrapods, with the exception of adelogyrinids (Carroll 1998).

Otic process

The posteriormost articulation between palatoquadrate and neurocranium is generally formed by the processus oticus palatoquadrati. This structure is primitive for tetrapods as a cartilage (Stadtmüller 1936). It is present in larvae of anurans, urodeles, and in many amniotes and can be identified in several capitosaurs. In these such an otic process appears to be borne by the lamina ascendens pterygoidei, namely at its most medial and dorsal edge. In contrast to the rather thin lamella, this process forms a stout strut either nearing the otic ossification or abutting against the skull roof or both. However, the processus oticus palatoquadrati is a perichondral ossification whereas the lamina ascendens clearly constitutes a dermal bone, being simply a dorsal protuberance of the pterygoid. A true otic process would therefore be expected in temnospondyls only close to, but not identical with the lamina ascendens of the pterygoid. This is exactly the situation in large specimens of *Mastodonsaurus*.

In *Mastodonsaurus* there is a pronounced yet structurally simple otic process which meets the above made definition. It is a thickened end of the thin-walled pterygoid process of the palatoquadrate, which covers the lamina ascendens (fig. 17). The process is directed posteromedially and has a convex dorsal surface. No attachment or articulation with any neurocranial structure is observed, though the process comes close to the anterolateral roof of the otic ossification (the cornu oticalis). These overcross each other as they approach upwards, whereby the otic horn is directed anterolaterally, the otic process anteromedially. Apparently the otic process nears the inner surface of supratemporal and postparietal.

Quadrate

The quadrate of tetrapods is by its embryonic origin the most posteroventral part of the palatoquadrate cartilage. It forms the jaw articulation throughout basal tetrapods by means of a trochlea, which is structurally throughout very similar in capitosaurs. The continuation of the palatoquadrate medial to the quadrate usually remains entirely unossified. In *Mastodonsaurus* there are traces of a (late ontogenetic) continuation of the quadrate dorsal to the pterygoid. The extent of this ossification is, however, very poorly known.

In capitosaurs the quadrate is a transversely elongated, cylindrical rod which broadens medially where it may grow to a high process that wedges between the quadratojugal and pterygoid in the occiput. The main body is formed by the trochlea quadrati: a screw-shaped, conical cylinder set in a frame formed by the quadrate ramus (pterygoid) and the processus ventralis (quadratojugal). This trochlea consists of an inner and outer spindle which are separated by a narrow, also convex rod. The two spindles are inclined at about 40° towards the sagittal axis, which gives the trochlea ist characteristic helicoid shape.

In *Mastodonsaurus* the quadrate trochlea is transversely longer than in primitive genera such as *Benthosuchus, Rhinesuchus,* or *Lydekkerina* (Bystrow & Efremov 1940; Broili & Schröder 1937a). In addition, the long-axis of the trochlea is orientated completely transversely and not anterolaterally such as in the aforementioned taxa (figs. 13, 16). This feature is shared with nearly all capitosaurids, as well as the genus *Eocyclotosaurus*. The occipital face of the quadrate is rather low. The trochlea connects by a roughly horizontal suture to the quadratojugal. There is no dorsal expansion such as reported for *Cyclotosaurus* cf. *posthumus* (Ingavat & Janvier 1981), thus resembling the usual and plesiomorphic structure in capitosaurs.

3.1.6. Neurocranium

General structure

Among the neurocranial regions, only the olfactory capsules remain entirely cartilaginous in *Mastodonsaurus giganteus*. The most extensive endocranial ossifications are the exoccipitals which bear the large, massive double occipital condyles and are in firm contact to posterior margin of the skull table.

Structure and surface morphology of all these elements suggest a cartilaginous continuation in several regions. In addition, size-related changes, such as in morphology and the extension of the ossified area, suggest a local developmental increase in mineralization. Most conspicuous among those is the anterior extension of the sphenethmoid ossification, a phenomenon that is frequently found in large *Mastodonsaurus* skulls.

Pfannenstiel (1932) attempted an analysis of the braincase and its relation to dermal ossifications in detail, studying transverse sections of several skulls of *Heptasaurus*. Unfortunately a major part of his material was destroyed during World War II; the remaining finds are according to my present knowledge little informative concerning the structure of the endocranium.

The nasal capsules, ethmoidal region, auditory capsules, and occipital region together comprise the neurocranium. The treatment of its units follows their embryonic origin and mode of mineralization as suggested by recent urodeles (Stadtmüller 1936; DeBeer 1937). The braincase of *Mastodonsaurus* is – rather unexpectedly – to a very large extent ossified and reveals a most interesting, hitherto largely unknown anatomy.

Braincases of temnospondyls have been studied in detail by Sushkin (1927), Pfannenstiel (1932), Dempster (1934), Case (1940), Sawin (1941), Romer & Witter (1942), and more recently by Shishkin (1968, 1973), Boy (1971), Shishkin & Ochev (1967 b), and Ochev (1972).

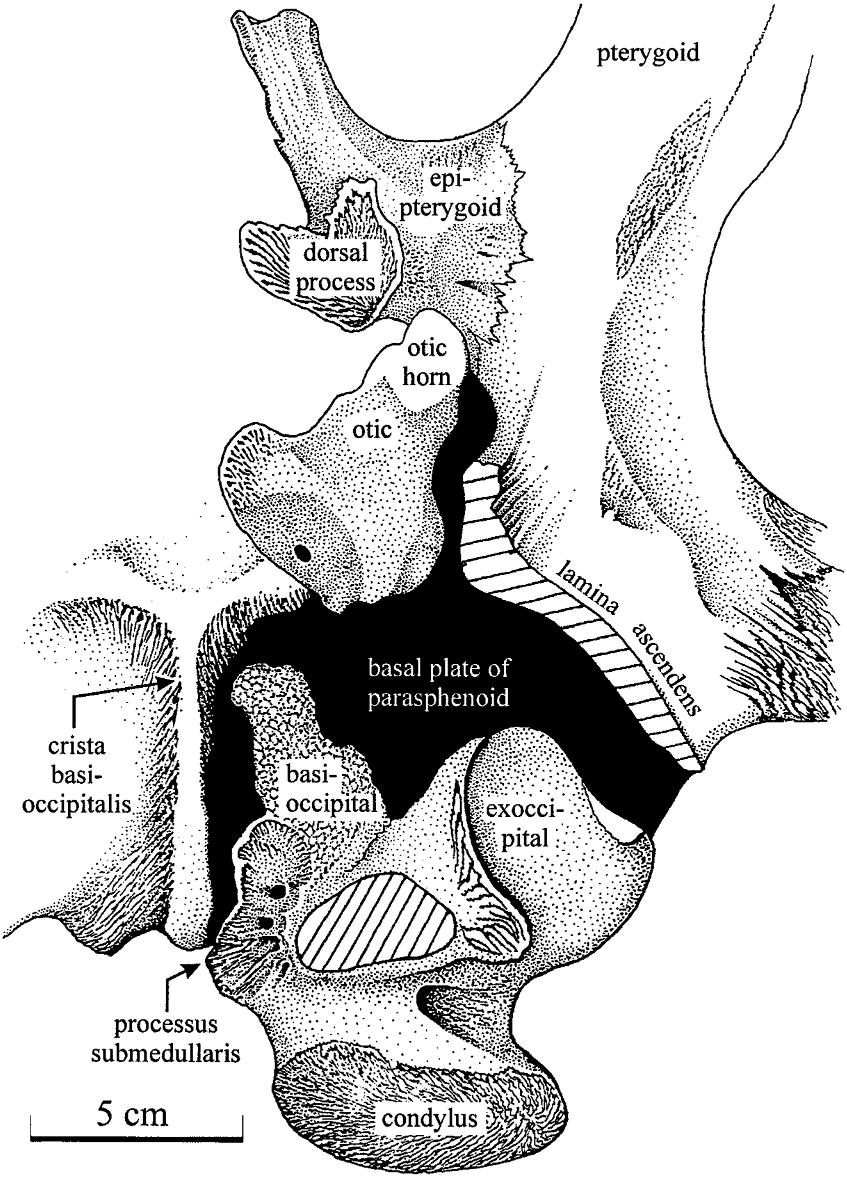


Fig. 18. Neurocranial ossifications in a medium-sized specimen of *Mastodonsaurus giganteus*. Only the anterior (prootic) portion of the otic is figured; in this stage it has no contact with any of the figured bones. The basioccipital overplates the exoccipital without forming a true suture. Both the otic horn and the dorsal process of the epipterygoid are attached to the skull roof. Based on several specimens (SMNS 54675, 81368, 80913).

Preservation and preparation

The braincase of *Mastodonsaurus giganteus* would be a major problem of reconstruction if there was not an exceptionally preserved, almost uncrushed skull available (SMNS 54675). Most crania are affected by compaction in the occipital, otic, and sphenethmoid regions, which has resulted in a mashing and distorting of the various neurocranial ossifications. On the basis of three partially crushed and one uncrushed specimen a near-complete reconstruction of the neurocranium of this species is possible. Among numerous other problems the position, articulation, and orientation of the stapes could be entirely clarified. Mr. J. G. WEGELE carefully prepared one specimen which revealed the beautifully preserved basement of the braincase.

The preparation of SMNS 54675 was carried out by TH. RATHGEBER who freed the neurocranium very thoroughly from its matrix, before he started fitting the broken dermal bones together in their original arrangement. The result is by far the best-preserved and most complete endocranium of any capitosaur, and it stands at one level with the best preserved endocrania of *Eryops megacephalus* (SAWIN 1941; pers. exam.).

The combined investigation of SMNS 54675, 80249, 81368, and 80913 allow the following perspectives on the posterior braincase: complete dorsal and ventral surfaces of the roof of ethmoidal and otic regions, lateral views of the lateral walls, the complete floor of the braincase, and the anterior aspect of sphenethmoid and epipterygoid.

Sphenethmoid region

Anteromedial to the otic there is a large, dorsally convex ossification which roofs the dorsum sellae and basisphenoid regions. It is elevated high above the otic roof. In dorsal view its shape is that of a wide rhombohedron. This structure is unpaired but has a midline suture in its anterior portion; the anlage is basically paired and generally resembles that of the sphenethmoid which is embryonically paired yet later ossifies as one unit. It continues anteriorly into the sphenethmoid without a suture. The reason to treat it separately is that the laterosphenoid roof is not found in small specimens and that it is an independent element in SMNS 54675.

The laterosphenoid roof is connected to the parasphenoid by a high column which rises anterior to the otic. There is a gap of 1 cm between these areas in which the basal plate is smooth. The laterosphenoid region in the largest specimen connects the otic with the sphenethmoid by forming an almost continuous ossification almost lacking sutures.

The sphenethmoid proper is a dorsally closed, roughly sphenoidal box which widens in the anterior part of the interorbital region. As mentioned, distortion and crushing have almost throughout precluded a detailed study, except for three isolated finds of different size. The anterior end eventually ossifies far into the snout region, almost reaching the posterior portion of the nasal capsule region.

Basisphenoid region

Mastodonsaurus giganteus lacks a definite basisphenoid ossification. As I demonstrate elsewhere, this is not necessarily typical of large capitosaurs, although it may be a common feature within the Capitosauridae (SCHOCH submitted 2). The primitive condition for this region is known from *Eryops* (Sawin 1941) and *Trimerorhachis* (Case 1935; Schoch submitted 3), where the basisphenoid is a bilaterally symmetrical, unpaired, and very low element wedged in between the sphenethmoid, epipterygoid, and otic and being floored by the anterolateral portion of the parasphenoid. There, the basisphenoid usually leaves characteristic, paired impressions. In *Mastodonsaurus* there is no ossification in this region, although clear impressions exist which suggest the presence of a cartilaginous basisphenoid.

Otic region

Mastodonsaurus giganteus is characterised by a well-ossified roof and lateral wall of the auditory capsule which are in their entirety referred to as otic region (figs. 18–20). The floor of the capsule remains wholly cartilaginous and is probably attached to the basal plate of the parasphenoid, as indicated by a concave, roughened dorsal surface of the latter. The otic is subdivided into the roof, the lateral walls, and the dorsal outgrowth (otic horn).

The otic is ventrally attached to (1) the paroccipital crest of the basal plate and (2) the basipterygoid ramus of the pterygoid. The otic roof reaches only about 1/3 the skull height in this region.

The anterior portion is elevated well above the centre of the otic roof especially in its lateral region. With the otic horn it reaches the internal side of the skull roof. This process has the cross-sectional area of a long triangle and abuts against the supratemporal, postparietal, and parietal. The abuttment is in part sutural and in part forms a complete synostosis. Probably this is controlled by age or rate of mineralisation as it varies between specimens of different size.

In a large specimen (SMNS 80249) the auditory capsules are exposed from their internal side and reveal a great deal of anatomical information (fig. 19). This is the largest braincase of *Mastodonsaurus giganteus* and has a remarkable degree of ossification. It clearly is the most strongly ossified basal tetrapod braincase. The general structure is very similar to the otic ossification as described from its dorsal surface with the exception that the tecta of the auditory capsules are fused along the entire midline, i.e. from a position right above the processus submedullaris (exoccipital) up to the laterosphenoid region.

The fused midline region is particularly thick and internally covered by a smooth sheet of bone. The remaining parts of the otic ossification are internally roughened. There are several large pits on each side of the otic roof. In addition both the fenestra ovalis and a large foramen between the otic and laterosphenoid are clearly preserved. The posterior rim of the fenestra is formed by two structures of different size but similar surface. The otic and laterosphenoid are almost co-ossified in the large specimen (fig. 19). The whole inner side of this portion is covered by smooth bone layers, and along the suture with the otic a groove runs laterally to finally end in the foramen prooticum.

The question whether the otic region of *Mastodonsaurus* comprises a compound element (prootic plus opisthotic) cannot be answered without detailed comparison that bases on a clarified phylogeny.

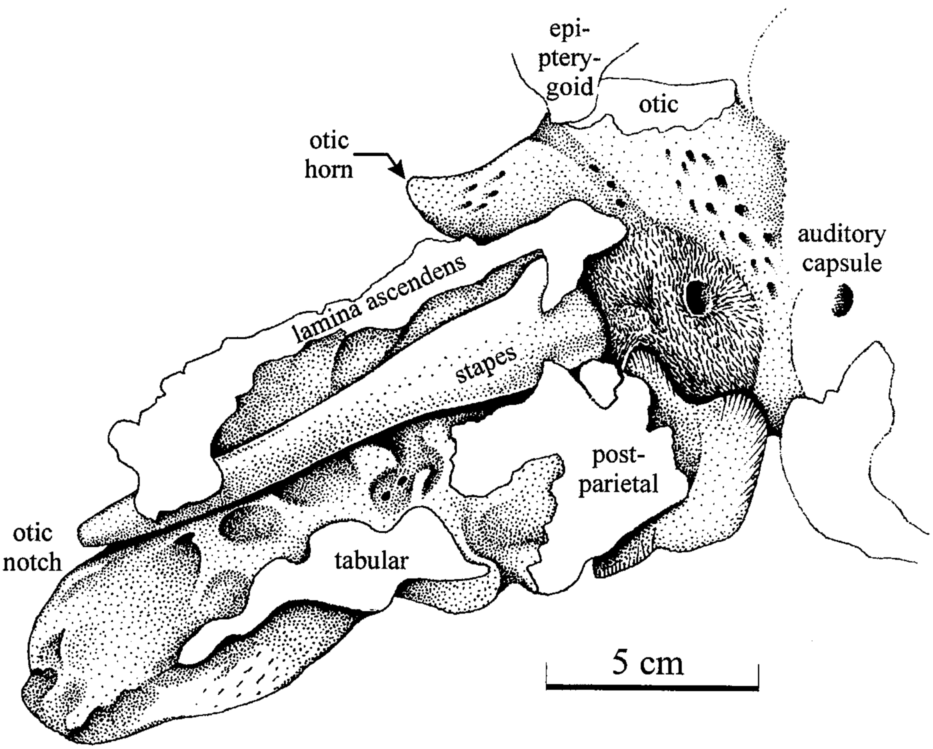


Fig. 19. The posterior neurocranium in a large specimen of *Mastodonsaurus giganteus*. Pterygoid (lamina ascendens), tabular, and postparietal are cross-sectioned. The figure depicts the internal side of the auditory capsule with the stapes in articulation, and the epipterygoid and otic partially cross-sectioned. It is noteworthy that the entire posterior braincase (otic, laterosphenoid, and sphenethmoid regions) is co-ossified. Based on a horizontally sectioned braincase (SMNS 80249).

The stapes

Some Kupferzell specimens of *Mastodonsaurus* have exceptionally well-preserved stapes in full articulation. In addition a respectable sample of disarticulated and even better preserved stapes is available. This is important because particularly the proximal ends are structurally very rich.

The stapes of *Mastodonsaurus* is a particularly long and slender, fragile bone reaching a length of 10 to 12 cm in large specimens (fig. 22). It consists of (1) an elongate shaft (stylus columellae) which ends abruptly on the distal side and (2) a bifurcating proximal end. The shaft is compressed anteroposteriorly to give a long-oval to rectangular cross-sectional area. The distal end is oval or subtriangular in cross-section and slightly concave; its surface is roughened suggesting a cartilaginous cover. The flat sides are orientated roughly anterior and posterior; the long axis of the cross-section has a small anteroventral slope throughout the length of the shaft. The shaft is generally smooth yet covered by fine parallel or anastomosing lines. These are most clearly expressed on the narrow flanks of the shaft, and are more dense in the proximal portion. The narrow flanks roughly speaking face dorsally and ventrally and are well-rounded.

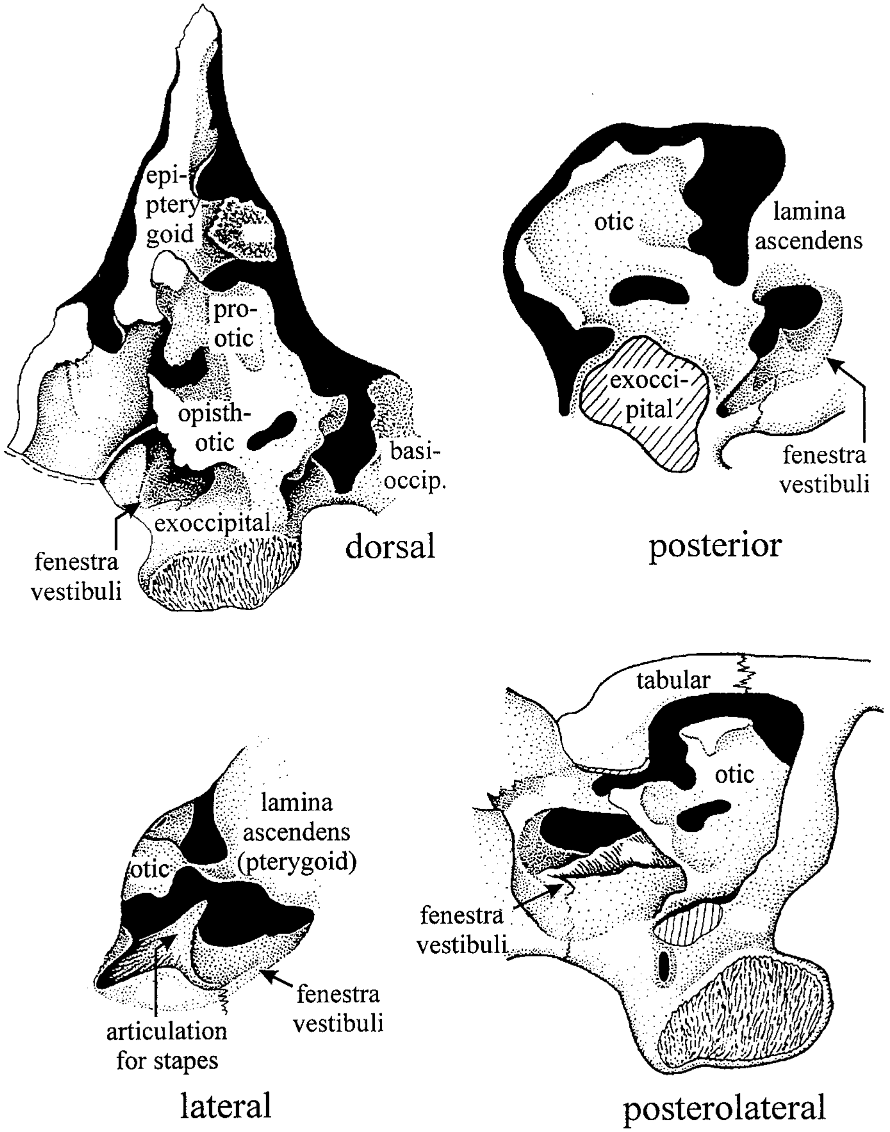


Fig. 20. The neurocranium of a medium-sized specimen of *Mastodonsaurus giganteus* from different perspectives. The otic forms a complicated element wedged in between the exoccipital, pterygoid, and epipterygoid. The fenestra vestibuli was located within a large fissure between the otic and parasphenoid. Based on SMNS 54675.

The proximal portion consists of two heads which are asymmetric in shape, size, and inclination towards the proper shaft. The proximal portion may be defined as the region in which the diameter of the cross-section enlarges. The proximal portion as understood here makes up 1/5 of stapedial length. Bolt & Lomard (1988) distinguished a ventral proximal head (VPH; processus basalis) and a dorsal proximal head (DPH; caput columellae or footplate of authors). The DPH is much larger and more distinctly inclined towards the long axis of the shaft. Diameter and shape of its cross-sectional area change exponentially to give an elongate oval proximal surface with strongly convex anterior and posterior margins. The proximal surface of the DPH is roughened and in most specimens concave. It may eventually bear a depression in the centre or slightly on the ventral side. BOLT & LOMBARD (1988: fig. 7) described a similar morphology in *Doleserpeton*.

Generally in tetrapods the footplate is the one proximal head which fits into the fenestra ovalis, and this situation has been often postulated for though rarely directly observed in temnospondyls (fig. 21). Two specimens from Kupferzell undoubtedly possess articulated stapes with their footplates associated with the fenestrae ovales. SMNS 54675 is threedimensionally preserved and permits to study the structure of the oval window. The stapes were found sticking to the oval windows on both sides and were removed by TH. RATHGEBER. His careful preparation and attentive proceeding make a restoration possible within very narrow limits. SMNS 80249 is larger and both stapes are preserved in articulation: their footplates firmly sit in the oval windows which are cross-sectioned by preservation. The ventral head is surrounded by a fork of bone (formed by parasphenoid and otic) which covers its flat ventral and dorsal flanks (fig. 22). One ramus of this fork touches the stapes at the incisura capiti into which it fits rather tightly. The other ramus attaches to the slightly curved ventral flank of the ventral head. In addition, an otic butress articulates with the fairly complex surface of the ventral head: it fits into the anteroposteriorly elongated bowl and is supported additionally by slender outgrowth of the ventral side of this depression (processus ventralis). The surface structure of the otic processes involved in this articulation is not adequately known. Nevertheless, there is clear evidence that in *Mastodonsaurus* a hitherto unexpectedly complex articulation connects the stapes to the anteroventral rim of the otic ossification, as well as the crista parapterygoidea of the parasphenoid.

The stylus columellae is in original articulation directed dorsolaterally with a minor anterior component. The footplate faces into the anterior part of the sagittally elongate oval window. Further distally, the shaft bends at about 1/3 of its length markedly upwards into a more steep angle towards the palatal plane. This bending is in most specimens rather abrupt, not curved. The distalmost part then bends again slightly, at about the posterior 1/10 stapedial length, into yet a more steep angle. It finally points into the squamosal embayment, not in its centre, but at the posteromedial margin close to the tabular. An abutting of the distal end to the tabular, supposed by SUSHKIN (1927), speculated in SAWIN (1941), and taken by WARREN & SCHROEDER (1995) as support for a "spiracle hypothesis" supposed to be non-consistent with a stapes pointing into the squamosal embayment. However, no temnospondyl specimen known to the author corroborates this reconstruction, and in Kupferzell *Mastodonsaurus* definitely the distal end of the stapes does not articulate with the tabular.

Basioccipital region

An ossified basioccipital region forms the most extended portion of the occipital condyle in the ground-plan of the Tetrapoda (HENNIG 1983). The successive size reduction of this ossification is clearly recognisable in the prevalent phylogenetic concept of temnospondyls (MILNER 1993). Supposedly plesiomorphic genera such as *Edops*, *Trimerorhachis*, *Saurerpeton*, and *Chenoprosopus* possess a rather large basioc-

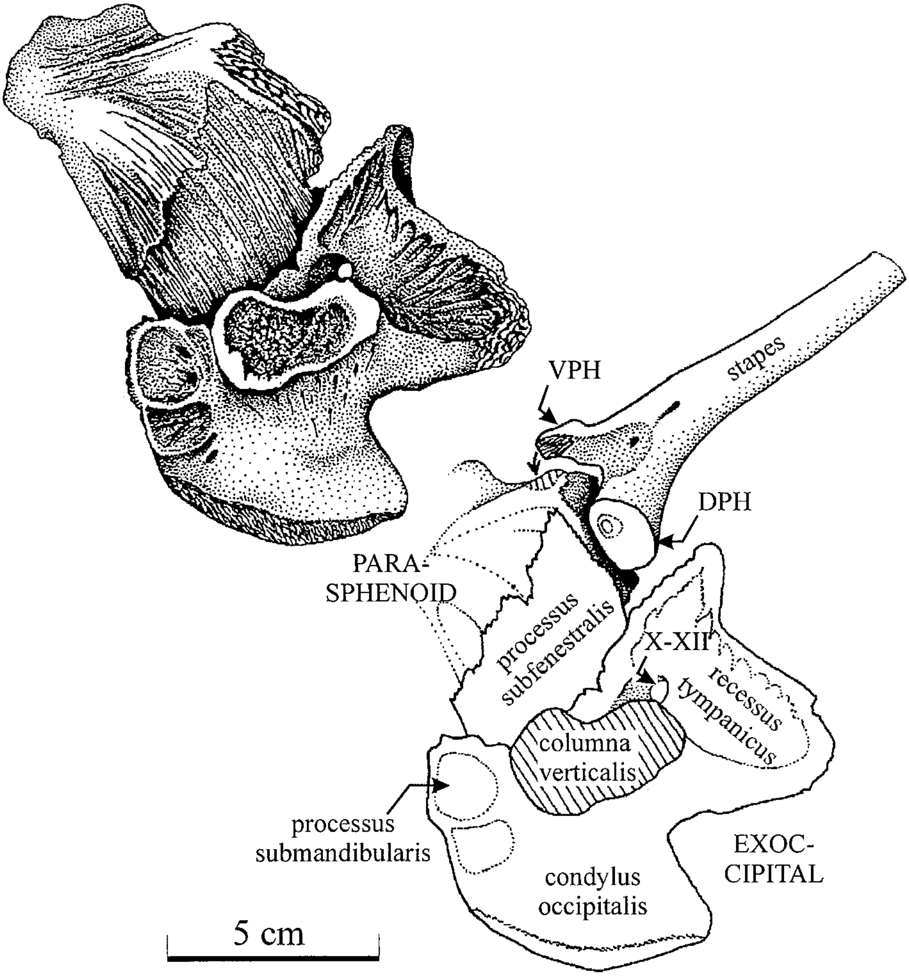


Fig. 21. The exoccipital in a medium-sized specimen of *Mastodonsaurus giganteus* in dorsal view, horizontally sectioned below the columna verticalis and parotic process. The attachment of the stapes in state of articulation is figured below; the fenestra vestibuli proper must have been located medial to the DPH.

cipital forming the ventral part of a structurally tripartite yet functionally single condyle (Broom 1913; Romer & Witter 1942; Watson 1956; Langston 1953). The basioccipital portion has become relatively smaller and finally disappeared in two higher groups convergently, the Brachyopidae and the Dissorophoidea plus Eryopoidea. In the latter group, the capitosaurs are the most advanced regarding this character: the basioccipital does not participate in the formation of the now completely bipartite condyle, and except for rare cases (*Wetlugasaurs angustifrons,* some trematosaurids) ossification is confined to a granular shagreen on the dorsal surface of the parasphenoid, which is the case in *Mastodonsaurus*. The original position of the main basioccipital body was between the exoccipital facets of the condyle (e.g. *Trimerorhachis insignis*). In *Mastodonsaurus* and other large capitosaurs the exoccipitals are very large and unite in the midline so that no space remains for a basioccipital participation.

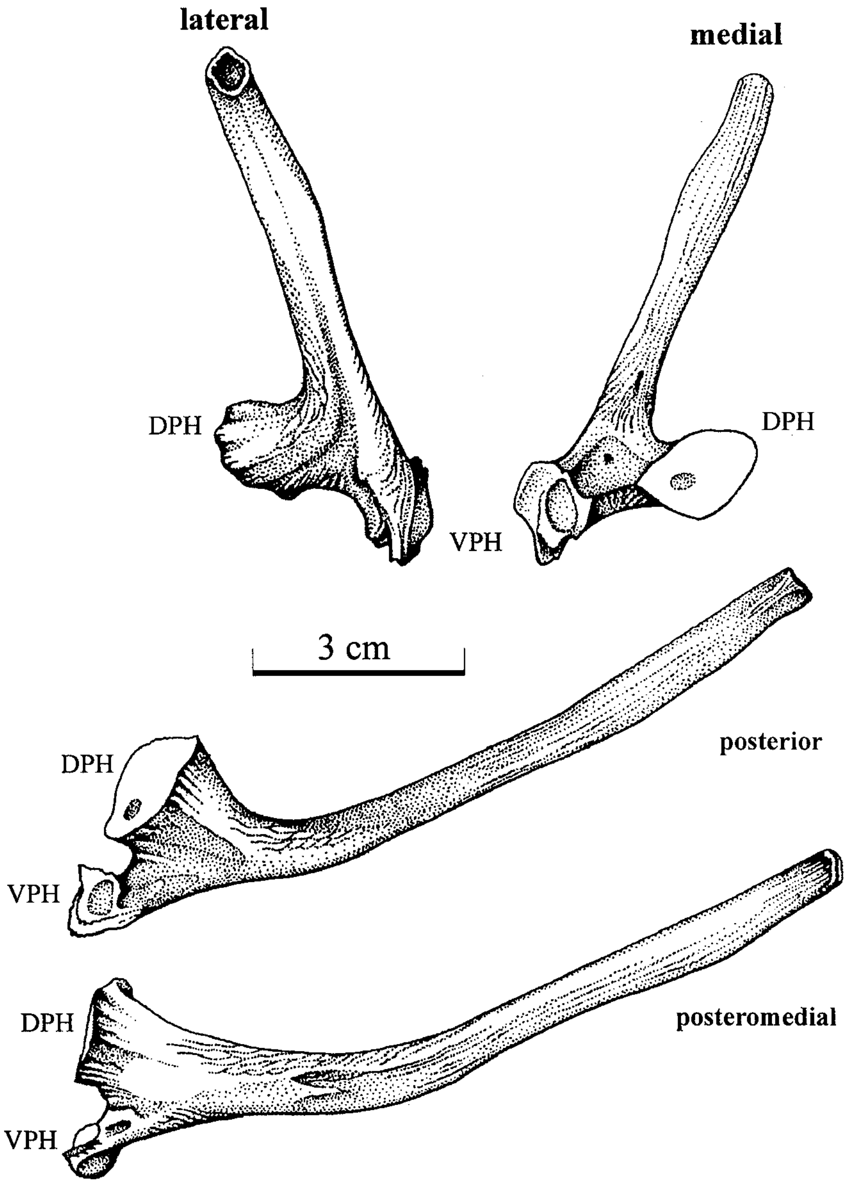


Fig. 22. Stapes of a medium-sized specimen of *Mastodonsaurus giganteus* from different perspectives. The oval depression on the medial face of the VPH forms the socket for the articulation of the stapes with the parasphenoid on the floor of the braincase (see fig. 21 for a different perspective). Partially reconstructed, based on SMNS 54675.

In well-preserved specimens the submedullar processes of the exoccipitals are anteriorly continued by a granular matrix of bone (fig. 18). This attaches to the exoccipital rather than fusing to it and extends ventrally to cover the dorsal side of the basal plate. The matrix is ill-defined in shape and partially worn-off by preparation in most specimens. According to available evidence the anlage of this ossification is paired. The general structure of these anlagen resembles the lateral portions of the unpaired basioccipital in *Eryops* (SAWIN 1941: pl. 7 B). In the largest available mastodonsaur specimen (SMNS 80249) the entire posterior part of the parasphenoid is covered by poorly ossified bone matrix. The basioccipital region in *Mastodonsaurus* was obviously anteriorly restricted to the area framed by the cristae paroccipitales. These cristae themselves aligne with the otic region dorsally. The crista basioccipitalis rising from the posteromedial surface of the basal plate are probably covered by a cartilaginous part of the basioccipital.

Supraoccipital region

PFANNENSTIEL (1932: 4) identified in *Heptasaurus* a thin trace of bone ventral to the tabulars and supratemporals as supraoccipital. In his reconstruction this ossification reaches anteriorly to the level of the epipterygoids. His interpretation obviously was influenced by WIMAN's (1913) reconstruction of the occiput in *Lyrocephaliscus euri*. In the Kupferzell specimens, there certainly is no separate ossification apart from the otic and laterosphenoid compound bones which reach that far anterior as concieved by PFANNENSTIEL. The remaining problem is whether the posteriormost part of the otic region contains a supraoccipital component. This concerns only the large specimen (SMNS 80249) where a single ossified unit reaches back below the postparietals (fig. 19). The degree of compaction, however, is considerable; examination of uncrushed SMNS 54675 makes clear that otic and postparietal are separated by a considerable vertical gap. The existence of this gap in turn strongly suggests the absence of an ossified supraoccipital and perhaps the persistence of cartilage in this region. True supraoccipital ossifications have been reported (among advanced temnospondyls) only for dissorophids (CARROLL 1964; GUBIN 1980), but even there an identification is ambiguous.

Exoccipital

The posteriormost portion of the endocranium is very well ossified in all capitosaurs, and as mentioned largely to exclusively formed by the exoccipitals. They give completely separated condyles, which in *Mastodonsaurus* reach an otherwise unparalleled size (fig. 21). This element is basically six-rayed represented by the following processes [I follow the terminology of BYSTROW & EFREMOV (1940)]:

(1) the columna verticalis is a massive strut abutting against the postparietal. It is longer and slenderer than in *Benthosuchus sushkini* (BYSTROW & EFREMOV 1940: fig. 14) and other basal capitosaurs, but it resembles that of *Cyclotosaurus* (KUHN 1942) and *Paracyclotosaurus* (WATSON 1958) more closely.

(2) The processus paroticus connects to the descending flange of the tabular and forms the lateral margin of the median occipital part, paralleling the course of the stapes, which runs anterodistal to it. In *Mastodonsaurus* the pr. paroticus is anteroposteriorly flattened and transversely wider than in most other capitosaurs, the aforementioned genera again being exceptions.

(3) The processus lamellosus is a short and rudimentary outgrowth at the medial base of (1). It reaches into the foramen magnum. In *Mastodonsaurus* it is comparatively small.

(4) The processus submedullaris rises from the ventromedial part of the ex-

occipital body, flooring part of the foramen magnum and separating it from the fenestra basioccipitalis. In *Mastodonsaurus* it is relatively short and stout, and anteriorly may be attached to the faint basioccipital ossification eventually.

(5) The processus subtympanicus raises lateral to the extensive suture with the basal plate of the parasphenoid. It is much more rudimentary than in *Benthosuchus*.

(6) The most massive outgrowth of the exoccipital body forms the condylus occipitalis itself, which is extraordinarily large in this genus. The facet is rather typical in shape, widening laterally and being markedly convex.

The capitosaur exoccipital encloses two particularly wide channels, the larger and more anterior of them traditionally is alternatively interpreted as the canalis for cerebral nerves IX and X (Bystrow & Efremov 1940), the jugular vein (Howie 1970), or as a common channel for the IX to XII nerves (Ochev 1972). In *Mastodonsaurus* both channels can be of nearly similar size, and the position of the entrance and exit foramina may be variable.

Review on the structure of the braincase

As an advanced Triassic labyrinthodont with obvious aquatic dispositions, *Mastodonsaurus* was long conceived as having a hypo-ossified braincase and possessing a rather simple endocranial organisation (Pfannenstiel 1932; Case 1933). The study of some excellent Kupferzell specimens reveals that the opposite is the case. The extent of ossification in the neurocranium of *Mastodonsaurus* parallels in most aspects, and even exceeds in others, the amount of bone developed in *Eryops* (Sawin 1941; pers. exam).

Nearly all regions of the braincase (with the significant exception of the nasal capsule) ultimately tend to ossify, and in the largest specimens examined most of the sutures between these ossifications have completely disappeared. This makes a homologizing difficult and in some cases (supraoccipital, basisphenoid) even impossible with the presently available knowledge. However, the enormous amount of new information on this very interesting and long-neglected anatomical region will be very valuable in comparative studies. The body of existing knowledge on both recent and fossil amphibian braincases is in a state of confusion, with a major gap between the fossil and recent taxa in particular. Such as with other regions in the skull, a firm basis for homologizing is urgently needed. *Mastodonsaurus* cannot resolve all of the often complex problems connected with these questions, especially because it is structurally so much advanced. However, a clarification of capitosaur braincase anatomy, which may now be somewhat more readily reached than before the discovery of the Kupferzell specimens, should in the long run also merge into a more extensive analysis of amphibian neurocrania that also includes modern groups.

3.1.7. Mandible

General structure

The lower jaw of *Mastodonsaurus giganteus* is despite its size a slender and partially delicate unit composed of eleven independent ossifications in each ramus. The basic structure is topographically and regarding its composition close to the groundplan condition of tetrapods (Jarvik 1996); see figs. 23–25. There are nine dermal bones and two replacement ossifications of Meckel's cartilage. The dermal elements are arranged throughout in the periphery of the mentomeckelian rod, and except for two extensive windows the mandible is entirely closed. The sutures are largely serrate and tight, some may eventually co-ossify.

The structure of Triassic temnospondyl mandibles was studied by MIALL (1874a), WILLS (1916), NILSSON (1943, 1944), ROMER (1947), WATSON (1962), OCHEV (1972), and lately by WARREN & BLACK (1985), and JUPP & WARREN (1986). The former knowledge of the lower jaw of *Mastodonsaurus giganteus* was very limited because of the poor condition of this unit in the Gaildorf specimens (FRAAS 1889). The mandible of the closely related *Heptasaurus* (WEPFER 1923a) was a little better known and frequently referred to as an example of large capitosaurs (e.g. NILSSON 1944). The Kupferzell material agrees in most aspects with WEPFER's data on the Buntsandstein mastodonsaurs, and in addition reveals a great deal of new information.

From anterior backwards there are lingually the splenial (below = b), precoronoid (above = a), postsplenial (b), intercoronoid (a), angular (b), coronoid (a), prearticular, and surangular. From posterior on forewards there are labially the surangular and articular, the angular (b), dentary, and mentomandibular (fig. 23). There are two dentigerous elements: the dentary bears in between 89 and 113 teeth (ten specimens), and the coronoid has variably either a single larger tooth or up to three rather small teeth.

The rami of the mandibles unite in an extended symphysis which is formed by the dentary and a partial ossification of the mentomeckelian. The symphysis proper bears in addition to the continuous marginal tooth row a pair of large tusks on each side. It is conspicuously broadened posterior to the dental arcade, but there are no additional teeth posterior to the tusks.

The shape of the jaw ramus and its strength are given by a stout, cylindrical rod on the ventral side. It is formed by three dermal bones: the splenial, postsplenial, and angular. This rod floors an elongate cavity that runs over most of the length of the mandible, the canalis primordialis (STADTMÜLLER 1936). In its middle part, this cavity is enlarged to form the adductor chamber, which housed the main body of the jaw-closing musculature. It has openings lingually (Meckelian window) and dorsally (adductor window). The Meckelian window is situated entirely anterior to the adductor window, in contrast to the majority of temnospondyls. The adductor chamber is deepest in the posterior third of the mandible, about at midlength of the Meckelian window.

The posterior portion of the mandible is extensively ossified. It integrates the tooth arcade of the dentary into the framework of the mandible, forms an unusually large articulation facet (area glenoidalis), and bears a long and deep postglenoid area (JUPP & WARREN 1986; retroarticular process of former authors). This is largely a posterior outgrowth of the surangular, with only minor participation of the angular and prearticular, and very variable participation of the articular. The postglenoid area (PGA) in *Mastodonsaurus giganteus* is longer than in any other capitosaur.

In *Mastodonsaurus* such as in most capitosaurs the prearticular forms part of the glenoid area in establishing an extended jaw articulation. In *Mastodonsaurus* however this hamate process is remarkably high and well-ossified (ROMER 1947). The glenoid region consists of two sagittal grooves separated about in the midline of the mandible by a broad ridge. The lingual fossa is conspicuously extended anteriorly and dorsally by participation of the prearticular to form the hamate process, which is very suggestive for the maximal gape angle in this species.

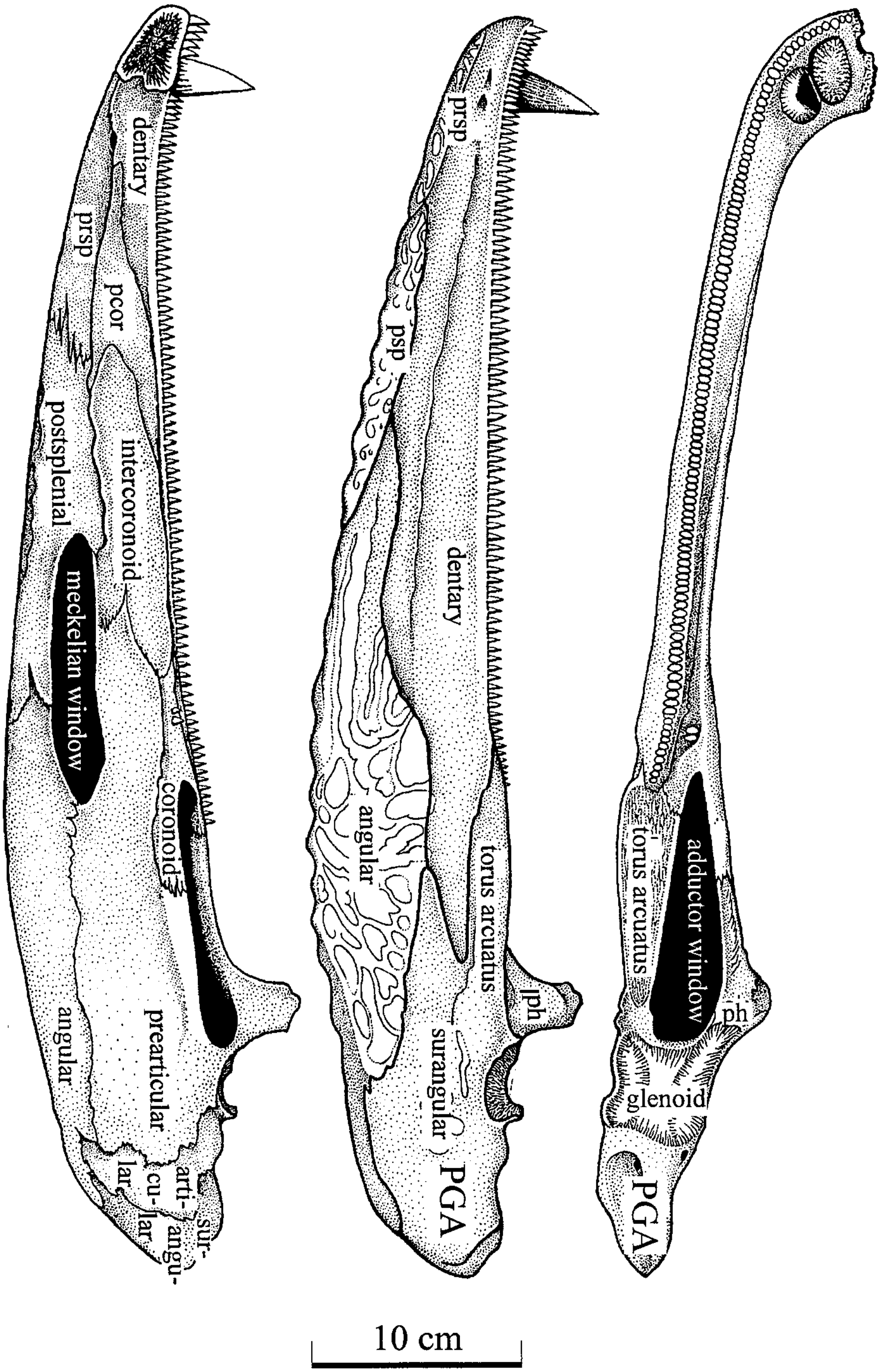


Fig. 23. Mandible of *Mastodonsaurus giganteus* from different perspectives. Most typical of the genus are the large symphyseal tusks, the elongated postglenoid area, and the hamate process of the prearticular. Based on several well-preserved and uncrushed specimens, particularly SMNS 56634 and 80880.

Preservation

As the mastodonsaur mandible contains some particularly delicate structures, compaction has affected most specimens quite seriously. Macroscopic fracturing frequently crushed or even largely destroyed the adductor chamber. The thin ossifications on the lingual side (prearticular, intercoronoid, and postsplenial) are usually broken and distorted, now being attached to the still articulated inner side of the thick labial bones (angular, dentary). The hamate process (prearticular) is often broken away or partially worn off, so that it is sometimes found isolated.

In addition to fractures, compaction also resulted in major continuous displacements with the result of considerable deformation of structures. Such deformation primarily affected the following regions and their relations to each other:

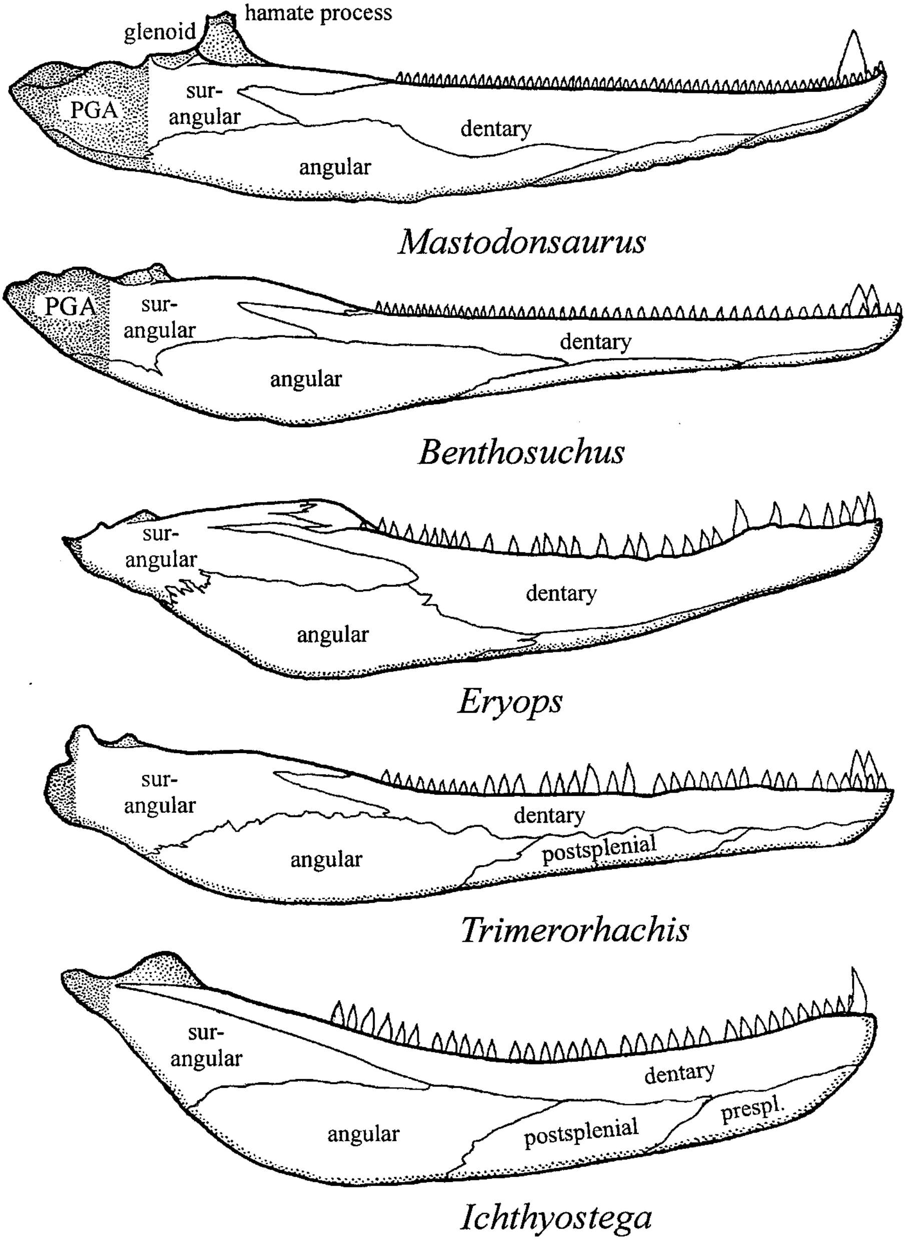
- Tooth-bearing top of dentary inclined lingually;
- Tusks of symphysis bent medially;
- Adductor chamber narrowed by deformation of prearticular and coronoid;
- Hamate process (prearticular) inclined lingually and glenoid facet torded thereby;
- Width of articular glenoid region decreased;
- Width of postglenoid area decreased;
- Height of postglenoid area decreased.

Surangular

The surangular wedges in between the dentary and angular by means of overlapping sutures, then frames the glenoid area of the articular lingually and posteriorly, and further backwards it forms the main body of the PGA (fig. 27). It comprises at least _ of the width of the PGA, and forms a massive ossification whereas the articular, prearticular, and angular are thin sheets of bone overlying it to a variable extent. The PGA is the only part of the mandible where a dermal bone forms such an extensive threedimensional block. Further anterior the surangular builds the complete labial margin of the adductor window and forms part of the bordering of the labial wall of the adductor chamber, as well. The top of the labial wall of the adductor chamber (torus arcuatus, Bystrow & Efremov 1940) borders a widened and slightly concave area medial to it (angulus adductoris), see fig. 23. This shelf is covered by numerous parallel stripes and ridges suggesting fleshy insertion of musculature. The surangular meets the coronoid in a broad, serrated suture about at the anterior fifth of the chamber.

The posterior border of the glenoid region (articular) and the dorsolabial margin of the postglenoid area form high crests. The latter is curved in a sigmoid fashion. Its anterior half is raised slightly above the level of the glenoid region and was therefore termed postglenoid ridge (Jupp & Warren 1986). The labial side of the PGA is characterised by heterogenous sculpturing: roughened surfaces alternate with thick tubercles and short ridges, and finally smaller grooves exist next to the well-established sulcus articularis and sulcus accessorius.

The suture with the dentary runs on the labial side somewhat ventral to the torus arcuatus (ta). A long posterior lappet of the dentary overlaps an elongate depression of the surangular. The bones differ in the type and amount of sculpturing. Lingually the surangular may form a large part of the PGA as well, or alternatively be overlapped to some extent by a posterolingual projection of the articular. The articular usually forms a posterior spine covering the dorsolingual margin of the PGA. From



Mastodonsaurus

Benthosuchus

Eryops

Trimerorhachis

Ichthyostega

Fig. 24. Comparison of mandibles in selected temnospondyls, viewed from labial side. *Ichthyostega* after JARVIK (1996), *Eryops* after SAWIN (1941), and *Benthosuchus* after BYSTROW & EFREMOV (1940); others from personal observation. Not drawn to scale.

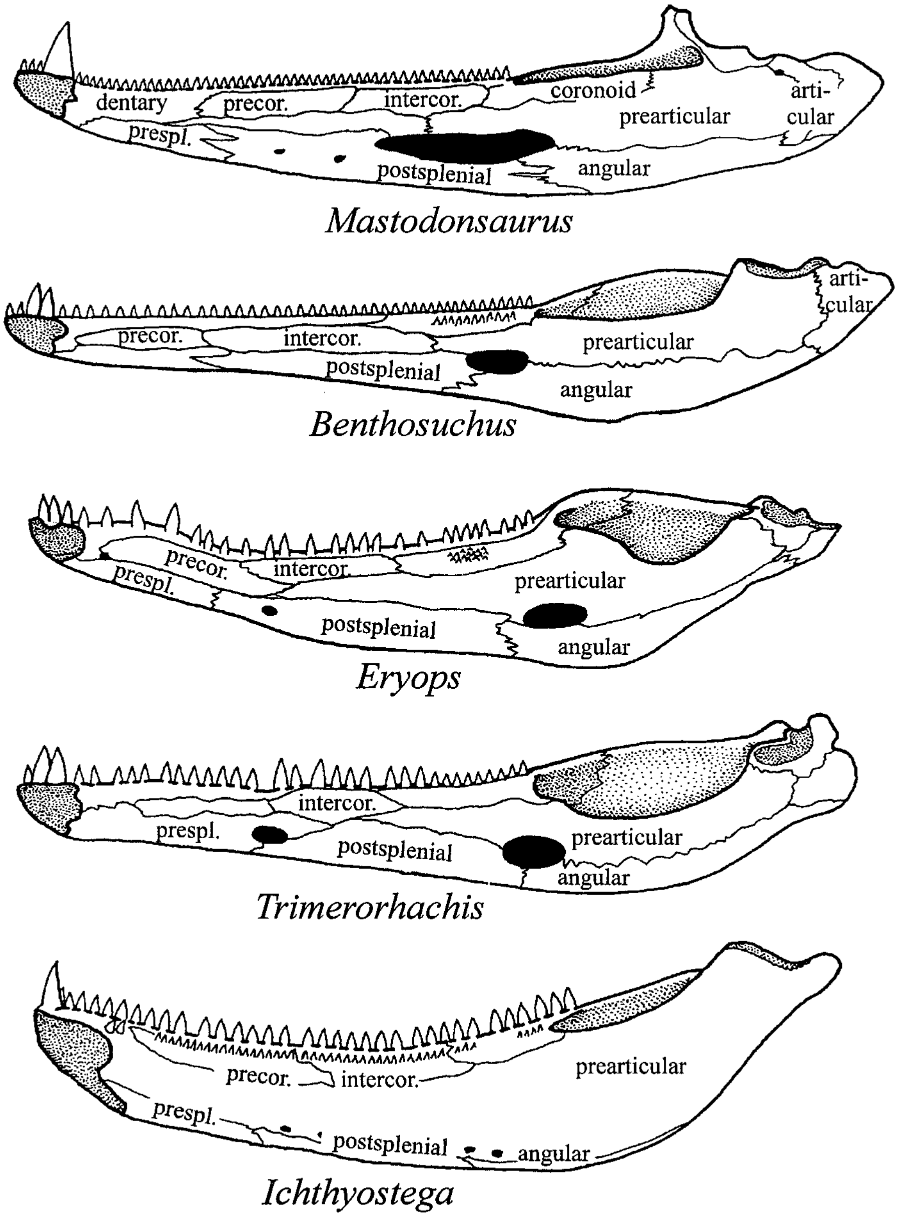


Fig. 25. Comparison of mandibles in selected temnospondyls, viewed from lingual side. *Ichthyostega* after Jarvik (1996), *Eryops* after Sawin (1941), and *Benthosuchus* after Bystrow & Efremov (1940); others from personal observation. Not drawn to scale.

there a thin sheet of bone may eventually grow ventrally to successively cover the roughened lingual surangular surface. The angular and prearticular meet the surangular in a double-sigmoid suture.

The postglenoid area of *Mastodonsaurus* is to a large extent formed by the surangular. The dorsal surface of the PGA has a deep groove aligned to the long axis of the mandible. This groove is by definition not an arcadian groove (Warren & Black 1985) as it is not situated between the articular and surangular, but is bordered on both sides by the surangular instead. A shallow arcadian groove is nevertheless present in *Mastodonsaurus*, resulting from the failure of the articular to entirely cover the concave lingual surface of the surangular (a consequence of poor ossification). To distinguish both these grooves, the deep surangular groove is termed fossa postglenoidalis. This is distinctly deeper than in all other temnospondyls and in may vary considerably in alignment, ranging from curved to entirely straight. The fossa originates at the top of the elevated hinder margin of the glenoid area. The surface of the groove may be smooth to roughened, but often there is a large foramen in its deepest point, which is usually in the anterior third of the PGA. The lingual wall of the fossa postglenoidalis is much lower than the labial (postglenoid ridge, see below) rounded, and often roughened. Variation in most morphological traits of the PGA is broad, hence a species identification based on only a mandible fragment is certainly problematic.

There is an immediately apparent problem with Jupp & Warren's (1986) concept, rising from the investigation of the Kupferzell material. These authors presented a welcome and useful discussion of lower jaw anatomy in temnospondyls. Among the invention of several useful descriptive terms they attempted a typological distinction of mandibles on the basis of the postglenoid area (PGA). Two types of PGA's were distinguished which are supposed to differ in 9 features from another. *Mastodonsaurus* displays considerable variation in the morphology of the PGA, and is especially variable regarding the proportion of elements and their participation to this region. Because of the broad variation of its PGA, the distinction of Jupp & Warren's two mandible types cannot be successful here.

Indeed *Mastodonsaurus* shares similarities with both types to an equal extent: it is similar to "type 1" in (1) the angular lying ventral to the articular, (2) the posterior extremity of the surangular forming an arcadian process, (3) a deep arcadian groove being present (exclusively bordered by the surangular though), and (4) the foramen chordae tympani separating articular and prearticular (in some specimens only).

PGA "type 2" shares with the mastodonsaur mandible the following features: (5) the prearticular almost always extends into the PGA, (6) the angular lies labial to the articular, (7) the posterior extremity of the articular never forms a true retroarticular process (sensu Warren & Black 1985), and (8) the surangular always forms the posteriormost extremity of the PGA. It is apparent that most characteristics of the two types need not exclude one another but may occur in combination. Nevertheless Jupp & Warren's work forms a serious and necessary approach towards a better understanding of this long-neglected yet complex and potentially phylogenetically informative structure. Maryánska & Shishkin (1996) have recently also focussed on PGA morphology, dealing with capitosauroids in more detail. Their results, particularly regarding *Mastodonsaurus torvus*, are largely corroborated by the study of the mandible in *M. giganteus*.

Angular

This is one of the major ossifications in the posterior half of the mandible, forming the lateral and bottom walls of the adductor musculature. It constitutes the largest area of the mandible covered by dermal sculpturing (figs. 23, 27). The angular is wedged in labially between the surangular, dentary, and postsplenial and lingually the prearticular and surangular, sometimes the articular. The sutures are mostly squamate and interfinger with mirror-imaged lappets of the partner elements (surangular, dentary, postsplenial, articular partim). The high degree of ossification correlates with the apparent role as main resistance against the most profound (and longest) portions of the adductor musculature.

The entire element is relatively low, having its deepest measure shortly behind the anterior end of the adductor chamber. Its (labial) shape is that of a longitudinally elongated oval, with a pronounced anteroposterior asymmetry in that the anterior part is much longer and terminates in a long, delicate process. In excellently preserved specimens the angular is considerably vaulted in the transverse plane, the adductor chamber hence having a markedly convex lateral wall. The angular is throughout relatively thick, but most strongly ossified ventrally where it forms the bottom of the adductor chamber. Lingually it contributes about 1/3 to the formation of the medial wall of the adductor chamber. Its lingual surface is largely smooth; the sculpturing starts abruptly exactly at the turning point towards the labial side. The border between sculptured and smooth bone runs along the edge of the angular up to the posterior third of the bone, where the edge becomes more rounded and bears numerous rough, curved ridges.

Almost the entire labial side of the element is covered by intense sculpturing. This suggests a shallow position of the labial bone surface within the dermis. Unlike in the skull roof the sculpturing ridges make up one half of the thickness of the bone. The sculpturing pattern consists of long radial rays of ridges which converge towards a small area slightly posterior to half length of the bone. Distally from the point of convergence these ridges are well-defined and single, whereas they proximally unite to give a reticulate pattern. Most of them are not straight but irregularly curved and of variable thickness along their course.

The sutures to the surrounding elements are mostly squamate. The surangular is labially overlapped by the angular which results in a complex, serrated suture. Sculpturing ridges grow along overlapping parts of the angular and take over to the surangular, resulting in a firm stabilisation of these regions. The dentary is also overlapped along its entire contact to the angular. There the sculpturing ridges end abruptly at the margin of the angular; the dentary ascends rapidly and is easily recognised by its intense covering with numerous stripes and fine ridges that run parallel to the mandibular long axis. Anteroventrally the angular is overgrown by a thin lappet of the sculptured postsplenial. The sculpturing of both elements does not have a continuation though. The angular forms the ventral keel almost up to the posterior end of the postglenoid area. The surangular articulates both labially and lingually by sticking to the internal sides of the V-shaped frame formed by the angular. The angular-surangular suture is lingually straight and labially serrated. A thin posteroventral projection of the articular may wedge between the surangular and angular lingually, and in this case it overlaps the angular largely, almost reaching the ventral keel. In one specimen the articular even separates the angular from the surangular medially for a short distance. The angular meets the prearticular in an only little serrated, slightly squamate suture.

Postsplenial

The postsplenial is a long and well-ossified strut on the lingual side of the mandible. It forms a predominant part of the ventral keel and extends dorsally well beyond the level of the angular and splenial (fig. 23). Its length is almost half the measure of the lower jaw, and lingually it is exposed over almost its whole length.

On the lingual side the postsplenial contacts the angular posteriorly, the prearticular and intercoronoid dorsally, and the splenial anteriorly. Labially it borders the angular, dentary, and splenial. The postsplenial makes only a minor contribution to the labial side, however. The surface of this part is intensively sculptured by short, reticulate ridges. As with the angular, there is a well-defined ventral edge of the bone where sculpturing starts abruptly by a long groove.

The labial surface of the bone is convex and throughout smooth. Posteriorly it borders the elongate Meckelian window, forming 2/3 of its ventral margin. The suture with the angular there is curved like a V and strongly serrated. The suture with the splenial extends over a larger area and forms a complex zig-zag line. Dorsally the postsplenial extends to build the anterior, pointed margin of the Meckelian window. The dorsal process involved in this is stout and abuts against the prearticular. Generally the structure and proportions of the postsplenial are very much like in plesiomorphic capitosaurs such as *Benthosuchus sushkini* (BYSTROW & EFREMOV 1940). The major difference is caused by the proportionately much longer Meckelian window which exceptionally expands in *Mastodonsaurus* up to about postsplenial midlength. In this feature *Heptasaurus* (WEPFER 1923a) is very similar whereas trematosaurids which also possess elongated Meckelian windows differ (NILSSON 1943).

On the ventral side the margin of the lower jaw forms a stable rod in which the angular, postsplenial, and splenial are very tightly integrated. Sutural serration is strengthened by ridges which bridge and overprint the proper bone contacts. There are two large foramina anterior to the Meckelian window which open posteriorly, suggesting an exit of nerves or vessels in that direction (anterior Meckelian foramina of authors). On the lateral side of the lingual part the foramina unite as an elongate oval opening in a larger depression. This side is also nearly completely smooth.

Splenial

The shallow splenial aligns to the postsplenial anteriorly and participates in the shaping of the symphyseal region (figs. 23, 26). It contacts the postsplenial posteriorly on both sides, the intercoronoid and pre-coronoid dorsally on the lingual side, and the dentary again on both sides dorsally. There is, however, variation as to how far the splenial reaches anteriorly. In most specimens it completely floors the dentary, contacting its contralateral element at the floor of the symphysis. The suture of this contact is roughened, and the splenial markedly expands in the region. Labially the splenial contribution is larger than lingually, which reverses the presymphyseal state, such as to form the structure of a screw. The splenial portion of the symphysis, moreover, juts out of the vertical plane of the dentary suture surface. This suggests a rather loose articulation of the two lower jaw rami. In a few specimens the splenial ends slightly anterior and ventral to the precoronoid. In these the dentary fails to completely fuse at the ventral edge of the symphysis, which produces a narrrow slit. In transverse section the splenial is U-shaped anteriorly and nearly V-shaped posteriorly. The precoronoid overgrows the splenial lingually, forming only a very thin sheet of bone. Further backwards the precoronoid increases in thickness and almost completely roofs the canalis primordialis. Close to the symphyseal region the splenial runs through a large foramen (foramen postsymphysealis) which is throughout present. Additional foramina of smaller size eventually appear further posteriorly, close to the suture between the splenial and dentary or splenial and precoronoid. The lingual side of the splenial is smooth except for a small, roughened platform close to the anterior end of the precoronoid in some specimens. Finally the sculpturing of the labial side is much weaker than that of the postsplenial. It mainly consists of shallow pits and short grooves of similar length, which end in the lower fourth of the height of the symphysis. The onset of sculpturing is abrupt and demarcated by a single, narrow ridge.

Articular

The articular is primitively the only mandibular bearer of the jaw articulation. It is a solid unit which has the surface of a saddle. The entire periphery of this perichondral replacement bone is made of rather thin dermal ossifications which converge ventrally to it completely. The articular is surrounded by the surangular posteriorly and anterolaterally on the labial side, and the prearticular lingually and anteriorly at the hinder end of the adductor chamber (fig. 23).

The general structure of the articular, especially the proper articulation facet is very similar throughout temnospondyls. It is basically tripartite: an outer and inner groove are separated by a broad bulge. Grooves and bulge are aligned subparallel with the long axis of the mandible, or eventually markedly inclined obliquely towards the lingual side. In *Mastodonsaurus* the inner groove is larger and particularly elongated anteriorly where it connects to a projection of the prearticular. The facet proper is easily recognised by its rough, poriferous surface typical of perichondral ossifications with cartilaginous cover. It remains unclear how deep the articular participates in the posterior bordering of the adductor chamber, because it is covered by the prearticular there.

The articular does never form the main component, nor does even reach the extent of the surangular in the PGA. Apparently there are two most frequent structural types possible in *Mastodonsaurus giganteus* from Kupferzell: either the articular forms a narrow shaft which strengthens the dorsolabial margin of the postglenoid area, or it expands labioventrally to firmly contact the angular and separating the prearticular from the surangular.

Prearticular

The prearticular is the largest element on the lingual side of the mandible and entirely confined to it. It may be divided into two structural different parts: (1) the thickened dorsal region which forms part of the jaw articulation and borders the adductor window lingually, and (2) the modestly ossified wall of the adductor chamber that is often only fragmentarily present. The prearticular contacts the surangular posteriorly, forms the cover for the lingual and front sides of the articular, meets the

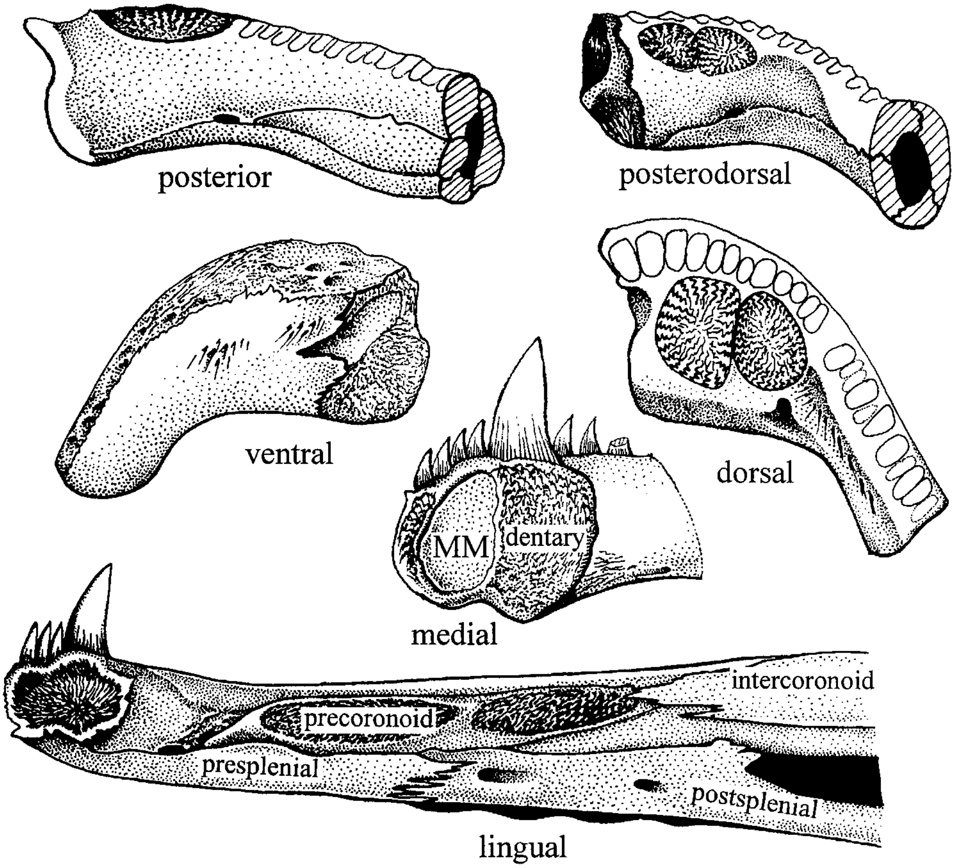


Fig. 26. Symphyseal region of *Mastodonsaurus giganteus* from different perspectives. The sockets of marginal teeth are characteristically oval. Note the existence of an additional replacement bone in the symphysis, the mentomandibular ossification (MM). The precoronoid and intercoronoid are thin sheets of bone, which overplate the massive dentary.

angular near the ventral edge and the postsplenial at midheight, and is finally covered dorsally by the coronoid and intercoronoid (fig. 23).

The dorsal, thickened part starts slightly anterior to the glenoid area which it frames lingually. The inner groove of the glenoid articulation facet extends anteriorly far beyond the margin of the central bulge and the outer groove of the articular. At the same time it curves dorsally to form the highest point of the mandible. The whole area in which this groove is set is formed by the articular. In lateral view, the articulation facet describes a quarter circle; this feature is unique for a small group of capitosaurs (Schoch 1997a). The prearticular forms the complete dermal envelope of the extended inner glenoid fossa. This whole projection was termed processus hamatus by Bystrow & Efremov (1940); I shall use this term only for the prearticular part (fig. 27). The hamate process widens as it ascends and finally ends in a dorsally convex edge. All edges framing the articular component are thickened and protrude the slightly concave glenoid surface. The back of the hamate process (which runs anteroventrally) is keeled and roughened. Its thick lateral flank is a broad frieze which participates in the framing of the large upper part of the adductor chamber. Lingually the hamate process is strengthened by a central column that continues anteriorly into the edge of the adductor window (torus lingualis).

Prearticular and coronoid nearly fuse at this lingual bulge, whereas anteriorly their suture is well-established. Further ventrally the lingual bulge is separated from the rather thin bone by a step. The coronoid overlaps the prearticular in its anteriormost portion. Conversely, at about 2/3 the length of the Meckelian window, the prearticular meets and clearly overlaps the intercoronoid. The result is a zig-zag suture strengthened by numerous parallel ridges. The entire lingual surface of the prearticular is smooth and solely covered by isolated tiny pores. Especially the posterodorsal rim of the Meckelian window is very weakly ossified and almost always broken.

Coronoid

In the plesiomorphic condition for tetrapods, the dentary tooth arcade is accompanied by a series of three dentigerous bones on the lingual side. This is the coronoid series, consisting (from anterior backwards) of the precoronoid, intercoronoid, and coronoid (Nilsson 1944; Jupp & Warren 1986; Schoch 1998). Numerous temnospondyl species, however, exemplify the loss of teeth on the anterior two of these elements. Throughout capitosaurs only the coronoid bears teeth, and their number is generally very limited (an exception is a new benthosuchid from southwestern Russia which bears a tusk pair on each element of the coronoid series; M.A. Shishkin, pers. comm.)

The coronoid of *Mastodonsaurus* is more firmly integrated and by itself more important for the stability of the adductor window than it is in most other capitosaurs (fig. 23). In particular it contributes to the formation of the bulges (torus arcuatus and torus lingualis) which frame the adductor window on both sides of its front. The shape of the coronoid is that of a fork, with the region anterior to the adductor window being the shaft and the window-framing rami the spikes. The lingual ramus is, however, distinctly longer and more slen-der than the labial which is flattened to give the anterior surface of the angulus adductoris.

The element bears three teeth arranged in a row and situated near the suture with the dentary, anterior to the margin of the adductor window. The teeth are generally similar to and of the same size as those of the dentary. The region surrounding these teeth forms a shallow, longitudinal depression which is covered by pores and small grooves. Prearticular and surangular are overlapped by the coronoid, with sutures facing straight dorsally and having parallel ridges. The suture with the dentary instead runs in a broad groove lingual to the tooth row of the dentary, with the greater part of this groove formed by the coronoid in the posteriormost part, but the dentary further anteriorly. Towards its anterior end the coronoid expands somewhat down the lingual flank, where it contacts the intercoronoid in a broad suture whose topography is unknown.

Intercoronoid

This is the longest element in the coronoid series and in contrast to the coronoid entirely confined to the lingual side. It reaches nearly the length of the postsplenial to which it relates like a mirror-image on the dorsal side of the mandible. The intercoronoid roughly speaking forms an elongate rectangle which is posteroventrally expanded. It contacts the coronoid posteriorly and dorsally, the prearticular posteriorly, the postsplenial ventrally, the precoronoid anteriorly, and finally the dentary labially.

In contrast to all known capitosaur mandibles, the intercoronoid of *Mastodonsaurus* forms the anterodorsal margin of the Meckelian window (figs. 23, 26). This is the consequence of the extraordinary size and position of this window and the proportions of the intercoronoid. Its posteriormost portion reaches unusually far ventrally where it meets the prearticular in a relatively broad suture. The situation might be similar in *Cyclotosaurus robustus* which also possesses a large Meckelian window, but unfortunately the sutures are not preserved in the available material (SCHOCH submitted 1).

The intercoronoid is not dentigerous such as in many basal tetrapods, but instead has a smooth surface. The only exception is its dorsal margin which is thickened like in the coronoid and additionally gives rise to a small, elongate platform with a roughened surface. The intercoronoid is overlapped by the postsplenial and the coronoid; conversely it overlaps the precoronoid and interfingers with the prearticular is a very tight suture. The contact with the dentary runs ventral to the upper margin of the lingual side and appears to be squamate with the intercoronoid overlapping the dentary. Dorsal and ventral areas of the intercoronoid differ much in thickness: while the upper portion is transversely oval and well-ossified, the ventral margin which borders the postsplenial (and sometimes the splenial, as well) often is only a thin sheet tending to get crushed in the region where it roofs the canalis primordialis.

Precoronoid

This is the anteriormost, smallest, and most weakly ossified element in the coronoid series. Having the shape of an elongated rhomboid, the precoronoid wedges in between the splenial and dentary anteriorly and closes up to the intercoronoid posteriorly (figs. 23, 26). A contact to the postsplenial may eventually be established. Along its entire dorsal margin it is bordered by the dentary. Its orientation is almost completely vertical and mainly forms a thin cover of the lingual flanks of splenial and dentary. At the anterodorsal edge of the element there is a slightly raised area with an irregular surface. The anterior contact with the splenial and dentary is pointed, and in this region several parasymphyseal foramina may occur; one larger foramen exactly situated on the suture between dentary and precoronoid is throughout present. The sutures are smooth and all squamate, and among the neighbouring elements the intercoronoid is the only which overlaps the precoronoid.

Dentary

The tooth arcade of the lower jaw is practically formed by the dentary, as the coronoids largely lack teeth in *Mastodonsaurus* (fig. 23). The dentary is a broad strip of bone set in the framework formed by the coronoids, angular and prearticular. Whereas it is hardly exposed lingually, there is a broad labial portion which underlaps the angular and splenials. This flank is peculiar because of its unique mode of sculpturing, consisting of numerous parallel stripes and ridges which are aligned to the upper margin of the bone. The whole latus dentalis has an undulating surface in transverse section.

The dentary is the largest element of the mandible, and altogether 8 bones contact it: the surangular, angular, postsplenial, splenial, mentomandibular, and the three coronoids. It is labially overlapped by the splenials and the angular, but posteriorly wedges in between surangular and angular by means of a long cultriform process. The transverse sections range (from posterior forwards) between transversely oval over vertically oval to U-shaped.

The element thickens markedly as it bends into the transverse plane at the symphyseal region. The symphysis proper is short but very broad, almost doubling the width of the dentary. The plane floor of the dental arcade narrows to about half its width as the tooth arcade curves medially. The teeth diminish in size, and the tooth sockets attain a more rounded, short-oval shape different from the predominant shape in the rest of the arcade. The tusk pair is situated rather laterally, leaving a well ossified, smooth region medially to it. Naturally they match with the lateral position of the aperturae praemaxillares and the penetration sites of the alary processes. Such a lateral position of symphyseal tusks (and the existence of paired anterior windows in the palate) is a state of numerous temnospondyls, such as *Ichthyostega* (JARVIK 1996), *Trimerorhachis* (CASE 1935), trematosaurids (NILSSON 1943), and the capitosaur *Eocyclotosaurus* (KAMPHAUSEN 1989). However, the size of this tusk pair in *Mastodonsaurus* is unique. The sculpturing of the anterior symphysis is characterised by numerous pores embedded into an ill-defined pattern.

Dorsal to the mentomandibular ossifications a part of the medial margins where the symphsysis pairs are attached remains unossified. The mentomandibulars themselves do not have a bony contact, but end slightly lateral to the suture between the dentary halves. In contrast to several other capitosaurs (*Eryosuchus, Parotosuchus* partim, *Wellesaurus*, and *Kupferzellia*) there is no additional tooth row posterior to the tusks.

Mentomandibular ossification

The large symphysis of *Mastodonsaurus giganteus* contains a solid, entirely ossified replacement bone which may be called mentomandibular ossification (fig. 26). The mentomandibular occurs in recent amphibians and was often concieved a unique feature for lissamphibians (STADTMÜLLER 1936: 651). It is defined as a separate ossification of the mentomeckelian in the symphyseal region. *Mastodonsaurus* is the first temnospondyl in which such an ossification can be documented unambiguously. The shape of the cross-section of this bone (taken at the articulation surface of the symphysis) varies from circular to transversely elliptical and vertically oval. The structure of the bone is homogenous and clearly differs from that of the dermal elements covering it. It has a fine-grained fabric yet forms a solid mass with considerable potential to resist compaction. In contrast to the dermal bones the mentomandibular is never fractured by compaction, but at best slightly deformed; it might be crucial for the throughout excellent preservation of the symphysis.

The length of the mentomandibular is not exactly known, but it does not reach the region of the precoronoid/intercoronoid suture, of which numerous transverse sections exist at different growth stages.

Mandibular windows

A strong and differentiated adductor musculature is considered primitive for tetrapods. This is supported by direct neontological evidence and palaeontological data on the morphology of the muscle chambers. The insertion sites for these muscles are situated to a large extent in an elongated groove anterior to the articulation facet and framed by the prearticular lingually and angular labially. In many basal tetrapods the dermal investing bones form a relatively high, dorsally widening chamber rather than a mere groove, which is referred to as cavitas adductoris here. There is no clear concept whether this chamber is a unique feature of some higher group or rather a convergent acquisition. *Mastodonsaurus* has a long adductor chamber whose both walls are relatively high which is typical of capitosaurs (fig. 23).

The side walls of the chamber differ in size, height, thickness, and extent of vaulting. The adductor window is the dorsal opening of the adductor chamber. Typically, it is almost completely edged by the prearticular, surangular, and coronoid. The latter element gives particular stability to the window by forming its anterior, pointed margin on both sides. Its sutures to the surangular and angular are tight and eventually co-ossify.

The adductor window opens straight dorsally which contrasts the situation found in most other temnospondyls, and certainly bears functional significance. This window is anteriorly narrow and widens continuously backwards, until it reaches up to three times the anterior width posteriorly. On the lingual side the rim of the window is straight and has a thickened margin (torus lingualis). The lingual wall (prearticular) is further only slightly convex and aligned parallel to the long axis of the mandible. The labial wall (angular) is more clearly convex. The labial edge of the window ends in a broadened bulge (torus arcuatus) and runs fairly straight, by which it differs from other genera such as *Eryops* or *Trimerorhachis*. In *Mastodonsaurus* there is an exceptionally broad, concave adductor edge (angulus adductoris), running medial to the convex torus arcuatus. This edge is especially broad anteriorly where it constricts the adductor window. It slopes continuously in posterolateral direction.

The back wall of the adductor chamber is posteriorly convex and slopes anteriorly. The chamber narrows towards the bottom and its main axis changes, thereby aligning to the course of the ventral rod of the mandible. There is a large foramen in the posterior wall which is rather close to the foramen chordae tympani, suggesting the entrance of a larger nerve branch. The anterior end of the adductor window does not descend to form a closed wall, but instead the adductor chamber continues, being confluent with the canalis primordialis. The latter narrows and shallows only slightly in anterior direction, but further along narrows rapidly having almost disappeared at level of the suture between the anterior coronoids. Supposedly the canalis primordialis persists as narrow, laterally compressed channel, supposedly up to the posterior end of the mentomandibular. The extent of cartilage present inside this channel is difficult to estimate, especially on the bottom of the adductor chamber proper.

The fenestra Meckeli is a relatively large opening throughout basal tetrapods and therefore referred to as window here, following the tradition of classical morphology (fig. 25). It is best defined as the lingual opening of the adductor chamber. The widespread term 'foramen' should not be used in this case and instead be reserved for small openings which are caused by the penetration of vessels and nerves. In the majority of cases a distinction between these two types does not pose problems. The term 'anterior Meckelian foramen' relates to the fact that the Meckelian window was frequently termed 'posterior Meckelian foramen' (NILSSON 1944; JUPP & WARREN 1986); the former term is useful, because sometimes additional foramina occur further posteriorly.

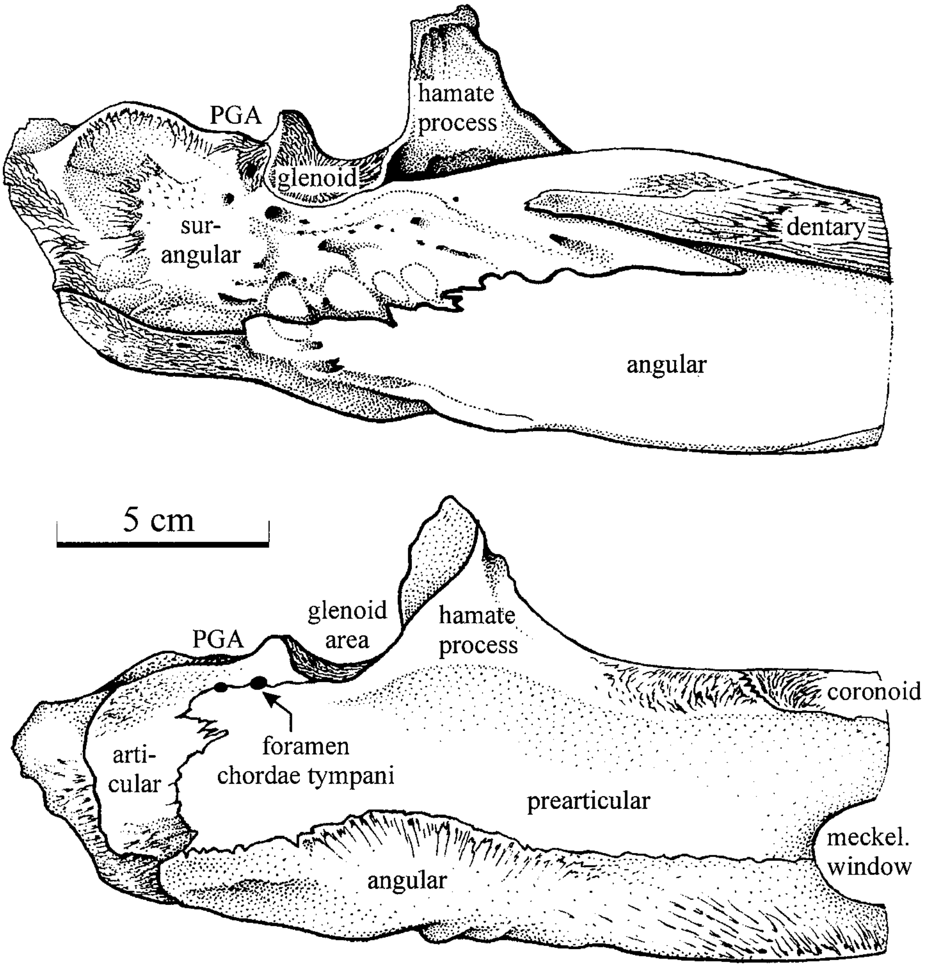


Fig. 27. Posterior portion of mandible in *Mastodonsaurus giganteus* from labial (above) and lingual sides (below). The hamate process forms a dorsal extension of the prearticular, which accommodates an anterodorsal projection of the articular glenoid facet. The postglenoid area (PGA) is much elongated with characteristically straight dorsal margins on both sides; the dorsal surface of it is well concave.

Review on the structure of the mandible

It was emphasised that there are marked differences in the extent of ossification. The strongest bones may be distinguished according to their apparent integrative role. Firstly, the elements of the ventral rod control the shape of the ramus and stabilise the floor of the adductor chamber (dentary, splenials, angular). Secondly there are ossifications involved in the jaw articulation (articular, hamate process, and their immediate periphery). And thirdly there are all bones which connect the dentary arcade to the walls of the adductor chamber (coronoid, articular, surangular).

Among all mandibular elements the surangular, angular, and coronoid certainly have the highest degree of ossification, as measured by thickness, density, and amount of sculpturing.

The structure of the sutures on the lingual side is relatively straightforward: (1) rims of windows are thickened with sutures there tending to co-ossify, (2) sutures near or perpendicular to windows are strongly serrated and may eventually be strengthened by sculpturing, (3) sutures connecting elements of the strong ventral rod likewise, (4) the upper margins of splenial and postsplenial are strengthened and abut against the lingual surface of the ventrally thinning dentary, (5) these are overlain by thin plates (coronoids) that overlap one another successively.

3.2. Postcranial anatomy

3.2.1. Historical sketch

The study of the postcranial anatomy of basal tetrapods started, among few other finds, with the description of the Lower Permian *Archegosaurus decheni* from the Saar-Nahe Basin (Meyer 1858) and the first Triassic capitosaurs from Baden-Württemberg (Meyer & Plieninger 1844; Quenstedt 1850; Fraas 1889). Surely the finds of *Mastodonsaurus giganteus* were the most impressive among these, and the articulated Lettenkohle specimens from Gaildorf, unspectacular as they seem today, challenged the works of Plieninger and Fraas. Both already arrived at a variety of fairly sound conclusions about the general structure of the postcranial skeleton of this species.

The knowledge on capitosaur postcranial anatomy grew comparatively slowly thereafter, which is explained by the disarticulated nature of most capitosaur finds and the widespread tendency to collect mainly the massive and impressive skulls. Huene (1922) was the last to pay attention to the articulated mastodonsaur material from Gaildorf. His reconstruction, though carried out very sketchy, gives a good impression of the gross structure and proportion of the capitosaur axial skeleton. The variety of ribs in *Mastodonsaurus* and their assignment to particular positions within the axial skeleton had long posed considerable problems (R. Wild, pers. comm.). Because of the largely disarticulated rib finds, none of the authors was able to give a comprehensive idea about the composition of the rib skeleton. Only the Kupferzell material provides a fairly complete sample of well-preserved ribs; the structure of their proximal ends, in combination with the costal skeletons in other capitosaurs, allows a reconstruction of the axial skeleton in articulation.

The Russian palaeontologists Bystrow & Efremov (1940) were very active in the field of capitosaur anatomy, and Konzhukova (1955), Ochev (1966, 1972) and Shishkin (1968, 1980) followed this tradition. These workers thoroughly described postcranial remains of several capitosaurs and other advanced actinodontids from the East European Platform (*Intasuchus, Platyoposaurus, Melosaurus, Benthosuchus, Eryosuchus*). Most of these finds were, however, disarticulated so that a reconstruction of the complete postcranial skeleton remained difficult (Ochev 1972: 128, 151).

Watson (1958) and Howie (1970) focussed on well-preserved, articulated postcranial material of two advanced capitosaurs. Their results can be regarded as the most complete accounts on the case, and especially Watson's near-complete skeleton of the West Australian *Paracyclotosaurus davidi* has served as a reference point in the reconstruction of capitosaurs ever since.

3.2.2. General structure

The postcranial skeleton is fairly conservative in basal tetrapods. The present knowledge on *Ichthyostega* (Jarvik 1980, 1996), and the comparison of the data on different groups of basal tetrapods suggest that basal tetrapods are essentially similar in the construction of neural arches and ribs, the basic structure of the limbs and girdle elements. However, the structure and arrangement of the vertebral centra is much more diverse, and the numerous differences long served as a major guide in the classification of basal tetrapods (Watson 1919; Romer 1947; Huene 1956; Panchen 1977, 1980). Jarvik's (1942, 1980) detailed work on *Eusthenopteron* and *Ichthyostega* revealed that the plesiomorphic condition most likely is the rhachitomous vertebra (in the trunk), which is present in both osteolepiforms and basalmost tetrapods and from which all other vertebral types can be derived without major problems (Panchen 1979). This idea challenged and finally overcame the notion supported by Watson (1919) that the embolomerous (diplospondylous) structure was the ancestral condition. Concommitantly, there was a major and long-going debate about the embryological origin of the components of the vertebral centra, wherein the study of Recent amphibians played a predominant role. This debate, reviewed by Gardiner (1982), apparently did not arrive at a final, clear-cut conclusion, and cannot form a matter of interest here.

The vertebral design of capitosaurs was briefly described in most of the aforementioned monographs, and the widely accepted concept is that they are derived from rhachitomous vertebrae, such as possessed by many yet not all temnospondyls (cochleosaurids: Langston 1953; trimerorhachids: Case 1935, Chase 1965; actinodontids: Meyer 1858, Konzhukova 1955, Boy 1988; eryopids: Moulton 1974, Boy 1990; zatrachydids: Case 1911, Langston 1953, Boy 1989; dissorophoids: Williston 1910, Boy 1972).

The general structure of the postcranial skeleton of capitosaurs is only known in three or four species, and there must be serious doubts as to how far we are informed about the actual vertebral diversity in this clade.

The finds of *Mastodonsaurus giganteus* are, next to those of Watson's *Paracyclotosaurus davidi*, the most complete remains of a capitosaur postcranium. The major advantage with the finds of *Mastodonsaurus* is the possibility to combine studies of old and new material. Nearly all elements of the skeleton, with the exception of the pes and the posterior part of the tail, are preserved and can be studied in great detail.

The vertebrae are composed of three types of elements: a massive cylindrical intercentrum, a relatively weak neural arch with an obliquely oriented and low processus spinosus, and small paired pleurocentra. This composition persists throughout the presacral column with certain proportional changes, up to the base of the tail (W. Kugler, pers. comm.). The presence of both neural arches and pleurocentra in the caudal skeleton is unknown, although from all evidence in other genera neural arches can hardly be conceived absent in the tail.

The ribs are very remarkable and most diverse structures in *Mastodonsaurus*. There are at least twenty different morphological costal types in the trunk, and an array of tail ribs. The trunk ribs differ in length, extent of bending, presence and expression of uncinate processes, and the structure of the proximal end. Because of uncertainties in the assignment of rib types with particular vertebral positions, the description does not specify which type may occur in which region. Instead, evidence

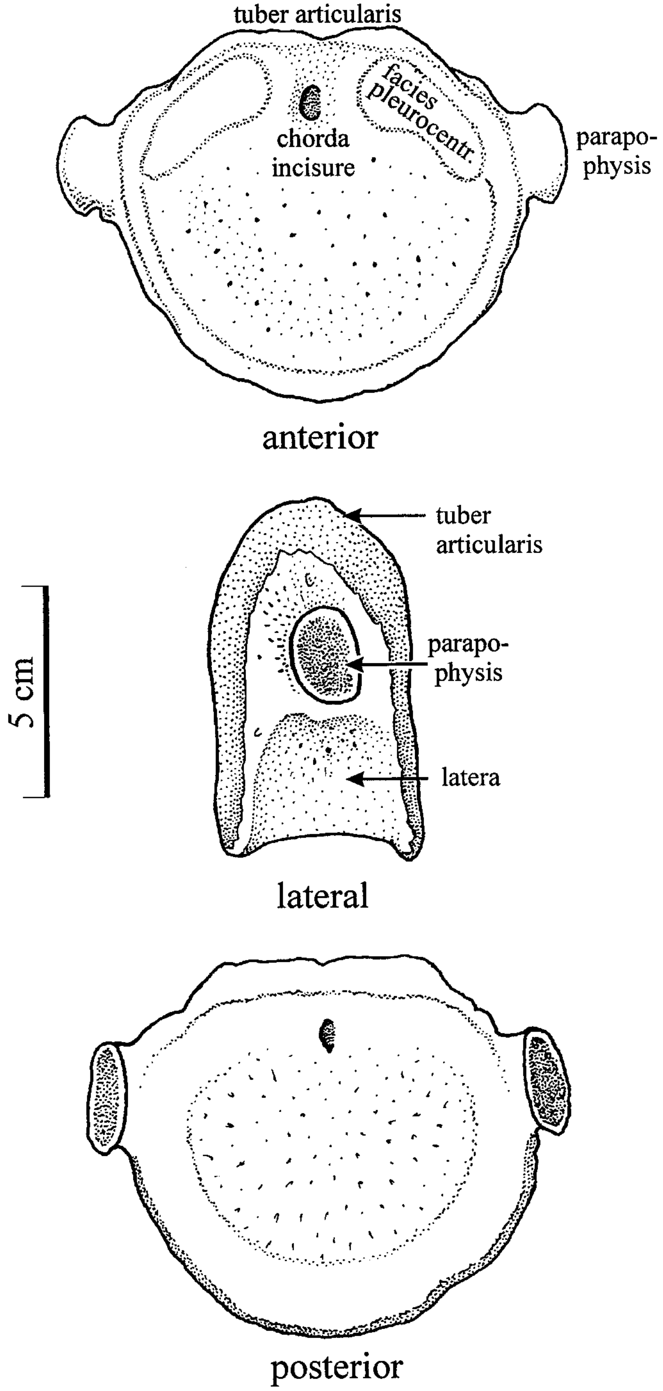


Fig. 28. Main vertebral centrum (intercentrum) in a medium-sized specimen of *Mastodonsaurus giganteus* in different views. This type is characteristic only for the anterior portion of the trunk in this species. The so-called stereospondyl condition is most elaborate in this type of temnospondyl intercentra.

will be listed in section 4 (reconstruction) whereby the different sources of information are distinguished and discussed in detail.

The trunk is nearly two times longer than the skull roof (see reconstruction), and the tail evidently consists of a large number of vertebrae, according to the various types of caudal intercentra in the sample. The proper assignment of intercentra, neural arches, and ribs is a matter of reconstruction and thus discussed in section 4. The various rib types are described according to their morphology and size.

The pectoral girdle and arm are well known since PLIENINGER in MEYER & PLIENINGER (1844), FRAAS (1889), and HUENE (1922). Among these the fore limb is almost completely preserved, but to a large extent known only from isolated material. The pectoral girdle is dominated by extensive dermal ossifications, the large interclavicle and the massive clavicles (FRAAS' Kehlbrustplatten). The scapula is usually well-ossified, but rather small at first and only later in development ossification expands into the coracoid region. The humerus is an unusually long bone which is slender and undifferentiated in medium-sized specimens. The largest humerus (SMNS 4707) is stronger and somewhat stouter than in smaller specimens, but still much more slender than in most other large basal tetrapods. The lower arm is supported by well-developed, yet relatively small bones, and the manus is elongate, with slender elements and probably four digits.

3.2.3. Axial Skeleton
Architecture and Arrangement

Mastodonsaurus giganteus has at least 27 presacral vertebrae, and an unknown but probably high number of caudal vertebrae (see section 'reconstruction'). The structure and morphology of the presacral vertebral column is well-known from two articulated specimens found at Gaildorf in the 1830s (MEYER & PLIENINGER 1844; HUENE 1922); see fig. 50). The exact number of vertebrae poses only a minor problem regarding the relative length of the trunk, because the uncertainty is a matter of two or three vertebrae only. PLIENINGER, FRAAS, and HUENE estimated the number as in between 27 and 30, and among the new material two specimens from Kupferzell suggest a similar presacral count (27–29). The proportions of the presacral column relative to the skull and limb elements is also relatively clear, because there are at least two specimens in which associated finds were made (SMNS 56633 from Gaildorf and SMNS 80913 from Kupferzell).

The historical development of the various popular reconstructions of *Mastodonsaurus giganteus* is very interesting. OWEN (1841) among others stressed the idea that the species belongs to amphibians, but he conceived anurans as the most appropriate Recent equivalents rather than salamanders which were favoured by JAEGER (1828). QUENSTEDT (1850) explicitly followed OWEN, although his main interest lay in the tympanum. Ever since then, numerous life reconstructions appeared with *Mastodonsaurus* being a giant frog-like amphibian. Both OWEN and QUENSTEDT were highly influential, which may have contributed to the long persistence of this concept. A second reason may be the predominance of cranial material and also the tendency to largely neglect the scanty postcranial remains, a tendency typical of capitosaur palaeontology in general (see however WATSON 1958, OCHEV 1972, and HOWIE 1970 for exceptions). Therefore reconstructions of the whole animal remained a subject of popular treatments to a large extent. HUENE

(1922), who still could rely on all original material from Gaildorf, only tentatively figured a series of intercentra. WATSON (1919), having seen parts of the material only during a brief visit, drew a sketch of a much too short trunk and did not give a presacral count. After the disappearance of parts of the material to which PLIENINGER (1844) had referred, no further attempts to reconstruct the skeleton of *Mastodonsaurus* were published.

Other capitosaur reconstructions were exclusively guided by the vast existing knowledge on other basal tetrapods. These studies already demonstrated a fairly conservative morphology within capitosaurs, especially regarding the proportion of the capitosaur trunk (HUENE 1956; WATSON 1958; OCHEV 1972). The study of the original material reveals that the finds from Gaildorf were nearly sufficient to reconstruct the skull, the girdles, and the axial skeleton of *Mastodonsaurus* appropriately, with the exception of the morphology of the trunk ribs and the structure of the tail base. PLIENINGER (1844), FRAAS (1889), and HUENE (1922) did not hesitate to mention that the trunk was elongate and the overall proportions that of a crocodile. In addition, the length of the tail was in the literature of the last decades throughout considered similar to that of other tailed amphibians (see already HUENE 1922).

Fortunately there are at least two partially articulated specimens from Kupferzell with supposedly complete presacral columns, a medium-sized (SMNS 80913) and a truly giant specimen (SMNS 81310). They supplement the data gathered from the Gaildorf material, and in sum there can be no doubt that the trunk of *Mastodonsaurus giganteus* was fairly long, reaching nearly two times the length of the skull roof . This matches almost exactly WATSON's (1958) reconstruction of *Paracyclotosaurus davidi.* Herein the reconstruction relies on several, independent lines of evidence, as listed in section 4. I am much indebted to R. WILD, J.G. WEGELE, H. HAGDORN, and W. KUGLER for various valuable observations.

SMNS 80913 comprises a fragmentary skull and a disarticulated presacral column of 28 vertebrae. Both skull and intercentra are affected by compaction, but only moderately crushed or distorted. SMNS 81310 (Riesenexemplar) is an assemblage of skull fragments, a complete lower jaw, 30 presacral vertebrae, 6–8 neural arches, about 20 ribs, and 6 caudal vertebrae.

Each vertebral segment consists of (1) an intercentrum, (2) a pleurocentrum, and (3) a neural arch. The intercentra are very well ossified, high, and form almost complete disks, whereas the pleurocentra are minute, supposedly rudimentary ossifications. This architecture was termed the stereospondylous condition (ZITTEL 1887; FRAAS 1889; WATSON 1919: 60). Moreover, mastodonsaur morphology was generally regarded as a 'terminal point' of vertebral evolution in stereospondyl temnospondyls. WATSON (1919) and ROMER (1947) conceived the Stereospondyli to be a natural group because of the widespread tendency to enlarge the intercentrum and reduce the pleurocentrum in capitosaurs. *Rhinesuchus* and *Benthosuchus* were seen as perfect intermediate (neorhachitome) stages, connecting Lower Permian eryopids with Triassic capitosaurs.

Mastodonsaurus has the most strongly ossified presacral intercentra among capitosaurs. Despite differences in transverse section, they are remarkably similar throughout the trunk (fig. 28). In particular their height does almost not decrease towards the sacrum. The most similar intercentra are known from *Eryosuchus*, particularly *E. tverdochlebovi*, which are relatively large, well-ossified capitosaurs from the Southern Urals (OCHEV 1972). In this species the intercentra are not entirely closed dorsally, but despite this are very high and thickened such as in *Mastodonsaurus giganteus*. Their characteristic shape in lateral view is that of a trapezoid (fig. 30). Metoposaurids are similar to the aforementioned species in that the intercentra form complete disks and are comparably thick. They differ clearly by being much lower and opisthocoelous, with a ball-and-socket articulation between one another. Irrespective of the size, all other capitosaurs differ from *Mastodonsaurus* much more than *Eryosuchus* and the metoposaurs.

There is no proatlas (in contrast to the temnospondyls *Eryops* and *Sclerocephalus*), and both the atlas and axis are much more differentiated than in plesiomorphic genera (fig. 29). The structure of atlas and axis is fairly constant among well-known capitosaurs (*Paracyclotosaurus* WATSON 1958, *Eryosuchus* OCHEV 1972) and metoposaurs (SAWIN 1945). It is clearly correlated with the structure and size of the unusually large occipital condyles in these groups. The axis and third vertebra of *Mastodonsaurus giganteus* are generally similar in structure, differing clearly from both the atlas and all subsequent vertebrae (fig. 29). In both units the intercentra are low and fairly broad, the apophyses closely set and aligned in a vertical line, and the neural arches are fused dorsally to the intercentra. Thus the first three vertebrae also differ from all following ones by the position of the neural arch relative to the intercentrum: they together make up one single ossification, and the neural arches do not alternate with the intercentra such as is typical of rhachitomous and stereospondylous vertebrae.

The trunk vertebrae are basically very similar in size, breadth, and composition (fig. 30); however, their morphology becomes more rudimentary tailwards (fig. 31). The pleurocentra are apparently present throughout the presacral column, and the alternating position of intercentra and neural arches is found at least up to the sacral vertebra. The situation in the tail skeleton, however, needs to be partially reconstructed by inference of data from other capitosaurs. Differences between trunk intercentra affect mainly their height, the structure of the dorsal side, and the size of the unossified region in the vicinity of the supposed chorda rudiment. In addition, on the flanks the position and shape of the parapophysis differ, and ventrally the general relief of the intercentrum changes while approaching tailwards. The neural arches of different trunk regions vary with respect to the length of the transverse process and the structure of the rib articulation (diapophysis), as well as the height and orientation of the processus spinosus. In the middle trunk region (understood here as the largest part of the trunk except the first four and the last three vertebrae) the transverse processes are markedly longer than elsewhere, and the processus spinosi highest and most strongly ossified.

Preservation

The Kupferzell material, as well as isolated finds from other localities in the Untere Graue Mergel, is peculiar in that most intercentra are badly crushed, conspicuously deformed, or both. In general, both intercentra and pleurocentra have a spongious internal structure, which becomes more clearly established during later development and reaches an extreme in the largest known mastodonsaur intercentra (catalogued as 'Riesenexemplar'). There the outer bone increments have suffered conspicuously more damage by compaction than the central parts. The characteristic effect of this compaction is a wrapping of the peripheral bone layers around the more massively ossified, spool-shaped centre. Reconstruction of these largest intercentra needs to rely on rare finds of uncompacted specimens, which were largely made in other localities, notably the Eschenau quarry. In the latter site generally a mode of compaction different to that in Kupferzell is observed (R. Wild, pers. comm.).

The raised anterior margins of the parapophyses are frequently fractured, as they are very delicate and thin-walled structures. In other specimens the parapophyses are flattened and have the appearance of large ears which increase the breadth of the intercentrum as compared to unaffected specimens. Apparently in posterior intercentra, in which the parapophyses are less massive than further anterior, such a flattening occured more frequently.

Contrary to the intercentra, the neural arches are generally rarely found. Their degree of ossification is much lower than that of the intercentra, and their processes and zygapophyses readily go into pieces even in well-preserved specimens. In many cases the zygapophyses are entirely worn off. At least in some of these cases a limited predepositional transport of the bones is probable. There are basically two different modes of preservation among the neural arches at Kupferzell. (1) Complete elements which are dorsoventrally flattened and tend to be rather deformed than crushed, and (2) medially separated arch elements with the transverse process broken, but well-preserved zygapophyses. In order to gain a complete understanding of mastodonsaur neural arch structure, specimens of both preservational types need be considered. The small number of neural arches in the Kupferzell sample allows reconstruction of only three types of neural arches. The articulated presacral column fragment from Gaildorf complementarily permits observation of gradual changes in the morphology of the neural arches.

Terminology for vertebrae

The vertebral segment of *Mastodonsaurus giganteus* has often been figured throughout the literature, although it had not been particularly well studied. The Gaildorf material is not very informative in the present, rather poor state of preparation. The new material, particularly from Kupferzell, allows much deeper insight into the anatomy of each vertebral component, revealing various hitherto unknown structures.

Howie (1970) gave a valuable review of the structure and arrangement of the components in the vertebral segment, to which I shall return in the reconstruction section. The state of knowledge on the vertebral segment now reached by the Kupferzell and Ilshofen material, however, makes a revision and refinement of terminology necessary. Most of these terms will be applicable to other temnospondyl groups, as well.

I should like to add the following terms (see figs. 28, 32, 33):

1. Intercentrum:

- Latera: The smooth and concave flank of the cylindrical intercentrum (which varies in height as viewed from the side).
- Facies pleurocentralis: The facet for the pleurocentrum on the anterior face of the intercentrum.
- Tuber articularis: The attachment site for the neural arch, in most intercentra situated dorsal and posterior to the facies pleurocentri.

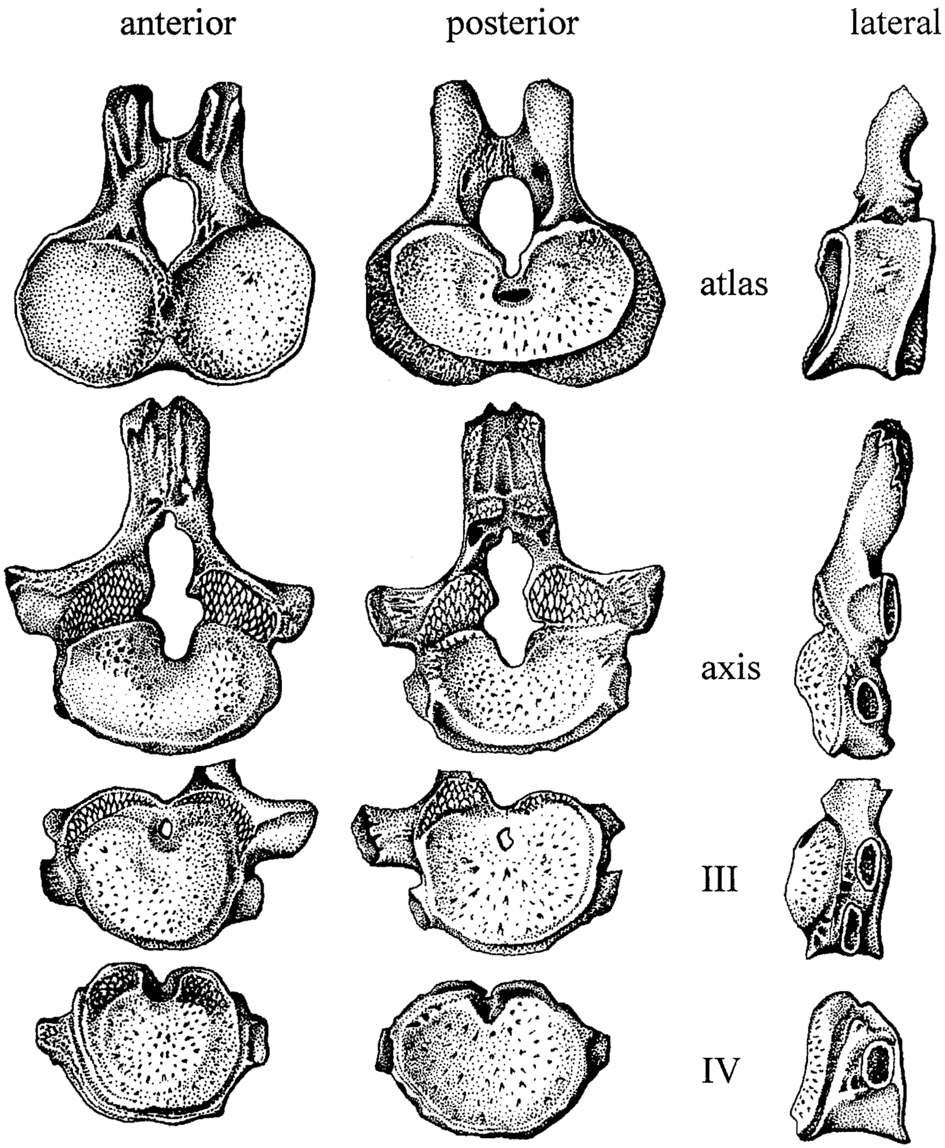


Fig. 29. The first four (or 'cervical') vertebrae of *Mastodonsaurus giganteus* from different perspectives. The shape changes of the intercentrum and spinal process are particularly remarkable. Note that there are no pleurocentra figured (they are present from the axis on), and that in the fourth (IV) vertebra the neural arch was loosely attached to the intercentrum, and therefore is not figured here.

2. Neural arch:
- Arcus vertebri: The arc framing the neural canal, formed by the processus spinosus dorsally and the processus transversi laterally.
- Facies pleurocentralis: The articulation facet for the pleurocentrum, situated entirely on the posterior side of the processus transversus and facing posteromedially.

- Facies intercentralis: The facet for the attachment to the tuber articularis of the intercentrum.
- Sulcus medialis: The unpaired and medial countersunk area on the anterior and posterior sides of the neural arch, where the countersided elements are fused, the term being applicable to both front and back side.

3. Pleurocentrum:

- Sulcus anterior: The markedly curved and laterally narrowing groove on the anterior facet of the pleurocentrum, which articulates with the neural arch.

The atlas

The atlas of *Mastodonsaurus* was identified and described by PLIENINGER (1844) and later again mentioned and figured by FRAAS (1889). Further, both PLIENINGER (cit.) and HUENE (1922) briefly described the element on the basis of the rather poor Gaildorf material. The most conspicuous feature mentioned by these early authors is the bilobed anterior surface, forming the articulation facets for the giant occipital condyles.

Capitosaur atlantes have been long known as elaborate structures which differ markedly from those of plesiomorphic genera such as *Eryops* (MOULTON 1974), *Sclerocephalus* (BOY 1988), *Platyoposaurus* (KONZHUKOVA 1955), and even *Lydekkerina* (BROILI & SCHROEDER 1937a). In these genera, the atlas has a minute neural arch which is dorsally slender and pointed and the intercentrum is not larger than those of the following vertebrae. The atlanto-occipital articulation facet may be single as in *Eryops megacephalus* (pers. exam.) or bilobed such as in *Platyoposaurus stuckenbergi* (KONZHUKOVA 1955: fig. 16), but it is throughout strongly concave.

The atlas of *Mastodonsaurus* is typical capitosaurid in being clearly larger and especially wider than the axis and all subsequent vertebrae (fig. 29). It lacks a parapophysis, and the neural arch has no transverse process and consequently lacks a diapophysis (see HUENE 1922: 401), and finally also has no postzygapophyses. As compared to all subsequent intercentra, that of the atlas is the most completely ossified, meaning that it practically forms a complete cylinder, which anteriorly widens to give two completely rounded and separated facets. Throughout the known developmental stages, it forms a dorsally completed cylinder with a smooth, equally broad latera vertebrae that is only interrupted by the small articulation facets for the tiny neural arch. The posterior side is strongly concave, forming a single, transversely elongated oval.

The neural arch elements are low, orientated straight vertically, and tightly fit onto the otherwise smooth dorsal surface of the atlantal intercentrum. They are often found in isolation and may not readily appear as elements of the axial skeleton, therefore fewer specimens are available than of atlantal intercentra. In *Mastodonsaurus* (HUENE 1922) they are much stouter than in other temnospondyls, and their dorsal ends are broadened with and covered by marked crests suggesting fleshy muscular origins. The general structure of each element is tetrahedral, with a rather small facies intercentralis but a broad, rectangular attachment face for the countersided element. There is no proper arch present, as the elements fail to meet dorsally where they are only very rudimentarily ossified leaving unfinished posteromedial surfaces. In sum, the neural arch of the atlas consists of rudiments of the transverse process (namely only its medialmost portion which attaches to the intercentrum) and a dorsomedially low, unfinished spinal process.

The axis

The axis is smaller than the atlas and in most aspects resembles the structure of the subsequent trunk vertebrae. It consists of a relatively low intercentrum and a straight vertical, complete neural arch which is broadly fused to the intercentrum. In *Mastodonsaurus* the axis is nevertheless a peculiar and diagnostic element, which differs in several aspects from axes of other temnospondyls (fig. 29). First it is specialised in having a convex anterior surface. Second the latera is distinctly narrower than in all subsequent intercentra. Third the intercentrum is much lower than those of most other trunk vertebrae, and consequently the chordal canal is dorsally open. HUENE (1922) interpreted the low height of the axial intercentrum as a result of deformation in the single specimen he examined, but the Kupferzell material demonstrates that indeed it is much lower than the succeeding ones.

There are definitely paired pleurocentra posterior to the axis, as they are found attached to large facies pleurocentrales on the posterior side of the axial neural arch. Anterior pleurocentra, belonging to the atlas, were not found, but cannot be ruled out from the depressions on the dorsolateral parts of the anterior face of the axial intercentrum which are suggestive of this.

The shape of the convexity of the anterior face is transversely oval, with the paired apices sitting lateral to the well-established chorda incisure. The surface of the anterior side is covered by numerous very large pores and minor depressions. The posterior face is markedly concave, very much like that of the atlantal intercentrum. The latera of the axial intercentrum is smooth, except for the parapophysis which it bears about in the ventral third of its height. The parapophyseal facet is round to slightly vertically oval, and relatively close to the diapophysis. The transverse process is short, and the diapophyseal facet is a vertically elongate oval.

The neural arch is of nearly the same height as subsequent arches but according to the articulated finds it sits straight vertically on top of the intercentrum. Rather weak pre- and postzygapophyses are present.

Third intercentrum

In the third vertebra the neural arch is more clearly separate from the intercentrum and is less firmly attached to it than in the axis. The intercentrum is much higher than that of the axis, attaining a nearly circular transverse area (fig. 29). There is a marked vertical slit-like chorda foramen in the upper third of the bone. The anterior surface of the intercentrum is very markedly convex, with the unpaired apex situated ventral to the centre of the element. The most elevated region of this convexity is heart-shaped. The facies pleurocentralis is large and strongly curved dorsoventrally.

The dorsal fusion of the intercentrum above the chorda canal is only very faint, leaving a larger area especially posterior to the chorda foramen unossified. Ventrally the latera of the intercentrum is broad and has a prominent relief. There is a medial, sagittal groove and marked, paired lateral depressions. The convex anterior surface of the bone excels the ventral margin by far. Contrary, the posterior side is clearly concave such as in the axis.

The rib articulation facets are closely set, but farther apart than in the axis. In addition, the geometry of their articulation facets differs. They are long-oval, the diapophysis being larger than the parapophysis.

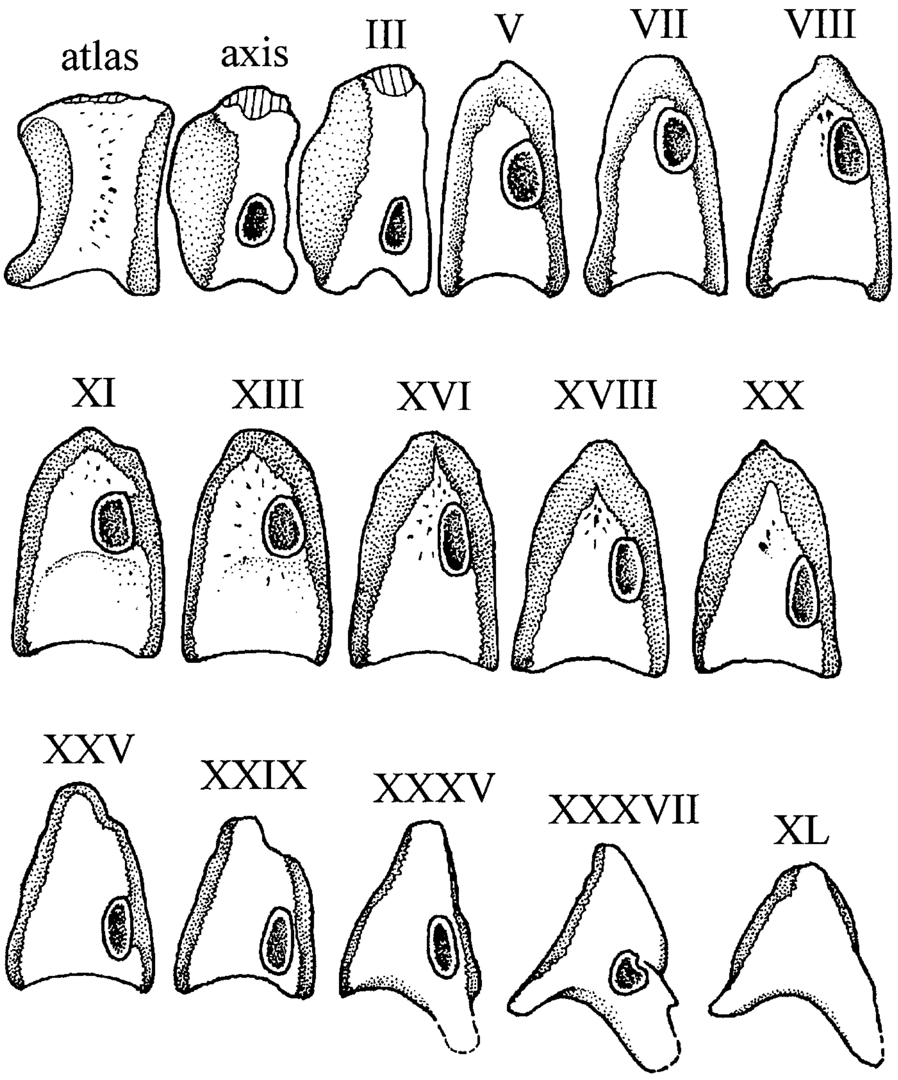


Fig. 30. Selected intercentra of medium-sized specimen of *Mastodonsaurus giganteus* in lateral view. The relative position and morphology of the parapophysis, the height, and the shape of the latera are features according to which the relative sequence of intercentra and ribs within the vertebral column can be approximated.

Anterior thoracal intercentra

The following suite of features characterizes the typical thoracal intercentrum in *Mastodonsaurus giganteus*: (1) it is a nearly complete disk with slightly concave anterior and posterior surfaces (hence very weakly amphicoelus), (2) the latera of the disk is throughout very markedly concave and smooth, ending at the margins of the distinctly flattened top of the disk, (3) this top is roughened and has an irregular relief, which is roughly concave dorsally, bearing the facies pleurocentralis anteriorly and the tuber articularis posteriorly, (4) the parapophysis rises from variable positions within the latera, this position depending on that of the vertebra in the column, and (5) near the top there is a well-established foramen for the chorda rudiment, which is to a variable degree emplaced on a small convexity, dorsal to the concave centre of the disk (figs. 28, 30, 31). The parapophysis is often extended posteriorly to expand onto the posterior rim of the latera, and the distal length of the parapophysis varies also with respect to the position of the vertebra.

Further characteristics are as follows: paired facies pleurocentrales are found throughout lateral to the chorda foramen, matching well the size, orientation, and shape of the pleurocentra attached to them. The intercentra of the first vertebrae are readily recognised by their relative size, the great thickness of their dorsal part, and most importantly the relative position of the parapophysis. Unlike in all other capitosaurs, mastodonsaur intercentra generally constitute almost complete disks in transverse view. This is what was formerly concieved the stereospondylous condition (Watson 1919; Bystrow & Efremov 1940; Romer 1947, 1966), but its convergent acquisition in the Metoposauridae demonstrates that this term is problematic. The mastodonsaur intercentrum originates by a complete fusion of the typical, crescent-shaped centrum of other capitosaurs. *Heptasaurus* and *Eryosuchus* exemplify this, having slightly less massive intercentra than *M. giganteus*; the former might be interpreted as a phylogenetical morphocline towards the condition of the latter. The resulting shape is very characteristic, and definitely diagnostic for the genus *Mastodonsaurus*: a dorsally slightly narrowing disk, weakly amphicoelous, with high reaching, concave lateral flanks that reach dorsally well beyond the parapophysis.

The anteriormost intercentra are peculiar in being transversely broader than all subsequent intercentra. This is especially obvious in the ventral part of the centrum, which tends to be laterally constricted in elements of further posterior positions. The pleurocentral grooves are oriented almost horizontally, whereas further posteriorly they curve more clearly in ventral direction.

Posterior thoracal intercentra

The intercentra of the posterior trunk region are characterised by a gradually increasing size and dorsal widening of the chorda foramen, a narrowing of the ventral face of the latera, and an overall decrease in extent of ossification (figs. 30, 31). The latera vertebrae successively fails to fuse dorsally, which starts anteriorly, and in XXVII finally arrives at a dorsally open intercentrum. Concomitantly the tubera articulares of the neural arch become thinner and finally disappear, indicating looser attachment of the transverse processes to the intercentrum. The parapophysis of all these intercentra is clearly longer and migrates ventrally towards the sacrum. The shape and size of the diapophysis and parapophysis become very similar caudally, which results in the characteristic morphology of the head region in the corresponding ribs. The transverse processes also greatly decrease in length in the posteriormost presacral column.

Sacral intercentrum

Irrespective of the developmental stage, the sacral intercentrum of *Mastodonsaurus* is typically dorsally open, with a broad and deep reaching chorda incisure. The pleurocentral facets at the posterior side form the most elevated regions of this ele-

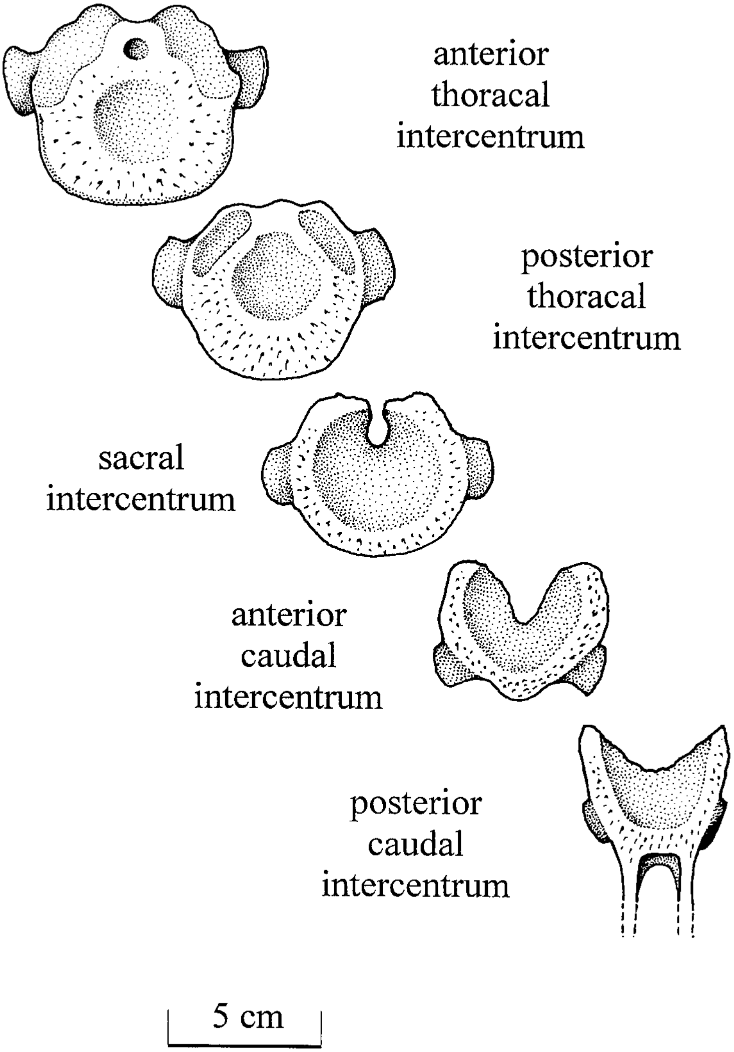


Fig. 31. Selected intercentra of the trunk and tail in *Mastodonsaurus giganteus* from an anterior perspective. The anterior intercentra are high and form complete disks; the position of the chorda is indicated by a marked depression. Backwards, the intercentra become ever more rudimentary in morphology, resembling typical intercentra of other stereospondyls. Note that the size of the pleurocentral facets, the degree of concavity, the position of the parapophysis, and the size of the chorda incisure change gradually along this cline. The posterior caudals possess well-developed haemal arches, whose length is uncertain.

ment. Anteriorly the chordal incisure of the intercentrum is much wider. The sacral intercentrum is distinctly lower than that of the foregoing vertebrae. In addition the parapophysis is relatively smaller than that of most trunk intercentra, and the ventral flank of the element is narrower than in other vertebrae.

Anterior caudal intercentra

The first four postsacral vertebrae differ only slightly from the sacral intercentrum. They are lower and more incomplete dorsally, leaving a wide chorda incisure (figs. 30, 31). The parapophysis is situated very low, their lower margin being at one level with the ventral rim of the element. They bear an elongated, long-oval to triangular facet, which is markedly directed posterolaterally. The capitulum must have abutted at an angle of 45° towards the sagittal axis.

The outline of these intercentra in lateral view is triangular with a markedly concave ventral rim, that of the dorsal view horizontally rectangular. Anterior and posterior aspects are basically similar. Pores are aligned concentrically in several narrow zones of reduced ossification. The amount of cartilage cover was larger than in trunk intercentra, as indicated by the clearly more roughened surfaces. The dorsal side, which entirely forms the border of the large incisura chordalis, is covered by numerous tubercles which are typical of cartilage-bone interfaces. In none of these vertebrae is there a facet for the neural arch. In the transverse plane the intercentrum differs from that of trunk vertebrae in being narrower and ventrally pointed.

Intermediate caudal intercentra

By the fifth caudal well-established haemal arches are present. The intercentra become successively crescent-shaped, generally resembling the structure in the capitosaur ground-plan (e.g. such as in *Eryops*, see MOULTON 1974). The extent of ossification is much smaller than in the anterior caudal intercentra. At the same time, the surface structure differs in that transversely elongate grooves and short channels dominate over pores. The haemal arches instead are weakly ossified and smooth; in most cases their ventralmost portions lacking.

The lateral flanks of the intercentra are much lower than in the anterior caudals, and the position of the parapophysis is more ventral, at the posteroventral edge of the bone. The facet is vertically oval and borne in part by the haemal arch. The direction of the articulation is unclear because of the strong preservational bias. The haemal arch is long and directed slightly posteroventrally. Parapophyses are apparently present at least up to the seventh or eighth caudal vertebra.

Posterior caudal intercentra

The identification and proper assignment of the posteriormost caudals is difficult for two reasons. The first is the occurrence of the small capitosaurid *Kupferzellia* (SCHOCH 1997a) at the same locality, and that to date only the cranial anatomy of this species is known. The second problem is that posteriormost caudals of capitosaurs might be generally very similar even among distantly related genera. This is suggested by the great general resemblance of capitosaur intercentra throughout the Triassic worldwide (HOWIE 1970; OCHEV 1972; WARREN & SNELL 1991).

The presence of haemal arches is the only criterion by which the position is unambiguously clarified. Imperfect ossification, as frequently observed among these finds, may be a feature related to the posterior position or alternatively the small size of the vertebra, and thus cannot be decisive. In conclusion, the presence of mastodonsaur posteriormost caudal intercentra is very probable and suggested by the stout appearance and imperfect morphology of these vertebrae, although a belonging to a smaller capitosaurid genus cannot be ruled out.

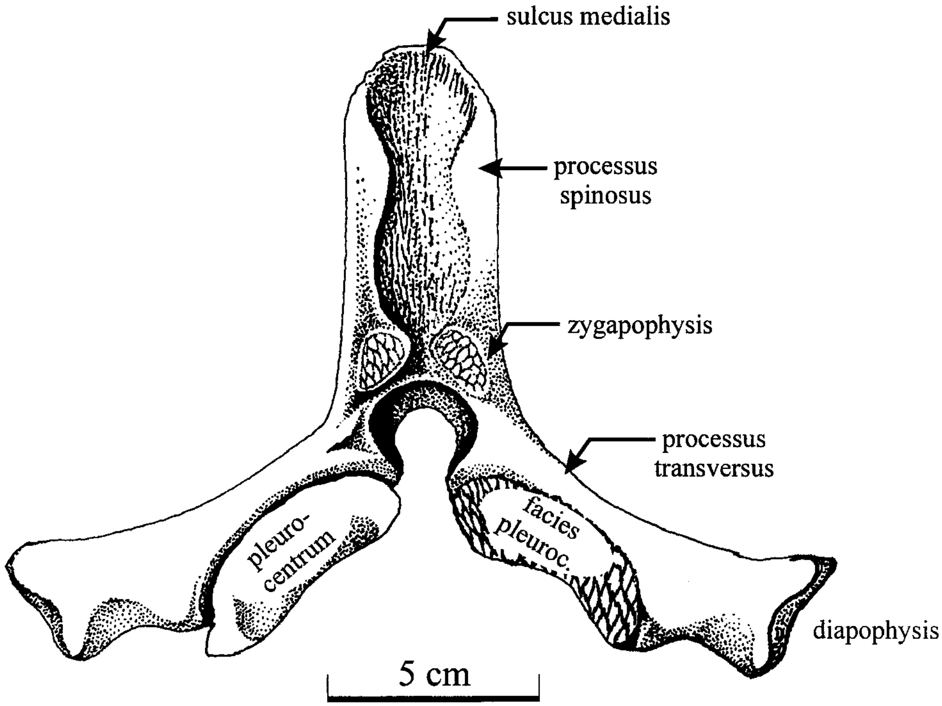


Fig. 32. The neural arch in a medium-sized specimen of *Mastodonsaurus giganteus* in posterior view. The transverse process and the morphology of the facies pleurocentralis are subject to high variation, but the height of the spinal process is usually constant within the axial skeleton of the trunk. On the left side the pleurocentrum is figured in articulation.

Neural arches

In contrast to the long bones and intercentra, the neural arches of *Mastodonsaurus* are weakly ossified and only very rarely well preserved in the Untere Graue Mergel horizon. Much more information, both about their anatomy and articulation, is gathered from Gaildorf specimens housed in the collections at Stuttgart and Tübingen. In addition, there are a few disarticulated, but very well-preserved and almost undistorted remains of very large neural arches from Kupferzell.

Meyer & Plieninger (1844) and Fraas (1889) briefly described and figured neural arch fragments from Gaildorf. A comparison of these elements with data on other basal tetrapods, however, was not carried out. Wepfer (1923) described poorly preserved neural arches of *Heptasaurus* from the Upper Buntsandstein locality Kappel, and Konzhukova (1955) described and figured a fairly complete neural arch of *Mastodonsaurus torvus* from Bashkortostan (see also Shishkin et al. 1995). Both agree largely with the Gaildorf and Kupferzell material, which shall be described in detail below.

The neural arches appear to be morphologically rather similar throughout the presacral column (figs. 32, 33, 50). Their appearance first strikes by the low and strongly posteriorly inclined processus spinosi. Each side of an arch pair consists of (1) the low and posterodorsally directed processus spinosus, (2) the large and bowl-shaped prezygapophysis, (3) the small and weakly developed postzygapophysis, and (4) the processus transversus which carries the diapophysis and comprises the most extended and massive, yet variable portion of the neural arch.

The processus spinosus is inclined at an angle of 30° towards the horizontal plane of the zygapophyses. It differs in size with respect to the position in the vertebral column. It appears from isolated finds that neural arches with the largest transverse processes also have the highest and most massive spinal processes. As I shall argue, this probably means that the neural arches were highest in the middle trunk region, and that their height decreased towards the tail less rapidly than towards the head. The sulcus medialis is present throughout the presacral column, but more clearly developed in less massive neural arches. This suggests that the sulcus medialis is principally only an artifact of the generally poor ossification, and the failure of the processes to completely fuse in the midline.

The prezygapophysis forms a laterally broadening bowl whose floor inclines anteriorly. It is comparatively long, almost reaching the length of the base of the processus spinosus. The prezygapophysis rises from the anterior contact zone between the processus transversus and spinosus. Its articulation facet has a long-oval outline and a laterally elevated margin. The floor of the facet is roughened, and continues posteromedially by bending into the oblique plane of the processus spinosus. There might have been an almost continuous cartilage cover from the prezygapophysis along the entire anteriomedial surface of the processus spinosus.

In contrast to the latter, the postzygapophysis is rather small and only faintly grows out of the oblique plane of the processus spinosus. The surface of its facet is only 2/3 the size of the prezygapophysis. This has a shape of an anteriorly constricted oval, and its margins are throughout not elevated above the level of the flat articular surface. The facet inclines anteriorly to the same angle as the prezygapophysis, by which a tight and complete fitting of the articular surfaces is accomplished. This does, however, not preclude a limited lateral movement of two subsequent neural arches.

Finally the processus transversus is the largest and most complicated component of the neural arch. It has a broad and very well-ossified base that is fused broadly to the processus spinosus. In anterior view the processus spinosi and pr. transversi of both sides unite to form the solid arcus. The latter becomes higher but not broader posterodorsally, so that its moderately flattened roof lies in the oblique plane of the prae- and postzygapophyses. The arcus is ventrally constricted by medial projections of the processus transversus; the surface of these paired projections is roughened. There the neural arch attaches to the dorsal bosses of the intercentrum (facies intercentralis). Posterior to this, the posteroventral side of the processus transversus tightly attaches to the pleurocentrum, leaving a well-defined facet for this element (facies pleurocentralis).

The neural arches of vertebrae III through XXVIII are of similar structure, but differ especially in the length of the transverse processes, the morphology of the diapophyseal facet, and the expression of the zygapophyses. In section 4 the morphological differences of the neural arches in the different trunk regions are discussed.

Pleurocentra

The pleurocentra are small, imperfectly ossified and widely separated elements (fig. 32, 33). They were first recorded among the Capitosauroidea by Howie (1970)

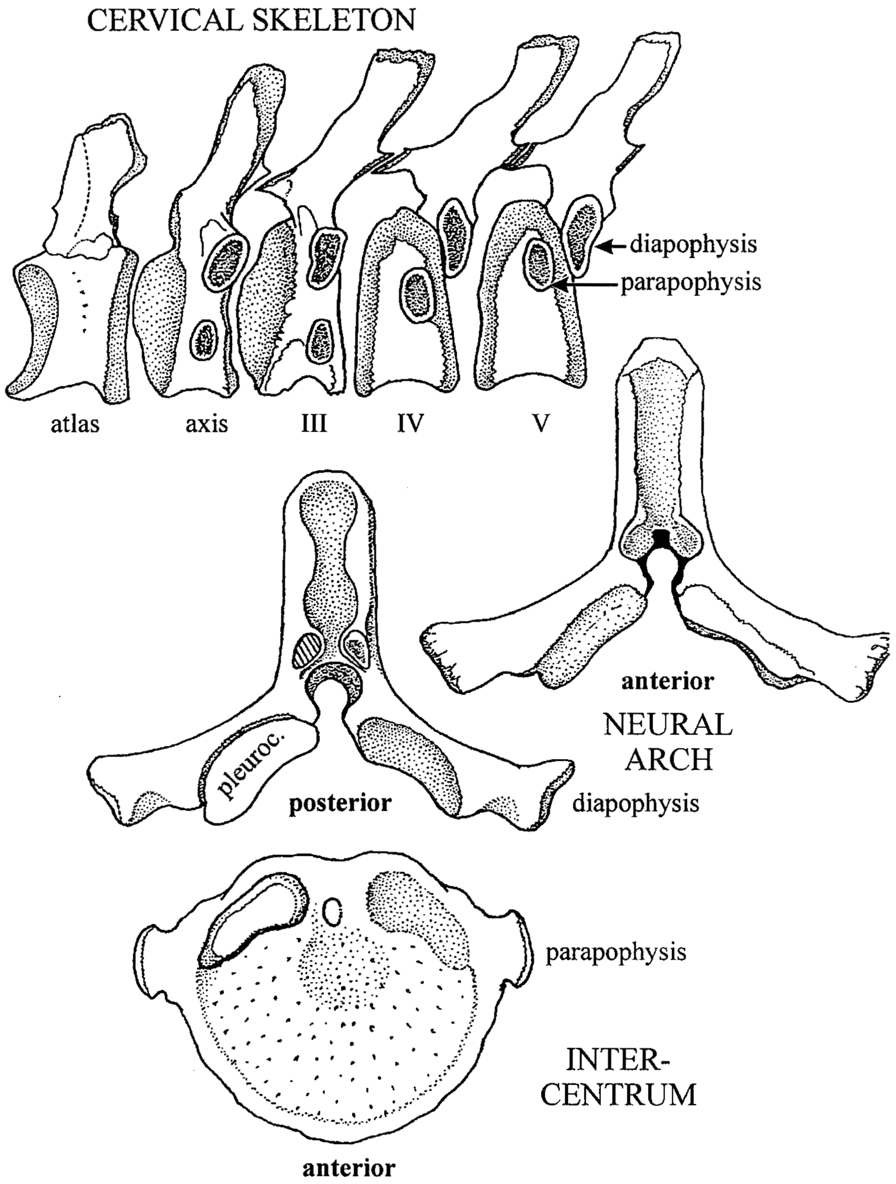


Fig. 33. The spatial relations between intercentrum, pleurocentrum, and neural arch in *Mastodonsaurus giganteus*, and a reconstruction of the cervical portion in the axial skeleton. See section 4 on the lines of evidence for these reconstructions.

in the East African *Parotosuchus pronus*, and subsequently found by Ochev (1972) in *Eryosuchus tverdochlebovi* from the Southern Urals. Dutuit (1976) found true pleurocentra in the metoposaurid *Metoposaurus ouazzoui*.

The plesiomorphic, "true rhachitomous" pleurocentra of *Eryops* (Moulton 1974), *Sclerocephalus* (pers. exam.), *Archegosaurus* (Meyer 1858), and *Platyoposaurus* (Konzhukova 1955) generally agree among another in the following features:

they are relatively large quarter circles, sometimes fused dorsally, and form a dorsal mirror-image of the low, crescent-shaped intercentrum. Consequently, the intervertebral borders run obliquely between pleurocentrum (vertebra A) and intercentrum (vertebra B). The architecture in capitosaurs is not much different: yet, the intervertebral boundaries run largely subvertically between the large intercentra, but dorsally they bend into the oblique plane typical of the "rhachitomous" vertebrae.

The pleurocentra of *Parotosuchus pronus* instead are throughout very similar to those of *Mastodonsaurus giganteus*. They are attached to the posteroventral side of the processus transversi and near the posterodorsal surface of the intercentrum without actually attaching to it. There is no contact between a pleurocentrum of vertebra A and the intercentrum of vertebra B as has been sometimes suggested. Intercentrum, neural arch, and pleurocentrum (right sequence !) of each vertebra form a closed unit, whose only ossified contacts to other vertebrae are established by means of the zygapophyses. This was clarified by HOWIE (1970), but the "stereospondylous" condition of capitosaurs is still largely cited in the traditional restoration which based on an erroneous interpretation of *Mastodonsaurus giganteus* (e.g. CARROLL 1988).

The pleurocentra become more massive and differentiated with increasing size in *Mastodonsaurus*. The shape of the posterior trunk pleurocentra is stouter; they are shorter (matching the shortness of the transverse processes) and deeper. The three-dimensional shape of these elements is, however, uncertain as all finds from this region are seriously affected by compaction.

Trunk ribs

Numerous ribs were found associated with disarticulated or partially articulated specimens during the Kupferzell excavation. In addition there is a large sample of isolated ribs, many of which are well-preserved and fairly complete, from the same and similar localities of the same horizon (H. HAGDORN, pers. comm.). The Gaildorf material has not produced many valuable costal remains. The best-preserved ribs among the material found before the Kupferzell excavation came from the Muschelkalk-Keuper Grenzbonebed, housed at Stuttgart and Tübingen.

MEYER & PLIENINGER (1844), FRAAS (1889) and HUENE (1922) described and figured largely fragmentary rib material, and also pointed out the conspicuous polymorphism of mastodonsaur ribs. However, the assignment of a certain rib type to a vertebral position within the column remained entirely obscure, and none of the authors seems to have been aware of the extent of rib polymorphism, which is by itself a most characteristic feature of *Mastodonsaurus* as compared to many other temnospondyls.

Among the 27–29 presacral vertebrae, there are at least twenty different rib shapes (figs. 34–37), and in most cases the relative position in the trunk can be ascertained relatively precisely for these ribs (see reconstruction). This is possible because of the limited individual variation and the minor ontogenetic changes in rib morphology, as exemplified by various similar ribs of very different size. The costal apparatus of *Mastodonsaurus* was more elaborate than that of *Eryops* or *Sclerocephalus*, and certainly excells the morphological diversity found usually among capitosaurs. *Eryosuchus* is, judging from OCHEV's (1972) reconstruction, the most similar taxon in this respect. The sequence of rib types treated below follows the results of the reconstruction as discussed in section 4. The distinction of rib types is made according to (1) morphology of the head region, (2) presence and expression of proximal and distal uncinate processes, (3) length, (4) relative position of bending point, and (5) morphology of the distal end. There is a fewer number of designated types than morphologies found, because some morphologies appear to have been subject to continuous variation; this concerns particularly the anterior and intermediate thoracal costae.

The following rib terminology is suggested (fig. 34):

- Caput tubercularis: The process bearing the tuberculum,
- Tuberculum: Only the facet for the articulation with the diapophysis,
- Caput capitularis: The process bearing the capitulum,
- Capitulum: The facet for the articulation with the parapophysis,
- Stylus costae: The shaft of the rib,
- Incisura capitis: The region that separates the two heads,
- Crista tubercularis and crista capitularis: They run on the proximal-dorsal side of the rib heads,
- Processus uncinatus proximalis: A crest or irregular outgrowth on the posterior flank of the dorsal rib face, proximal to the bending point of the stylus,
- Processus uncinatus distalis: Same as before, but distal to the bending point.

Rib type A

This rib type is moderately long, markedly bent at about midlength, and has only slightly broadened proximal and distal ends (fig. 34, below). Capitulum and tuberculum are closely set, both almost round, and of nearly similar size. There are clearly two proximal heads which are separated by a well-established incisura capitis. The shafts of the capitular and tubercular heads converge distally at about one third of the rib's length, proximally being divided by a furrow on the ventral side. The dorsal side of the rib is largely smooth, with a tenuous crest rising from the caput tuberculi. This is highest at about the point where the shafts of the proximal heads meet, and continuously decreases towards the bending point of the costa; following the before mentioned criteria, this is (serially) homologous to the processus uncinatus proximalis (UPP). The geometry of capitulum and tuberculum is similar, both are oval to round, and the former is only slightly larger than the latter. Finally the distal end is moderatley wide, with an dorsoventrally compressed cross-sectional area.

Rib type B

This type is longer than A, and its most diagnostic feature is the broadened stylus immediately distal to the head region (fig. 34, below). There are well-defined capitular and tubercular crests, which unite relatively further distal than in type A. A definite proximal uncinate rises close to the bending point of the shaft, being inforced by a medial column which converges with the long axis of the proximal portion of the rib at an angle of 30°. The size and morphology of a distal uncinate process (UDP) is uncertain, but apparently was much elongate and blade-like, unlike the rather small proximal process. The tuberculum is much longer than the capitulum, and dorsally widens markedly. In cross-section, the rib attains the shape of a comma, which is a rather typical feature of large capitosaurs (HOWIE 1970). In addition, the

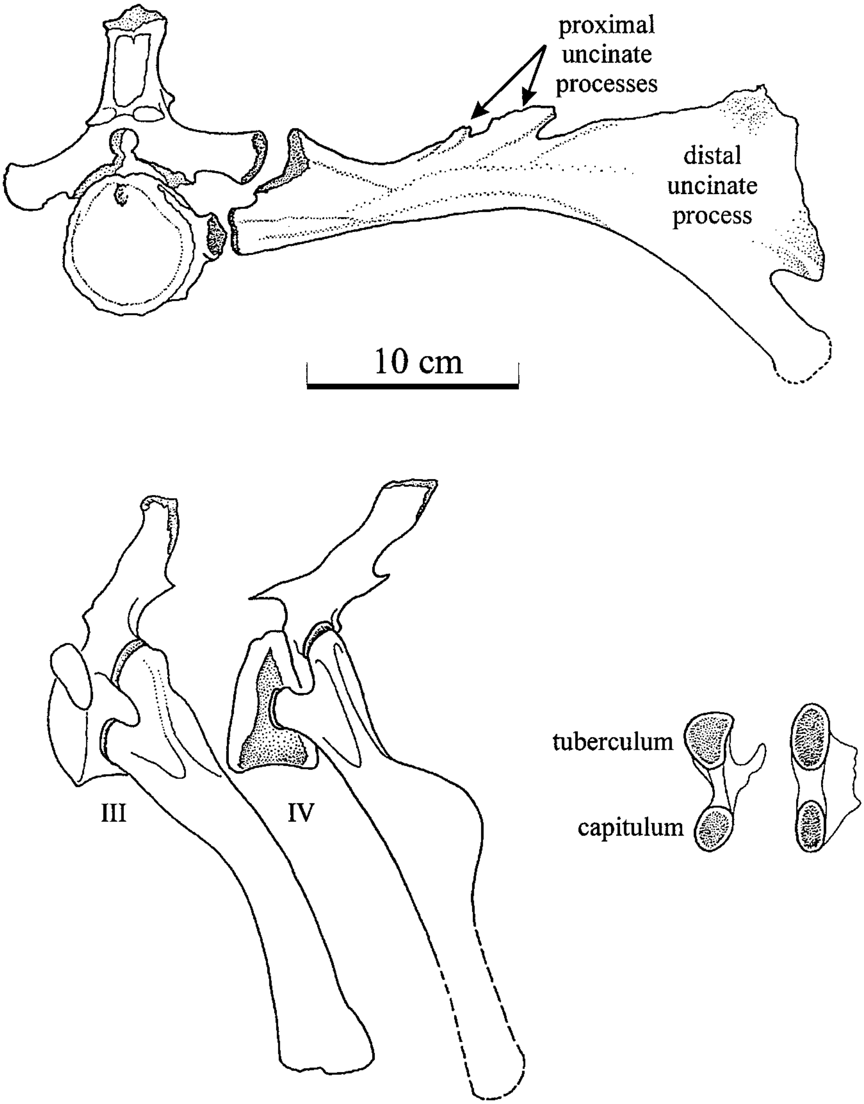


Fig. 34. The morphology and articulation of ribs in medium-sized specimens of *Mastodonsaurus giganteus*. Above, anterior trunk rib with associated intercentrum and neural arch. The rib is well bent in the distal part and bears two or more uncinate processes. One of these, the distal uncinate, may form an extensive blade. Below, third and fourth intercentra with probably matching ribs, types A and B as descibed in the text. Right, the two rib heads in rib types A (left) and B (right).

centre of the proximal portion, about at the level where the tubercular and capitular crests unite, is the most elevated part of the rib. The distal portion shallows continuously, but the stylus does not loose its blade-like appearance up to the end. In posterior view the rib is curved in sigmoid fashion and bears a proximally widened plate between the proximal uncinate process and the tuberculum, which has several prominent muscle scar fields.

Rib type C

This is the most complicated among the thoracal costae. It basically is of the same design as the aforementioned, especially in the morphology of the caput region, the overall curvature, and the course and point of convergence of the capitular and tubercular crests. It differs in being more stout proximally in having a larger UDP with stepped margin, and in the longer distal stylus. The bending point is generally not as pronounced as that of all subsequent rib types, and the head region is lacks the differentiation into an elongated tuberculum and a short capitulum, which corresponds with a distally elongated transverse process.

Rib type D

This is a characteristic rib type with a fairly general design that may be found among many large actinodontid-grade and capitosaur temnospondyls (FRAAS 1889; MOULTON 1974; KONZHUKOVA 1955; LEHMAN 1955). There are two very pronounced and well separated uncinate processes (fig. 35). The capitulum is longitudinally oval and slender, the tuberculum wider and larger, and the two are separated by a strongly asymmetrical incisura capitis, which tapers towards the tuberculum in side view, and actually forms a continuous articulation facet for the ventral rim of the transverse process. Thus, not only the tuberculum itself but also the incisura capitis forms the tubercular joint, and the corresponding transverse process bears a ventral facet additional to the diapophysis.

The rib is not curved in the transverse plane, but almost flat. Dorsally clear-cut tubercular and capitular crests are borne which have a more marginal position as compared to the aforementioned rib types. There is a third and more stout crest in between, which does, however, not reach the caput region proper. The main crests unite at about the level of the proximal uncinate process, which is smaller and better defined than in the other ribs. It is medially thickened and has a pointed end. Distal to their point of unification the crests form a higher and wider keel, which finally opens to give a rapidly sloping and flattened surface, which entirely merges into the distal uncinate process. The latter forms a prominent, but throughout thin blade with well rounded, convex posterior margin. The rib is longer than the previously described ones, and the stylus broadens in the distalmost part, where still an anterior columnar portion and a posterior blade-like portion can be distinguished in cross-section. The anterior rim of the rib is rather shallow proximally and distally, but bends into a more vertical plane in the middle, where it bears muscle scars.

Rib type E

The principal architecture is similar to that of rib type D (fig. 35). The differences are (1) the longer and slenderer proximal portion (especially proximal to the proximal uncinate process), which suggests a widening of the trunk region, and (2) a more clearly established differentiation of tuberculum and capitulum. The crests are shorter and shallower, and the distalmost portion of the stylus is slightly shorter. Consequently, the bending point is farther outside than in the aforementioned ribs, but the distal portion does not reach as deep as in more anterior rib types.

Rib type F

It differs from the forerunners in (1) the larger and further distally situated UDP, (2) the clearer differentiation of capitulum and tuberculum, suggesting a distally elongate transverse process, and (3) a stronger bending of the stylus in general (fig. 35). The tuberculum is trilobed, distally orientated in an oblique, proximally almost horizontal plane (where it articulates with the ventral part of the transverse process), whereas the capitulum is longitudinally oval. The degree of curvature in the horizontal plane is larger than in the aforementioned ribs, and it differs from that of the first trunk ribs by not being sigmoidal, but simply convex with the apex at about midlength. Both uncinate processes are larger, and the distal portion of the UDP parallels the course of the stylus. Eventually there may be a thin crest proximal to the UPP.

Rib type G

In this rib type the degree of bending has reached a maximum, and the position of the UDP is much further distal, nearing the distal end of the element (fig. 35). This rib is of the same length as the last mentioned, but lacks definite crests on the proximal end. Instead, there runs a well-defined groove which rises at the incisura capitis and disappears proximal to the UPP. The UDP is shallower than in F, and its posterodorsal margin is convex; there is no pointed distal end.

Rib type H

This rib bears only a tiny distal uncinate process, which rises from the otherwise completely rod-like shaft (fig. 36). The diameter of the shaft is similar for more than 2/3 of the element, but proximally changes continually to give a much elongated tubercular facet. The main differences to G are the lesser degree of curvature and the greater length of the tuberculum.

A medial crest runs from the dorsal edge of the capitulum distally, but terminates before the long axes of the two proximal heads meet. The proximal portion of the dorsal surface again is covered by numerous ridges and striations. On the contrary, the ventral side is smooth, but bears a central groove that originates from the separation of the two proximal heads and finally converges into a more distal crest that runs along the main axis of the shaft up to the distal end. The latter is tripartite and has a median, raised area. There are many intermediate morphologies conceivable between ribs G and H, although the similar length of the ribs and the comparable position of the centre of the distal uncinate process suggests that they were rather close to one another.

Rib type I

This element has a more slender and shorter shaft and a faintly developed uncinate shelf over more than half of its length (fig. 36). The tuberculum more clearly rises from the main axis, but the facet is slightly shorter than in the latter rib types. The dorsal surface of the proximal portion is largely smooth with only a few tiny and very faint ridges. Instead of an uncinate process there is a continuous shelf; this cannot be subdivided into a proximal and a distal portion such as in the more anterior ribs.

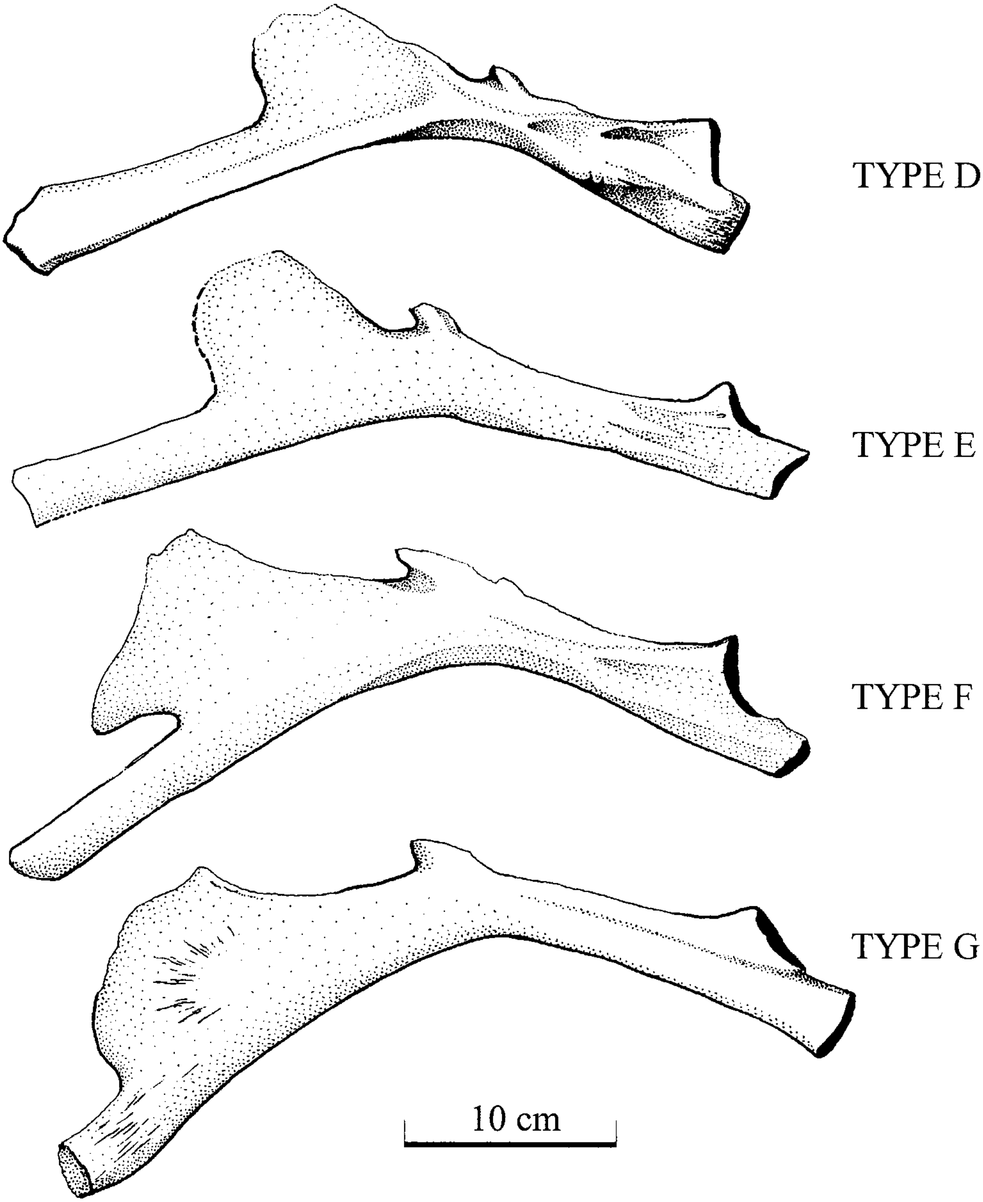


Fig. 35. The morphology of four anterior thoracal rib types in a medium-sized specimen of *Mastodonsaurus giganteus*. Remarkably, the distal uncinate process migrates distally with increasing distance to the atlas. Also, the distance between proximal and distal uncinates becomes larger. The dorsal rib head, or tuberculum, becomes shorter to accommodate a larger transverse process in the middle of the trunk.

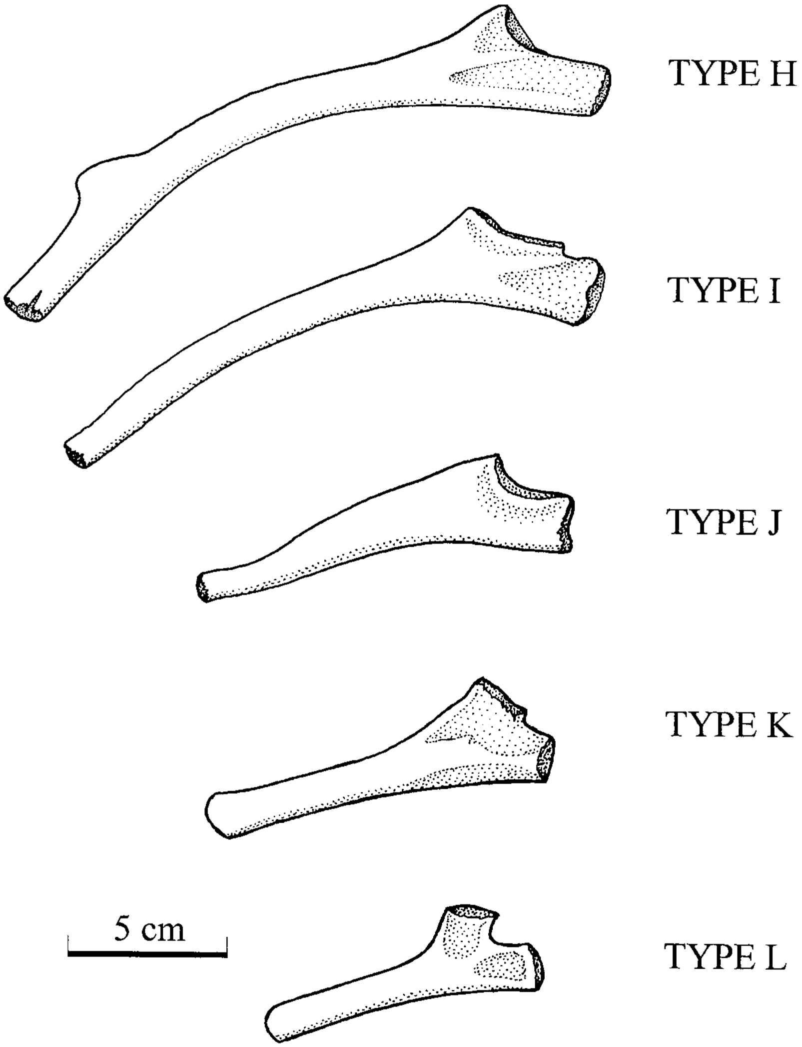


Fig. 36. The morphology of five posterior thoracal rib types in a medium-sized specimen of *Mastodonsaurus giganteus*. The uncinate processes have almost disappeared in this region, and the ribs become clearly shorter and more simple in morphology.

Rib type J

Much shorter and less curved than I, this rib type has a more pronounced uncinate shelf and a similar tuberculum (fig. 36). The distal end is thinner, and in contrast to the latter two rib types it has a simple oval cross-section. The stylus is more flattened than in all aforementioned ribs.

Rib type K

The following ribs – there are manifold variations to a simple general type – are short, straight and flattened rods with a relatively very large head. The tuberculum is proportionately smaller than in the former rib types, and there are almost no traces of an uncinate shelf. The distal end may be broadened, but always has a long-oval distal face.

Rib type L

These ribs are the shortest in the whole series, being even smaller than most caudal ribs (fig. 36). Their structure is utmost simple, with an almost symmetrical head (tuberculum and capitulum are of almost similar size and shape) and a stylus which is only faintly longer than the head region. The latter bears thin crests, but otherwise the rib surface is largely smooth.

Rib type M

The sacral rib of *Mastodonsaurus giganteus* is a fairly diagnostic element (fig. 37), and the SMNS possesses a good sample of well-preserved specimens of different sizes. These are throughout isolated finds, so that an assignment of this rib to a particular vertebra must rely on anatomical evidence and comparison to other taxa.

HUENE (1922: fig. 3) identified a questionable rib find as sacral rib on the basis of CASE's (1911) description of the sacrum in *Eryops megacephalus*. His specimen is, however, fragmentary and quite different from the generally similar capitosaur ribs; moreover there is little resemblance to the sacral rib of *Eryops*. According to all presently available evidence, HUENE's specimen is the proximal end of a posterior trunk rib.

Sacral ribs of temnospondyls were described in the dissorophid *Cacops* (WILLISTON 1910), the eryopid *Eryops* (CASE 1911; OLSON 1936), and the capitosauroids *Uranocentrodon* (VAN HOEPEN 1915: pl. 9fig. 2), *Metoposaurus ouazzoui* (DUTUIT 1976: fig. 47), *Benthosuchus* (BYSTROW & EFREMOV 1940), *Parotosuchus pronus* (HOWIE 1970), and *Eryosuchus garjainovi* (OCHEV 1972). From the aforementioned genera, the sacral rib of *Parotosuchus pronus* bears the greatest resmblance to rib type M. The morphology of this element is so unique that a confusion with other ribs from the same locality can be ruled out. There is, however, much variation in the morphology of this element.

The element is relatively short and stout, and proximal and distal portions are roughly symmetrical. The rib is clearly two-headed, with a narrow capitulum and a rather broad tuberculum. The distal end is posteriorly longer, its ventrally directed margin tapering continuously upwards. The lateral side has a more distinct relief than the medial one; it has a sculptured elevation about at midlength of the element, where the shaft reaches its narrowest width. The capitulum bears a prominent central ridge that converges towards the sculptured region. The region distal to the tuberculum is depressed and covered by numerous pores. In general, the surface of the sacral rib contains numerous tiny (? nutritive) foramina which are sometimes found at the end of a groove. From the sculptured and elevated region there runs a diagonal, flattened ridge towards the anteroventral margin of the distal end. Adjoining to this ridge there runs a narrow zone of intensely roughened bone which resembles muscular attachments such as found on the ilium or humerus. It is most obvious that this formed the attachment site for the ilio-sacral ligament (OLSON 1936).

Caudal ribs

The presence of caudal ribs in *Mastodonsaurus* is indicated by well-defined parapophyses in the anterior caudal intercentra (figs. 30, 31). The diversity among these intercentra and the variable position of their parapophyses suggests a larger number of caudal ribs. There are rib-bearing intercentra with and without haemal arches.

Few tail skeletons of other capitosauroids are known, notably the rhinesuchid *Uranocentrodon senekalensis* (van Hoepen 1915: 138), the metoposaurid *Metoposaurus ouazzoui* (Dutuit 1976: 119), and the capitosaurid *Paracyclotosaurus davidi* (Watson 1958: 247). The number of caudal ribs in these species is 9 (8?) in *Uranocentrodon*, 8 in *Paracyclotosaurus*, and unknown in *Metoposaurus*. In all these the caudal ribs are rather similar and uniform, being short and well-bent rods with a single head. The case is different in *Mastodonsaurus*, where the diversity of caudal ribs is much greater, and the morphology unexpectedly more complicated. Their general design can be derived from that of the sacral rib. In particular, the tuberculum and capitulum are similar in shape and size, so that the proximal portion of the rib is symmetrical. By this they differ from most thoracal rib types, except for the anteriormost ("cervical") and the last presacral ribs. They differ from the latter types by being longer and by the existence of uncinate processes of a special design. The structure of these processes is similar to the distal end of the sacral rib, where only the uncinate process is thicker and takes part in the formation of the distal end. The sequence of caudal ribs as treated here follows the reasoning explained in section 4. Only the most distinct types are described here, but there may be manifold intermediate morphologies, suggesting either individual variation or an even greater length of the rib-bearing tail portion.

Anterior caudal rib types (N–Q)

The first caudal ribs are generally similar to the sacral rib (fig. 37). The main difference is that the uncinate process is much slenderer in these. Throughout these ribs, the uncinate process is an elongate, cultriform outgrowth of the posterodorsal margin, sometimes embedded in a continuous and shallow crest or shelf. The main difference to the anterior thoracal ribs is that this uncinate process is nearly perpendicular to the main axis of the stylus, and has a stilette-like appearance. The ribs are only slightly curved, with the apex at about the level of the uncinate process. The length is similar to that of the sacral rib. Their distal portions are narrow and straight, with a flattened cross-sectional area.

The dorsal surface of the proximal portion is covered by three high and well-defined ridges. The medial one is the most prominent, it runs obliquely and converges into the posterior, thickened rim of the uncinate process. The two outer ridges run along the main axes of the capitulum and tuberculum, respectivey.

The uncinate process may be embedded into a broad shelf. Distal to this, like in the trunk ribs, a second uncinate process is present in some ribs, such as in rib type N. I shall apply the same terminology as for the thoracal ribs, without implying a true serial homology. On the ventral side the proximal uncinate process has a depressed posterior area and a thickened anterior rim. Capitulum and tuberculum are essentially similar to those of the sacral rib. From the perspective of caudal ribs, the sacral rib appears as a distally slightly enlarged type with a swollen anterior uncinate process, or rather shelf, which is confluent with the distal end of the stylus proper.

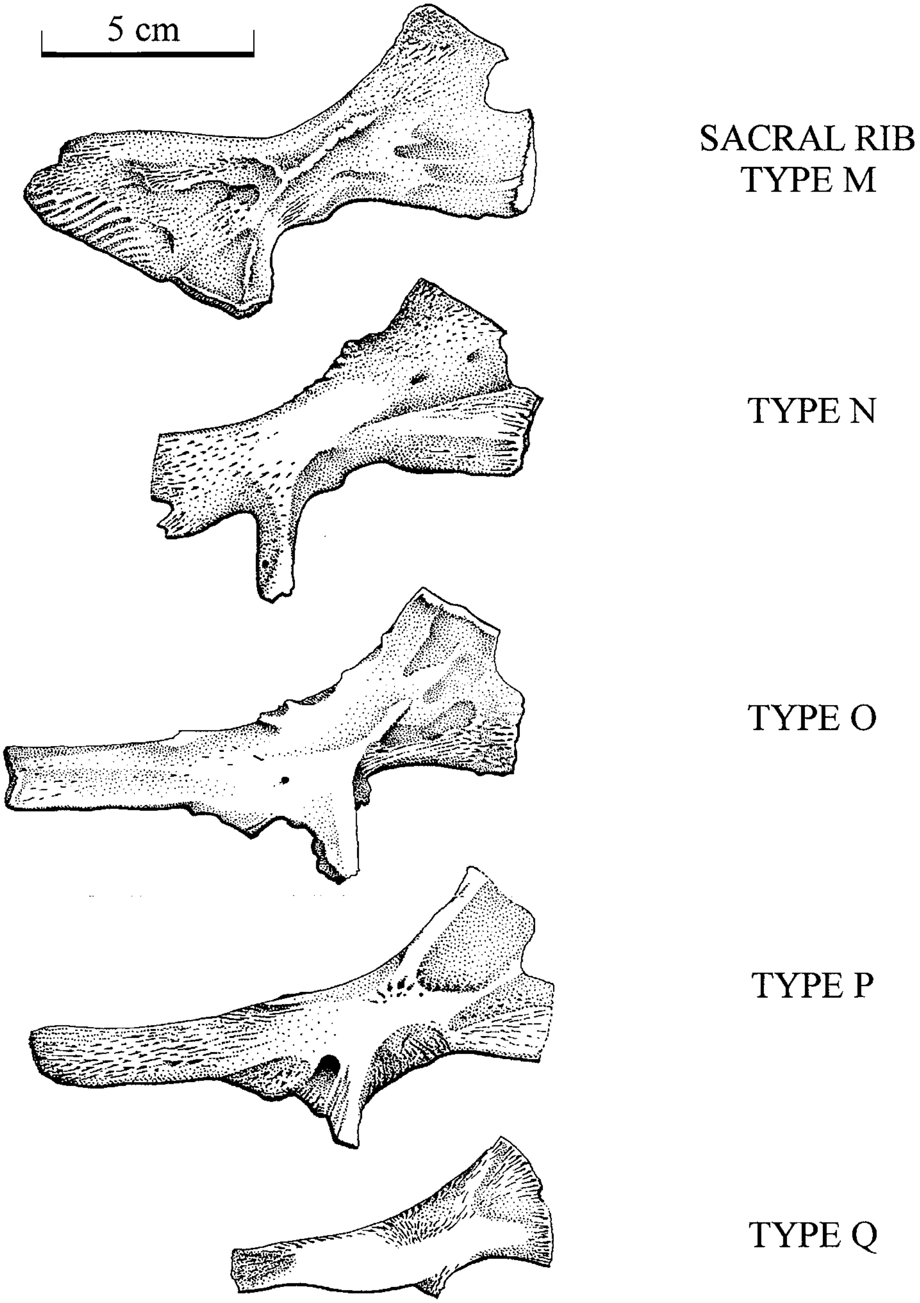


Fig. 37. Ribs of the sacral and anterior caudal regions in *Mastodonsaurus giganteus*. The morphology of the sacral rib is basically similar to that of the first caudal ribs (types N and O), especially in having almost symmetrical rib heads, the presence of a proximal uncinate process and the degree of bending.

The main body of the proximal portion may bear, posterior to the base of the proximal uncinate process, a large foramen, which is set into a groove that runs parallel to the process. This morphology is characteristic of more posterior caudal ribs, which are further characterized by a smaller head and a shorter and posteriorly thinner anterior uncinate process, as well as the lack of a true UDP. The Kupferzell material consists of numerous such ribs which display a broad spectrum of variation.

Posterior caudal rib types (R-T)

These ribs are tiny and usually rudimentary in structure, although their design is very similar to that of the anterior caudal ribs (fig. 37). This encompasses (1) the general outline, (2) the existence of a proximal uncinate process, and (3) the presence of a foramen on the main body of the stylus. The only questionable, usually poorly preserved region is the head, so the separation into two facets, such as in all other rib types, cannot be proved.

3.2.4. Appendicular skeleton preservation

The appendicular skeleton is throughout excellently preserved in the Kupferzell material. Most of the long bones are massive and well ossified, so that they remained relatively little affected by compaction. Crushing is sometimes observed in the hollow dorsal end of the ilium, and the distal end of the humerus. Even these bones are much more solid than the frequently crushed and distorted intercentra. Fractures are more common than distortion and large-scale deformation. Most of them are, however, of minor size, running obliquely across the broadened ends of the long bones in particular.

Interclavicle

This element evoked as much interest as the huge and heavy skull in the history of capitosaur studies. Like the skull this element has a good chance of preservation, and many labyrinthodont finds made in the last century were fragments of interclavicles. Because of its most characteristic sculpturing, this was the most readily identified bone among capitosaurs (fig. 38). Meyer & Plieninger (1844), Quenstedt (1850), and Fraas (1889) all payed particular attention to this bone, and there was a debate about how to orientate the bone in the living animal (Quenstedt 1850) which was clarified by studies on articulated archegosaurid material from the Lower Permian (Meyer 1858; see also Fraas 1889).

The presence of an interclavicle is a ground-plan feature of the Tetrapoda (Hennig 1983; Jarvik 1996) and in temnospondyls in particular the element attained a considerable size. Plesiomorphic temnospondyl interclavicles share *Trimerorhachis* (Case 1935), *Balanerpeton* (Milner & Sequeira 1993), and *Cochleosaurus* (Steen 1938), and it is of nearly perfect rhomboidal shape. It can be derived from interclavicles such as that of the primitive anthracosaur *Crassigyrinus* (Panchen 1985) or the colosteids, such as *Pholidogaster* (Panchen 1975). In eryopoids and dissorophoids (Milner 1990a; Boy 1990; Schoch 1997b) a particularly large interclavicle is also a ground-plan feature. Especially in the large capitosauroids the interclavicle forms a long and very massive rhomboid (van Hoepen 1915; Bystrow & Efremov 1940; Watson 1951, 1958).

The Capitosauridae then possess most massive and extended interclavicles, and in *Mastodonsaurus* this reaches a peak. The size of the interclavicle is much greater than in actinodontids such as *Sclerocephalus* (MECKERT 1993), both in relation to the skull and the presacral column, and particularly the anterior process which excels the anterior margin of the clavicles, is greatly extended. In the living animal this process reached far anterior below the hyobranchial apparatus. A slightly extended anterior rim of the interclavicle is found in the plesiomorphic, rhomboidal interclavicle of actinodontids, which in turn is basically similar to that of eryopids and dissorophids, although never a comparably long, stilette-shaped outgrowth is present. Shared is this feature with most known capitosaurs (an exception being *Paracyclotosaurus*, see WATSON 1958), as discussed by WELLES & COSGRIFF (1965), OCHEV (1972), and others. The clavicles overlap the interclavicle especially in the posterior part of the lateral wings, whereas they abut against the lateral rim of the anterior portion of the latter. The clavicles fail to meet in the midline, separated by the narrow and much sculptured anterior process of the interclavicle.

The ornament is very clear and strongly developed throughout the ventral face of the element. It encompasses short and radially symmetric polygons in the centre (which lies in between the posterior third and midlevel of the bone). These polygons very rapidly elongate, especially anteriorly and posteriorly. In anterolateral direction the ridges may be curved but are otherwise straight, high, and sharp-cut. The depressions framed by them bear numerous openings, of which the ones close to the centre are the largest, leading into a channel which runs towards the centre of the bone. The connection between sculpturing and design of suture surfaces is most apparent on the interclavicle. The roughened ridges that guarantee tight fitting of the clavicles on the lateral wings of the interclavicle are merely the continuation of the polygonal ridges of the sculpturing. The dorsal surface of the interclavicle is largely smooth. The lateral wings are strengthened by a posteriorly convexly curved, broad ridge which unites in the middle with a single median posterior ridge, together forming a T. The lateral ends of this are much broadened and thicker than the other parts.

Clavicle

The clavicles are sagittally elongated, generally slender and very strongly ossified plates. Their medial and anteromedial shields overly the lateral wings of the interclavicle to a large degree, and posteromedially directly connect to the interclavicular sculpturing with their own ornamentation (fig. 39). More anteriorly the sculpturing is, however, aligned at a steep angle towards that of the median element. The strongest portion is the base of the ascending process, where the sculpturing ceases and the element is almost completely smooth. A marked furrow, bordered by a high crest, forms the attachment site for the cleithrum. There the ascending process thins and forms a stilette-like spike which partially underlies the base of the cleithrum, paralleling the main axis of the latter. The ascending process was orientated at a more shallow angle towards the sagittal axis than in *Eryops*, *Proterogyrinus*, or *Archeria*. The ventral side of the clavicle is entirely smooth.

Scapulocoracoid

The scapulocoracoid ossification of *Mastodonsaurus* was first described by FRAAS (1889), but for obscure reasons erroneously identified as ischium by him. PLIENIN-

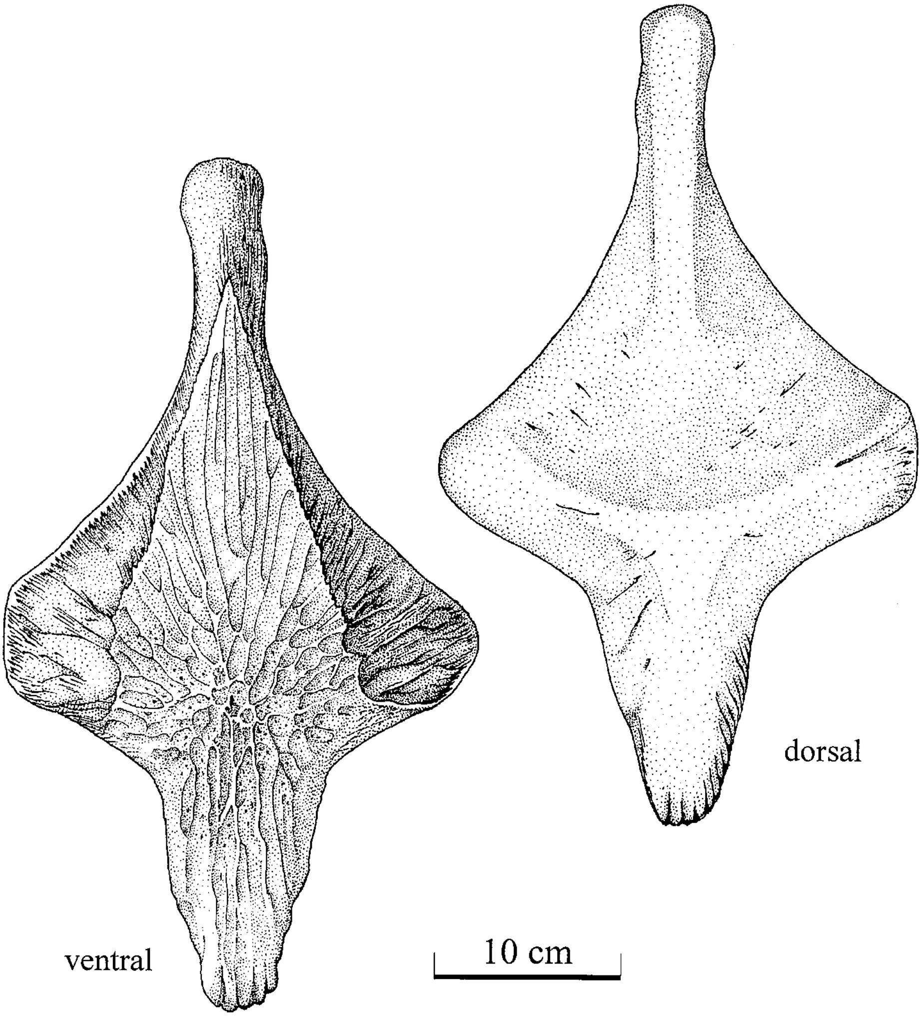


Fig. 38. The interclavicle of *Mastodonsaurus giganteus* from two perspectives. The element is very large and well-ossified, so that it constitutes one of the most frequently found fossil items in the Lettenkeuper. The sculpturing and the anteriorly extended and widened process are typical features of *Mastodonsaurus*. The apex of the concave ridge on the dorsal side points posteriorly, and helps in orienting fragmentary specimens.

GER in MEYER & PLIENINGER (1844) wrongly identified the clavicula as scapula proper. The first authors to mention and describe the scapula among labyrinthodonts were BURMEISTER (1849) in *Trematosaurus*, MEYER (1858) in *Archegosaurus*, and finally ZITTEL (1890). HUENE (1922) recognised FRAAS' mistake and correctly identified the scapula and ischium in *Mastodonsaurus giganteus* by referring to the same material as all previous authors.

In early tetrapods the scapula and coracoid are frequently co-ossified and consequently generally referred to as scapulocoracoid in their entirety (ROMER 1947, 1957; MECKERT 1993). This is of course only correct as long as both components

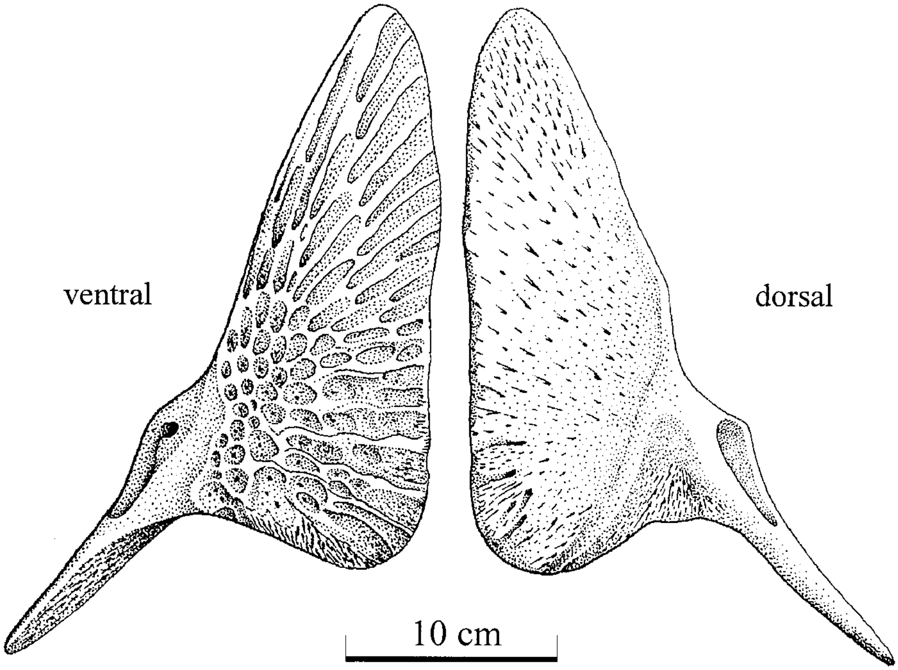


Fig. 39. The clavicle of *Mastodonsaurus giganteus* from two perspectives. The ascending process pointed posterodorsally, but is usually rotated into the same plane as the blade.

(scapula and coroacoid) actually participate in this compound bone. In the fairly large capitosaur *Benthosuchus sushkini* for instance only the scapular blade is known to ossify (BYSTROW & EFREMOV 1940), such as in small paedomorphic Branchiosauridae (BOY 1974; SCHOCH 1992), among numerous other examples. In the eryopid *Onchiodon labyrinthus* onset of coracoid mineralisation is late, but a complete fusion to the scapula is soon established (BOY 1990).

Mastodonsaurus giganteus has a well-ossified scapula which is only in later developmental stages fused to the coracoid (fig. 40). No small, isolated coracoids are known, but a variety of different stages of scapulae exist. The morphology of the scapula is very similar throughout temnospondyls and basal tetrapods in general. It is, unlike most other girdle elements, obviously little dependent on the mode of locomotion in the particular species. In smaller specimens the scapula is especially slender, but already strongly ossified with well-defined bone margins. In lateral view it is a posterodorsally elongate plate with convex anterior and concave posterior margins. The dorsal end is rounded and has a thin, flattened edge, whereas the ventral end is larger, flattened, and medially broadened to give a large facet for the coroacoid portion. The scapula thus basically has an asymmetrically lunate shape with a greatly extended dorsal portion. It is similar to the large scapula of *Eryops megacephalus* (pers. exam.) in which a comparably high degree of ossification is reached. Only in *Eryops* the dorsal portion is still more elongated and reaching far upwards. In most other capitosaurs the scapula is a rather weak ossification (BYSTROW & EFREMOV 1940; WATSON 1958). Exceptions are *Platyoposaurus stuckenbergi* (KON-

ZHUKOVA 1955) and *Eryosuchus garjainovi* (OCHEV 1972) in which the scapula has proportions nearly identical to that of *Mastodonsaurus*.

MECKERT (1993) analysed the anatomy and development of the scapulocoracoid in *Sclerocephalus haeuseri* in detail. According to his findings, there is only a single ossification centre (namely that of the scapular blade) which later on successively expands over the area of the coracoid. *Mastodonsaurus* instead has a clearly established surface of unfinished bone at the interface between the scapular and the coracoid ossification. In larger specimens there is no such gap, but instead a complete ossification without any trace of synostosis or a secondary co-ossification of a sutural plane. The specimen that FRAAS (1889: fig 6) used to reconstruct what he concieved the ischium is a well-established scapulocoracoid of that kind. Thus a difference in the development and number of ossification centres appears to exist among temnospondyls which urges a cautious treatment of this matter.

The scapula has a large foramen supraglenoidalis which is framed by a pronounced anteroventral rim. The foramen is situated posterodorsal to the upper edge of the glenoid facet. A second major opening, the foramen supracoracoidalis, is found anterior to the area glenoidalis, perforating the scapulocoracoid suture. Most of the surface of the scapula and coracoid is smooth or covered by minor striations. Exceptions are well-defined muscle attachments in the following regions: (1) ventral to the supracoracoidal foramen and posterior to the glenoid facet, (2) in the anteriormost portion near to the anterior edge and on the lateral side, (3) dorsally in the anterior portion of the scapula, posterior to the bifurcation point of lateral and medial branches, and (4) at the inner edge of the medial branch (processus medialis). The markedly elongated glenoid area is obliquely orientated and distinctly curved, with the convex side facing posterodorsally. Dorsally it is widest where it separates the foramina. Among these, the supraglenoid foramen opens posterodorsally and the supracoracoid foramen ventrally. The supraglenoid foramen gives rise to a large groove (fossa supraglenoidalis) which roughly parallels the posterior and posteroventral margin of the scapular blade.

The medial side of the scapula bears an elongate and broad ridge which widens both dorsally and ventrally where it rises from the otherwise planar and smooth element. It parallels the fossa supraglenoidalis but starts at a more ventral position than the latter. The medial opening of the supraglenoid foramen is anterodorsal to, that of the supracoracoid foramen posteroventral to that ridge (torus medialis). This torus is found for instance in *Eryosuchus garjainovi* (pers. exam.), and *Archeria crassidisca* (ROMER 1957), but lacks in many other basal tetrapods.

Anteriorly the scapula is only faintly thickened, by which it differs from that of *Eryops* (pers. examination). The margins there are not completely ossified, as is indicated by the roughened flat ridge by which it terminates. This margin is curved in sigmoid fashion if viewed dorsally.

The coracoid portion is much smaller than the scapular blade, reaching only half of the area of the latter (fig. 40, above). It has two oval attachment surfaces for the junction with the scapula. These are separated by the large foramen supracoracoidale. The medial side of the element bears two stout columns, one of them giving rise to the glenoid area and the other continuing dorsally on the scapular blade as the columna supraglenoidalis. These columns are separated by a narrow but deep furrow on the inner side, which is a ventral continuation of the foramen supracoracoidale. Laterally the coracoid is planar and has a smooth surface.

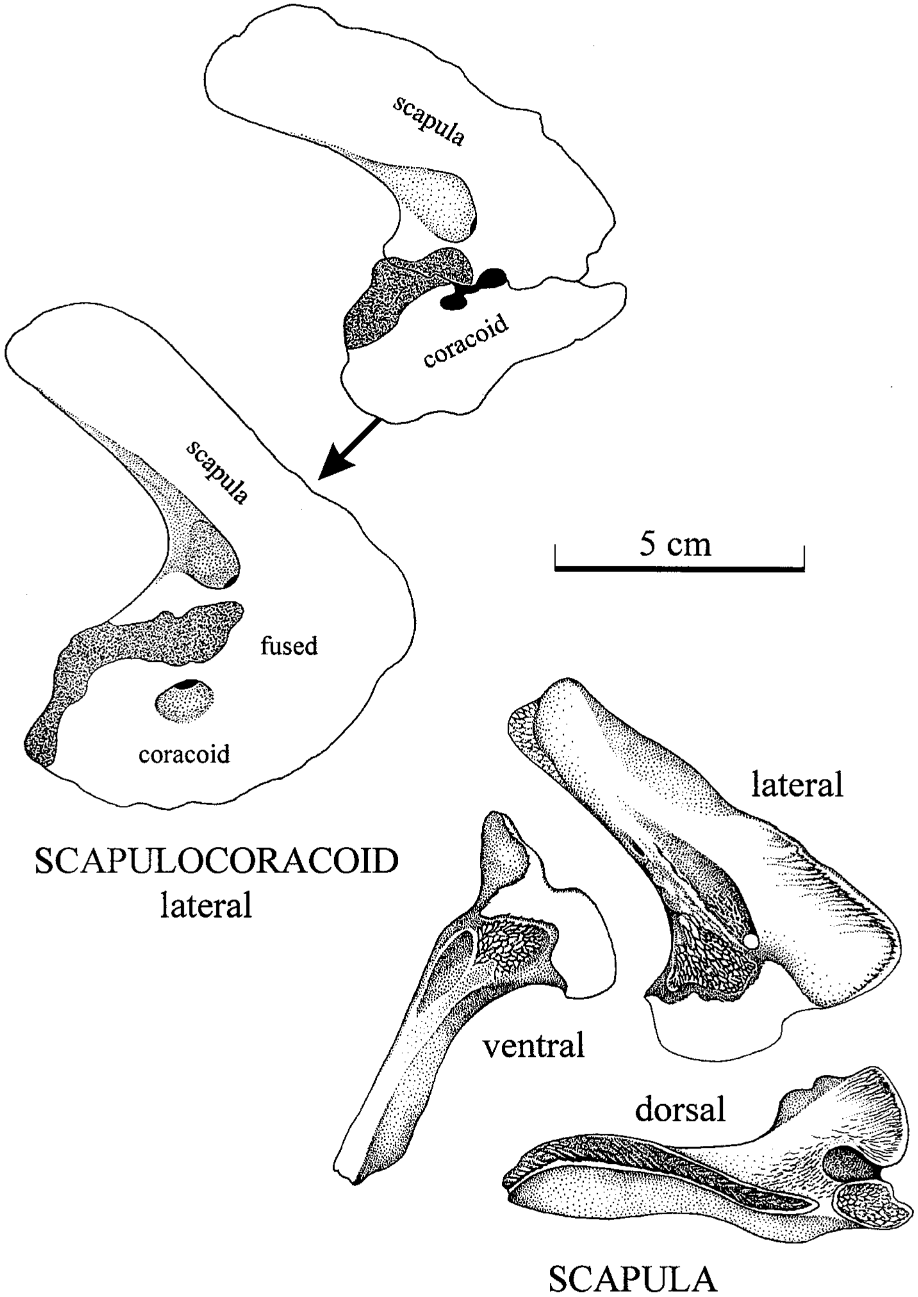


Fig. 40. The scapulocoracoid of *Mastodonsaurus giganteus* from different perspectives and in different ontogenetic stages. Below, the scapula of a relatively small specimen, above right, the scapula and coracoid in a somewhat larger specimen still separated by a suture, and left, a co-ossified scapulocoracoid of a large specimen.

Cleithrum

The cleithrum has a stout and well-ossified shaft and a most dorsally situated head (fig. 41). The external and internal surfaces of the element are flattened to slightly concave, and the internal face bears a curved ridge and is much more rugose. The articulation with the scapula and the clavicula is upheld by an abutting of that ridge against the anterior margins of these elements and by the underlapping of the posterior part of the bone, marked by a well-developed depression in this region. Towards the dorsal end the element broadens on both sides to give a short head, where the element underlaps the scapula to a larger extent than ventrally. The suture surface is roughened and sculptured by numerous parallel ridges and bosses. The outer (lateral) surface is striped along the main axis and bears radially arranged rugosities in the head region which face posteroventrally.

Humerus

The humerus of *Mastodonsaurus giganteus* was described by PLIENINGER in MEYER & PLIENINGER (1844), FRAAS (1889), and HUENE (1922), who all referred to the same, very large specimen (SMNS 4707). However, practically all other humeri available for *Mastodonsaurus* differ in being much smaller and less differentiate; I shall therefore distinguish arbitrarily two growth stages here, and describe them separately in detail.

The general structure of the humerus is similar in most basal tetrapods (MINER 1925; ROMER 1957; HOLMES 1980; JARVIK 1980; MECKERT 1993). It is short, markedly widened at both ends and forms a tetrahedron. The Choanata (PANCHEN & SMITHSON 1987) are characterized by two prominent outer processes at the distal end of the humerus, the ect- and entepicondyle. The humeri of tetrapods are characterized by convex heads, and the glenoid facet is consequently (at least weakly) concave. In temnospondyls the humerus differs from that of most anthracosaurs (ROMER 1957; HOLMES 1980; PANCHEN 1972, 1985), *Ichthyostega* (JARVIK 1996), and microsaurs (CARROLL & GASKILL 1978) in that it is more clearly torded, longer and more clearly differentiated. Yet *Mastodonsaurus* departs from this scheme quite considerably, particularly in untypically low extent of humeral torsion and the length and slenderness of the element.

The humerus of *Mastodonsaurus* has a long and slender shaft, a rather narrow head, and a pronounced ectepicondyle (figs. 42, 43). A supinator process is present in larger specimens and grows to a prominent boss in the largest known animals. The entepicondyle is initially thin and rudimentary, but thickens considerably during late ontogeny, reaching almost the size of the ectepicondyle. The head is at first narrow and the joint simple and dorsally convex, but in large specimens the posterior portion grows ventrally, corresponding to the late-ontogenetic ventral extension and ‘curling’ of the glenoid facet. The initially throughout narrow head thus becomes thickened posteriorly and very massive. On the dorsal side a rather well-defined radial column is present from small stages on. The supinator process ultimately rises from it at about midlength of the bone, and through development rotates at an angle of 50° to finally stand perpendicular to the shaft. The ventral surface is mostly flat, and towards the ends slightly concave even. At the posterior rim of the entepicondyle rises a ridge which runs proximally and thereby rotates into the horizontal plane, entering the ventral side of the element. The anterior face is proximally up to

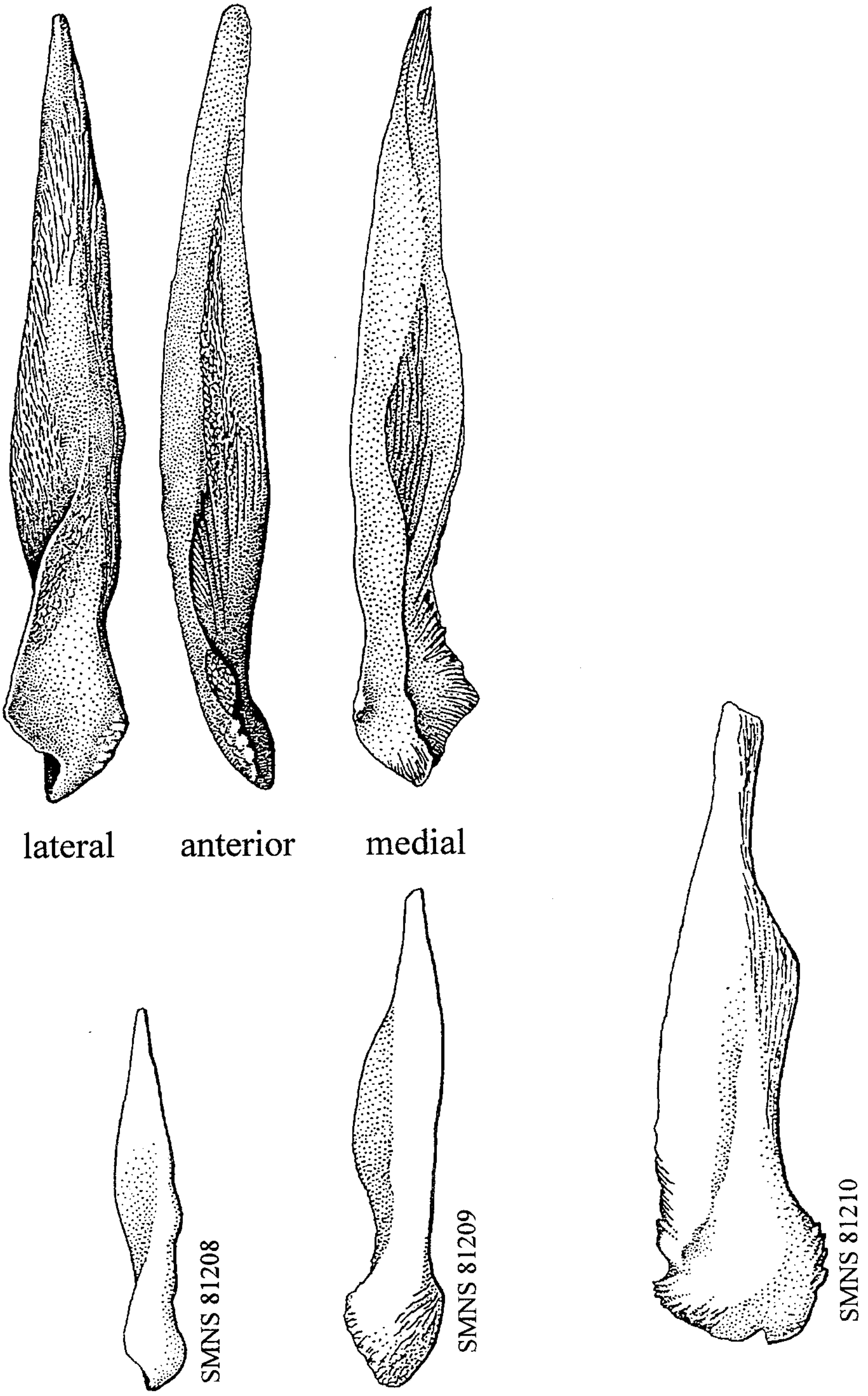


Fig. 41. The cleithrum of *Mastodonsaurus giganteus* from different perspectives (above) and in different growth stages (below).

midlength much thickened and rough, bearing a very prominent attachment site for musculature that later in development forms a marked boss.

The ectepicondyle has a distinctly concave, transversely triangular to oval facet, which is orientated almost exclusively laterally, with a very minor anterior component. Instead the entepicondyle is much compressed and faces laterally and posteriorly. In the largest specimens the ectepicondyle shifts slightly into a little more anterolateral direction.

Small Specimens

The humerus at this stage is more slender and elongate than in any other large capitosaur hitherto described. The head is curved, with the convex side facing anterodorsally (fig. 42). It is nearly equally wide along most of its longitudinal extension. The margins are raised, ventrally to a larger degree than dorsally, giving the head a slightly concave surface. This is roughened, indicating a cartilaginous cover. Anteriorly the head ends in a single, very weakly defined process. The posterior process instead bifurcates into a faint dorsal (PPD) and a strong ventral portion (PPV). Both give rise to smooth crests which run at the posterior margin distally along the shaft. The lower of these crests (torus ventralis of Ochev 1972) faces posteriorly and disappears at about midlength of the bone. In contrast the upper crest (torus dorsalis of Ochev 1972) faces posterodorsally and widens towards the distal end. It is confluent with the posterior margin of the columna radialis. At the distal end the ectepicondyle is the broadest portion, but as compared with most other temnospondyls it is only weakly developed. It is separated by a well-defined incision from the supinator region, whereas posteriorly it narrows rather gradually towards the entepicondyle. The most pronounced muscle scars are found at the anterior edge, on the ventral side anteriorly, and in the front region of the dorsal side; most of the other parts are smooth.

Large Specimens

The humerus of large specimens of *Mastodonsaurus* is generally stouter and more differentiated than in earlier developmental stages (fig. 43). Distally being much wider, it has a more clearly established entepicondyle and supinator region (Plieninger in Meyer & Plieninger 1844; Huene 1922). The latter has grown to a definite process, resembling that of *Sclerocephalus* (Meckert 1993). In addition, the caput humeri in large *Mastodonsaurus* has a very well-established, additional process (PM). It is much more pronounced than the anterior and posterior processes and situated ventrally, somewhat closer to the posterior processes. The proximal shape of the caput is V-shaped with the bifurcating broad end formed by the three posteriorly oriented condyles (Huene 1922: fig.7). The ventral and dorsal crest (CPD and CPV) are more clearly established than in smaller individuals. The distal end is posteriorly slightly broader, and especially the entepicondyle is expanded proximally. Consequently the whole bone appears to be wider than in smaller specimens.

Antebrachium

The lower arm of *Mastodonsaurus* is documented by several growth stages. It was described and figured in part by Fraas (1889) and Huene (1922). There are only isolated elements available in the rich Kupferzell material, and solely one specimen

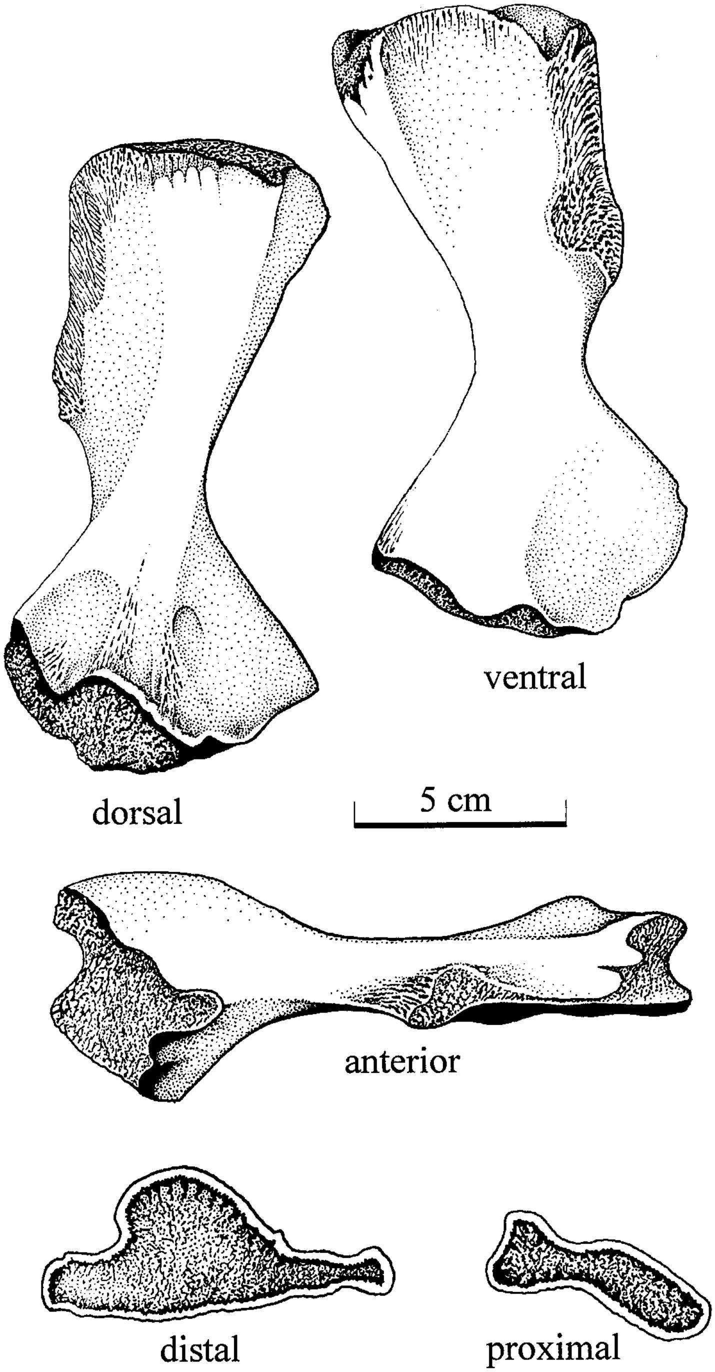


Fig. 42. The humerus in a medium-sized specimen of *Mastodonsaurus giganteus* from different perspectives. The bone is rudimentary in morphology, having no supinator process and only faintly developed epicondyles. The prominent muscle scars on the ventral and anterior sides may be interpreted as associated with the pectoralis and deltoideus musculature.

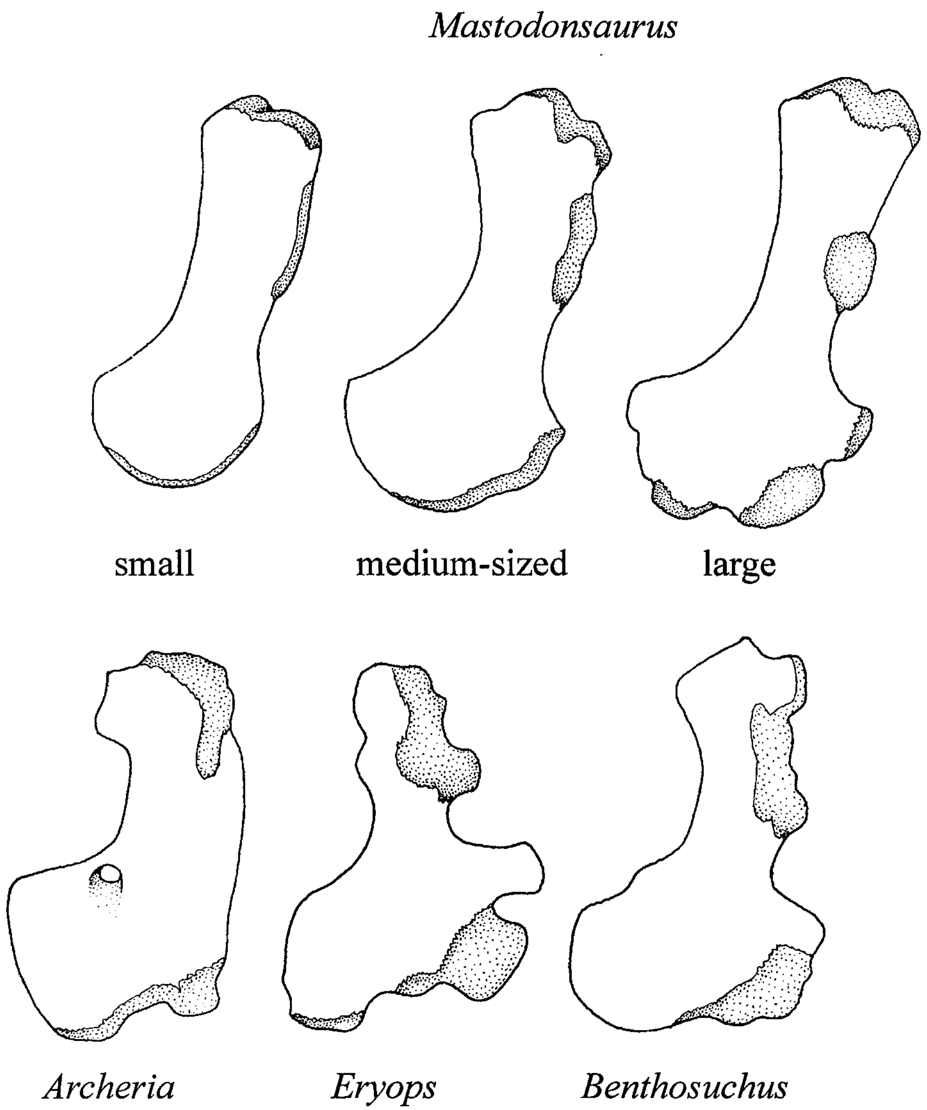


Fig. 43. Humeri in selected temnospondyls (below) and different growth stages of *Mastodonsaurus* (above), all in ventral view. The humerus of *Mastodonsaurus* is peculiar in its relatively great length and the immature state of development, even in the largest stage, which was associated with a skull of 74 cm length. *Archeria* after Romer (1957), *Eryops* after Miner (1941), and *Benthosuchus* after Bystrow & Efremov (1940). *Mastodonsaurus*: small and medium-sized humeri from Kupferzell specimens, large specimen from Gaildorf (Meyer in Meyer & Plieninger 1844: tab. 1).

from Gaildorf, an ulna with carpal elements, metacarpals and phalanges, is articulated.

The following description exclusively treats the preserved elements without inferring data from other taxa. In general, both elements are well-differentiated and thereby more easily identified than those of most other actinodontids and capitosaurs. The extent of ossification is high, and because of the strength of the bones most specimens are threedimensionally preserved. The relative size of the lower arm can be estimated by the large humerus specimen, which is associated with a radius. Following all available data, the lower arm was short, reaching slightly more than half the length of the humerus. Closest resemblance in the structure and proportions of the antebrachium is found with two capitosaurs, namely *Eryosuchus garjainovi* (OCHEV 1972) and *Parotosuchus pronus* (HOWIE 1970).

The radius is about the same length as the ulna, by which it differs substantially from that of *Eryops* (MINER 1925) and rather is similar to that of *Sclerocephalus* and *Archegosaurus*. However, it is relatively longer and more differentiate than in many other temnospondyls (figs. 44, 45).

It is a strong yet slender element, with distinctly different proximal and distal ends and much different dorsal-anterior and ventral-posterior surfaces. Among capitosaurs it resembles that of *Eryosuchus garjainovi* closest, which was described in great detail by OCHEV (1972: 147). Some aspects are, however, more similar to the radii of *Parotosuchus pronus* (HOWIE 1970) and *Wetlugasaurus kzilsaensis* (OCHEV 1972), such as the slightly more massive appearance and the straight and markedly convex margin of the distal end.

The posterior-ventral surface of the radius is convex and bears a medial ridge (‘a.l.’ of OCHEV) that is strongest developed towards the ends of the bone. The dorsal surface is striated, and more so medially than laterally. On the anterodorsal surface, which is clearly concave much like in *Eryosuchus*, with the depression asymmetrically opening towards the lateral margin. The medial margin is concave, with the apex lying in the distal third of the bone, whereas the lateral margin is irregular, with two successive bosses on the distal side. The more distal of these is larger and bears a well-defined rugosity. Distally the end of the radius is laterally compressed and oval in outline and has a much flattened surface. The proximal end is more rounded and the bone is of unfinished appearance, especially on the ventral side. The posterior-ventral face of the proximal end is oval to triangular (cf. HOWIE 1970). In medial view, the element is sigmoidally curved and bears a crest which ends distally in the prominent tuberosity just mentioned.

In contrast to the rather symmetrical radius, the ulna is more distinctly curved and torded. Its flat surfaces were not oriented anterodorsally and -ventrally in the living animal, but roughly anterolaterally and posteromedially. The description here follows a simplified orientation, in which the long axis of the element is regarded as strictly vertical, although this was probably held obliquely in the living animal.

The following features are characteristic of this bone in *Mastodonsaurus*: (1) the olecranon process is prominent, making up roughly one third of the total length, (2) the posterolateral side is straight while the anteromedial margin is distinctly curved to give both proximal and distal extensions, the medial heads of the bone. The olecranon process is thickened at both ends, and its depressed posteromedial surface gives rise to an extensive bowl which covers almost one half of this flat side of the bone. Distally the depression aligns with a groove that finally separates the two unequally large distal heads. Among these the medial head is larger, curves medially, but does not reach that far distally as the lateral head. The latter has a flattened posterior flank. In posterior view, the ulna is distinctly curved proximomedially. The cross-section of the distal head is L-shaped, that of the proximal head is roughly

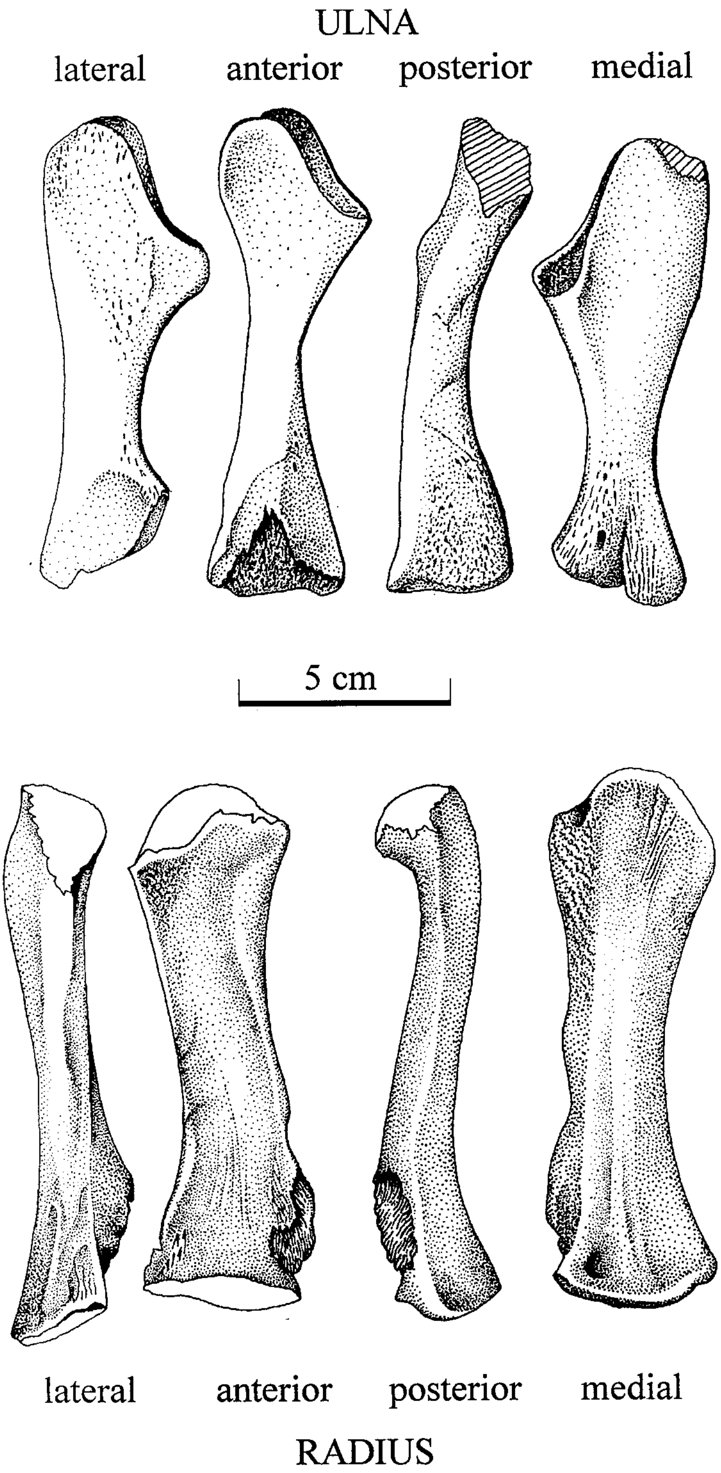


Fig. 44. The lower arm bones in a medium-sized specimen of *Mastodonsaurus giganteus*, from different perspectives each.

transversely oval. The surfaces of the ulna are, except for the strongly roughened articulation facets, throughout smooth with only minor striations.

Manus

The hand of *Mastodonsaurus giganteus* is only partially known. There are various isolated metacarpals and proximal phalanges from both Gaildorf and Kupferzell. Isolated carpals have hitherto not been found, and distal phalanges are very rare, which probably results from the small size of these elements. The extent of ossification in the carpus is consequently not sufficiently known. There is a single articulated, but fragmentary specimen from Gaildorf. It encompasses the distal end of the ulna, two proximal carpal elements from the lateral side, four metacarpals, and three proximal phalanges. The assignment to a particular specimen – and thus certain size relations – is possible. A phalangeal count, however, cannot be given.

The autopodium of *Mastodonsaurus* consists of well-ossified elements of moderate length and size (fig. 45). Apparently there are only four digits (SMNS 4706; see discussion in Huene 1922), which is the condition found almost throughout temnospondyls and microsaurs. The metacarpals are well 1 1/2 times longer than the adjoining proximal phalanges. There are conspicuous size differences between the metacarpals. Their proximal heads are throughout broader than the distal ends. The inner (I+II) metacarpals are thinner and shorter than the third which is slightly larger than the fourth. The first is definitely the smallest element. The carpal elements are relatively large plates and articulated. The inner one is broad-rectangular, with the distal margin slightly convexely curved, while the medially situated second bone is quadrangular and narrower than the first, about of the width of the third metacarpal.

The pectoral limb as a whole

The pectoral girdle and limb are particularly impressive by their size and architecture. The dermal ossifications, notably the interclavicle, reach a size unparalleled among other early tetrapods. The position of the pectoral girdle poses problems for the function of the lower jaw and shall be a matter of discussion in the reconstruction section. The clavicles fit neatly onto the lateral flanks of the huge interclavicle and overlap it quite considerably posteriorly. The suturing is very tight, as indicated by the specially designed surfaces of these overlapping bone regions. The main direction of the rugosities on the sutures appear to resist particularly stresses from anterior and lateral. The anterior extension of the interclavicle establishes a connection to the floor of the intermandibular region, which shows that the heavy skull and the pectoral girdle must have been highly coupled; this must have posed important constraints on both the feeding and locomotory systems. The very clearly developed dermal ornament of the clavicles and interclavicle demonstrates that these shields lay shallowly in the dermis, but rather contrary to many other temnospondyls the posterior portion of the interclavicle does not have a shelf for the attachment of osteoderms. In the steady absence of such dermal scutes, which is very striking because of their permanent appearance in most (and especially the larger) basal tetrapods, I am inclined to assume that they were absent altogether. Watson (1958) figured osteoderms in the pelvic region of *Paracyclotosaurus*, but these are loosely set and morphologically different from the spindular ventral osteoderms so characteristic of

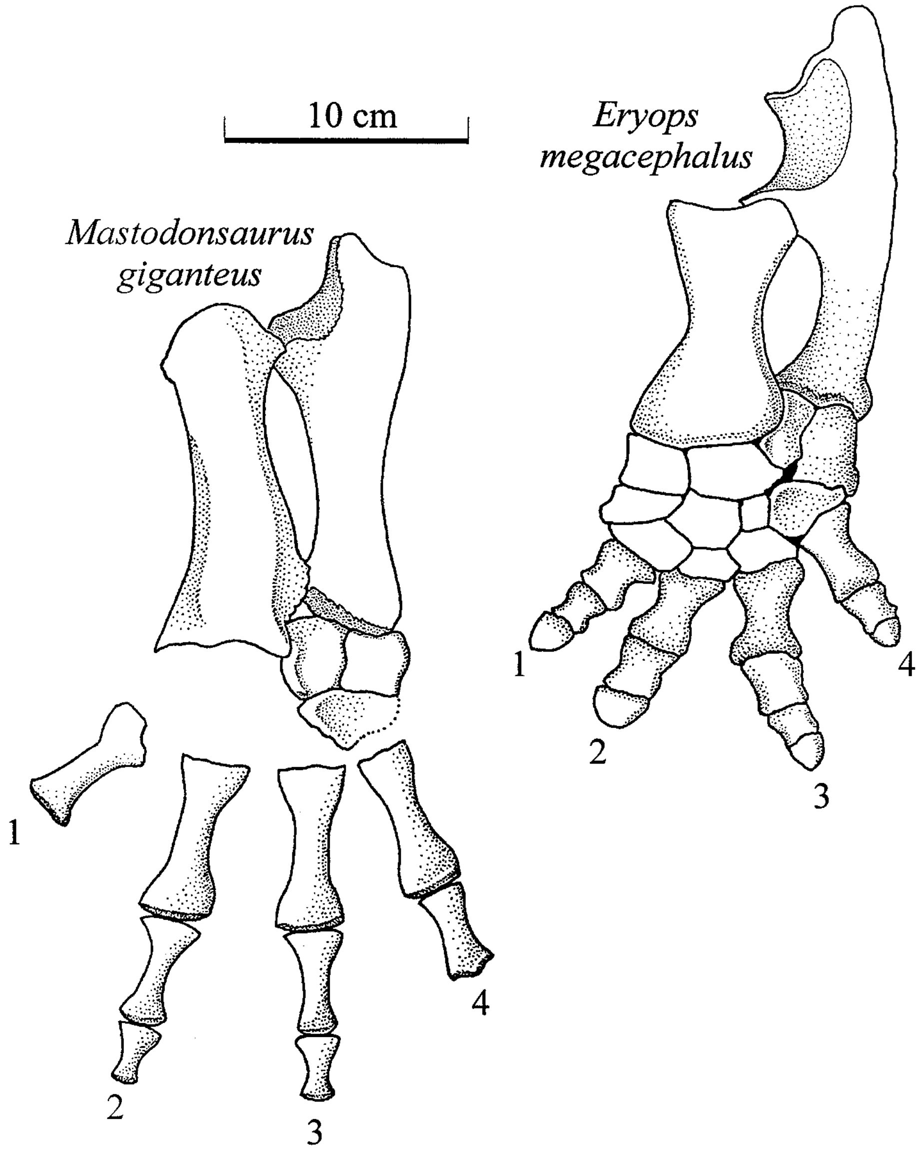


Fig. 45. Below, the lower arm, carpus, and manus in a large specimen of *Mastodonsaurus giganteus*, based on both isolated finds and partially articulated specimen (SMNS 4706). Above, the same region in the terrestrial temnospondyl *Eryops megacephalus* from the Lower Permian of North America and Europe.

most temnospondyls, which lack in this genus. The scapulocoracoid apparently forms from two centres of ossification, among which the coracoid appears much later than the scapula. In addition, the scapula extends dorsally with growth, although its width is rather small throughout development. In specimens of the size of 2,5 m the fusion of the bones is finally established. The glenoid facet at first is horizontally orientated, but later on it extends ventrally to attain a subvertical posterior face as well. To this a very marked expansion of the caput humeri neatly fits, also recorded for the latest phase in ontogeny. In specimens of about 4 m size (75 cm skull length) the humerus is much stouter and bears a supinator process as well as well-established epicondyles, in addition to the mentioned, posteroventrally extended caput. There is much to be discussed about the position of the antebrachium and the spatial constraints imposed by the design of the articulation facets, which in concert permit a detailed reconstruction of the pectoral limb. The lower arm is surprisingly strong yet relatively short.

The enormous width and flatness of the interclavicle, the articulation of the clavicles and scapulocoracoids, and the rather small height of the whole apparatus show that the anterior trunk was much flattened, as WATSON (1958) had already presumed in his reconstruction of *Paracyclotosaurus*. This is in agreement with the design and arrangement of the ribs and the striking morphology of the neural spines. The pectoral girdle must have directly connected to the skull and had the same lateral extension as this. The resulting proportions of the whole anterior trunk, from a superficial perspective, are best compared to that of cryptobranchid salamanders, especially to the largest specimens known.

Ilium

An abundant postcranial element in the Kupferzell material is the ilium. It is a comparatively small and slender bone with a narrow dorsoposterior shaft, a broadened but flat dorsal end, and a posteriorly much widened base (fig. 46). The acetabulum is well-established in the stage referred to in the following description. The frequency of occurrence in the collected material is probably due to both its characteristic shape and the high degree of ossification. Because of its thickness the ilium is almost throughout complete and very well preserved. The extent of compaction is further very limited, probably it has only affected the distal end.

In general, the shape of the ilium is quite variable in basal tetrapods and there are even conspicuous differences within temnospondyls. Frequently the shaft bifurcates posteriorly, giving an anterior and posterior process, the latter being usually a continuation of the shaft proper. This appears to be the plesiomorphic condition in tetrapods (ROMER 1957; JARVIK 1996). *Benthosuchus sushkini* has a marked anterior process in most specimens, but some smaller individuals may have an ilium which is almost identical to that of *Mastodonsaurus* (BYSTROW & EFREMOV 1940: figs. 53, 82). In most capitosaurs the ilium is rather short and stout, such as in *Paracyclotosaurus* (WATSON 1958), *Parotosuchus pronus* (HOWIE 1970). Among those capitosaurs in which ilia can be assigned to articulated and diagnostic cranial material, the mastodonsaur ilium is most similar to that in *Eryosuchus garjainovi* (OCHEV 1972: pl. 31).

The cross-sectional shape of the shaft is oval to nearly round ventrally, close to the base of the shaft. Further dorsally it abruptly flattens at about the midlength of the element, but only gradually broadens both anterior and posterior to the long axis. The latter is inclined at an angle of approximately 15? ° towards the vertical plane. The distal end is compressed, its shape being that of an elongated oval. The margins excell the markedly concave, slit-like surface distinctly. Instead the outline and structure of the proximal end are more complex. Anteriorly it has a straight transverse margin which gives rise to a transversely flattened anterior face of the iliac base. Further posteriorly both lateral and medial margins are markedly concave, while the posterior end widens somewhat again. The lateral margin is more strongly curved

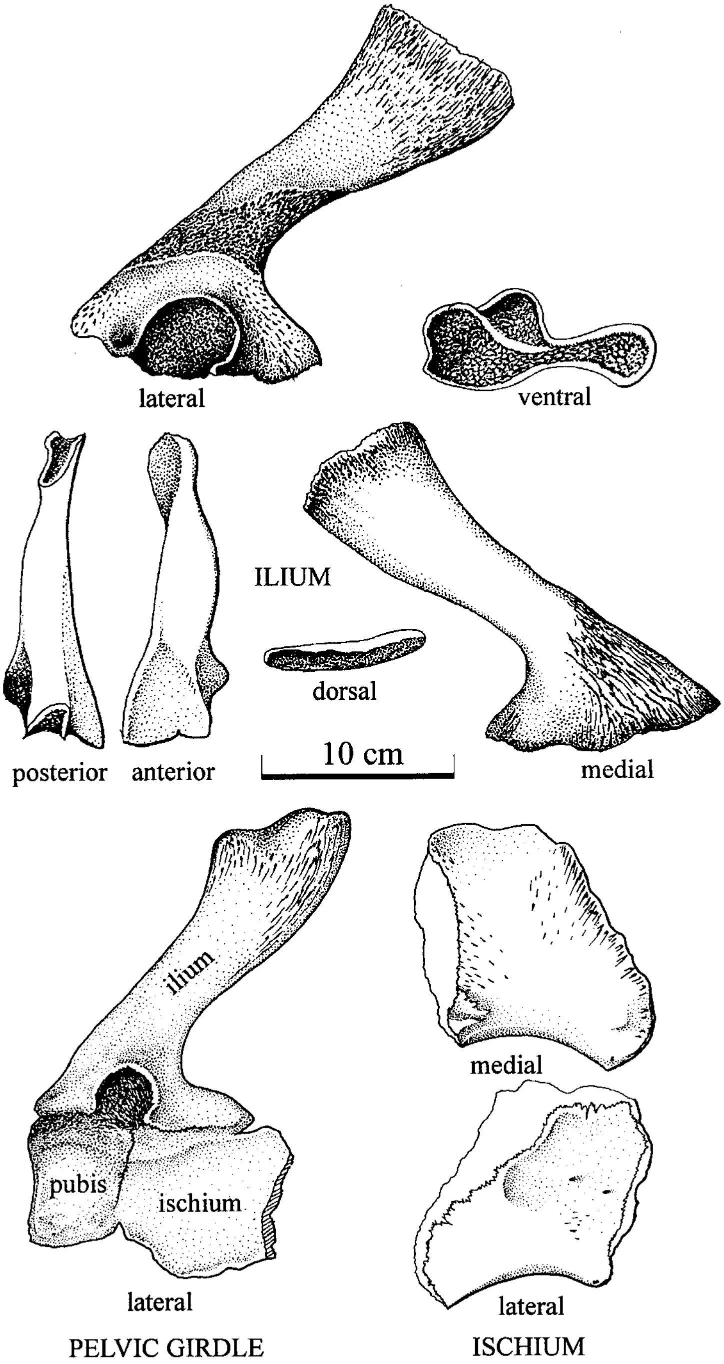


Fig. 46. The pelvis in medium-sized specimens of *Mastodonsaurus giganteus*, drawn in different views. Above, an isolated ilium; below, left an ilium with ischium in articulation and a part of the pubis. Below right, the ischium from two perspectives.

and in its anterior part the rough, cartilage-flooring surface extends over this margin to expand over the subcircular area of the acetabulum. The latter is emplaced within a depression and has very distinctly demarcated margins which rise from the smooth surface of this depression. The anterodorsal margin of the acetabulum is most clearly elevated and bends ventrolaterally. The acetabular surface hence expands dorsolaterally somewhat. The surface of the ilium is throughout relatively smooth. The dorsal end of the element is covered by numerous fine furrows and ridges. Obliquely crossing the shaft, there runs a marked muscle attachment zone which originates at the anterior, flattened margin of the shaft.

Ischium and pubis

The ischium was first correctly identified by WATSON (1919) who commented somewhat bitterly on FRAAS' (1889) misidentification of the scapula as ischium and that of the ischium as pubis. He did, however, not describe the element, which was finally carried out by HUENE (1922).

It is a small element of trapezoidal outline and simplified morphology (fig. 46). Its medial and lateral, flat surfaces are very similar. The lateral surface is identified by its possession of an anteriorly unfinished and broadened margin, which closes up to the iliadic rim of the acetabulum. Also it is unfinished more anteromedially, where the pubic cartilaginous region was attached. Medially, the ischia also must have been attached to a cartilaginous ischiadic element, as they show no traces of a suture with each other and the bone surface suggest cartilaginous cover.

In practically all Kupferzell specimens the ischia were found in isolation from the ilia, but often occur as paired elements. Perhaps this indicates a more tight integration of the ischia within the pelvic girdle than to the ilia. A definite pubis only occurs in one large specimen, in which the bone is confluent with the ischium. The position of this structure relative to the ilium unequivocally tells its identity. As this fragmentary specimen is relatively badly preserved, no significant details of this bone could be found out. Apparently, ossification of the pubis was a late-ontogenetic event in *Mastodonsaurus*, although an artificial bias (excavation) in the largely disarticulated Kupferzell material cannot be entirely ruled out.

Femur

This element is the strongest and largest in the pelvic girdle, although it does not compare to the much more massive and differentiated humerus, particularly in large specimens. FRAAS (1889), HUENE (1922), WATSON (1958), HOWIE (1970), and OCHEV (1972) have paid particular attention to the femora of capitosaurs, and the bone is among the best known in that group. Closest resemblance is shared with that of *Parotosuchus pronus*, which agrees in both proportions and structural details very precisely.

The bone forms a strong and stout rod which is distally more clearly broadened (fig. 47). Its dorsal side is axially symmetrical, convex with the apex at midlength, and almost smooth, with the exception of a medial groove at the distal end, by which it attains a two-headed shape in this region. The ventral side is generally concave, but asymmetrical. It bears a medial ridge (adductor crest) that rises from the posterior rim of a rugose depression at the distal epicondyles, and widens proximally to merge into the internal trochanter.

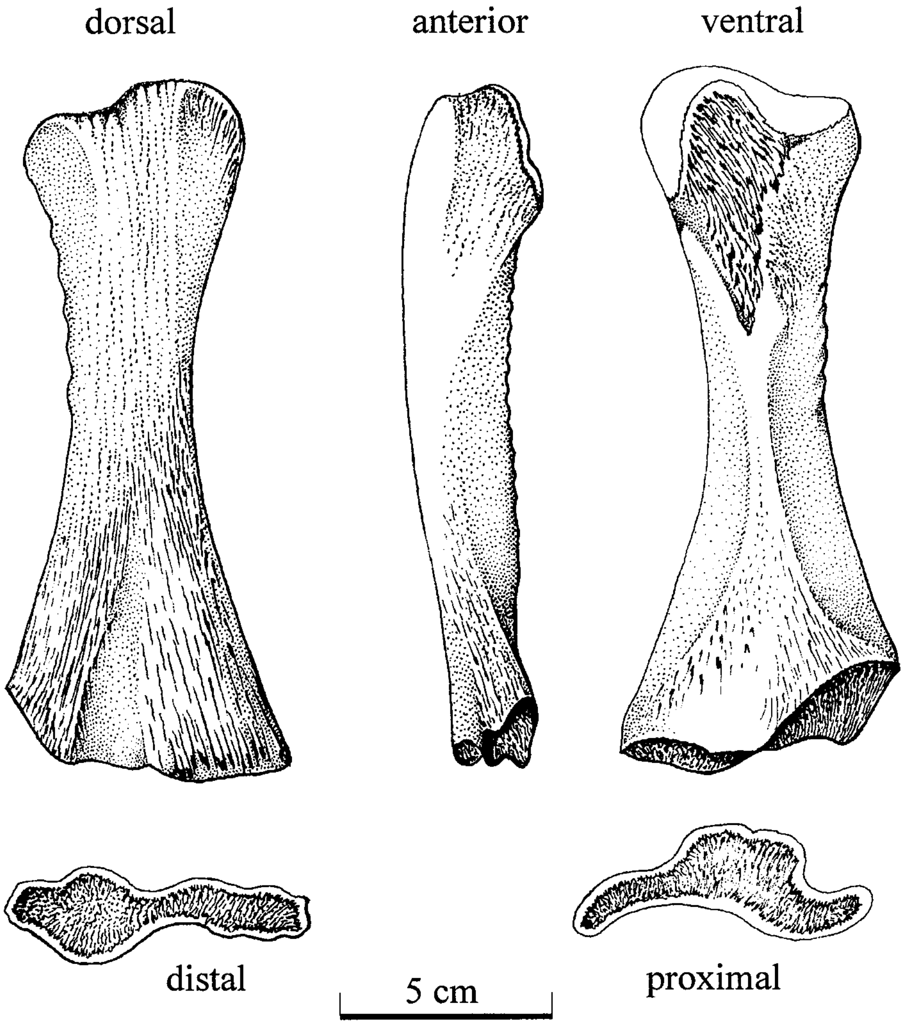


Fig. 47. The morphology of the femur in a medium-sized specimen of *Mastodonsaurus giganteus*, seen from different perspectives.

The proximal articular surface is an oval which is dorsoventrally compressed and anteriorly widened. The distal articular surface is vaulted in a convex manner, but of equal width throughout. The crest, as well as the depressions between the epicondyles and trochanters become very pronounced during ontogeny.

Lower leg

The lower leg of *Mastodonsaurus* is short and rudimentary. As far as can be gathered from comparisons, the lower leg bones have only half the length of the femur, which is itself a rather poorly developed element, as compared to *Eryops* (pers. exam.) or *Archeria* (Romer 1957) for instance.

The tibia has the following features, which are characteristic in many temnospondyls (fig. 48): (1) The proximal end is 1/3 wider than the distal end and two-headed in anterodorsal view, (2) the midline of the anterodorsal side is covered by a groove which broadens proximally and finally separates the two heads, (3) the medial margin is straight, whereas the lateral one curves towards the extended lateral head, and (4) the margins of the distal end are throughout raised and vaulted externally. The radius is slightly concave dorsally but clearly convex on its ventral side. In the latter the narrow distal end is almost two-headed. Otherwise the ventral side is entirely flat but covered by numerous parallel furrows. The dorsal surface is much smoother. Dorsally the surface is formed by a single column distally which bifurcates in the distal third of the longitudinal extension, and by then gives rise to two smaller, but more clearly established columns which finally form the proximal heads.

The fibula is longer than the tibia, but more simple in structure (fig. 48). It was described by OCHEV (1972) and HOWIE (1970) in the only other well-known capitosaurs, and from observation of *Mastodonsaurus* little is to add. The distal head is broader and extended medially, where it gives rise to a prominent ridge that runs along the medial side of the element. The face of the distal head is compressed in the middle and of symmetrical appearance, markedly sloping medially.

In addition, the distal end is flat with a marked central elevation that bears a strong, sigmoidal tuberosity. Further proximally, the lateral half of the bone gives rise to a proximally widening ridge. The ventral-posterior surface is smooth and more clearly flattened than the opposite face, and the lateral margin is rounded and bears an additional tuberosity towards the proximal half of the bone.

Pes

Little can be fixed about the anatomy and size of the foot of *Mastodonsaurus giganteus*, for the only elements potentially belonging to it are two small elements found attached to a femur which were interpreted as metatarsals (HUENE 1922). They do not differ in any feature from the better known metacarpals, so that a similar shape and perhaps size of the foot as the hand may be roughly estimated. In agreement with all knowledge on temno-spondyls, particularly actinodontids, the foot consists of five digits, of which the fourth is by far the longest – a condition not necessarily primitive for tetrapods, see the situation in *Archeria* (ROMER 1957). The closest form to *Mastodonsaurus* of which complete foot skeletons are known is *Uranocentrodon senekalensis* (VAN HOEPEN 1915). In this form, the pes has the following phalangeal formula: 2–3-3–4-3. This is in accordance with that of *Sclerocephalus* (BOY 1988), but is higher than in *Eryops* (MINER 1925: 2–3-3–3-3).

One additional, indirect evidence on the morphology and size of the pes is the structure and putative arrangement of the lower leg bones. The fact that the fibula widens distally suggests a broad tarsus, which would give a fairly large foot. Such a morphology is best known from *Archeria* (ROMER 1957), which has, however, a much more developed lower leg than *Mastodonsaurus*.

The pelvic girdle as a whole

The contrast between the size and architecture of the anterior and posterior appendages is striking in *Mastodonsaurus*. The problem, however, is that there are no articulated specimens which would allow a direct comparison of the sizes of pectoral and pelvic limbs.

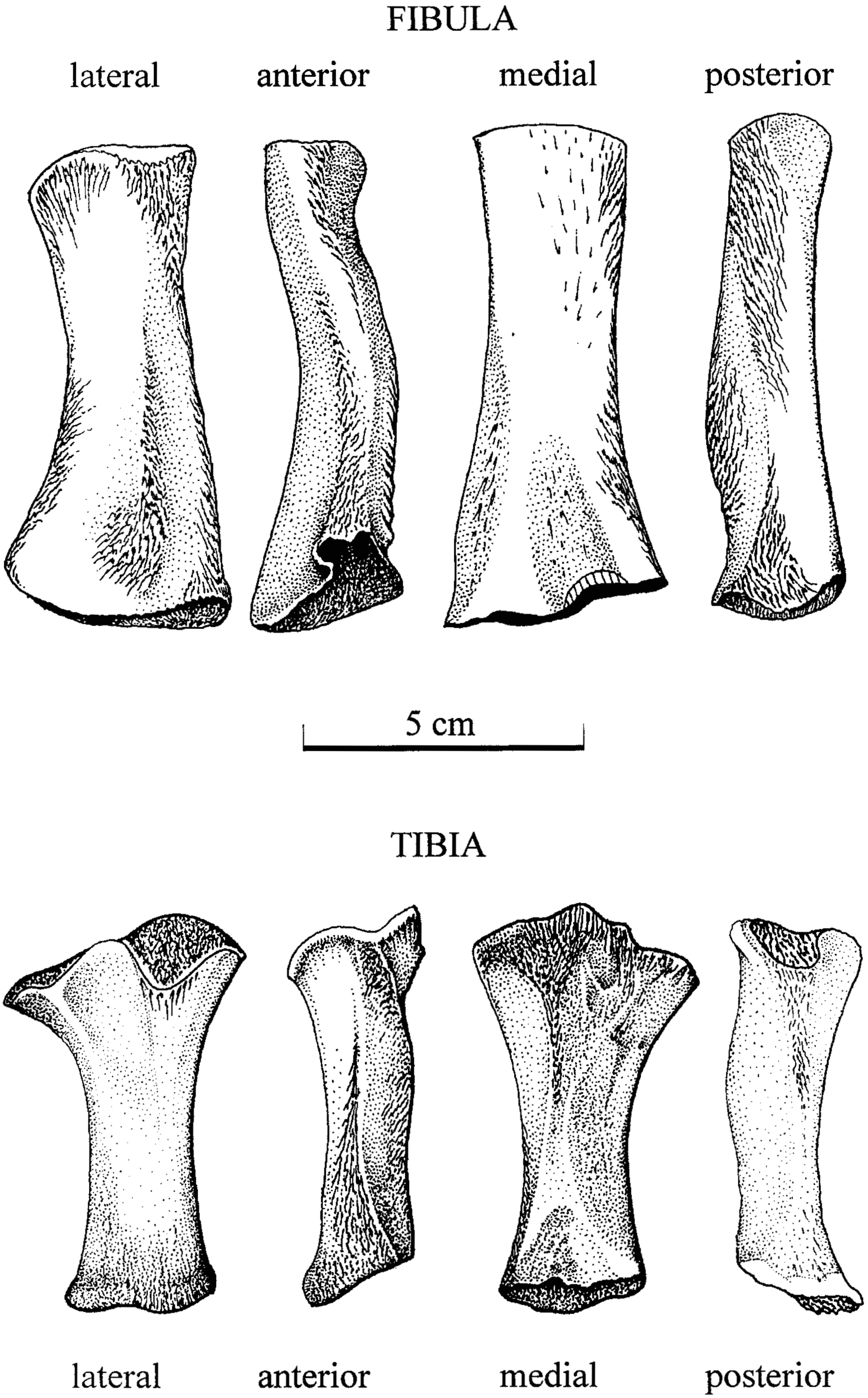


Fig. 48. The lower leg in a medium-sized specimen of *Mastodonsaurus giganteus*. Above, fibula; below, tibia.

Whereas the shoulder girdle ossifies extensively both by dermal and replacement bone formation, the pelvis keeps an immature morphology and a low extent of ossification until late in development. The extent of the obviously late-ontogenetic ossification in the pubic region is not known, but the ischia still had a considerable amount of cartilage between them by that stage. The ilium strikes by its tininess and the low angle by which it attached to the rather moderately-sized sacral rib. There was apparently no significant growth change in the ilium, and its structure is very much as in *Eryosuchus* and differs from that of most other capitosaurs by being very narrow and straight. The entire pelvic region must have been much lower than the pectoral region and skull, a fact that underlines the already supposed flattened nature of the whole body. The hind limb was supported by a rather typical basal tetrapod femur, which however is only moderate in size. The lower leg was short and its bearers surprisingly undifferentiated, reaching only about half the length of the femur.

4. Reconstruction of skeleton

4.1. Introduction

The skeleton of *Mastodonsaurus giganteus* is the most excellently preserved and complete of all capitosaurs, and the magnificent material from Kupferzell certainly forms one of the most advantageous information sources for the reconstruction of a basal tetrapod. Especially temnospondyls, whose skulls are abundant from the Lower Carboniferous through the Upper Triassic, are a widespread group, and their occurrence in many terrestrial faunas indicates a predominant role in late Palaeozoic to early Mesozoic ecosystems. The skull finds are often beautifully preserved and reveal numerous data on the feeding apparatus of these early tetrapods. Yet without the knowledge of fairly complete skeletons ecological studies are utopical. Reconstructions of complete basal tetrapod skeletons are therefore one of the major goals in this field of palaeontological research.

The frequent lack of postcranial material in labyrinthodonts is probably related to the discrepancy between the heavy, well-ossified skulls and interclavicles and the rather feebly mineralised postcranial, especially axial skeleton. Certain terrestrial basal tetrapods possessed heavy axial skeletons and sometimes rigid dermal armour and are therefore relatively well known. Complete aquatic temnospondyls, on the other hand, are least represented in the fossil record. Exceptional are finds in lacustrine sediments of the Rotliegend (Lower Permian) in Central Europe (Saar-Nahe Basin, Thuringian Forest, Saxony, Podkrkonose Basin), where aquatic temnospondyls in great number and excellent preservation were excavated.

Descriptions of most Permo-Triassic labyrinthodonts have long seemed to entirely neglect postcranial material, and therefore reconstructions of whole skeletons remained few in number. There are no more than a dozen basal tetrapod species whose skeletons were tentatively restored. These are the stem-tetrapod *Ichthyostega* (JARVIK 1952, 1996), the stem amniotes *Eogyrinus* (PANCHEN 1972), *Seymouria* (WHITE 1939), and *Kotlassia* (BYSTROW 1944), the basal temnospondyls *Trimerorhachis* (WILLISTON 1916) and *Dvinosaurus* (BYSTROW 1938), the terrestrial temnospondyls *Eryops* (MINER 1925; MOULTON 1974), *Cacops* (WILLISTON 1910), *Trematops* (CASE 1911), and *Micropholis* (BROILI & SCHROEDER 1937a), and the aquatic temnospondyls *Sclerocephalus* (pectoral girdle: MECKERT 1993) and *Paracyclotosaurus* (WATSON 1958).

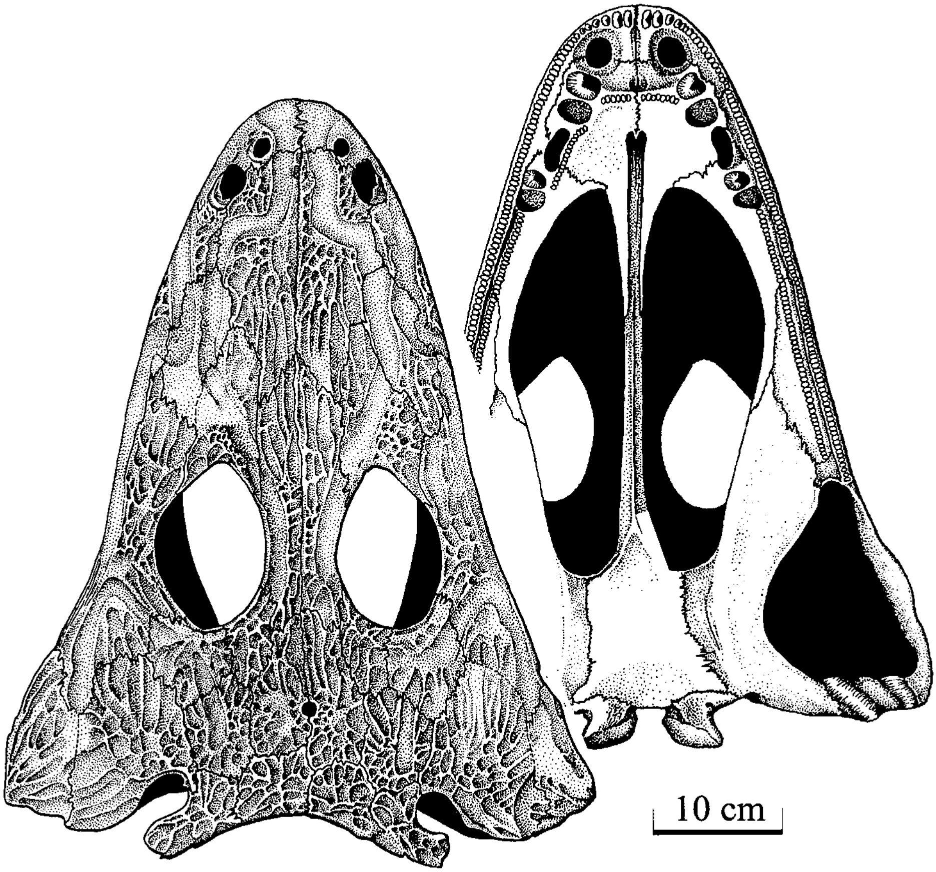


Fig. 49. The skull of *Mastodonsaurus giganteus* from dorsal and ventral sides, depicting the state of an almost uncrushed specimen (SMNS 54675; see also plate 2).

Most other reconstructions were largely carried out with one or several of the aforementioned results in mind, and a clear separation of the actual sources of information is only rarely maintained.

The following effort is an attempt to reconstruct the skeleton of the giant capitosauroid *Mastodonsaurus giganteus* for the first time. Until recently the scanty, only by its size intriguing material was little inviting, because the preservation of the old Lettenkohle material is far from optimal. However, the discovery, excavation, and metucolous preparation of *Mastodonsaurus* specimens from Kupferzell helped forming an ideal basis for such a task.

4.2. Problems and open questions

The extraordinary preservation of mastodonsaur skulls at Kupferzell may not readily appear to leave major questions open, yet there is a number of uncertainties. These result largely from differential effects of compaction on the skeleton, which is itself a consequence of differences in the solidity, fine structure, and composition of the various bones. Whereas the skull roof and palate are nearly threedimensionally preserved, the braincase, neural arches, and intercentra usually have suffered considerable deformation and fragmentation. Articulated specimens generally have undergone more modifications than isolated remains. In addition, the particular mode of preservation, such as the position (e.g. 'roof-up' or 'palate-up') may play a predominant role. The following problems emerge from the study of the preservational peculiarities of the Kupferzell and Gaildorf material.

1. The threedimensional structure of the mandible.
2. The structure of the occiput, and its articulation with the atlantal intercentrum.
3. The structure of the vertebral segment (intercentrum, neural arch, pleurocentrum).
4. The sequence of intercentra through the axial skeleton.
5. The sequence of rib types through the axial skeleton.
6. The structure, composition, and length of the tail.
7. The restoration of the appendicular skeleton.
8. The skeleton as a whole.

4.3. Lines of evidence

Information on the threedimensional arrangement of bones in a skeleton may be gathered by two direct and two indirect sources. These are the following:

A) Articulated specimens. Bones in their supposedly original setting often inform about the nature of contacts such as sutures, joints, or partial co-ossification. They bear, however, the disadvantage that the contact zones themselves cannot be studied, and therefore often the degree of preservational bias in the articulated specimen is difficult to assess.

B) Articulation facets and other direct osteological markers complementarily inform about the anatomy of bone contacts, and only from these reasonable guesses can be made on which arrangement was the most likely. This procedure involves at least partial restoration of units of the skeleton.

C) Spatial constraints are a more general and rough means to assess the limitations on the manifold thinkable arrangements of parts of a skeleton. They become important whenever more direct osteological indicators are lacking.

D) A phylogenetic bracket (Witmer 1995) may sometimes be a means to restore certain arrangements which are badly preserved in a particular species, but well known in others. Given that the phylogenetic position of the species under study can be reasonably determined, ground-plan reconstruction may help deciding which architectural type may have been present. This is of course only possible when the architectural types vary in such a way among the taxa that ancestral and derived states can be determined at all.

In the following discussion of the aforementioned problems the sources of information are throughout indicated.

4.4. Reconstruction

4.4.1. Threedimensional structure of the mandible

Although the structure of the mandible is preserved in great detail, the threedimen-sional arrangement of the bones and the orientation of the lower jaw as a whole is distorted in many specimens. The anterior portion of the mandible is frequently rotated into a more shallow plane towards the symphysis. In addition, the regions of the Meckelian window, adductor chamber, and hamate process are often crushed and/or flattened. Moreover, the postglenoid area sometimes is laterally compressed.

The first important question is that regarding the original shape of the mandible in the distorted and fragmented regions. There are few isolated mandible specimens in which the adductor chamber is not crushed and the fenestra Meckeli is completely preserved. These demonstrate that the adductor chamber was relatively wide, especially posteriorly, resulting in a convex lingual surface of the elements (prearticular, angular). The following problems remain, resulting from the exposed position of the regions: (1) The hamate process is markedly inclined labially, resulting in an obliquely orientated glenoid facet. (2) In most specimens the proper glenoid area is distinctly shortened and sagittally somewhat elongated. In both cases the original condition can be reconstructed relatively precisely by the morphology of the quadrate trochlea; this structure is practically never deformed because of its massiveness. (3) The postglenoid area is often laterally compressed, which is indicated by a strongly narrowed glenoid facet and unusually high and fragmented lingual crest. Reconstruction relies on well-preserved specimens with wider postglenoid areas and uncrushed margins. The morphology of this region is, however, variable in many aspects which are not affected by compaction. Thus reconstruction remains difficult here. (4) The adductor chamber is frequently considerably deformed, which affects both the shape of the adductor window and the thin lingual wall of the chamber. The latter is, however, known nearly uncrushed from three articulated specimens, wherefrom it is apparent that it was markedly convex. The deformation of the adductor window largely results from a crushing of the lingual frame (formed by the coronoid and prearticular). Isolated finds of coronoids help restoring this region: the coronoid curves markedly laterally at the anterior, pointed end of the adductor window, converging towards the sagittal tooth arcade of dentary and coronoid.

A more difficult problem is that of the orientation of the mandible with respect to the skull. The dental tooth arcade suggests that the deep, laterally flattened anterior part of the mandible lays in a near-vertical plane. The orientation of the dentary teeth is well constrained by the narrow slit in the upper jaw (between maxilla and palatine and ectopterygoid) into which they fit. As in undistorted skulls, the upper tooth rows are strictly parallel and point straight ventrally, not much variation in the direction of the dentary teeth is possible. Furthermore, as the dentary teeth are largely straight and lie in the same plane as the whole bones of the mandible, the general orientation of the latter must have been also nearly vertical. The reconstruction finally reveals that the mandible in articulation was slightly wider than the skull at its narrowest point, lateral to the orbit. The cranium of *Mastodonsaurus* thus formed a nearly perfect triangle in life.

4.4.2. The structure of the occiput and its articulation with the atlas

The occiput is the most problematic region in the cranium of *Mastodonsaurus*, as well as in many other large temnospondyls. Despite of the largely flattened skulls of these forms the occiput was often relatively high, a fact which became apparent only by rare finds of nearly uncrushed skulls. The long-believed general tendency of actinodontid temnospondyls to successively flatten their occiputs through the Permo-Triassic (Watson 1919, 1951) is in fact much more difficult to assess, now that threedimensionally preserved skulls are available for a variety of taxa. A good example is *Cyclotosaurus hemprichi* (Kuhn 1942) which has an occiput nearly as high as that of most other taxa. The generally believed characteristic of *Cyclotosaurus robustus*, the most extremely flattened occiput among the Capitosauridae, is also a matter of revision. New threedimensional finds from the Lower Stubensandstein show that this species had a fairly high occiput (Schoch submitted 1). Finally, *Mastodonsaurus giganteus* now turns out to be another such case: one specimen out of the Kupferzell sample has a nearly uncrushed occiput (SMNS 54675) in which also a complete endocranium is preserved (fig. 49).

The following regions of the occiput of *Mastodonsaurus* are affected by compaction even in the best-preserved specimens.

1. Processus paroticus (tabular, exoccipital).
2. Columna verticalis (postparietal, exoccipital).
3. Condylus exoccipitalis.

The structure of the atlanto-occipital articulation was such that the strongly concave and bilobed atlantal facets faced anterodorsally. This is evident from the structure of the atlas, which is much longer ventrally than dorsally, and irrespective of distortion has an anteroventrally sloping anterior face. Well-preserved occiputs have occipital condyles which face slightly posteroventrally. It thus appears that the design of the atlanto-occipital articulation favoured an elevation of the skull rather than a depression. This is particularly interesting as both possibilities might be theoretically conceiveable (see Erdmann & Cundall 1984 on *Amphiuma tridactylum*).

4.4.3. Structure of the vertebral segment

The presacral vertebrae of *Mastodonsaurus* consist throughout of three components per segment: the intercentrum, neural arch, and pleurocentrum (fig. 33). The peculiar structure of the capitosauroid vertebral segment has long been referred to as stereospondylous, a term coined by Zittel (1887). The greek term is a composite of stéreos (massive) and spondylé (vertebra), and must be viewed in a relative sense, compared to other temnospondyls. Fraas (1889), who referred to the mastodonsaurid vertebrae from the Gaildorf locality, adopted this expression. Watson (1919) identified the massive central element in the axial skeletons of *Mastodonsaurus* and *Metoposaurus* as intercentrum and demonstrated that it can be readily derived from the intercentrum of Permian rhachitomes such as *Eryops*. The composition of the vertebral segment, such as described by Plieninger (1844) and Fraas (1889) for *Mastodonsaurus*, was often cited and figured, although its morphology was not that well understood. Plieninger (1844) figured a fragmentary vertebral column of a small temnospondyl specimen which he identified as juvenile *Mastodonsaurus*. This specimen shows pleurocentra and an overall typically rhachitomous structure; an assignment to a particular group is, however, not possible (Huene 1922: 427). Fraas (1889: 83) was inclined to assume pleurocentral ossifications in the posterior part of the trunk, emphasising the decreasing amount of bone in the intercentrum. He also referred to a fragmentary find of uncertain affinity in which pleurocentra are present. Huene (1922) on the other hand, the last to describe certain aspects of vertebral anatomy in *Mastodonsaurus giganteus*, did not find any evidence for pleurocentra.

The transverse processes of the typical “rhachitomous” temnospondyls, such as *Trimerorhachis*, *Eryops*, *Sclerocephalus*, or *Archegosaurus*, are relatively short and directed posterolaterally. Their diapophyses are long-oval and obliquely orientated, allowing the rib only to run very close to the long axis of the trunk. The capitulum is small and nearly confluent with the tuberculum; the parapophysis is consequently very small. In capitosaurs, especially in large-growing genera such as *Eryosuchus*, *Mastodonsaurus*, *Paracyclotosaurus*, and *Parotosuchus pronus*, the transverse processes are long and the tuberculum thus much larger than in the aforementioned genera. The capitulum is much larger and the ribs are very clearly two-headed. The orientation of the ribs must have been different to that of the “rhachitomes”: they run more clearly in lateral direction and were much longer, with a marked bending point at about midlength, which contours the shape of a markedly broader and flattened trunk. The gross morphology of the capitosauroid trunk is therefore stout, best compared to the appearance of a large cryptobranchid specimen (e.g. *Andrias japonicus*).

The neural spines are throughout very low in capitosaurs. This is either a result of imperfect ossification, such as the morphology of the neural arches in *Benthosuchus* or *Parotosuchus pronus* suggest, in which case a cartilaginous dorsal continuation cannot be ruled out.

The massive pleurocentra, which nearly completely fill the gap between two successive intercentra, are attached to the posterior and ventral side of the transverse processes. This is a condition found in *Eryops* for instance, and it similarly occurs in *Platyoposaurus* (Bystrow & Efremov 1940). As these authors noted, a general tendency in old specimens is the synostosis of intercentrum and pleurocentrum, as exemplified in *Dvinosaurus* and *Platyoposaurus*. They considered this tendency to be one among four possible ways by which stereospondylous intercentra may have been formed in evolution. The condition in *Benthosuchus* and *Wetlugasaurus*, namely a loss of an ossified pleurocentrum, for a long time appeared to be the typical condition of Triassic ‘stereospondylous’ temnospondyls.

The study of the structure of the vertebral segment in *Mastodonsaurus* hence reveals that basically the rhachitomous architecture is retained. The particular, but not unique condition found in *Mastodonsaurus* is the great height and overall massiveness of the intercentrum. Whereas there are clear differences to the intercentra of metoposaurids (cf. Sawin 1945; Colbert & Imbrie 1956), those of *Eryosuchus* are well compared to those of *Mastodonsaurus* and in fact the most similar among capitosaurs.

4.4.4. The sequence of intercentra through the axial skeleton

Plieninger (1844), Fraas (1889), Watson (1919) and most recently Huene (1922) commented on the structure and composition of the presacral vertebral column. Huene arranged a series of 28 intercentra according to the articulated specimen formerly described by Plieninger, and in particular emphasized that there is a marked height decrease through the sequence. Although his figure is much generalised and schematic, the general arrangement is corroborated by the present re-investigation.

There are several independent sources for the reconstruction of this sequence:

1. The articulated specimens described by Meyer & Plieninger (1844), and new finds from Kupferzell.

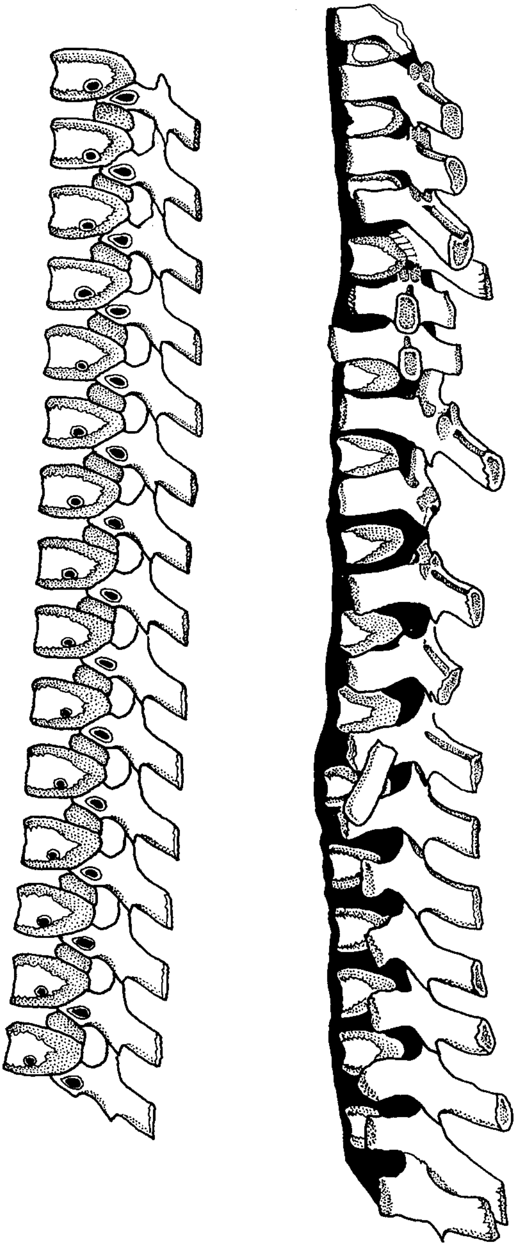


Fig. 50. Vertebral column of *Mastodonsaurus giganteus* from the alum shale at Gaildorf (SMNS 4698). Right, original in dorsolateral view; left, reconstruction of the preserved sequence of intercentra and neural arches. The height of the processus spinosi remains almost constant.

2. Relative height of the intercentra decreases caudally.

3. Degree of closure of the chorda foramen decreases, and the intercentra loose successively contact to both the pleurocentra and the neural arch.

4. The transverse breadth of ventral part decreases, and the ventral side possesses marked depressions and lateral constrictions.

The articulated finds clearly lead to the concept that the height of the intercentra first increases (from the axis through the fifth vertebra), then keeps a rather similar height up to the 22nd presacral, and then again decreases to the 27th which has an open chorda incisure instead of a foramen (figs. 30, 50). In the near-articulated specimen from Kupferzell (SMNS 80913) the last six intercentra clearly differ among each other so significantly that a definite sequence can be established according to the criteria mentioned before.

4.4.5. The sequence of rib types through the axial skeleton

The proper assignment of the various ribs with particular vertebrae poses more problems than that of the intercentra, and it cannot be ultimately resolved for all regions. All authors so far failed to establish such a series, and the reasons have to be sought entirely with the poverty of the disarticulated rib material from the Gaildorf and other Alaunschiefer localities.

The following criteria appear to be correlated with the relative position of the ribs:

1. Rib length distal to the ventral bending point.
2. Presence and morphology of proximal and distal uncinate processes.
3. Degree of separation and morphology of capitulum and tuberculum.
4. Morphology of distal rib shaft.
5. Length of the portion proximal to the bending point.
6. Morphology and distance of diapophysis and parapophysis.

In the axis, the diapophyses and parapophyses are nearest and of almost round shape. The corresponding rib (A), whose head approaches most closely this structure, is fairly long yet little differentiated as compared to other anterior trunk ribs. The following ribs are very similar in the morphology of their heads, such as the di- and parapophyses of the corresponding vertebrae are. Instead of establishing a detailed and speculative sequence, I should like to rather grossly arrange the rib types according to: (1) the length of the distal shaft (the longer the more anterior), (2) the size of the distal uncinate process (the larger the more anterior), and (3) the position of the distal uncinate process relative to the distal end (the more distal the more anterior). The length of the proximal rib portion (i.e. proximal to the bending point) is throughout the same for the anterior ribs. According to this scheme, the proximal shaft which bears the proximal uncinate process decreases in thickness caudally, and the region is less differentiate, especially in lacking the various additional crests which are characteristic of the posterodorsal side of the anteriormost trunk ribs. At the prominent bending point the ribs usually turn at an angle of 50–55° ventrally, thus paralleling the supposed body outline. According to this evidence, the anterior trunk region was much flattened (Watson 1958), with a transversely long-oval, dorsally compressed transsectional area.

Further posterior (at about the 8th or 10th vertebral position) first the proximal and then the distal uncinate processes disappear. The former are borne by a crest on the dorsoposterior side of the rib and may persist eventually in a rudimentary state up to the sacrum, which is a matter of individual variation. The latter, throughout found distal to the bending point, disappear fairly soon, which gives the rib a much more slender appearance. The distance between capitulum and tuberculum increases in these vertebrae, indicating a distally extended neural arch. The bending point of the ribs has disappeared, resulting from the smaller length of the ribs in which this distal point is simply not reached. The articulation facet of the tuberculum is also much extended, and by its structure reveals a very tight fitting of rib and vertebra.

The next series of trunk ribs (15–20) are both shorter and more slender, with uncinate processes almost lacking. The head region is, however, similar to that of more anterior ribs, and it differs from the somewhat similarly shaped tail ribs foremost by the well-differentiated tuberculum and capitulum. The distal end and shaft are much thinner than in the aforementioned rib types.

Finally, the last presacral ribs tend to differentiate again, develop uncinate processes and a rather flat, proximal region. The articulation facets for the vertebra have also changed substantially: capitulum and tuberculum have become increasingly similar to each other, and strongly suggest that the length of the transverse processes is also reduced. The proximal portion, distal to the immediate rib head region, is flattened and bears numerous crests and bosses respectively. The last three rib types are very similar in head structure to the sacral rib, which is not significantly larger than the more anterior ones.

4.4.6. Structure and length of the tail

The caudal skeleton, as far as can be concluded from available remains, is moderately large and has a massive base with a relatively high number of caudal ribs and haemal arches (fig. 51). Both of the latter data indicate the presence of a transversely deep and not too short caudal skeleton. There are at least 8 caudal ribs, as suggested by both partially articulated material and the diversity of caudal parapophyses. The haemal arches are found from the fifth or sixth caudal backwards, but their length is uncertain. The presence of caudal ribs and haemal arches suggests that the anterior portion of the tail had a large cross-sectional area. The known tail skeleton in the largest specimen has a length of 50 cm, with the last vertebra being rib-bearing, haemal arch-bearing, and still well differentiated. A posterior continuation of the tail is hence obvious. Modest estimation, derived from an extrapolation of the direct data on the height and diameter of the last definitely known tail segment, gives a tail of about 140 cm length. The entire animal, to which the giant specimen belonged, consequently must have been slightly longer than 5 m. An estimation which draws data from other capitosaurs into consideration, arrives at a very similar result: if the pro-

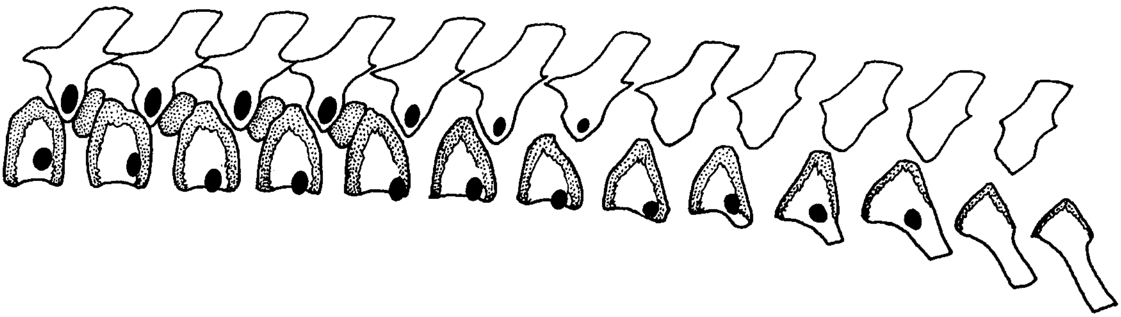


Fig. 51. Reconstruction of the caudal skeleton in *Mastodonsaurus giganteus*, based on isolated caudal intercentra and indirect evidence from closely related genera.

portions of *Paracyclotosaurus davidi* are taken as additional guide, a head-to-tail length of nearly 5 m is obtained. Finds of mastodonsaur tusk, exceeding the size of those of the giant specimen by far, suggest the presence of much larger animals in both Kupferzell and Gaildorf localities. JAEGER's original specimen, SMNS 55911, is in fact the largest amphibian tooth ever reported on, and tentative estimation would give an animal of nearly 6 m length.

4.4.7. Appendicular skeleton

The posture of the fore limb is constrained by the geometry and topography of the articulation facets, which are generally relatively well ossified, though obviously were covered by cartilaginous caps. The glenoid faces laterally and posterolaterally, whatever orientation of the scapula is preferred (fig. 52). There is, however, little doubt that the scapula faced rather steeply upwards, as results from all attempts to fit the scapulocoracoid, cleithrum, and clavicula together. The massiveness and rigidity of the latter suggest that most specimens are undistorted in that region, and the minimal number and amount of fractures agrees with this. The structure of the glenoid thus permits a posture in which the humerus directed strictly laterally, and rotation along the head of the latter would bring it into a more posteriorly directed position. Other movements, such as a foreward rotation of the humerus, appear to be strongly constrained by the glenoid and largeley impossible. On the other hand, a vertical rotation of the humerus around a sagittal axis, such as to lift the body, cannot be ruled out.

The orientation of the antebrachium towards the humerus is constrained by the morphology of the ectepicondyle in particular (fig. 52). This faces entirely to the side, permitting only a lateral articulation of the radius. The posture must consequently have been a sprawling one, with the arms held straight to the side and only minimally to the back, and the forearms facing to the side rather than the front as in *Eryops*, *Sclerocephalus*, *Archeria*, and *Proterogyrinus*. In old specimens the proximal articulation facet extends both to the side and ventrally, and in addition the convexity increases, so that the angle of rotation with maintained bone contact is larger than in smaller specimens.

The attachment of the ilium to the sacral rib is indicated by a triangular rugose and sculptured area, which in some specimens neatly mirrors the shape of the dorsal iliadic end (figs. 37, 46). As the orientation of the sacral rib with respect to the axial skeleton can be ascertained by the structure of the diapophysis and parapophysis, the distance between the acetabula and hence the width of the body in the sacralregion can be estimated. The depth of the body at this level is given by the length of the ilium and ischium, but ventral to the latter a considerable amount of cartilage may be presumed. Hence there is doubt about this measure, although by any assumption one arrives at a narrow and very shallow posterior trunk. The hind limb was according to all evidence similar to that of other large temnospondyls, such as *Sclerocephalus* and *Uranocentrodon*, with the difference that it was proportionately smaller and in particular also absolutely smaller and slenderer than the fore limb.

4.4.8. The skeleton as a whole

The proportions of the postcranial skeleton of *Mastodonsaurus giganteus* have been a major point of discussion for more than 150 years. In fact, only the combina-

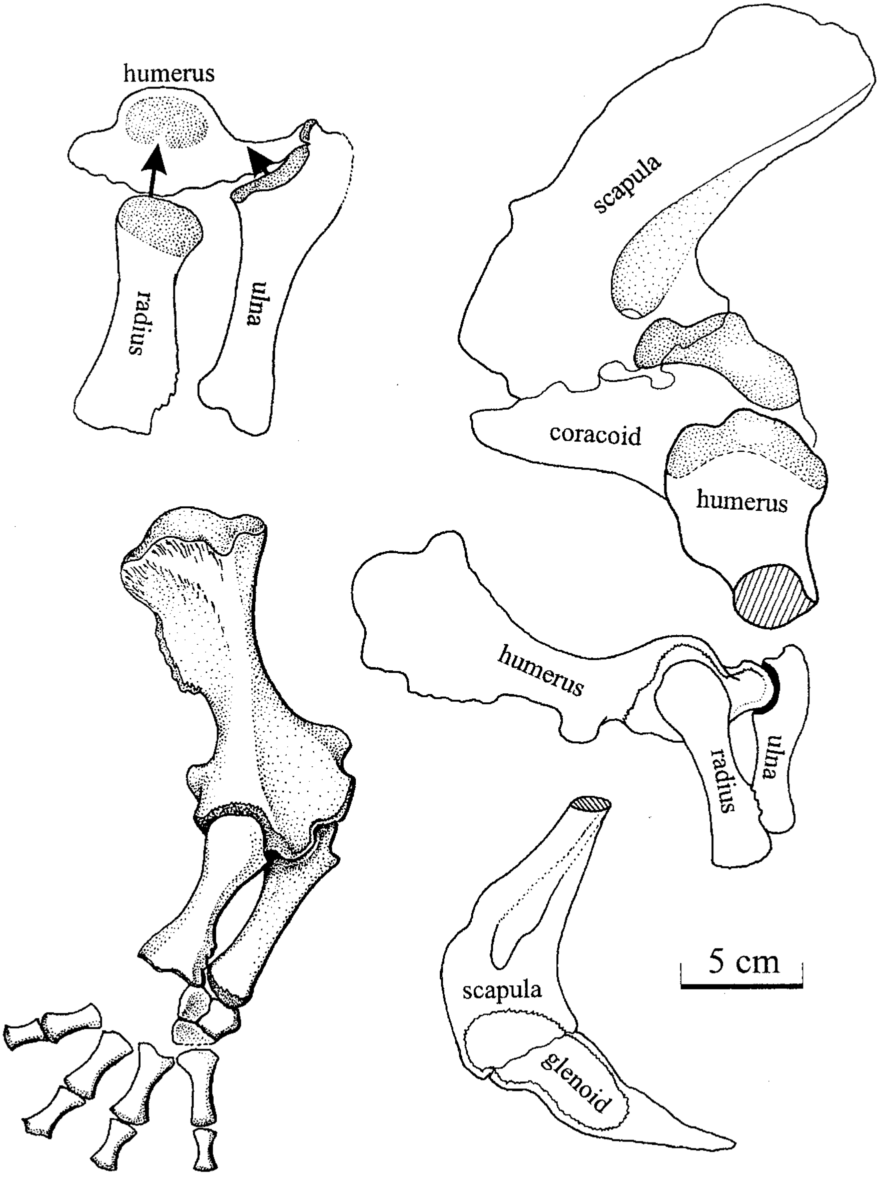


Fig. 52. The structure and articulations of the pectoral girdle and fore limb in *Mastodonsaurus giganteus*.

tion of knowledge gathered from the two main samples, the old from Gaildorf and the new from Kupferzell, provides sufficient data to reconstruct the skeleton as a whole. Both sources are equally important.

The articulated Gaildorf material originally consisted of two long vertebral columns (SMNS: Meyer & Plieninger 1844; Huene 1922) and various additional specimens of fragments of the presacral skeleton (SMNS 4698, GPIT 1804).

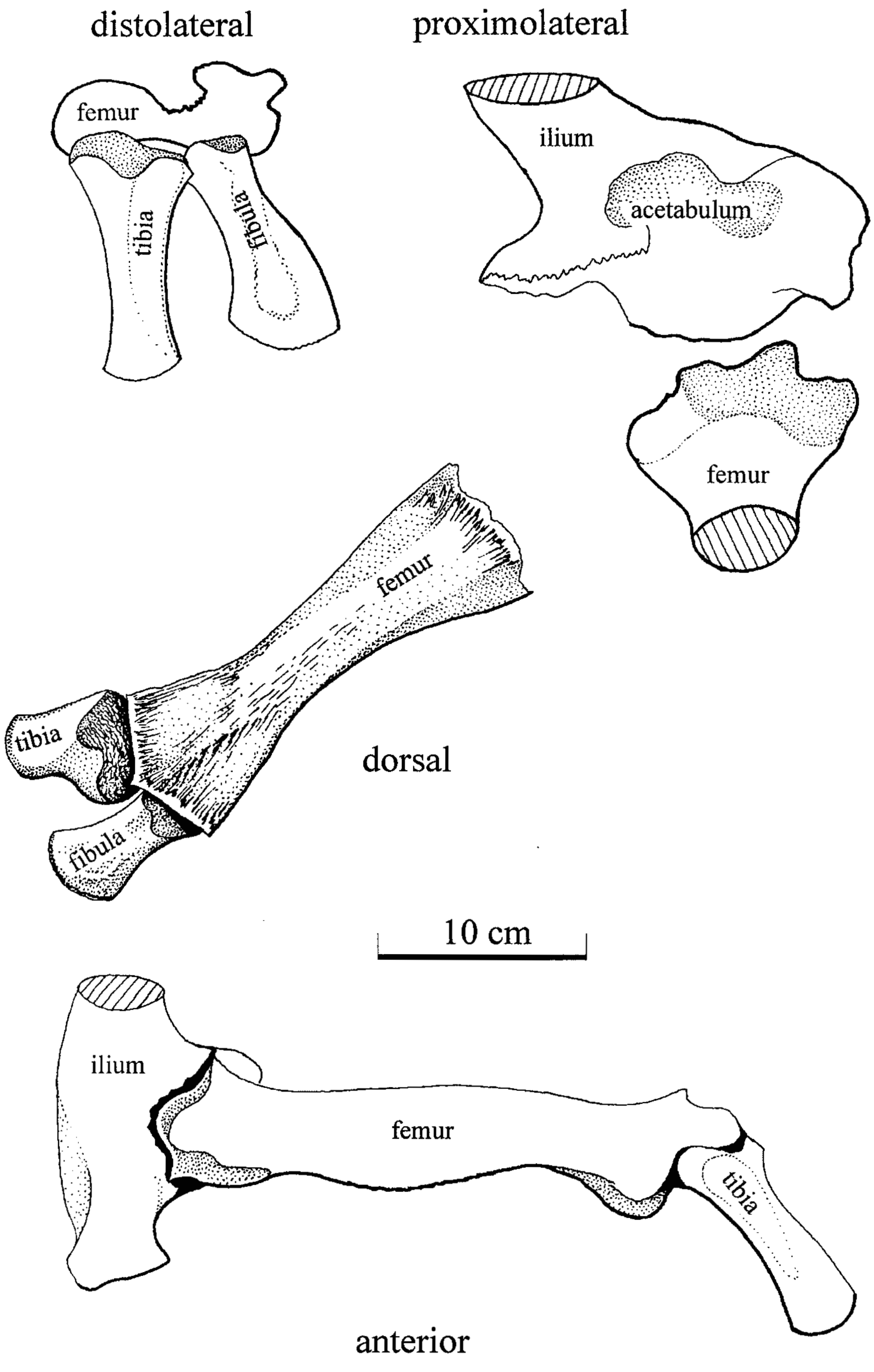


Fig. 53. The structure and articulations of the pelvic girdle and hind limb in *Mastodonsaurus giganteus*.

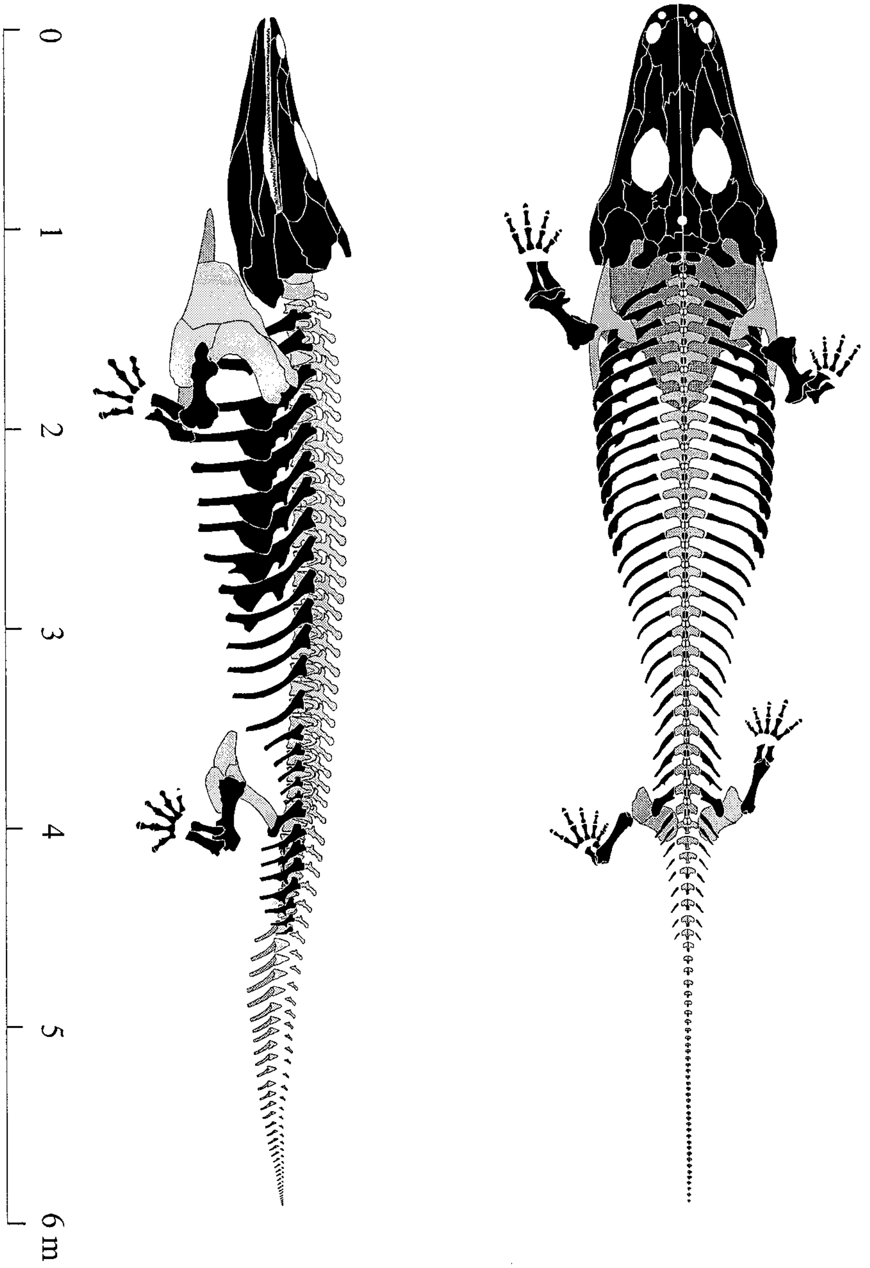


Fig. 54. The complete skeleton of a large specimen of *Mastodonsaurus giganteus* from two perspectives. Reconstruction based on numerous observations mentioned in the text. The skeleton is markedly stouter and broader than that of primitive temnospondyls, and the trunk is flattened dorsoventrally. While the length of the trunk is given by articulated specimens and the spatial relations of the vertebrae and ribs, the tail is of unknown length. The figured caudal skeleton depicts the minimal size, which results from the diversity of vertebral and rib types in the tail.

The trunk of *Mastodonsaurus giganteus* is almost exactly two times longer than the skull roof (fig. 54). This proportion can be derived from several independent lines of direct evidence, and it corresponds well with the structure of other capitosaur trunks (*Uranocentrodon*: VAN HOEPEN 1915, *Paracyclotosaurus*: WATSON 1958, *Eryosuchus*: OCHEV 1972, *Metoposaurus*: DUTUIT 1976). The greatest resemblance in trunk proportion is between *Mastodonsaurus* and *Paracyclotosaurus*. The lines of evidence supporting this reconstruction are as follows.

(1) The complete articulated specimen from Gaildorf (SMNS 4707, see MEYER & PLIENINGER 1844; FRAAS 1889; HUENE 1922) encompasses the complete skull (74 cm), the presacral column (145 cm), and parts of the appendicular skeleton (humerus: 24 cm). The length of the presacral column is a minimal measurement, given that the last preserved vertebra (the 28th) actually is the sacral.

(2) The incomplete articulated specimen from Gaildorf (SMNS 4698) in which 20 vertebrae are preserved in tight articulation. The size of the vertebrae is nearly the same as that of (1). The column is bent to give a dorsally concave line. The length of a vertebral segment was measured and counted to 28, which gave a presacral length of 145 cm. This result matches very precisely with the result of (1). Size and length of the vertebral centra is nearly similar throughout the presacral column, which is known from (1) and (3).

(3) A specimen from Kupferzell, including a fragmentary skull (75 cm) and 28 vertebral centra (SMNS 80913). The latter were found partially disarticulated, but closely associated with the skull. The last vertebra is crescent-shaped and dorsally with an open chordal incisure. Arranged in a sequence, with distances allowing articulation of proportionately matching neural arches, the trunk will have a length of between 135 and 145 cm, thus giving a trunk nearly two times longer than the skull.

(4) A giant specimen from Kupferzell with a partial skull (fragments of palate and two complete mandibles), 35 intercentra, numerous fragments of neural arches, and a large number of morphologically diverse ribs (SMNS 81310). The skull was about 125 cm long (mandibles: 140 cm), the arrangement of 28 presacral vertebrae (in the way explained before) gives a length of 240 cm. As all intercentra are strongly affected by compaction, their length must be estimated, comparing them to uncrushed specimens of similar size. This specimen is particularly important, as it has a series of definitely articulated caudal intercentra, and a variety of associated trunk and tail ribs.

In sum, reconstruction of trunk proportions relies on the articulated Gaildorf material to (1) estimate the length of an average vertebral segment, (2) count the minimal number of presacral vertebrae, and (3) study the variation in structure and proportions of vertebral segments according to their positions within the column. The results of (3) help correcting an oversimplified estimation gained from (1).

The presacral count of *Mastodonsaurus giganteus* is suggested by (a) the first Gaildorf specimen (MEYER & PLIENINGER 1844), (b) the giant Kupferzell specimen (SMNS 81310), and (c) phylogenetic ground-plan reconstruction. The latter relies on data from *Uranocentrodon senekalensis* (VAN HOEPEN 1915; HUENE 1956: 28 presacrals) and *Paracyclotosaurus davidi* (WATSON 1958: 28 presacrals).

The tail of *Mastodonsaurus* was, for the reasons mentioned and discussed before, much longer than previously considered by certain authors (figs. 51, 55). Although the general morphology of caudal skeletons in capitosaurs is rather well understood, complete finds are extremely rare. *Paracyclotosaurus davidi* is the only find known in which the tail is completely preserved (Watson 1958). As both the structure and length of the presacral skeleton and the morphology of the tail base are very similar in *Mastodonsaurus*, and especially the proportions with respect to the cranium, I conclude that the tail of the latter was very likely to be slightly shorter or as long as the skull, which would mean a length of about a metre in a large specimen.

In conclusion, the general appearance of the skeleton of *Mastodonsaurus giganteus* comes very close to that of other large capitosaurs and related genera (fig. 55). Keeping the numerous and far-reaching anatomical differences in mind, the overall resemblance to a crocodile is compelling. This has been stressed numerous times (starting with Meyer & Plieninger 1844), but is certainly not a fortunate comparison. The extremely flattened and platybasic skull and especially the large degree of flattening in the trunk are striking features of capitosaur body architecture. The bodily appearance of *Mastodonsaurus giganteus* is much better and physiologically more reasonably compared to that of the largest specimens of the Japanese Giant Salamander, *Andrias japonicus*, with the exception that capitosaur skull design bears many plesiomorphic features not found in extant groups. Among urodeles, *Amphiuma tridactylum* resembles *Mastodonsaurus* most closely in the appearance of the skull, both by its narrow outline and the exceptionally high degree of ossification. The flatness of body architecture is a very frequent, if not general phenomenon among the largest species of Recent lissamphibians, with such different forms as *Conraua goliath* (the West African Goliath Frog), the cryptobranchid *Andrias japonicus* (The Japanese Giant Salamander), and *Dicamptodon ensatus* (The Pacific or Marbled Giant Salamander).

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Glossary of anatomical terms

The following list of anatomical terms summarizes the existing and useful names for morphological features in temnospondyls. Many of them have been invented by comparative morphologists early in this century, and therefore are in Latin language. Some terms which are more general are even older and have gained universal acceptance. Other, younger terms are either English or somehow modified Latin, depending usually on the mother language of the author who suggested them. It is reasonable to keep all terms that have gained general acceptance, or at least which have experienced a continued use, and to prefer them over less widely used (and known) synonyms. While a mixture of Latin and English terminology is unavoidable, this strategy is certainly more useful than attempting to establish a new and standardized terminology, either Latin or English.

The translation of all Latin terms into English would pose major problems in some cases, as it would be difficult to keep the higher degree of precision characteristic of many words in the Latin language. I have invented new terms (in Latin) for features which have been inadequately referred to by English terms. In addition, new features, of which this study has yielded a relatively large number, are referred to by new terms. I suggest Latin names in this case, although often an English translation would not pose problems; in this case the use of the language may be decided by subsequent authors.

Adductor chamber: The widened mandibular cavity anterior to the glenoid articulation which terminates somewhat before the anterior rim of the adductor window.

Adductor window: The dorsal opening of the adductor chamber framed by prearticular and surangular lingually, coronoid and surangular labially, and articular posteriorly. Synonyms: fenestra adductoris, adductor fossa of some authors.

Alary process: An ascending process of the premaxilla by which this bone contacts the nasal medial to the naris. Synonym: Processus alaris.

Angulus adductoris: A broadened and flat depression on the labial side of the mandible, running along the labial margin of the adductor window. Its name refers to the probable insertion of adductor musculature on this area, as suggested by its characteristic surface.

Apertura praemaxillaris: Paired or unpaired opening(s) in the palate, bordered by vomers posteriorly and premaxilla anteriorly, accommodating the tusk of the symphysis.

Arcus: The arc which frames the neural canal, formed by the processus spinosus dorsally and the processus transversi laterally.

Basal plate: The posterior portion of the parasphenoid, behind the interpterygoid vacuities, by which the bone is sutured with the pterygoids.

Canalis primordialis: The slender cavity between the lingual and labial walls of the mandible.

Capitulum: The ventral facet on the head of the rib which articulates with the parapophysis.

Caput capituli: The process bearing the capitulum.

Caput humeri: The proximal head of the humerus.

Caput tuberculi: The process bearing the tuberculum.

Choana palatalis: The superficial outline of the internal narial opening situated in the main plane of the palate.

Choana proprieta: The proper outline of the internal narial opening, which is often situated dorsal to the main plane of the palate, arranged in an oblique plane relative to the palate, and which is generally smaller than the choana palatalis. This distinction is useful within the Capitosauridae, where the morphology and size of the choana differs considerably and might be a phylogenetically significant feature.

Columna verticalis: A straight dorsal process of the exoccipital, connecting the occiput with the postparietal.

Commissura anterior: The transverse connection between the paired sulcus infraorbitales and s. supraorbitales.

Condylus occipitalis: The only bearer of the articulation between the skull and the vertebral column (proatlas or atlas). In many, especially primitive temnospondyls formed by basioccipital (ventral) and exoccipitals (dorsolateral), it is solely formed by the exoccipitals in certain advanced, large-growing capitosaurs such as *Mastodonsaurus* and *Cyclotosaurus*, as well as the Metoposauridae.

Conical recess: A nearly round depression on the dorsal side of the parasphenoid, in the basisphenoid region anterior ro the otic, medial to the epipterygoid, and lateral to the laterosphenoid region of the sphenethmoid. It probably housed the cartilaginous lateral portion of the basisphenoid in stereospondyls. Synonym: Recessus conoideus.

Crista basioccipitalis: A medial and unpaired crest rising from the posterior, raised margin of the parasphenoid and running sagittally along the dorsal surface of the bone, dividing the fossa basioccipitalis by half.

Crista falciformis: A posterior outgrowth of the superficial, skull-roofing portion of the squamosal, forming part in the posterior rim of the skull roof. In *Cyclotosaurus* and other so-called 'closed-notched' capitosaurs the crista falciformis is sutured or fused to the tabular posterior to the otic notch, thus encircling an otic window.

Crista laterosphenoidalis: Paired crests attached to the laterosphenoid portion of the sphenethmoid, on the dorsal side of the parasphenoid, at the interface between basal plate and cultriform process.

Crista muscularis: A transverse crest at the posterior rim of the basal plate, suggesting the origin of hypaxial musculature.

Crista parapterygoidea: A transverse, dorsal outgrowth of the parasphenoid at the posterior rim of the conical recess in the basipterygoid region. It continuously rises laterally, and forms a dorsolateral process by which it articulates with the ventral proximal head (VPH) of the stapes.

Crista paroccipitalis: A high ridge or crest rising from the posterolateral margin of the parasphenoid, running obliquely anteromedial on the dorsal surface of the bone.

Crista tubercularis and crista capitularis: Medial crests running on the proximal-dorsal side of the rib heads.

Cultriform process: The anterior portion of the parasphenoid, which is bordered by the interpterygoid vacuities and that interconnects the vomer with the basal plate. Synonym: Processus cultriformis of some authors.

Dental ramus: The tooth-bearing portion of the premaxilla. Synonym: Ramus dentalis.

Diapophysis: The rib articulation facet of the neural arch.

Dorsal proximal head: The footplate of the stapes, or dorsal portion of the head in temnospondyls, which points into the fenestra ovalis (DPH). Note that the dorsal head of the temnospondyl stapes is probably not homologous with the dorsal head of the amniote stapes (see LOMBARD & BOLT 1988). Synonyms: Processus vestibularis, caput columellae, footplate.

Dorsum sellae region: The ventral ossification in the laterosphenoid region, named after the characteristic region of the hindbrain.

Ectepicondyle: The antero-ventral condylus of the distal end of the humerus, articulating with the radius.

Entepicondyle: The postero-dorsal condylus of the distal end of the humerus, articulating with the ulna.

Epipterygoid footplate: The ventral facet of the epipterygoid by which the element is suturally connected with the pterygoid.

Facies intercentralis: The facet for the attachment to the tuber articularis of the intercentrum.

Facies pleurocentralis: The articulation facet for the pleurocentrum, situated entirely on the posterior side of the processus transversus and facing posteromedially.

Fenestra ovalis: An opening which in *Mastodonsaurus* is framed by the otic, exoccipital, pterygoid, and parasphenoid and into which the footplate of the stapes fitted in natural articulation. By definition (articulation of stapedial footplate) this opening includes, if not represents the fenestra ovalis as known from Recent amphibians and amniotes. Synonyms: Fenestra vestibuli, Oval window.

Flexura lacrimalis: A sigmoid curvature of the sulcus infraorbitalis, in most temnospondyls situated on the lacrimal.

Fodina vomeralis: An elongated, countersunk area on the ventral surface of the palate, separating the vomers in the midline and exposing the anterior portion of the cultriform process. Anteriorly the fodina continues as a channel enclosed by the vomers which opens anterior to the dentes postfenestrales, right behind the apertura praemaxillaris.

Foramen chordae tympani: Relatively large opening ventrolingual to the glenoid area of the mandible, in *Mastodonsaurus* situated at the articular-prearticular suture.

Foramen magnum: The largest opening in the occiput, bordered by the exoccipital laterally, the parasphenoid ventrally, and the processus lamellosus dorsolaterally.

Fossa basioccipitalis: A medial depression in the posterior portion of the parasphenoid, on its dorsal side.

Fossa parasphenoidalis: Paired grooves or pockets in the posterior portion of the ventral side of the basal plate, posterior to the crista muscularis. Synonym: parasphenoid pocket, muscular pocket.

Glenoid facet: The articulation facet for the humerus head, formed by the scapulocoracoid.

Glenoid area: The articulation facet for the articular in the mandible.

Incisura capitis: The region separating the two rib heads.

Interpterygoid vacuities: Medium-sized to large openings in the palate, ventral to the orbital windows, bordered by the pterygoids, vomers and eventually palatines, and separated in the midline by the cultriform process.

Lamina ascendens: A sheet-like, curved and irregularly shaped outgrowth of the pterygoid, connecting to the squamosal dorsally, the epipterygoid anteroventrally, the otic posterodorsally, and the quadratojugal posterolaterally.

Lamina descendens: The counterpart of the lamina ascendens, formed by the squamosal, and in capitosaurs usually closing the occipital face of the cheek.

Lamina supraoccipitalis: A continuous descending flange of the postparietal and tabular, forming the posterior face of the skull roof in occipital view.

Latera vertebrae: The smooth and concave flank of the cylindrical intercentrum.

Laterosphenoid roof: The medial and unpaired roof of the posteriormost portion of the sphenethmoid region, which in later stages fuses with the otic in *Mastodonsaurus*.

Meckelian window: The large fenestra on the lingual side of the mandible, bordered by prearticular, postsplenial, dentary, and angular.

Mentomandibular ossification: A paired bone in the symphysis, representing the anterior portion of the mentomeckelian, the primordial cartilage of the mandible in gnathostomes, which ran along the canalis primordialis (MM).

Otic horn: The ascending process of the otic by which the neurocranium contacts the postparietal and supratemporal.

Parapophysis: The rib articulation facet of the intercentrum.

Postglenoid area: The region posterior to the glenoid facet of the mandible

(PGA). This term was introduced (WARREN & BLACK 1985) to generally refer to this region without specifying by which elements it is formed.

Processus anterior: An anterior outgrowth of the epipterygoid.

Processus ascendens palatoquadrati: In its strict sense, this structure is confined to the embryonic and early larval stages of primitive tetrapods and the embryonic stages of amniotes. The ossified, late-ontogenetic counterpiece has long been referred to as the epipterygoid, although this ossification often encompasses more than just the processus ascendens palatoquadrati. In *Mastodonsaurus* the sphenethmoid process of the epipterygoid is most likely to represent an ossified portion of the processus ascendens.

Processus basalis: A posteromedial rudimentary process or simple facet rising from the epipterygoid footplate on its medial side.

Processus dorsalis: A rod-like, dorsomedial outgrowth of the epipterygoid connecting to the parietal lateral to the pineal foramen.

Processus hamatus: An anterodorsal extension of the glenoid area, formed by the articular, and framed by a dorsal ougrowth of the prearticular, forms a strong abutment against the quadrate trochlea.

Processus paroticus: An oblique, dorsolateral outgrowth of the exoccipital, which is blade-like in large capitosaurs and connects to the underside of the tabular; in older literature usually referred to as processus paroccipitalis.

Processus parasphenoidales: Posteromedial outgrowths of the vomers which underplate the cultriform process. In many capitosaurs these processes form prominent bulges, and are separated by a markedly countersunk area, the fodina vomeralis.

Processus posterior: A short and straight posterior outgrowth of the epipterygoid, by which the element connects to the lamina ascendens of the pterygoid.

Processus sphenethmoidalis: An anterodorsal process of the epipterygoid, connecting to the neurocranium in the sphenethmoid region, either by means of a simple abuttment, or sutural such as in *Mastodonsaurus*.

Processus submedullaris: A ventrally situated, anterior outgrowth of the exoccipital, situated below the foramen magnum and below the basioccipital rudiment of higher temnospondyls.

Processus subtympanicus: The process by which the exoccipital contacts the pterygoid in advanced capitosaurs.

Processus vomeralis: The ventral, posteriorly directed process of the premaxilla by which it connects to the vomer.

Processus uncinatus distalis: Crest or blade-like outgrowth of the stylus distal to the processus uncinatus proximalis and usually also distal to the main bending point of the rib.

Processus uncinatus proximalis: A crest or irregular outgrowth on the posterior flank of the dorsal rib face, proximal to the bending point of the stylus.

Stylus costae: The cylindrical shaft of the rib.

Sulcus accessorius: A short and blindly ending lateral sense canal immediately ventral and labial to the glenoid area, passing through the surangular and branching from the sulcus articularis.

Sulcus articularis: An oblique lateral sense canal running through the surangular and connecting the sulcus accessorius with the sulci dentalis and marginalis.

Sulcus dentalis: A long lateral sense canal running in parallel with the dental arcade of the mandible and passing through the surangular and dentary.

Sulcus infraorbitalis: The lateral sense canal lateral and ventral to the orbit, passing through squamosal, jugal, lacrimal, and maxilla.

Sulcus marginalis: A short lateral sense canal running through the angular and surangular, where it merges into the sulcus accessorius.

Sulcus supraorbitalis: The lateral sense canal medial and dorsal to the orbit, passing through premaxilla, nasal, lacrimal, prefrontal, frontal, postfrontal, postorbital and finally unites with the sulcus infraorbitalis on the jugal.

Sulcus temporalis: The lateral sense canal on the posterior skull table posteromedial to the orbit, passing through tabular, supratemporal, and postorbital, where it merges into the sulcus supraorbitalis.

Supinator process: An outgrowth of the anterodistal face of the humerus, facing anteroventrally. It is presumed that this process served as an attachment site for the supinator musculature, although the broad size and shape spectrum among early tetrapods and stem-amniotes suggests that this interpretation may not be universally correct.

Torus arcuatus: A bulge or thickening topping the labial wall of the adductor chamber and forming the labial margin of the adductor window, labial to the angulus adductoris.

Torus lingualis: A bulge or thickening topping the lingual wall of the adductor chamber and forming the labial margin of the adductor window.

Tuber articularis: The attachment site for the neural arch, in most intercentra situated dorsal and posterior to the facies pleurocentri.

Tuberculum: The dorsal facet on the head of the rib which articulates with the diapophysis.

Ventral proximal head: A stilette-like protuberance of the stapedial head ventral to the footplate, and usually separated from the latter, forming an articulation with the crista parapterygoidea of the parasphenoid (VPH). Synonym: processus ventralis.

Plate 1

Skull of *Mastodonsaurus giganteus* (Jaeger, 1828) in dorsal view. This specimen was found in the alum mine at Gaildorf, and is the best preserved skull of this species among the finds made in the nineteenth century. Skull length 60 cm. SMNS 4698.

Plate 2

Skull of *Mastodonsaurus giganteus* in dorsal view. Best preserved specimen from Kupferzell, with completely preserved and uncrushed braincase. Skull length 60,5 cm. SMNS 54675. See also textfigures 1 and 9.

Plate 3

Skull of *Mastodonsaurus giganteus* in dorsal view. Kupferzell. Skull length 54,5 cm. SMNS 54678.

Plate 4

Skull of *Mastodonsaurus giganteus* in ventral view. Kupferzell. Same specimen as in plate 3.

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