A revision of *Askeptosaurus italicus* and other thalattosaurs from the European Triassic, the interrelationships of thalattosaurs, and their phylogenetic position within diapsid reptiles (Amniota, Eureptilia)

Dissertation
zur Erlangung des Grades

„Doktor
der Naturwissenschaften“

am Fachbereich Geowissenschaften
der Johannes Gutenberg-Universität
in Mainz

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geb. in Frankfurt am Main

Mainz, 2002

Tag der mündlichen Prüfung: 17.07.2002

Zusammenfassung: Thalattosaurier sind eine rein auf die Trias beschränkte Grupper mariner Diapsiden, die derzeit aus Nordamerika, Europa und China bekannt ist. Die europäischen Formen sind über längere Zeit vernachlässigt worden, was speziell für *Askeptosaurus italicus* aus der Mitteltrias des Monte San Giorgio gilt. Die hier durchgeführte anatomische Revision des Taxons ergibt einige Korrekturen im dorsalen Schädeldach, und ermöglicht erstmalig eine detaillierte Darstellung des ventralen Teils von Gaumen und Gehirnkapsel. Im postcranialen Skelett ergeben sich ebenfalls wichtige Korrekturen, so fehlt z. B. im Gegensatz zu bisherigen Annahmen ein Thyroidfenster im Becken. Weiterhin zeigt die Hand von *Askeptosaurus* eine intraspezifische Variation in der Verknöcherung.

Das aquatische Reptil *Endennasaurus acutirostris* aus dem Nor der Lombardei wird ebenfalls neu untersucht, speziell im Hinblick auf eine potenzielle Zugehörigkeit zu Thalattosauriern. Letzteres wird bestätigt, zudem werden einige Korrekturen im Schädel durchgeführt, so ist z.B. der für Thalattosaurier typische Prämaxillare/Frontale-Kontakt vorhanden. Im Postcranium wird u.a. erstmals die vollständige Phalangenformel für die Hand ermittelt.

Zwei weitere aquatische Trias-Reptilien werden ebenfalls untersucht. Zum einen ein bisher unbeschriebenes Postcranium eines relativ kleinen, hochschwänzigen Thalattosauriers aus der Obertrias von Österreich, der sehr viele Ähnlichkeiten mit dem chinesischen *Xinpusaurus* zeigt, und zum anderen die nur an Hand von Wirbeln bekannte Form *Blezingeria ichthyospondyla* aus dem Muschelkalk/Lettenkeuper der Germanischen Trias. Trotz einiger anatomischer Gemeinsamkeiten mit Thalattosauriern kann eine definitive Zugehörigkeit zu dieser Gruppe nicht bestätigt werden.

Zur Klärung der verwandtschaftlichen Position der Thalattosaurier innerhalb der diapsiden Reptilien wird eine computergestützte phylogenetische Analyse basaler Diapsiden unter der Verwendung von 182 Merkmalen und 31 Taxa durchgeführt. Thalattosaurier gruppieren sich hierbei außerhalb der Sauria, und zeigen zudem ein gewisses Signal zu einer Monophylie mit Ichthyosauriern. Weitere Ergebnisse sind eine Gruppierung von Schildkröten mit Lepidosauriern, ein Schwestergruppenverhältnis von Drepanosauriern und Kuehneosauriern außerhalb der Sauria, sowie der Verlust des unteren Schläfenbogens in der frühen Evolution der Diapsiden und dessen sekundäre Aquirierung innerhalb der Archo- und Lepidosauromorpha.

Eine Innengruppen-Analyse der Thalattosaurier ergibt auf der Basis von 35 Merkmalen eine basale Dichotomie, die *Endennasaurus* und die monophyletischen *Askeptosaurus/Anshunsaurus* von den übrigen Thalattosauriern abgrenzt. Die Monte San Giorgio-Taxa *Hescheleria* und *Clarazia* sind ebenfalls monophyletisch und zudem die Schwestergruppe zu *Thalattosaurus*. Die verbleibenden Thalattosaurier sind basal zu diesen drei Taxa positioniert, wobei der chinesische *Xinpusaurus* und der kalifornische *Nectosaurus* monophyletisch sind, und die Einbeziehung des österreichischen Thalattosauriers diesen innerhalb letzterer Taxa gruppiert. Auf der Basis dieser Ergebnisse wird ein vorläufiges biogeographisch-evolutives Szenario entworfen.

Eine Kiefermuskelrekonstruktion von *Askeptosaurus* ergibt eine eher plesiomorphe, von posterodorsal nach anteroventral verlaufende Schläfen-Muskulatur. Zusammen mit weiteren osteologischen Merkmalen resultiert daraus eine Konfiguration, die die effektivste Beißkaft bei nur gering geöffneten Kiefern erlaubt. Die lange Schnauze, der flache Kopf und der bewegliche Hals legen eine Jagdstrategie nahe, bei der die wahrscheinlich aus kleinen bis mittelgroßen Wirbeltieren bestehende Beute durch schnelle Seitwärtsbewegungen des Kopfes gefangen wurde. Die übrige aquatische Fortbewegung des Taxons bestand aus einer subundulatorischen Lokomotion ohne Beteiligung der Extremitäten. Im Gegensatz zu *Askeptosaurus* bevorzugte der vollständig zahnlose *Endennasaurus* vermutlich nur Invertebraten und kleine Wirbeltiere als Beute, und schien seine Extremitäten im Rahmen eines paraxialen „Pectoropelvical-Ruderns“ explizit mitbenutzt zu haben.

Abstract: Thalattosaurs represent a clade of marine reptiles that remained exclusively restricted to the Triassic period, and they are currently known from North America, Europe, and China. In the last decades, especially the European taxa were strongly neglected, and this is especially true for *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio. For that reason, a re-investigation of this taxon is conducted in the present study. The anatomical revision results in the correction of several cranial features, as well as in a much more detailed documentation of palate and braincase anatomy. Also in the postcranial skeleton several corrections are performed. It is shown, e.g., that a thyroid fenestra was absent in the pelvis, and moreover, *Askeptosaurus* shows intraspecific variation in the degree of carpal and phalangeal ossifications.

Next to *Askeptosaurus*, also the enigmatic reptile *Endennasaurus acutirostris* from the Norian of Lombardy is re-studied. The assumption that this taxon may belong to thalattosaurs is corroborated. Furthermore, several anatomical features are corrected as well. *Endennasaurus* shows, e.g., a contact between premaxilla and frontal, a configuration that is very typical for thalattosaurs. Also the postcranial skeleton is revised in detail, and for the first time, the phalangeal formula of the manus can be given.

Two further Triassic reptiles are investigated in this study. From the Upper Triassic of Austria, a formerly unknown thalattosaur postcranium is described, which shows strong resemblances to the Chinese taxon *Xinpusaurus*. Besides, the enigmatic taxon *Blezingeria ichthyospondyla* from the Germanic Triassic is re-studied. The taxon is only known from vertebrae, which make a systematic assignment difficult, and although there are similarities to the vertebrae of thalattosaurs, the lack of sufficient evidence precludes a definite assignment of the taxon to this clade.

Since the phylogenetic position of thalattosaurs within diapsid reptiles still remains controversial, a computer-aided, cladistic analysis is performed, including 31 basal diapsid taxa and 182 informative characters. Thalattosaurs turn out as the sister-taxon of the Sauria, and they show furthermore a signal towards a closer affinity to ichthyosaurs. Further results of the analysis are a monophyletic grouping of lepidosaurs and turtles, a monophyly of kuehneosaurs and drepanosaurs with a position outside the Sauria, as well as the loss of the lower temporal arcade in early diapsid evolution and its re-acquisition within archosauromorphs and lepidosauromorphs.

An analysis of thalattosaur ingroup relationships on the basis of 35 characters reveals that *Endennasaurus* and the monophyletic *Askeptosaurus* and *Anshunsaurus* are the sister-group of all other thalattosaurs. Among the latter, the Monte San Giorgio taxa *Clarazia* and *Hescheleria* are monophyletic and the sister-group of *Thalattosaurus*. The remaining thalattosaurs are positioned basally to this clade, whereas the Chinese *Xinpusaurus* and the Californian *Nectosaurus* are sister-taxa. The inclusion of the above mentioned Austrian thalattosaur places this taxon in a trichotomy together with *Xinpusaurus* and *Nectosaurus*. On the basis of these findings, a tentative evolutionay scenario is presented.

Finally, the restoration of the jaw muscles of *Askeptosaurus* results in a relatively plesiomorphic, posterodorsally to anteroventrally trending alignment of the cheek musculature. Along with further osteological features, this configuration allows the most effective bite force when the jaws are near to closure. With regard to the long snout, the low skull, and the movable neck, it is assumed that *Askeptosaurus* caught its prey, which probably consisted of small to medium-sized vertebrates, by lateral sweeps of the head. The way of aquatic locomotion can be assumed to have been axial-subundulatory, with no significant participation of the limbs. By contrast, *Endennasaurus* presumably fed on invertebrates and only occasionally on (very small) vertebrates, while the locomotory habits consisted of a so-called paraxial “pectoropelvical rowing”, in which mainly the extremities are used for propulsion.

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1. Introduction

1.1. History of research on thalattosaurs and the aim of the present study

At the end of the Palaeozoic, several different tetrapods like the Permian mesosaurs or the early diapsid *Claudiosaurus* became secondarily adapted to an aquatic mode of life, and this development continued during the early Mesozoic, when diverse groups such as eosauropterygians or ichthyosaurs originated and existed nearly until the end of the Cretaceous. There were, however, also groups of lower diversity like placodonts or thalattosaurs which remained restricted exclusively to the Triassic.

Thalattosaurs represent a clade of marine reptiles with modest specializations towards aquatic life, but with a notable ecological heterogenity. Typical anatomical features are an elongation of the premaxillae and thus a relatively large snout, as well as a small or absent upper temporal fenestra. While some species remained relatively small, others reached a total length of up to 3 m.

The first known taxa were *Thalattosaurus* and *Nectosaurus* from the upper Triassic of California, which had originally been described by MERRIAM (1904, 1905, 1908). *Thalattosaurus* is today also known from the lower/middle Triassic of British Columbia (NICHOLLS & BRINKMAN 1993). The taxon reaches a length of probably 3 m in total. The holotype of *Nectosaurus* appears to be much smaller, but some additional specimens suggest that the taxon may have also reached an equivalent size. On the basis of a re-preparation of the type specimens, NICHOLLS (1999) recently conducted a revision of *Nectosaurus* and *Thalattosaurus*.

Askeptosaurus from the Grenzbitumenzone (Anisian/Ladinian) of Monte San Giorgio, Switzerland/Italy, had been investigated by KUHN (1952) on the basis of three specimens. Later (KUHN-SCHNYDER 1960, 1971), he added some further anatomical details and corrected some of his previous assumptions. As a result, however, there are several contradictory statements today, like the presence or absence of a quadratojugal, and furthermore there is still a notable lack of anatomical knowledge. Although most of the specimens are only about 2 m long, some additional, incomplete specimens indicate a length of 3 m at least.

From the same locality, two further thalattosaur species are known, *Clarazia* and *Hescheleria*, each represented by only a single specimen and originally described by PEYER

(1936 a,b). Both are comparatively small (approximately 1 m in total) and show blunt and bulbous teeth. Later, RIEPPEL (1987) re-investigated the two taxa, but as there are no further specimens in different exposures, many details still must remain unknown.

From the Norian of Italy, RENESTO (1984) described *Endennasaurus*, which he investigated more detailed a few years later (RENESTO 1992). The author considered this very interesting form without any trace of teeth as a thalattosaur, and supposed affinities to *Askeptosaurus*. The animal is relatively small and reaches a total size of 1 m.

The lower/middle Triassic of British Columbia not only yielded another form of *Thalattosaurus* (see above), but also two new, very incomplete taxa of relatively small size (?1 m), *Agkistrognathus* and *Paralonectes*, as well as an additional undetermined form (NICHOLLS & BRINKMAN 1993). The incomplete preservation of *Agkistrognathus* and *Paralonectes* has hitherto hampered well-corroborated statements about their phylogenetic affinities.

From the Guizhou Province of China (?early late Triassic), two further thalattosaur taxa, *Anshunsaurus* and *Xinpusaurus*, have been recently described by RIEPPEL et al. (2000) and LIU & RIEPPEL (2001), respectively. While the former taxon closely resembles *Askeptosaurus* in size and morphology, the second species, which apparently grew also relatively large (MAISCH, pers. comm.), is slightly similar to forms like *Nectosaurus*.

The enigmatic and very incompletely known taxon *Blezingeria* from the Ladinian of the Germanic Triassic was for a long time considered to be an ichthyosaur (VON HUENE 1951), but in the last years, the informal view arose that this animal might be a thalattosaur (e.g. RIEPPEL 1998). If this is the case, *Blezingeria* would represent the only known thalattosaur from the Germanic Basin.

Additionally, there are several fragmentary records of thalattosaurs from the Norian of British Columbia (STORRS 1991), the Carnian of the Julian Alps (DALLA VECCHIA 1993), the middle/upper Triassic of Nevada (SANDER et al. 1994), and the Muschelkalk of Spain (RIEPPEL & HAGDORN 1998). In the present study , further remains of a thalattosaur from the Norian of Austria will be presented, and it should be noted that there is another Chinese thalattosaur housed in the Staatliches Museum für Naturkunde Stuttgart, which can currently not be described as it was obviously not legally exported.

The phylogenetic relationships between thalattosaurs have been discussed on various occasions, but up to now a consensus has not been achieved. Dependent on new findings and revisions, different families or suprafamilies were established, but computer-aided analyses had not been conducted prior to NICHOLLS (1999). In the last two years, two additional computational analyses were added (RIEPPEL et al. 2000, LIU & RIEPPEL 2001). All of them, however, present contradictory results.

The general position of thalattosaurs within amniotes is even more problematic. With the exception of KUHN-SCHNYDER (1988), there is a consensus that the group is of diapsid nature, but the more exact affinities are not clear. In former times, the group was considered to be lepidosaurian and should either belong to squamates or rhynchocephalians (KUHN 1952, ROMER 1956, VON HUENE 1957). Later, BENTON (1985) stated that thalattosaurs should be preliminarily regarded as Neodiapsida inc. sed., a view that was followed by RIEPPEL (1987) and NICHOLLS (1999). On the contrary , EVANS (1988) supposed archosauromorph affinities, while RIEPPEL (1998) suggested a nesting with sauropterygians. The problematical status of thalattosaurs is surely not only due to character incongruences, but also a result of incomplete preservation or poor anatomical knowledge of the better preserved specimens. Additionally, other aspects like, e.g., functional morphology have hitherto been completely neglected.

The purpose of the present investigation is to revise the anatomy of *Askeptosaurus*, *Endennasaurus*, and *Blezingeria*, as well as to describe the Norian thalattosaur from Austria. The taxa will be compared with other European representatives like *Clarazia* and *Hescheleria* and the thalattosaurs from North America and China. Additionally, a jaw-muscle restoration will be presented for *Askeptosaurus*, coupled with an interpretation of its functional morphology and autecology. The anatomical results will be used to evaluate the ingroup-relationships and palaeobiogeography of thalattosaurs, and to assess the phylogenetic position of thalattosaurs by entering them into a large-scale analysis of early diapsid reptiles.

1.2. Central Europe during the Triassic

Since in the present study faunal elements from the Triassic of Germany, Austria, Switzerland, and northern Italy will be investigated, a short introduction of the central European Triassic will be given. The following sections are mainly based on BEUTLER & SZULC (1999), PARRISH (1999), and RÜFFER (1999).

During the early Mesozoic, Central Europe was part of the supercontinent Pangaea, situated in its eastern part, slightly north of the equator, and formed the western most shoreline of the Tethyan ocean. Climatically, the large landmass Pangaea caused a so-called “megamonsoonal climate“, which means that each year must have included an extremely dry

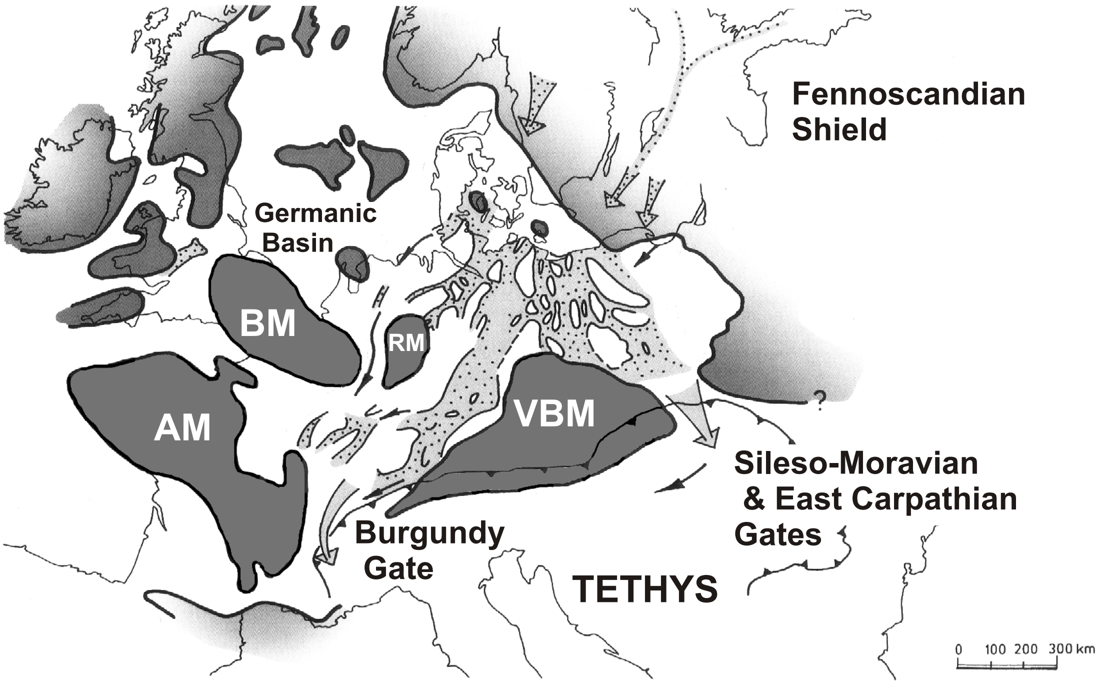


Fig. 1: Central Europe during the early Late Triassic (from BEUTLER & SZULC 1999, modified). AM: Armorican Massif, BM: Brabant Massif, RM: Rhenian Massif, and VBM: Vindelico-Bohemian Massif. For further details see text.

period and a prominent rainy season. The reason is that Pangaea was distributed on both hemispheres, and thus cooling in wintertime and warming in summertime were contrarily distributed in the north and the south of the continent. As a consequence, the difference between the high and low pressure zones caused air streaming across the equator and the Tethyan Ocean for most of the time, but the direction changed twice a year.

Contrarily to today, Central Europe did not completely consist of land, but was subdivided into a suite of different islands, separated from each other by an epicontinental sea, the Germanic Basin (fig. 1). The eastern border of the basin was formed by a large landmass, the Fennoscandian Shield, while the Vindelico-Bohemian Massif built the southern delimitation. The western part of the Germanic Basin was more heterogenously developed. In the west and southwest, the Armorican Massif, the Brabant Massif, and the Rhenian Massif formed differently sized islands, and in the northwest there were several other landmasses of varying size. In the middle and late Triassic, most of these islands formed a single, relatively large landmass. South of the Vindelico-Bohemian Massif and the Armorican Massif the Tethyan Ocean was located. Generally, the area of the Germanic Basin is today called “Germanic Triassic“, while the more southern, Tethyan region is named “Alpine Triassic“.

It is not clear whether the Germanic Basin had a marine connection to the Arctic Sea, but there were obviously several streets that connected the basin with the Tethyan Ocean, at latest from the beginning of the late early Triassic. In the eastern part, situated between the Fennoscandian Shield and the Vindelico-Bohemian Massif, the East Carpathian Gate and the Silesian-Moravian Gate formed such connections, and between the latter landmass and the Armorican Massif another street, the Burgundy Gate, was situated. During the remaining Triassic, the importance of the different streets changed. In the Anisian, the two eastern gates were the most influential seaways, while in the Ladinian and Carnian, the Burgundy Gate formed the main connection to the Tethys. In the late Carnian and Norian, the Germanic Basin was probably completely isolated from the Tethyan Ocean, but a re-connection took place during the Rhaethian global transgression. Additionally, there were also some western seaways to the proto-Atlantic Ocean, formed by several rift systems.

During the existence of the Germanic Basin very different sedimentary environments developed, caused both by global sea-level changes and regional tectonic events, like the opening of the proto-Atlantic Ocean. At early Triassic time (Unterer/Mittlerer Buntsandstein), a fluviatile-terrestrial sedimentation dominated, and a very restricted marine connection may have persisted only to the Arctic Sea. Later in the middle Scythian (Mittlerer/Oberer

Buntsandstein), when the East Carpathian Gate opened, an increasing Tethyan influence took place, resulting in prominent evaporitic and carbonatic sediments in the eastern Germanic basin. The marine transgression extended in the early middle Triassic (Unterer Muschelkalk) to the western part of the basin and resulted in the deposition of further carbonatic sediments, but then a global regression during middle Muschelkalk time changed the conditions into a more evaporitic environment. Beginning with the late Anisian (Oberer Muschelkalk), the Burgundy Gate opened and a major transgression filled the basin again with carbonates, and only in the northern parts the deposition of evaporites persisted. At this time, marine influence had reached its highest extent during the whole Triassic. On the contrary, the eastern part of the basin experienced clastic sedimentation caused by tectonic uplift of the eastern landmasses. Beginning with the late Ladinian (Lettenkeuper), a marine regression changed the environment into a very shallow epicontinental sea and caused a wide-ranging deposition of clastic, i.e. fluviatile and terrestrial, sediments, along with the successive formation of prominent evaporites (Gipskeuper). The above mentioned complete isolation from the Tethyan Ocean in the late Carnian and Norian (Mittlerer Keuper), which was only interrupted for very short intervals, increased the influence of terrestrial sedimentation. The scenery completely changed during the Rhaethian global transgression (Oberer Keuper), which again resulted in the deposition of marine sediments in the western part of the basin, while in the eastern region clastic sedimentation still persisted due to tectonic uplift. The sedimentation in the Germanic Basin was terminated by a regression in the late Rhaethian, resulting in the deposition of mainly limnic and brackish sediments.

Many facies of the Alpine Triassic distinctly differ from those of the Germanic Basin, mainly because fully marine environments often prevailed here. The following will be focussed on the northern Alpine Triassic, as the southern area will be considered in detail in the sections on Monte San Giorgio (see below).

The region of the Alpine Triassic originally represented a continental shelf. During early Scythian time, terrestrial clastic sedimentation dominated (“continental red-beds“), but later a marine transgression coming from southeastern direction resulted in the increasing deposition of shallow-marine siliciclastics, carbonates, and evaporites. During the transition to the Anisian, carbonatic/evaporitic sedimentation was present throughout the region. In the late Anisian, Tethyan influence increased and the conditions partially changed into an open-marine environment. There were pelagic platform-carbonates and a few turbidites, but also carbonatic intrashelf-basin sediments and shallow-marine deposits. At the Anisian/Ladinian boundary, reefs began to develop, resulting in the formation of bioclastic carbonates and related sediments typical for reefs and lagoons. Open-marine environments still existed, but they became restricted and were interestingly interrupted by short intervals of terrestrial sedimentation. The late Anisian development persisted and increased throughout the Ladinian, and prominent carbonate platforms constituted the major geomorphological element. During the transition to the Carnian, however, a notable terrestrial influence took place in the northern most part of the area, and prominent shales, but no clastics, were deposited. As a result, many intraplatform basins were filled with shales and platform detritus in the early Carnian, and productive reef environments existed only at the shelf margin, very close to the Tethyan Ocean. The filled basins and former carbonate platforms now experienced a time of extensive terrestrial sedimentation, i.e. shales and sandstones were being deposited, and only more in the south, shallow-marine carbonates were formed. In the late Carnian, however, the terrestrial influence decreased, and carbonates and evaporites were the prevailing sediments throughout the region. The development continued in the Norian and resulted in the formation of prominent carbonate platforms, lagoons, and reefs. Terrestrial influence returned at the transition to the Rhaethian, when shales and marls filled the shallow depressions between the Germanic Basin and the carbonate platforms of the Alpine Triassic. In some areas, also an extensive clastic sedimentation took place. Nevertheless, high-productive, carbonate-dominated depositional environments still persisted. At the transition to the Jurassic, the platforms drowned due to tectonic influence, and the conditions changed into a deep-marine environment.

1.3. The Monte San Giorgio

The Monte San Giorgio, which yields three different thalattosaur taxa (*Askeptosaurus*, *Clarazia*, *Hescheleria*), is situated in the southern part of Switzerland, Kanton Tessin, close to lake Lugano (fig. 2A). Some parts of the Monte San Giorgio area also belong to Italy, and the fossil-bearing horizons can be found on both sides of the border. Geologically, the Monte San Giorgio area is part of the Southern Alps, a S-vergent fold and thrust belt (FURRER 1995). Lithologically, the region consists of Palaeozoic basement ("Insubrisches Kristallin", i.e. gneisses and phyllites; late Carboniferous conglomerates; Permian lavas, pyroclastics, sandstones, conglomerates, and shales) and Mesozoic deposits (Triassic and Jurassic sediments, mainly carbonates but also shales or radiolarites). The latter are subdivided into a

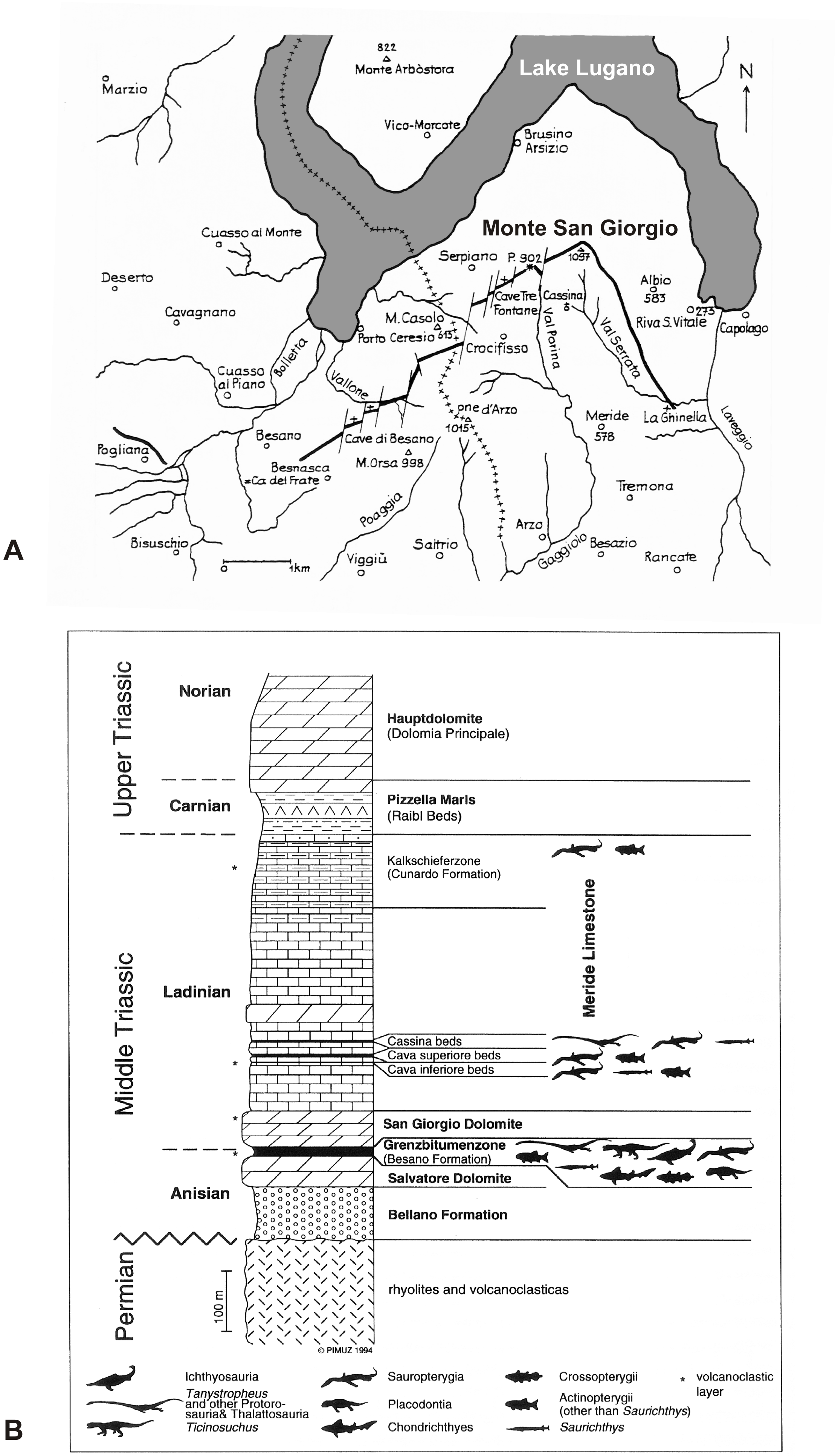


Fig. 2: A) topographic map of the Monte San Giorgio area (after BRINKMANN 1994, modified), B) stratigraphy of the Triassic sediments in the Monte San Giorgio area, with special reference to the vertebrate beds (from FURRER 1995).

short Anisian section, followed by Ladinian and upper Triassic layers (fig. 2B), and a termination formed by Jurassic strata of Liassic age. The major fossil-bearing horizon is the so-called “Grenzbitumenzone“(= Besano Formation, FURRER 1995), in which the Anisian/Ladinian boundary is situated. It is formed by 16 meters of interbedded dolomites, bituminous shales, and a few thin ash-fall tuffs (SANDER 1989a), distinguished by RIEBER (1973) into 190 respective beds. Approximately 85% of the Grenzbitumenzone are formed by the dolomite layers, and most of the remaining beds consist of bituminous shales. The thalattosaur taxa all come from different points of this formation (“Cave di Besano“, “Cava Tre Fontane“, “P. 902"). Tetrapods, however, were also found in middle and upper Ladinian strata, namely from three horizons in the lower part of the Meride Limestone (“Cava inferiore horizon“, “Cava superiore horizon“, “Alla Cassina horizon“; SANDER 1989a), and in the „Kalkschieferzone“ (Cunardo Formation; fig. 2B), the upper termination of the Meride Limestone (FURRER 1995).

The above mentioned bituminous layers of the Grenzbitumenzone yield a high amount of organic material, sometimes reaching up to 40%. For that reason, the fossil-bearing horizons also raised some economical interests. Between 1902 and 1946 the bituminous layers were mined, destilled, and a special oil, “Saurol“, was produced. The rentability, however, was too low and therefore mining and oil production were finally shut down.

The fossil potential of Monte San Giorgio had already been recognized by Italian scientists in the 19th century, and in the years 1863 and 1878, the Museo Civico di Storia Naturale di Milano conducted successful excavations in the Grenzbitumenzone (BRINKMANN 1994). Later, also Swiss palaeontologists began to do field work in the region, and it was BERNHARD PEYER who initiated professional excavations in 1924. The project was extended and continued until 1973, then under the supervision of EMIL KUHN-SCHNYDER, and covered all fossil horizons mentioned above. In recent years, some new excavations in the Ladinian Meride Limestone were started (FURRER 1999), mainly with the purpose to investigate the sedimentology and taphonomy of the fossil-bearing deposits. Furthermore, also Italian scientists are still working in different horizons of Monte San Giorgio (DAL SASSO, pers. comm., but see also LOMBARDO et al. 1999).

The mainly autochthonous Triassic fauna of Monte San Giorgio is world-famous for its diversity and importance (see e.g. BÜRGIN et al. 1989, or BRINKMANN 1994). Among invertebrates, foraminifers, ammonoids, nautiloids, bivalves, gastropods, crustaceans, echinoids, and conodonts are known. The vertebrate fauna consists of a suite of different actinopterygians (many still undescribed), chondrichtyhans, crossopterygians, and tetrapods. Among the latter, marine reptiles constitute the major part, and there are several very different forms like ichthyosaurs, pachypleurosaurs, nothosaurs, placodonts, thalattosaurs, and the enigmatic *Helveticosaurus*. The terrestrial elements are represented by the rauisuchian *Ticinosuchus* and the archosauromorphs *Tanystropheus* and *Macrocnemus*. Plant fossils are only rarely found.

1.4. The Monte San Giorgio area during middle Triassic time

Recently, FURRER (1995) presented a comprehensive scenario of the evolution of the Monte San Giorgio area from the late Anisian to the Carnian (see also fig. 3). If not noted otherwise, the following will refer to this study.

The Monte San Giorgio area represented an intraplatform basin in the southern part of the Alpine Triassic for most of the time of its existence. Between the continent and the Monte San Giorgio basin a lagoon must have been situated, while the Tethyan Ocean was in the south. In the Anisian, a marine transgression affected the area of the Western Lombardian Alps, and the result was the deposition of the first marine sediments of Monte San Giorgio, the Salvatore Dolomite, a shallow-marine carbonate overlying red sandstones, conglomerates, and shales of the (?early Anisian) Bellano Formation. As a consequence of tectonic activity associated with extensive volcanism during the latest Anisian and Ladinian, the Monte San Giorgio area was then split into several single carbonate platforms.

At the same time, a starved basin with restricted water circulation formed in the southern part of the region, the above mentioned Grenzbitumenzone (= Besano Formation; figs. 2B, 3). It represented a typical stagnation deposit, and the generally low sedimentation rate caused the impression of a high accumulation of vertebrate skeletons. There were no bioturbations, and the sediments were apparently deposited under permanently anoxic conditions within a time span of two to five Million years. The basin of the Grenzbitumenzone had a minimal diameter of 10 km and was not deeper than 150 m. Stenohaline invertebrates, whose existence usually requires normal marine surface water, indicate strong connections to the open sea. As far as known today, the vertebrate fauna of the Grenzbitumenzone consisted of at least 16 reptile taxa, three crossopterygians, 47 actinopterygians, and five chondrichthyans. The reptilian fauna in particular is represented by eosauropterygians, placodonts, thalattosaurs, ichthyosaurs, archosauromorphs,

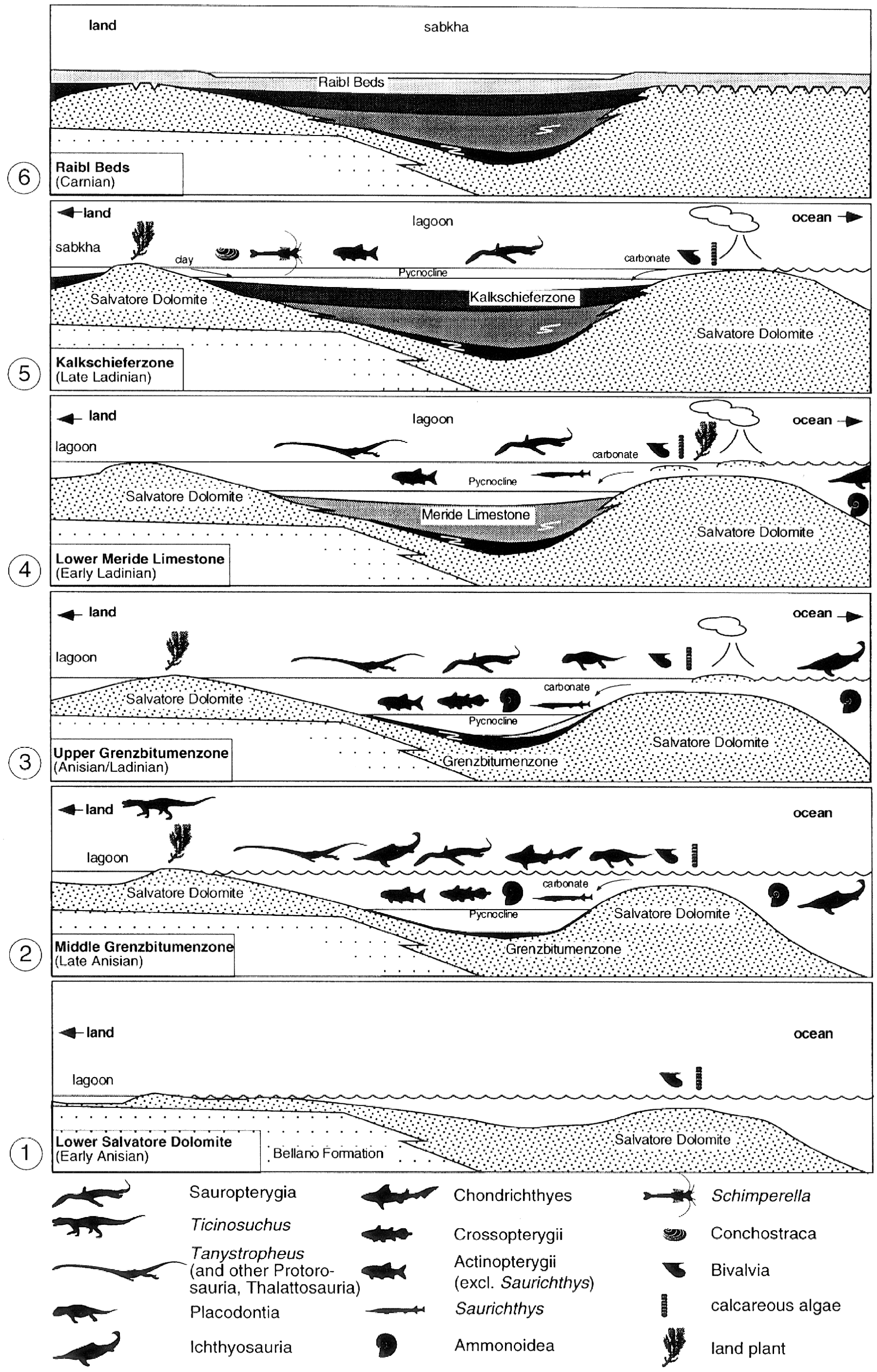


Fig. 3: The evolution of the Monte San Giorgio area during Triassic time (from FURRER 1995).

Helveticosaurus, and *Ticinosuchus*. Remarkably, the latter form is strictly terrestrial (like one of the archosauromorphs, *Macrocnemus*), but its presence is not surprising as also terrestrial plant material from small surrounding islands was apparently brought into the basin. Palaeoecologically, it is assumed that most of the Grenzbitumenzone vertebrates had a life style associated with reef habitats or other coastal areas (RIEPPEL 1993a). This is indicated both by a suite of different trophic specializations, especially among fishes, and the overall small size of most of the vertebrate fossils found, as well as a high intrageneric species diversity like in the actinopterygian genus *Saurichthys*. On the other hand, there were apparently also large epipelagic animals, e.g. the actinopterygian *Birgeria* or the ichthyosaur *Cymbospondylus*, but as they are more rarely found than the other taxa, it is probable that they only occasionally entered the basin.

During the remaining early Ladinian, the prominent carbonate formations of the San Giorgio Dolomite (60 m thick) and most of the Meride Limestone (400 to 600 m thick) were deposited in the basin (figs. 2B, 3). The lower part of the latter formation mainly consists of alternating micritic limestones and marls, occasionally interrupted by volcanoclastic beds. During this time, the area represented a deep basin environment with a carbonatic sedimentation below the normal wave base, and also turbidity and storm currents were sometimes deposited. A good connection to the open sea along with stenohaline surface waters only existed during short intervals. Bioturbation again was very rare, and the bottom of the basin must have been mainly of anoxic nature. The preserved vertebrate fauna of the three above mentioned horizons in the lower part of the Meride Limestone is relatively poor when compared to the Grenzbitumenzone. Until now, 16 actinopterygian species and two eosauropterygian taxa are known from the Cava inferiore and superiore beds, while the slightly younger Alla Cascina beds yield two eosauropterygians, two archosauromorphs, and two actinopterygians, indicating a very restricted environment. Remarkably, there are again small animals such as pachypleurosaurs and the actinopterygian *Saurichthys*, but also larger vertebrates like *Birgeria* and nothosaurs.

In the late Ladinian, the basin became increasingly shallow due to the continuous deposition of limestones, marls, and siliciclastic mud. The progressive filling of the basin resulted in a lagoonal environment, today known as the Kalkschieferzone (figs. 2B, 3), representing the termination of the Upper Meride Limestone and being the youngest fossil vertebrate locality of Monte San Giorgio. The laminated strata suggest that the sedimentation was obviously seasonally controlled by the monsoonal climate, i.e. a notable fresh-water influence occurred during the wet-season, while mud-cracked stromatolites and halite crystal casts indicate drier periods, along with carbonate sediments that must have been deposited under high salinity conditions. The bottom water of the lagoon again was anoxic and the region of organic productivity therefore very shallow, which resulted in a stable density stratification. The vertebrate fauna of the Kalkschieferzone again is comparatively poor, consisting currently of two (maybe only one, RIEPPEL 2000a) small species of sauropterygians and eight actinopterygian taxa lacking the large predator *Birgeria*.

At the transition to the Carnian, an increasing siliciclastic input, probably caused by the erosion of a southern Mobile Belt, strongly affected the carbonatic sedimentation of the lagoon. In the Carnian, the conditions had therefore changed into a sabkha environment with the local deposition of evaporites, and the Raibl Beds were formed. This period of detrital input corresponds to a general marine regression in the Alpine Triassic during Carnian time (see above).

1.5. Taphonomy

As mentioned already in the previous section, the high number of vertebrates in a relatively small horizon like the Grenzbitumenzone is most probably not the result of sudden mass extinctions or similar scenarios, but only due to a usual attritional mortality coupled with a low sedimentation rate, causing a considerable time-averaging. Further taphonomical investigations, however, have so far only rarely been conducted for the Monte San Giorgio area. SANDER (1989a) presented a detailed study of the carcass positions of *Neusticosaurus* from the fossil localities of the Lower Meride Limestone, but a similar analysis is lacking for the Grenzbitumenzone. For that reason, although the following refers to SANDER (1989a), one must be aware that there may be some differences concerning the taphonomy of the vertebrates from the Grenzbitumenzone, and therefore also for the thalattosaurs from that horizon.

The *Neusticosaurus* specimens are mainly preserved in a dorsoventral position, only in a very few cases a lateral exposure is observed. The orientation of the vertebral column is mostly straight, the forelimbs are apressed to the body, and the hindlimbs are obliquely oriented, with either a more anterior or more posterior direction, a typical position of many relaxed and floating tetrapods as well as “Wasserleichen“ (WUTTKE 1988a). The long neck of the *Neusticosaurus* specimens often shows a certain degree of curvature, whereas this degree varies considerably. In some cases, the single skeletal elements are isolated from each other, although the animal is still complete. A notable lack of completeness can generally be recognized only for the elements of the manus and for parts of the tail. SANDER (1989a) was able to combine all the different preservational stages of the tail into a decay series: complete tails, tails with one break, tails with several breaks, the loss of several elements, and the complete disarticulation into discrete vertebrae and haemal arches. The author interpreted his observations as a result of a carcass positioning in weak bottom currents under anoxic conditions. After the carcass sank to the bottom, it would be oriented according to weak oscillatory currents. As the basin was relatively deep, a rising of the carcass back to the surface was not possible because water pressure was stronger than the gas pressure in the abdominal cavity of the dead animal. The trunk of the body soon became anchored, and the neck was still able to swing freely above the bottom due to its greater buoyancy as resulted from the large eyeballs. Consequently, the neck often became differently oriented in comparison to the trunk. Dependent on the degree of microbial decay, the carcass then became more or less disarticulated. The fact that usually no limb, head, or neck is missing, may be explicable by the anoxic conditions on the bottom of the basin, preventing that another animal could swim downward and eat parts of the carcass. Breakage of bones occurred later during compaction and diagenesis of the sediment.

The number of preserved thalattosaur specimens from the Grenzbitumenzone is much lower than that of *Neusticosaurus,* and therefore a statistical analysis of the carcass positions would be useless. Anyhow, it can be noted that the *Askeptosaurus* specimens are generally fairly complete (with the occasional exception of autopodium and tail). The vertebral columm and the tail are usually preserved in lateral view, which probably is the result of the relatively high neural spines. On the contrary, skull, girdle, and limb elements are mostly dorsoventrally exposed and only rarely preserved laterally. Additionally, stages of considerable disarticulation occur, and the neck of *Askeptosaurus* is always recurved, while the remaining vertebral column is mostly straight. The two single specimens of *Clarazia* and *Hescheleria* are roughly dorsoventrally and laterally positioned, respectively, whereas the elements of the latter animal are fully isolated from each other. Although further investigations are surely needed, it seems that SANDER´s (1989a) taphonomical scenario can at least partially be assumed also for the thalattosaurs from the Grenzbitumenzone. The slight contradictions in the position of the vertebral column are likely due to anatomical differences between thalattosaurs and *Neusticosaurus*.

There are only a few records for soft-part preservation among the fossils of Monte San Giorgio. SANDER (1989a) reports on several cases in *Neusticosaurus*, i.e. the partial preservation of scales, integument, eyeballs, and undefinable stomach contents. While the originally keratinous scales are now of apatitic nature (for unknown reasons), the remaining preserved kinds of soft-parts are actually fossilized bacterial mats that replaced the original tissue, as it has been observed in the Eocene fossils of the Grube Messel (WUTTKE 1988b).

2. Methods & Abbrevations

2.1. Methods

The anatomical investigations were conducted either macroscopically or by using the stereo microscopes of the respective institutions where the investigated material is housed. Drawings of the smaller specimens were done by using a camera lucida, while the larger fossils like, e.g., the *Askeptosaurus* specimens, were drawn on the basis of photographs that were either taken personally or by HEINZ LANZ (Zürich). A ROTRING RAPIDOGRAPH (0.25 and 0.35 mm) served as major drawing tool. The three-dimensional restorations of skull, pectoral and pelvic girdle were modelled with wax. The presented restorations are based on these wax models, with exception of the reconstruction of the complete skeleton, which was performed only on the basis of drawings. Biometric data were ascertained by using a slide gauge, and the ratios were calculated with the software package MICROSOFT EXCEL2000 (see chapter 3.2 for a definition of the respective measurements). Dissections of extant lizards were conducted personally under a WILD M3Z stereo microscope equipped with a camera lucida. The phylogenetic analyses were performed by using the software package PAUP* 4.0b8 (SWOFFORD 2001; see also chapters 4.1 & 4.2).

Lists of the investigated material will be presented in the respective chapters.

2.2. Institutional abbrevations

GPIM: Geologisch-Paläontologisches Institut der Universität Mainz; **GPIT:** Geologisch-Paläontologisches Institut der Universität Tübingen; **PIMUZ:** Paläontologisches Institut und Museum der Universität Zürich; **MMHI:** Muschelkalk Museum Hagdorn Ingelfingen; **MSNM:** Museo Civico di Storia Naturale Milano; **MSNB:** Museo Civico di Scienze Naturali “Enrico Caffi” Bergamo; **SMNS:** Staatliches Museum für Naturkunde Stuttgart; **UCMP:** University of California Museum of Paleontology Berkeley; **ZFMK:** Zoologisches Forschungsinstitut und Museum Alexander Koenig Bonn.

2.3. Anatomical abbrevations

act: acetabulum; **ang:** angular; **ant pr:** additional anterior process of the cervical rib; **ar:** articular; **as:** astragalus; **at ic:** atlas intercentrum; **at na:** atlas neural arch; **at rb:** atlas rib; **ax:** axis; **ax rb:** axis rib; **BA:** bodenaponeurosis; **bas tub:** basal tubercle; **bpt pr:** basipterygoid process; **bs:** basisphenoid; **bo:** basioccipital; **c:** coronoid; **ca:** calcaneum; **cd rb:** caudal rib; **cl:** clavicle; **cn:** centrale; **co:** coracoid; **co fo:** coracoid foramen; **cul pr:** cultriform process; **cv rb:** cervical rib; **d:** dentary; **dc:** distal carpal; **dp cr:** deltopectoral crest; **dt:** distal tarsal; **ec:** ectopterygoid; **ect gr:** ectepicondylar groove; **ept:** epipterygoid; **EPX:** epaxial neck musculature; **eo:** exoccipital; **f:** frontal; **fe:** femur; **fen vest:** fenestra vestibuli; **fi:** fibula; **gl:** glenoid; **gst:** gastral rib; **ha:** haemal arch (chevron); **ha f:** haemal arch facet; **hu:** humerus; **hy:** hyoid; **hyp fo:** hypoglossal foramen; **ic:** intercentrum; **icl:** interclavicle; **il:** ilium; **in:** intermedium; **int trc:** internal trochanter; **is:** ischium; **j:** jugal; **l:** lacrimal; **m:** maxilla; **MAMEM:** musculus adductor mandibulae externus medialis; **MAMEM3A:** 3a-head of the musculus adductor mandibulae externus medialis; **MAMEP:** musculus adductor mandibulae externus profundus; **MAMES:** musculus adductor mandibulae externus superficialis; **MAP:** musculus adductor posterior; **MDM:** musculus depressor mandibulae; **MLAO:** musculus levator anguli oris; **mnd:** mandible; **MPSP:** musculus pseudotemporalis profundus; **MPSPA:** anterior profundus portion; **MPSPP:** posterior profundus portion; **MPSS:** musculus pseudotemporalis superficialis; **MPT:** musculus pterygoideus; **mc:** metacarpal; **met fi:** metotic fissure; **mt:** metatarsal; **n:** nasal; **na:** neural arch; **na f:** neural arch facet; **ncs:** neurocentral suture; **obt fo:** obturator foramen; **ol:** olecranon; **op:** opisthotic; **op ve ra:** opisthotic ventral ramus; **p:** parietal; **pl:** palatine; **pm:** premaxilla; **pra:** prearticular; **prf:** prefrontal; **pob:** postorbital; **pof:** postfrontal; **poz:** postzygapophysis; **pro:** prootic; **prat:** proatlas; **pro cr:** prootic crest; **prz:** prezygapophysis; **pt:** pterygoid; **ps-bs:** parabasisphenoid; **pu:** pubis; **q:** quadrate; **QMX:** quadratomaxillary ligament; **ra:** radius; **rb:** rib; **rb f:** rib facet; **RPT:** rictal plate; **s:** stapes; **sang:** surangular; **sc:** scapula; **scl:** scleral ossicles; **sc rb:** sacral rib; **sm:** septomaxilla; **sp:** splenial; **soc:** supraoccipital; **sq:** squamosal; **st:** supratemporal; **ti:** tibia; **tr pr:** transverse process; **trc 4:** 4th trochanter; **tri cr:** crest for the triceps muscle; **ul:** ulna; **uln:** ulnare; **v:** vomer; **V2:** palatal branch of the trigeminal nerve; **V3:** mandibular branch of the trigeminal nerve; **V3d:** posteroventral offshoot of the mandibular branch of the trigeminal nerve; **vid can:** vidian canal.

3. Results

3.1. The osteology of *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio

The marine reptile *Askeptosaurus italicus* is exclusively known from the Anisian/Ladinian Grenzbitumenzone of Monte San Giorgio, and was originally described by NOPSCA (1925) on the basis of very fragmentary postcranial remains from Besano, the Italian part of Monte San Giorgio. In subsequent years, better preserved, completely articulated specimens were recovered and prepared by Swiss palaeontologists. As a result, three additional specimens were then described by KUHN (1952). Later (KUHN-SCHNYDER 1960, 1971), the author also added further information on palate and shoulder girdle. As already illustrated in chapter 1.1, however, many anatomical details still remained only superficially known, and in some respects, e.g. braincase morphology, knowledge was almost completely lacking. In the last decades, several additional specimens have been prepared by the staff of the Paläontologisches Institut und Museum der Universität Zürich, and therefore the necessary revision of the anatomy of *Askeptosaurus*, which will be conducted in the following chapter, can be based on more material than previously possible.

Eureptilia OLSON 1847
Diapsida OSBORN 1903
Thalattosauriformes NICHOLLS 1999

Askeptosaurus italicus NOPSCA 1925

Material (see also figs. 4-7): MSNM V456 (Cava di Besano, Minerale matto), well-preserved, almost complete skeleton (fig. 4); V3931 (Cava di Besano), slab and counterslab of a disarticulated, badly preserved skeleton; V3550 (Cava di Besano), holotype consisting of an isolated ilium as well as a few ribs; PIMUZ T 0050 (Valle Stelle, sopra Minerale 1), badly preserved skeleton; T 1554 (pt. 902, stratum 141/24) unprepared skeleton; T 1830/1830a (Cave di Besano) slab and counterslab of a skeleton, badly preserved; T 4831 (Valle Stelle), complete skeleton, well-preserved (fig. 5); T 4832 (Cava Tre Fontane, Minerale del Sasso 1), complete but disarticulated skeleton, relatively well-preserved (fig. 6); T 4839 (Cava Tre

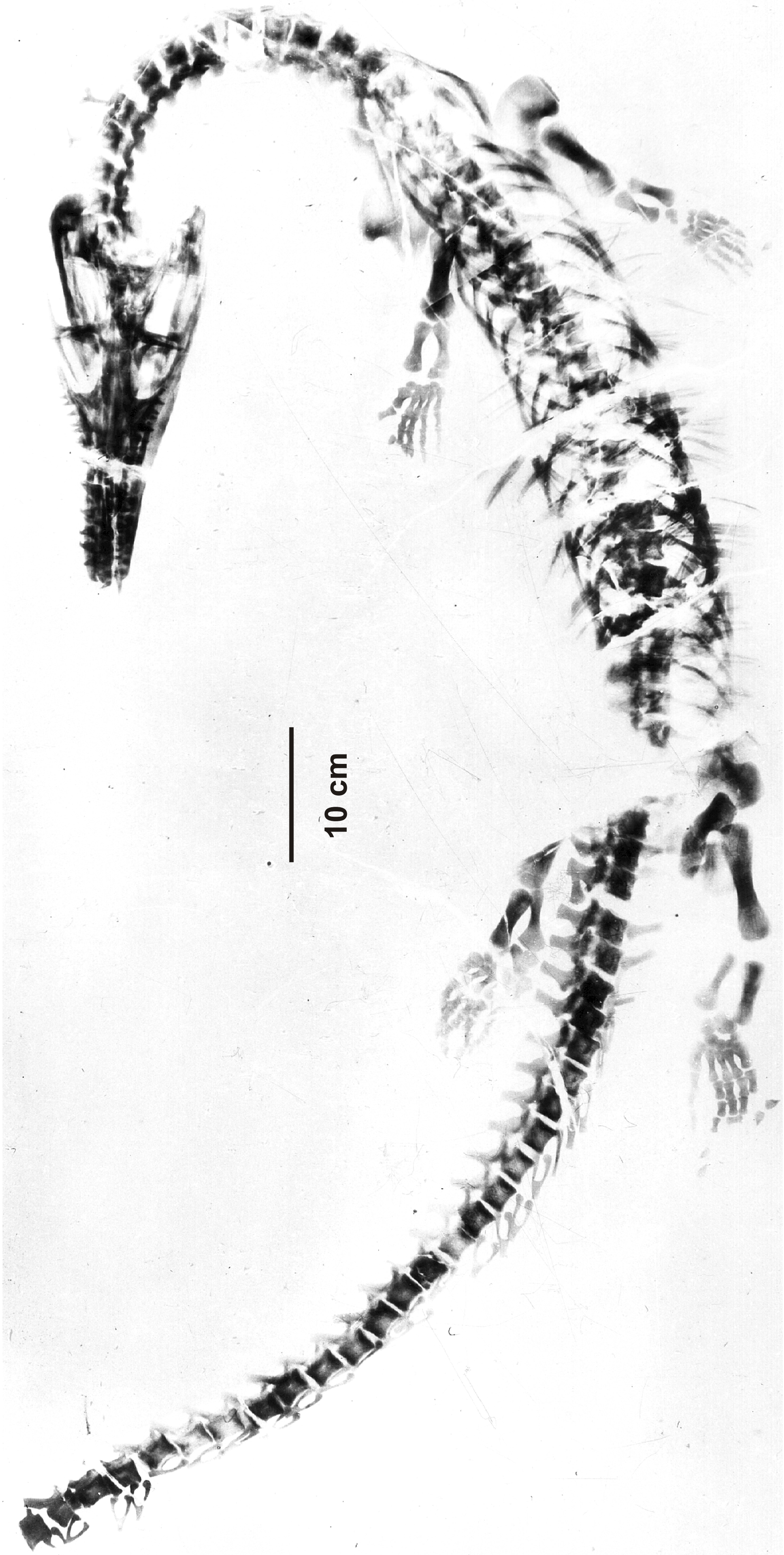


Fig. 4: *Askeptosaurus italicus*, x-ray photograph of MSNM V456 (preserved in dorsal view).

Fig. 5: *Askeptosaurus italicus*, PIMUZ T 4831, preserved mainly in lateral view (posterior part of the tail omitted).

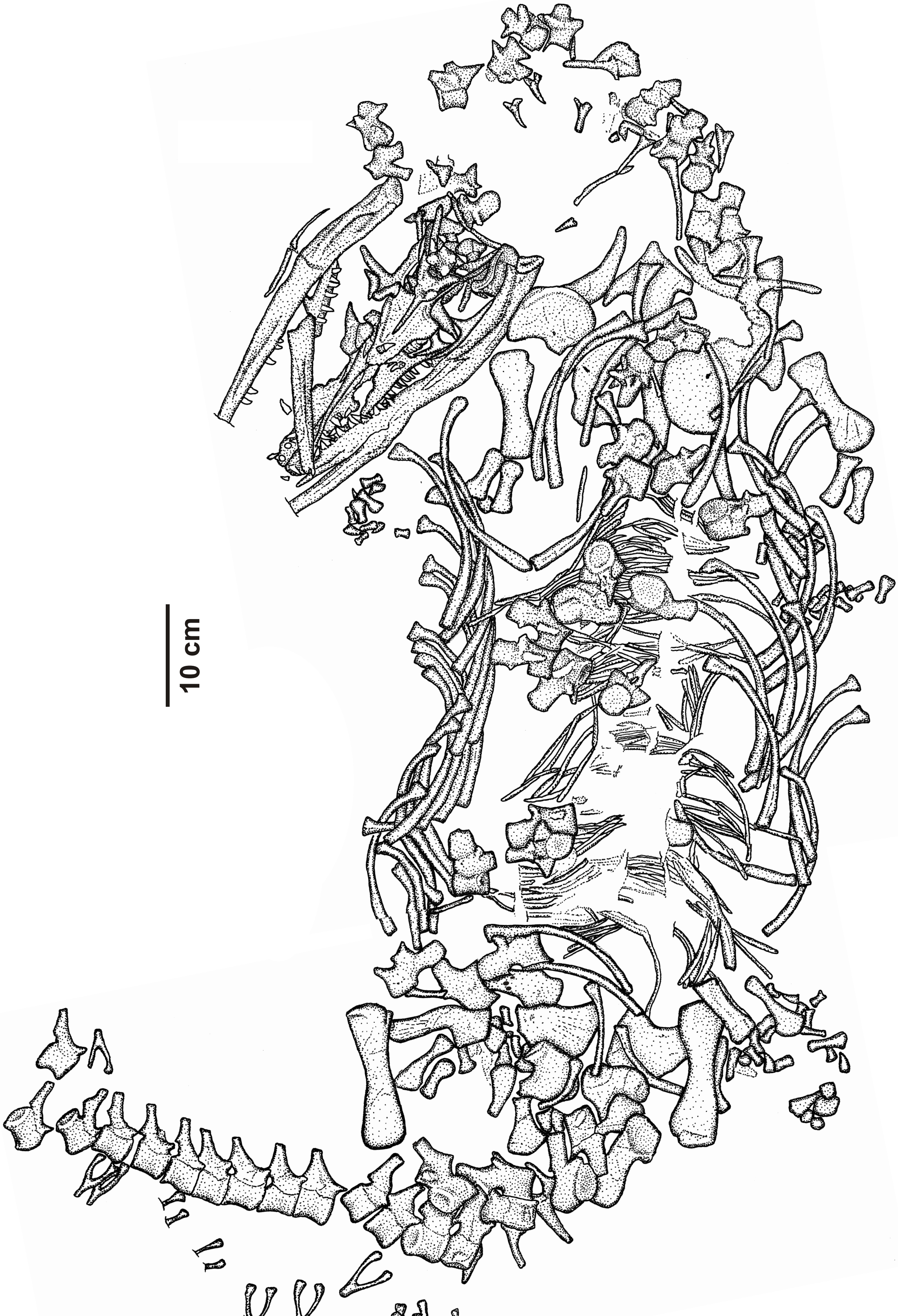


Fig. 6: *Askeptosaurus italicus*, PIMUZ T 4832, specimen preserved in ventral view.

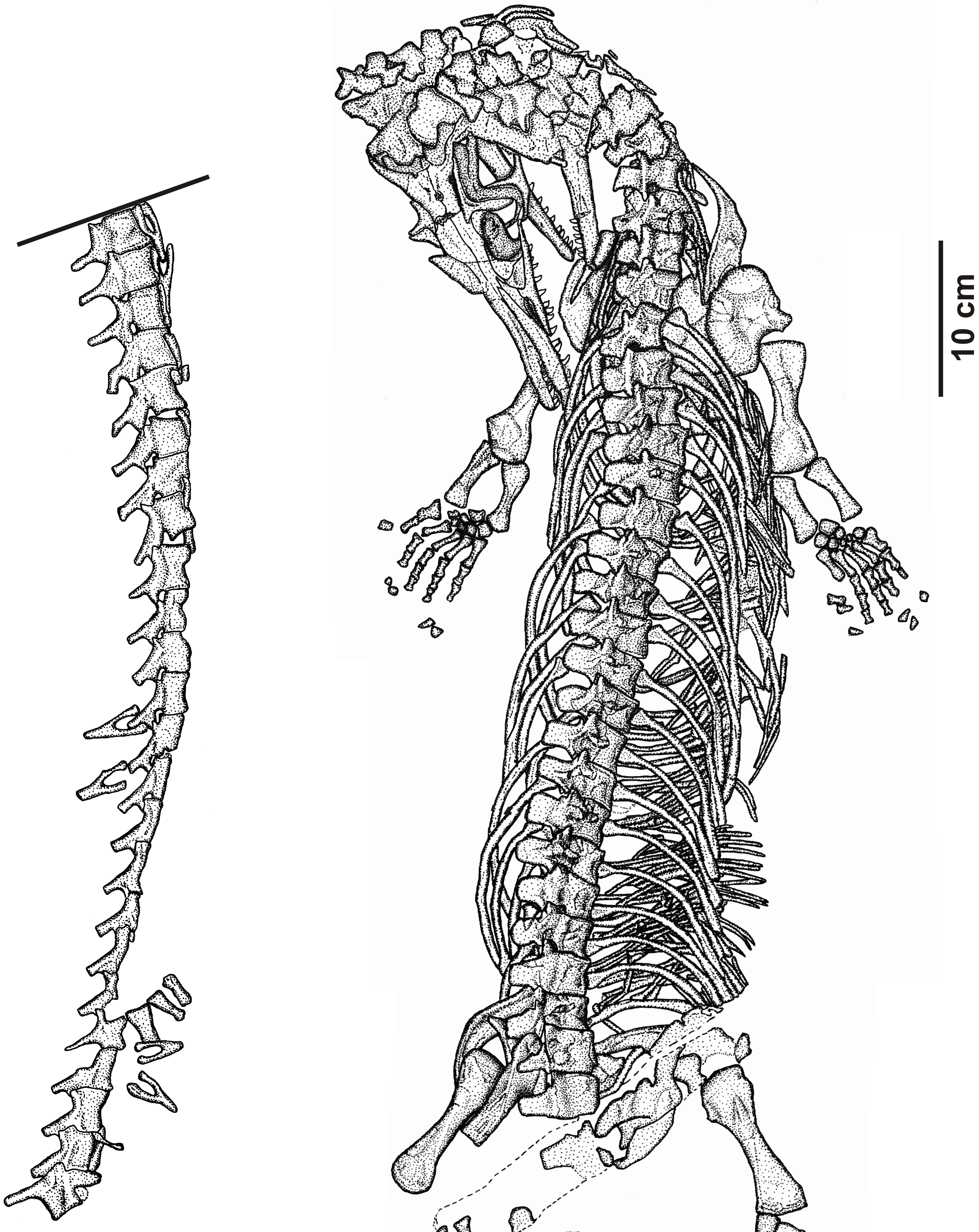


Fig. 7: *Askeptosaurus italicus*, PIMUZ T 4846, specimen preserved in dorsolateral view.

Fontane), badly preserved skeleton; T 4840 (Valle Stelle, Minerale del Sasso 1), badly preserved skeleton; T 4842 (Cave Tre Fontane, Minerale del Sasso 1), relatively well-preserved, but mostly disarticulated skeleton; 4846 (Cava Tre Fontane, Corso sop. Min: Nu.) well-preserved, complete skeleton (fig. 7); T 5392 (Cava Tre Fontane, Minerale del Sasso), slab and counterslab of a skull, badly preserved; T 5392 (Valle Stelle), isolated trunk fragments, badly preserved.

Locality and horizon: Grenzbitumenzone (Anisian/Ladinian) of Monte San Giorgio, Switzerland/Italy.

Diagnosis: large thalattosaur with a maximum length of at least 3m; skull flat and with a distinctly elongated, straight rostrum; premaxilla/frontal contact present; lacrimal/frontal contact present; frontal/supratemporal contact absent; postorbital and postfrontal unfused; upper temporal fenestra very small, slit-like; quadratojugal absent, lower temporal bar therefore interrupted; teeth in the upper and lower jaw sharp and homogenously developed, no diastema; palatal dentition absent; neck elongated with at least 13 cervical vertebrae; at least 25 thoracal, 2 sacral, and more than 60 caudal vertebrae; cervical ribs double-headed and with an additional anterior process; neural spines broad and low; pelvic girdle without a thyroid fenestra; limbs short and stout; manus with a variably reduced degree of ossification; pes also with reduced ossification, but not variable among specimens.

Anatomical description

3.1.1. The skull (figs. 8-13)

The restoration of the skull (fig. 8) shows that *Askeptosaurus* possessed a very slender and relatively flattened skull. The snout was significantly elongated, the orbits were comparatively large, and the posterior skull table was greatly emarginated. Further notable features are a posterior shifting of the external nares as well as a slit-like upper temporal fenestra. A quadratojugal, whose probable existence was proposed by KUHN (1952), is not present. The so-called “quadratojugal“ in specimen PIMUZ T 4831, supposed to be a broken piece of bone by RIEPPEL (1987) and NICHOLLS (1999), is in fact the squamosal (fig. 9; but see also below).

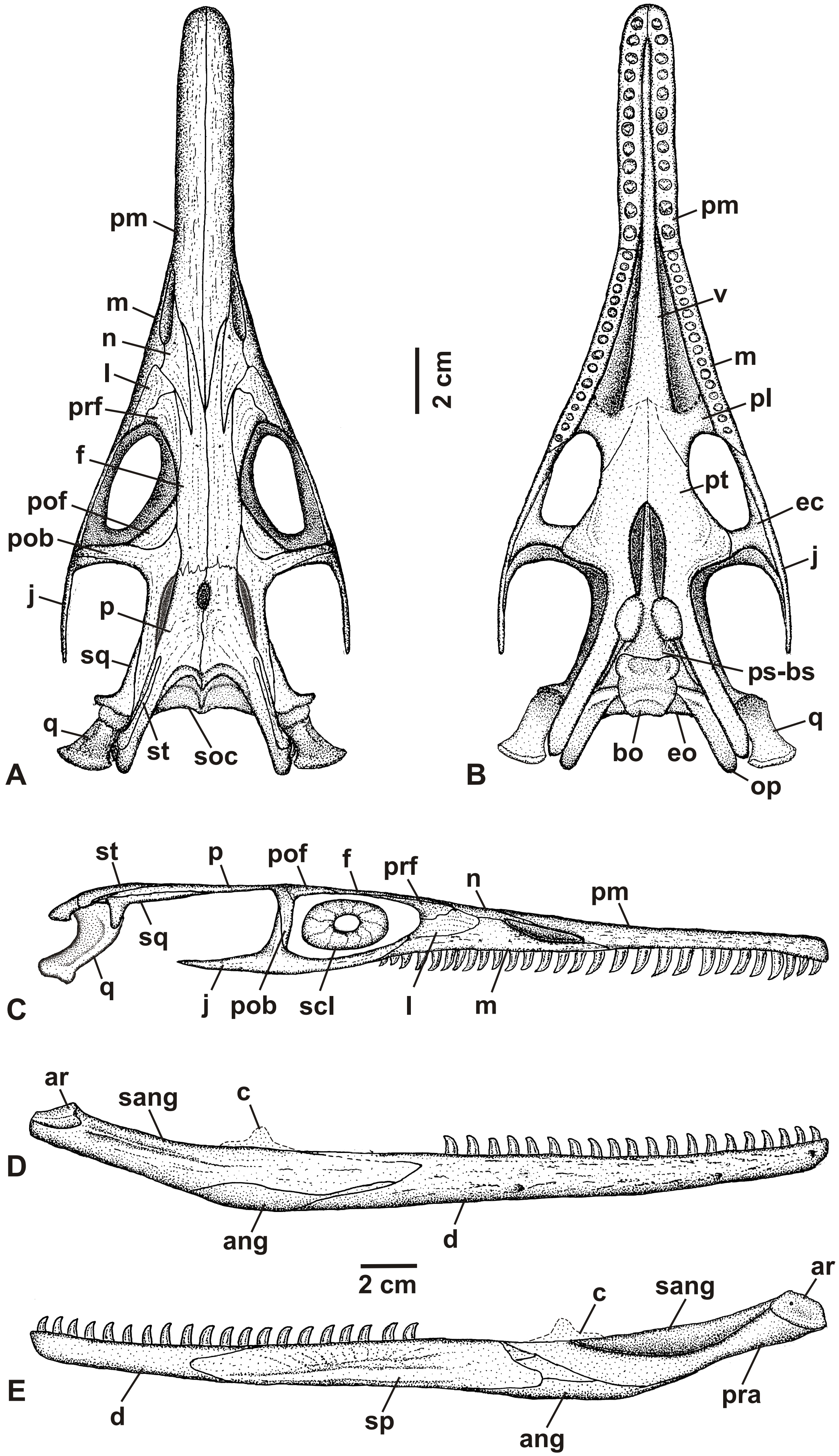


Fig.8: *Askeptosaurus italicus,* restoration of skull and mandible. A) dorsal view, B) ventral view, and C) lateral view of skull. D) lateral and E) medial view of lower jaw.

3.1.1.1. Skull roof and cheek (figs. 8A, C)

The bones of the skull roof and the cheek are among the best preserved portions of *Askeptosaurus*. The following description is mainly based on specimens PIMUZ T 4831 (fig. 9), MSNM V456 (fig. 10), PIMUZ T 4846 (fig. 11; the latter three specimens mainly display the external side), and PIMUZ T 4832 (fig. 12; this specimen shows the internal side).

Premaxilla

The paired premaxillae are preserved in dorsal and ventral view. As is typical in all thalattosauriform reptiles, they are slender and rather elongated elements, reaching nearly one half of the whole skull length. The bones meet each other in a straight suture. In the upper jaw, the premaxillae form more than one third of the tooth row. In dorsal view, the bones define the anteromedial margin of the external nares. They possess gradually tapering and sharply pointed posterior processes that contact the anteromedial processes of the frontals, thus separating the nasals from each other. The rostral tips of the bones are rounded and slightly tapered, the snout is therefore relatively small. In the mid region, the premaxillae meet the maxillae dorsolaterally in a posteromedially directed suture, extending to the anterior margin of the external nares. There is only a small area contacting the nasals which is situated at the medial margin of the nares, but for the most part the bones are separated by the anteromedial processes of the frontals. Laterally, the premaxillae show several depressions in which the teeth of the dentaries obviously fitted during closure of the jaw. Dorsally, the bones show several straight, craniocaudally directed striations throughout their whole surface. In ventral view, the premaxillae extend far medially, meeting each other in the rostral area. The bones bear 6 to 11 teeth, respectively, taking the empty alveoles into account, the maximum number may have reached at least 12. In the rostral portion, the tooth implantations are shifted into the median area of each bone. Unfortunately, it could not be determined whether the position of the alveoles changes more posteriorly. Tooth implantation is pleurothecodont (sensu EDMUND 1969), the teeth are unicuspid and apically recurved, the anteriormost ones being smaller than the others. There is a certain kind of striation present in the apical area of each tooth. Approximately one half to two thirds of each tooth reaches above the edge of the ventral margin of the premaxillae.

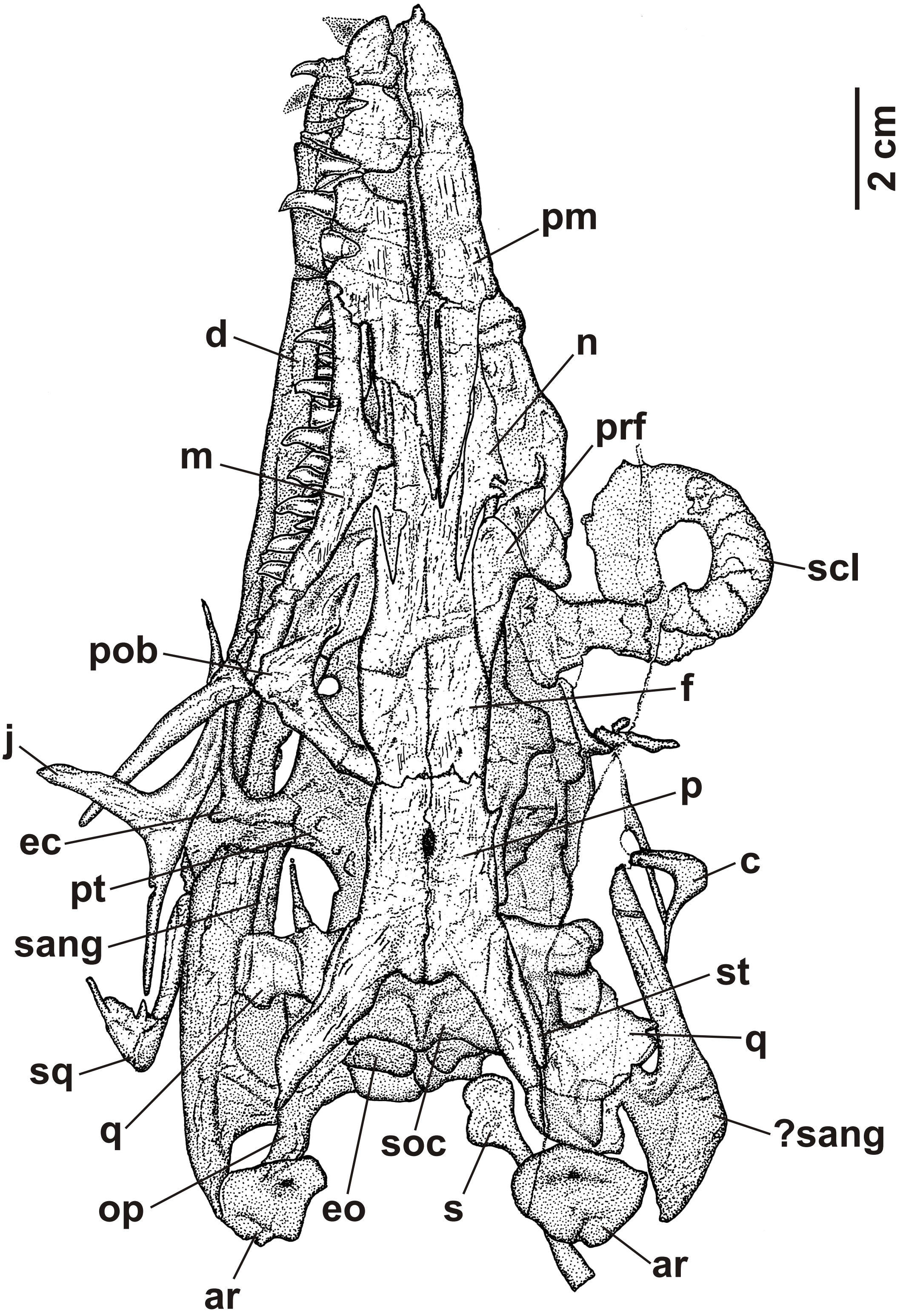


Fig. 9: *Askeptosaurus italicus*, skull of PIMUZ T 4831 in dorsal view.

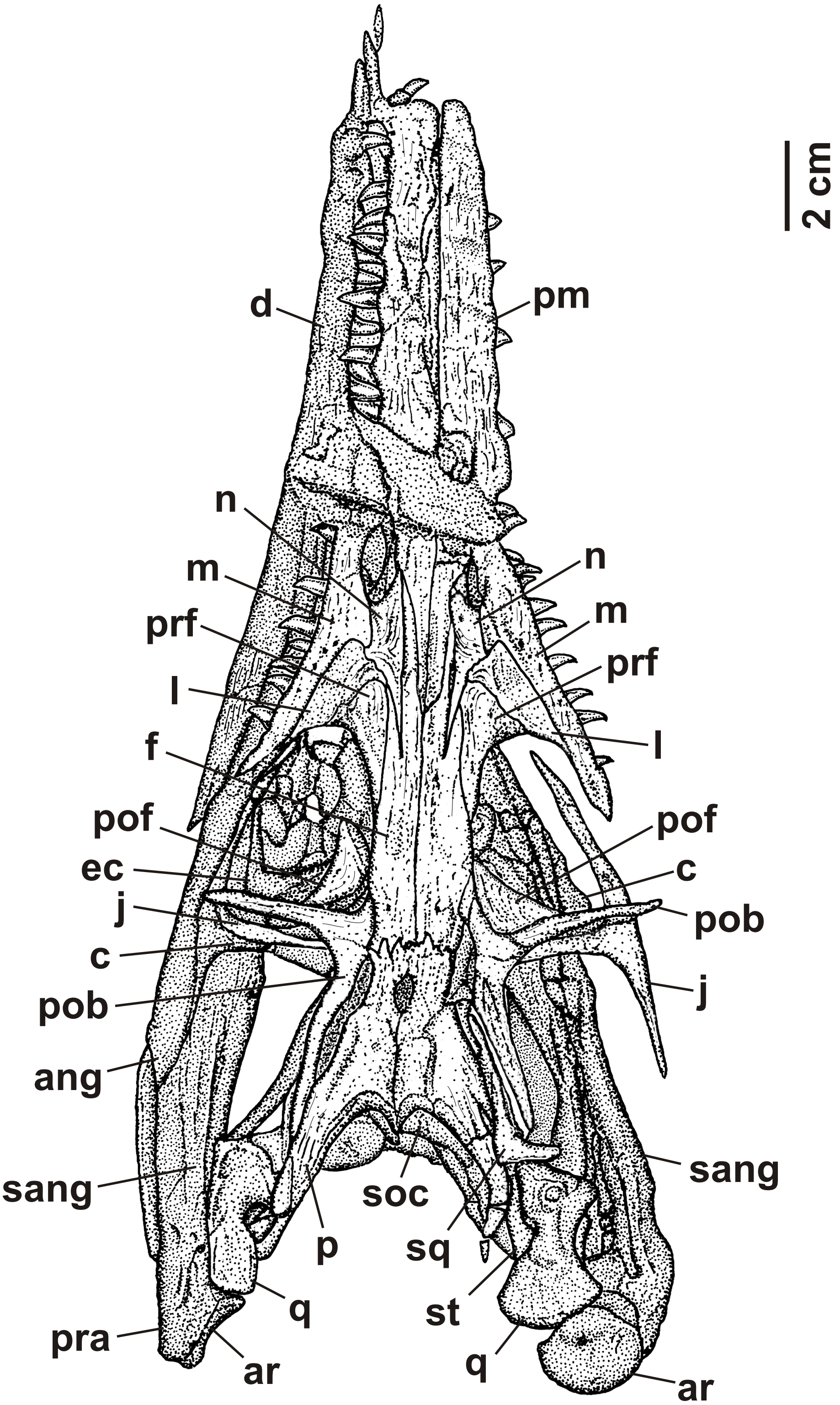


Fig. 10: *Askeptosaurus italicus,* skull of MSNM V456 in dorsal view.

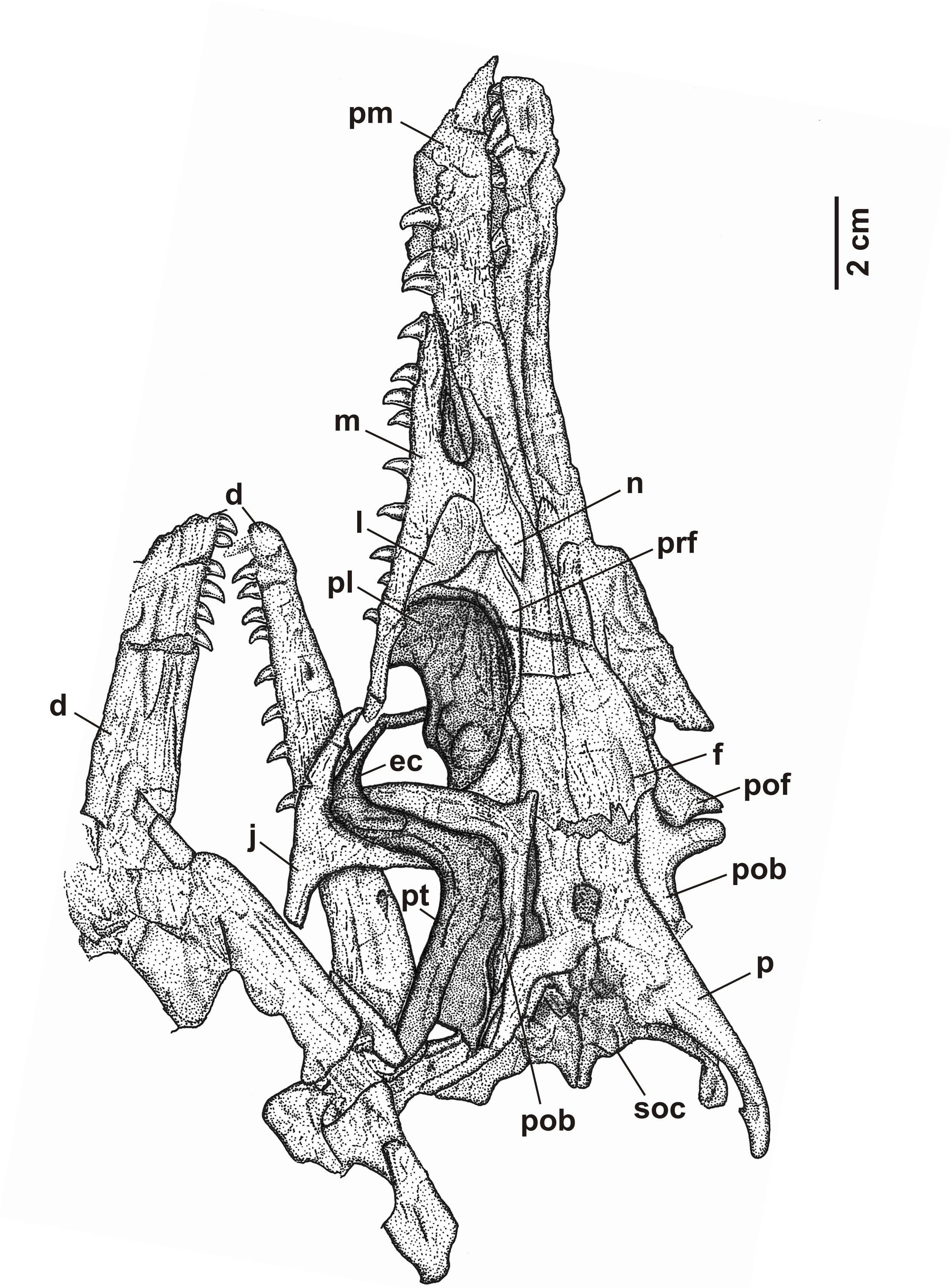


Fig. 11: *Askeptosaurus italicus,* skull of PIMUZ T 4846 in dorsolateral view.

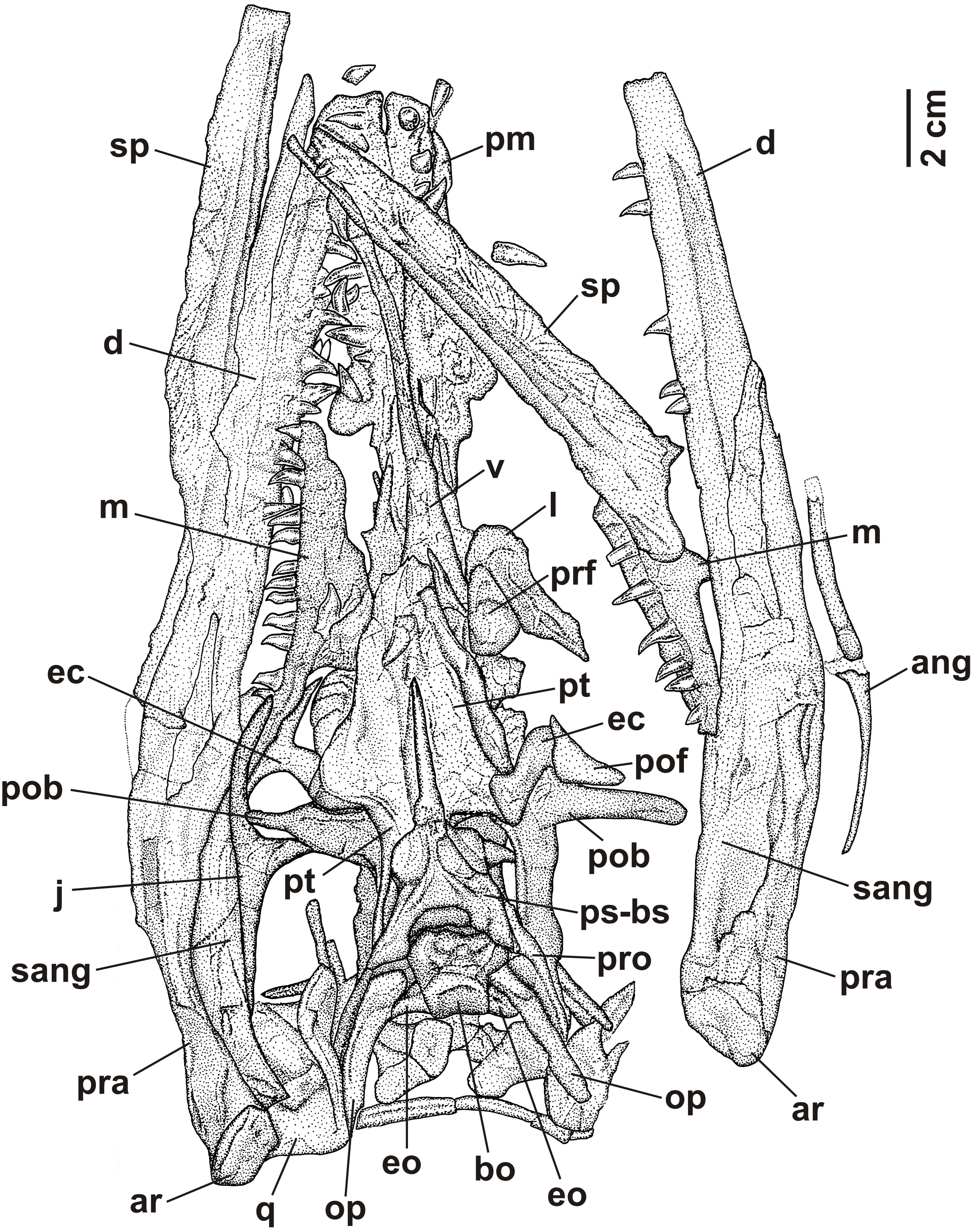


Fig. 12: *Askeptosaurus italicus,* skull of PIMUZ T 4832 in ventral view.

Septomaxilla

A definite septomaxilla could not be detected. In PIMUZ T 4832 (fig. 12), there are two heavily damaged pieces of bone medially to the external nares. They are very slender elements, posteriorly slightly expanded, and show a tapering anterior projection with a sharp rostral tip. It should be noted, however, that these bones could also represent the nasals. In PIMUZ T 4831 (fig. 9) and 4846 (fig. 11), narrow parts of bone are exposed within the nasal openings, but since they are mostly covered by upper jaw bones, a determination as septomaxillae is being difficult.

Maxilla

The maxillae are exposed in lateral and medial view. They are slender and elongated elements, relatively small in comparison to the premaxillae. The bones define the lateral margin of the external nares and contribute to the ventral formation of the orbital rim, although they are excluded from the margin itself by lacrimal and jugal. The maxilla is tapered anteriorly and posteriorly, in its central part it is somewhat dorsoventrally expanded. Anteriorly to the external naris, the bone meets the premaxilla in an anteroventrally directed suture (see above). Directly behind the narial opening, a broad and relatively short process originates, trending into posterodorsal direction and ending in a small tip. The process enters between nasal and lacrimal but divides the two bones only partially. The posterior portion of the maxilla tapers into caudal direction. Its dorsal edge meets the lacrimal and, more posteriorly, already well within the orbital rim, also the anterior process of the jugal. The external surface sometimes shows a striation that more or less follows the direction of the ventral margin in the lower area, and that of the dorsal margin in the upper one. 2 to 4 lateral foramina are present, distributed in the central and posterior portion of the bone. In medial view, the dorsal part of the maxilla possesses a more or less smooth surface. Its ventral portion forms a modestly developed lamina horizontalis on which the teeth are implanted. The number of functional teeth extends from 9 to 11, together with the empty alveoles the total number may have reached 16 at least. Implantation is pleurothecodont, the tooth bases are massively cemented within the lamina horizontalis. The shape of the teeth strictly resembles those of the premaxillae, but their size is distinctly smaller, both in height and in width. One half to two thirds of each tooth reaches above the margin of the maxilla in lateral view.

Nasal

The two nasals are preserved in dorsal view. They are small bones, situated nearly in the mid region of the skull due to the conspicuous elongation of the premaxillae. The nasals define the posterior borders of the external nares, reaching also parts of their medial margin by a relatively short but well developed process which is anteriorly in contact with the respective premaxilla. Laterally, the nasals meet the frontal bones, whose anterior margins are deeply indented by a far posteriorly extending process of each nasal. The process is very sharp and reaches even the height of the anterior margin of the orbit. Nasal and prefrontal do not meet, the two bones are separated from each other by a contact between lacrimal and frontal. Hence, the lateral edge of each nasal is rather bordered by the lacrimal and anterolaterally by the maxilla that meets the two bones in a slightly undulating suture. The dorsal surface of the nasals shows several more or less recurved striations: Anteriorly, they correspond to the shape of the posterior margin of the naris. Posteriorly, however, the striations follow the orientation of the posteromedial edge of each nasal. In MSNM V456 (fig. 10), as already mentioned by KUHN (1952), two small foramina are present, situated close to the external nares.

Lacrimal

The lacrimals are exposed in lateral and medial view. They define the anteroventral margin of the orbital rim. In *Askeptosaurus*, the lacrimals are distinct bones and very characteristic of the genus. They equal the size of the prefrontals and their shape is more or less semilunar with two small but well developed processes, a dorsal and a posterior one. The latter tapers posteriorly and contributes to the formation of the orbital rim. Ventrally it extends along the posterodorsal margin of the maxilla, together with the anteriorly remaining ventral edge of the lacrimal. The dorsal process is triangular, entering between nasal and prefrontal and meeting the frontal by a sharp and very small tip. The resulting fronto-lacrimal contact is a special feature of *Askeptosaurus*. The posterior, undulating margin of the lacrimal trends into posteroventral direction and thereby meets the prefrontal. The anterior tip of the lacrimal is rounded and fits into a concavity of the dorsal process of the maxilla, whereas the anterodorsal edge of the bone meets the nasal. In lateral view, the lacrimal shows a distinct depression nearly along its whole surface, only in the upper part, where the dorsal (frontal) process originates, it forms a rounded and slightly dorsally convex ridge. This ridge may simply be the result of the conspicuous depression in the central part of the bone, as is probably a similar structure in the contact area between lacrimal and maxilla. Several striations are present on the outer surface. In the upper part of the bone, they follow the orientation of the described dorsal ridge, whereas the striations of the ventral portion correspond to the direction of the posterior process. The medial side of the lacrimal is badly preserved. In its central part, a small groove originates and trends into posterior direction. This groove may be interpreted as part of the lacrimal duct.

Prefrontal

The prefrontals, preserved in dorsal and ventral view, are triangular elements and form the anterodorsal rim of the orbit. Their anteroventral margins meet the lacrimals, their dorsal ones the frontals. The anterior tip of the prefrontal is rounded and short, whereas the anteroventral and -dorsal projections are more prominently developed, the anterodorsal one being the largest. The suture between lacrimal and prefrontal is undulating, the contact to the frontal is more or less straight. Within the contribution of the prefrontal to the orbital rim, a slightly indented depression is present, situated close to the edge of the lacrimal. This structure was interpreted as entrance of the so-called canalis orbitonasalis by KUHN (1952). Although the posterior edges of the prefrontals extend far into occipital direction due to the elongation of the anterodorsal processes, the bones do not contact the postfrontals. There are several striations on the surface of the bone, reflecting the curvature of the anterodorsal and -ventral suture. In ventral view, the prefrontal extends well downwards by a broad ventral projection, originating in the medial area of the bone. The process tapers ventrally and is more or less cone-shaped. The development of this process shows that the posterior wall of the nasal capsule was at least partially ossified, as it is the case in *Thalattosaurus* and *Nectosaurus* (see e.g. NICHOLLS 1999). This interpretation is also supported by PIMUZ T 4846 (fig. 11) where the prefrontal reaches far downwards along the medial margin of the lacrimal, and most probably contacted the palatine.

Frontal

The paired frontals are exposed in dorsal view. They are slender elements and define the mediodorsal margin of the orbit. The two bones meet each other in a straight suture and they are not laterally constricted between the orbits, rather they show a slight lateral expansion in their middle part. Two slender processes project into anterior direction, externally divided from each other by the overlap of the posterior edge of the nasal. The medial process extends far anterolaterally and nearly reaches the external naris, its medial margin being in contact with the premaxilla. The lateral process enters between nasal and prefrontal, its anterior tip meeting the lacrimal and thus preventing a nasal-prefrontal contact (see above). The posterior area of the frontals is slightly indented at its posterolateral edge, in which the anteromedial process of the postorbital as well as the posterior part of the dorsomedial margin of the postfrontal fit. The anteromedial margin of the latter bone extends along the straight lateral edge of the frontal. The posterior end of the frontals meets the parietal bones in a strongly interdigitating suture. There are again several striations on the dorsal surface of the frontal bones, resembling those of the premaxillae in development and direction. In MSNM V456 (fig. 10), two small foramina occur on both frontals, as already described by KUHN (1952). The first one is situated directly behind the posterior process of the nasal and the second one at the beginning of the posterior third of each bone. The latter foramen could also be detected in PIMUZ T 4831 (fig. 9).

Postfrontal

The postfrontals are preserved in dorsal and ventral view. They are triangular to semilunar bones and define the posterodorsal margin of the orbits. There is no sign of a fusion with the postorbitals. The anterodorsal and posteroventral processes are short but well developed and possess a sharp tip, respectively. They are nearly equal in length, intraspecific variation may sometimes result in an elongation of one of the two projections. The anteromedial margin of the postfrontal shows a distinct edge along which the bone meets the frontal. The posteromedial and -ventral margin is fully in contact with the postorbital, fitting into a concavity of the latter bone. The dorsal surface of the postfrontal shows again a certain striation which follows the shape of the medial and posterodorsal edge. The ventral surface does not bear any significant structure.

Parietal

The paired parietals are exposed in dorsal view. They are relatively slender elements, the posterior part being increasingly expanded into lateral direction, and define the complete medial margin of the slit-like upper temporal fenestra. The bones meet each other in an undulating suture, clearly different from that of the frontals or premaxillae. The prominently developed pineal foramen is situated well within the anterior half of the bones. Its size differs in the investigated specimens: In MSNM V456 (fig. 10), it is relatively large in relation to the rest of the parietals, whereas in PIMUZ T 4831 (fig. 9), it is comparatively small. Anteriorly, the parietals contact the frontals in the aforementioned interdigitating suture. It is not possible to determine whether there is a certain underlap by anteroventral projections of the parietals. The posterolateral processes are prominently developed and laterally expanded. Their size is nearly equal to the rest of the bones. Their posterior tip is tapered and meets the paroccipital process of the opisthotic and probably also the quadrate. More anteriorly, the process shows a slender groove on its dorsolateral surface in which the supratemporal fits. Anterolaterally, the process meets the posterior portion of the squamosal and the posteromedial edge of the postorbital, together with the latter the parietal forms the posterior margin of the upper temporal fenestra. The posterior edge of the parietal is greatly emarginated, thus exposing the dorsal surface of the supraoccipital. In the middle part of the edge, however, a slight triangular projection is present, divided by the median suture of the parietals. It possesses a sharp posterior tip and is situated well above a median ridge of the supraoccipital (described below in more detail). The posterior edge as well as the posterolateral processes are ventrally expanded into posterior and medial direction, respectively, most probably serving for the insertion of the epaxial neck musculature. As in the other bones of the skull roof, the dorsal surface of the parietals is striated. In the anterior part, around the pineal foramen, the direction of the striations is craniocaudal, as in the frontals and premaxillae. More posteriorly, however, the striations are increasingly posterolaterally directed, following the orientation of the posterolateral processes. The median area shows furthermore several dermal rugosities which trend, to some extent, also into lateral direction.

Postorbital

The postorbitals are preserved in dorsal and, partially, in ventral view. They are prominent triradiate elements, defining the posteroventral rim of the orbit as well as the lateral margin of the upper temporal fenestra. The ventral and posterior processes are very long and nearly equal in length, the posterior one may be somewhat longer. The ventral (orbital) process extends far down the orbital rim, its posterior edge being flattened for the contact of the ascending process of the jugal by which it is covered laterally. The anterior process is very short, horizontally arranged, and with a medially convex recurvation, fitting into a slight indentation of the frontal (see above). Its posteromedial margin is notched, thus forming a small slit between the frontoparietal contact area and the postorbital. The notch extends further into posterior direction up to the end of the anterior third of the parietal which is therefore also separated from the postorbital edge. The posterior process of the postorbital forms the main part of the upper temporal arcade. Its tapering posterior end meets the mid and posterior portion of the parietal table medially and covers the anterior process of the squamosal dorsally. A possible medial contact to the supratemporal could not be determined. The anterodorsal surface of the postorbital does not show a significant striation, only some dermal rugosities are present, if at all. The orbital process, however, possesses a certain striation that trends into ventral direction, and also the posterior process shows a craniocaudally striated dorsal surface. In ventral view, the postorbital does not bear any remarkable structure.

Jugal

The jugals are exposed in lateral and medial view. They are triradiate bones and define the ventral part of the orbital rim, contributing also to the posterior formation of the latter. Furthermore, the jugals form partially the anterior and anteroventral margin of the lower temporal fenestrae. Three processes are present. The first one is the longest and extends, slightly recurved, into rostral direction. It tapers anteriorly, meeting the posterior projection of the maxilla by its anteroventral edge and contacting the lacrimal by its distal tip. At least 3 small foramina can be located laterally, arranged in a straight row and equally separated from each other, probably serving for the passage of nerves and blood vessels. The medial side of the process shows a distinct groove on its proximal and middle portion. This groove may represent the posterior part of the lacrimal duct. The slender second process is straight, posteriorly directed, and with a sharp distal tip. It represents the rest of the reduced ventral bar of the lower temporal fenestra and reaches up to the level of the anterior tip of the supratemporal. The third process extends dorsally and contacts the postorbital by a slight lateral overlap of the posterior edge of the latter, bordering nearly two thirds of the descending postorbital projection. The lateral surface of the jugal shows again several striations on each projection, following the direction of the respective process.

Squamosal

The squamosals are preserved in lateral view. They are pistol-shaped and generally slender, participating in the formation of the upper temporal arcade and thus defining the posterodorsal margin of the lower temporal fenestra. The “quadratojugal“ of specimen PIMUZ T 4831 (fig. 9), situated in the posterior area of the left side of the skull, can be determined as squamosal due to its similarity to the squamosal of MSNM V456 (fig. 10) as well as to the squamosal of *Anshunsaurus* (RIEPPEL et al. 2000) The bone consists of two processes, an anterior one and a ventral one. The anterior process is approximately twice as long as the ventral projection. Its distal portion is dorsally flattened and tapers anteriorly, underlapping the posterior process of the postorbital and reaching nearly up to the level of the posterior margin of the pineal foramen. Medially, the process meets the supratemporal proximally and most probably also parts of the parietal distally, but the exact contact area could not be determined. The ventral projection of the squamosal is straight in MSNM V456 and as broad as the proximal portion of the anterior process, only its distal tip is slightly tapered. In PIMUZ T 4831, the ventral process is slightly anteroventrally directed and somewhat expanded, with an irregular anterior margin. In *Anshunsaurus,* which is considered to be closely related to *Askeptosaurus* by RIEPPEL et al. (2000), the ventral projection is extremely elongated and overlaps laterally the anterior edge of the quadrate. This may have also been the case in *Askeptosaurus*, since there is no posterior articulation surface which had to be supposed otherwise. Hence the situation in *Askeptosaurus* seems to be similar to *Anshunsaurus*, the only difference being a shorter ventral extension of the process. Contrary to most other bones of the skull roof and the cheek, the lateral surface of the squamosal does not bear a significant striation.

Supratemporal

The supratemporals are exposed in lateral view. They are slender but relatively elongated slivers of bone, mediating between the posterior area of the skull roof and the upper temporal arcade. Along its whole extension, the supratemporal fits into a groove present on the dorsolateral surface of the posterolateral process of the parietal, beginning at the proximal base of the projection and extending nearly up to its distalmost tip. Although the supratemporal is generally narrow, its posterior end is slightly expanded posteroventrally. The remaining portion of the bone is relatively straight and shows a sharp anterior tip. As in the squamosal, it is again difficult to determine the way of contact to the other bones next to the parietal. In its anteriormost region, the supratemporal is slightly recurved into medial direction, hence there may be no contact to other bones at all. In the mid region, the supratemporal contacts the squamosal and eventually also the posteromedial part of the postorbital. More posteriorly, the bone meets the quadrate, most probably in a movable joint, as it is the case in the contact between quadrate and squamosal (see above). The posterior end of the supratemporal may also have contacted the paroccipital process of the opisthotic, but this determination must remain speculative.

Quadrate

The quadrates, misidentified as opisthotics by KUHN (1952), are sufficiently preserved only in posterior view. Although there is also a lateral exposure in PIMUZ T 4831 (fig. 9) and MSNM V456 (fig. 10), as well as a more or less ventral one in PIMUZ T 4832 (fig. 12), its preservation is too bad for a detailed description. In posterior view, the quadrate has generally an hour-glass-shape, whereas the lateral margin is more concave than the medial one. The dorsal end of the bone contacts the squamosal/supratemporal/parietal-complex along which it probably slid during the movement of the jaw. It is distinctly thickened, its posterodorsal edge being almost straight. Laterally, the dorsal margin slightly reaches above the outer extent of the quadrate shaft and forms a rounded lateral knob. The mid part of the bone shows posteriorly a small curvature. In the right quadrate of MSNM V456, a rounded depression occurs dorsally to this curvature, but its function could not be determined. The posteroventral area of the bone is strongly expanded and half-rounded. It possesses a slightly developed crest at its ventralmost margin, indicating that cartilage was probably present there, serving for the support of the quadrate movement. As already mentioned above, the lateral exposure of the quadrate is so badly preserved that only a tentative interpretation can be given. It seems that the anterior margin of the quadrate was convexly formed into rostral direction, thus representing a half-rounded edge, as it is typical in many movable reptilian quadrates. On the contrary, the posterior margin was greatly emarginated and gently concave. The preservation and the thereby inferred morphology suggests that most probably a tympanum laterally covered the quadrate in *Askeptosaurus*. In PIMUZ T 4832, another exposure of the quadrate is preserved, a ventral one (see above), situated posteromedially to the right mandible. However, the preservation is very scarce, and the only finding that could be obtained is that the bone was generally a relatively broad and massive element. The ascending medial edge present there may be identical with the anterior margin described above, but a more definite statement is impossible.

Scleral ossicles

Well-ossified scleral ossicles are always developed in *Askeptosaurus*. Especially in PIMUZ T 4831 (fig. 9), they are clearly visible close to the right orbit. There, at least 12 single elements are preserved. This does most probably not reflect the total number, as further impressions can clearly be recognized, but the preservation does not allow a more detailed differentiation. The total number can therefore only be estimated and must have amounted to 14 ossicles at least.

3.1.1.2. Palate (fig. 8B)

Of the whole skull, the palate is the most badly preserved part. The following description is mainly based on PIMUZ T 4832 (fig. 12), as it is the only specimen which is sufficiently preserved in ventral view.

Pterygoid

The relatively large pterygoids are partially exposed in dorsal view and fairly well preserved ventrally. They define the mid and posterior portion of the palate and contribute to the formation of the suborbital fenestra. Unlike the rest of the bone, the anteriormost region is badly damaged, making a detailed description of that portion problematical. It is only possible to state that the two elements meet each other along a straight midline in the anterior half and that they taper increasingly into rostral direction. However, the structure of the contact to vomer and palatine could not be determined exactly. The mid region of the pterygoids is expanded into posterolateral direction due to the prominent development of the pterygoid flange, defining the posteromedial border of the suborbital fenestra. However, its exact contribution to this opening could not be determined. The lateral edge of the bone runs diagonally, the medial margin is indented posteriorly but in general craniocaudally directed. The pterygoid flange possesses a rounded posterolateral edge on which the bone meets the ectopterygoid. There is a small but sharp ventral crest posteromedially to the flange, right at the origin of the quadrate ramus that extends into posterolateral direction. The crest reaches also onto the posterior area of the flange and serves for the insertion of parts of the pterygoideus muscle. Anteriorly to the flange, there is another more or less craniocaudally directed scarce, most probably another area of muscle insertion, trending to the lateral edge of the bone. Posteriorly, the pterygoid tapers significantly and forms the aforementioned quadrate ramus. This structure is approximately as long as the remaining anterior portion of the pterygoid. It is very slender and extends to the quadrate which it contacts medially by a movable joint.

Ectopterygoid

The ectopterygoids, exposed in dorsal and ventral view, are relatively well preserved. They are slender T-shaped elements, slightly recurved, and define the posterolateral border of the suborbital fenestra. Generally, their shape closely resembles that of generalized diapsids. Laterally, the bone presents an anterior and a posterior process. Both are very narrow and show a sharp distal tip, the anterior projection being slightly longer than the posterior one. Together they form a straight lateral edge that meets the jugal along its full extension. Most obviously, a contact to the maxilla was not present. The ectopterygoid is medially rounded but relatively stout, its meeting point with the pterygoid being slightly expanded. The surface of the bone does not bear any significant crests or other structures which could indicate muscle attachment.

Palatine

Unfortunately, the palatines are only very fragmentarily preserved, making a description practically impossible. In specimen PIMUZ T 4846 (fig. 11), the posterolateral portion is slightly exposed in the anterior half of the left orbit. It possesses a concave posterior margin, indicating that the palatine formed the anterior border of the suborbital fenestra. The structure of the border to pterygoid and vomer cannot be determined, nor the shape of the internal nares whose posterior margin is normally supposed to be formed by the palatine.

Vomer

The exposure in specimen PIMUZ T 4832 (fig. 12) suggests that the vomers were obviously fused to a single bone. It represents a very slender and elongate bar which is slightly expanded in its posterior portion, and extends nearly along the whole length of the premaxilla. As already mentioned in the descriptions of pterygoid and palatine, neither the border to the other palate bones nor the structure of the internal nares can be determined as a result of the poor preservation.

3.1.1.3. Braincase (fig. 13)

The braincase is only preserved in PIMUZ T 4832 (fig. 12) and for the most part exposed in ventral view, making a complete documentation impossible. However, the neurocranium of *Askeptosaurus* is one of the best preserved among all thalattosauriform reptiles, a detailed description of the data at hand may therefore be very important.

Basioccipital

The basioccipital, only preserved in ventral view, is a broad element with a more or less trapezoid shape. The bone contributes to the formation of the occipital condyle as well as the metotic fissure and the foramen magnum. The latter structure is unfortunately not preserved. Anteriorly, the basioccipital meets the parabasisphenoid in an undulating suture. Its anterolateral portions bear prominent knob-like structures, the basal tubercles, which serve for the attachment of subvertebral muscles (EVANS 1986). The basal tubercles are ventrolaterally

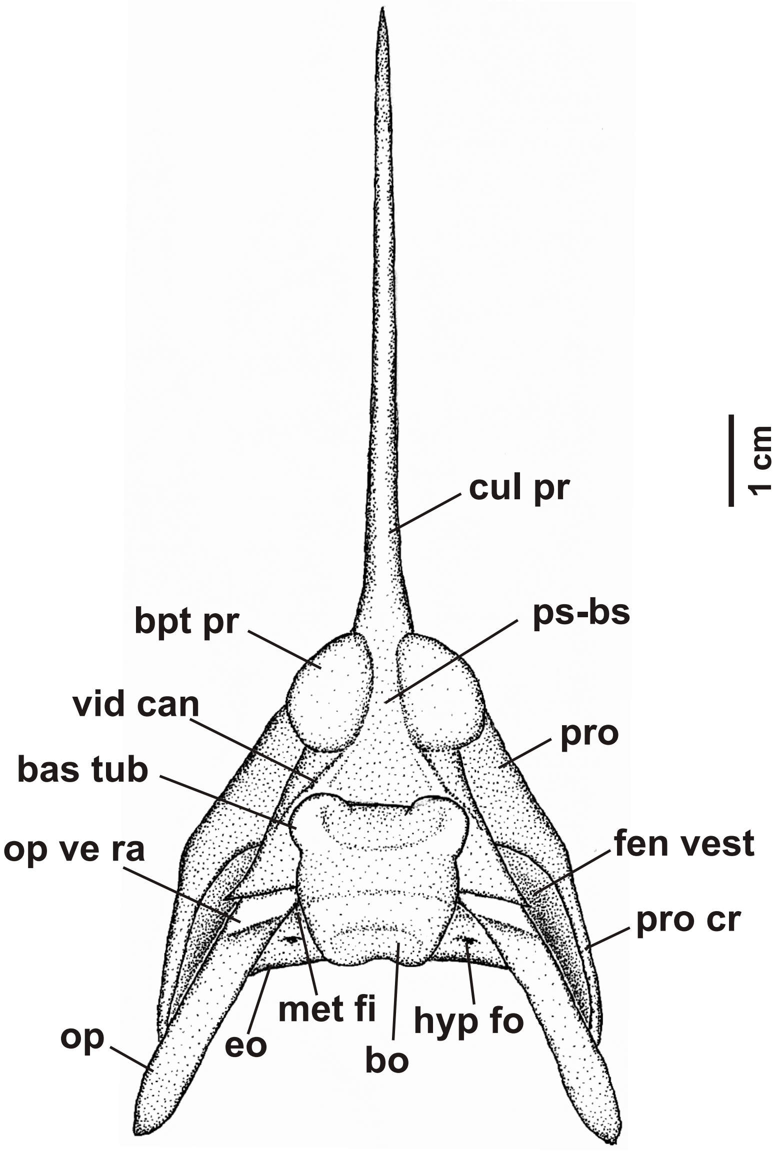


Fig. 13: *Askeptosaurus italicus*, restoration of braincase in ventral view, stapes omitted.

directed, their medial surface being oblique and their lowermost tips forming semilunar edges. The middle portion of the bone is depressed. More posteriorly, however, the basioccipital shows again a ventral expansion and the posterior edge is slightly concave. These structures form part of the ventral formation of the occipital condyle. Laterally, the basioccipital bears a prominent concave facet between the posterior margin of the basal tubercle and the anterolateral edge of the posteroventral expansion. This facet is obliquely directed, its dorsal margin extended obviously more into a lateral direction than the ventral one, thus the anterior portion of the basioccipital seems to have “roofed over“ the ventral part of the bone. The facet serves for the contact of the proximal end of the opisthotic. The posterolateral edge of the bone meets the exoccipital. Since the braincase is generally flattened as a result of tectonic deformation, it is difficult to determine the exact participation of the basioccipital in the formation of the metotic fissure, which serves for the passage of the glossopharyngeal and vagal nerve as well as the posterior cerebral vein (RIEPPEL 1979). The exposure suggests that the bone formed its ventromedial margin.

Exoccipital

The exoccipitals are only partially preserved, both in ventral and in dorsal view. They were obviously not fused neither to the basioccipital nor to the opisthotics. The bones define the lateral margins of the foramen magnum and participate in the formation of the metotic fissure. Whether they also make a contribution to the occipital condyle, which would therefore not be formed solely by the basicoccipital, must remain open to question. Dorsally, the exoccipitals approach each other very closely, but they did not meet at their dorsomedial margins, thus the supraoccipital still enters the dorsal margin of the foramen magnum. Along its anterodorsal edge, each exoccipital meets the supraoccipital and laterally the opisthotic. In ventral view, most of the exoccipital is covered by other braincase bones, only a triangular exposure is visible which represents the dorsomedial border of the metotic fissure, whose general morphology will be discussed below in the opisthotic section. The posterior margin of the left exoccipital of PIMUZ T 4832 (fig. 12) shows a small foramen that possibly represents the opening for the hypoglossal nerve.

Supraoccipital

Of the supraoccipital, only the posterodorsal portion is exposed. The bone roofs the cranial cavity and defines the dorsal border of the foramen magnum. The dorsal surface of the bone extends into posteroventral direction, its caudal edge being slightly concave on each half and forming the contact area with the respective exoccipital. The posterolateral edge meets the opisthotic. There is a conspicuous median crest on the dorsal surface, tapered at its posteriormost point and increasingly expanded into anterior direction, until it finally passes into a broad mediolateral curvature which is, unfortunately, mainly covered by the parietals. While the curvature most probably represents the posterodorsal part of the semicircular canals, the median crest may serve for the attachment of tendons dividing the subvertebral muscles. Since neither the anterior portion nor the ventral portion of the supraoccipital are preserved, the exact contact to the prootic, meeting the bone normally at its anteroventral edge, could not be determined.

Opisthotic

The opisthotics are preserved in ventral view, their distal portions are also exposed dorsally. They were misidentified as pterygoids in specimen PIMUZ T 4831 (fig. 9) by KUHN (1952). The bones form the posteroventral part of the otic capsule, contribute to the formation of the metotic fissure, and mediate between the skull roof and the braincase by the development of prominent paroccipital processes. Anteriorly, the opisthotic presents an elongated ventral ramus. Due to the poor preservation, its downward extension could not be completely determined. The ramus forms the lateral wall of the metotic fissure. The preservation indicates that the metotic fissure was not divided into a recessus scalae tympani, characterized by the exit of the glossopharyngeal nerve, and into a jugular foramen, serving for the passage of the vagal nerve and the posterior cerebral vein (RIEPPEL 1979). Thus the structure of the metotic fissure is relatively plesiomorphic in comparison to, e.g., squamates, and rather corresponds to the conditions found in *Sphenodon* (RIEPPEL 1979), *Prolacerta* (EVANS 1986), and *Captorhinus* (PRICE 1935, cit. in FOX & BOWMAN 1966), where the metotic fissure is not divided either. Together with the dorsal portion of the opisthotic, the ventral ramus furthermore forms the posterior border of the fenestra vestibuli and meets the basioccipital ventromedially. Dorsomedially, the opisthotic contacts the exoccipital, meeting the supraoccipital dorsolaterally to this border. The paroccipital process arises posterolaterally to the otic capsule, being elongated and slightly recurved. It does not show a significant tapering into distal direction and extends to the posterior tip of the corresponding projection of the parietals. As already mentioned in the description of the skull roof, it is difficult to determine whether the paroccipital process also met the supratemporal.

Prootic

Only the ventrolateral margin of the prootic is preserved. The bone is clearly expanded into posterior direction and presents a significant crest anterolaterally, the crista prootica, roofing over the parabasisphenoid and serving for a protective passage for the vena capiti lateralis as well as for fibre attachment of the protractor pterygoidei muscle (EVANS 1986). Posteriorly, the bone forms the anterodorsal border of the fenestra vestibuli by a broad lateral expansion. The caudal end of the prootic meets the opisthotic ventrally, the contact to the other bones, supraoccipital and parabasisphenoid, cannot be described due to the poor preservation.

Parabasisphenoid

This element is a composite bone, resulting from the fusion of the dermal parasphenoid to the ventral surface of the basisphenoid, which represents the anterior ossification of the embryonic basal plate (EVANS 1986). It is unfortunately only exposed in ventral view. Anteriorly, the bone possesses a long and relatively broad cultriform process that extends far into rostral direction, its anteriormost portion being ventrally covered by the palate. The projection shows a rounded ventral edge. The proximal base is slightly expanded. In its central portion, the parabasisphenoid presents two prominent drop-shaped ventral expansions situated posterolaterally to the base of the cultriform process, representing the basipterygoid processes. Between them, two slender grooves follow the medial edge of the expansion and extend into posterolateral direction, then accompanied by small medial crests. The grooves represent the open vidian or parabasal canals and carry the internal carotid artery as well as the palatine branch of the facial nerve. In modern reptiles, the internal carotid artery is divided into palatine and cerebral branches, the latter entering the hypophysial fossa on the dorsal side of the bone via a short canal situated close to the basipterygoid processes (EVANS

1986, RIEPPEL 1979). The palatine branch remains on the ventral side of the parabasisphenoid and runs into rostral direction, together with the palatine branch of the facial nerve. Since this division of the internal carotid artery already occurs in younginiform diapsids (EVANS 1987), the same situation can also be supposed for *Askeptosaurus* (see also chapter 4.1). However, due to the poor preservation it is difficult to detect the entry foramina for the cerebral branch. As inferred from the morphology in a relatively unspecialized diapsid like *Sphenodon* (RIEPPEL 1979), they were most probably situated next to the medial margin of the basipterygoid processes. The better preserved right basipterygoid process indeed shows a small depression close to its posteromedial edge. The depression may be interpreted as entry foramen, but this inference must remain speculative. Between the medial crests accompanying the posterolateral portions of the parabasal canals, the parabasisphenoid shows a triangular depression that extends to the posterior edge where the bone meets the basioccipital. Along the margin to the aforementioned medial crests, another pair of grooves defines the anterior and lateral borders of the depression. Their function is unknown, and maybe they are simply the result of a “rigid“ preparation. The parabasisphenoid presents two prominent posterolateral projections. They are broad and with a relatively sharp distal tip, originally underlying the fenestra vestibuli which was situated dorsally to the projections. Semilunar depressions, as they occur on the posterolateral projections of archosauromorph reptiles (EVANS 1986, GOWER & SENNIKOV 1996, GOWER 1997, GOWER & WEBER 1998), could not be detected. In PIMUZ T 4832 (fig. 12), a broken triangular piece of bone is situated laterally to the left basipterygoid process. Although the determination is doubtful, this structure may represent the clinoid process, originally situated on the dorsal side of the parabasisphenoid and forming the contact area with the prootic.

Stapes

An elongated rod of bone with a blunt two-headed knob at its left (?medial) end, exposed under the right articular in PIMUZ T 4831 (fig. 9), may be interpreted as stapes, even though it cannot be definitely excluded that it alternatively represents a part of the hyoid apparatus. Given the determination is correct, the stapes would correspond to the slender morphology found in younginiforms and the more derived diapsid reptiles (EVANS 1987).

3.1.1.4. Lower jaw (figs. 8-12)

Although the lower jaw is preserved in several specimens, a detailed determination of the respective morphology is difficult due to the high influence of tectonic deformation and the covering by skull roof bones. Generally, the slender mandibular ramus possesses an elongated and very straight tooth-bearing portion, while the posterior part, on which the trigeminal jaw musculature and the depressor mandibulae muscle attach, is comparatively short and slightly recurved, with a relatively prominent mandibular fossa. A true retroarticular process is not developed. The following description is mainly based on the same specimens as in the description of the skull roof.

Dentary

The dentary is preserved in lateral and medial view. In relation to the remaining mandibular bones, the dentary is the longest element, being very straight and increasingly expanded into posterior direction. It covers the complete anterolateral portion of the mandibular ramus, thus there is no lateral exposure of the splenial as shown in KUHN´s (1952) restoration. The symphyseal area is rounded. Due to the flattened preservation it is not possible to determine whether it was medially recurved or not. In any case, the two mandibles did obviously not fuse anteriorly, as they are always separately preserved. In lateral view, the bone shows several foramina for the passage of nerves and blood vessels along its lateral surface. At least five such openings could be detected, arranged in a straight series, situated dorsally in the symphyseal region and then trending into posteroventral direction. The mid and posterior foramina are elliptic and slightly larger than the rounder anterior ones. Posteriorly, the dentary presents an elongated ventrolateral projection, tapering increasingly and ending in a sharp tip. The projection covers the anterolateral portion of the angular and the latter bone borders also its anterior edge. The remaining posterior margin meets the surangular, but the exact structure of the contact could not be determined. As indicated by specimen PIMUZ T 4831 (fig. 9), the dorsal half of the posterior dentary margin presented two moderately developed posterior projections with sharp ends. The surangular may have entered the indentation between the two and bordered also their distal tips. The morphology of the contact to the coronoid cannot be determined due to the extremely poor preservation of the latter (see below). The lateral surface of the dentary shows a distinct striation, the respective striae extend either into posterodorsal or posteroventral direction. Furthermore, the bone possesses several depressions in the dorsolateral area of the anterior portion. As in the premaxilla, the teeth of the complementary (upper) jaw probably fitted into these depressions when the mouth was closed. In medial view, the dentary shows an elongated but relatively large groove, the Meckelian sulcus. The sulcus is broader posteriorly and tapers increasingly into rostral direction, but it does not reach the symphyseal area. Dorsally, the Meckelian sulcus is bordered by the lamina horizontalis, ventrally its extension reaches the lowermost edge of the dentary, and only in the anteroventral area, a small curvature is developed that separates the sulcus from the ventralmost margin. The curvature extends into symphyseal direction and fuses with the anterior portion of the lamina horizontalis. Posteroventrally, the dentary meets the angular, however, the preservation does not allow a more precise description of the respective suture. As inferred from the lateral contact of the two bones and also indicated by the right mandible of PIMUZ T 4832 (fig. 12), the angular most probably covered the posteroventral edge of the dentary medially. The contact to the surangular can be determined in a better way. This is also shown in PIMUZ T 4832, where the surangular forms a prominent anterior projection that extends far into the Meckelian sulcus, thus covering even its complete posterior half. The posterodorsal edge of the dentary most probably met also the prearticular and the coronoid, but a precise description is not possible. The lamina horizontalis bears at least 12 functional teeth, together with the remaining alveoles the total number can be estimated as 20. The teeth are implanted in a pleurothecodont fashion and their shape is principally similar to the teeth described for the upper jaw. However, there is a certain difference in size, because even in the anterior portion, the tooth size corresponds more to that of the maxilla than of the premaxilla, the dentary teeth being therefore relatively small. Within the tooth row of the dentary, the teeth of the mid portion are the largest.

Splenial

The splenial is relatively well preserved in internal and medial view. It is completely restricted to the medial side of the mandible and covers the Meckelian sulcus along its full extension, including also the anterior projection of the surangular. It does not contribute to the formation of the symphysis. Generally, the bone is an elongated and broad element that shows a slight tapering in its anterior portion. Posteriorly, the splenial presents an expanded posterior process that reaches above the medial contact of angular and dentary. The surface of the bone is very significant. In internal view, there is a conspicious groove right above the ventral edge, being very straight and posteriorly expanded nearly up to the dorsal margin of the bone, representing the medial wall of the Meckelian sulcus. The groove originates anteriorly to the base of the aforementioned posterior projection and extends far rostrally. While the mid portion of the groove is very well developed, it increasingly diminishes in the anterior area and close to the anterior splenial tip, the groove cannot be detected any more. From the dorsal margin of its mid portion, a distinctive fan-shaped striation originates, the respective striae extend in all directions and cover the complete area dorsally to the groove. In medial view, the bone is principally similarly developed, the only difference is that the groove is consequently a curvature.

Coronoid

The coronoid is badly preserved. KUHN (1952) did not detect any bone which he considered to be a possible coronoid. In PIMUZ T 4831 (fig. 9), a more or less semilunar piece of bone is situated directly beneath the right prearticular, named as questionable squamosal by KUHN (1952). Its anterior leg is straight and slender, while the posterior one, caudally recurved, tapers increasingly into distal direction. The mid part of the bone is distinctly expanded. It is clear that this structure does not represent the squamosal, since it differs significantly from the pistol-shaped squamosals in the other specimens of *Askeptosaurus*, and maybe it is part of the coronoid. KUHN (1952) described a coronoid in the left mandible of the same specimen, but he did not name it in his figure. It is therefore unclear whether he referred to the squamosal or whether he designated the left ectopterygoid as possible coronoid. In MSNM V456 (fig. 10), there is a slender and sharp bony projection directly posteriorly to the ventral process of the left jugal. This structure can be determined as dorsal coronoid process, as it closely resembles the coronoid morphology known in other thalattosaurs. Furthermore, an elongated triangular element is situated laterally to the right mandible within the right orbit, its posterior portion being covered by jugal and postorbital. The structure may represent the anteromedial area of the coronoid.

Angular

The angular is exposed both laterally and medially, however, the flattened preservation renders many details difficult to determine. The bone is a slightly recurved and relatively slender element, defining the most part of the ventral margin of the posterior half of the mandible. In lateral view, the angular is exposed on the posteroventral area of the mandible. Anteriorly, it is recurved dorsally, and, as already described above, borders the dorsal edge of the posterior dentary projection, while the latter covers the anteroventral portion of the angular. The straight dorsal margin of the bone meets the surangular along its full extension and may have overlapped the ventrolateral portion of the latter bone. Posteriorly, the angular is again slightly dorsally recurved and presents a rounded end, situated anteriorly to the level of the articulation surface for the quadrate. In medial view, the angular is more slender. Anteriorly, it is covered by the splenial (see above), and the anterodorsal margin meets the surangular, while the remaining dorsal edge is sutured to the prearticular. The anterior and posterior portions of the bone are again recurved dorsally.

Surangular

The surangular is relatively well preserved in lateral and medial view, only the anteriormost lateral part is missing. The bone forms the posterodorsal part of the lower jaw ramus and defines the lateral and dorsal portion of the mandibular fossa. In lateral view, the surangular is an elongateD but relatively broad element which is somewhat recurved, but not as strong as the angular. Anteriorly, it meets the dorsal part of the posterior dentary edge. Most probably, the anterodorsal margin was bordered by the coronoid, but the suture could not be determined. The ventral edge meets the angular, and as already mentioned in the latter section, the angular possibly overlapped the lowermost portion of the bone. Posteriorly, the surangular forms the lateral part of the ventral base on which the articular is situated. The base is relatively short, its ventral margin being half-rounded and the tapered posterior tip slightly recurved dorsally. In dorsal view, the lateral margin of the base is recurved medially. The dorsal edge slopes posteroventrally and is gently concave, together with the prearticular it forms a facet for the overlying articular. A true retroarticular process is not developed, as there is no caudal projection posteriorly to the articular facet. The lateral surface of the surangular presents a small but very sharp crest in its posterior half, most probably serving for the attachment of the superficial layer of the external jaw adductor muscle. The crest originates at the proximal base of the retroarticular process and extends more or less straight into rostral direction. Anteriorly, the crest flattens rapidly and is, as a consequence, not present any more on the anterolateral half of the bone. Especially in dorsal view, it is visible that the posterior portion of the crest is distinctly expanded into lateral direction. Next to this conspicuous structure, there is a small foramen in the dorsolateral area of the posterior part, which most probably served for the passage of a branch of the trigeminal nerve (possibly identical with the “foramen auriculo-temporalis“ that was mentioned but not figured by KUHN 1952). Furthermore, it laterally shows a slight depression in its dorsalmost part of the anterior area which may be correlated with the insertion of the medialis-part of the depressor mandibulae muscle. Several striations are also present laterally, situated ventrally to the crest and trending into rostral and anteroventral direction. In medial view, the surangular forms the broad dorsal margin of the mandibular fossa as well as its lateral wall. The dorsal margin shows posteriorly a sharp medial edge, together with a general expansion of the posterodorsal border of the mandibular fossa. More anteriorly, the edge diminishes and the margin becomes less expanded. The lateral wall of the mandibular fossa is slightly concave, especially in its posteroventral portion. The anterodorsal margin of the surangular slopes anteroventrally and the bone extends far into the Meckelian sulcus by a sharp projection (see above), the latter being externally separated from the remaining bone by the anterodorsal portion of the medial margin of the mandibular fossa which is formed by the prearticular. The ventromedial margin of the surangular is not well preserved any more, but it can be assumed that it met the prearticular at the bottom of the mandibular fossa. More anteriorly, the ventromedial edge was sutured to the angular.

Prearticular

The prearticular is restricted to the medial side of the lower jaw and completes its posteroventral portion, defining the medial half of the mandibular fossa. In medial view, the base is horizontally expanded. It tapers proximally and then passes into the recurved medial margin of the mandibular fossa. The margin is posteriorly expanded into medial direction, then it tapers in its middle part and becomes anteriorly again medially expanded. Furthermore, the anteriormost portion is dorsally recurved and overlaps the surangular (see above). In dorsal view, it is visible that the margin approaches very closely the surangular especially in the anterior half, thus resulting in a generally very narrow but elongated mandibular fossa. The anterior edge of the prearticular meets the dentary and was most probably medially covered by the coronoid, while the ventral edge was medially bordered (or slightly overlapped) by the angular and laterally sutured to the surangular.

Articular

The articular is well preserved in dorsal and lateral view (the so-called “articular“ described by KUHN (1952) can be assigned to the prearticular). It represents an oval lense covering the entire dorsal surface of the aforementioned posteroventral base that is formed by prearticular and surangular. There are no signs of any fusion to the prearticular, as it sometimes occurs in other reptiles. The chorda tympani foramen is situated in the anterior half of the central area. In PIMUZ T 4831 (fig. 9), there is also another small opening posteriorly to this foramen. The anterior margin of the articular is slightly recurved into dorsal direction, thus forming the posterior edge for the articulation of the quadrate with the mandible.

3.1.2. The axial skeleton

3.1.2.1. Vertebral column (figs. 14-16)

As it is widely observed in marine reptiles, the vertebrae of *Askeptosaurus* are clearly amphicoelous throughout the complete extension of the vertebral column, although this amphicoely cannot be compared to the conditions found in, e.g., ichthyosaurs. Also, there is no sign of pachyostosis in the postcranium. Intercentra could not be detected, but they may have been present in chondrified fashion, as already supposed by KUHN (1952). *Askeptosaurus* possessed at least 38 presacral vertebrae (at least 13 cervicals and at least 25 thoracals), two sacral and more than 60 caudal vertebrae.

Cervical vertebrae (fig. 14)

As in many other reptiles, it is generally difficult to distinguish the posterior cervicals from the anterior thoracals. CARROLL & GASKILL (1985), when investigating a pachypleurosaur, characterized the cervical vertebrae by a different rib articulation. The same method can be used in *Askeptosaurus*, because the cervicals articulate with double-headed ribs, instead of one-headed in the thoracals. Therefore they show two attachment sites, and the cervical number can thus be given as 13 at least.

In MSNM V456, the atlas is relatively well preserved, although completely disarticulated (fig. 14). This appears to be a primitive feature, since in more derived reptiles the respective elements tend to fuse at least partially. Two neural arches are present in *Askeptosaurus*. Interestingly, the neural arches present a low but well-developed neural spine. The presence of such a projection is surprising, because in other relatively basal or generalized diapsids like *Sphenodon* or *Champsosaurus*, the neural arch does not develop a notable dorsal extension (see e.g. ROMER 1956, fig. 120). In *Askeptosaurus*, this neural spine has a rectangular shape with rounded ends, its dorsolateral area being slightly striated. The base of the neural arch shows posteriorly a well-developed postzgygapophysis, originally articulating with the complementary prezygapophysis of the axis. The postzygapophysis is slender but laterally thickened and slightly posterodorsally directed. A prezygapophysis is certainly not present, the anterior side of the neural arch rather possesses a vertical margin, whose direction slightly trends posteroventrally. The anterodorsal edge of the neural arch base

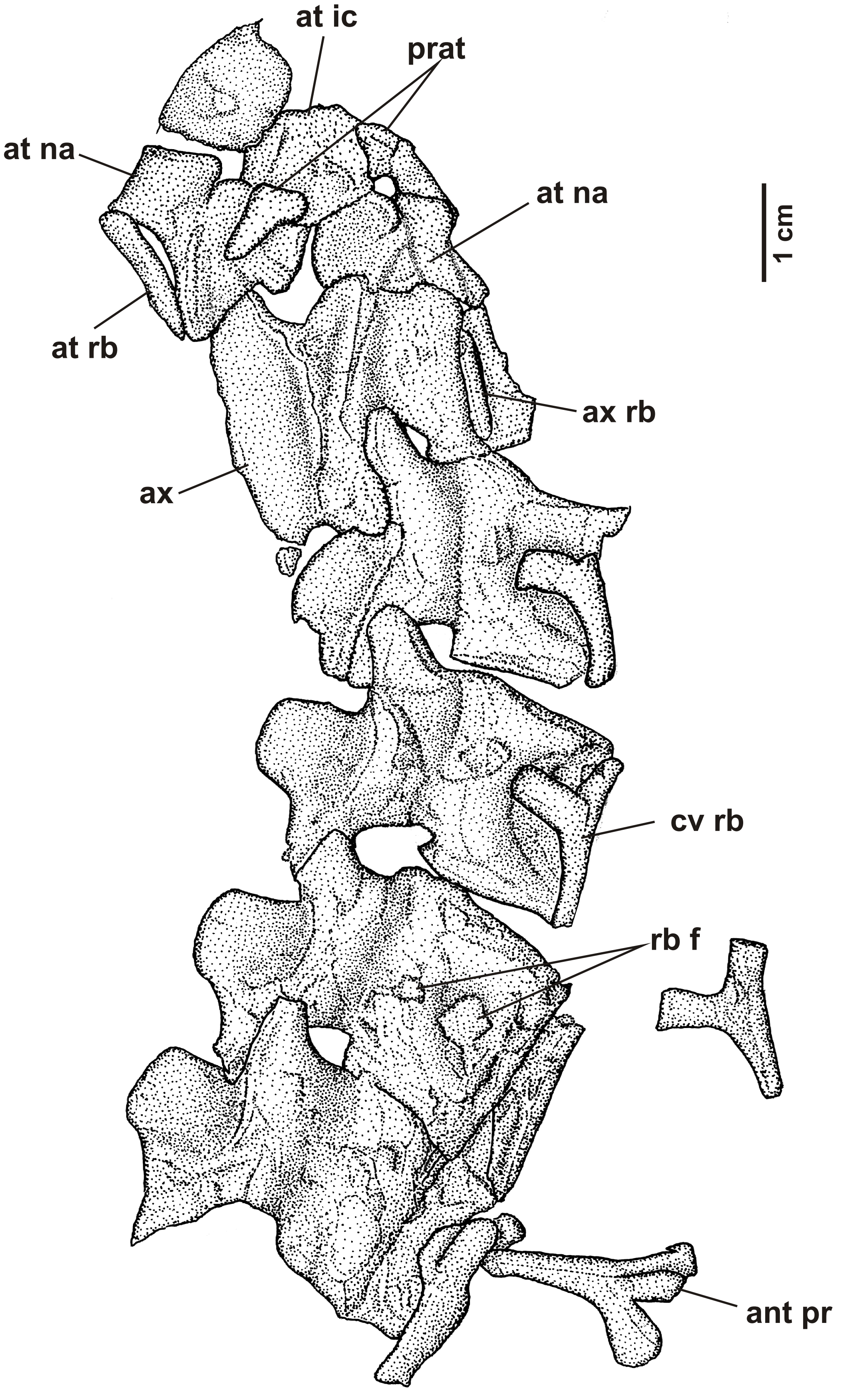


Fig. 14: *Askeptosaurus italicus*, cervical vertebrae in lateral view, MSNM V456.

projects somewhat dorsally, reaching above the level of the anteroventral origin of the neural spine. Although this feature had already been noted by KUHN (1952), his restoration shows the dorsal projection as too slender, suggesting that it is a small dorsal tip rather than a real expansion. The posterior margin of the base trends posterodorsally in an angle of approximately 45°, however, the margin is not completely straight but slightly concave, especially in its middle part. The remaining central part of the base is convexly built. Its lateral surface does not show notable structures.

It is difficult to determine the exact morphology of the atlas intercentrum due to the poor preservation. The element is situated anteriorly to and slightly above the right neural arch of the atlas of MSNM V456 and is of roughly rectangular shape. KUHN (1952) also noted a possible centrum lying anteriorly to the atlas neural arches, but this determination is problematical. It may be only a somewhat broken part of the braincase, which is also indicated by its position directly posteriorly to the parietal.

In MSNM V456, two small bones are situated medially to the left neural spine of the atlas and posteriorly to the right half of the exposed braincase, respectively. They have an elongated triangular shape, whereas the longest edge is slightly indented. The shorter and stouter end is rostrally directed. These bones highly resemble the proatlas in *Sphenodon* (ROMER 1956, fig. 120c), and since even the preserved position is nearly identical to the condition in the articulated atlas-complex of *Sphenodon*, they are therefore interpreted as such. A proatlas was previously not recorded in *Askeptosaurus*.

The axis is generally better preserved than the atlas, which may also be due to the fact that it does not consist of unfused elements. It is generally a prominent, elongated bone. The axis centrum is longer than high and distinctly depressed in its ventrolateral part. Its dorsolateral area is convexly curved and presents a sharp, laterally expanded edge slightly below its mid-dorsal margin, most probably serving for rib articulation. The neural arch of the axis is laterally constricted at its ventral base and presents a small but well-developed pre- and postzygapophysis. The former originates in the central area of the neural arch and then seems to trend into anteroventral direction. The projection generally remains broad and is only slightly tapered in its distalmost region. The anterior tip is of triangular shape. The morphology of the postzygapophysis is principally similar, although it seems that it was somewhat shorter. The process runs into posteroventral direction and ends in a rounded tip. Its proximal base is thickened and passes into the posteroventral margin of the well-developed neural spine, whose outline is low and relatively elongated. The dorsal margin of the spine is straight but presents a ventrally recurved distal tip on its posterodorsal and anterodorsal edge, while the remaining ventral part is significantly indented. The lateral surface of the spine shows a slight striation.

The remaining cervical vertebrae are modest elements as a result of the relatively low neural spine. They slightly increase in size into posterior direction. Neurocentral sutures are sometimes visible, being then of more or less horizontal alignment. KUHN (1952) misinterpreted the rib articulation, supposing that only the capitulum of the double-headed ribs met the vertebra, whereas the tuberculum articulated with a proposed chondrified intercentrum. However, the cervicals show in several cases that there were indeed two points of articulation, a diapophysis for the capitulum and a parapophysis for the tuberculum. The first one can be found directly below the lateral base of the neural arch on the dorsalmost part of the centrum, more or less in the middle of the vertebra, consisting of an irregularly rounded or rectangular depression. The second one, being of the same morphology, is present in the central area of the centrum and somewhat more posteriorly directed than the diapophysis. The centrum itself is slightly constricted in its central part and generally longer than high. On its ventrolateral area, it often shows a semilunar depression that opens into ventral direction. The development of this depression is not equally strong in all specimens of *Askeptosaurus*, therefore it cannot be excluded that tectonic deformation strengthened the impression to some extent. The remaining lateral part of the centrum consists of a convex curvature. The ventral base of the neural arch is distinctly more slender than the centrum, which results in a notable depression in the mid region of the vertebra. Pre- and postzygapophysis are relatively stout. The former shows a more prominent development, presenting a broad proximal base that passes into a horizontally flattened dorsal articulation surface distally. The postzygapohysis is somewhat shorter, but it presents also a broad base that tapers only slightly into posterior direction. Also here, the articulation surface on the ventral side of the distal tip is nearly horizontally flattened. The neural spine is of roughly rectangular shape, its anterodorsal and posterodorsal edges being rounded. The posterior margin passes into the base of the postzygapophysis and is therefore not as vertically directed as the anterior one.

Trunk vertebrae (fig. 15)

Especially the trunk vertebrae generally resemble those observed in younginiform reptiles like *Thadeosaurus* (CARROLL 1981) and therefore retain a relatively primitive shape.

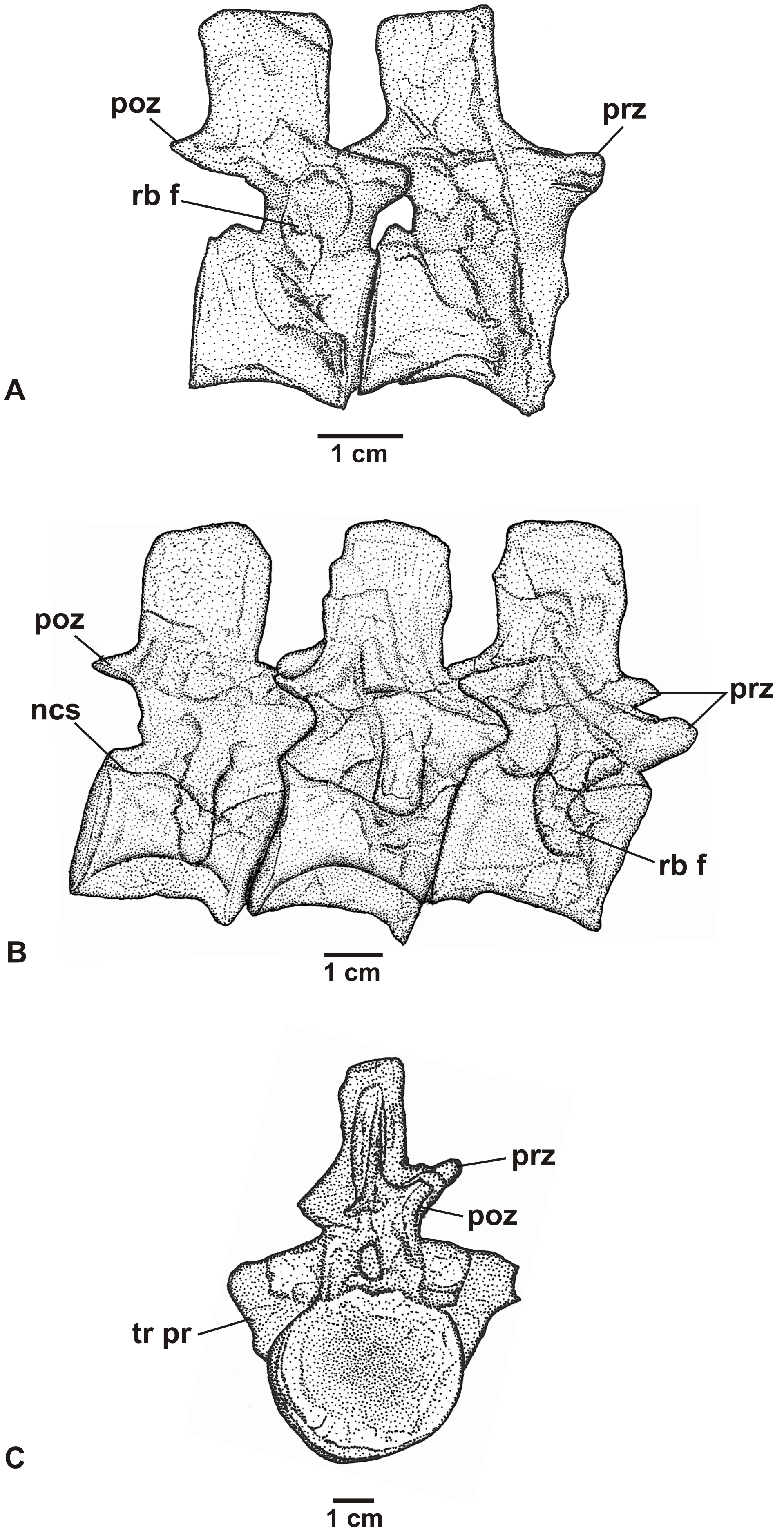


Fig. 15: *Askeptosaurus italicus*, thoracal vertebrae. A) and B) lateral view (MSNM V456 and PIMUZ T 4846), C) medial view (PIMUZ T 4832).

A neurocentral suture is often visible, running along the dorsal edge of the centrum, with a certain ventrally directed notch in the mid region. There is no notable change in size from front to back, only the anteriormost vertebrae are slightly smaller. However, all trunk vertebrae are larger than any of the cervicals, mainly as a result of the dorsal extension of the neural spine (to be described below). Another significant difference to the cervicals is that the trunk vertebrae do not possess a single diapophysis and parapophysis, due to the holocephalous condition of the thoracal ribs. The rib articulation facet is anteroventrally directed, originating in the mid-ventral region of the neural arch and then extending across the neurocentral suture down to the anteroventral margin of the centrum (fig. 15A, B). Sometimes the direction of the facet is also dorsoventral. In this case, the ventral end does not reach the anterior edge of the centrum. In lateral view, it is visible that the middle part of the articulation facet is often more slenderly built than the outer edges. In posterior view, it becomes evident that the attachment site indeed develops a modestly built transverse process. Its dorsal edge extends prominently into lateral direction, slightly recurved ventrally. The ventral edge is not expanded in this way and remains situated directly on the lateral surface of the centrum, the connecting outer edge of the middle part therefore runs diagonally into ventromedial direction. This condition results in a triangular shape of the transverse process, as seen in posterior view. The centrum is generally longer than high, its middle part being slightly constricted. In cross-section, the centrum is more or less circle-shaped. The neural arch is relatively long in most trunk vertebrae, but it does not equal the length of the centrum, because the latter extends slightly more into posterior direction. The ventral part of the neural arch is pierced by a small neural canal of elliptic shape (such a condition can at least be observed in a trunk vertebra of specimen PIMUZ T 4832, fig. 15C). The prezygapophyses are anterolaterally directed, their dorsal edges being very straight, only the distalmost edges are slightly recurved dorsally. However, the anterior extension is not very prominent, which results, together with the broad proximal base, in a stout impression. The complementary postzygapophyses are distinctly shorter and not that broad, but the dorsal recurvation of the distalmost tip is present as well. Furthermore, the posterior exposure in PIMUZ T 4832 suggests that the lateral extension of postzygapophyses was not as strong as in the prezgyapophyses. Thus the latter do not seem to have been fully overlain by the postzygapophyses, a condition that probably allowed a better lateral movement between the vertebrae. (It should be noted that specimen PIMUZ T 4846 superficially indicates the presence of a zygosphene-zygantrum articulation (fig 15B). However, this is certainly not the case but rather the result of tectonic deformation that shifted one of the two prezygapophyses into a position similar to that of a probable zygosphene). The neural spines are broad and of rectangular shape. They are more or less straight dorsally directed, only in a few cases a slight posterodorsal recurvation can be recognized. As mentioned above, the neural spines of the trunk vertebrae are distinctly higher than those of the cervicals. In many spines a dorsolateral striation can be observed.

Sacral and caudal vertebrae (fig. 16)

Only in MSNM V456 there is one sacral vertebra sufficiently preserved (fig. 16A). There are no signs of any fusion between the vertebrae, nor do the sacral ribs fuse to centra or neural arches. In general, the sacral vertebrae retain the shape of the preceding thoracals, but there is one significant difference in the development of the rib attachment site. The sacral rib does not articulate in the way the thoracal ribs do, but meets the vertebra more ventrally, in the lower half of the centrum. The articulation facet originates anteriorly to the lateral mid point of the centrum and then runs slightly posteroventrally, but it does not reach the posterior edge. The facet itself represents a modest concavity in which the sacral rib originally fitted. Hence there is no development of a transverse process like in the trunk vertebrae. As mentioned above, the remaining morphology of the sacral vertebrae shows no significant differences to the preceding elements, thus the post- and prezygapophyses as well as the neural spine cannot be distinguished from similar structures more anteriorly.

The caudal vertebrae (fig. 16A, B) are of a distinct morphology that is similar to the condition found in other thalattosauriform reptiles. A neurocentral suture occurs occasionally but it is not visible in every caudal element. If present, the suture runs along the upper margin of the centrum, sometimes being slightly concave into ventral direction. One striking feature is that the vertebrae do not show any sign of a transverse process, rather they possess unfused short ribs in the first six anterior caudals. Beginning with the fourth caudal, well-developed haemal arches are present between each vertebra. As the ribs, they are not fused either and diminish in the posteriormost portion of the tail.

Similar to the sacral vertebrae, the rib attachment site of the anterior caudals represents a half-rounded lateral depression on the centrum, but it is situated more ventrally. Therefore the centra of the anterior caudals show a well-developed curvature in their mediolateral part as a result of the ventral concavity and the lateral constriction of the contact zone to the neural

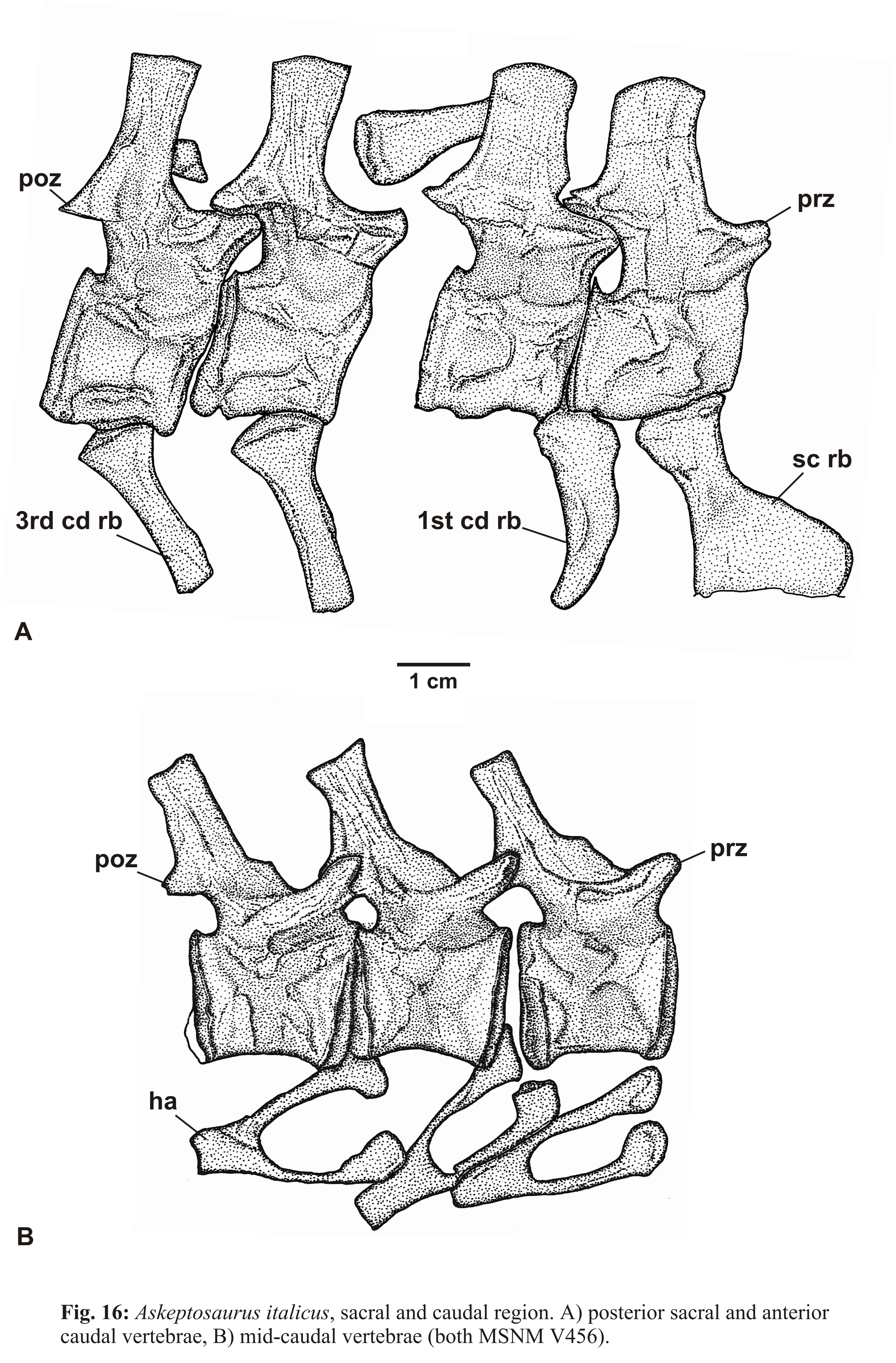


Fig. 16: *Askeptosaurus italicus*, sacral and caudal region. A) posterior sacral and anterior caudal vertebrae, B) mid-caudal vertebrae (both MSNM V456).

arch. In the more posterior caudals, where no ribs attach, this morphology is certainly different. In this area, the centra show a vertical depression in the mid region, running from the ventrolateral margin up to the dorsal edge. As a result the centra are more or less dorsoventrally constricted. Another feature, changing from the anterior to the posterior part, is the lateral outline of the centra. In the anterior caudals, the centra are not longer than high, the relation is at least equal, sometimes the centra are even higher than long. This morphology alters more posteriorly, the centra become increasingly elongated and are then longer than high, as the trunk vertebrae. Already KUHN (1952) describes a lateral foramen in the middle part of some caudal centra, but these openings are not visible in all vertebrae. Relatively similar to the condition of the thoracals is the development of the neural arches in the anterior caudals. They are also comparatively high and with stout pre- and small postzygapophyses. The neural spines are dorsally directed, but they are not as broad as the thoracal neural spines, rather they only reach two thirds of the width of the latter as maximum. As in all other neural spines of *Askeptosaurus*, a lateral striation can be observed in nearly every caudal element. The neural arches of the more posterior caudals differ in many respects. The ventral base is not that high, and almost directly above the contact to the centrum the prominent prezygapophysis originates. It is distinctly more elongated than in the anterior portion of the tail and is strictly anterodorsally directed. On the contrary, the postzygapophysis remains very small, representing only a small, posterolaterally projecting triangle. The neural spine becomes increasingly shorter in the middle and posterior portion of the tail. Furthermore, it gets more slender and the direction of the alignment changes from more or less dorsal to strictly posterodorsal. The distal edge is very straight and leads to an impression as if it was cut in an angle of 90°. Especially in the middle part of the tail, the anteroproximal base of the neural spine shows a prominent anterodorsal expansion. The haemal arches are posteroventrally directed and V-shaped, with each end, both dorsally and ventrally, being distinctly expanded. The two dorsal knob-like tips show small articulation surfaces, whereas the ventral tip of the arch is elongated and rectangular in shape. Corresponding to the condition found in the neural spines, also the haemal arches decrease in size into posterior direction.

3.1.2.2. Ribs

The morphology of the ribs distinctly differs along the vertebral column. So the cervical ribs do not have the same morphology as the thoracal ribs, and can therefore be easily distinguished from the latter. The tail does not bear many ribs, only the six anterior caudals possess some. Gastral ribs, however, are fairly present, but their total segment number can only be estimated as about 60-70.

Cervical ribs (fig. 14)

Generally, the cervical ribs of *Askeptosaurus* are of dichocephalous fashion, the only exception being obviously the ribs of the atlas-axis-complex. However, preservation makes it difficult to determine the exact structure of the latter. Posteriorly to the left atlas arch of the MSNM V456, there is a small and slender rod of bone, whose morphology suggests that it is indeed a small holoceophalous rib, articulating with the neural arch of the atlas. Its anterior head is slightly expanded and shows an obliquely directed, straight surface which obviously served for articulation. The posterior end of the bone is tapered and seems to have ended in a sharp tip.

In the same specimen, another small bar of bone is situated on the lateral side of the axis centrum, which can also be determined as rib element. Preservation suggests that this rib is holocephalous too, as no additional process could be detected.

The following anterior cervical ribs are Y-shaped. The two heads, the dorsal tuberculum and the ventral capitulum, nearly reach the length of the distal process, the tuberculum being the longer projection. Both heads show rectangular articulation surfaces. As already indicated in the description of the vertebrae, the cervical ribs articulate completely with the respective vertebrae, and the capitulum does not contact a chondrified intercentrum, as proposed by KUHN (1952). Rather the ribs meet the vertebrae at the points described in the latter section, i.e. close to the border of the neural arch and in the anteroventral portion of the centrum, respectively.

More posteriorly, the cervical ribs become increasingly more elongated, and also the capitulum gets notably longer than the tuberculum. Furthermore, at latest in the fifth cervical rib, an additional process is present in the proximal portion. This process lies on the external side, between capitulum and tuberculum, and is anteriorly directed, being shorter than the two other projections. In the posteriormost cervical ribs, this additional process appears to be reduced again, but it is still visible as a small ridge between tuberculum and capitulum.

Thoracal ribs (figs. 4-7)

All trunk vertebrae bear ribs, which are of distinctly different morphology than those of the cervical region. None of them seems to have fused to the respective vertebra, although KUHN (1952) states that the last two thoracal ribs did so. The articulation surfaces of the ribs are strictly holocephalous, the proximal heads being of flattened appearance, corresponding to the elongated articulation facets of the trunk vertebrae. In the anterior region, the heads appear to be slightly expanded in their dorsal portion, while more posteriorly, the heads are equally developed on both edges. With the exception of the posteriormost ribs, the thoracal ribs are notably longer than the cervical ones, whereas it is difficult to determine whether the anterior thoracal ribs are more elongated than posteriorly. In general, all respective elements are relatively long, strongly recurved and with a slightly expanded distal portion. However, there are no signs of a pachyostotic development. As just mentioned, the posteriormost thoracal ribs decrease abruptly in length, which can be noted at latest in the last four ribs. The last two thoracal ribs are slightly differently built, however, a clear determination is difficult due to the generally poor preservation of that portion in all specimens. They appear to be relatively short and almost straight laterally directed, without showing a significant recurvation.

Sacral and caudal ribs (figs. 16A, 19B)

Sacral and caudal ribs are all significantly shorter than the thoracal ribs and bear holocephalous proximal heads.

Askeptosaurus possessed obviously two sacral ribs on each side. They are not ankylosed to the vertebrae, as they always occur dissociated in the specimens. They can be easily distinguished from all remaining ribs by their expanded morphology, which practically affects the whole element, especially the distal portion. The latter is broadly expanded and of fan-shaped morphology, contacting the ilium with its distal margin.

There are only a few caudal ribs present, the number is not higher than five. They are all unfused to the caudal vertebrae. At least the following two vertebrae show slight expansions laterally, indicating the rest of a transverse process. The five caudal ribs decrease in size from front to back and show different morphologies. So the first caudal rib is relatively broad proximally, but tapers distally, showing a posterior recurvation. The following ribs are entirely different. They do not taper into distal direction, they are generally slender, and anterolaterally directed. Their distal tip is of an angular fashion. The last two caudal ribs are not straight anterolaterally directed, but are more recurved into the same direction. Furthermore, they appear to be generally expanded and each of them shows a nearly pointed distal end. Both are significantly shorter than the preceding ribs, thus the last one is of almost triangular shape.

Gastral ribs (figs. 4-7)

The gastralia are situated between pectoral and pelvic girdle. Due to the slenderness of the gastral ribs, the preservation of these elements is relatively bad. PIMUZ T 4832 shows the gastralia to be exposed in ventral view, but a suitable description is still rendered difficult. There appears to be a slender, paired medioventral element, being slightly expanded internally, and tapering into lateral direction. Both halves overlap each other in the ventral midline of the body. Each paired medioventral element is anteriorly accompanied by a lateral one, respectively, which is very slender and gracile along its full extension. KUHN (1952) supposes that each vertebral segment contained two complete gastral sections, but this cannot be corroborated with absolute certainty, although it would not be unusual (for example, such a condition can be observed in *Sphenodon* (ROMER 1956)). Preservation does not allow to determine whether the morphology of the gastralia changes along the extension of the trunk. Maybe there were no lateral elements in the anteriormost portion.

3.1.3. The appendicular skeleton

3.1.3.1. Pectoral girdle (figs. 4-7, 17, 18)

The elements of the pectoral girdle of *Askeptosaurus* are preserved in ventral (lateral) and dorsal (medial) view, but often covered by other bones. The girdle consists of coracoids, scapulae, clavicles and interclavicle, other elements are not present. The shoulder girdle obviously constituted a highly mobile construction, since none of the respective elements appears to be firmly fused to one another. It must remain open to question whether there were originally additional chondrified elements, e.g. a suprascapula. The following description is mainly based on MSNM V456, PIMUZ T 4831, 4832, 4842, and 4846.

Interclavicle

The interclavicle is an arrow-shaped, broad, and elongated element of flattened appearance. Its anterior tip is relatively slender, rounded, and straight rostrally directed. The lateral projections are slightly longer and trend into posterolateral direction, their distal ends being increasingly more tapered, while the proximal base is expanded. Their anterior margin is slightly depressed, most probably because of the contact with the clavicles. In dorsal and ventral view, the lateral projections show several small crests. The posterior projection of the interclavicle is the largest part of the bone. Its caudal elongation is almost four times as long as the remaining portion. Generally, there is no tapering into posterior direction, the distalmost tip appears to be broad and rounded as well. The surface of the bone does not bear any further remarkable structures.

Clavicle

The clavicle is a thin and slender element whose internal and external regions are significantly recurved into ventromedial and dorsolateral direction, respectively. The medial area of the bone shows a rounded internal end, but generally, the medial part appears to be relatively flattened, its surface being of roughened impression. It passes into the mid-portion of the bone by an increasing expansion, thus the bone gets even more flattened and thinner, while its dorsal margin becomes rounded. The dorsolateral shank of the clavicle continues this

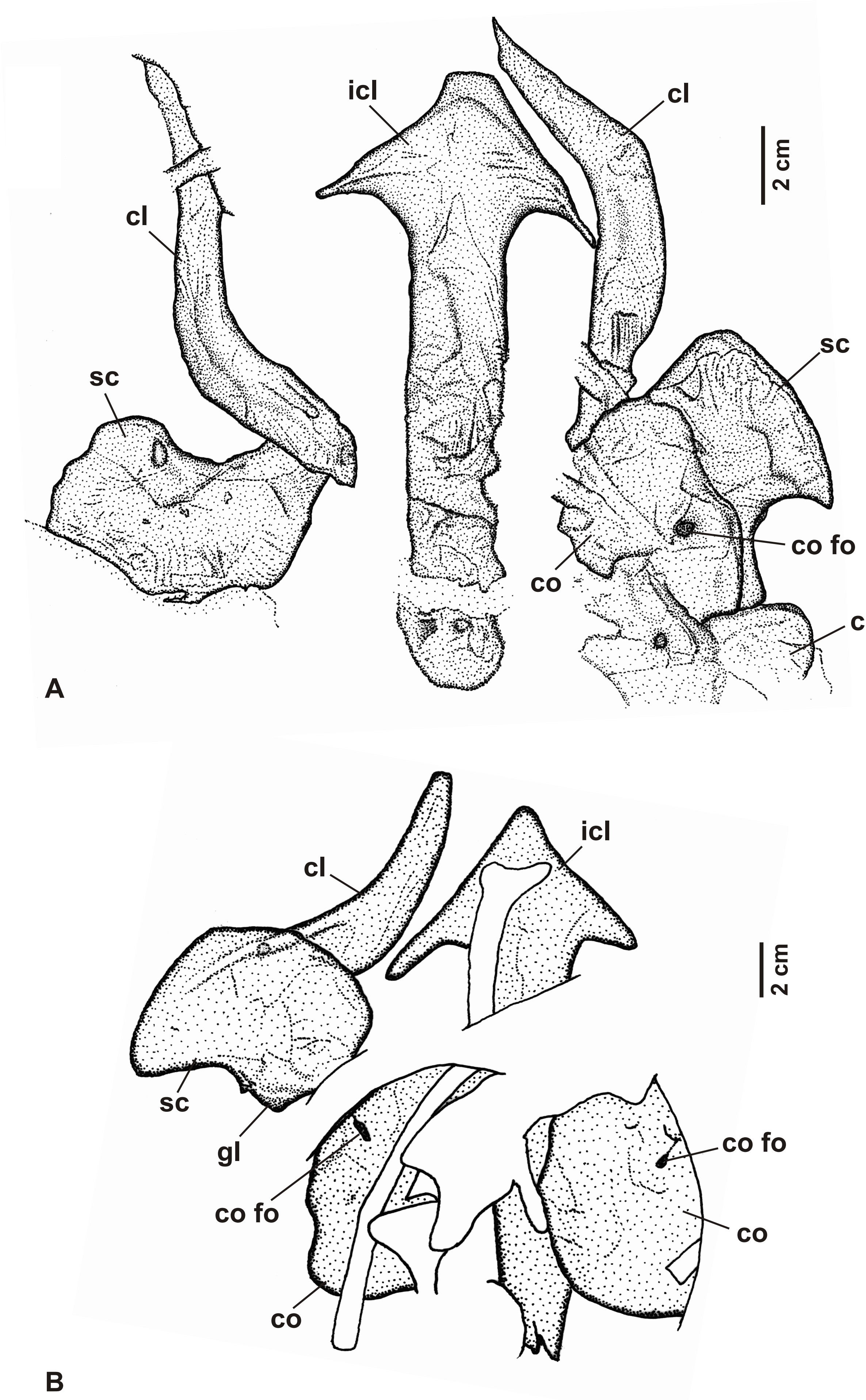


Fig. 17: *Askeptosaurus italicus,* pectoral girdles in ventral view. A) PIMUZ T 4842, B) PIMUZ T 4832.

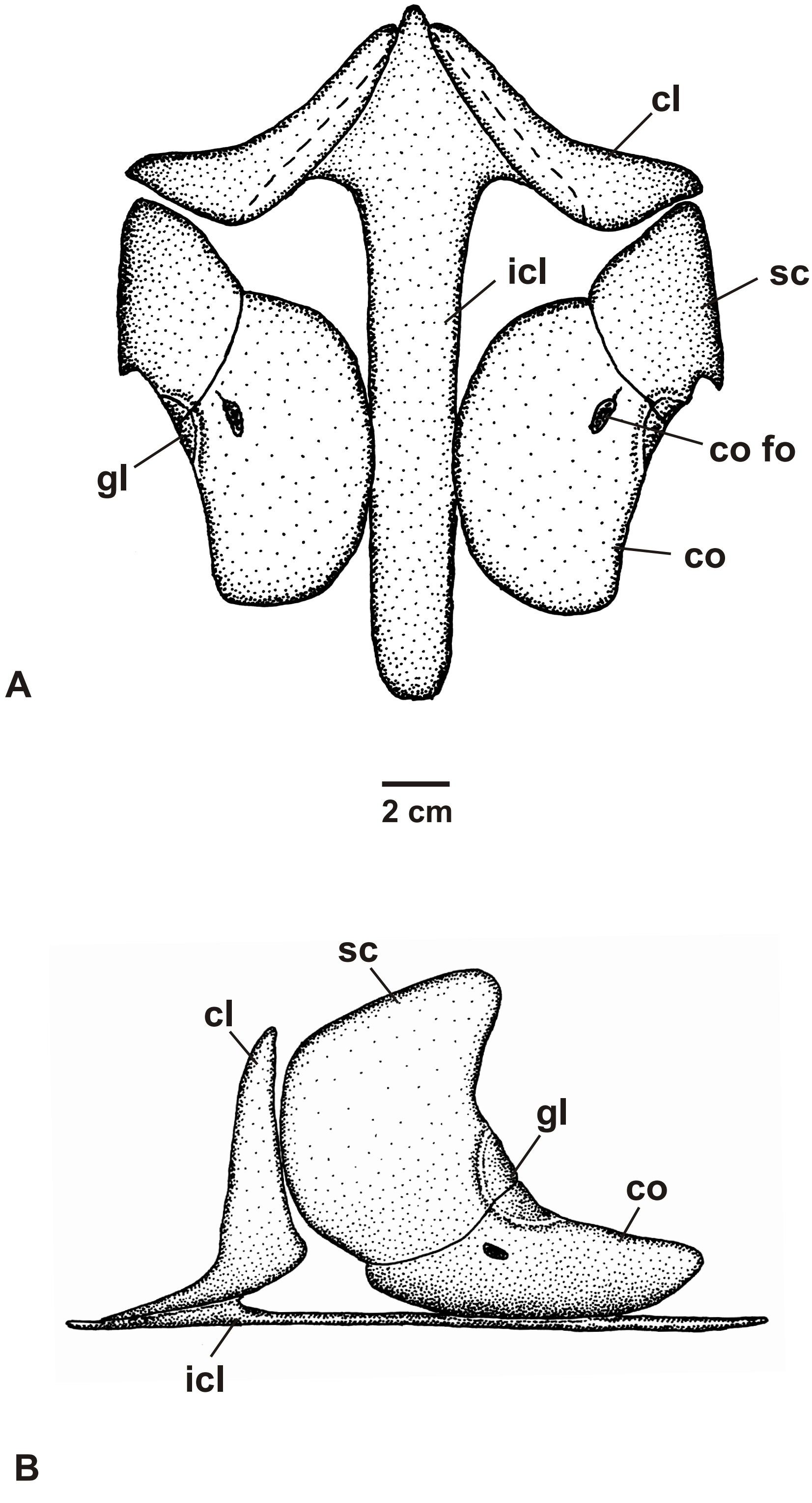


Fig. 18: *Askeptosaurus italicus*, restoration of pectoral girdle. A) ventral view, B) lateral view.

flattened expansion proximally, but the distal portion tapers again and represents a rounded and slender rod, which formerly originated from the rounded dorsal margin of the mid-portion. The ventral margin of the tapering expansion shows sometimes a slightly serrated morphology, while in all specimens the surface of this region bears a distinct striation. It appears that the clavicles contacted the anterolateral margin of the interclavicle medially and the anterior edge of the scapula dorsally. The degree of this contact obviously changed during body movement, a condition roughly resembling the one in squamates.

Coracoid

The coracoid is a broad, half-rounded element, being the only bone of the shoulder girdle that appears to have a relatively stable contact to a neighbouring element, i.e. the scapula, which the bone meets at its dorsal edge. However, even there the suture was obviously loose, as both elements mostly occur dissociated from one another in the investigated specimens. The ventromedial margin of the coracoid is strongly convexly built and passes smoothly into the anterior and posterior margins, without showing a significant difference. The posterodorsal edge, however, is separated from the remaining posterior margin by a rounded corner. Its alignment is different, instead of a convex margin the edge is rather concave. The anterodorsal margin is relatively straight, most probably as a result of the contact to the scapula. Close to its mid-level, the coracoid foramen is situated, being very small and of elongated impression. It may be even the case that the foramen is dorsally not completely embraced by the bone, which is at least indicated in PIMUZ T 4832 (fig. 17B), where anterior and posterior margin of the foramen seem to approach each other dorsally, but without showing a fusion. In the dorsal portion, the bone appears to be thickened to some extent, showing also some rugosities there, especially in the posterodorsal area, where the coracoid forms the ventral portion of the glenoid. However, the articulation surface for the humerus is only modestly developed, being just a small transverse expansion at the dorsal end of the posterior margin. The remaining surface of the coracoid does not possess many remarkable structures, the only exception being a slight fan-shaped striation that can be noted laterally as well as medially.

Scapula

As the coracoid, the scapular blade is a broad element. However, its shape differs from the latter in the sense that the posterior margin is strongly concave, especially in its mid-portion. With the exception of the straight posterodorsal part, the dorsal and the anterior edge together show a convex outline and are only separated from another by a rounded anterodorsal corner. The ventral margin is slightly convex, corresponding to the morphology of the dorsal edge of the coracoid, to which it is sutured (see above). The posteroventral portion of the bone is thickened and forms the dorsal part of the glenoid region. As can be seen in lateral view, this area possesses a more or less transversely orientated surface for humerus articulation, being dorsally followed by a short but prominent keel that passes into the posterior margin of the scapula. The medial side of this region shows several rugosities. Both surfaces of the scapula present again fan-shaped striations, as well as irregularly distributed rugosities and small foramina. Presence and development of these structures appear to vary within the specimens.

3.1.3.2. Pelvic girdle (figs. 19, 20)

The pelvis consists of three elements, ilium, ischium, and pubis, and there are no signs of a prepubis or other structures. Contrary to previous assumptions, the girdle does not show a derived diapsid condition in having a thyroid fenestra, but presents a puboischiadic blade, as is typical of more primitive diapsids. The following description mainly rests on MSNM V456, PIMUZ T 4831, 4832, 4842, and 4846.

Ilium

The ilium, preserved laterally and medially, is a bone of typical thalattosauriform appearance. The bone forms the dorsal part of the acetabulum and mediates between the pelvis and the vertebral column by a contact to the sacral ribs at its medial side. A possible fusion between ribs and ilium could not be detected. That there was indeed only a loose contact is also indicated by the dislocation of the pelvic elements in several specimens, never showing a fusion to the ribs. The ventral part of the ilium is distinctly expanded and presents a convex ventral margin, whose anterior and posterior half meet pubis and ischium, respectively. The side of the ventral portion bears, as mentioned above, the dorsal part of the acetabulum, consisting of a smooth depression, divided from the dorsal part of the ilium by a dorsally-convex edge. The medial side of the ventral portion presents a median curvature, most probably as a result of the lateral acetabular depression. The dorsal part of the ilium consists of an elongated process being strongly directed posterodorsally. The medial side of the process presents a well-visible ridge at the proximal base that runs along the proximoventral edge. The dorsal side of this ridge may have served for muscle attachment, i.e. iliofemoralis and iliofibularis muscles. Posterodorsally, the process becomes increasingly flattended into distal direction, its end being of almost rectangular shape, with a sharp dorsal and ventral edge. Both laterally and medially a significant striation occurs along the mid and posterior portion of the process that trends into posterodorsal and posterior direction. There is no development of a preacetabular spine on the dorsal margin of the ilium, as is often observed in other reptiles.

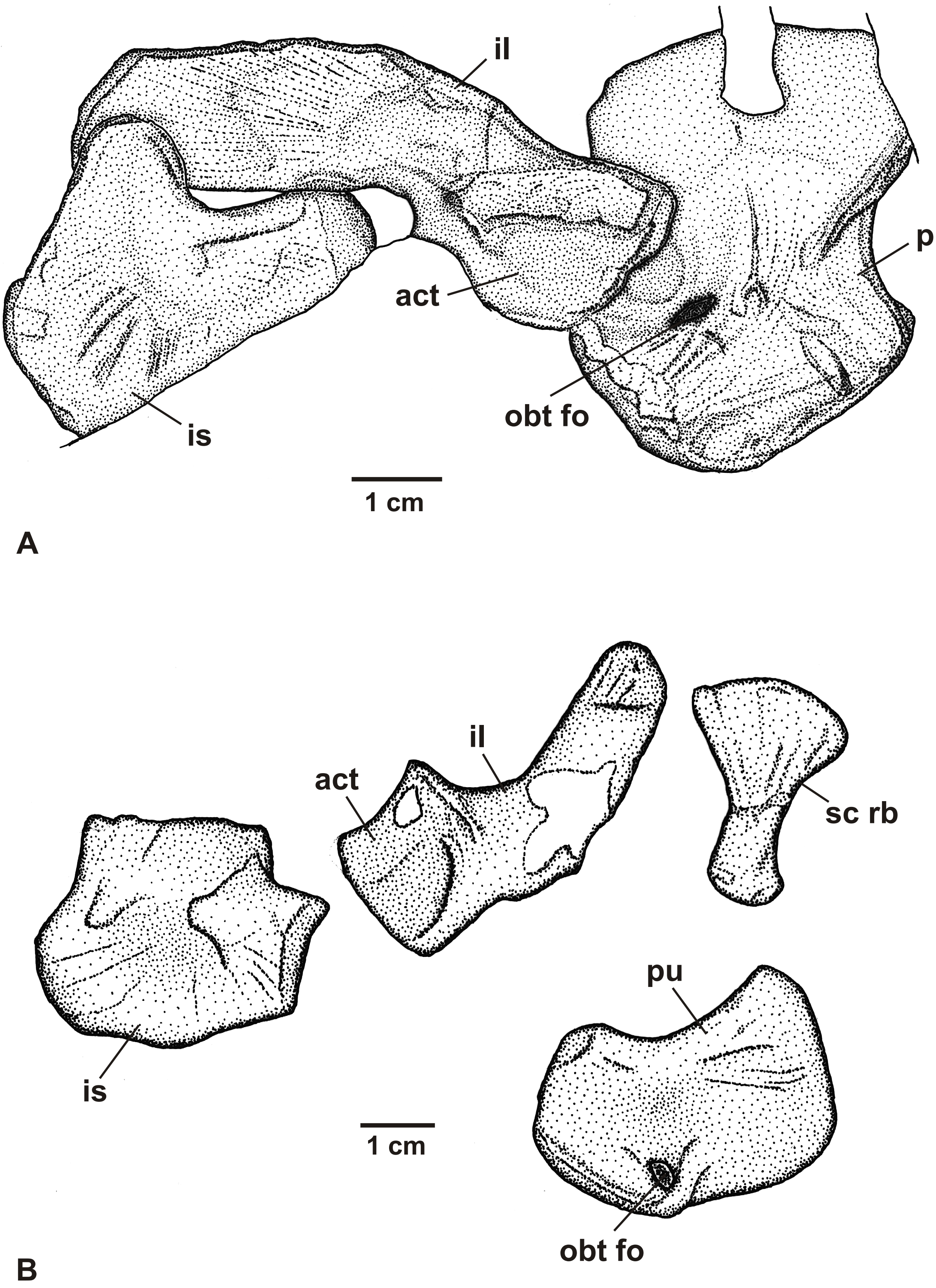


Fig. 19: *Askeptosaurus italicus,* isolated pelvic elements. A) right pelvis of MSNM V456, ilium and ischium in lateral, pubis in medial view. B) right pelvis of PIMUZ T 4642, all elements in lateral view.

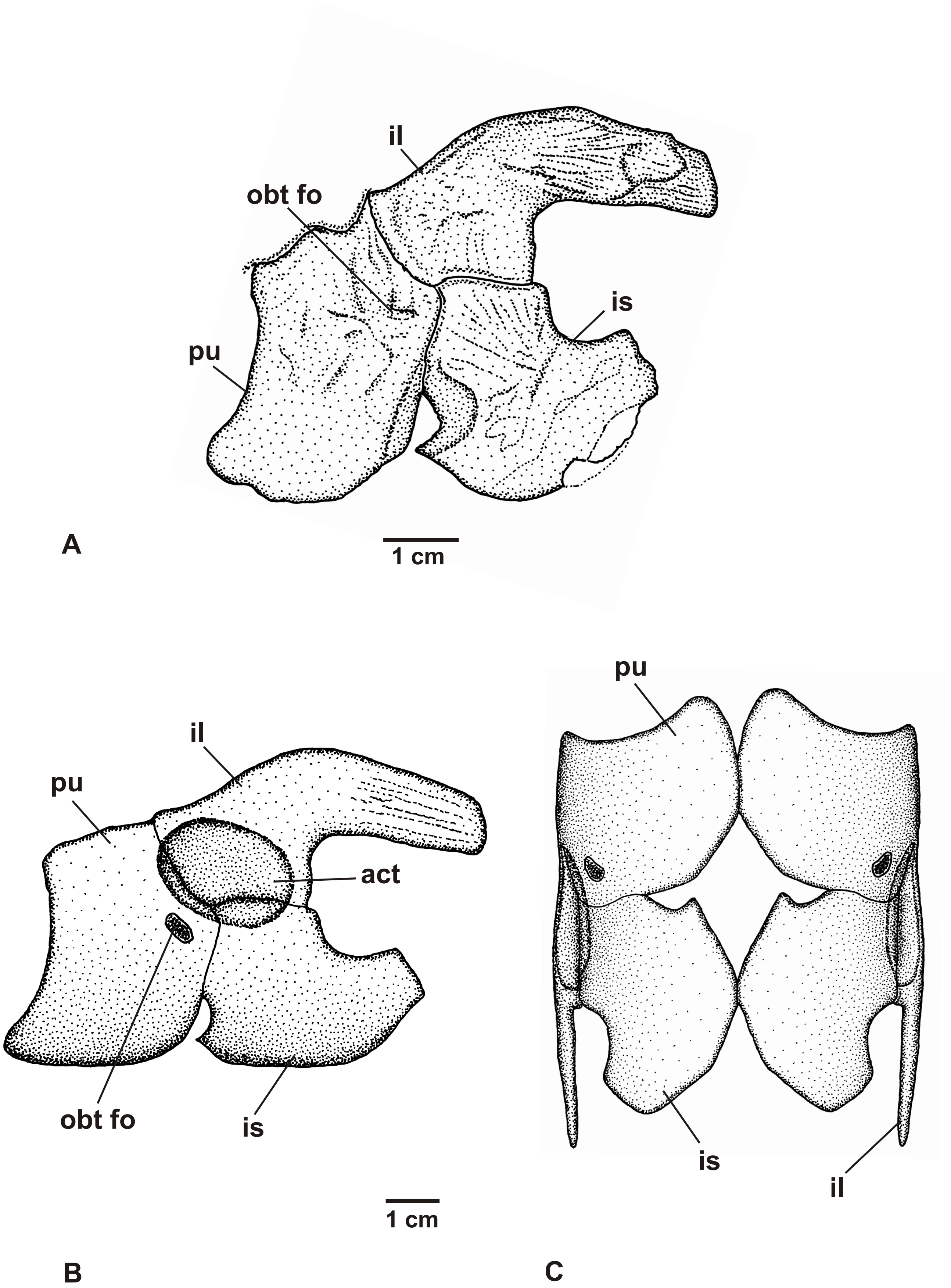


Fig. 20: *Askeptosaurus italicus*, articulated pelvis. A) right pelvis of PIMUZ T 4831 in medial view, B) restoration of pelvis in lateral view, C) restoration of pelvis in ventral view.

Ischium

The ischium is preserved in lateral and medial view. It is a broad element and forms the posteroventral portion of the acetabulum. KUHN (1952) describes the ischium to show a concave anterior margin, however, it is not clear how KUHN came to this conclusion. So he states that in MSNM V456, the anterior margin of this bone shows such an alignment, but this remains difficult to understand since there is only one ischium preserved whose anterior part is covered by the femur (fig. 19A), and the x-ray picture of the specimen does not corroborate this interpretation either (fig. 4). The photograph rather suggests that the ischium has a straight anterior margin. The only other structure which KUHN (1952) also referred to, was an impression in PIMUZ T 4831, but here he misinterpreted a breakage with a suture (fig. 20A). In fact, the true borders of the bone are still visible there and show that the margin was more or less straight. Disarticulated ischia in specimens PIMUZ T 4832 and 4842 (figs. 6 & 19B, respectively) also show that the anterior margin was straight, although slightly trending into posteroventral direction. Hence, concerning the general outline of the ischium it can be stated that the dorsal margin is the only concave edge, the anterior and posterior margins are generally straight, the latter slightly trending anteroventrally, and that the ventral edge is of convex fashion. The bone meets the ilium at its anterodorsal edge in an anteroventrally trending suture. In this region, the ischium is furthermore relatively thickened. This thickening is also present in the remaining dorsal area, although less well-developed. Into ventral direction, the bone becomes increasingly flattened. The lateral area around the anterodorsal edge bears a slight depression, representing the acetabulum. With the exception of a slight fan-shaped ventral striation, the lateral and medial surfaces do not show significant structures.

Pubis

The pubis, preserved in lateral and medial view, is the most expanded element of the pelvic girdle. It is a broad plate of bone whose dorsal and ventral portions are somewhat enlarged. The bone forms the anteroventral part of the acetabulum and the small, oval obturator foramen lies anteroventrally to the contact with the ilium. The ventral margin of the bone is more or less straight, only sometimes a slight convexity can be recognized. The dorsal margin is nearly triangular. Its posterior shank, shorter than the anterior one, is thickened, like the entire posterodorsal area of the bone at least medially, and meets the ilium along its complete extension. The anterior margin of the pubis is strongly concave, while the outline of the posterior edge is more or less straight. The large thyroid fenestra, as reconstructed by KUHN (1952), can therefore not be corroborated. Rather, ischium and pubis met each other to a great extent and the respective margins diverged only in the ventralmost area, which is, however, often observed in reptiles with a puboischiadic plate (ROMER 1956). The observed condition strongly corresponds to the one seen in *Hescheleria* (PEYER 1936b, RIEPPEL 1987). Next to the obturator foramen, there are several crests and striations in the dorsomedial portion of the bone. Moreover, two relatively prominent crests originate in the central part and trend far anteroventrally and posteroventrally, respectively, the former closely approaching to the anteroventral margin. Both crests are probably related to the attachment of the puboischiofemoralis internus muscle (ROMER 1956), while the anteroventral crest may reflect the inferred border to the ischiotrochantericus muscle, whose attachment appears to be responsible for the rugosities in the anterodorsal area. In this region, MSNM V456 shows furthermore a small elongated ridge close to the anterodorsal edge, but its function could not be determined (fig. 19A). Laterally to the pubis, there are no significant features, with the exception of the depressed acetabular area in its dorsalmost part.

3.1.3.3. Limb skeleton

Askeptosaurus bears well-developed fore- and hindlimbs, although both are relatively short in relation to the length of the trunk. The anterior extremity is shorter than the posterior one. As is typical in aquatic reptiles, ossification is reduced to certain extent, the respective structures being made up by cartilage only. Hence, in comparison to a terrestrial reptile, muscle scars, processes and epiphyses are not preserved or at least very difficult to detect, rendering several details of the extremities problematical to describe. It seems that at least the stygopodial and zygopodial elements had originally been embraced by cartilage at their proximal and distal heads, which is especially apparent in humerus and femur.

3.1.3.3.1. Forelimb (figs. 21, 22)

Preservation allows both the flexor (dorsal) and the extensor (ventral) side of the forelimb to be described. The forelimb is preserved in most specimens.

Humerus

The humerus is generally the most prominent and longest element of the forelimb skeleton. There is a notable torsion in the bone so that both heads are distinctly twisted to one another (fig. 21B), but this is not visible in every specimen, probably due to tectonic deformation. A certain variation in the morphology of the proximal and distal head can be recognized in the specimens. So PIMUZ T 4846 shows the two articular surfaces not to be as strongly rounded as in MSNM V456 (figs. 7 & 21A, respectively), they rather have an angular impression. Thus, it is probable that a different degree of ossification may be the responsible cause. This assumption is corroborated by the indication of cartilage on both heads of the humerus. The area where cartilage was obviously present embraces the complete articular surface of the heads and can be distinguished from the remaining bone by a slight depression that lacks striations, as they often occur on the rest of the bone. Furthermore, a small keel divides the cartilage area from the remaining surface of the humerus. All this is especially well-developed on the dorsal surface of the bone. This side also shows a prominent crest at its posterior margin, serving for the attachment of the triceps muscle (according to ROMER 1956). Its proximal origin is situated where the dorsal head tapers and begins to pass

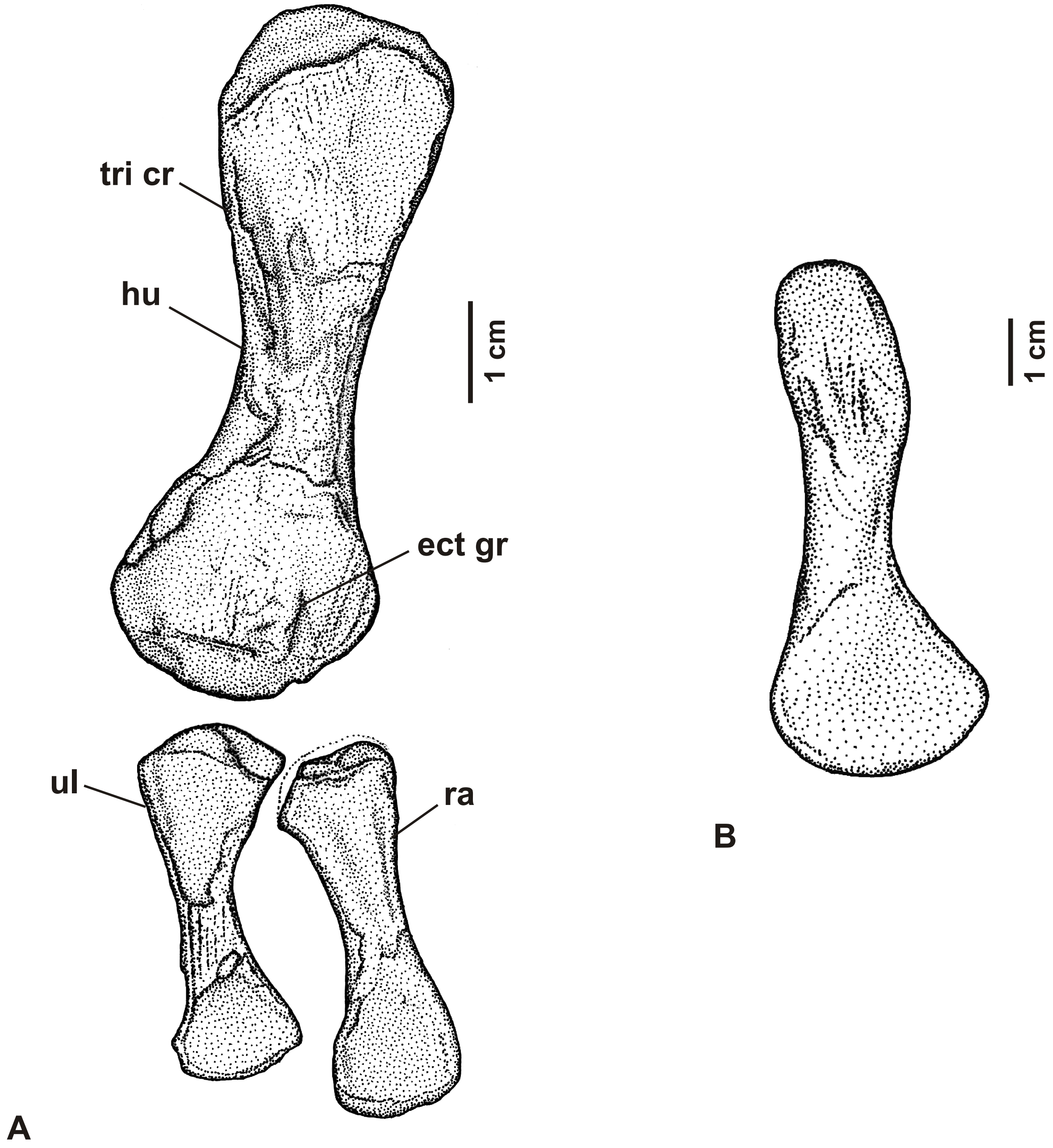


Fig. 21: *Askeptosaurus italicus*, stylo- and zeugopodium. A) right stylo- and zeugopodium, dorsal surface (MSNM V456), B) right humerus in more or less lateral view, showing the torsion of the distal and proximal heads relative to each other (PIMUZ T 4842).

into the shaft of the bone, the end of the crest lies in the mid part of the humerus. Proximally, the crest is more slender than distally, and it passes finally into a broad curvature, running along the posterodistal margin of the shaft. Laterally to this crest, a well-visible curvature covers the central surface of the shaft, being slender distally and becoming increasingly broader and flattened into proximal direction. It nearly extends up to the proximal head region. In the mid-level of this curvature, a small knob-like structure is present that most probably also served for the attachment of muscles or tendons. With the exception of a slight anterior and posterior expansion, there is no significant development of supinator process, ectepicondyle, or entepicondyle, nor is there any trace of a respective foramen. The only indication for such a structure is a groove in the anterior (lateral) area of the distal head, which already KUHN (1952) considered as the remainder of an ancestral ectepicondylar foramen. Distally to the reduced entepicondyle, a short but broad crest is sometimes present, situated at the posterior margin of the base of the ventral head. The structure surely is also an area for muscle or tendon attachment, but a more precise statement is impossible. Corresponding to the reduced condition of the aforementioned structures of the distal articular surface, radial and ulnar condyle are not well-developed either. It should be noted, however, that due to a different degree of ossification the structures of the distal head might have been variably developed, as at least the humeri of PIMUZ T 4846 appear to be slightly more differentiated (fig. 7). The ventral side of the humerus also shows only a very few features. The right humerus of PIMUZ T 4832 (fig. 6) presents a small edge at its proximomedial margin, which possibly represents the reduced deltopectoral crest.

Radius

The radius (fig. 21A) is a relatively stout bone whose articular surfaces are slightly expanded and nearly equal in size, their margins being almost straight. In general, the bone does not show significant structures, neither flexor nor extensor surface. However, in PIMUZ T 4846, the proximal head of the left radius is more expanded than the distal articular surface. This impression may be an artefact of preservation, indicating that the dorsal head was originally triangular in cross-section. Thus, tectonic deformation forced one of the three proximal curvatures into a position that makes the head seem to be more expanded than it was formerly the case.

Ulna

The ulna (fig. 21A) is a bone which is significantly constricted in the shaft area. It is slightly shorter than the radius and lacks an olecranon, which was probably present in chondrified fashion. Both articular surfaces show convex margins and are prominently expanded, whereas the proximal head is notably larger than the distal one. The lateral edge of the former is rounder than the medial edge, the latter being relatively sharp and also more expanded. The remaining proximal area seems to be flattened, but this may also be a consequence of tectonic deformation. The distal portion does not show notable features, the articulation surface is equally developed both laterally and medially.

Manus

The manus of *Askeptosaurus* is of special interest since there occurs a notable degree of intraspecific variation. So in MSNM V456 (fig. 22A), six ossified elements are present in the carpus, whereas in PIMUZ T 4846 (fig. 22B), seven bones can be recognized. The condition in the former specimens has already been described by KUHN (1952). There, two proximal elements are present, ulnare and intermedium, as well as four distal ones, distal carpals 1 to 4. The intermedium is distinctly larger than the ulnare and of rectangular shape, with rounded edges. The ulnare is stouter and more oval in shape. PIMUZ T 4846 interestingly presents another proximal element situated distally to the intermedium. It is of irregular oval shape and approximately half as large as the intermedium, articulating with the latter bone proximally, and with distal carpals 2, 3, and 4 distally. Whether there had also been an occasional contact to the ulnare or distal carpal 1, the latter being at least indicated in the left forelimb of the same specimen, must remain open to question. The topology suggests this bone to represent the centrale, and it is therefore interpreted as such.

In MSNM V456, all distal carpals are small, circle-shaped elements, while in PIMUZ T 4846, distal carpals 1 and 4 are larger than the remaining two. Distal carpals 3 and 4 also slightly differ in shape. They are more oval, and distal carpal 4 has even a somewhat rectangular impression. Every distal carpal articulates with its neighbouring one as well as with the respective metacarpal. Distal carpal 4 also meets, as mentioned above, the centrale in PIMUZ T 4846, and the ulnare at its proximal edge. Since distal carpal 5 is not present any

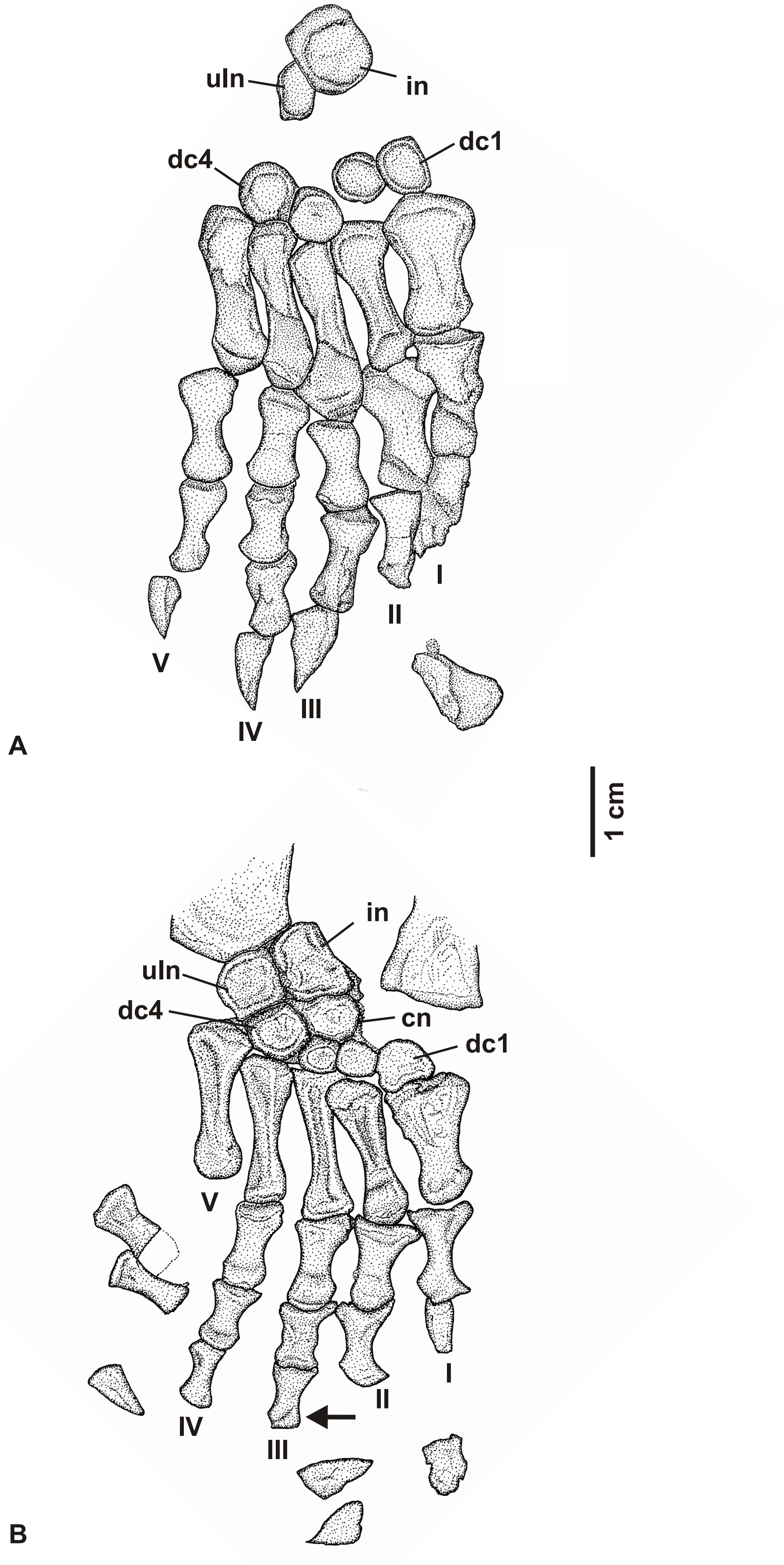


Fig. 22: *Askeptosaurus italicus*, manus. A) right manus of MSNM V456, B), right manus of PIMUZ T 4846. Note the presence of a centrale as well as the ossification of an additional phalangeal element in the third digit (arrow) of PIMUZ T 4846.

more, the bone occupies also this position and shows therefore a further contact to metacarpal 5.

As indicated in the previous section, the metacarpus shows five elements. Metacarpal 1 is the shortest bone, being prominently thickened both on its two heads and in the shaft area. The proximal articular surface is the most expanded part. The remaining metacarpals are relatively slender elements, with metacarpal 5 being somewhat more expanded. All are nearly equal in size, only metacarpal 2 is slightly shorter. It should be added that especially metacarpals 2-4 show well-developed sharp crests on their shafts.

As in the carpus, the phalanges are also subject of a certain intraspecific variation. So MSNM V456 and PIMUZ T 4831 present a phalangeal count of 2-3-3-4-3, whereas PIMUZ T 4846 shows a formula of 2-3-4-4-3. The third digit possesses therefore one additional eleent. Since the ungual is not shifted away in MSNM V456, a preservational cause for this difference can be excluded. Thus also here, the manus of *Askeptosaurus* shows a notable variability. The phalanges are generally smaller than the metacarpals. Especially the proximal phalanx of the first digit is slightly more expanded than the other ones, but this is only true for MSNM V456. Apart from that, shape and size of the proximal phalanges remain almost constant, showing only a slight irregular variation. This is also true for all other phalanges, although the more distal ones tend to become somewhat smaller. The ungual phalanges consist of modestly developed claws that do not present a significant recurvation. Nevertheless, their distal tip is very sharp. The claws show furthermore small dorsomedian grooves, which already KUHN (1952) interpreted as sites for tendon attachment.

Given that only these two specimens currently allow a detailed comparison of carpal ossifications, any taxonomical consequences will be avoided. Furthermore, at least in the case of the additional phalange, an intraspecific variation has already been reported for pachypleurosaurs (e.g. SANDER 1989a; see also CALDWELL 1997 for a more general view), and there is also embryological evidence that an additional phalange can easily develop (TICKLE 2002).

3.1.3.3.2. Hindlimb (fig. 23)

The hindlimb, although it can be seen in most specimens, is sufficiently preserved mainly in dorsal (anterior) view, and only sometimes in ventral (posterior) view, whereas it is then not so well preserved.

Femur

The femur is an elongated bone of cylindrical shape which is longer than its complementary element in the forelimb. The articular heads are rounded, sometimes also of slight angular impression, and with the proximal head being somewhat larger than the distal one. Their margins again indicate that they had originally been embraced by cartilage, as there are some rugosities recognizable. Specimen PIMUZ T 4846 suggests that the two heads were affected by a slight torsion (fig. 7). Generally, the reduction of ossified structures as a result of aquatic adaptation renders many features of the femur difficult to determine. Nevertheless, the ventral side is roughly visible in some specimens, e.g. in PIMUZ T 4832 (fig. 6). At the proximomedial edge of the right femur of this specimen, a small crest is visibe, which probably represents the internal trochanter. Presumably the same structure is visible in dorsal view (fig. 23A), developed as a modest expansion at the posterior (medial) edge of the proximal articular surface. The shaft of the right femur of MSNM V456 (fig. 23A) presents a slight angular ridge on its anterior margin, as well as a sharp keel at its posterior side, but their function must remain undetermined. The distal head does not show many structures on its dorsal side. The left femur of PIMUZ T 4846 (fig. 7) presents a modest depression in its distal region, which may be the intercondylar fossa for the attachment of triceps tendon (according to ROMER 1956). Generally, the femur does not appear to have developed prominent condyles for the articulation with tibia or fibula.

Tibia

The tibia (fig. 23B) is a stout bone of cylindrical shape. The shaft area does not show a significant constriction. The proximal articular surface presents a distinct expansion, being somewhat more developed into lateral direction and maybe representing the relic of a crest serving for the attachment of the triceps or quadriceps femoris muscle (ROMER 1956). On the

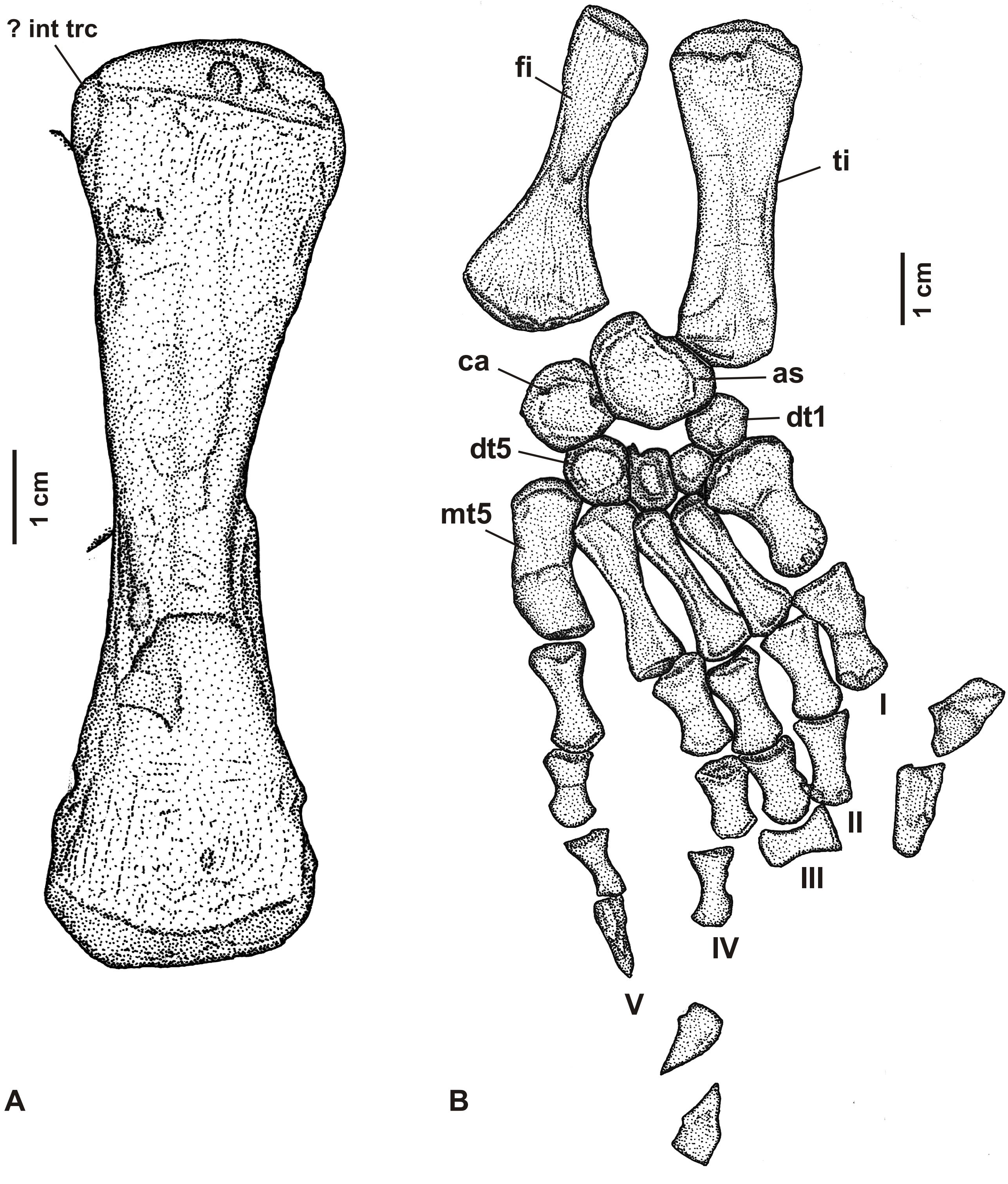


Fig. 23: *Askeptosaurus italicus*, hindlimb. A) right femur, dorsal view, B) right zeugo- and autopodium, dorsal view (MSNM V456).

contrary, the distal head is rarely expanded. The margins of both heads are convexly built. The shaft surface does not show many notable features, only two slight curvatures are present on the dorsal side.

Fibula

Unlike the relatively straight and structureless tibia, the fibula (fig. 23B), although of roughly the same size, shows a distinctly different shape. The bone has generally a more flattened appearance and bears a stronger constriction of the shaft as well as a greatly expanded distal head. The latter is fan-shaped and nearly twice as broad as the shaft, with the medial edge being slightly sharper than the external one. The margin of the distal articular surface is convex, the proximal margin varies to a certain extent, but is generally straighter. The proximal head is also only slightly broader than the shaft and mirrors more or less the condition of the distal head of the tibia, whereas its lateral edge tends to show a little greater expansion. The anterior side of the shaft shows a small triangular ridge, which may have served for the distal attachment of the iliofibularis muscle (according to ROMER 1956). The remaining surface of the fibula is without notable features.

Pes

Contrary to the conditions found in the manus of *Askeptosaurus*, the pes (fig. 23B) remains constant in the development of ossifications, both in the tarsus as in the phalanges. The tarsus presents six bones in total, two proximal and four distal elements. The proximal bones had been interpreted as fibulare and intermedium by KUHN (1952). Today, however, it is widely accepted that in reptiles, those elements should be rather considered as astragalus and calcaneum (see e.g. RIEPPEL 1993b). The distal elements represent distal tarsals 1-4. The astragalus is the most prominent element, being approximately one and a half times larger than the calcaneum. It is generally broad and roughly kidney-shaped, its proximomedial facet articulating with the tibia, and the proximolateral edge meeting the fibula. Laterally, there is a contact to the calcaneum. The distal articulations are difficult to determine, maybe there was originally a potential articulation with all other tarsal elements. The shape of the calcaneum resembles a rectangle with rounded edges. Distal, lateral, and proximal margins are convexly built, while the medial edge shows a small notch, serving for the passage of the perforating artery that usually pierces the contact between astralagus and calcaneum in many reptiles (ROMER 1956, RIEPPEL 1993b). The bone articulates, as just mentioned, with the astragalus, its proximal edge meeting the fibula. Distally, it obviously articulates only with distal tarsal 4.

The distal tarsals are not all of the same size. Distal tarsals 1-3 are more or less equally large, whereas the first distal tarsal is sometimes slightly more expanded. The largest element is always distal tarsal 4. The latter articulates distally with metatarsals 4 and 5, the remaining distal tarsals all meet their respective metatarsal, but also seem to have contact to the neighbouring ones, which is at least suggested by the preservation. As in the manus, each distal tarsal contacts its adjacent equivalent laterally.

The five metatarsals are more differently built than the complementary elements in the manus. So a notable expansion can be recognized in metatarsals 1 and 5. The first metatarsal approximately equals the shape of the first metacarpal, i.e. it is shorter and stouter than the remaining elements and shows a distinct proximal expansion. Metatarsal 5 is a slightly curved (“hooked“) bone that is generally expanded and only slightly constricted in the shaft area. Hence, proximal and distal head cannot be well distinguished from the rest of the bone. Metatarsal 5 is only slightly longer than the first one, the longest elements are therefore metatarsals 2-4. They correspond to the shape of the respective metacarpals and are slender, elongated elements with slightly expanded heads, showing also a lateral and medial keel in their shaft area. There appears to be a slight increase in length from metatarsal 1 to 4.

The phalangeal formula of the pes is 2-3-4-4-4. The proximal phalanges of the first and fifth digit are the longest elements, the remaining proximal phalanges are shorter and stouter. Into distal direction, all phalanges decrease in size. The ungual phalanges are of the same shape as in the manus.

3.2. Size and proportions of *Askeptosaurus*

The following quantitative/biometric analysis roughly corresponds to the criteria established by RIEPPEL (1989a) and SANDER (1989a). If possible, measurements were taken for both sides of the respective animal.

The glenoid-acetabulum length represents the distance from the posteromedial corner of the proximal humerus head to the posteromedial corner of the proximal femur head. In case of a flexion of the body, the mean value of both body sides was calculated.

The standard length is the length of four articulated vertebrae in the posterior part of the trunk. Usually, only the four posteriormost thoracals are taken (RIEPPEL 1989a, SANDER 1989a), but due to poor preservation, such a restrictive approach was not possible in most of the *Askeptosaurus* specimens. The measurement was taken across the pre- and postzygapophysis.

The head length was measured from the anterior tip of the snout up to the level of the posterior end of the opisthotics, while the mandible length represents the distance from the symphysis to the caudal tip of the articular.

Unfortunately, the here presented analysis is strongly hampered by the low number and partial incompleteness of the *Askeptosaurus* specimens, which makes the following analysis very preliminary and tentative. A complete list of measurements is presented in Appendix I.

Although some remarks will be given in every section, a final, summarizing conclusion will be presented at the end of the chapter.

3.2.1. Relative head length

Head length : glenoid-acetabulum length ratio

Four ratios were obtained, extending from 0.460 (PIMUZ T 4832) to 0.545 (MSNM V456). Interestingly, these two values come from specimens with the largest heads of all. The results could simply be due to a high amount of intraspecific variability, but also aspects like a possible sexual dimorphism may be responsible.

Head length : standard length ratio

Six ratios could be calculated, extending from 1.512 (PIMUZ T 4842) to 2.231 (PIMUZ T 4831). It is interesting that these two extremes were obtained from specimens with relatively small heads of almost equal size (18.78 and 18.76, respectively). Their standard lenghts, however, differ greatly (12.42 and 8.41).

Head length : humerus length ratio

Five ratios could be calculated for the right side of the body, the same number of calculations was possible for the left side. MSNM V456 shows the highest ratio (3.540 dex [= right], 3.465 sin [= left]), whereas the lowest could be recorded in PIMUZ T 4842 (2.346 dex, 2.199 sin). The remaining values vary between 2.5 and 3.1, with an individual variability of up to 0.3. MSNM V456 presents a relatively large head (26.09), whereas PIMUZ T 4842 has a distinctly smaller one (18.78). Thus these ratios could superficially indicate a negative allometric growth of the humerus, coupled with a positive allometric growth of the head. However, the specimen with the largest head (28.39; PIMUZ T 4832) presents a ratio of 2.727 dex and 2.676 sin. Hence individual variation appears to be high. Due to the low number of values a possible sexual dimorphism is difficult to determine.

3.2.2. Forelimb proportions

Humerus length : glenoid-acetabulum length ratio

Four calculations were possible for the right side of the body, and three for the left side. The highest ratio was recorded in PIMUZ T 4846 (0.181 dex), the lowest in MSNM V456 (0.154 dex, 0.157 sin). Individual variability nearly extends up to 0.02. Due to this variability and the close association of all values, there is obviously no important significance in this ratio.

Humerus length : standard length ratio

Six calculations could be conducted for each side of the body. The range of ratios extends from 0.616 (dex) in MSNM V456 to 0.789 (sin) in PIMUZ T 4831, whereas individual variability reaches up to 0.09. Hence, the significance of these values appears to be strongly restricted.

Humerus length : femur length ratio

Four calculations were possible for the right side of the body, and three for the left side. The range of ratios is relatively restricted and extends from 0.769 (sin; PIMUZ T 4832) to 0.853 (sin; PIMUZ T 4831), with an individual variability reaching up to 0.03. Despite the close association of all values, it seems, however, that the highest ratios are present in the largest specimens, which would indicate either a positive allometric growth of the humerus or a negative allometric growth of the femur.

Humerus length : length of metacarpal 3 ratio

Only two ratios could be recorded for each side of the body, ranging from 2.778 (sin; PIMUZ T 4831) to 3.569 (dex; PIMUZ T 4846). MSNM V456 is the only in which two values could be measured (3.084 dex, 3.218 sin). Even though there is a relatively high range of variability, the low number of ratios makes any interpretation difficult.

Humerus length : radius length ratio

Five ratios could be recorded for the right side of the body, seven calculations were possible for the left side. The range of ratios extends from 1.681 (dex; PIMUZ T 4842) to 2.135 (sin; PIMUZ T 4831), with an indivdual variability of up to 0.13. No correlation to specific size classes could be recorded, as MSNM V456, for example, also has relatively low ratios (1.755 dex, 1.776 sin), although the head is significantly larger than in PIMUZ T 4842. Furthermore, PIMUZ T 4831 is of approximately the same size as the latter and has the highest value. It should be noted, however, that sexual dimorphism could be involved.

Humerus length : distal width ratio

Whereas only three calculations were possible for the right side of the body, ratios from the left side could be recorded in five specimens. The highest value was calculated for specimen PIMUZ T 4846 (2.452 dex), the lowest for PIMUZ T 1830 (1.802 sin), individual variability extending up to 0.01. The latter specimen has the highest standard value and also relatively large humeri, contrary to the former specimen. However, the inference of a possible size correlation is contradicted by PIMUZ T 4832 and MSNM V456, which both have relatively high ratios but very different humerus lengths.

Radius length : standard length ratio

Four ratios were possible to calculate from the right side of the body, and seven ratios from the left side. The lowest value was recorded in MSNM V456 (0.351 dex), the highest in PIMUZ T 4846 (0.457 sin), individual variability extends up to 0.02. The lowest values are present in specimens with very different humerus lenghts, so no size correlation seems to be present. The general trunk lenghts of PIMUZ T 4846 and MSNM V456 are very similar, which may indicate the possible involvement of sexual dimorphism.

Length of metacarpal 3 : standard length ratio

Only a very few ratios could be recorded, two for the right side of the body and three for the left side. The range of ratios extends from 0.197 (sin; MSNM V456) to 0.284 (sin; PIMUZ T 4831), with an individual variability of up to 0.09. The low number of values makes any interpretation very doubtful. Nevertheless, a certain difference can be recorded between MSNM V456 and PIMUZ T 4846, where the latter again has higher values, although trunk length is almost equal.

Humerus minimal width : humerus distal width ratio

Three ratios were possible to calculate for the right side of the body, and six for the left side. The lowest value was recorded in PIMUZ T 0050 (0.467 sin), the highest in PIMUZ T 4846 (0.716). The latter value is significantly higher than all the remaining ones, even that of the right side of the same specimen (0.490!). So either taphonomic reasons are responsible, or there is a great range of individual variability, which makes any further interpretation doubtful.

3.2.3. Hindlimb proportions

Femur length : glenoid-acetabulum length ratio

Four calculations could be made for the right side of the body, three for the left side. The range of ratios extends from 0.199 (dex; MSNM V456) to 0.224 (sin; PIMUZ T 4832), with an individual variability reaching up to 0.01. Again, MSNM V456 has the lowest value, while the remaining ratios are very close to each other.

Femur length : standard length ratio

For the right side of the body, five values could be calculated, and three ratios for the left side. Their range extends from 0.794 (dex; MSNM V456) to 1.027 (dex; PIMUZ T 4840), individual variability is up to 0.066. MSNM V456 also here differs from all others, even though it is not the smallest specimen and the remaining ratios cannot be correlated to size.

Length of metatarsal 4 : standard length ratio

Four ratios could be calculated for the right side of the body, and three for the left side. The range of ratios extends from 0.233 (dex; MSNM V456) to 0.312 (dex; PIMUZ T 4840), with an individual variability of up to 0.022. It is interesting that again these two specimens represent the extremes. Unfortunately, PIMUZ T 4840 is very fragmentarily preserved and could be calculated for only a few ratios, it may have given some useful insights otherwise.

Femur length : fibula length ratio

While five values could be obtained from the right sides of the specimens, only three calculations were possible for the left side. The lowest ratio was recorded in PIMUZ T 4846 (1.718 dex), the highest in PIMUZ T 4832 (1.872 sin). Individual variability extends up to 0.028. The present values may be correlated to size, as the lowest ratio was obtained from a smaller specimen, whereas the highest was calculated for a relatively large (if not the largest) animal. The remaining ratios do not significantly contradict to this interpretation.

Femur length : length of metatarsal 4 ratio

Four ratios could be calculated for the right side of the body, and only two for the left side. The range of ratios extends from 2.996 (dex; PIMUZ T 4831) to 3.836 (dex; PIMUZ T 4846), with a relatively high amount of individual variability of up to 0.45. Due to this and the low number of values obtained, any interpretation is rendered difficult, even though it is interesting that PIMUZ T 4846 has the two highest values of all.

3.2.4. Conclusion

As already mentioned in the beginning of this chapter, the incompleteness of many specimens as well as the low sample number render most statistical inferences generally difficult, and there is furthermore a high amount of non-correlated (?) variation. Moreover, many of the specimens were recovered by miners without making an exact stratigraphic assignment, which additionally hampers a better resolved distinction. Hence, every of the following interpretations has to be treated with caution.

The confusing distribution of values becomes a little more clear when the specimens are subdivided into different size classes. The material consists of more or less two size classes, one with relatively small heads of approximately 20 cm (PIMUZ T 0050, 4831, 4842, 4846) and one with larger heads of up to 28 cm (PIMUZ T 4832, 5392, MSNM V456, possibly also PIMUZ T 4839 and MSNM V3550). Within the first size class, there appears to be a certain difference in several ratios, which becomes especially apparent in the head length : standard length ratio, or the humerus length : radius length ratio. In the second size class, there is a notable difference in that PIMUZ T 4832 has a large head and also large extremities, whereas MSNM V456 possesses a head of almost the same size but with a distinctly smaller postcranium.

One possible explanation for these values could be that the smaller specimens are younger individuals with certain differences perhaps already related to sexual dimporhism, and that later in ontogeny, the different sexes grew strongly differently, i.e., one sex with negative allometry in the postcranium, and the other with positive allometric or isometric growth.

The above interpretation would imply that PIMUZ T 4846 is a younger individual. On the other hand, this animal shows an additional bone in the carpus as well as an additional phalangeal element in the third digit of the manus (see above). Given that the large-headed MSNM V456 lacks these ossifications, it seems problematical to infer that PIMUZ T 4846 is juvenile or semi-adult. So another explanation could be that the animals of the smaller size class belong to a different species with a certain degree of sexual dimorphism, or that at least MSNM V456, which strongly differs from all others in many biometrical respects, is different at the species level. The remaining larger specimens would then possibly represent only relatively old animals. None of these interpretations, however, can currently be corroborated on the basis of the present material. New specimens have to be discovered until a more precise assessment is possible.

3.3. Comparison of *Askeptosaurus* with other thalattosaurs

3.3.1. Comparison with the remaining thalattosaurs from Monte San Giorgio

Two further thalattosaur taxa are known from Monte San Giorgio, *Clarazia schinzi* and *Hescheleria ruebeli*, both described by PEYER (1936 a,b).

3.3.1.1. *Clarazia schinzi* (figs. 24, 25)

The Monte San Giorgio reptile *Clarazia schinzi* was originally described by PEYER (1936a) on the basis of a fairly complete specimen, which was originally prepared in ventral view only (fig. 24). PEYER (1936a) established the new family Claraziidae and recognized several similarities with *Thalattosaurus*, concluding that these formes are probably related to Rhynchocephalians, and thus being included within the Tocosauria (=Lepidosauria). Nevertheless, the systematic status of *Clarazia* remained problematical, and in the following it was either assigned to Rhynchocephalians or Eosuchians (see e.g. ROMER 1956), whereas BENTON (1985) treated it as Diapsida inc. sed. This unsatisfiying situation stimulated RIEPPEL (1987) to re-investigate the anatomy of *Clarazia* in the light of the increasing knowledge of diapsid phylogeny. Furthermore, due to a re-preparation of the only known specimen, he was also able to describe the dorsal side of the skull for the first time. RIEPPEL (1987) confirmed PEYER´s (1936a) view of a closer relationship to *Thalattosaurus*, and postulated that it is the sister-group of the Thalattosauridae, and both together form a taxon opposed to *Askeptosaurus*. Regarding the position of the whole group, however, the author roughly followed BENTON´s (1985) conclusion and treated it preliminarily as Neodiapsida inc. sed. Since both PEYER (1936a) and RIEPPEL (1987) presented thorough descriptions of *Clarazia*, it was here considered unnecessary to completely re-describe this taxon, but rather to name its general anatomical characteristics, as compared to the new results obtained from *Askeptosaurus*.

Clarazia schinzi is a sharp-snouted animal (fig. 25), even though the skull appears to be stouter than that of *Askeptosaurus*. The surface of the dermal skull bones often has a striated ornamentation. The dorsal side of the skull shows the nares to be retracted and shifted dorsomedially. The premaxilla forms the rostrum and the anterior portion of the upper jaw, presenting furthermore 4 stout and blunt teeth, of which the anteriormost one is the smallest.

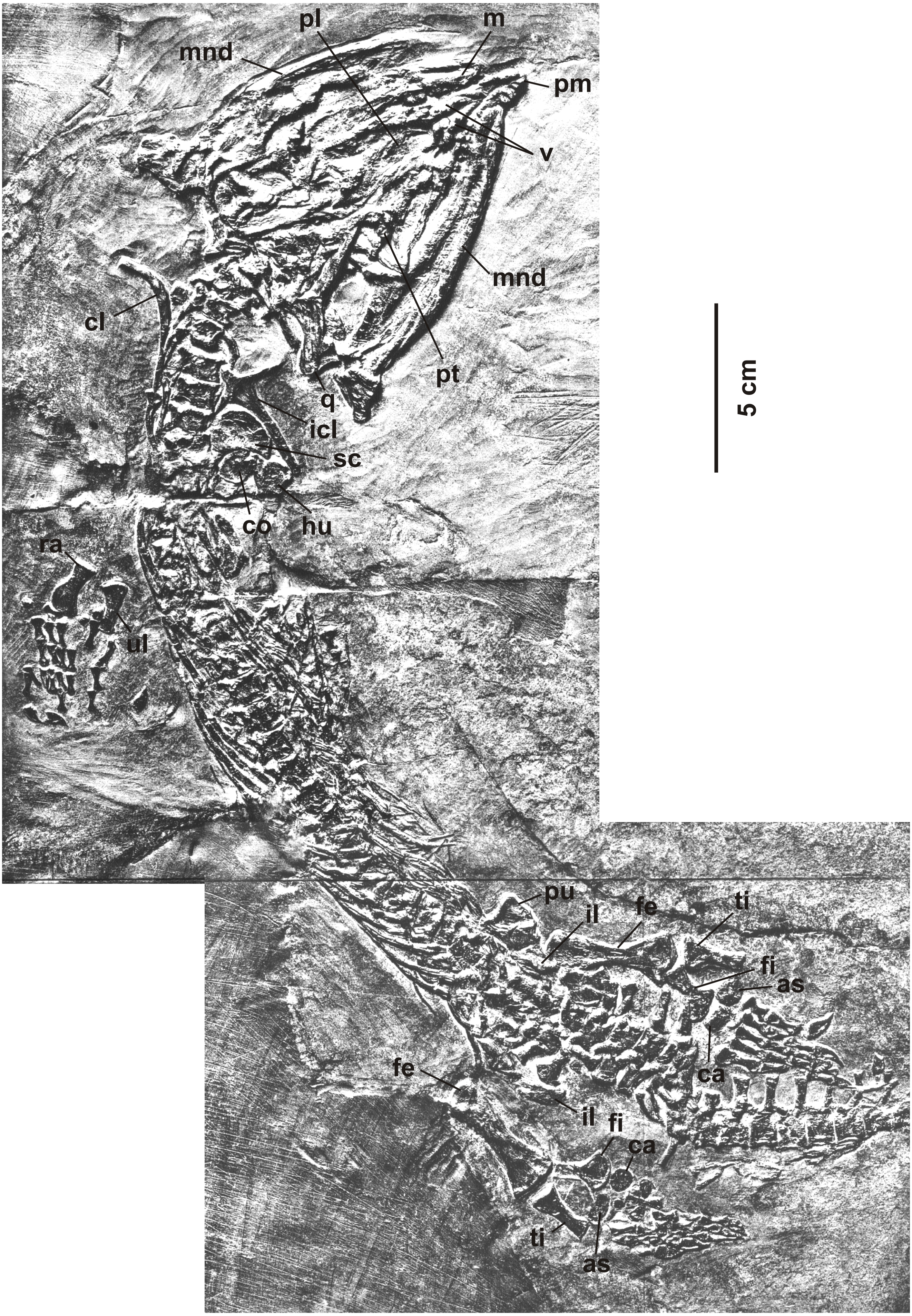


Fig. 24: *Clarazia schinzi*, skull and thoracal region of the holotype (PIMUZ A/III 211), preserved in ventral view (from PEYER 1936a, modified).

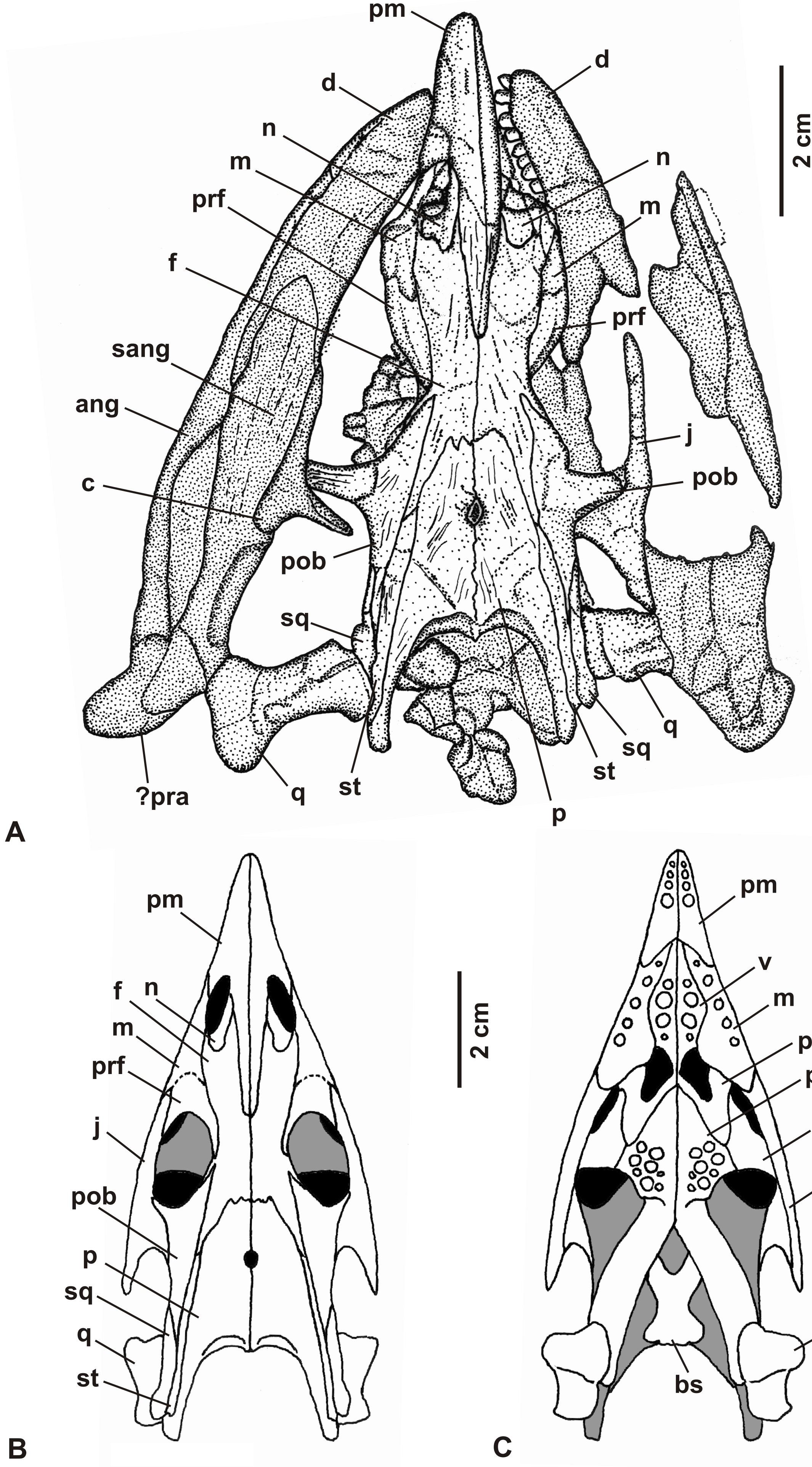


Fig. 25: A) *Clarazia schinzi,* holotype, dorsal view of skull. B) dorsal and C) ventral restoration of skull (after RIEPPEL 1987, but modified in the antorbital and temporal area).

The premaxilla contacts the frontals, thereby separating the nasals from one another. A personal re-evalutation of the dorsal skull morphology revealed that the nasal was obviously much shorter than previously assumed (fig. 25A, B). Possibly the nasal did even not contact the maxilla due to an anterolateral projection of the frontal, but this cannot be stated with absolute certainty. The maxilla forms the posterior portion of the upper jaw, bearing 5 blunt teeth of which the anteriormost one is again distinctly smaller than the others. The teeth are separated from those of the premaxilla by a conspicuous diastema. A prefrontal is well-developed, but it is not clear whether also a lacrimal was originally present. Postorbital and postfrontal are fused to a single bone. The upper temporal fenestra is closed. The frontal meets the narrow, but very long supratemporal by a slender, elongated posterolateral projection, resulting in an exclusion of the parietal from the cheek region. Also the parietal possesses long posterolateral extensions, thus the posterior margin of the skull roof is greatly emarginated. The jugal has a prominent posterior process, but the lower temporal bar is reduced due to the absence of a quadratojugal. The quadrate was obviously attached to the posterolateral edge of the skull roof by a movable joint.

The ventral side of the skull (fig. 25C) presents a paired vomer with 4 small, blunt teeth on each side. The bone is sutured to maxilla and premaxilla along its anterior and lateral margin and thus forms some sort of a secondary palate. The vomers contact the palatines by a posteromedial projection, which at the same time separates the internal nares from one another. The palatines do not bear any teeth, nor do the ectopterygoids. The broad pterygoids, however, present a well-developed dentition in their anterolateral part, bearing about 8 teeth on each half, being similar to those of the premaxilla but very different from each other in size. The pterygoids have furthermore prominent quadrate rami, extensively contacting the medial aspect of the quadrate.

The braincase of *Clarazia* is too badly preserved and therefore not characterizable.

The lower jaw is a broad and massive structure. The dentary bears 8 to 9 blunt teeth, and the surangular comprises the major part of the lateral side of the mandible. The angular forms the posteroventral margin of the lower jaw, while the splenial is exposed at the anteroventral edge. Unfortunately, most of the remaining bones of the jaw ramus are not clearly identifiable, nor is the detailed structure of the medial side. It seems, however, that Meckel´s canal was covered by bone and therefore externally not visible. Medially of the central portion of the left mandible there is a triradiate bone that has been interpreted as jugal by RIEPPEL (1987). However, the ventral portion of this bone is not curved as typically observed in thalattosaurian jugals, and its position in relation to the remaining mandible indicates that it is rather the coronoid, showing a distinct dorsal apex. Even though the anteroventral portion is longer than in many other reptilian coronoids, an enlarged anterior portion can also be observed in, e.g., the thalattosaur *Nectosaurus* (fig. 30D), and thus does not contradict this alternative interpretation.

The exact vertebral number cannot be given, but at least 32 precaudal vertebrae were present, whereas at least two of them are sacrals. None of them possesses intercentra. A total of 59 caudal vertebrae is preserved, which, however, represent an incomplete number. All vertebrae are amphicoelous. Of the presacrals, at least 7 vertebrae appear to be referable to the cervical region, maybe this number was slightly higher. Due to preservation, the structure of dia- or parapophysis of the cervical vertebrae is unknown. The cervical ribs, however, are clearly dichocephalous and possibly without an additional anterior process, but this cannot be stated with absolute certainty. The thoracals appear to have developed slight transverse processes for the attachment of the holocephalous ribs. Their neural spines are stout and low. The sacral vertebrae are very similar to the thoracals. The associated ribs are distally expanded and not ankylosed to the vertebrae. The caudals differ from all other vertebrae in having long and slender neural spines that become increasingly inclined more posteriorly in the tail. With the exception of the first caudal, all tail vertebrae have slender haemapophyses.

The shoulder girdle consists of interclavicle, clavicle, scapula, and coracoid. The interclavicle is very slender and cruciform, the clavicle narrow and curved. The coracoid is broad and rounded, whereas the scapula is kidney-shaped.

Of the forelimb, only zeugo- and autopodium are sufficiently preserved. The radius is an expanded element, while the ulna is more slender, but with a distinctly broadened proximal head. The carpus shows five elements, the radiale as well as four distal carpals. The metacarpals are slender, the 4th being the longest. The phalangeal formula of the manus is 2-3-4-5-3.

The pelvic girdle consists of the usual elements, ilium, ischium, and pubis, but is only scarcely preserved. While PEYER (1936a) considered *Clarazia* not to have a thyroid fenestra, RIEPPEL (1987) restored the girdle with a notable emargination of the pubo-ischiadic plate. A definite statement is difficult due to the disarticulated condition and the partial breakage of the elements.

The femur is relatively slender and elongated. Tibia and fibula are both very broad, whereas the former shows the proximal head to be the most expanded portion, while in the latter it is the distal head. The tarsus consists of three elements, astragalus, calcaneum, and one distal tarsal. The metatarsals are short and slightly increasing from the 1st to the 5th digit. Metatarsal 5 is somewhat expanded. The phalangeal formula of the pes is 2-3-4-5-4.

Askeptosaurus and *Clarazia* share, of course, the typical features of all thalattosaurs, like the premaxilla/frontal contact or the distinct rostrum, and there are some further similarities like the low neural spines or the blade-like scapula. However, it is also evident that there are many prominent differences between these two forms. First, *Clarazia* is much smaller (although size is not a firm criterion for difference), and the antorbital portion of the generally much higher skull is distinctly shorter. Furthermore, the upper temporal fenestra of *Clarazia* is completely obliterated, and the blunt teeth indicate a very different way of nutrition than in *Askeptosaurus*. In the postcranium, a conspicuous difference is that the neck of *Clarazia* is much shorter and possesses a lower number of cervical vertebrae. In the shoulder girdle, the cruciform interclavicle is a notable, possibly unique feature. Moreover, carpus and tarsus seem to possess fewer ossified elements, indicating that the degree of aquatic adaptation was higher in *Clarazia*. In conclusion, the major differences cited here preclude any confusion of these two taxa.

3.3.1.2. *Hescheleria ruebeli* (fig. 26)

Hescheleria ruebeli, also described by PEYER (1936b), is only known from one completely disarticulated specimen. The author assigned this taxon to the Claraziidae, and therefore the confusion concerning the systematic status of claraziids outlined above was also true for *Hescheleria*. For that reason, RIEPPEL (1987) revised this taxon as well.

Hescheleria represents a small thalattosaur with an estimated total length of approximately 1 m (fig. 26). One of the most conspicuous structures of the skeleton is the distinctly ventrally recurved snout, formed by the anterior curvature of the premaxilla. RIEPPEL (1987) doubted PEYERS´s (1936b) restoration, but a recent re-analysis confirmed the original interpretation (RIEPPEL, MÜLLER, & LIU in prep.). Unfortunately, palatal elements are only insufficiently known, which would be of certain interest especially in comparison with *Nectosaurus* that obviously also possessed a recurved rostrum. The premaxilla of *Hescheleria* contacts the frontals and carries at least 5 teeth with slightly expanded crowns in its anteriormost part, being followed by a marked diastema separating them from 3 blunt teeth on

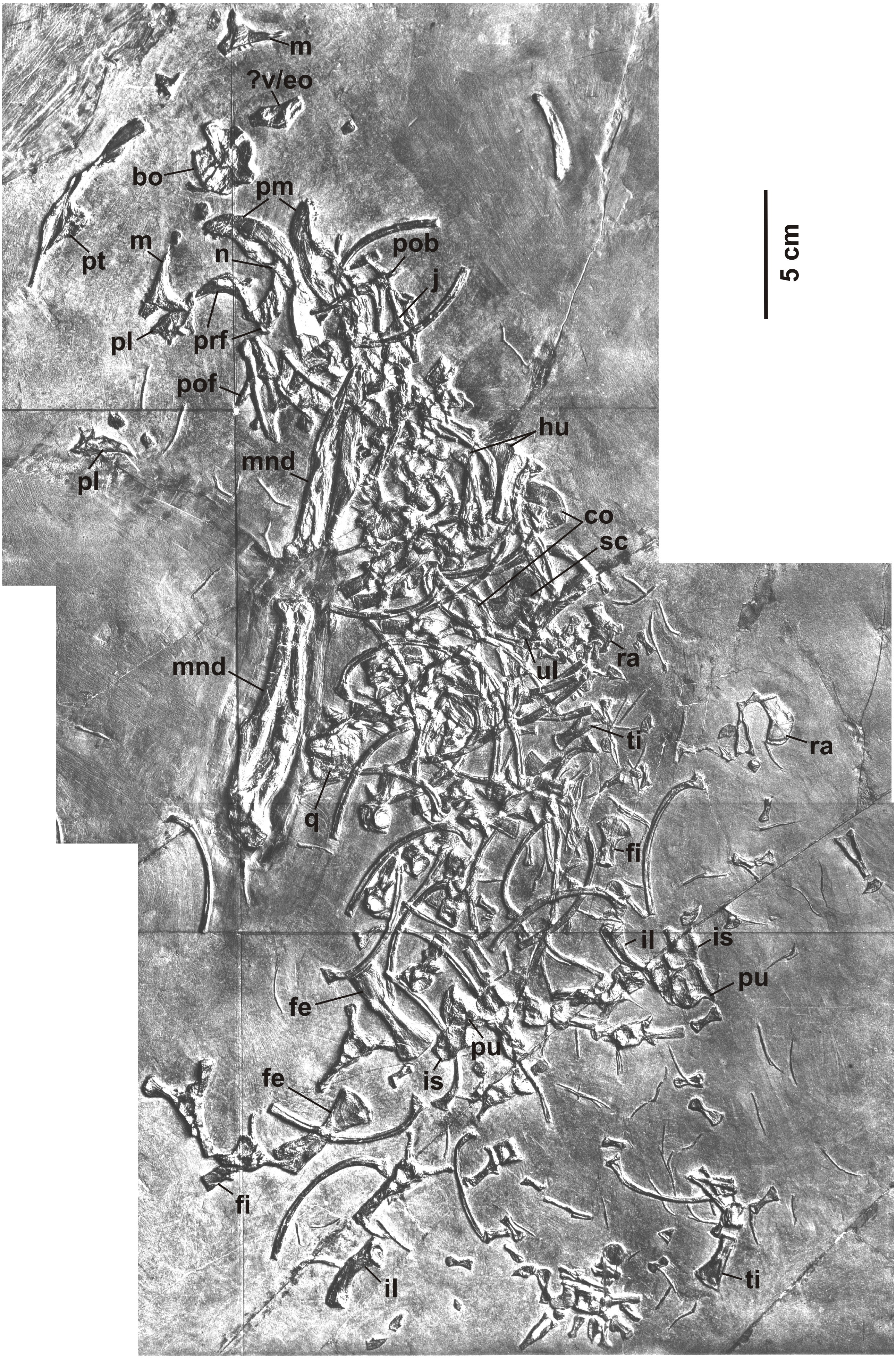


Fig. 26: *Hescheleria ruebeli,* anterior half of holotype (PIMUZ T 2469), showing most of the significant anatomical features (from PEYER 1936b, modified).

the short maxilla. Palatal dentition could not be positively identified. Unfortunately, many elements of the skull roof are not preserved, so it is only possible to state that the frontals were separate and that the lower temporal bar was most probably open. Postfrontal and postorbital were obviously fused, while the presence or absence of a lacrimal is difficult to determine. Also, whether or not the upper temporal fenestra was obliterated, must remain open to question. The lower jaw is massively developed and presents a short coronoid process. Preservation does unfortunately not allow a further satisfactory determination of the respective bones, with the exception of the posteriorly bifurcated dentary. A retroarticular process was present but short. An interesting feature is the mandibular dentition which is restricted to the symphysial region only, consisting of at least 4 pointed, conical teeth with the first one distinctly enlarged and situated lingually to the remaining ones. This tooth is possibly formed only by bone and might be interpreted as “symphysial protuberance“. All the teeth described above are followed by 4-5 distinctly smaller teeth with acrodont implantation.

The postcranium presents 32 presacral vertebrae with 7-8 cervicals, 5 possible sacrals, and at least 52 caudals. All vertebrae are characterized by the lack of a neurocentral suture and the relatively straight upwards directed neural spines, which are also relatively broad. Only in the caudal portion, the spines become lower and posteriorly inclined. Rib articulation is double in the cervicals and single in the thoracals, with the articulation facets also extending onto the neural arch. The cervical ribs have a distinct additional anterior process, and the sacral ribs are not ankylosed to the vertebrae. The attachment of the chevrons was possibly intervertebral, as clear facets for articulation cannot be observed on the caudal centra.

The shoulder girdle is characterized by a broad coracoid and an expanded scapular blade, the interclavicle is cruciform, and the clavicle is slender and recurved. The stylopodium consists of a stout humerus with a prominent entepicondyle and a well-visible supinator process, no foramina were obviously present. Radius and ulna are short, the former being distinctly broader than the hour-glass-shaped ulna. Three carpal ossifications were recognized by PEYER (1936b), while RIEPPEL (1987) considers it impossible to determine the definite number of bones due to the complete disarticulation of the specimen. The phalangeal formula was probably 2-3-4-5-3.

A conspicuous feature of the pelvic girdle is the lack of a thyroid fenestra. Pubis and ischium both form broad plates. The ilium is typical for thalattosaurs in having a distinct posteriorly recurved dorsal process without any trace of an additional anterior projection. The femur is well-preserved and shows a shallow intertrochanteric fossa and a prominent 4th trochanter, while the epiphysis is not ossified. Tibia and fibula are short. While the former has a broad distal head, the latter presents an even more expanded proximal end. As in the forelimb, it is difficult to identify all the tarsal elements of the autopodium. Astragalus and calcaneum were definitely present, as were at least 2 distal tarsals. The phalangeal formula probably was 2-3-4-5-4.

It is obvious that next to the great difference in size, also several other aspects clearly distinguish *Hescheleria* from *Askeptosaurus*. Surely the most conspicuous difference is the lack of a ventrally recurved rostrum in the latter taxon, furthermore it does not possess a diastema nor a symphysial protuberance, but a homogenously arranged row of well-developed pointed teeth. However, both taxa obviously lack palatal dentition. In the postcranium, there are several interesting similarities. So the anterior process of the cervical ribs is present in both taxa, and the morphology of the scapula is very similar. While these similarities have already been noted previously (e.g. RIEPPEL 1987), the new interpretation of the pelvic girdle of *Askeptosaurus* adds another one, namely the well-developed pubo-ischiadic plate instead of a thyroid fenestra. On the other hand, notable postcranial differences include the more elongated neural spines throughout the vertebral column in *Hescheleria*, as well as the more expanded radius and fibula.

3.3.2. Comparison with the thalattosaurs from North America

3.3.2.1. The taxa from the Triassic of California

From the late Triassic of California, two thalattosaur genera, *Thalattosaurus* and *Nectosaurus,* were described by MERRIAM at the beginning of the last century (MERRIAM 1904, 1905, 1908). Of the former, two species, *T. alexandrae* from California and, additionally, *T. borealis* from British Columbia, are currently accepted to be valid, whereas *Nectosaurus* actually consists only of one species, *N. halius*. Both genera have recently been acid-prepared and re-described by NICHOLLS (1999), but the type material, which is housed in the UCMP (*T. alexandrae*, UCMP 9085; *N. halius*, UCMP 9127) and in both cases consists of isolated elements of skull and postcranium, could also be investigated personally.

3.3.2.1.1. *Thalattosaurus* (figs. 27-29)

Thalattosaurus is a relatively large form whose size approximately equals that of *Askeptosaurus*. The anterior tip of the snout is slightly ventrally recurved. As typical for thalattosaurs, the premaxillae meet the frontals and the nares are posteriorly positioned. Additionally, however, they are also dorsally shifted and situated narrowly to one another. The skull roof shows prominent frontals, each with a distinct posterolateral projection contacting the slender and elongated supratemporal, which is additionally met by the postorbital. As a result, the parietals have a strongly convex anterior margin, while their posterior edge is greatly emarginated. The quadrate was obviously moveably suspended, and a quadratojugal is lacking, hence the lower temporal bar is not closed. Postorbital and postfrontal were fused, as well as prefrontal and lacrimal. NICHOLLS (1999) restored the skull of *Thalattosaurus* with a slit-like upper temporal fenestra (fig. 27A, B), which was questioned by RIEPPEL et al. (2000). Personal re-investigation corroborates these doubts. A clear evidence for a supratemporal opening is lacking, and it rather seems that breakage may have led to NICHOLLS´ impression. A conspicuous element of the palatal area is the fused vomer, which is a massive, prominent bone.

The lower jaw (fig. 27C, D) presents a relatively long tooth-bearing portion and a short posterior area for jaw muscle insertion. The retroarticular process is unfortunately not sufficiently preserved. The coronoid shows a distinct dorsal apex, splenial and angular are both long and well-developed.

The dentition of *Thalattosaurus* has several peculiarities. In the upper jaw, the premaxilla is edentulous but presents several pseudodont protuberances in its anteriormost portion, while the maxilla shows five blunt teeth that are very low and set in sockets. The result is a prominent diastema between the “teeth“ of the premaxilla and the maxilla. Vomer and pterygoid additionally have a considerable dentition, the former bone presents a number of 8 to 11 striated teeth on each half, and the dentition of the latter consists of 5 rows. With the exception of the lateralmost row which has only 2 teeth, the remaining ones present 4 to 5 teeth, respectively. All palatal teeth are blunt and were probably set in sockets, and the teeth of the pterygoid are smaller than those of the vomer. The mandibular dentition is again heterogenous. Anteriorly, at least 5 sharp and slender teeth are present, the anterior ones clearly extending around the symphysial area. Posteriorly, a short, blunt tooth is present, followed again by distinct diastema. The remaining tooth-bearing portion consists of at least

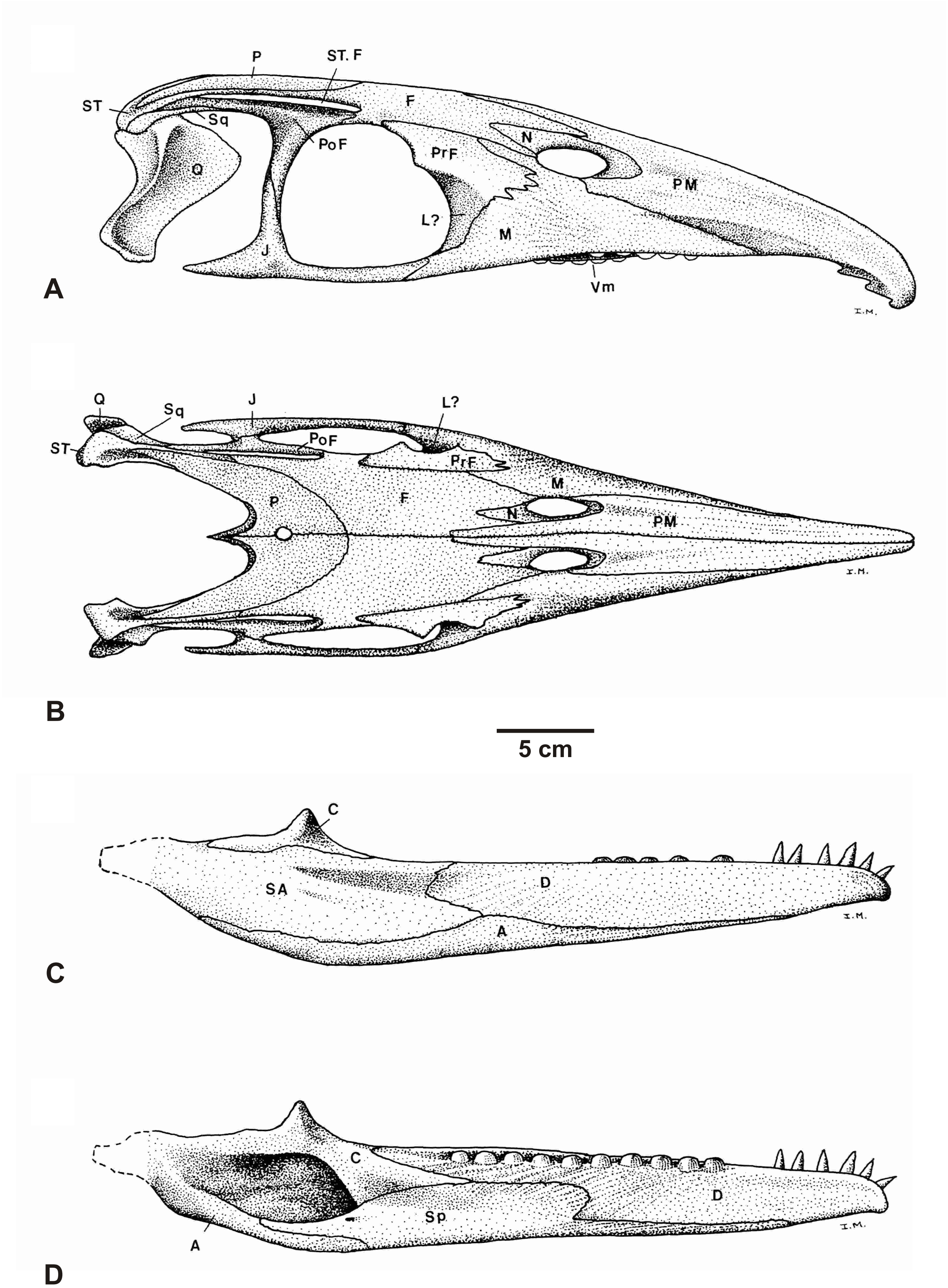


Fig. 27: *Thalattosaurus alexandrae*, cranial restoration (from NICHOLLS 1999). A) skull in lateral and B) dorsal view, C) mandible in lateral and D) medial view. Contrary to NICHOLLS (1999), I doubt the presence of a slit-like upper temporal fenestra ("ST.F"; see text for details). Abbrevations differing from those of the present work are "SA" (surangular) and "A" (angular).

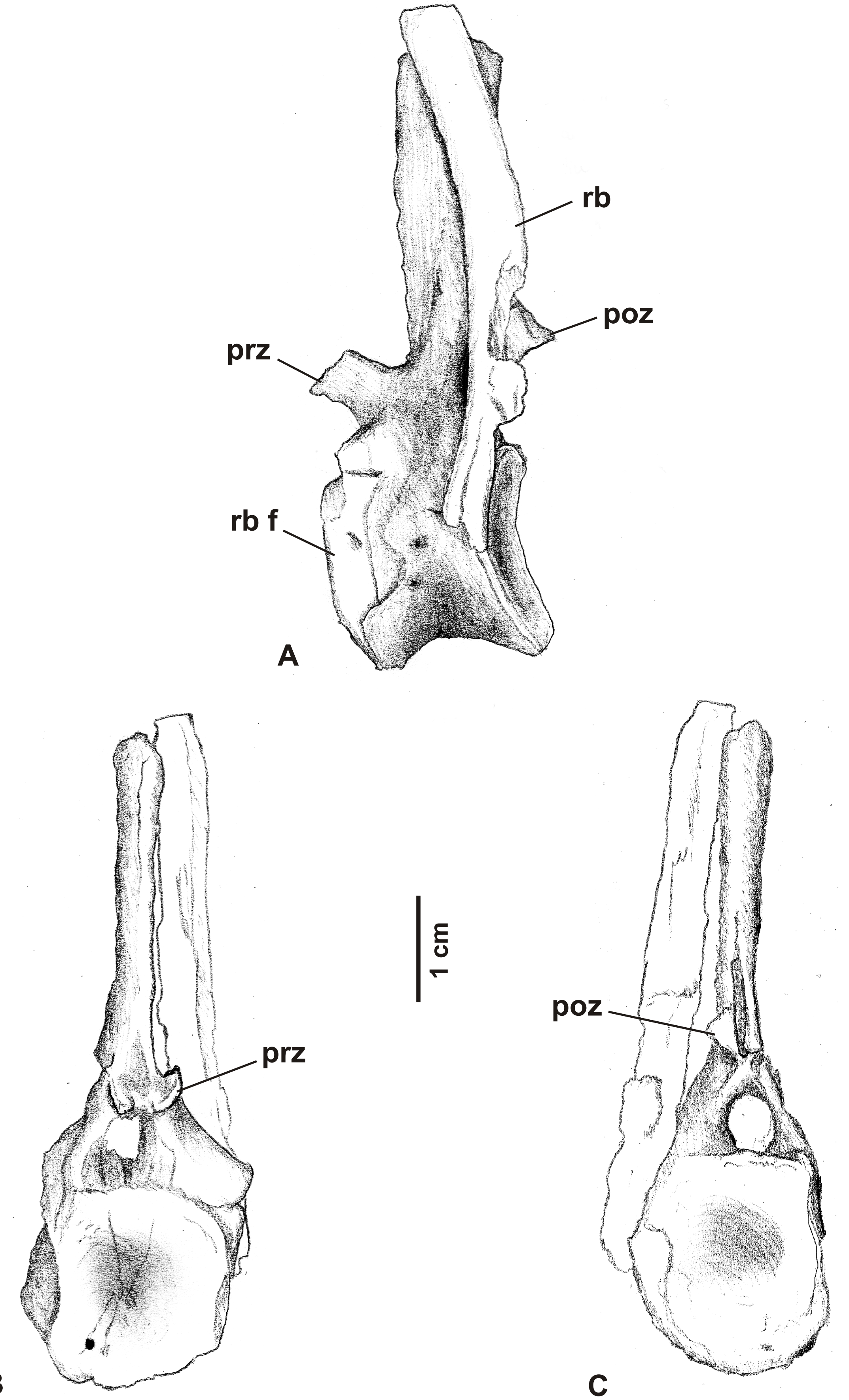


Fig. 28: *Thalattosaurus alexandrae.,* isolated thoracal vertebra (UCMP 9085). A) lateral, B) anterior, and C) posterior view.

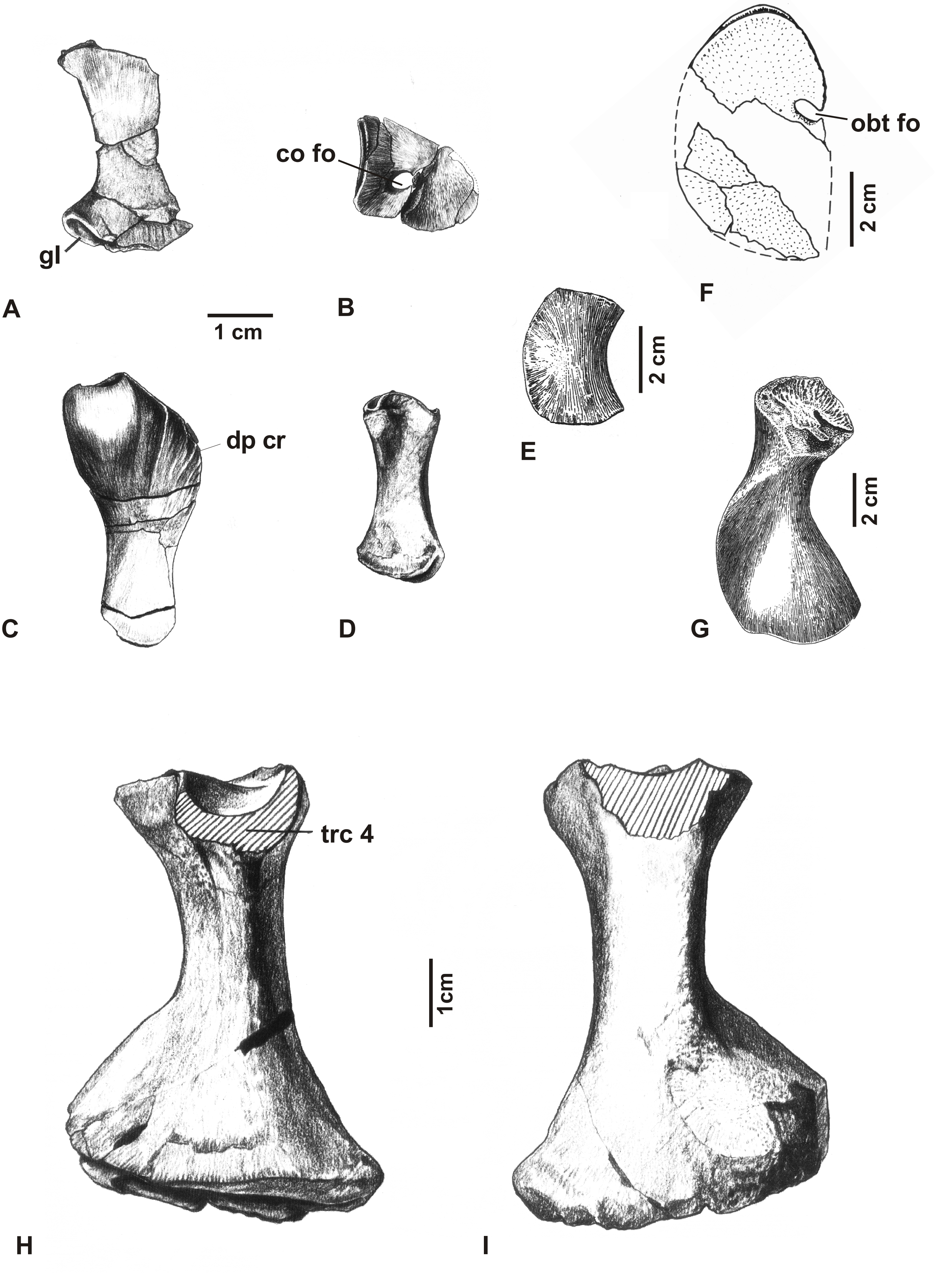


Fig. 29: *Thalattosaurus alexandrae*, appendicular skeleton (UCMP 9085; E) & G) from MERRIAM 1905, remaining figures from NICHOLLS 1999). A) scapula, B) coracoid, C) proximal head of humerus, extensor surface, D) ulna, E) radius, F) pubis, G) supposed ischium, H) flexor and I) extensor surface of femur.

10 teeth that are low crowned, blunt, and radially striated. The teeth appear to be fused to a deep socket in the bone and implantation can therefore be regarded as ankylothecodont *sensu* CHATTERJEE (1974).

The postcranium is by far not as well-preserved as in *Askeptosaurus*. The opisthocoelous axis shows a single rib articulation, as does the amphicoelous third cervical vertebra. The remaining vertebrae are all amphicoelous (fig. 28), but their exact position within the vertebral column cannot be determined. Some of them show a single rib articulation extending from the centrum to the neural arch, while others present a double one. The neural arches are often not firmly fused to the centra. Small, blade-like intercentra were obviously present at least in the anterior cervical region. There are only a few further postcranial elements. The scapula is elongated and slender (fig. 29A), while the coracoid is only insufficiently preserved (fig. 29B). Of the forelimb, only the incomplete humerus with a well-visible deltopectoral crest (fig. 29C) as well as radius and ulna are preserved. The kidney-shaped radius was formerly interpreted as ulna by MERRIAM (1905) and then considered to be an ichthyosaurian epipodial by NICHOLLS (1999). LIU & RIEPPEL (2001) then interpreted the element in question to be a radius, a view which is followed here due to its similarity with the radius of *Nectosaurus*, *Xinpusaurus*, and the Salzburg thalattosaur (fig. 29E). The ulna (fig. 29D) is more slender and straighter than the radius and again very similar to the ulnae of *Xinpusaurus* or the Salzburg thalattosaur. Of the pelvic girdle, the broad pubis (fig. 29E) and a possible slender ischium (fig. 29G; labeled as pubis by MERRIAM 1905, Pl. VIII, figs. 8, 10) are preserved. The femur is the only known bone of the hindlimb, being extremely expanded in its distal portion (fig. 29H, I).

As can be seen, there are numerous differences between *Askeptosaurus* and *Thalattosaurus*. In the skull, a conspicuous difference is the dentition, being roughly homodont in *Askeptosaurus* and with sharp, slightly recurved teeth, whereas in *Thalattosaurus*, there are pseuododont protuberances, procumbent teeth, and low-crowned, blunt teeth, being separated from the others by a distinct diastema. Furthermore, palatal dentition is lacking in *Askeptosaurus*. Further notable differences in the skull are the frontal/supratemporal contact, the postorbital/supratemporal contact, as well as the absence of a slit-like upper temporal fenestra in *Thalattosaurus*. Moreover, *Askeptosaurus* has a distinct lacrimal and a postfrontal. In the postcranium, the latter taxon differs in having dichocephalous cervical ribs beginning from the third vertebra, and holocephalous ribs throughout the thoracic region. Also, no traces of intercentra can be found in *Askeptosaurus*. The scapula of *Thalattosaurus* is very disctinct and slender, and thus bears no similarity with the same element of *Askeptosaurus*, which is blade-lake and comparatively short. In the forelimb, it appears that the extremity of *Askeptosaurus* was less well-ossified, furthermore the radius is not as expanded as in *Thalattosaurus*. The pelvic region of the latter is insufficiently preserved for a thorough comparison, whereas the femur is strongly different from that of *Askeptosaurus* due to its extreme distal expansion.

3.3.2.1.2. ***Nectosaurus halius*** (figs. 30-32)

The second Californian thalattosaur genus, *Nectosaurus* (including *Nectosaurus* sp. from the same locality) was probably smaller than *Thalattosaurus*, although notable size differences among the respective specimens suggest that this impression may simply be the result of an insufficient number of fossil finds.

The skull of *Nectosaurus* (figs. 30A, B, 31A) is again typical for thalattosaurs in having a paired premaxilla that obviously met the frontal bones, thereby separating the nasals from each other. Furthermore, the lower temporal bar is open. Lacrimal and prefrontal were fused, as is the case for postfrontal and postorbital. The frontal again contacts the supratemporal due to a development of a prominent posterolateral projection. Also in this taxon, NICHOLLS (1999) assumed that there was a slit-like upper temporal fenestra, personal investigation, however, has shown that the isolated postorbital fits perfectly well into a facet of the frontal (fig. 31A), with no remainder of a supratemporal fenestra. The preserved elements of the snout, especially the maxilla, strongly resemble *Hescheleria*, suggesting that the rostrum was equally recurved anteroventrally (fig. 30A, B). The premaxilla, however, is not completely preserved any more, rendering this assumption slightly equivocal, although the recurved vomer indicates a certain degree of curvature. The overall dentition is peculiar in having small, needle-like, and heavily-striated teeth both on the upper and the lower jaw, whereas in the posterior portion of the latter the teeth are somewhat shorter and blunter. While the small, semilunar-shaped palatine is smooth, pterygoid and vomer again bear a certain kind of dentition (fig. 30C). Blunt teeth are present on the vomer, and at least 4 rows of irregularly distributed, very tiny and sharp teeth can be found on the pterygoid. Unfortunately, so far it is not possible to present a well-confirmed interpretation of the mode of tooth implantation.

The anatomy of the lower jaw cannot be fully established due to insufficient

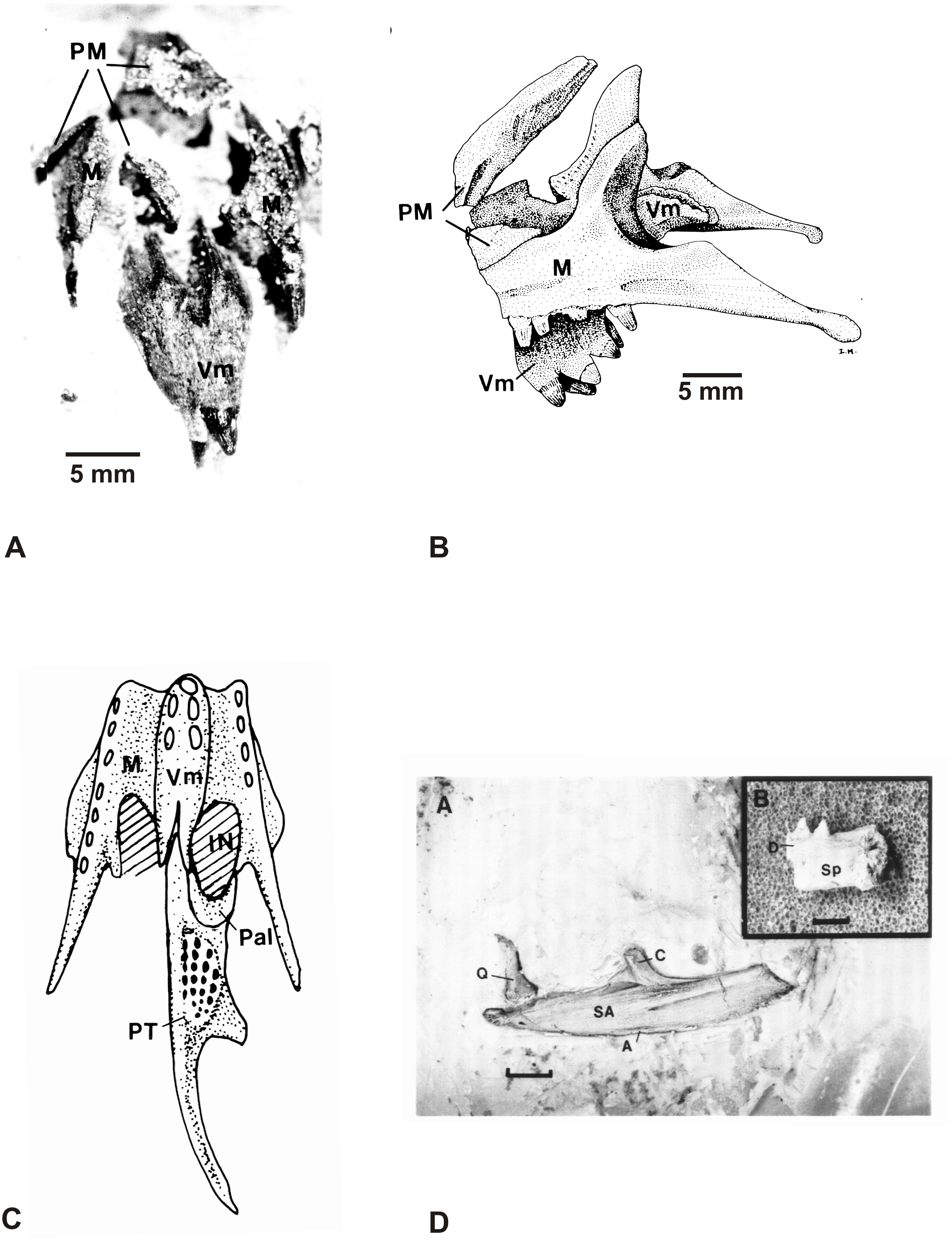


Fig. 30: *Nectosaurus halius*, cranial elements. A) rostrum in anterior and B) left lateral view (type, UCMP 9124), C) restoration of palate, D) right mandible from lateral view as well as a part of the splenial (UCMP 9124, scale bars equal 5 mm). All figures from NICHOLLS (1999). Abbrevations differing from those of the present work: “Vm” (vomer), “Pal” (palatine), “SA” (surangular),“A” (angular).

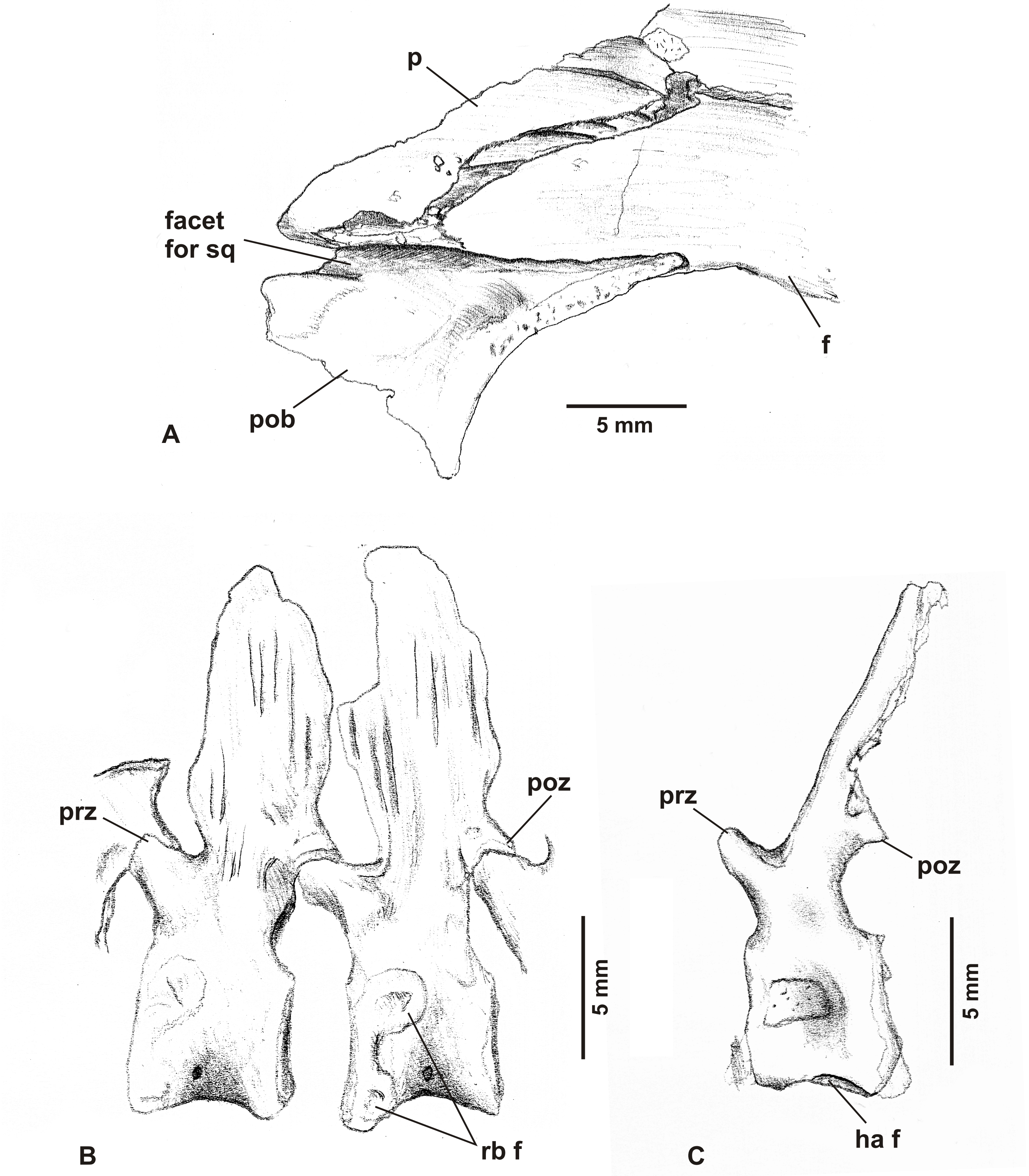


Fig. 31: *Nectosaurus halius*, cheek and vertebrae. A) anterodorsal part of the right cheek with the isolated postorbital put into a facet formed by frontal and parietal, in order to show that there is no slit-like upper temporal fenestra (UCMP 9124). B) ?thoracal vertebrae (UCMP 9124), C) caudal vertebra (UCMP 10779).

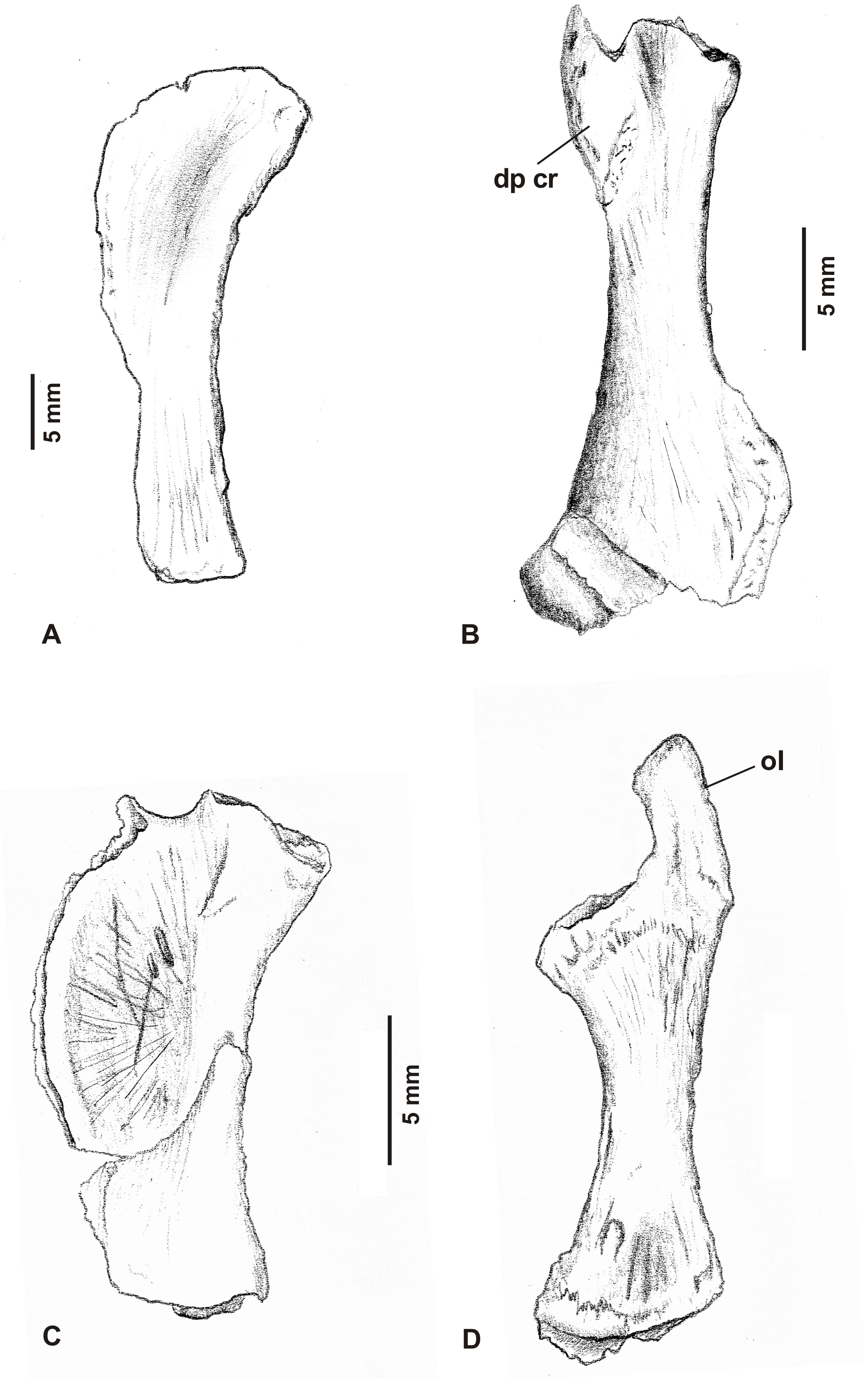


Fig. 32: *Nectosauru halius*, appendicular skeleton. A) right scapula (UCMP 9120), B) right humerus (UCMP 9124), C) right radius, D) right ulna (all UCMP 9124).

preservation. However, it can be stated that the coronoid was well-developed and possessed a distinct dorsal apex, and the presence of a small retroarticular process can also be confirmed (fig. 30D).

As in *Thalattosaurus*, also the postcranium of *Nectosaurus* is only insufficiently preserved, and even less elements are known than in the latter taxon. A row of 10 vertebrae with double rib articulations and straight upwards directed neural spines (fig. 31B) were interpreted as anterior thoracals by NICHOLLS (1999), due to their association with elements of the forelimb and the length of the accompanying ribs. The ribs articulated mainly with the centrum, but a slight extension onto the neural arch may have been present as well. A definite statement in this aspect, however, is difficult due to the lack of a neurocentral suture. Additional isolated vertebrae, which can only questionably be referred to *Nectosaurus*, include a centrum with a single rib articulation, probably a posterior thoracal, as well as a caudal vertebra that shows well-developed facets for the haemapophyses, but lacks any trace of rib attachment (fig. 31C). The scapula is a long and slender element and unfortunately the only preserved part of the pectoral girdle (fig. 32A). The humerus is generally narrow, but slightly broadened distally (fig. 32B), whereas the kidney-shaped radius is very expanded (fig. 32C). On the contrary, the ulna is slender and, interestingly, still retains an olecranon (fig. 32D). Additional preserved elements include some propodials and epipodials as well as dichocephalous ribs.

Again it is evident that *Askeptosaurus* strongly differs from this taxon, and certainly not only in size. As the above described morphology of the anterior skull portion suggests, the snout of *Nectosaurus* was obviously distinctly anteroventrally recurved, contrary to *Askeptosaurus*. A further difference is the palatal dentition of the former, as well as the posterolateral frontal process that meets the supratemporal. Also, at least the presence of a single postfrontal can be excluded for *Nectosaurus*. In the postcranium, notable differences include the absence of anterior thoracals with double rib articulations in *Askeptosaurus*, and this taxon also lacks a long and slender scapula, an expanded radius, and an ulna with ossified olecranon.

3.3.2.2. The thalattosaurs from the Triassic of British Columbia

From the early/middle Triassic Sulphur Formation of British Columbia, Canada, two additional thalattosaur taxa, *Paralonectes merriami* and *Agkistrognathus campbelli*, were described by NICHOLLS & BRINKMAN (1993). Unfortunately, the material is very fragmentary, and a comparison with *Askeptosaurus* can therefore only be conducted on a very restricted basis.

3.3.2.2.1. *Paralonectes merriami* (fig. 33A)

Paralonectes, including *Paralonectes* sp. described also by NICHOLLS & BRINKMAN (1993), shows a large maxilla with a rectangular anterior edge that is also slightly curved upwards, and a dorsal margin that is conspicuously notched close to the anterior end of the naris. The latter opening is unfortunately incompletely preserved due to the missing of most of the premaxillae, but interpreted to have been relatively large. Negative impressions and isolated remains suggest that the premaxillae formed an elongated rostrum. Posteriorly to the maxilla there is a bone originally considered to be the lacrimal, however, the semilunar appearance of the bone rather suggests that it is a composite element resulting from the fusion of lacrimal and prefrontal. The nasals were obviously separated from each other, most probably by the premaxillae, as is typical for thalattosaurs. The space between naris and orbit is narrow, the latter being very large and ventrally bordered by the jugal. A quadratojugal is lacking, the lower temporal bar was apparently incomplete. The quadrate, however, is present and was suspended to the squamosal, the point of articulation was interpreted to be situated ventrally to the dorsal rim of the orbit. However, preservation does not allow a definite statement, and it cannot be excluded that the ventral projection of the squamosal bordered the quadrate laterally, as seen, e.g., also in *Anshunsaurus* (RIEPPEL et al. 2000), which would imply that the point of articulation was situated more dorsally. The remaining skull roof is only insufficiently known, the frontals obviously contacted the parietals, but whether there was also a posterolateral frontal projection meeting a possible elongated supratemporal, cannot be determined. The vomer is a prominent, stout element with an enlarged posterior margin, the palatine V-shaped, and the pterygoid very similar to that seen in *Clarazia*, having a plate-like palatal portion and a flat quadrate ramus. Known braincase elements include a prootic and a possible basisphenoid, the former being elongated, dorsally convex, and

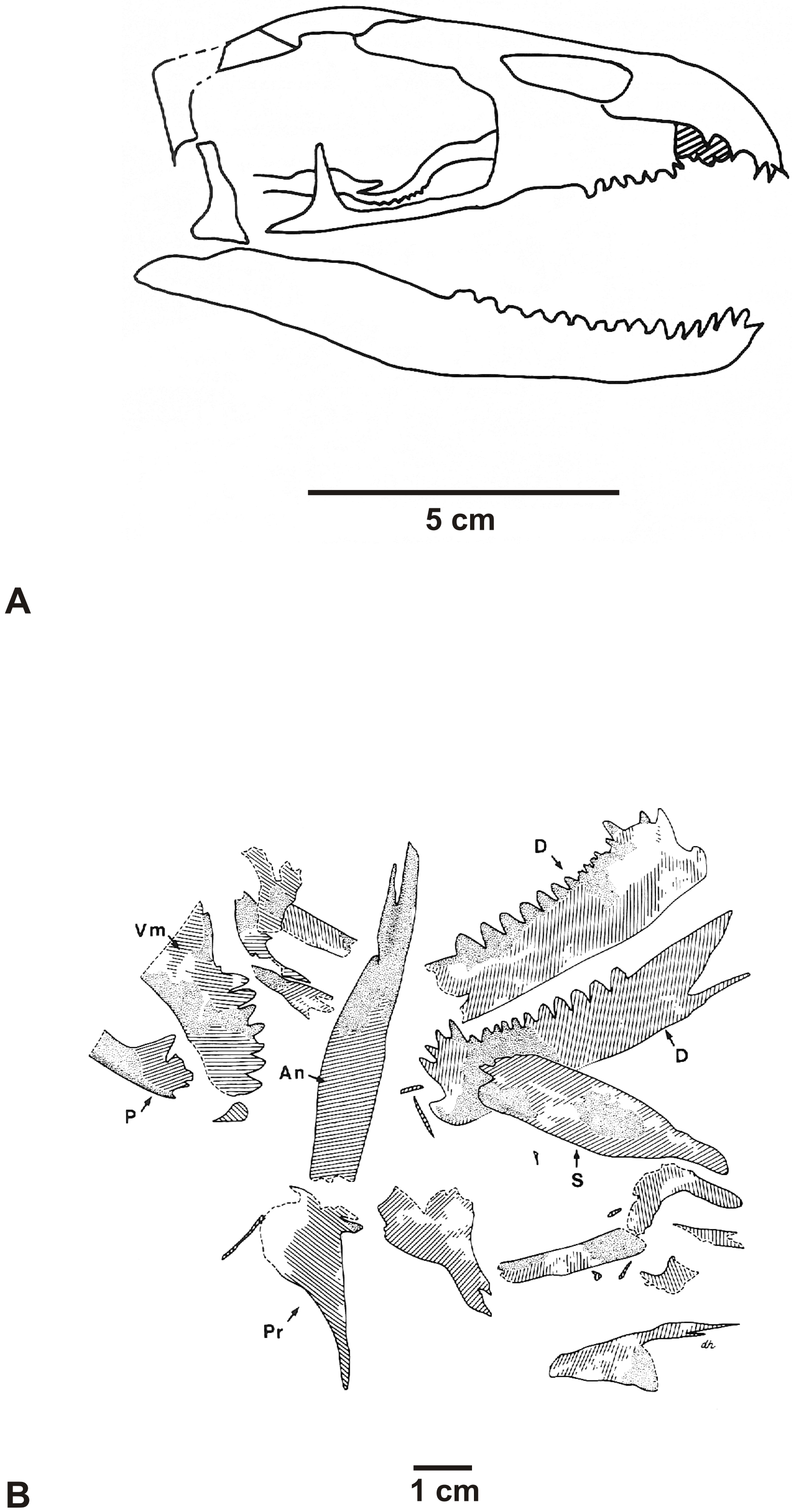


Fig. 33: The thalattosaurs from the Lower/Middle Triassic of British Columbia (from NICHOLLS & BRINKMAN 1993). A) cranial restoration of *Paralonectes merriami*. B) *Agkistrognathus campbelli*, holotype (all material is housed in the Tyrrel Museum). Abbrevations differing from those of the present work: "An" (angular), "P" (premaxilla), "Pr" (preorbital area), "S" (splenial/surangular), and "Vm" (vomer).

participating in the formation of the anterior margin of the foramen ovale, while a trigeminal notch was obviously absent. The supposed basisphenoid is of a roughly semilunar appearance. The dentition of the upper jaw is peculiar in showing 3 conical teeth on the premaxilla, separated by a diastema from those of the maxilla, the latter bone bearing at least 7 teeth with the anterior two procumbent and the posteriormost one bulbous and enlarged. Tooth implantation is ankylothecodont. Palatal dentition is also present, the vomer shows at least 7 narrow based teeth situated in a single row with probably the same mode of implantation. The pterygoid possesses several smaller teeth on its palatal portion, arranged in three rows of at least 3, 3, and 2 teeth, respectively.

The mandible is badly preserved and the identification of the single elements is not possible for most of it. Anyhow, the jaw ramus was obviously slender and with a short retroarticular process, a shallow mandibular fossa, and a low dorsal coronoid projection. Dentition consisted of at least 15 teeth on the dentary, the 4 conical teeth of the symphyseal region being procumbent and closely spaced, followed by 7 increasingly bulbous and smaller teeth. Finally, the posteriormost teeth are extremely bulbous and very low. Implantation again is ankylothecodont.

Of the very incompletely preserved postcranium, only remains of the vertebral column, a girdle element, and a few problematic limb elements are known. The preserved vertebrae come from the posterior dorsal region and from the caudal region. The thoracal centra are amphicoelous and higher than long, articulating with widely expanded neural arches. The centra of the caudal vertebrae are more elongated and strongly concave laterally, neural spines are only rudimentarily preserved. A few haemal arches as well as ribs are additionally known, the former having slightly expanded proximal articular surfaces and the latter being all single-headed and possibly assignable to the trunk region.

The aforementioned girdle element can most probably be considered as ischium. It represents a long, rectangular plate with a slightly convex medial edge and straight remaining margins.

A comparison with *Askeptosaurus* certainly has to focus mainly on the skull and the dentition, as the remaining skeletal elements are clearly too badly preserved. Again, also *Paralonectes* strongly differs from *Askeptosaurus*, as practically all other thalattosaurs do. Main differences are the large nares, the anteroventrally notched maxilla, and, surely, shape and implantation mode of the teeth as well as the presence of a palatal dentition. It should be noted, however, that if NICHOLLS´ & BRINKMAN´S (1993) identification of a lacrimal were true, which has been questioned above, this would be an interesting shared similarity of both taxa, as most other thalattosaurs lack a lacrimal. Also, if the supposed ventral position of the squamosal/quadrate articulation were interpreted differently (see above), this would be another notable resemblance.

3.3.2.2.2. *Agkistrognathus campbelli* (fig. 33B)

The material of *Agkistrognathus campbelli* only consists of a few distarticulated cranial bones. The premaxilla is ventrally recurved at its anterior tip, while the posterior region is unfortunately not preserved. Further incompletely preserved elements are maxilla, jugal, frontal, and lacrimal. Of the palate, only the anterior end of the vomer could be identified, showing a straight dorsal edge and a crescent-shaped ventral margin with at least 8 high, conical, and striated teeth. The remaining upper jaw presents two conical, procumbent teeth at the anterior region of the snout, followed by a marked diastema. The more posterior tooth-bearing portion, if originally present, is not preserved. Tooth implantation is ankylothecodont.

The mandible possesses a deep and elongated dentary which is posteriorly deeply emarginated and thus separated into a posterodorsal and a posteroventral projection. Anteriorly there is a small bony protuberance, and posteriorly to this there are 4 stout, conical, and coarsely striated teeth that are strongly procumbent. They are followed by two smaller teeth being offset from the main tooth row, and then by 4 very tiny and low teeth. The remaining 5 teeth succesively increase in size, and the posteriormost tooth is the largest of all. All teeth are closely spaced, and tooth implantation is acrodont or ankylothecodont. Further questionable mandibular elements include a badly preserved, elongateD splenial or surangular, and a thin angular.

Only a very restricted comparison with *Askeptosaurus* is possible. *Agkistrognathus* may share one feature, the presence of a lacrimal, with *Askeptosaurus*, but in general there are many differences: These are mainly the ventral curvature of the premaxilla, the shape of the vomer, and certainly the dentition with procumbent teeth and a marked diastema in the upper jaw.

3.3.3. Comparison with the thalattosaurs from China

In recent years, two new thalattosaur genera, *Anshunsaurus* and *Xinpusaurus*, have been described from middle/upper Triassic deposits of the Chinese Guizhou Province. These interesting taxa add important knowledge to the understanding of thalattosaur evolution, also with respect to *Askeptosaurus*.

3.3.3.1. *Anshunsaurus huangguoshuensis* (fig. 34)

Anshunsaurus huangguoshuensis, the first known thalattosaur taxon from China (LIU 1999, RIEPPEL et al. 2000), is currently only known from the skull, although the postcranial skeleton is also preserved but yet unprepared. *Anshunsaurus* presents an elongated premaxilla contacting the frontals in typical thalattosaur fashion, and the rounded nares appear to be retracted due to the anterior elongation of the snout. The frontal presents a well-developed posterolateral process, but it does not meet the supratemporal. The latter bone is elongated, its complete posterior half being notably expanded as compared to the anterior portion, and contacts the postorbital with its anterolateral edge. The fronto-parietal suture is interdigitating. Lacrimal and prefrontal are fused, as are postfrontal and postorbital. Moreover, the upper temporal fenestra is obliterated, and the skull roof is posteriorly emarginated. The lower temporal bar is incomplete due to the lack of a quadratojugal, the obviously movable quadrate is laterally covered by a distinct ventral projection of the squamosal. The dentition is homogenously developed, teeth are pointed and slightly recurved, and there is no sign of a diastema.

On the first sight, the similarity of the *Anshunsaurus* skull with that of *Askeptosaurus* is astonishing. There are, however, several important differences. So the former differs from *Askeptosaurus* in the fusion of lacrimal/prefrontal and postfrontal/postorbital. Further differences are the presence of a posterolateral process in the frontal and the shape of the supratemporal that even meets the postorbital, and the complete obliteration of the upper temporal fenestra. Additionally, the ventral projection of the squamosal covering the quadrate appears to be longer than in *Askeptosaurus*. Hence, although a close relationship may possibly be present, a synonymy can be exlcuded.

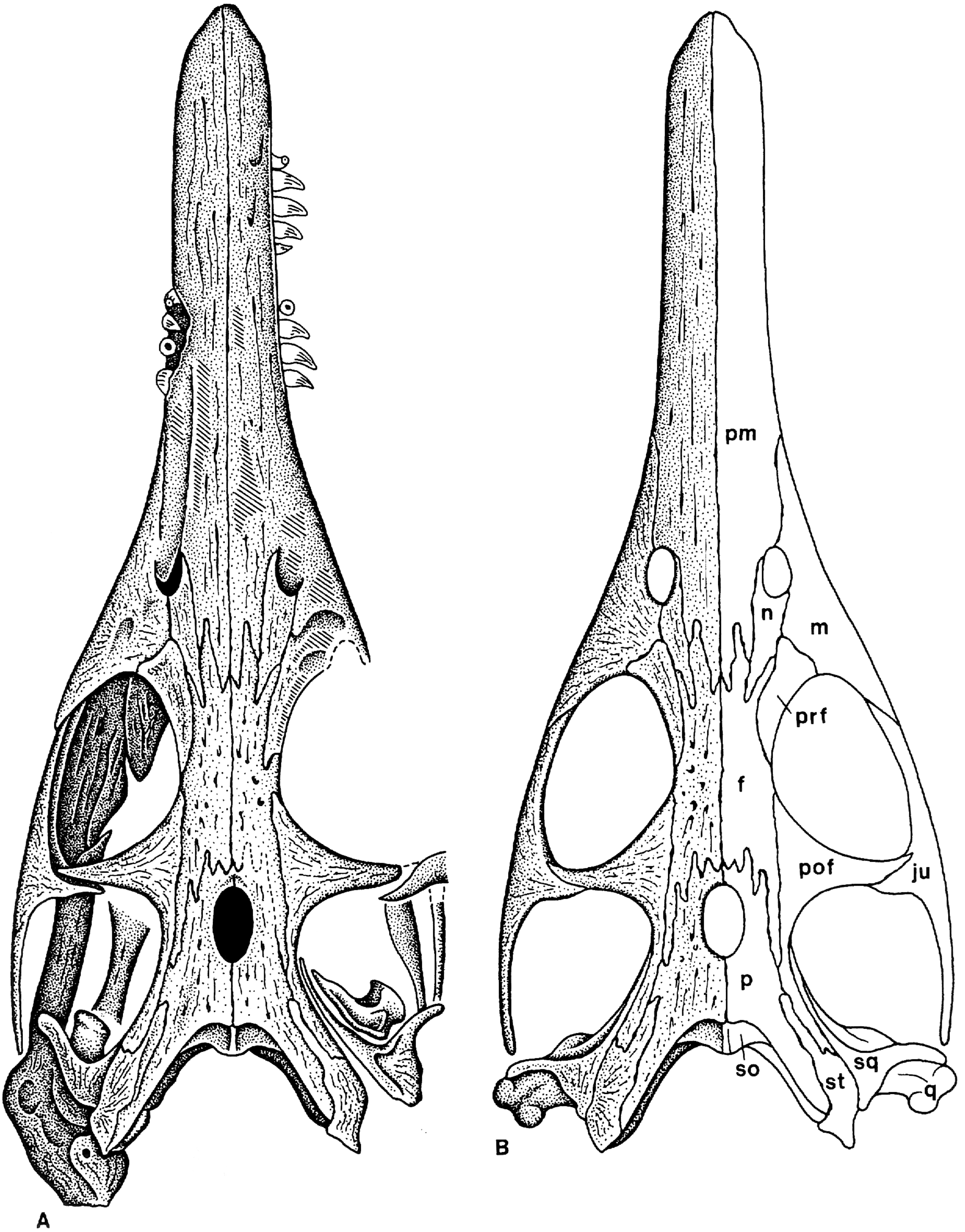


Fig. 34: *Anshunsaurus huangguoshuensis* (from RIEPPEL et al. 2000). A) holotype skull in dorsal view, B) cranial restoration (material housed in Bejing). Abbrevations differing from those of the present work: “ju” (jugal), “so” (supraoccipital).

3.3.3.2. *Xinpusaurus suni* (fig. 35)

Xinpusaurus suni, first described by YIN et al. (2000) and revised by LIU & RIEPPEL (2001) is a thalattosaur superficially resembling *Clarazia*, although at least the holotype is distinctly larger than the latter taxon (MAISCH, pers. comm.). The premaxilla/frontal contact is present, the nares are relatively posteriorly situated but not shifted dorsally (fig. 35B). The maxilla is anteroventrally distinctly emarginated. The frontals are broad elements with prominent posterolateral expansions, but without a contact to the supratemporal. A notable posterior emargination of the skull roof is present. The supratemporal meets the postorbital at its anterolateral edge. Postorbital and postfrontal were fused. The upper temporal fenestra is closed, and the lower temporal bar open due to the lack of a quadratojugal. The squamosal is small and the prootic very large with a distinct trigeminal notch and a transverse crest. Opisthotic and exoccipital are fused posteriorly. Ossified scleral ossicles are fairly present. The dentition of the upper jaw consists of 7 conical, pointed, and distinctly striated teeth on the premaxilla, followed by at least 2 further teeth on the maxilla, without a separating diastema. The latter teeth are procumbent due to the anteroventral emargination of the bone, the posterior tooth being also prominently enlarged. More posteriorly, 4 broad and blunt teeth are additionally present. Palatal dentition can also be identified, 6 large and blunt teeth are shown on the vomer, while the pterygoid bears plenty of small teeth of irregular distribution.

The lower jaw (fig. 35C) presents a prominent dentary whose dorsal margin is distinctly projecting dorsally directly behind the symphyseal area. The coronoid is well-developed and presents a notable dorsal process. Splenial and angular are relatively long, but the surangular is comparatively short. The retroarticular process is present but not very elongated. Dentition is restricted to the portion just behind the symphysis, and to the central part of the more posterior area of the dentary, both tooth-bearing portions being separated from each other by a marked diastema. The 7 anterior teeth are conical and pointed, with the tooth opposing the enlarged one of the maxilla being posteriorly inclined. The at least 3 posterior teeth are blunt and lower.

The postcranial skeleton is only insufficiently known (fig. 35A). The atlas-axis-complex corresponds to the usual condition of reptiles. With exception of the axis intercentrum, intercentra are obviously lacking in the trunk. The remaining amphicoelous vertebrae do not differ significantly from front to back, they all have neural arches being fused to the centra, whereas the height of the generally prominent neural spines slightly

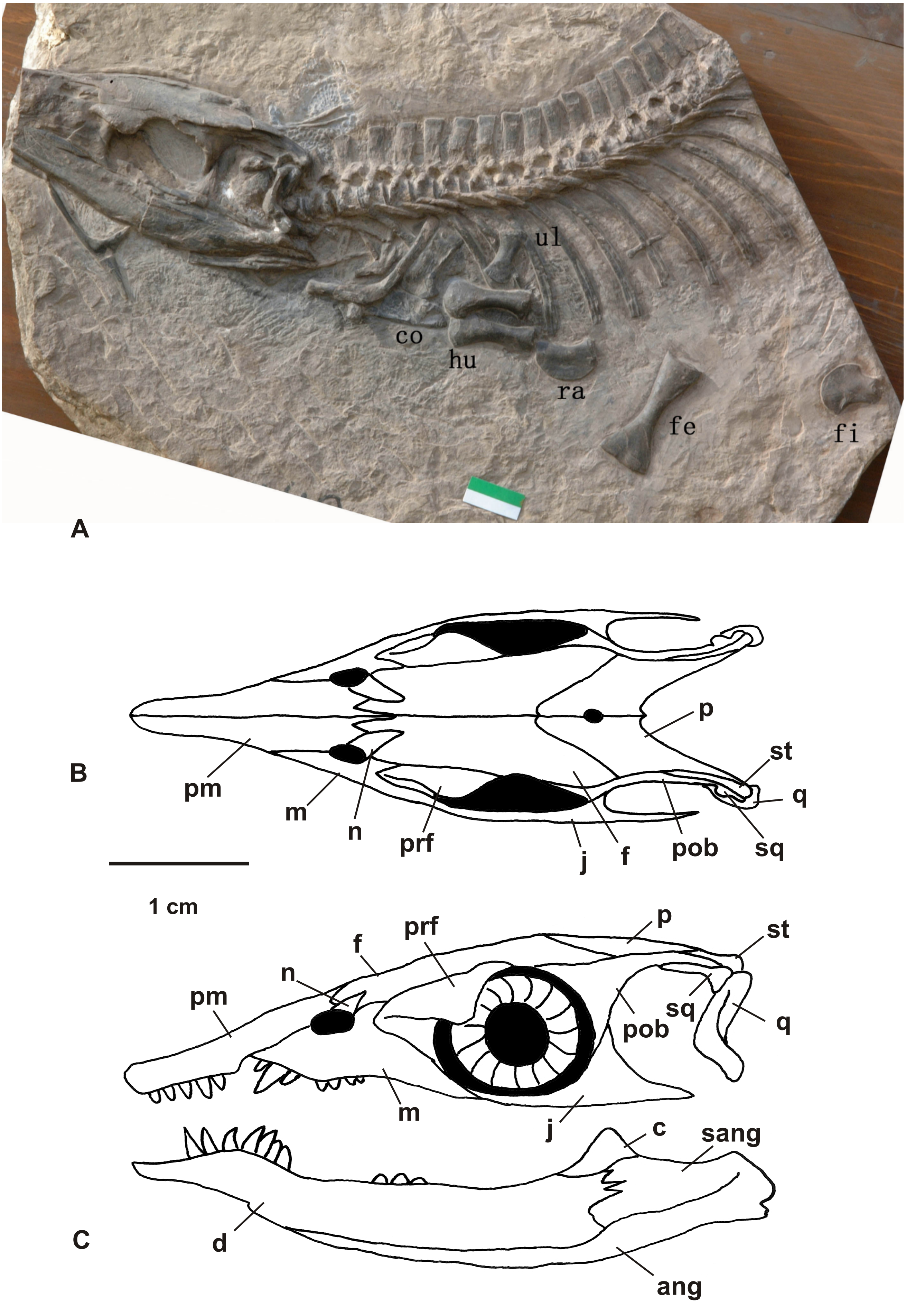


Fig. 35: *Xinpusaurus suni* (from and after LIU & RIEPPEL 2001, material housed in Bejing). A) photograph of the investigated specimen in lateral view, B) cranial restoration in dorsal view, C) restoration of skull and mandible in lateral view.

increases into posterior direction. In the cervical region, rib articulation was apparently double, whereas it changes into a single articulation more posteriorly. An additional anterior process was obviously not present in neither rib. Generally, *Xinpusaurus* has a very short neck.

Of the pectoral girdle, only scapula, coracoid, and clavicle are known. The latter is slender and recurved, and the coracoid is arch-shaped with a straight ventral margin. The scapula is peculiar in being broad but relatively elongated.

The stout humerus shows a notable expansion of its proximal head, which therefore is distinctly larger than the distal end. No trace of an ectepicondylar foramen can be detected. The radius is kidney-shaped, as, e.g., in *Nectosaurus*, and the ulna is stout with slightly expanded heads. No autopodial elements are currently known, as is unfortunately the pelvic girdle.

The slender femur is longer than the humerus and is distinctly hour-glass-shaped due to an expansion of the heads and an elongated constriction of the shaft. The fibula is notably broadened and almost fan-shaped. With exception of two probable phalangeal bones, no further hindlimb elements are known.

Xinpusaurus is certainly very different from *Askeptosaurus*, although both interestingly share the lack of a frontal/supratemporal contact. Anyhow, next to the overall size, the distinct shape of snout and mandible as well as the aberrant dentition are some of the most conspicuous differences in the skull, followed by the generally high cranium, the obliteration of the upper temporal fenestra, the fusion of postfrontal and postorbital, the postorbital/supratemporal contact, and the presence of a distinct retroarticular process. In the postcranial skeleton, *Xinpusaurus* differs from *Askeptosaurus* mainly by the high neural spines and the short neck, furthermore it seems that the cervical ribs did not possess additional anterior processes. Also, the scapula of *Xinpusaurus* is very different in being tall and with a roughly rectangular dorsal margin. The two taxa can furthermore be distinguished by the different morphology of the zeugopodia, with *Xinpusaurus* having notably expanded radius and fibula.

3.4. A revision of the enigmatic aquatic reptile *Endennasaurus acutirostris* from the Upper Triassic of Lombardy

The Norian Zorzino Limestone of Northern Italy is famous for its diversity of late Triassic organisms. Originally, the Zorzino Limestone was deposited in intraplatform basins surrounded by the Dolomia Principale (Hauptdolomit) carbonate platform, which belongs to the Alpine Triassic of the Southern Alps (PINNA 1993). These basins, although more than 200 meters deep and comparatively large (with an extent of several kilometers), had only a very restricted connection to the open sea, and the result was a lack of extensive water circulation and thus the presence of anoxic conditions in the deeper part of the basins. The preserved fauna mainly consists of nectonic, benthic, and, interestingly, also terrestrial organisms. Among vertebrates, there is a suite of fishes with many different ecological specializations (actinopterygians, coelacanths, sharks), and a variety of reptiles, both aquatic and terrestrial (*Endennasaurus*, placodonts, phytosaurs, aetosaurs, drepanosaurids, pterosaurs, lepidosaurs, prolacertiforms). The invertebrate fauna comprises crustaceans, bivalves, gastropods, corals, brachiopods, and a few echinoderms. Contrary to the Anisian/Ladinian of the Monte San Giorgio area, the preserved fossils are interpreted to be allochthonous (PINNA 1993), as, e.g., benthic faunal elements are absent. Besides, other, more pelagic representatives like, e.g., ichthyosaurs were apparently not able to enter the basins. A similarity, however, is that also here attritional mortality coupled with a low sedimentation rate rather than mass extinction events caused the large number of preserved specimens (TINTORI 1992).

The Endenna quarry of the Bergamo Prealps is stratigraphically located at the transition of the massive carbonatic beds of the Zorzino Limestone to the black shales of the Riva di Solto Shale, forming a layer of 3-4 m of thickness. The deposition of these sediments was obviously related to a marine transgression in the middle/late Norian (TINTORI 1995).

The enigmatic reptile *Endennasaurus acutirostris* was originally described by RENESTO (1984) in a preliminary note. The author suggested lepidosaurian affinities, but at the same time he added that a more definite assignment had to await a final preparation of the holotype (MBSN 5170), represented by an almost complete skeleton, preserved in ventral view and lacking only part of the left hindlimb and most of the tail, as well as the paratype (MBSN 27), in which only tail, femur, and pelvis are exposed. In the following, CARROLL (1988) placed *Endennasaurus* into the monotypic family Endennasauridae, which he

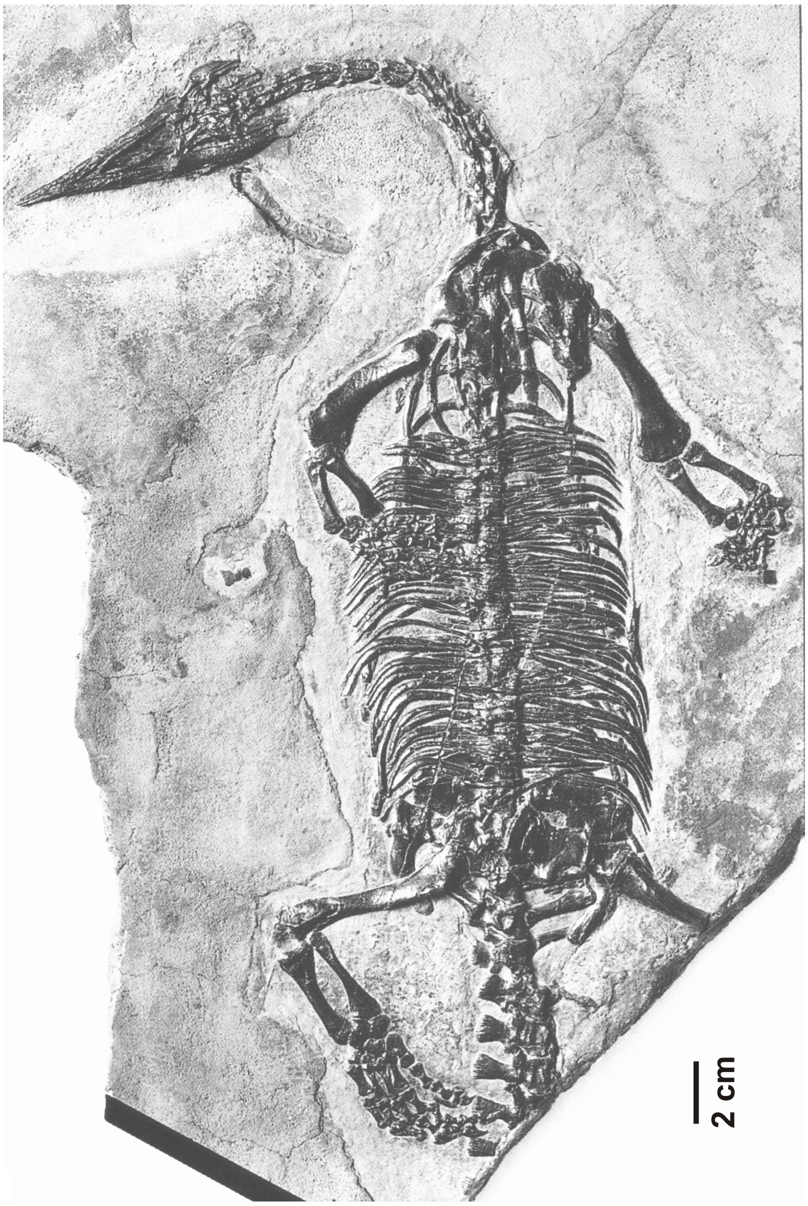


Fig. 36: *Endennasaurus acutirostris*, holotype skeleton (MBSN 5170), preserved in ventral view. Photograph taken by the staff of the Museo Civico di Scienze Naturali Bergamo.

considered as a taxon of uncertain affinities. Later, RENESTO (1992) presented a more detailed interpretation of the relationships of *Endennasaurus*, based on the preparation of also the dorsal side of the holotype skull. In his new investigation, RENESTO (1992) interpreted *Endennasaurus* as being closely related to thalattosaurs, especially *Askeptosaurus*, which, in his opinion, was mainly indicated by the shape of the ilium, the way of how the ribs are attached to the vertebrae, and the elongation of the premaxillae which form a distinct rostrum. This view was accepted by NICHOLLS (1999) in her recent revision of *Thalattosaurus* and *Nectosaurus*, where *Endennasaurus* was included within the new taxon Thalattosauriformes, even though the result of the phylogenetic analysis showed this reptile to stand in a polytomy together with *Askeptosaurus* and the remaining thalattosaurs. The latter result, however, brought RIEPPEL et al. (2000) to the conclusion that *Endennasaurus* should be excluded from thalattosaurs, as the clear evidence of a closer relationship could currently not be given.

In the light of these contradicting opinions and due to the here presented anatomical revision of *Askeptosaurus*, it was considered useful also to re-investigate the osteology of *Endennasaurus*, in order to make a hopefully more consistent hypothesis of probable relationships possible.

It should be added that the following description forms part of a joint project conducted together with SUSAN E. EVANS (University College London) and SILVIO RENESTO (University of Milan).

Eureptilia OLSON 1847
Diapsida OSBORN 1903
Thalattosauriformes NICHOLLS 1999

Endennasaurus acutirostris RENESTO 1984

Material: holotype, MBSN 5170 (see above; fig. 36), paratype, MBSN (27 (see above), both coming from the upper Triassic (Norian) Zorzino Limestone of Endenna, Lombardy, Italy.

Locality and horizon: from the Norian Zorzino Limestone, Endenna, Lombardy, Italy.

Diagnosis: Relatively small thalattosaur of slightly more than 1 m in total length; rostrum sharp, straight, and not ventrally recurved; nares posteriorly retracted; premaxilla/frontal contact present; orbits dorsally exposed; dentition absent in the upper and lower jaw as well as in the palate; jugal obviously very long posteriorly; neck elongated with at least 12 cervical vertebrae; 16 thoracal, two sacral, and more than 60 caudal vertebrae; neural spines generally low with a slight tendency towards pachyostosis; well-developed, relatively massive shoulder girdle; prominent gastral basket; limbs comparatively long, with relatively well ossified manus and pes.

Anatomical description

3.4.1. The skull

As already mentioned in the previous section, there is only one slightly incomplete skull of *Endennasaurus* preserved, both in dorsal and ventral view. The dorsal side of the occipital region as well as the posterior portion of skull roof and cheek are unfortunately not preserved any more.

3.4.1.1. Snout and skull roof (figs. 37, 38)

The skull of *Endennasaurus* is very sharp and elongated (fig. 37; the holotype skull has a length of 77 mm). The nares are relatively far posteriorly positioned, and the orbits are situated dorsally rather than laterally.

Premaxilla

The paired premaxilla is one of the largest cranial bones of *Endennasaurus*, reaching almost half the length of the whole skull and forming the major part of the snout as well as of the dorsal margin of the external naris. The premaxilla is very sharp and slender anteriorly and broadens into posterior direction, but generally the bone remains very narrow. The posterior region terminates in a relatively sharp tip that deeply enters between the frontal(s) and thus separates the nasals from one another. Since the posterior area of the premaxillae is broken, RENESTO (1992) originally misinterpreted these broken parts as nasals, and stated that

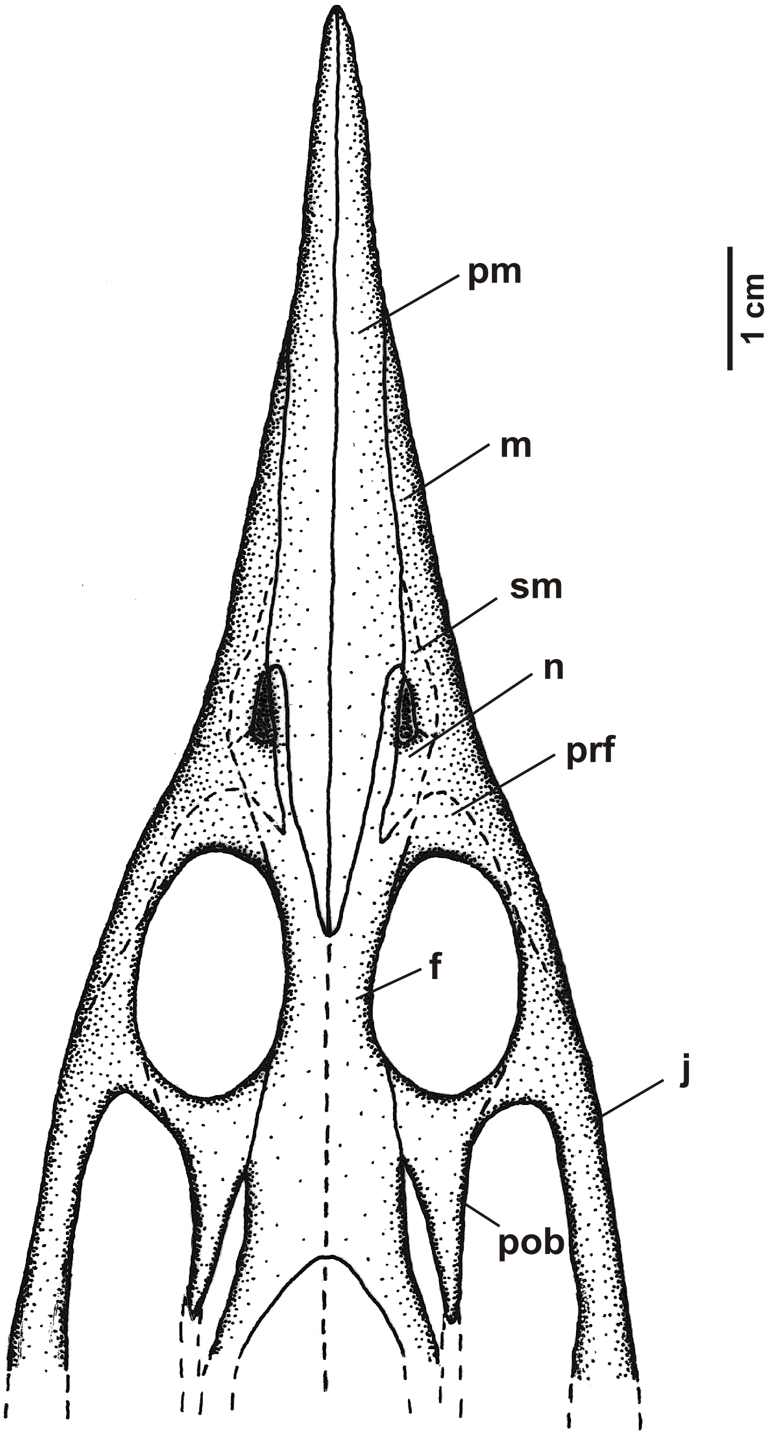


Fig. 37: *Endennasaurus acutirostris,* tentative restoration of the dorsal side of the skull.

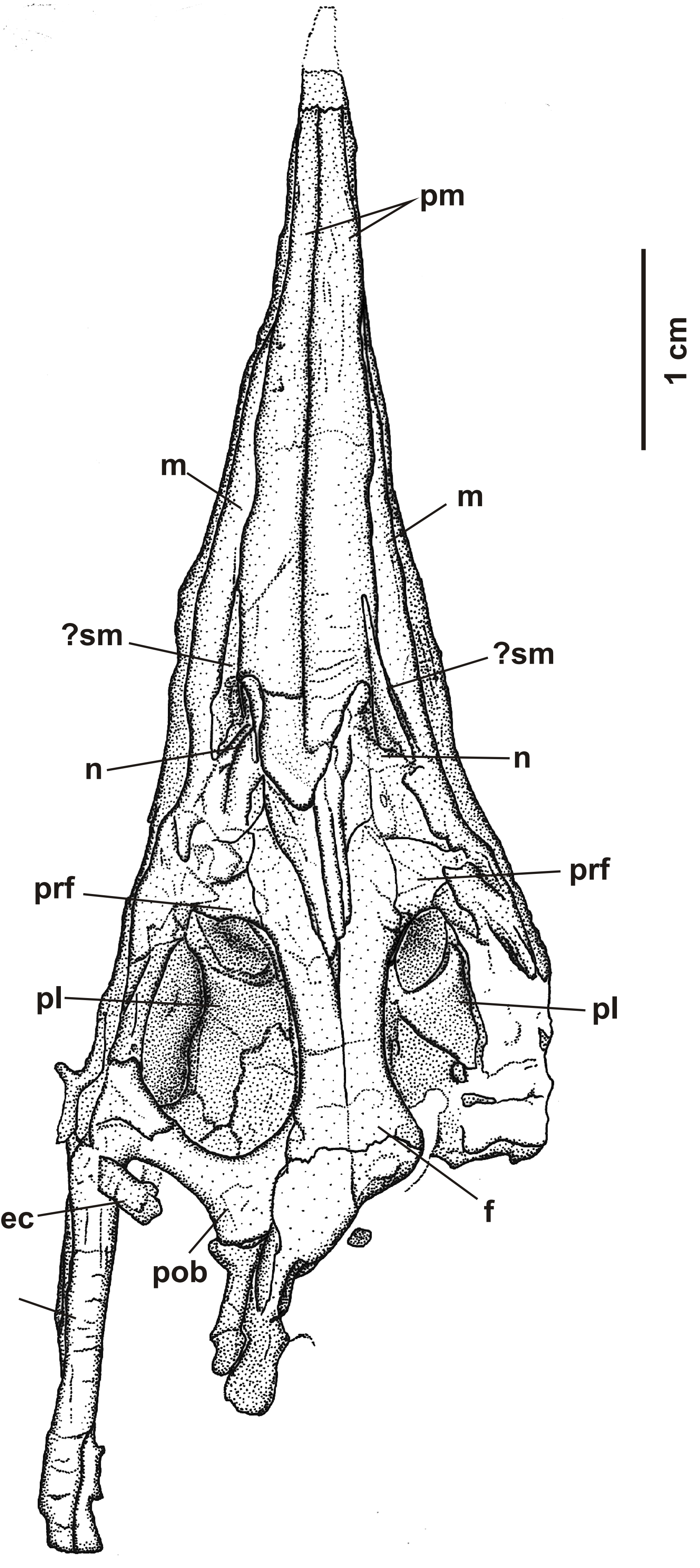


Fig. 38: *Endennasaurus acutirostris,* holotype skull (MBSN 5170) in dorsal view.

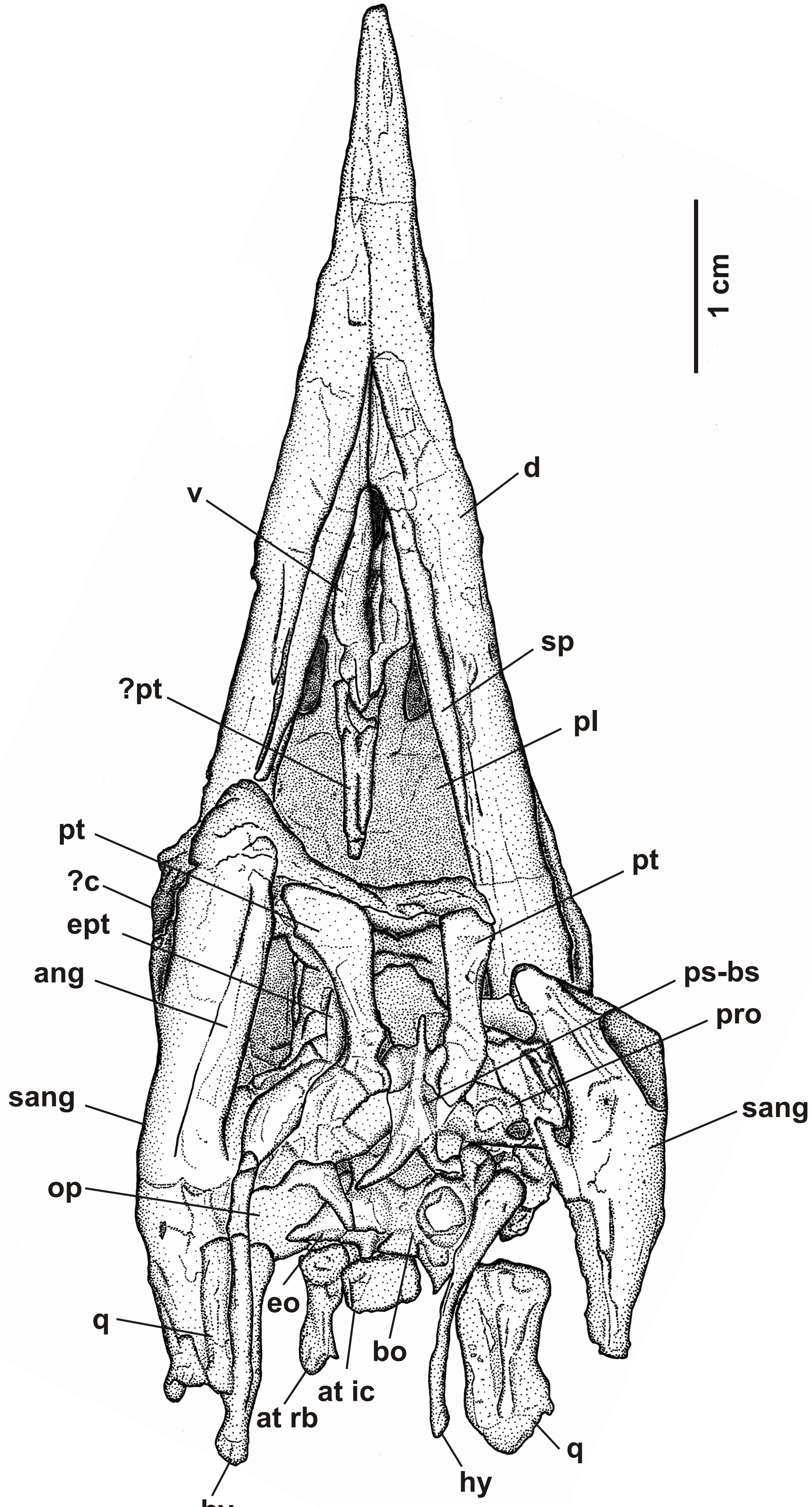


Fig. 39: *Endennasaurus acutirostris*, holotype skull (MBSN 5170) in ventral view.

the premaxilla would not have contacted the frontal. The central portion of the lateral edge of the premaxilla meets the maxilla in a relatively straight suture, while the anterior portion of the snout is exclusively built by the premaxilla. The posterolateral region borders the laterally exposed ?septomaxilla as well as the external naris (see above). A premaxillary dentition is not detectable and the bone was obviously edentolous, as already described by RENESTO (1984, 1992). Moreover, there are no external foramina present, and the whole dorsal surface is very smooth and without significant structures.

Maxilla

The maxilla appears to be a slender and elongated bone that forms a significant part of the ventrolateral portion of the snout and the upper jaw, respectively, also contributing to the formation of the external naris as well as of the anteroventral portion of the orbital arch. The rostral half is very slender anteriorly and broadens only slightly into a posterior direction. The dorsal (dorsomedial) edge of the maxilla meets the premaxilla anteriorly and, almost exactly in the mid portion of the bone, also the ?septomaxilla (see below). Due to the poor preservation it is difficult to establish whether the bone contributed to the formation of the external naris. Preservation does furthermore not allow a thorough description of the antorbital portion of the bone, and it must remain open to question which element of that area was actually contacted by the maxilla. At least it seems that the bone developed a slightly ascending flange. The posterior most part of maxilla forms part of the anteroventral orbital rim and tapers distinctly into caudal direction. It was posteriorly bordered by an oblique contact to the jugal, beginning at the anterior level of the orbital arch. As the premaxilla, the maxilla does not show any sign of a possible dentition, nor are there traces of foramina or striations.

?Septomaxilla

The dorsal exposure of the skull of *Endennasaurus* suggests that there was a slender, drop-shaped septomaxilla which was not restricted to the inner part ot the nasal opening, but reached obviously also onto the external side of the skull. If correctly interpreted, the bone is generally very small and narrow, but posteriorly slightly expanded. The latter portion lies directly within the narial opening and forms furthermore the ventral border of the naris.

Anteriorly, the septomaxilla forms a sharp spine that projects onto the dorsal surface of the skull, situated between the dorsomedial margin of the maxilla as well as the lateral edge of the premaxilla.

Nasal

The nasals are very badly preserved and it is difficult to determine much about their morphology. Due to the posterior elongation of the premaxillae, the two bones were broadly separated from one another. Each nasal must have contacted the premaxilla medially in a straight suture, and it seems that the anterolateral border of the nasal formed the medial margin of the external nares. The anterior portion of the nasal appears to be drop-shaped and also bordered by the premaxilla. The posterior outline of the bone is difficult to judge due to the poor preservation of the antorbital skull portion, so it is not possible to determine whether the nasal met, for example, the prefrontal, or whether it was separated therefrom by a fronto-lacrimal contact, like in *Askeptosaurus*.

Lacrimal

A lacrimal could not be positively identified, as the respective region anteriorly to the orbit is crushed. It cannot be excluded, however, that such a bone was originally present.

Prefrontal

The exact morphology of the prefrontal must be left open to question, due to the poor preservation of the antorbital region of the skull. It is only possible to state that the prefrontal met the anterolateral edge of the frontal medially, thereby contributing to the anterodorsal formation of the orbit. The way how the bone contacted the maxilla or a possible lacrimal could not be determined.

Frontal

It is difficult to judge whether the frontals were fused or not. The deep anterior facet in which the premaxillae enter suggests a separation, but more posteriorly both elements appear to be fused. A sagittal groove in the posterior most preserved portion, however, again seems to contradict a frontal fusion. Better preserved specimens are therefore necessary for a definite conclusion. The exact morphology of the anterior most portion of the frontal could not be established due to poor preservation, but it seems that there was a long rostral projection like in other thalattosaurs. Whether the bone, however, actually contributed to the formation of the external naris cannot be definitely determined, also there is a slight indication. The caudal portion of the bone is broad in comparison to the constricted interorbital area and posterolaterally meets the postorbital. Furthermore, the incomplete, crushed area which was originally interpreted to represent part of the parietal (RENESTO 1992) also belongs to the frontal and the supposed suture indeed is only a breakage. The original suture was therefore more posteriorly situated and, as indicated by the preserved bony parts in that area, was probably U- or V-shaped. Furthermore, it now appears that the frontal also developed a distinct posterolateral elongation, like in many other thalattosaurs. Contrary to most of these forms, however, the outline of the projection indicates that a slit-like upper temporal fenestra might have been present. Unfortunately, the posterolateral projection is posteriorly incomplete.

Parietal

The parietal is not preserved.

Postorbital

The postorbital forms the posterior margin of the orbital arch, but unfortunately is not completely preserved. The postfrontal was obviously fused to the bone. Anteromedially, the postorbital is comparatively short and borders the posterolateral edge of the frontal. The caudal portion of the postorbital is incomplete and it is difficult to determine whether the preserved remains all belong to this bone or form already part of the squamosal. Anyhow, the medial edge of this area is slightly concave, suggesting that there eventually was a slit-like upper temporal fenestra. The ventral region of the postorbital meets the jugal in the posteroventral portion of the orbital arch, but the exact morphology of the respective suture could not be established.

Squamosal

As just mentioned, maybe the caudal portion of the postorbital already belongs to the squamosal, but this is speculative. Moreover, possible remains of a squamosal appear to be present at the posteriormost part of the lower temporal arch.

Jugal

The jugal is a very conspicuous cranial element of *Endennasaurus* as it obviously retained a distinct posterior projection, suggesting that the lower temporal bar may not have been reduced. The posterior elongation of the bone is straight and most probably oval in cross-section. The posterior most portion does not appear to be complete, but nevertheless, at the posterolateral (posterodorsal) edge one can find traces of a possible suture, indicating that a posteroventral extension of the squamosal contacted the jugal at this point. At its anterior origin, the elongation is slightly expanded and turns clearly into the orbital arch, corroborating the interpretation that this structure really belongs to the jugal. The remaining portion of the bone is difficult to describe in detail. Anyhow, the remains suggest that the jugal met the maxilla at its posterodorsal edge, and by that , both elements form the ventral part of the orbital arch. The dorsal extension of the jugal cannot be established in detail either, but also here the general configuration indicates a typical contact between jugal and postorbital, i.e. the jugal met the ventral extension of the postorbital in an oblique suture.

Quadrate

Originally, RENESTO (1992) considered two small, roughly rectangular bones lying medially to the posterior end of the two mandibles as the quadrates. The left element is the better visible one. It shows rounded anterior and posterior ends, with the latter being smaller and more sharpened. Furthermore, there is a longitudinal crest in the mid portion of the bone. RENESTO´s interpretation that these elements are quadrates will be followed here, although it should be noted that if *Endennasaurus* really possessed a closed lower temporal bar, the quadrate was probably firmly suspended and, like in *Sphenodon,* developed an anteromedial flange sutured to the pterygoid. This interpretation would exclude a determination of the here described bones as quadrates, as the rounded surfaces would indicate a movable suspension.

The elements would then rather represent isolated parts of the lower jaw, possibly articulars, which are relatively similarly developed in *Sphenodon* (pers. obs.), and should also be found in the same relative position within the skull. However, as the posterior palatal area of *Endennasaurus* unfortunately is badly crushed, the identification of a different bone as quadrate is impossible, and the alternative assumption can therefore not be tested.

Quadratojugal

Due to the coverage by the mandibles, a quadratojugal could not be positively identified.

3.4.1.2. Palate (fig. 39)

The preserved elements of the palate can for the most part only be described in ventral view.

Vomer

The paired vomer is a slender, elongated bone. The two elements were obviously slightly obliquely oriented and met one another in the posterior portion only. In their caudal most part, the vomers taper distinctly and probably contacted the anterior end of the pterygoids, thereby separating the anterior portions of the palatines from each other. The rostral part of the vomers cannot be described due to the coverage by the lower jaw.

Palatine

The paired palatine is a prominent element forming the posterior half of the internal naris. Unfortunately, its definite outline cannot be determined as it is covered both dorsally and ventrally by several other bones. It can be stated, however, that the central part of the palatine represents a broad plate whose lateral edge did not contact the ventral orbital arch and thus formed a slender suborbital fenestra. Anteriorly, the palatine most probably met the maxilla by a narrow anterolateral projection, the anterior margin of which represents the posterior border of the internal naris. The dorsal surface of this projection shows a slight curvature, probably an attachment site for eye muscles. The medial outline of the palatine cannot be definitely established , but both elements were apparently separated from one another by pterygoids and vomers. Unfortunately, also the posterior termination of the palatine cannot be determined due to poor preservation.

Pterygoid

The two pteryoids are crushed, and therefore difficult to describe in detail. Anteriorly, they were obviously very slender, and contacted the vomers, thereby separating the palatines from one another. It is not clear whether all of the exposed slender bones posteriorly to the vomers belong to the pterygoids, maybe some parts can be assigned to descending processes of the frontal(s), the so-called cristae cranii, which would then indicate that the pterygoids did not meet one another anteromedially. More posteriorly, the pterygoids definitely diverge and become more expanded. A possible pterygoid flange that usually contacts the ectopterygoid is not preserved any more, but was most probably present, as the right pterygoid shows a slight lateral expansion close to the region where such a flange should normally be expected. At the point where the pterygoids reach the level of the braincase, they show a slight, half-rounded emargination at their medial edges, serving for the articulation with the basipterygoid processes of the parabasisphenoid. Posteriorly to this, the pterygoids turn strongly posterolaterally and become obviously distinctly more expanded. However, this region is badly crushed and therefore any further interpretation would have to be considered doubtful.

Ectopterygoid

The ectopterygoid is practically not visible on neither side. Only the dorsal exposure of the skull shows a small, elongated piece of bone lying posteriorly to the orbital arch, slightly reaching onto the posterior projection of the jugal. This piece most probably represents part of the ectopterygoid, but it does not allow to determine the way in which the ectopterygoid was associated with the pterygoid and the formation of the suborbital fenestra.

Epipterygoid

Laterally to the posterior edge of the pterygoids, a more or less vertically oriented bone is visible, following the alignment of the pterygoid and having an irregular ventral margin that appears to be slightly thickened. This structure is here interpreted as the epipterygoid.

3.4.1.3. Braincase (fig. 39)

All the identified braincase elements are only preserved in ventral view.

Basioccipital

The basioccipital is a stout element with very prominent basal tubercles. Both tubercles are of more or less rounded outline and with a slight rectangular ventral tip. Anteriorly to the tubercles, the basioccipital shows a half-rounded depression. Originally, this area was probably ventrally covered by the parabasisphenoid. Immediately posterior to this depression, a small groove of unknown function is visible. The posterior portion of the basioccipital presents a comparatively small condyle, being trapezoid in shape and laterally contacted by the exoccipitals. The posterior edge of the condyle is very straight. The lateral edges of the basioccipital are slightly convex and were obviously contacted by the opisthotic. Due to the disarticulated nature of the braincase elements it is not possible to determine the structure of the (undivided?) metotic fissure, to whose formation the basioccipital usually contributes.

Exoccipital

The exoccipital is only scarcely preserved, some small remains of which are only exposed at both lateral edges of the basioccipital condyle, as well as at the posteromedial margin of the right opisthotic. The left exoccipital shows a concave medial margin, which most probably represents the lateral border of the foramen magnum, while the right exoccipital projects laterally, showing a sharp distal tip. More details are not detectable.

Opisthotic

The opisthotic is a prominent element forming the paroccipital process and part of the otic capsule. Medially, it touches the basioccipital and presents a well-developed, roughly semilunar ventral ramus, which usually separates the metotic fissure from the more anteriorly situated fenestra vestibuli. The bone is proximally (medially) relatively expanded. The anteroventral region is unfortunately not well preserved any more, and therefore a description of the fenestra vestibuli cannot be given.

Parabasisphenoid

No distinction can be drawn between the basisphenoid and the parasphenoid, therefore the two elements are here considered as a single, composite bone. Generally, the parabasisphenoid is badly crushed in the specimen, making a detailed investigation very difficult. However, it can be stated that there were two posterolateral projections of elongated, distally tapering shape, which obviously bordered the anterior and anterolateral margins of the basioccipital, and possibly also reached the opisthotic. Anteriorly to this projections, the parabasisphenoid becomes slightly expanded and finally turns into a flat anterolateral expansion, the basipterygoid process, being of butterfly-shape and articulating with the pterygoid. Posteromedially to the right process, a small groove is detectable in the central area of the bone, eventually representing the vidian canal, carrying the internal carotid artery and the palatal branch of the facial nerve. A possible foramen for the cerebral branch of the carotid artery can be detected at the posteromedial base of the right basipterygoid process. The anterior portion of the parabasisphenoid is represented by a slender cultriform process whose anterior part is unfortunately not preserved, so that the rostral extension of the element cannot be established.

Prootic

Due to the crushed preservation of the braincase as well as the coverage by other bones, the prootic cannot be described in detail. There are, however, some remains detectable laterally to the pterygoid-parabasisphenoid complex, especially in the left half of the skull. In this area , a slight curvature as well as a foramen can most probably be assigned to the ventral part of the semicircular canal and its surroundings, and thus to the prootic. A more precise treatment is unfortunately not possible.

Hyoid

Remains of the hyoid apparatus, i.e. the ceratobranchials 1, can be seen on both sides laterally to the occiput, consisting of slender and elongated rods of bone.

3.4.1.4. Lower jaw (fig. 39)

For the most part, the mandible is exposed in ventral view, only a few lateral structures are also visible. The two mandibles are anteriorly not significantly displaced from each other, suggesting that the symphyseal contact was very strong. Posteriorly, both mandibles taper and form a retroarticular process. Generally, almost every suture is badly visible, if at all, and the following description is based on personal observations that may not be shared by different workers.

Dentary

The dentary is a long element that appears to take part even in the formation of the posterior portion of the mandible. Anteriorly, if forms the major part of the symphysis, which is, corresponding to the elongated rostrum of the upper jaw, very extended and with a sharp anterior tip. More posteriorly, the dentary is dorsally sutured to the coronoid, but the way in which this contact took place cannot be established. Due to preservation it is also difficult to determine whether the dentary also extented to the posterior part of the lower jaw or whether it was instead replaced by the surangular. At least there is no suture detectable. Thus one may assume that the posterolateral portion of the jaw ramus was also formed by the dentary, which then met the angular at the posteroventral egde, and possibly the surangular posteriorly. Obviously the dentary did not possess any teeth, an interpretation that is also corroborated by x-ray.

Splenial

In the anterior portion of both mandibles, there are elongated pieces of bone that do not only form the medial margin of the central part of the jaw ramus, but also appear to contribute to the formation of the symphysis. These structures may be interpreted as splenials.

Right posteriorly to the symphyseal contact of the dentaries both bones turn medially and meet each other in a straight suture. Laterally, each structure contacts the dentary, posteriorly it tapers increasingly and seems to terminate in a small tip. Whether this posterior most tip slightly contacted the angular, cannot be stated with absolute certainty.

It should be noted that an alternative interpretation of the anterior splenial portion could be that this area does not belong to the mandible, but, instead, is an exposed part of a secondary palate formed by the maxilla (SUSAN EVANS, pers. comm.). However, I was not able to determine a bony margin between the posterior part of the splenials and the portion that is interpreted here as symphyseal area , which otherwise must be expected. Furthermore, a comparison with other long-snouted reptiles like, e.g., the marine crocodile *Steneosaurus*, shows a very similar configuration, i.e. the splenials are anteromedially recurved and meet in a straight suture, thus forming the posterior part of the symphysis (pers. obs.).

Coronoid

At the anterior beginning of the posteroventral third of each mandible, there is a badly preserved bony mass laterally to the dentary, which may be interpreted as remains of the coronoid. It is not possible to state whether the major part of the coronoid was laterally covered by the dentary, as it sometimes occurs in other diapsid reptiles.

Angular

The angular forms most of the posteroventral margin of the lower jaw. It represents an elongated bone, whose dorsolateral edge contacted the dentary. It is difficult to establish how far posteriorly the angular originally extended.

Surangular

It is problematical to determine the morphology of the surangular. It probably formed the posterodorsal most portion of the lateral side of the lower jaw ramus and thus contributed to the formation of the retroarticular process, which can be seen on both sides as a slender, distally tapering structure.

Prearticular and articular

A prearticular could not be identified, although it surely must be situated somewhere in the posterior portion of the mandible. Maybe it was fused to other bones. Also the morphology of the articular could not be established due to the lack of visible sutures, but see the discussion in the quadrate section.

3.4.2. The postcranial skeleton

The ventral side of the holotype skeleton of *Endennausaurus* is relatively well preserved, even though not all extremities are complete.

3.4.2.1. Vertebrae and ribs (figs. 40, 41)

3.4.2.1.1. Vertebral column

As already noted by RENESTO (1984), there are at least 12 cervical, 16 dorsal, two sacral, and 67 caudal vertebrae. All of them are amphicoelous. Especially in the posterior thoracal and the sacral region, vertebrae and ribs show a certain kind of “swollen“ impression, and thus can be interpreted to have been pachyostotic.

Cervical vertebrae

The cervical elements are all of roughly the same size.

The atlas-axis complex is not fully preserved. The atlas intercentrum (fig. 39) is ventrally exposed and has the shape of a slightly rounded rectangular. Laterally to its right , an atlas rib is preserved, consisting of a slightly expanded proximal portion and a tapered distal part. It finally terminates in two small projections, of which one is broad and rounded, while the other one is very slender. The axis centrum (fig. 40A) is a narrow and slightly elongated element. Unfortunately, the exposure does not allow the description of a possible neural arch, nor can facets be seen for the attachment of the ribs.

The remaining cervical vertebrae (fig. 40B, C) are all very low elements. The centrum is prominently developed and relatively elongated, being only slightly constricted in its central portion. A well-developed rib facet was obviously not present, but slight depressions in the central lateral portion indicate that the lower process of the cervical rib, i.e. the capitulum, obviously was attached there. Dorsally, the centrum appears to be separated from the neural arch by traces of a neurocentral suture that runs more or less concavely along the dorsal margin of the former. The base of the neural arch is much shorter than the extension of the centrum, and no clearly defined rib facets are visible, but some rugosities in the central portion of the ventral base may have served for the articulation with the tuberculum. More

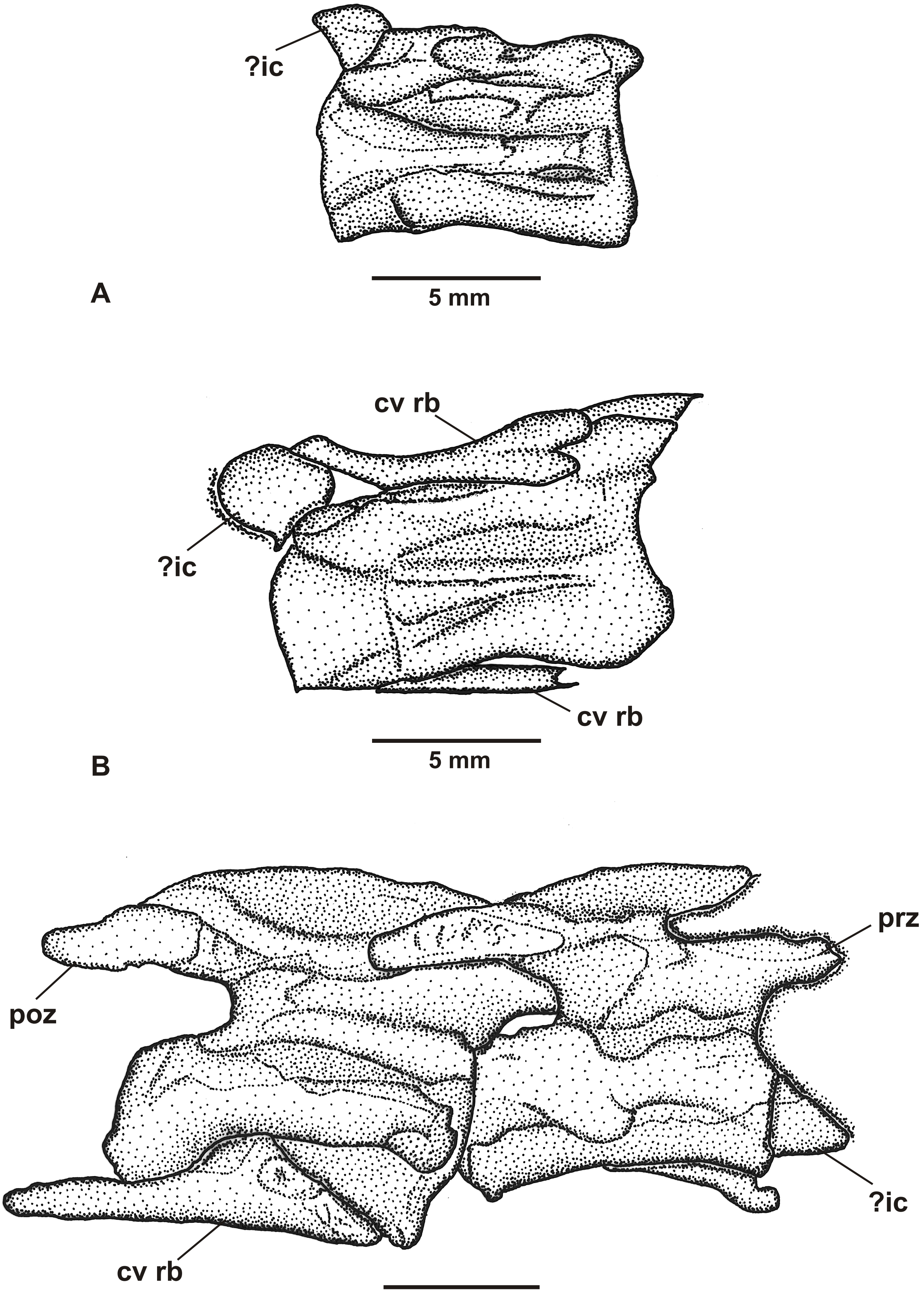


Fig. 40: *Endennasaurus acutirostris*, cervical region (MBSN 5170). A) axis in ventral view, B) 4th cervical vertebra in ventral view, C) 8th and 9th cervical vertebrae in lateral view.

dorsally, the neural arch presents prominent and elongated zygapophyses, of which the postzygapophysis is twice as long as the prezygapophysis. Both zygapophyses are relatively straight anteriorly and posteriorly directed, respectively, and have a flattened dorsal margin. The neural arch is extremely low and consists only of a slight dorsal extension that originates anteriorly at the level of the base of the prezygapophysis, extending slightly beyond the height of the posterior edge of the centrum.

In the anterior half of the neck, there may have been some intercentra at least up to the 8th cervical, more posteriorly these elements obviously diminish. They all are relatively small, without any sign of a notable ventral extension or curvature, and attached to the anteroventral edge of each centrum. It should be noted that this is only a tentative determination and that breakage may have led to the impression of intercentra.

Thoracal vertebrae

Unfortunately, the trunk vertebrae are mostly covered by gastral ribs, hence a detailed description is very difficult. However, one anterior thoracal is still fairly well visible in the type specimen, and the following description will mainly be based on this element.

The trunk centrum (fig. 41A) is relatively elongated and only slightly constricted, and thus it corresponds more or less to the extension of the cervical centra. In the central area of its dorsolateral portion, the thoracal centrum participates in the formation of the prominent rib articulation facet, of which it forms its ventral portion. Ventrally to this, the centrum is slightly depressed. As in the cervicals, the ventral base of the neural arch is much shorter than the extension of the centrum. A neurocentral suture is obviously missing. The mid portion of the neural arch is very extended again. Only the prezygapophyis is sufficiently preserved, consisting of a sharp and stout anterior projection that reaches beyond the level of the anterior edge of the centrum. Posteriorly to the prezygapophysis, the dorsal portion of the rib articulation facet can be found, giving the complete facet a roughly rectangular outline. Also, it slightly projects laterally. In the here described anterior thoracal, the neural spine is covered by other bones. However, the visible parts of the remaining trunk vertebrae as well as an x-ray photograph indicate that the neural spines were relatively broad, stout, and rectangular, but distinctly higher than those of the cervicals. Obviously, there were no dorsal intercentra present.

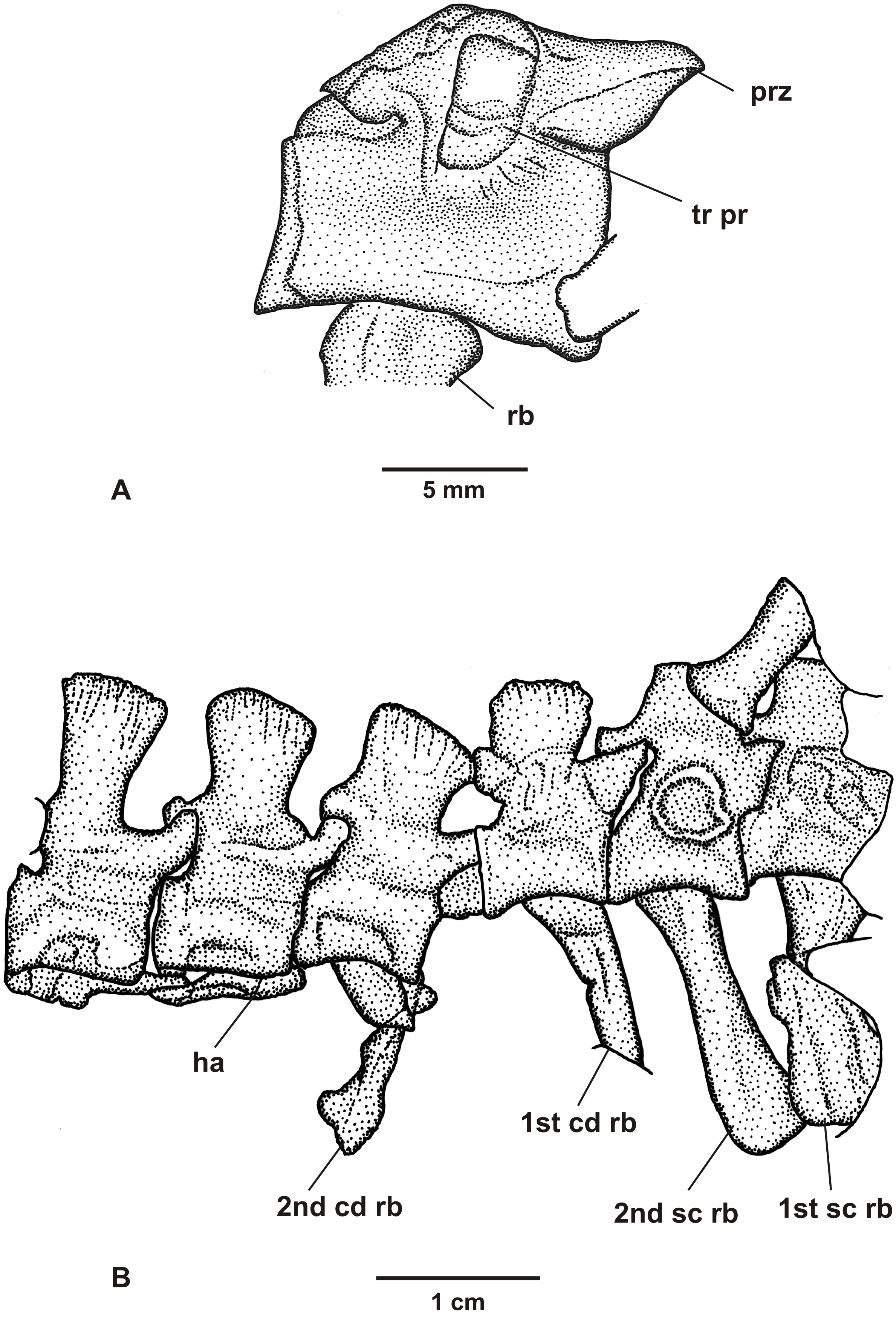


Fig. 41: *Endennasaurus acutirostris*, thoracal, sacral, and caudal region (MBSN 5170). A) anterior thoracal vertebra in lateral view (neural spine not visible), B) sacral and anterior caudal vertebrae in lateral view.

Sacral and caudal vertebrae

The two sacral vertebrae (fig. 41B) are generally shorter than the thoracals. The centrum appears to be stouter and not as elongated as the zygapophyses. Instead of a lateral extension of the rib facet like recorded in the trunk vertebrae, the facet for the unfused sacral ribs consists of a rounded depression lying again both on the centrum and on the neural arch. Within the articulation facet, traces of a neurocentral suture are visible. As in the thoracals, the neural spine is broad and stout.

The caudal vertebrae (fig. 41B) are, as it is usually observed in many reptiles, shorter and higher in the anterior portion, and they become relatively more elongated and lower posteriorly, even though their size generally decreases. In the anterior part of the tail, the overall shape of the centra resembles that of the sacrals, only the articulation facet for the unfused caudal ribs changes into a more elliptic outline, and the neural arch participates in the formation of the facet to only a minor extent. At least in the anterior most vertebrae, also remnants of a neurocentral suture can be detected. The neural spine of the proximal caudals is almost fan-shaped, i.e. its ventral base is shorter than the dorsal margin and projects straight into dorsal direction. Significant striations can be recognized in the dorsal portion of the spine. More posteriorly, the neural spines become increasingly posterodorsally directed, taper significantly, and decrease in size. In the posterior most portion of the tail, the spines are not detectable any more. The haemapophyses are V-shaped and can already be recognized at the second caudal. They are not fused to the vertebrae and show slightly expanded distal ends. Furthermore, they are generally small and do not significantly decrease in size more caudally. The posteriormost portion of the tail does not appear to possess haemapophyses.

3.4.2.1.2. Ribs

The cervical ribs (fig. 40B, C) are clearly double-headed, whereas it seems that the capitulum was slightly longer than the tuberculum. Generally, the cervical ribs are relatively short and about as as long the cervical centra. Sometimes they are slightly recurved. Posteriorly, they terminate in a slender tip. An additional anterior projection, as it occurs in some other diapsids and *Askeptosaurus,* is not present.

The ribs of the trunk region are of common diapsid appearance and without significant peculiarities. They are posteriorly recurved and do not show a pachyostotic development. The anterior most and posterior most thoracal ribs are slightly shorter than the remaining ones, but there are no great differences in size. Although the proximal end of the ribs is holocephalous (fig. 41A), it appears to be somewhat hour-glass shaped in cross-section.

As already mentioned above, the two sacral ribs (fig. 41B) are not fused to the respective vertebrae. They are massive, but elongated elements with a distinctly expanded distal portion for the articulation with the pelvis. The posterior rib is slightly longer and not straight laterally directed, but extends anterolaterally. Also the proximal end of the ribs is slightly expanded, whereas the posteroproximal edge appears to be somewhat flattened and extended.

Only one caudal rib could be recognized (fig. 41B), situated on the first caudal vertebra, to which it is not ankylosed. It consists of an anterolaterally directed, shovel-like projection whose distal part is relatively sharp.

The gastral ribs are numerous and well-developed (fig. 36), at least 31 slightly pachyostotic composite elements are laterally visible. Each element consists of a single median and an associated lateral component, and all of them were obviously strongly articulating with each other, as the lateral components show small grooves in which the outer portion of the median component must have fitted. A certain degree of overlap may have also occurred between the recurved lateral most parts of the neighbouring composite elements. Thus, *Endennasaurus* obviously possessed a very rigid gastral basket.

3.4.2.2. Pectoral girdle (fig. 42)

The following elements of the shoulder girdle are present in the holotype specimen of *Endennasaurus*: Clavicles, interclavicle, scapula, and coracoid. Especially the last two bones appear to be very massively developed and together they form a broad plate. All elements are only ventrally (laterally) exposed and not very well preserved.

Clavicle

The clavicles are small, elongated, and dorsolaterally recurved bones situated anteriorly to the interclavicle. The medial portion is extremely slender and terminates in a sharp tip, while more laterally, the bone becomes somewhat expanded. The dorsolateral part of the clavicle is not preserved any more.

Interclavicle

The interclavicle is a long and narrow element, whose anterior portion is distinctly expanded and of an arrow-like shape with broadly extended lateral shanks. The craniolateral margins are articulating with the clavicles. Posteriorly to this, the interclavicle presents an elongated caudal projection that is almost five times as long as the anterior expansion. The projection posteriorly terminates in a slightly tapered tip.

Coracoid

The prominent coracoid is a long and broad element that participates in the posteroventral formation of the glenoid for the articulation with the humerus. The medial margin is irregularly preserved, indicating that the cartilage was attached there. However, it seems that the edge ran relatively straight in a posterior direction and then turned laterally, resulting in a rounded posterior coracoid margin. The lateral margin of the coracoid has a slightly irregular outline as well, but generally it trends anterolaterally and finally forms the half-rounded posterior emargination of the glenoid. Close to the glenoid, the small coracoid foramen is situated. The border to the scapula is relatively straight and runs obliquely in an anteromedial direction. On neither side, the coracoid is displaced from the scapula, suggesting

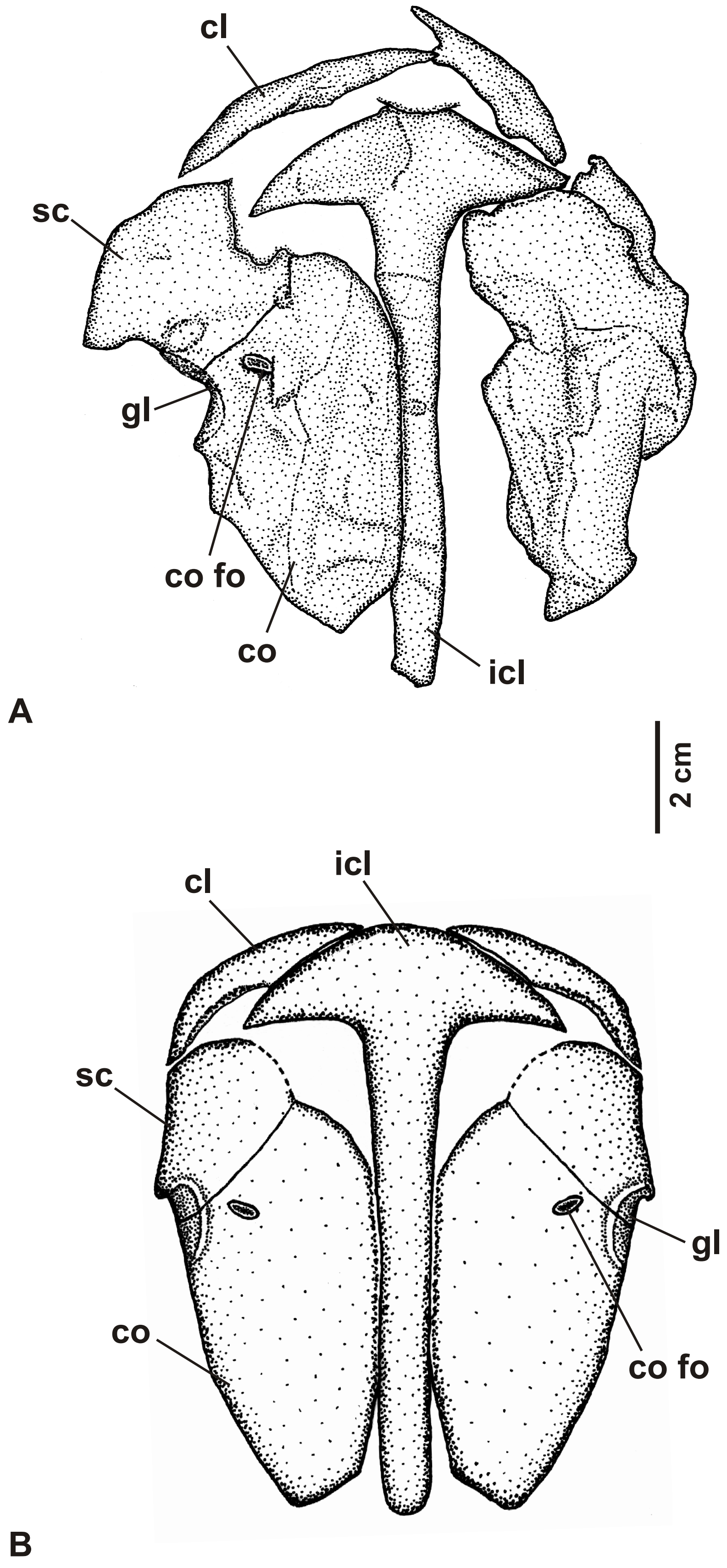


Fig. 42: *Endennasaurus acutirostris*, shoulder girdle. A) pectoral elements in ventral view (MBSN 5170), B) restoration of the shoulder girdle in ventral view.

that the contact between these two elements was relatively strong.

Scapula

The broad, plate-like scapula appears to be distinctly smaller than the coracoid. It forms the anterior half of the glenoid, the outline of the respective emargination being again half-rounded. The anterior margin of the scapula is clearly convex, while the medial margin is not well enough preserved for a consistent description.

3.4.2.3. Forelimb (fig. 43)

The holotype specimen of *Endennasaurus* has both forelimbs still preserved, but unfortunately only in ventral view.

Humerus (fig. 43A)

The humerus has a length of 50 mm. It is a prominent, elongated, and relatively massive element, being almost as long as the remaining extremity. Proximal and distal head of the humerus are distorted to one another in angle of surely more than 20°, and the shaft is relatively massive and not very slender. The proximal head was seemingly broad in cross-section, but exposes only its ventral edge, thus it is not possible to describe its complete outline. Anyhow, the proximal margin obviously formed a prominent dorsal projection, and then sloped slightly into ventrolateral direction. It turns into a distinct ventral edge that shows a prominent curvature, representing the attachment site for the pectoralis muscle (sensu ROMER 1956). This curvature extends along the ventral side of the humeral shaft, forms almost a sharp crest in its mid portion, and smoothly diminishes at the base of the distal expansion of the bone. The distal head presents a rather convex and rugose margin, thus there appears no clear differentiation in ectepicondyle and entepicondyle. Traces of a small ectepicondylar groove can be detected close to the posterodistal margin of the bone.

Radius and ulna (fig. 43A)

Both elements are distinctly shorter than the humerus, each having a length of 27 mm.

The radius is an elongated, cylindrical, and only very slightly recurved bone which is clearly longer than the ulna. Proximal and distal head are expanded and of almost the same rounded outline and size. The shaft of the bone appears to be slightly thicker in comparison to the flattened heads and shows no significant structures on its surface.

The ulna is a stout and cylindrical bone that is only slightly recurved as well. Proximally, it presents an expanded head with a modest dorsolateral projection of rounded outline, being obviously the remaining part of the reduced olecranon. The shaft of the bone is not very tapered and turns finally into the expanded distal head of rounded shape. Further

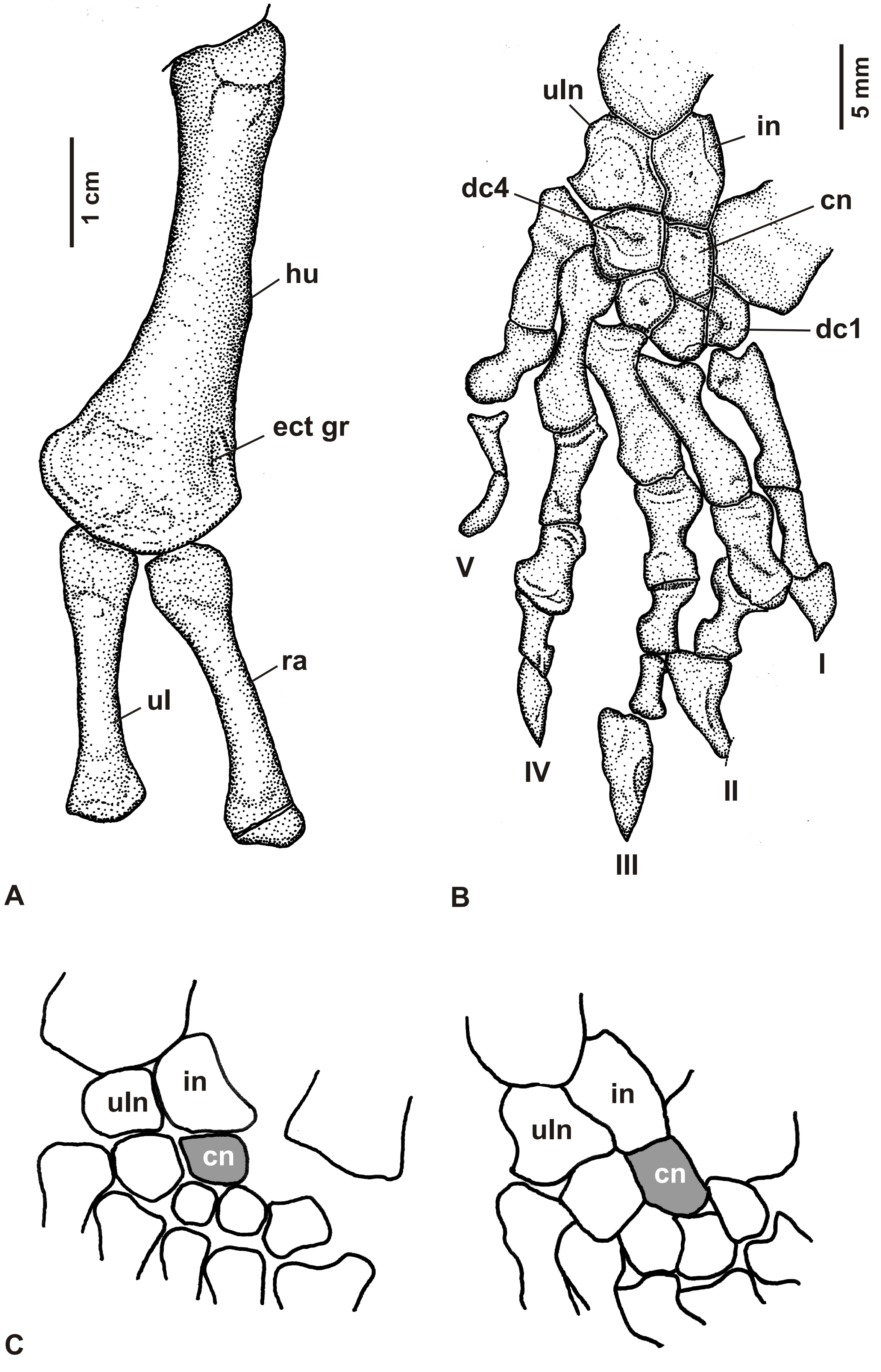


Fig. 43: *Endennasaurus acutirostris*, forelimb (MBSN 5170). A) right stylo- and zeugopodium in ventral view, B) left manus, C) schematic drawings of the carpus of *Askeptosaurus* (PIMUZ T 4846, left) and *Endennasaurus* (right) to show the topological identity of the elements here interpreted as centralia (not to scale).

notable structures are not present.

The manus (fig. 43B, C)

The carpus consists of seven elements: ulnare, intermedium, centrale, and distal carpals 1-4.

The ulnare is the largest of the carpal bones. It has a polygonal outline, whereas the lateral margin is concave and the medial edge convex. The ulnare proximally articulates with ulna and intermedium, distally it meets distal carpal 4.

The intermedium is almost as prominent as the ulnare, slightly longer, but not that expanded. It has the shape of a rounded rectangular and proximally articulates with the ulna, while it distally meets ulnare, centrale, and possibly distal carpal 4.

The centrale has a slight trapezoid shape and is only half as large as the ulnare. It proximally meets radius, intermedium, and distal carpal 1, and distally it articulates with distal carpals 2-4. Due to the close association with the radius, one may alternatively consider the centrale to be a radiale, but a comparison with a well-ossified specimen of *Askeptosaurus*, where the preserved manus is not that compressed, shows a similar carpal configuration but with a definite centrale that is widely separated from the radius (fig. 43C). Hence, the view that in *Endennasaurus* the element in question also is the centrale appears to be more likely in my opinion. A different interpretation may be caused by a misleading impression due to taphonomy.

The series of the distal carpals show a slight increase in size. Distal carpal 1 appears to be the smallest, distal carpals 2 and 3 are somewhat larger, and distal carpal 4 is the most prominent element. Distal carpal 1 and 3 are rounded, while the remaining two are of polygonal shape. Distally, they all articulate with the respective metacarpals, whereas distal carpal 4 also meets the 5th metacarpal.

The five elements of the metacarpus are not of the same size either. Metacarpals 1 and 5 are slightly smaller than the remaining ones. The shape, however, is relatively similar in showing expanded proximal and distal heads connected by a massive shaft.

For the first time, the complete phalangeal formula can be given for the manus of *Endennasaurus*: 2-3-4-4-3. The terminal phalange is always developed as a claw, the rest consists of short and stout elements with the subterminal phalanges being slightly smaller than the others.

3.4.2.4. Pelvic girdle (fig. 44)

The pelvic girdle consists of the usual elements ilium, ischium, and pubis. Additional bones, e.g. a praepubis, are not developed. All respective elements are only laterally (ventrally) exposed.

Ilium

The ilium forms the dorsal third of the pelvis and almost completely the acetabulum for the articulation with the femur. The latter structure comprises the complete proximal (ventral) portion of the bone and consists of a distinct rhomboedrical depression. The straight anteroventral and posteroventral edges of the ilium meet pubis and ischium. Dorsally to the acetabulum, the bone tapers distinctly and presents a notable posterior recurvation of the mid and distal portion. The bone becomes also slightly thicker, only the distalmost part flattens again and shows a broad termination without any tapering. This region also presents a distinct striation on the surface, possibly for the contact of the caudifemoralis muscle. There is no sign of any additional anterior process, i.e. a preacetabular spine.

Ischium

The ischium is an expanded and relatively flattened element. The dorsal margin slopes slightly anteroventrally and meets the ilium. Close to the dorsal border, the ischium presents a distinct edge that represents the posteroventral margin of the acetabulum. At the anterior corner of the dorsal margin, the termination of the ischium turns ventrally and meets the pubis along this extension. However, there is no complete pubo-ischiadic contact, but the anterior edge runs slightly concavely in a ventral direction, thus producing a small fenestra in the central region between the two bones. Ventrally, the bones again meet each other (fig. 44A). RENESTO (1992) restored the pelvis without a ventral contact, but the preserved pelvic elements of *Endennasaurus* are not disarticulated and therefore clearly demonstrate that there was an original contact in this area (fig. 44B, C). The ventromedial border of the ischium has a convex shape and shows a rugose edge, indicating that the contact between the two ischia was of cartilaginous nature. The posterior margin of the bone runs anterodorsally in the ventral area, but presents a prominent caudal projection in the central portion. This process is

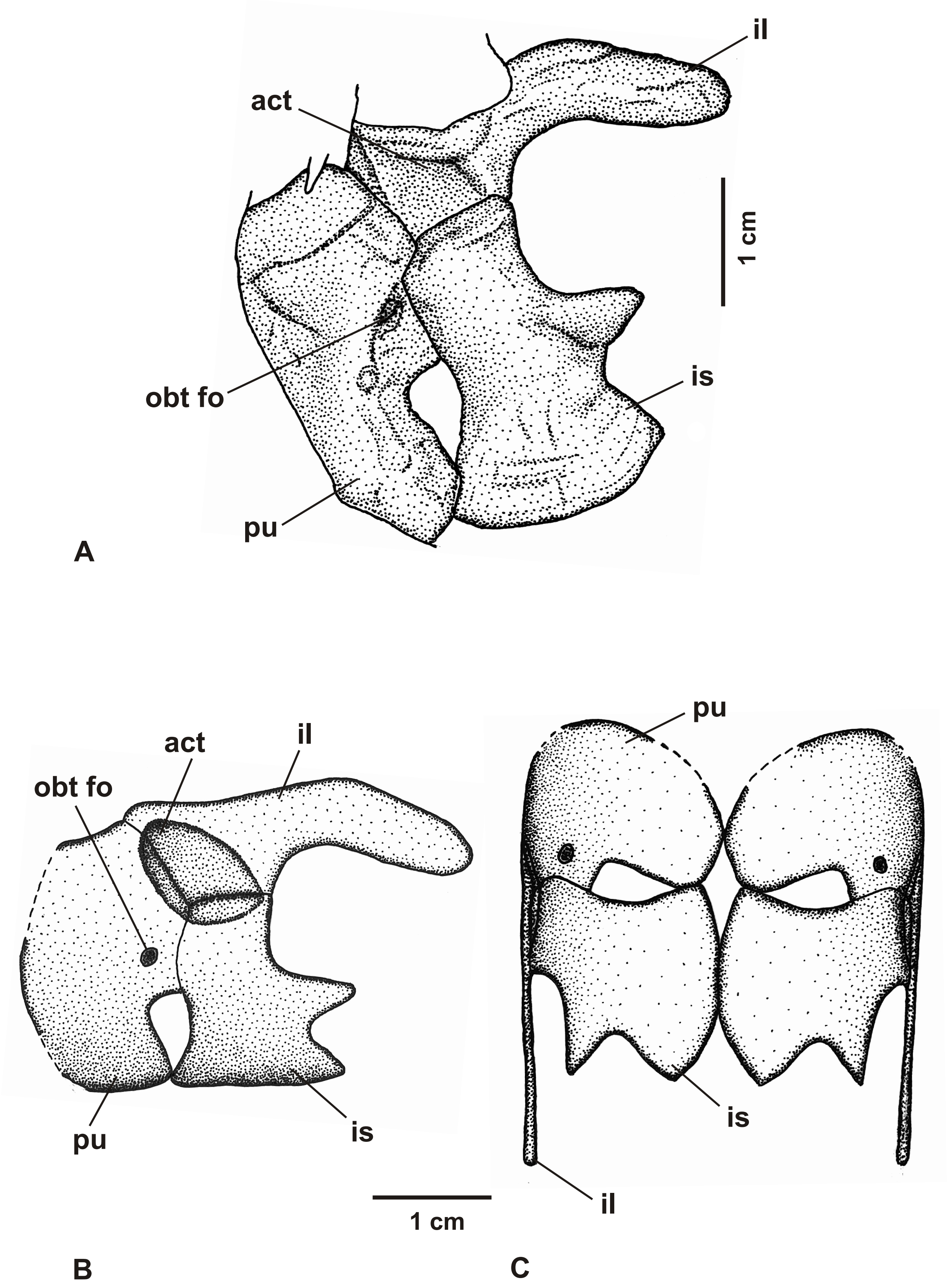


Fig. 44: *Endennasaurus acutirostris*, pelvis. A) left pelvis in lateral view (MBSN 5170), B) restoration of pelvis in lateral view, C) restoration of pelvis in ventral view.

of triangular shape and presents a sharp distal tip. The proximal base of its dorsal edge turns into the dorsal portion of the posterior margin, which is relatively straight. The lateral surface of the ischium presents a fan-shaped striation as well as a rounded knob in the posterior region of the central part.

Pubis

The pubis represents the anteroventral third of the pelvis and is a prominent broad plate. Its posterodorsal margin meets the ilium in the dorsal two thirds of its extension, thereby forming the anteroventral border of the acetabulum, while the remaining portion contacts the ischium. More posteroventrally, the bone presents a slight emargination, corresponding to the concave anterior margin of the ischium, and meets the latter bone again at the posteroventral corner (see above). The anterior margin is convexly formed and runs anteroventrally. Unfortunately, this region, as well as the ventromedial edge, are mostly covered by bones (fig. 44A), making a description difficult. It seems, however, as if the ventromedial margin was relatively straight. The small, elliptic obturator foramen is located in the posterodorsal part, close to the contact with the ischium.

3.4.2.5. Hindlimb (fig. 45)

As the forelimb, the hindlimb is mostly preserved in ventral view, only the paratype also exposes the posterior side of the femur.

Femur (fig. 45A, B)

The femur of the holotype has a length of 58 mm, the one of the paratype 56 mm. The bone is a very elongated and slightly sigmoidally recurved element, being almost twice as long as tibia and fibula. Proximal and distal head are somewhat distorted to one another, but not as strong as in the humerus. The proximal head has a roughly rectangular outline. At the level where the head turns into the shaft, the ventral surface presents a distinct process of irregular structure, which continues as a distinct curvature onto the posteroventral surface of the shaft. This process most probably represents the fourth trochanter. From a posterior view, it becomes evident that the fourth trochanter consists of a notable caudal projection that is of a spoon-like shape. Proximomedially to the trochanter, the femur head shows a depression that can be interpreted as the intertrochanteric fossa (sensu ROMER 1956). With the exception of the aforementioned curvature, the surface of the massive shaft does not show further significant structures. The distal head has a relatively straight and somewhat rugose distal edge, indicating that cartilage was possibly present there. The complete outline of the head resembles that of its proximal counterpart. There is no clear differentiation into separate articular surfaces for tibia and fibula. A slight depression in the central area of the distal head may be interpreted as the popliteal space.

Tibia and fibula (fig. 45A)

Both elements are equal in size, having a length of 31 mm.

The tibia is a massive element with a greatly expanded proximal head. The head has a rounded, trapezoid outline and a relatively straight proximal edge. Obviously it was also relatively thick and probably triangular in cross-section. The shaft of the tibia is distinctly tapered in comparison to the proximal end and broadens distally to only a minor extent. The distal edge is very straight and rugose.

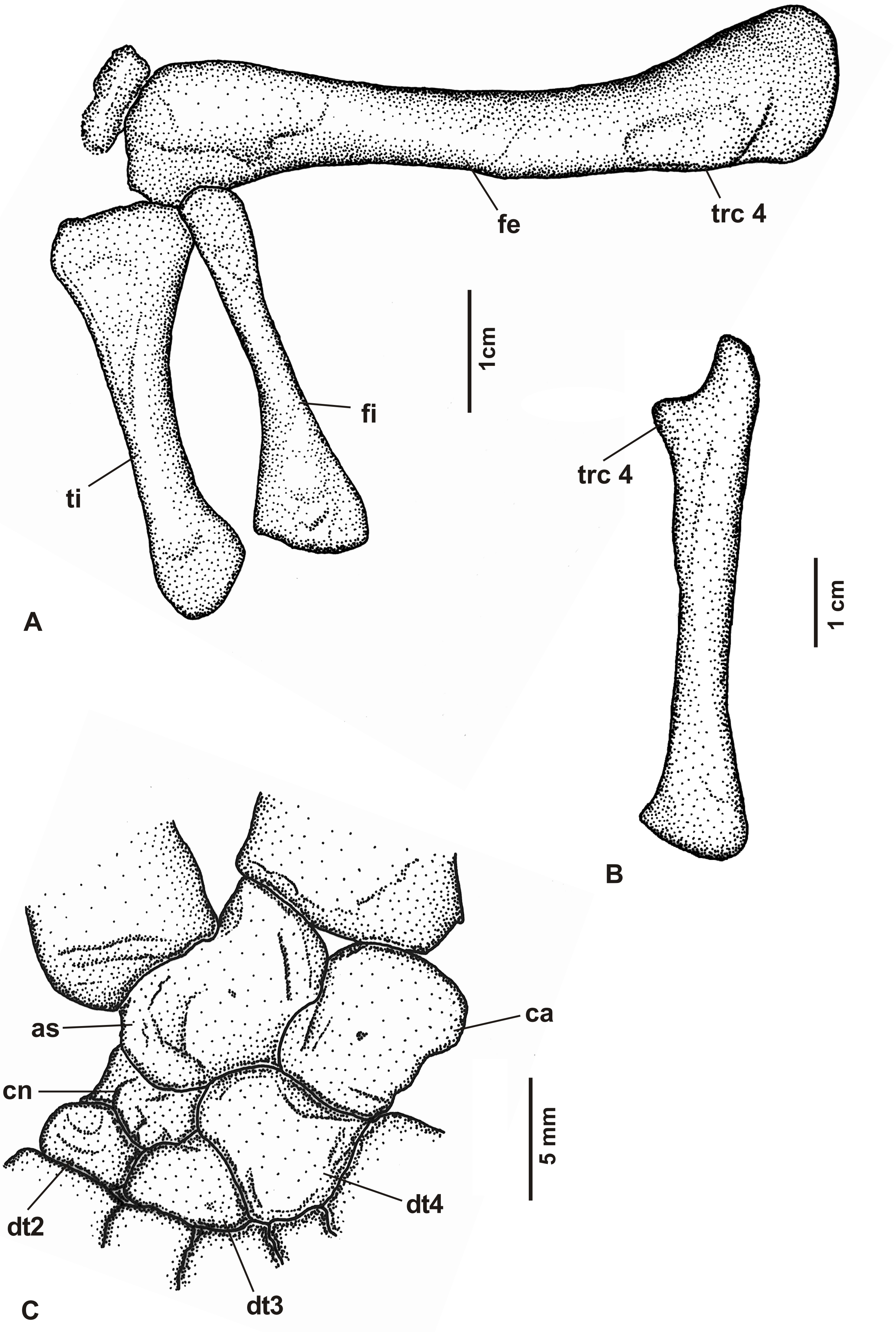


Fig. 45: *Endennasaurus acutirostris*, hindlimb. A) right stylo- zeugopodium in ventral view (MBSN 5170), B) right femur in posterior view (MBSN 27), C) right tarsus (MBSN 5170).

The fibula is as long as the tibia and presents a very narrow proximal head which is almost as slender as the shaft. On the contrary, the distal portion of the bone is greatly expanded, having a conspicuous rounded head which is twice as broad as the remaining bone. The shaft of the fibula presents a small curvature along its complete extension.

The pes (fig. 45C)

The tarsus of the pes consists of the following elements: astragalus, calcaneum, centrale, and distal tarsals 2, 3, 4.

The astragalus is the largest element of the tarsal bones. It is of kidney-like shape and meets the tibia with its concave proximolateral edge, while the straight proximomedial margin articulates with the fibula. Distomedially, the astragalus meets the calcaneum, and there is obviously no foramen for the perforating artery. Distolaterally, the astragalus articulates with distal tarsal 4 and with the centrale.

The calcaneum has the shape of a slightly rounded rectangular and reaches about two thirds of the size of the astragalus. It articulates with the fibula proximally, medially with the astragalus and distally with distal tarsal 4.

The centrale is a very small and elongated element. It meets the astragalus at its proximal edge, distal tarsal 4 medially, and the remaining distal tarsals distally.

All the three distal tarsals are of irregularly rounded shape and show a significant increase in size. Distal tarsal 2 is the smallest, distal tarsal 3 slightly larger, and distal tarsal 4 about twice as large as the others. Next to the aforementioned proximal articulations, distal tarsal 2 contacts metatarsal 1 distally, distal tarsal 3 meets metatarsals 2 and 3, and the 4th distal tarsal articulates with metatarsals 4 and 5.

In the metatarsal series, a significant difference in shape and size can be recognized. So metatarsals 1 and 5 are distinctly shorter and stouter than the remaining ones, the latter having clearly expanded heads, slender shafts, and are of almost the same length. Metatarsal 5 is of the stoutest appearance and has a very broad proximal head.

The phalangeal formula of the pes is 2-3-4-5-4. The shape of the phalanges is similar to that described for the manus.

3.4.3. The status of *Endennasaurus*

The new results clearly show that *Endennasaurus* is a thalattosaur, as the taxon has all the striking features typical for this group, such as the elongated premaxillae that meet the frontal(s), the prominent anterolateral and posterolateral extent of the frontal(s), the reduction of the upper temporal fenestra, the retracted nares, and the strongly posteriorly recurved ilium.

There are, however, also some significant differences that may be regarded as autapomorphies of the taxon. In the skull, one of the most significant features is the absence of any teeth. Furthermore, the preserved temporal area suggests that the lower temporal bar perhaps was closed, since the jugal extends far posteriorly and shows no trace of any tapering, contrary to other thalattosaurs. In the postcranium, it is notable that there is a certain degree of pachyostosis both in the vertebral column and in the ribs. Another prominent feature is the rigid gastral basket. A possible retaining of ancestral terrestrial traits is the strong ossification of carpus and tarsus, the relatively long limbs in relation to the trunk, and the massive pectoral plate formed by scapula and coracoid.

Within thalattosaurs, *Endennasaurus* shows the closest resemblances to askeptosaurids. Both taxa have an elongated neck with more than 10 cervical vertebrae and well-developed atlantal ribs, and manus and pes are still relatively well ossified. Furthermore, the skull proportions are also roughly similar, most other thalattosaurs have a comparatively shorter antorbital portion. Unfortunately, the configuration of the upper temporal fenestra cannot be definitely established for *Endennasaurus*, but a slit-like opening is indicated, which would then be another similarity.

Differences mainly include the specific peculiarities cited above, but also the lack of an additional process on the cervical ribs. This process is definitely present both in *Askeptosaurus* and in *Hescheleria* (RIEPPEL 1987, pers. obs.), while preservation does not allow, in my opinion, a precise statement for *Clarazia*, although RIEPPEL (1987) notes that the process would lack in the latter form.

A further possible difference to *Askeptosaurus* can be found in the tarsus. So it seems that there is no distal tarsal 1 in *Endennasaurus*, and moreover, there is no foramen or indentation between astragalus and calcaneum that would indicate a passage for the pedal artery. Unfortunately, the pes of other thalattosaurs is not sufficiently known, hampering a wider comparison.

Finally, the pelvis also appears to be different in being slightly emarginated in the central area of the pubo-ischiadic plate rather than in the ventral most portion. Anyhow, the thalattosaur status of *Endennasaurus* seems out of debate, and the phylogenetic analyses (chapters 4.1 & 4.2) will provide more detailed information.

The supposed autecology of *Endennasaurus* will be discussed in chapter 4.3.4.

3.5. Postcranial remains of a deep-tailed thalattosaur from the Upper Triassic of Austria

In the collection of the Staatliches Museum für Naturkunde Stuttgart, a plate with parts of the postcranium of a small marine reptile is housed (SMNS uncatalog.), coming from Norian deposits ("Kössener Schichten") of Gaissau near Salzburg, Austria. As will be shown in the following (see the discussion), these remains belong to a small thalattosaur and deserve special consideration due to its aberrant morphology relative to other European thalattosaurs.

Eureptilia OLSON 1847
Diapsida OSBORN 1903
Thalattosauriformes NICHOLLS 1999

Thalattosauria indet.

Material: 1 specimen (SMNS uncatalog.), displaying parts of the trunk, the limbs, and the tail (fig. 46).

Locality and horizon: Kössener Schichten (Norian) of Gaissau near Salzburg, Austria.

3.5.1. Anatomical description

Vertebrae

At least 25 true caudal vertebrae are preserved. They are all of almost the same size with an average height of 50 mm (measured from the distal tip of the neural spine to the distal end of the haemal arch) and of deeply amphicoelous morphology, but obviously not notochordal, which is at least indicated by the few anteriorly and posteriorly exposed elements. The centra are clearly higher than long, roughly elliptic in cross-section, and with slightly thickened anterior and posterior margins. In the ventrolateral portion, the centra present distinct transverse processes. These are relatively long and flat, but unfortunately broken away in most cases. The ventral portion of the centra shows two crests for the attachment of the haemal spines (chevrons), being divided by a depression that even affects

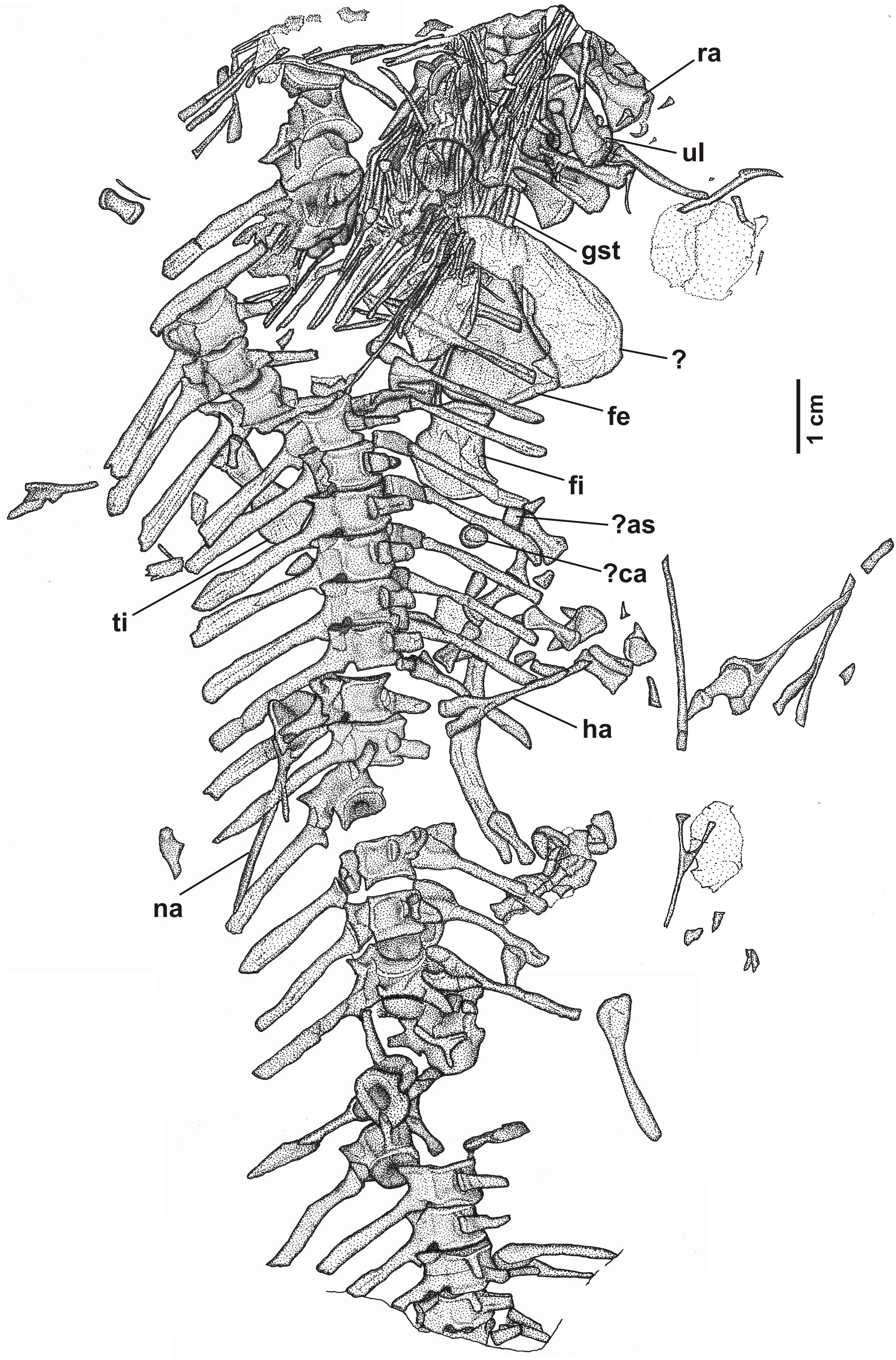


Fig. 46: The postcranium of a deep-tailed thalattosaur (SMNS uncatalog.) from the Kössener Schichten near Salzburg, Austria, preserved in lateral view.

the anterior and posterior edges of the centrum, so that in anterior view, for example, the centrum is ventrally slightly emarginated.

The slender and high neural arch is often completely fused to the centrum, but there are also several cases in which a neurocentral suture can be observed. The alignment of the suture is somewhat undulating, but generally very straight. Due to an emargination at the posterior edge of the arch, the base of the neural arch is slightly shorter than the length of the centrum. In posterior view, the main body of the neural arch is of triangular outline. Unfortunately, preservation renders it difficult to describe the way in which the neural canal was developed. It seems, however, that the canal was relatively broad and filled most the neural arch “triangle“. Pre- and postzygapophyes are extremely short and sharp. The prezygapophysis is strongly dorsally directed, its anteroventral margin being straight to slightly concave in lateral view. It does practically not reach beyond the anterior level of the centrum. The postzygapophysis is smaller than its anterior counterpart and more or less caudally directed. Its proximal base lies at the top of the neural arch “triangle“ and turns directly into the posteroventral edge of the neural spine. The latter is extremely high, slender, and strongly posterodorsally directed. Its distal half is often more expanded than the proximal portion, and the upper termination is of subangular outline. In many cases, a significant striation can be recognized on the lateral side of the spine.

In lateral view, the haemal arches are very similar to the neural spines. They correspond in length, width, and direction, and only the proximal base appears to be expanded. In anterior view, one can see that the two proximal shanks attaching to the centrum fuse relatively early, so that most of the chevron is formed by a single, flat rod of bone. In some cases, the points for the attachment to the centrum are somewhat thickened.

The forelimb

Of the forelimb, only the zeugopodial elements are preserved.

Radius

The radius, whose complete length is 15 mm, is of a very exceptional morphology. Generally, it is of broadened appearance due to a prominent lateral expansion extending along the complete external margin, the outermost part of which is unfortunately broken away. The expanded area is very thin in comparison to the remaining body of the bone. The proximal head of the radius is slightly expanded, as is the distal head to an even greater extent, the latter showing furthermore a slightly convex articulation surface with an indication of a small edge in the median area. The shaft itself is massive, thick, and with its medial margin being somewhat concave due to a strong constriction in the central area of the shaft. If the thin lateral expansion were not present, the radius would have a distinct hour-glass shape.

Ulna

The ulna has a length of 12 mm and is a straight bone of thickened appearance. The proximal head is roughly rectangular, the distal head, which is also somewhat larger, shows a slightly flattened, medial broadening that turns into proximomedial direction. The body of the shaft is almost as broad as the proximal head, and both its lateral and medial margins are not constricted.

The hindlimb and pes

Most of the the hindlimb elements are still present, although the proximalmost portion of the femur as well as parts of the phalangeal elements are not completely observable.

Femur

The femur is a long and prominent element, which was seemingly very flat. Its proximal portion is covered by other bones. Distally, the femur is greatly expanded and shows a convex, slightly thickened distal margin without any further differentiation. The exposed surface of the bone presents several proximodistally directed striations.

Tibia

The tibia is dislocated in the specimen, being situated on the opposite side of the vertebral column. It has a length of 15 mm and is generally relatively flat. The proximal head is slightly covered by a neural spine, but it does not appear to be much broader than the shaft. Both lateral and medial margins of the tibia are concave and turn into the expanded distal region of the bone, being, due to the convex distal margin, of half-rounded outline, whereas the alignment of the medial portion of the distal margin is straighter. The laterodistal edge of the bone is rounded, while its mediodistal counterpart presents a sharp corner.

Fibula

The fibula has a length of 13 mm and is a stout, flat, and extremely expanded element, so that, if there were not the articulation with the femur, it may superficially be confused with a part of the pectoral or pelvic girdle. Its proximal edge is only slightly convex and relatively straight. The margins of the shaft, however, are clearly concave in their alignment. The medial edge is distinctly more elongated, while the extension of the lateral edge is relatively short. The ventral portion of the latter already turns into the greatly expanded distal "head" of the fibula, being distinctly larger than the proximal area. The distal margin is notably convex, giving the whole ventral region of the fibula an almost half-rounded appearance, whereas its lateral portion is distinctly more recurved.

The pes

Due to the disarticulated preservation of the pes, it is difficult to determine its exact morphology or the definite number of tarsal and digital elements, respectively.

Anyhow, there are two bones situated close to the distal margin of the fibula. Due to topological grounds they can presumably be considered as astragalus and calcaneum. Given the correctness of this interpretation, the lateral element would then represent the astragalus, which is of rounded outline, and the medial bone could be considered as calcaneum, which is slightly smaller and of rectangular shape. Whether there were originally more ossified elements in the tarsus, is almost impossible to determine.

There is one relatively massive, stout element with expanded heads, situated directly next to the astragalus, which will be here considered as one of the metatarsals. The more expanded head of the bone lies ?distally, i.e. not at the contact to the astragalus. The remaining digital elements preserved close to the tarsus are more elongate and with slightly expanded heads as well, but it is not possible to differentiate between metatarsals and phalangeal bones. More "distally", there is one conspicuously broad element of unknown affinity. In the posterior portion of the specimen, badly preserved distal elements of the foot are visible, indicating that at least the subterminal phalangeal bones were distinctly smaller. One comparatively well-preserved ungual element can be detected, being of slightly curved appearance and with a sharp distal tip, the remaining possible unguals are only scarcely preserved.

Gastral ribs

A notable number of gastralia is still present. The elements are very slender and gracile, and for that reason not really well preserved. However, preservation suggests that there were probably two complementary median elements overlapping each other in the central area, accompanied by two lateral elements on each side, but the exact way of articulation must remain unknown.

Unidentifiable elements

Next to the here described bones, there are also several elements where a determination was not possible. So there are two elongated pieces of bone left to the zeugopodium of the forelimb.

The right element is very slender and obviously broken in its central area, leading to the impression as if the bone were distorted. There is only one end visible, being subangular and slightly thickened in comparison to the rest of the bone. The remaining portions of the element are covered by gastralia, making a further description impossible.

The left piece appears to be stouter and thinner, but is unfortunately covered for the most part. Anyhow, one can state that the left margin seems to be recurved so that the bone appears to be slightly concave. Again, only one end is visible, consisting of a slightly convex edge. Close to the covering by the gastralia, the element seems to turn a little upwards, but this may also be the result of possibly underlying bones that are not visible in external view.

3.5.2. The status of the Salzburg thalattosaur

A comparison of the Salzburg specimen with other thalattosaurs suffers, of course, from the fact the Salzburg specimen only displays its posterior postcranial morphology, a region which is by far not always preserved in thalattosaurs.

When compared to *Endennasaurus*, the Salzburg specimen is strictly different. Although both have a well-developed suite of gastral ribs, the tail and the limbs distinctly differ from one another. In *Endennasaurus*, the tail is much lower and the caudal centra are not as short and high as in the Salzburg specimen. Furthermore, *Endennasaurus* presents well-developed transverse processes only in the anteriormost portion of the tail. The limbs of this form are also strictly different, as they are relatively long and slender, and with obviously more tarsal ossifications, although one should keep in mind that the preservation of the tarsal area is very poor in the Salzburg specimen, and it can furthermore not be excluded that it was a young animal with yet incomplete ossification.

The differences of the Salzburg specimen to *Askeptosaurus* also are apparent. The latter has a distinctly lower tail with only a few well-developed transverse processes, and both forelimb and hindblimb elements are of a clearly different morphology. The latter is especially true for the fibula, which is slender in *Askeptosaurus* but broadly expanded in the Salzburg specimen. Also, preservation suggests that there were fewer tarsal elements than in the former so that the overall morphology contradicts a possibly closer relationship to *Askeptosaurus*.

A comparison with *Clarazia* and *Hescheleria* shows that also in these taxa the tail is much lower than in the Salzburg specimen, and transverse processes are lacking as well. However, both forms present a slight tendency towards an expansion of the limb bones, and also the number of the tarsal elements is reduced relative to the original terrestrial amniote condition. Furthermore, the overall size roughly corresponds to that of the Salzburg specimen.

As can be seen by this short comparison with the European thalattosaurs, a close relationship does not appear to be present. If at all, the Salzburg specimen seems to be most similar to the small taxa of the Monte San Giorgio area.

Regarding the thalattosaurs from North America, *Thalattosaurus* does not show significant resmblances either, but *Nectosaurus* may be useful for a more detailed comparison, as this taxon interestingly shows an expanded, kidney-shaped radius (NICHOLLS 1999) that is very close to the condition described for the Salzburg specimen. However, the caudal vertebrae assigned to *Nectosaurus* lack again transverse processes, although they also possess very elongated neural spines.

On the basis of this finding, it is intriguing that there in the Chinese thalattosaur *Xinpusaurus suni*, the tail is also relatively deeply developed, even though not as high as in the Salzburg specimen. Unfortunately, the presence or absence of transverse processes in the tail of *Xinpusaurus* can currently not be confirmed. A further possible difference may be the lack of gastral ribs in *Xinpusaurus*, but this determination has to await further well-preserved material. The limb bones, however, are notably similar and almost impossible to distinguish from those of the Salzburg specimen, which accounts both for the forelimb and hindlimb elements. Especially the expanded radius and fibula are of an astonishing similarity, whereas, unfortunately, the tarsal ossifications of *Xinpusaurus* still await a detailed description. Furthermore, their overall size is more or less equal.

Following the above discussion, it is intriguing that the Salzburg specimen has its apparently closest relative in China and not in Europe. It even cannot be excluded that the Salzburg specimen is congeneric with *Xinpusaurus*, whose stratigraphic age is furthermore roughly equivalent with that of the Kössener Schichten. The Salzburg specimen is therefore of a notable biogeographical importance, although too scarcely preserved for a well-corroborated inference of the underlying evolutionary process leading to this diversification and the specialized tail morphology. Nonetheless, the specimen well shows that our information about the diversity and evolution of thalattosaurs is still too poor and has been neglected for a long time, as compared to other marine reptiles of Triassic age.

3.6. The enigmatic aquatic reptile *Blezingeria ichthyospondyla* from the Germanic Triassic

Blezingeria ichthyspondyla from the upper Muschelkalk and lower Lettenkeuper of the Germanic Triassic (especially abundant in the “Grenzbonebed“) has originally been described by FRAAS (1896) as *Nothosaurus ichthyospondylus* on the basis of isolated, badly preserved vertebrae (type material housed in the GPIT). Later, VON HUENE (1951) placed the form into the newly erected genus *Blezingeria*, assuming that it is an ichthyosaur rather than a sauropterygian. In the following decades, *Blezingeria* had been widely neglected in studies on Triassic reptiles, but new material was increasingly collected, including a lot of non-vertebral elements that were questionably referred to this taxon.. In the last years, *Blezingeria* was informally assumed to be a thalattosaur (see e.g. RIEPPEL 1998, SCHOCH & WILD 1999), but until now, no anatomical study was conducted to corroborate this assumption.

In the following, the vertebral morphology of *Blezingeria* will be redescribed. It will only be focussed on this part of the axial skeleton, as all the remaining elements additionally assigned to this taxon either consist of misinterpreted sauropterygian or amphibian material (like, e.g, the mandibular fragments in VON HUENE 1951) or have not been found in close articulation with the vertebrae and thus lack any evidence of relationship. It should be noted that there are two size classes among the material, one consisting of relatively large specimens with a centra length of more than 15 mm (fig. 47), and one of very small size with a length of only 7-8 mm (figs. 48, 49). Specimens of the latter size class are relatively rare and may represent juveniles, therefore, as long as not additional material is known, they will be treated as conspecific.

Blezingeria ichthyospondyla FRAAS 1896

Vertebrae material examined: GPIT/RE 144 & 145 (casts), 1005/1, 1005/3, 1005/5, 1005/6, 1005/9, 1005/10, 1005/11, 1005/12, 1005/13, 1005/14, 1005/15, 1005/17, 1005/18, 1005/24, 1005/25, 1005/26, 1005/27, 1005/28; MMHI 4 uncatalogued specimens; SMNS 9 uncatalogued specimens (3 of them erroneously referred to *Askeptosaurus*), 56859, 58750, 81198, 81197.

Locality and horizon: widely known from the upper Muschelkalk and lower Lettenkeuper of the Germanic Triassic, Germany,

Diagnosis: marine reptile with short, disc-like, amphicoelous centra lacking a notochordal pit, and strongly elongated, slender neural spines; rib articulation facets situated both on the centrum and the neural arch; maximum centrum length at least 25 mm, maximum height of complete vertebra at least 110 mm.

3.6.1. Anatomical description

Generally, the material described by VON HUENE (1951) partly consists of strongly eroded material, making an assignment to a specific region in the vertebral column difficult. The result is, for example, that specimen GPIT/RE 1005/28, a deteriorated vertebra assigned to the cervical region by VON HUENE, has been figured upside down (VON HUENE 1951, fig. 1). Whether it is really a cervical, can currently not be confirmed.

For the most part, only thoracal centra could be found (figs. 47, 48). These are of a distinct morphology and are easy distinguishable from other, contemporaneous Triassic reptiles. They are strictly amphicoelous and always higher than long. In anterior view, the centra have a roughly rounded outline, whereas the dorsal area is slightly flattened and the ventral most portion laterally constricted, especially in the larger specimens. A further constriction can be detected in lateral view, between the anterior and posterior surface, the latter also extending more into ventral direction. The ventrolateral side exposes one small but well-visible foramen on each side. The rib articulation facet originates approximately at the mid-level of the centrum and extends up to the dorsolateral portion. It consists of a drop-shaped expansion with the narrower part situated ventrally. The shape of the attachment site varies, so the lateral expansion is sometimes relatively strong, but in other cases it is extremely reduced and barely visible in anterior view.

The dorsal side of the centrum shows well-visible facets for the attachment of the neural arch (fig. 48A, B). The craniocaudally directed facet is notably broader and of hour-glass shape, whereas the laterally directed one is distinctly thinner and more elongated, with the distal end extending onto the dorsolateral area and being slightly more expanded. It should be noted, however, that the shape of the latter facet is subject to a certain degree of variation, i.e., sometimes this structure is rather a broad depression than a narrow and distinct groove.

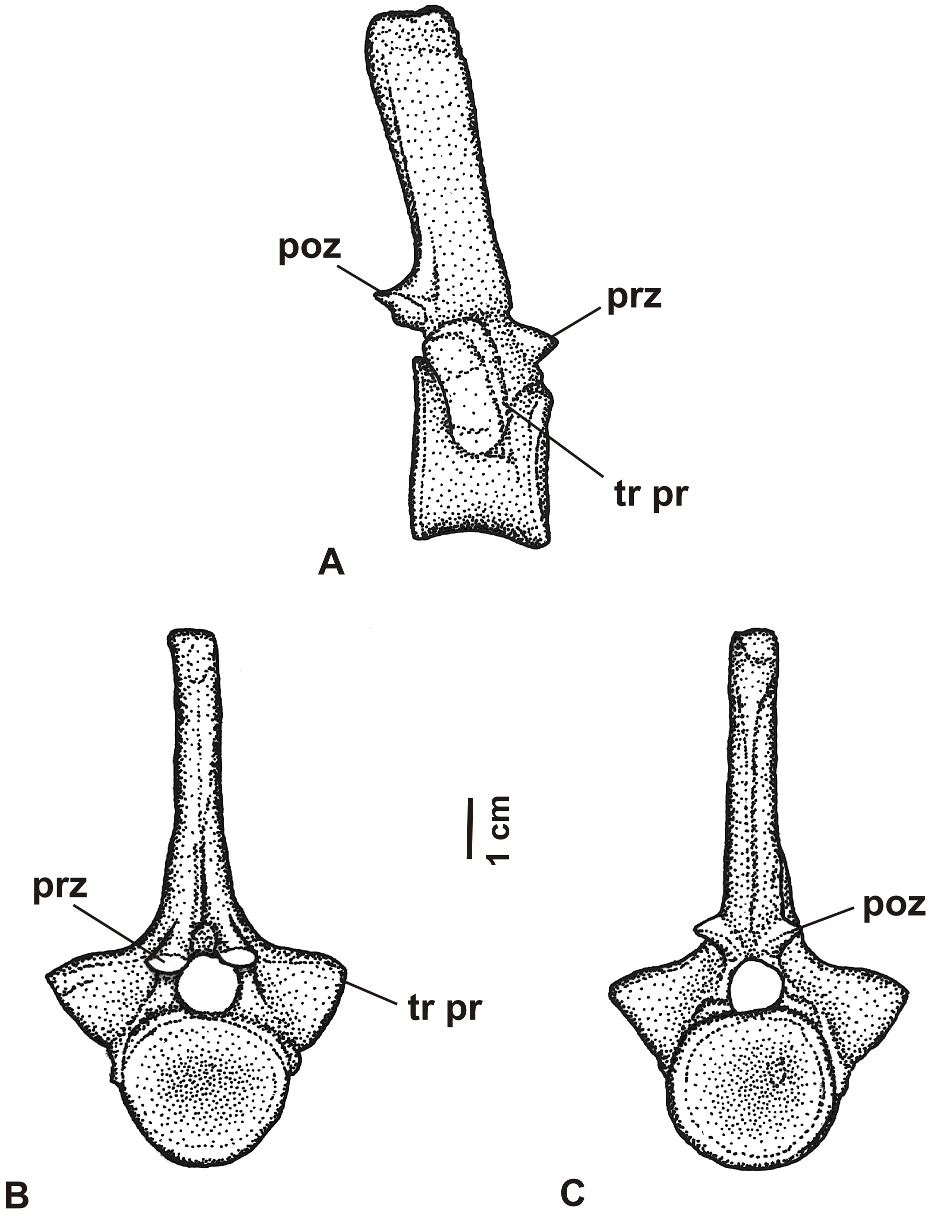


Fig. 47: *Blezingeria ichthyospondyla,* large thoracal vertebra (SMNS 81198). A) lateral, B) anterior, and C) posterior view.

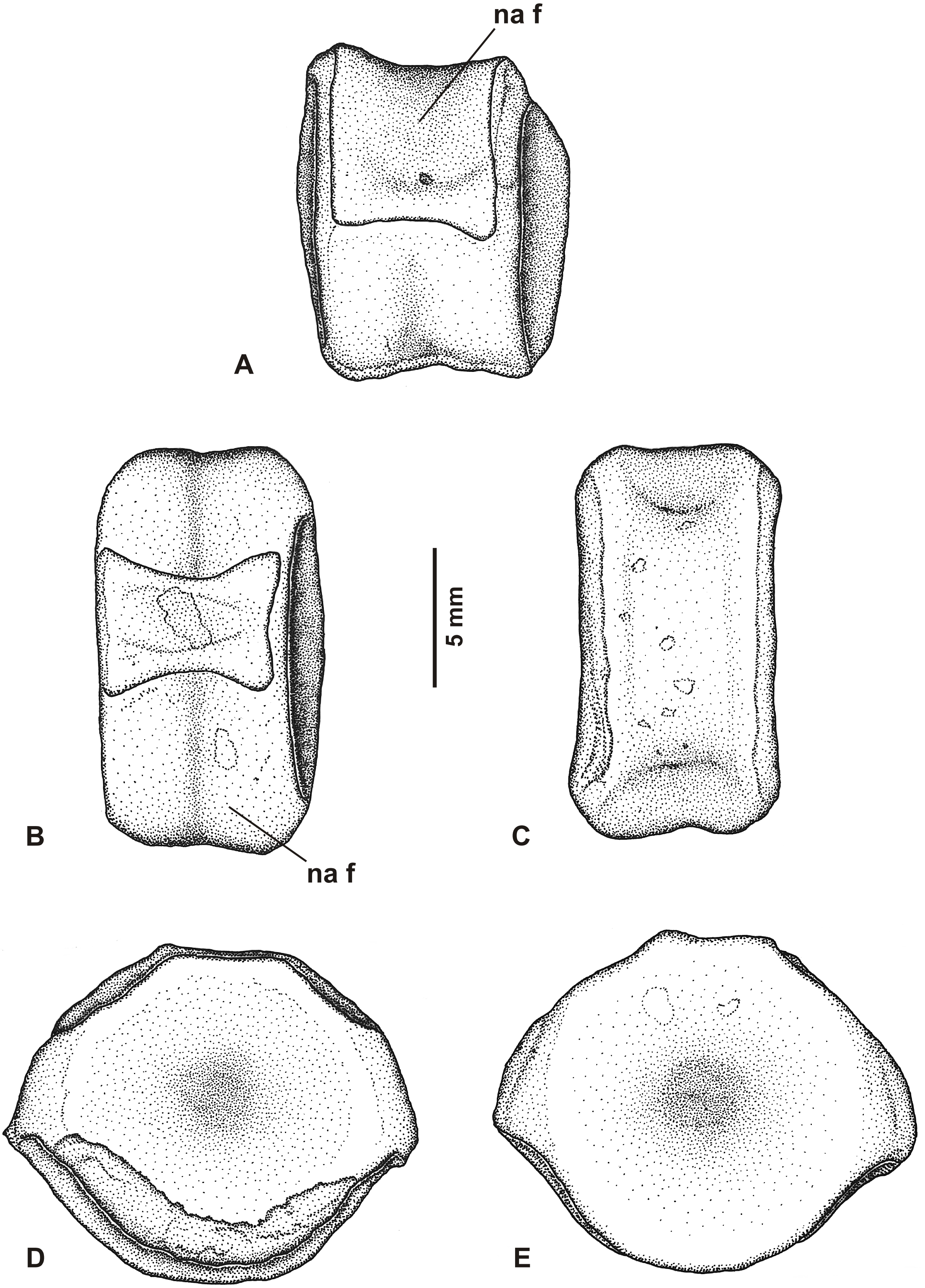


Fig. 48: *Blezingeria ichthyospondyla,* small thoracal centrum (GPIT/RE/145). A) lateral, B) dorsal, C), ventral, D) anterior, and E) posterior view.

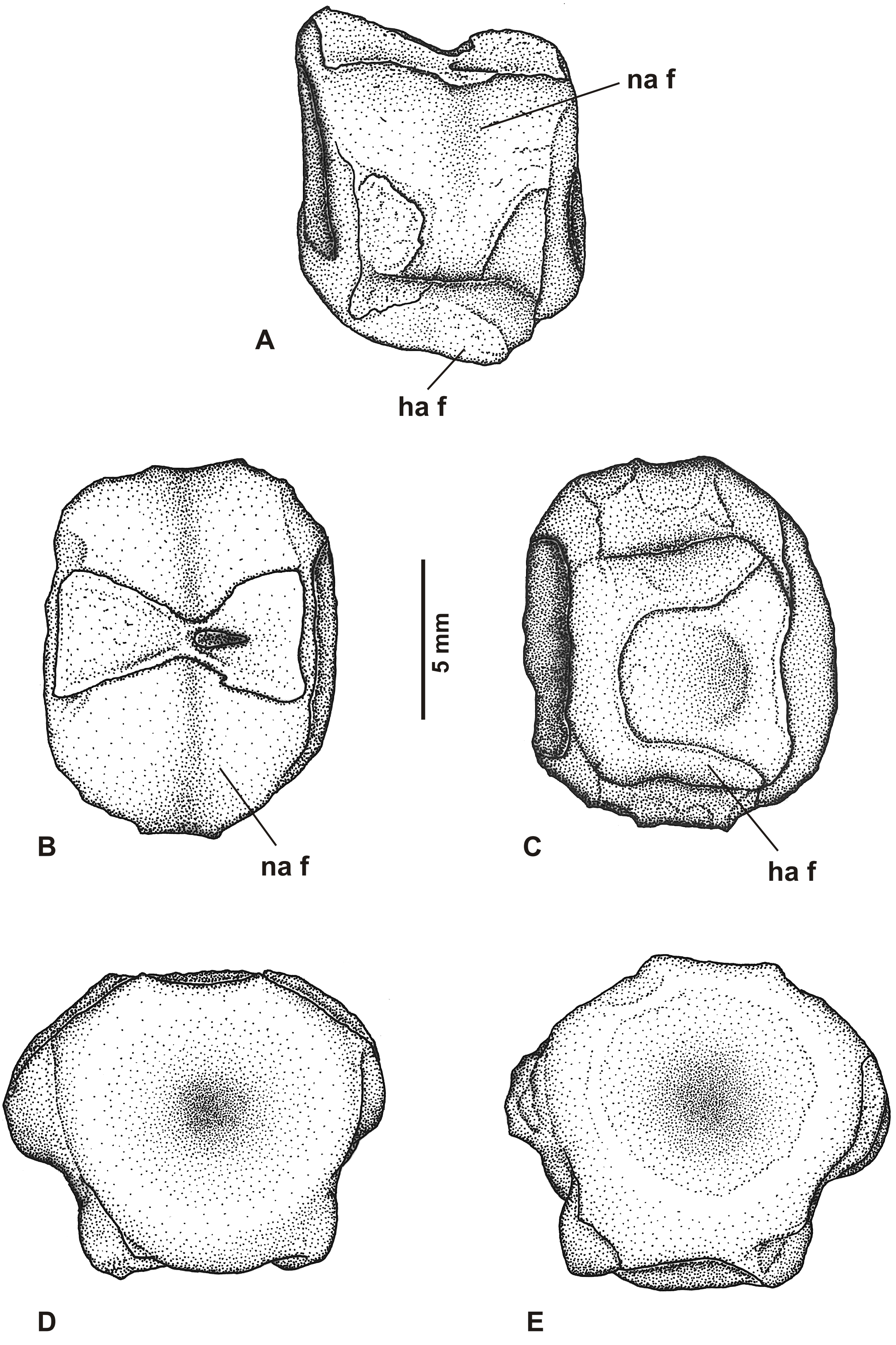


Fig. 49: *Blezingeria ichthyospondyla*, small caudal centrum (GPIT/RE/144). A) lateral, B) dorsal, C) ventral, D) anterior, and E) posterior view.

The facets are surrounded by a crenulated surface of elliptic appearance, but this is only the case if the lateral facet is slender and well-developed.

The neural arch is generally slender and possesses a long and narrow neural spine (fig. 47). The base of the arch surrounds the complete dorsal and dorsolateral area of the centrum. The ventrolateral portion of the arch develops a small transverse process and represents the dorsal part of the rib articulation facet, which comprises at least one half, sometimes even two thirds of the whole articulation surface.

The central portion of the ventral base of the neural arch is pierced by an oval neural canal. Dorsolaterally to this piercing, the prezgygapophyses are visible anteriorly. They are situated very close to one another and project into anterolateral direction. Their dorsal articulation surfaces are smooth and trend slightly ventromedially. The postzygapophyses are situated somewhat dorsally to the level of the prezygapophyses. Their proximal base is thicker, resulting in a more prominent appearance. Corresponding to the ventromedial direction of the dorsal articulation surfaces of the prezygapophyses, the ventral articulation surfaces of the postzygapophyses project ventromedially as well.

The neural spine projects posterodorsally and is slightly laterally constricted. Both anterior and posterior edges present a sharp median keel along their complete extension. On the anterior side, the keel originates from the fusion of two crests lying laterally to an oval depression situated right dorsally to the aforementioned opening. The situation on the posterior side is more or less similar, but there are sometimes additional lateral keels arising from the base of each postzygapophysis. Within both depressions, knob-shaped small expansions are occasionally situated in the central most part of each.

The caudal vertebrae (fig. 49) are principally relatively similar to the thoracals, but sometimes the outline of the centra turns into a more oval alignment, especially in the larger specimens. As in the trunk centra, the dorsal area, on which the neural arch attaches, is still markedly flattened. The ventrolateral side exposes a well-developed, posteroventrally trending oval expansion for the attachment of the chevrons, which are unfortunately not preserved. Since there are no neural arches of the caudal vertebrae currently known, a description of their morphology cannot be conducted.

3.6.2. The status of *Blezingeria*

VON HUENE (1951) suggested that *Blezingeria* should be regarded as an ichthyosaur. His opinion was obviously due to the high and relatively short centra, leading to the superficial impression of an ichthyosaurian centrum. However, the centra of *Blezingeria* strongly differ from the latter in that the ribs must have articulated not only with the centrum, but also extensively with the neural arch. In ichthyosaurs, rib attachment is restricted to the centrum, the only exception being a few shastasaurs where also the neural arch participates in rib articulation, but even then only to a low extent (MAISCH, pers. comm.). There are furthermore other strong differences like, e.g., the lesser degree of amphicoely in *Blezingeria* or the structure of the dorsal side of the centrum, which both differ from the morphology seen in ichthyosaurs. Hence, an ichthyosaurian affinity can be excluded.

On the other hand, the informal view that *Blezingeria* is a thalattosaur cannot be definitely confirmed either. Certainly, thalattosaurs also share the expansion of the rib attachment site onto the neural arch, and furthermore, the cross-sectional outline of the centra is relatively similar. However, the first feature still has the difference that in *Blezingeria*, the ribs articulate mainly with the neural arch and only slightly with the centrum, which is vice versa in those definite thalattosaurs that also have elongated neural spines, like, e.g., *Thalattosaurus*. The second feature, the outline of the centrum, is equally developed in choristoderes like *Champsosaurus* (pers. obs.), rendering a definite statement problematical. Further differences are that some thalattosaurs either have much broader but lower thoracal neural spines like, e.g., *Askeptosaurus*, or, if the spines are tall, they are still more expanded and straight dorsally directed, as in *Hescheleria* or *Nectosaurus*. Also, at least in some forms like *Endennasaurus*, *Askeptosaurus*, or *Clarazia*, the centra are not as short as in *Blezingeria*. After all, *Thalattosaurus* is the only form that shows a certain degree of closer similarity, at least the overall appearance resembles *Blezingeria* on the first sight. The vertebrae, however, differ from the latter in the more dorsally projecting neural spine as well as in the position of the rib articulation site situated at the anteroventral edge of the vertebra rather than within the central area (see above). So if *Blezingeria* is a thalattosaur, the plesiomorphic, intermediate position of the rib articulation site (see chapter 4.1 for a definition of the respective character) would indicate that it may represent a basal member of the clade.

A possible assignment of *Blezingeria* to thalattosaurs would be mainly based on negative evidence, i.e., because nothing else fits, thalattosaurs are the only group left and therefore the taxon is placed into this assemblage. Such a procedure, however, may be misleading for future research. Furthermore, there are also other marine reptiles of uncertain affinities, e.g. *Helveticosaurus* from Monte San Giorgio (PEYER 1955, RIEPPEL 1989b), which indicates that we are still too poorly informed about Triassic aquatic reptiles. *Blezingeria* may be a thalattosaur, but a definite assignment has to await additional material.

4. Discussion

4.1. Diapsid interrelationships and the phylogenetic position of thalattosaurs

4.1.1. Cladistic analysis

The aim of the following study is not only to evaluate the affinities of thalattosaurs, but also to investigate whether and how some basal diapsid clades which, until now, have only rarely been included in phylogenetic analyses, affect the placement of other, “more important“ clades.

For that reason, several well-understood diapsid taxa were included in the analysis, but also some problematic forms that are usually only considered in more inclusive investigations. Furthermore, clades like prolacertiforms or sauropterygians were split into several single taxa. Turtles and ichthyopterygians, for which a diapsid status is being increasingly accepted (RIEPPEL & REISZ 1999, MOTANI 2000), were also entered in the analysis. In total, the matrix consists of the hypothetical all-0-ancestor and the following 31 taxa, including one non-diapsid taxon: Captorhinidae (mainly on the basis of *Captorhinus*), Araeoscelidia, Rhynchocephalia, Squamata, Kuehneosauridae (mainly on the basis of *Kuehneosaurus*), Drepanosauridae (mainly on the basis of *Drepanosaurus*), Choristodera (see below for details), pachypleurosaurs (on the basis of *Serpianosaurus* and *Neusticosaurus*), *Simosaurus*, Pistosauridae, *Placodus*, *Helveticosaurus*, *Testudines* (mainly on the basis of *Proganochelys*), *Prolacerta*, *Tanystropheus*, *Macrocnemus*, *Trilophosaurus*, Rhynchosauria (see below for details), Archosauriformes (on the basis of early forms like *Protosuchus* or *Euparkeria*), *Askeptosaurus*, *Endennasaurus*, *Clarazia*, *Thalattosaurus*, *Ichthyopterygia* (see below for details), *Coelurosauravus*, *Palaeagama*, *Saurosternon*, *Claudiosaurus*, Younginiformes (mainly on the basis of *Youngina*), *Hupehsuchus*, and *Apsisaurus*.

182 informative characters were used in the analysis. Characters and codings were mainly taken from RIEPPEL (1993c, 1994), RIEPPEL et al. (1999) and DEBRAGA & RIEPPEL (1997), including the corrections performed by RIEPPEL & REISZ (1999). Characters were selected in the interest of informativeness with respect to the taxa included. However, character #27 (frontals parallelogramm-shaped or hour-glass-shaped) of DEBRAGA & RIEPPEL (1997) was ignored because the definition was not considered to be sufficiently well defined,

and furthermore, the coding did not correspond to my personal observations or interpretations with regard to the respective taxa. Also, it was followed MOTANI et al. (1998) in that characters #162 (limbs stout and short, or long and slender) and #163 (manus and pes stout and short, or long and slender) were excluded too, because there is a suite of different ways of how a foot or a limb can be shortened. Moreover, several characters concerning archosauromorph taxa were added from DILKES (1998), and some characters related to thalattosaurs were taken from NICHOLLS (1999). Furthermore, four additional, personally defined characters were also included (#177, skull roof is without (0) or with (1) distinct posterior emargination; #179, prefrontal and maxilla do not meet due to a contact of lacrimal and nasal (0), or prefrontal contacts maxilla and thereby separates lacrimal and nasal from one another (1); #180, nares are positioned anteriorly (0) or are situated in the central or posterior area of the antorbital skull portion (1); #181, lacrimal enters the orbital margin (0), or remains excluded therefrom due to an external contact between the posteroventral part of the prefrontal and the posterodorsal margin of the maxilla (1); #182, quadratojugal remains restricted to the ventral margin of the cheek (0), or shows a distinct dorsal extension (1)).

Generally, several characters were slightly modified or redefined in the interest of informativeness, and it was tried to correct some taxon codings on the basis of personal observations or interpretations. This was done for rhynchosaurs, where the revision of DILKES (1998) was very useful and allowed a recoding in a lot of cases, coupled with a clearing of multistate and therefore uninformative characters due to a strict reference to the two basalmost rhynchosaur taxa *Mesosuchus* and *Howesia*. As a consequence of the splitting of prolacertiforms, the respective taxa were recoded as well, and also the codings of choristoderes were revised on the basis of recent discoveries (GAO et al. 2000). In ichthyosaurs, most characters were taken from MOTANI et al. (1998), whereas in those cases where a coding had not been conducted previously for ichthyosaurs, the decision was made according to the morphology of *Utatsusaurus*, *Grippia*, *Mixosaurus*, or *Cymbospondylus*, which are considered to be relatively basal taxa by several authors (MOTANI 1999a, SANDER 2000, MAISCH & MATZKE 2000). In the remaining cases where a character had previously not been coded for a certain taxon, or where a complete new coding was necessary, the following additional references were taken into consideration (next to personal observations, when possible): BROILI (1912), PEYER (1936 a,b,c, 1955), ROMER (1956), FOX & BOWMAN (1966), CLARK & CARROLL (1973), WILD (1973, 1980), ROBINSON (1973), GOW (1975), CARROLL (1975, 1978, 1981), SIGOGNEAU-RUSSELL (1979), HEATON & REISZ (1980), EVANS (1980, 1982, 1984, 1988), REISZ (1981), REISZ et al. (1984), BENTON (1984, 1985), RIEPPEL (1987, 1989 a,b,c, 2000a), EVANS & HAUBOLD (1987), GAUTHIER et al. (1988 a,b), SANDER (1989 a,b), GAFFNEY (1990), CARROLL & CURRIE (1991), CARROLL & ZHI-MING (1991), LAURIN (1991), BERMAN & REISZ (1992), EVANS & HECHT (1993), RENESTO (1984, 1992, 1994a, b, 2000), RENESTO & PAGANONI (1995), RIEPPEL & WILD (1996), SANDER et al. (1997), GAO & FOX (1998), MOTANI (1999b).

Sometimes it was also necessary to change character polarity, which is particularly important in #53, where the anteroventral position of the clavicles relative to the interclavicle was now coded as plesiomorphic, along with a lot of changes of taxon states where the clavicle position had previously been coded vice versa. Further necessary comments are listed in Appendix II, the complete data matrix is shown in Appendix III. Generally, character polarity was evaluated by using taxa like seymouriamorphs, parareptiles, and synapsids as outgroups.

Using the heuristic search option of PAUP* 4.0b8 (SWOFFORD 2001; all characters unordered and with equal weight, multistate characters interpreted as polymorphism, random stepwise addition, branch swapping (on minimal trees only) affected by tree-bisection-reconnection) under both delayed (DELTRAN) and accelerated (ACCTRAN) character optimization, four equally parsimonious trees were obtained (fig. 50), with a tree length (TL) of 874 steps, a consistency index (CI) of 0.4130, a homoplasy index (HI) of 0.7517, a retention index (RI) of 0.5268, and a rescaled consistency index (RC) of 0.2176. All trees are very similar, lack of resolution only affects the clade comprising *Trilophosaurus, Rhynchosauria*, and Archosauriformes, as well as the relationships between the monophyletic *Askeptosaurus*, *Endennasaurus*, and *Clarazia/Thalattosaurus*.

In the following, each node within diapsids will be described including a listing of all synapomorphies, both those occuring only under ACCTRAN or DELTRAN character optimization and those which are independent of any optimization and therefore “unequivocal“.

Unequivocal synapomorphies diagnosing the Diapsida are the elongation of the preorbital region relative to the postorbital region (#8[1], consistency index of the character (ci) is 0.462), the presence of an upper temporal fenestra (#9[1], ci= 0.3), the presence of a posterolateral process of the frontal (#10[1], ci=0.25), the presence of a suborbital fenestra (#31[1], ci=0.5), the exclusion of the splenial bone from the mandibular symphysis (#37[1],

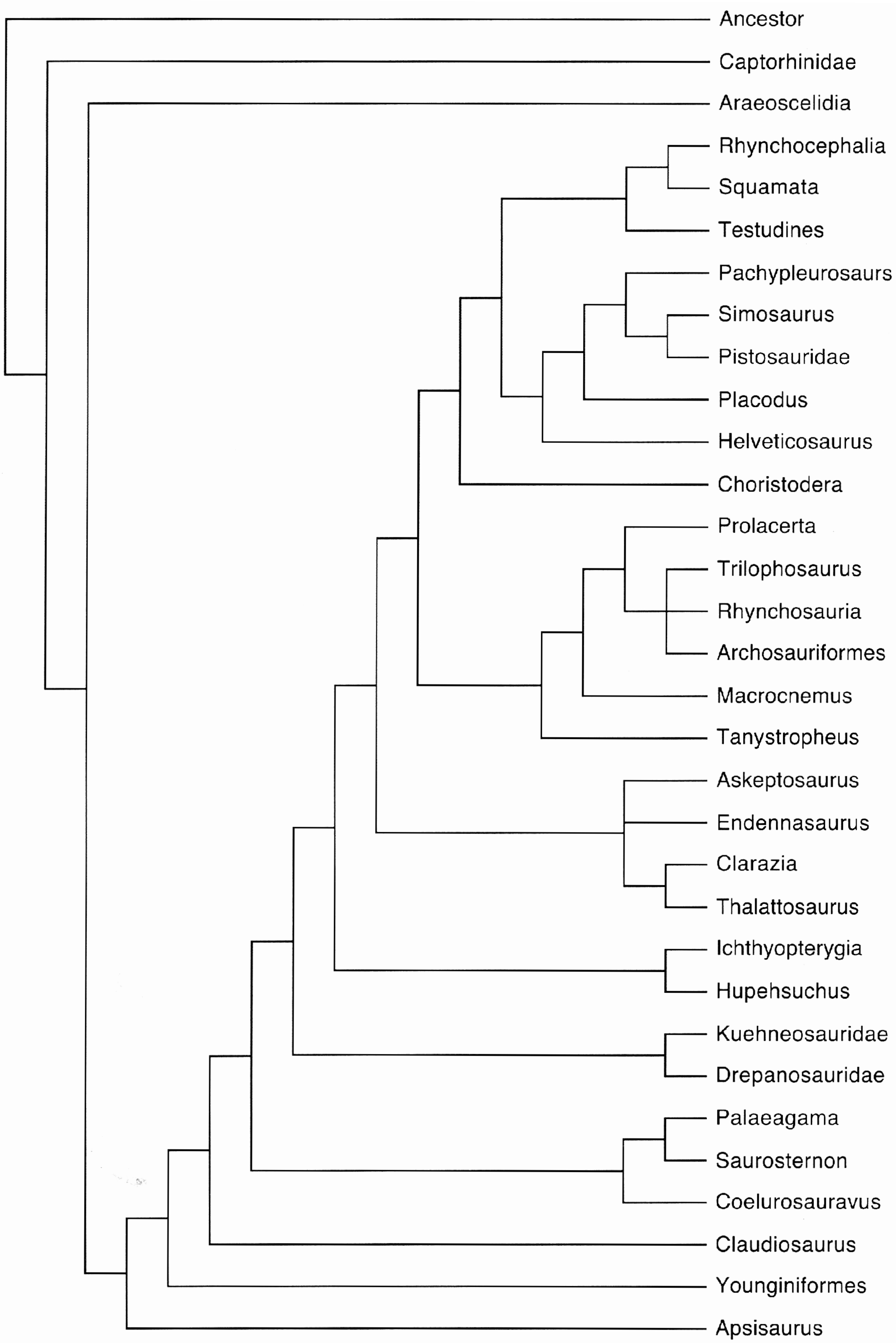


Fig. 50: Strict consensus of 4 equally parsimonious trees showing the relationships of basal diapsid reptiles (874 steps, CI: 0.4130, HI: 0.7517).

ci=0.5), and the loss of the medial pedal centrale (#151[1], ci=0.5). Synapomorphies only present under ACCTRAN character optimization are the presence of a closed lower temporal fenestra (#17[1], ci=0.444), the narrow dorsal wing of the epipterygoid (#28[1], ci=0.25), the T-shaped interclavicle (#55[1], ci=0.375), the absence of the sphenethmoid (#138[1], ci=0.5), the short metatarsal I in respect to metatarsal IV (#173[1], ci=0.286), and the modest elongation of the mid-cervicals relative to the mid-dorsal vertebrae (#174[1], ci=0.286). DELTRAN character optimization adds support to the node by the contact of the exoccipitals dorsal to the basioccipital condyle (#23[1], ci=0.5).

Unequivocal autapomorphies of araeoscelidians are the presence of a mineralized sternum (#81[1], ci=0.2), the deep excavation of the neural arches of the mid-dorsal vertebrae (#103[1], ci=0.5), the low caudal neural spines (#106[1], ci=0.312), the distally tapering haemal spines (#108[1], ci=0.462), the large coracoid process (#110[1], ci=0.333), and the anterolateral orientation of the basipterygoid processes (#140[1], ci=0.167). Under ACCTRAN character optimization, additional autapomorphies are the presence of tabulars (#15[0], ci=0.667) and parasphenoid teeth (#97[0], ci=0.333), and DELTRAN character optimization presents the T-shaped interclavicle (#55[1], ci=0.375), the notched cranial margin of the interclavicle (#111[1], ci=0.25), the presence of two coracoid ossifications (#123[1], ci=0.5), the lack of a caudal extension of the maxilla until to the posterior orbital margin (#127[1], ci=0.286), the shortened metatarsal I (#173[1], ci=0.286), and the modest elongation (ratio >1 and <1.5) of the mid-cervicals relative to the mid-dorsal vertebrae (#174[1], ci=0.286) as additional autapomorphies.

Apsisaurus and all other diapsid reptiles form a monophyletic taxon that corresponds to the term “Eosuchia”. The node is characterized by the following unequivocal synapomorphies: The cleithrum is absent (#51[1], ci=1], the femur is slender and sigmoidally curved (#70[1], ci=0.2), the anterior femoral condyle is roughly equal to the posterior condyle and of the same distal extent (#73[1], ci=0.5), the subtemporal process of the jugal is slender and distinctly lower than high (#91[1], ci=0.333), the double condyle of the humerus is low (#146[1], ci=0.6), and the olecranon is small (#147[1], ci=0.333). Under ACCTRAN character optimization, additional synapomorphies are the exclusion of the lacrimal from the external naris (#6[1], ci=0.8), the posterior excavation of the quadrate shaft (#26[1], ci=0.25), the absence of caniniform teeth on the maxilla (#39[1], ci=0.333), the reduced humeral epicondyles (#63[1], ci=0.444), the circular acetabulum (#69[1], ci=0.25), the presence of a postorbital/parietal contact (#89[1], ci=0.286), the presence of a paroccipital process/suspensorium contact (#98[1], ci=1), the lack of a notch on the cranial margin of the interclavicle (#111[0], ci=0.25), the presence of only one coracoid ossification (#123[0], ci=0.5), the caudal extent of the maxilla until to the posterior orbital margin (#127[0], ci=0.286), the caudal extent of the postorbital until to the posterior limit of the parietal (#131[1], ci=0.143), the slender stapes (#133[1], ci=0.5), the absence of a stapedial dorsal process (#134[1], ci=1), the lack of ossification of the atlantal ribs (#144[1], ci=0.5), the equal or smaller size of metacarpal IV relative to metacarpal III (#148[1], ci=0.25), and the presence of a parietal shelf for the adductor musculature (#157[1], ci=0.25). DELTRAN character optimization adds support to the node by the presence of a closed lower temporal fenestra (#17[1], ci=0.444), the narrow dorsal wing of the epipterygoid (#28[1], ci=0.25), and the absence of parasphenoid teeth (#97[1], ci=0.333).

Apsisaurus is diagnosed by the following unequivocal autapomorphies: cervical intercentra are absent (#43[1], ci=0.429), the ectepicondylar groove is without anterior notch (#64[1], ci=0.583), the radius is longer than the ulna (#66[1], ci=0.4), palatine teeth are absent (#99[1], ci=0.4), teeth on palatine ramus of the pterygoid are absent (#100[1], ci=0.375), and the internal trochanter is reduced (#120[1], ci=0.25). ACCTRAN character optimization lists the presence of a rhomboidal interclavicle (#55[0], ci=0.375), and DELTRAN character optimization presents the reduced humeral epicondyles (#63[1], ci=0.444), the absence of the sphenethmoid (#138[1], ci=0.5) and the modestly elongated mid-cervical vertebrae (#174[1], ci=0.286) as additional autapomorphies.

The next node comprises Younginiformes and all other diapsids, and therefore corresponds to the term “Neodiapsida” sensu BENTON (1985), even though also *Claudiosaurus* is surpisingly nested within the clade. Unequivocal synapomorphies diagnosing this dichotomy are the medially broad clavicles (#52[1], ci=0.333), the presence of a supraglenoidal buttress (#57[1], ci=1), the reduced intertrochanteric fossa (#71[1], ci=0.429), the holocephalous trunk ribs (#104[1], ci=0.333), and the lack of a ventral extension of the pterygoid flange below the level of the maxillary tooth row (#142[1], ci=0.25). With the implementation of ACCTRAN character optimization, additional synapomorphies are the lateral exposure of the quadrate (#27[1], ci=0.25), the presence of a retroarticular process (#35[1], ci=0.5), the fusion of the sacral (and caudal) ribs to their respective centrum (#50[1], ci=0.429), the fusion of basioccipital and basisphenoid to floor brain cavity (#137[1], ci=0.5), and the short mid-cervical vertebrae (#174[0], ci=0.286).

DELTRAN character optimization adds support to the node by the exclusion of the lacrimal from the external naris (#6[1], ci=0.8), the absence of caniniform teeth on the maxilla (#39[1], ci=0.333), the circular acetabulum (#69[1], ci=0.25), the presence of a postorbital/parietal contact (#89[1], ci=0.286), the presence of a paroccipital process/suspensorium contact (#98[1], ci=1), the caudal extension of the postorbital up to the posterior limit of the parietal (#131[1], ci=0.143), the slender stapes (#133[1], ci=0.5), the absence of a dorsal stapedial process (#134[1], ci=1), the absence of ossified atlantal ribs (#144[1], ci=0.5), the short metacarpal IV relative to metacarpal III (#148[1], ci=0.25), and the presence of a parietal shelf (#157[1], ci=0.25).

Younginiform reptiles show the following suite of unequivocal autapomorphies: a distinct coronoid process is present on the lower jaw (#36[1], ci=0.333), the illiac blade is reduced (#67[1], ci=0.25), metatarsal V is shortened (#79[1], ci=0.25), a mineralized sternum is present (#81[1], ci=0.2), the fibula is straight (#149[1], ci=0.4), caudal lateral projections are present beyond the fifth caudal vertebra (#169[1], ci=0.333), the supinator process is confluent with the femoral shaft (#176[1], ci=0.375), and the prefrontal contacts the maxilla and thereby separates lacrimal and nasal from one another (#179[1], ci=0.2). ACCTRAN character optimization shows the prominent humeral epicondyles (#63[0], ci=0.444) and the presence of the sphenethmoid (#138[0], ci=0.5) as additional autapomorphies, while DELTRAN character optimization lists the posteriorly excavated quadrate shaft (#26[1], ci=0.25), the lateral exposure of the quadrate (#27[1], ci=0.25), the presence of a retroarticular process (#35[1], ci=0.5), the straight fibula (#149[1], ci=0.4), and the short metatarsal I (#173[1], ci=0.286).

The next node consists of a sister-group relationship between *Claudiosaurus* and all other remaining diapsids. The node is diagnosed by the following unequivocal synapomorphies: the postparietals are absent (#14[1], ci=1), the lower temporal fossa is open ventrally (#17[2], ci=0.444), the quadratojugal lacks an anterior process (#20[1], ci=0.167), the distal femoral condyles are reduced (#72[1], ci=0.4), the postfrontal enters the upper temporal fenestra (#90[1], ci=0.375), the subtemporal jugal process is absent (#91[2], ci=0.333), the ectopterygoid is posteriorly elongated and reaches the corner of the transverse flange of the pterygoid (#95[2], ci=0.4), the presence of slender and tapering cervical ribs at low angle to the vertebrae (#102[1], ci=0.167), the low proximal caudal neural spines (#106[1], ci=0.312), the anterolateral orientation of the pterygoid transverse flange (#140[1|, ci=0.444), and the exclusion of the lacrimal from the orbital margin (#181[1], ci=0.5). When ACCTRAN character optimization is implemented, additional synapomorphies are the nonnotochordal vertebrae (#40[1], ci=0.75), the medially shifted external nares (#85[1], ci=0.125), the presence of an ascending process of the maxilla (#126[1], ci=0.4), the absence of a caudal extension of the maxilla up to the posterior orbital margin (#127[1], ci=0.286), the presence of an orbital exposure of the maxilla (#128[1], ci=0.444), and the elongated metatarsal I relative to metatarsal IV (#173[0], ci=0.286). DELTRAN character optimization adds support to the node by the absence of tabulars (#15[1], ci=0.667), the fusion of sacral and caudal ribs to the respective centra (#50[1], ci=0.429), and the restriction of the maxilla anterior to the posterior orbital margin (#127[1], ci=0.286).

Unequivocal autapomorphies characterizing *Claudiosaurus* are the absence of the supratemporals (#21[1], ci=0.556), the reduction of the pterygoid flanges (#32[1], ci=0.333), the presence of a free anterior process on the cervical ribs (#48[1], ci=0.25), the reduction of the deltopectoral crest (#61[1], ci=0.2), the reduction of the insertional crest for the latissimus dorsi muscle (#62[1], ci=0.25), the lack of an anterior notch in the ectepicondylar groove (#64[1], ci=0.583), the presence of gastralia (#109[0], ci=0.286), the broad basi/parasphenoid (#135[1], ci=0.25), and the termination of the anterior surangular extent prior to reaching the coronoid eminence (#143[1], ci=0.25). Under ACCTRAN character optimization, further autapomorphies are the straight posterior margin of the quadrate (#26[0], ci=0.25), the lateral coverage of the quadrate by squamosal and quadratojugal (#27[0], ci=0.25), the absence of a retroarticular process (#35[0], ci=0.5), and the modestly elongated mid-cervical vertebrae (#174[1], ci=0.286). When DELTRAN character optimization is implemented, additional autapomorphies are the T-shaped interclavicle (#55[1], ci=0.375), the reduced humeral epicondyles (#63[1], ci=0.444), the medially shifted external nares (#85[1], ci=0.143), the presence of an orbital exposure of the maxilla (#128[1], ci=0.444), and the elongated mid-cervical vertebrae (#174[1], ci=0.286).

The subsequent node consists of a dichotomy between a clade comprising *Coelurosauravus* as the sister-group of *Palaeagama* and *Saurosternon,* and all remaining diapsid reptiles. The node is supported by the following unequivocal synapomorphies: the squamosal is restricted to the dorsal region of the cheek (#18[2], ci=0.3), the absence of cervical intercentra (#43[1], ci=0.429), and the absence of the occipital flange of the squamosal (#132[0], ci=0.25). ACCTRAN character optimization adds support to the node by the large premaxilla (#1[1], ci=0.2), the absence of posterolateral frontal processes (#10[0], ci=0.25), the absence of dorsal intercentra (#42[1], ci=0.6), the equal length of radius and ulna (#66[2], ci=0.4), the presence of a contact between vomer and maxilla (#92[1], ci=0.333), the absence of palatine teeth (#99[1], ci=0.4), the absence of teeth on the palatine ramus of the pterygoid (#100[1], ci=0.375), the distally tapering haemal spines (#108[1], ci=0.462), the restriction of the ventral braincase tubera to the basioccipital (#136[1], ci=0.333), the presence of a shagreen of teeth on the pterygoid (#163[0], ci=0.333), and the small lateral exposure of the angular (#167[1], ci=0.286). Additional synapomorphies under DELTRAN character optimization are the posterior excavation of the quadrate shaft (#26[1], ci=0.25), the lateral exposure of the quadrate (#27[1], ci=0.25), the presence of a retroarticular process (#35[1], ci=0.5), and the absence of the sphenethmoid (#138[1], ci=0.5).

The clade including *Coelurosauravus*, *Palaeagama*, and *Saurosternon* is unequivocally diagnosed by the superficial attachment of the teeth (#38[3], ci=0.429), the posterior termination of the postorbital prior to reaching the caudal limit of the parietal (#131[0], ci=0.143), the presence of distinct trochlea and capitellum on the humerus (#146[0], ci=0.6), the long metacarpal IV relative to metacarpal III (#148[0], ci=0.25), and the straight fibula (#149[1], ci=0.4). Implementing ACCTRAN character optimization yields as additional synapomorphies the prominent epicondyles (#63[0], ci=0.444), the deep intertrochanteric fossa (#71[0], ci=0.375), the marginal position of the external nares (#85[0], ci=0.125), the dichocephalous trunk ribs (#104[0], ci=0.333), the elongated caudal projections (#107[0], ci=0.286), and the contact between maxilla and prefrontal (#179[1], ci=0.2). DELTRAN character optimization adds support to the node by the absence of posterolateral frontal processes (#10[0], ci=0.25) and the distally tapering haemal spines (#108[1], ci=0.462).

Palaeagama and *Saurosternon* share the following unequivocal synapomorphies: metatarsal V is shorter than the remaining metatarsals (#79[1], ci=0.25), a mineralized sternum is present (#81[1], ci=0.2), and the supinator process is confluent with the femoral shaft (#176[1], ci=0.375). Additional synapomorphies under ACCTRAN character optimization are the small premaxillae (#1[0], ci=0.2), the restriction of the squamosal to the dorsal region of the cheek (#18[2], ci=0.3), the lack of an anterior process of the quadratojugal (#19[1], ci=0.286), the presence of dorsal intercentra (#42[0], ci=0.6), the presence of a zygosphene-zygantrum articulation (#44[1], ci=0.5), the absence of slender and tapering cervical ribs at low angle to the vertebrae (#102[0], ci=0.167), the absence of an ascending process of the maxilla (#126[0], ci=0.4), the absence of an orbital exposure of the maxilla (#128[0], ci=0.444), and the well-defined astragalus/distal tarsal IV articulation (#150[1], ci=0.333). Implementing DELTRAN character optimization, additional synapomorphies are the T-shaped interclavicle (#55[1], ci=0.375), the deep intertrochanteric fossa (#71[0], ci=0.375), and the elongated caudal lateral projections (#107[0], ci=0.286).

Coelurosauravus is unequivocally diagnosed by the elongated nasals (#4[1], ci=0.143), the subequal length of the preorbital and postorbital skull portions (#8[0], ci=0.462), the prominent anterior femoral condyle (#73[0], ci=0.5), the well-developed olecranon (#147[0], ci=0.333), the posterolateral deflection of the paroccipital processes (#158[1], ci=0.5), and the distinct posterior emargination of the skull roof (#177[1], ci=0.2). One further autapomorphy under ACCTRAN character optimization is the short radius (#66[0], ci=0.4). When DELTRAN character optimization is implemented, the taxon is additionally diagnosed by the large premaxillae (#1[1], ci=0.2), the absence of dorsal intercentra (#42[1], ci=0.6), the dichocephalous trunk ribs (#104[0], ci=0.333), the presence of an ascending process of the maxilla (#126[1], ci=0.4), the orbital exposure of the maxilla (#128[1], ci=0.444), and the contact between maxilla and prefrontal thereby excluding lacrimal and nasal from one another (#179[1], ci=0.2).

Interestingly, the next node consists of a sister-group relationship between a monophyletic group formed by drepanosaurids and kuehneosaurids, and all remaining diapsid reptiles. Unequivocal characters diagnosing the clade are the anteriorly displaced pineal foramen (#12[1], ci=0.538), the absence of an entepicondylar foramen (#65[1], ci=0.4), the presence of a thyroid fenestra (#68[1], ci=0.2), and the absence of distal tarsal V (#77[1], ci=1). ACCTRAN character optimization adds support to the node by the rhomboidal interclavicle (55[0], ci=0.375), the elongated external nares (#86[1|, ci=0.4), and the dorsal extension of the quadratojugal (#182[1], ci=0.5). Under DELTRAN character optimization, additional synapomorphies are the nonnotochordal vertebrae (#40[1], ci=0.75), the absence of dorsal intercentra (#42[1], ci=0.6), the equal length of radius and ulna (#66[2], ci=0.4), the medial shift of the external nares (#85[1], ci=0.125), the absence of palatine teeth (#99[1], ci=0.4), the absence of teeth on the palatine ramus of the pterygoid (#100[1], ci=0.375), the presence of an ascending process of the maxilla (#126[16, ci=0.4), and the presence of ventral braincase tubera on the basioccipital (#136[1], ci=0.333).

The sister-group relationship between kuehneosaurids and drepanosaurids is unequivocally supported by the presence of a postnarial process (#2[1], ci=0.333), the absence of supratemporals (#21[1], ci=0.556), the posteriorly increasing inclination of pre- and postzygapophyses (#47[1], ci=0.429), the upturned retroarticular process (#101[1], ci=0.25), and the slender and high scapula (#119[1], ci=0.5). When ACCTRAN character optimization is implemented, additional synapomorphies are the open lower temporal fossa (#18[2], ci=0.3), the absence of the quadratojugal (#19[1], ci=0.286), the presence of a lateral conch on the quadrate (#29[1], ci=0.4), the presence of an ectepicondylar foramen (#64[2], ci=0.583), the presence of a calcaneal tuber (#75[1], ci=0.333), the absence of a postorbital/parietal contact (#89[0], ci=0.286), the presence of parasphenoid teeth (#97[0], ci=0.333), the equal proximal and distal width of the haemal spines (#108[0], ci=0.462), and the well-developed olecranon (#147[0], ci=0.333). DELTRAN character optimization lists no further synapomorphies.

The following major dichotomy consists of a clade comprising *Hupehsuchus* and ichthyopterygians, and all other remaining diapsids. The node is unequivocally supported by the sutured contact between the sacral ribs and the respective centra (#50[0], ci=0.429), the moderate height of the proximal caudal neural spines (#106[0], ci=0.312), the presence of gastralia (#109[0], ci=0.286), the absence of a processus lateralis (#114[1], ci=0.333), and the participation of the lacrimal in the formation of the orbital margin (#181[0], ci=0.5). ACCTRAN character optimization adds further support by the elongated nasals (#4[1], ci=0.143), the small upper temporal fossae (#9[3], ci=0.3), the reduced insertional crest for the latissimus dorsi muscle (#62[1], ci=0.25), the absence of a maxilla orbital exposure (#128[0], ci=0.444), the oblique naso-frontal suture (#154[1], ci=0.25), the absence of a transverse flange dentition (#163[2], ci=0.333), the presence of a posterior emargination of the skull roof (#177[1], ci=0.2), and the posterior position of the external nares (#180[1], ci=0.333). When DELTRAN character optimization is implemented, further synapomorphies are the large premaxillae (#1[1], ci=0.2), the elongate external nares (#86[1], ci=0.4), the fusion of basisphenoid and basicooipital to floor brain cavity (#137[1], ci=0.5), and the dorsal extension of the quadratojugal (#182[1], ci=0.5).

Ichthyopterygians and *Hupehsuchus* show the following unequivocal synapomorphies: The lower temporal fossa is absent (#17[0], ci=0.444), the posterior quadrate margin is straight (#26[0], ci=0.25), the premaxillae are excluded from the internal nares (#33[1], ci=0.5), the vertebrae are platycoelous (#41[1], ci=0.7), the deltopectoral crest is reduced (#61[1], ci=0.2), the femoral shaft is stout and straight (#70[0], ci=0.2), the absence of an intertrochanteric fossa (#71[2], ci=0.429), the internal trochanter is reduced (#120[1], ci=0.25), the short postorbital posterior extent (#131[0], ci=0.143), the reduced humeral torsion (#145[1], ci=0.333), and the relatively short frontals (#155[1], ci=0.333). When ACCTRAN character optimization is implemented, additional synapomorphies are the open ectepicondylar groove (#64[1], ci=0.583), the oval acetabulum (#69[0], ci=0.25), the absence of a passage for the pes artery between astragalus and calcaneum (#74[1], ci=0.4), the robust stapes (#133[0], ci=0.5), and the dorsal facing of the Meckelian fossa (#165[1], ci=0.333). Implementation of DELTRAN character optimization additionally lists the elongated nasals (#4[1], ci=0.143), the small upper temporal fenestra (#9[3], ci=0.3), the reduced insertional crest for the latissimus dorsi muscle (#62[1], ci=0.25), the reduced humeral epicondyles (#63[1], ci=0.444), and the posteriorly positioned extenal nares (#180[1], ci=0.333.

Ichthyopterygians are unequivocally characterized by the constricted snout (#3[1], ci=0.333), the absence of the ectopterygoid (#34[1], ci=0.4), the butterfly-shaped sutural facets on the centrum (#45[1], ci=0.2), the slender and tapering cervical ribs at low angle to the vertebrae (#102[0], ci=0.167), the oblique suture between palatine and pterygoid (#139[1], ci=0.429), the loss of the pedal centralia (#151[2], ci=0.5), and the close approach of the frontal to the upper temporal fenestra (#178[1], ci=0.4). When ACCTRAN character optimization is implemented, further apomorphies are the posterolateral frontal process (#10[1], ci=0.25), the absence of a contact between vomer and maxilla (#92[0], ci=0.333), the non-tapering haemal spines (#108[0], ci=0.462), and the presence of a large row of teeth along the posterior edge of the transverse flange (#163[1], ci=0.333). DELTRAN character optimization additionally presents the absence of an anterior notch of the ectepicondylar groove (#64[1], ci=0.583), the oval acetabukum (#69[0], ci=0.25), the absence of a passage for the pes artery between astragalus and calcaneum (#74[1], ci=0.4), the robust stapes (#133[0], ci=0.5), the oblique naso-frontal suture (#154[1], ci=0.25), the dorsal facing of the Meckelian fossa (#165[1], ci=0.333), and the distinct posterior emargination of the skull roof (#177[1], ci=0.2).

Unequivocal autapomorphies of *Hupehsuchus* are the absence of the lacrimal (#6[2], ci=0.8), the presence of a contact between prefrontal and postfrontal (#7[1], ci=0.6), the presence of an anterior extension of the quadratojugal (#20[0], ci=0.167), the absence of supratemporals (#21[1], ci=0.556), the lateral coverage of the quadrate by squamosal and quadratojugal (#27[0], ci=0.25), the posteriorly increasing inclination of the pre- and postzygapophyses (#47[1], ci=0.429), the marginal position of the external nares (#85[0], ci=0.125), the exclusion of the postfrontal from the upper temporal fenestra (#90[0], ci=0.375), the very tall proximal caudal neural spines (#106[3], ci=0.312), the absence of a premaxilla dentition (#152[1], ci=0.2), the absence of a lateral parietal shelf (#157[0], ci=0.25), and the absence of a sharp edge on the pterygoid transverse flange (#164[1], ci=0.25). Implementation of ACCTRAN character optimization additionally presents the transverse naso-frontal suture (#154[0], ci=0.25) and the lack of a posterior emargination of the skull roof (#177[0], ci=0.2). DELTRAN character optimization lists the absence of posterolateral frontal processes (#10[0], ci=0.25), the presence of a contact between vomer and maxilla (#92[1], ci=0.333), the distally tapering haemal spines (#108[1], ci=0.462), and the edentulous pterygoid transverse flange (#163[2], ci=0.333).

The subsequent node presents a dichotomy between thalattosaurs (*Askeptosaurus*, *Endennasaurus*, *Thalattosaurus*, *Clarazia*) and all remaining diapsid reptiles. The whole clade is characterized by the following unequivocal synapomorphies: metatarsal V is short and stout (#79[1], ci=0.25), the subtemporal process of the jugal is slender (#91[1], ci=0.333), the fibula is straight (#149[1], ci=0.4), the paroccipital processes are posterolaterally deflected (#158[1], ci=0.5), and the prearticular is relatively short (#168[1|, ci=1). The implementation of ACCTRAN character optimization yields as additional synapomorphies the broad prefrontal/palatine antorbital contact (#130[1], ci=0.333), the presence of a contact between prootic and parietal (#160[1], ci=0.5), and the ossfied medial wall of the inner ear (#161[1], ci=0.667). DELTRAN character optimization supports the node by the distally tapering haemal spines (#108[1], ci=0.462) and the distinct posterior emargination of the skull roof (#177[1], ci=0.2).

Askeptosaurus, *Endennasaurus*, *Thalattosaurus*, and *Clarazia* are diagnosed by the following unequivocal synapomorphies: nasals are separated from one another by the posterior processes of the premaxillae extending back to the frontal bones (#5[1], ci=0.667), the pineal foramen is close to the middle of the skull table (#12[0], ci=0.538), the quadratojugal is absent (#19[1], ci=0.286), the occipital crest is present (#25[1], ci=0.571), the lateral conch on the quadrate is present (#29[1], ci=0.4), and a distinct coronoid process is present on the lower jaw (#36[1], ci=0.333). Implementation of ACCTRAN character optimization additionally supports the node by the short nasals (#4[0], ci=0.143), the presence of a posterolateral frontal process (#10[1], ci=0.25), the displacement of the mandibular articulations to a level distinctly behind the occipital condyle (#22[1], ci=0.636), the butterfly-shaped sutural facets on the centra (#45[1], ci=0.2), the exclusion of the postfrontal from the upper temporal fenestra (#90[0], ci=0.375), the caudal expansion of the ectopterygoid (#93[1], ci=0.333), the long and slender supratemporal (#115[1], ci=1), the ossified atlantal ribs (#144[0], ci=0.5), the loss of the pedal centralia (#151[2], ci=0.5), and the narrow approach of the frontal to the upper temporal fenestra (#178[1], ci=0.4). DELTRAN character optimization adds support to the node by the small upper temporal fenestra (#9[3], ci=0.3), the reduced crest for the the latissimus dorsi muscle (#62[1], ci=0.25), the oblique naso-frontal suture (#154[1], ci=0.25), the edentulous transverse flange (#163[2], ci=0.333), and the posteriorly positioned nares (#180[1], ci=0.333).

The next major node consists of a dichotomy between what is usually known as Lepidosauromorpha, including turtles and sauropterygians, and Archosauromorpha, thus representing the traditional “Sauria”. The problematic choristoderes are interestingly positioned as sister-group of lepidosauromorphs instead of being nested with archosauromorphs, turtles are closer associated with modern lepidosaurs than with sauropterygians, *Helveticosaurus* is the sister-taxon of the latter clade, and prolacertiform reptiles form a paraphyletic unit. The whole saurian clade is unequivocally diagnosed by the free anterior process of the cervical ribs (#48[1], ci=0.25), the “hooked” 5th metatarsal (#80[1], ci=0.333), the presence of a contact between ectopterygoid and maxilla (#94[1], ci=1), the short anterior extent of the surangular (#143[1], ci=0.25), the presence of caudal lateral projections beyond the fifth caudal vertebra (#169[1], ci=0.333), and the presence of a contact between prefrontal and maxilla, thereby excluding lacrimal and nasal from one another (#179[1], ci=0.2). ACCTRAN character optimization adds support to the node by the postnarial process of the premaxilla (#2[1], ci=0.333), the subequal size of orbit and upper temporal fenestra (#9[1], ci=0.3), the prominent insertional crest for the latissimus dorsi muscle (#62[0], ci=0.25), the prominent epicondyles (#63[0], ci=0.444), the presence of palatine teeth (#99[0], ci=0.4), the lateral formation of the lacrimal duct by the maxilla (#129[1], ci=1), the lateral orientation of the transverse flange of the pterygoid (#140[0], ci=0.167), the prominent lateral exposure of the angular (#167[0], ci=0.286), and the anterior position of the external naris (#180[0], ci=0.333). Under DELTRAN character optimization, further support is provided by the presence of a prootic/parietal contact (#160[1], ci=0.5).

Lepidosauromorpha and choristoderes are unequivocally diagnosed by the absence of supratemporals (#21[1], ci=0.556), the T-shaped interclavicle (#55[1], ci=0.375), the reduction of the iliac blade (#67[1], 0.25), the oblique pterygoid/palatine suture (#139[1], ci=0.429), the short cultriform process (#141[1], ci=0.5), the laterally smoothly convex transverse flange (#164[1], ci=0.25), and the confluent supinator process (#176[1], ci=0.375). ACCTRAN character optimization adds support to the node by the subequal length of the preorbital and postorbital skull regions (#8[0], ci=0.462), the ventral extent of the squamosal (#18[0], ci=0.3), the presence of an anterior quadratojugal process (#20[0] ci=0.167), the presence of cervical intercentra (#43[0], ci=0.429), the rounded external nares (#86[0], ci=0.4), the presence of an occipital flange (#132[1], ci=0.25), and the transverse nasal/frontal suture (#154[0], ci=0.25). When DELTRAN character optimization is implemented, further synapomorphies are the ventral descent of the squamosal (#18[0], ci=0.3), the presence of a vomer/maxilla contact (#92[1], ci=0.333), and the presence of palatine teeth (#99[0], ci=0.4).

Choristoderes show the following suite of unequivocal autapomorphies: the pineal foramen is absent (#12[2], ci=0.538), the parietal is weakly constricted (#13[1], ci=0.556), the lower temporal fenestra is ventrally closed (#17[1], ci=0.444), the mandibular articulation is displaced behind the level of the occipital condyle (#22[1], ci=0.636), the occipital crest is present (#25[1], ci=0.571), the premaxillae are excluded from the internal nares (#33[1], ci=0.5), the vertebrae are platycoelous (#41[1], ci=0.7), the sutural facets on the dorsal side of the centrum are expanded (#45[1], ci=0.2), the number of sacral ribs is three (#49[1], ci=0.5), the thyroid fenestra is absent (#68[0], ci=0.2), the calcaneal tuber is present (#75[1], ci=0.333), the upper temporal fenestra is caudally elongated (#82[1], ci=0.5), the external nares are confluent (#84[1], ci=0.333), a postorbital/parietal contact is absent (#89[0], ci=0.286), the ectopterygoid is transversely broad at the suture with the pterygoid (#95[0], ci=0.4), the teeth on the palatine ramus of the pterygoid are present (#100[0], ci=0.375), slender and tapering cervical ribs are absent (#102[0], ci=0.167), the proximal caudal neural spines are low (#106[1], ci=0.312), the caudal stem of the interclavicle has a distinct expansion (#112[1], ci=0.333), the ascending process of the maxilla is absent (#126[0], ci=0.4), the absence of ventral braincase tubera (#136[0], ci=0.333), the pterygoid transverse flange extends ventrally below the level of the maxillary tooth row (#142[0], ci=0.25), the nasals are fused (#153[1], ci=0.75), metatarsal I is comparatively short (#173[1], ci=0.286), and the quadratojugal is low (#182[0], ci=0.5). Implementation of ACCTRAN character optimization additionally presents the elongated postorbital skull portion (#8[2], ci=0.462) and the presence of a large tooth row on the transverse flange (#163[1], ci=0.333), while DELTRAN character optimization lists as additional autapomorphies the postnarial premaxilla process (#2[1], ci=0.333), the elongated nasals (#4[1], ci=0.143), interestingly also the elongation of the postorbital skull region (#8[2], ci=0.462), the absence of a posterolateral frontal process (#10[0], ci=0.25), the presence of a quadratojugal anterior process (#20[0], ci=0.167), the presence of cervical intercentra (#43[0], ci=0.429), and the lateral orientation of the pterygoid transverse flange (#140[0], ci=0.167).

The Lepidosauromorpha share the following suite of unequivocal synapomorphies: the foramen for the passage of the pes artery is absent between astragalus and calcaneum (#74[1], ci=0.4), distal tarsal I is absent (#76[1], ci=0.667), the humeral torsion is reduced (#145[1], ci=0.333), and both pedal centralia are lost (#151[2], ci=0.5). ACCTRAN character optimization adds support to the node by the lack of a premaxilla postnarial process (#2[0], ci=0.333), the short nasals (#4[0], ci=0.143), the broad subtemporal jugal process (#91[0], ci=0.333), the caudal extent of the maxilla up to the level of the posterior orbital margin (#127[0], ci=0.286), the presence of a maxilla orbital exposure (#128[1], ci=0.444), the anterolateral orientation of the pterygoid transverse flange (#140[1], ci=0.167), the lateral orientation of the parocciptial processes (#158[0], ci=0.5), and the lack of a distinct posterior emargination of the skull roof (#177[0], ci=0.2). When DELTRAN character optimization is implemented, further support is given by the subequal length of the preorbital and postorbital skull regions (#8[0], ci=0.462), the rounded external nares (#86[0], ci=0.4), the broad prefrontal/palatine antorbital contact (#130[1], ci=0.333), the presence of an occipital flange (#132[1], ci=0.25), the ossification of the medial wall of the inner ear (#161[1], ci=0.667), and the edentulous transverse flange of the pterygoid (#163[2], ci=0.333).

As already mentioned above, turtles are closely associated with rhynchocephalians and squamates. They share the following unequivocal synapomorphies: The premaxillae are small (#1[0], ci=0.2), the cervical ribs lack an anterior process (#48[0], ci=0.25), the clavicles are positioned dorsally to the interclavicle (#53[1], ci=1), the radius is shorter than the ulna (#66[0], ci=0.4), a processus lateralis is present (#114[0], ci=0.333), a well-developed articulation between tibia and astragalus is present (#170[1], ci=0.5), and astragalus and calcaneum are fused (#171[1], ci=1). The implementation of ACCTRAN character optimization further supports the node by the ventrally short squamosal (#18[2], ci=0.3), the superficial tooth attachment (#38[3], ci=0.429), the presence of an ectepicondylar foramen

(#64[2], ci=0.583), the absence of gastralia (#109[1], ci=0.286), the well-defined astragalus/distal tarsal IV articulation (#150[1], ci=0.333), the presence of a surangular shelf (#166[1], ci=0.2), and small lateral exposure of the angular (#167[1], ci=0.286). DELTRAN character optimization adds support to the node by the lack of a frontal posterolateral process (#10[0], ci=0.273), the lack of a distinct posterior extension of the maxilla (#127[0], ci=0.286), the lateral orientation of the paroccipital processes (#158[0], ci=0.5), the small lateral angular exposure (#167[1], ci=0.286), and the lack of a distinct posterior emargination of the skull roof (#177[0], ci=0.25).

Testudines are unequivocally diagnosed by the absence of an upper temporal fenestra (#9[0], ci=0.3), the absence of a pineal foramen (#12[2], ci=0.538), the absence of a lower temporal fossa (#17[0], ci=0.444), the contact of the exoccipitals dorsal to the basioccipital condyle (#23[0], ci=0.5), the broad dorsal wing of the epipterygoid (#28[0], ci=0.25), the absence of the ectopterygoid (#34[1], ci=0.4), the medially broad clavicles (#52[0], ci=0.333), the position of the coracoid foramen between scapula and coracoid (#58[1], ci=0.75), the oval acetabulum (#69[0], ci=0.25), the stout and straight femoral shaft (#70[0], ci=0.2), the deep intertrochanteric fossa (#71[0], ci=0.429), the absence of the septomaxilla (#87[1], ci=0.5), the absence of a postorbital/parietal contact (#89[0], ci=0.286), the elongated caudal lateral projections (#107[0], ci=0.286), the posteromedially deflected choanae (#125[1], ci=0.333), the short posterior extent of the postorbital (#131[0], ci=0.143), the broad basi/parasphenoid (#135[1], ci=0.25), the absence of a premaxilla dentition (#152[1], ci=0.2), the short frontal (#155[1], ci=0.333), the long anterior process of the quadrate (#156[0], ci=0.5), the absence of a parietal shelf (#157[0] ci=0.25), the broad paroccipital processes (#159[1], ci=0.5), and the dorsal facing of the Meckelian fossa (#165[1], ci=0.333). There is no further support under the implementation of ACCTRAN character optimization, but DELTRAN optimization lists as additional autapomorphies the dorsal restriction of the squamosal (#18[2], ci=0.3), the presence of a quadratojugal anterior process (#20[0], ci=0.167), the robust subtemporal process of the jugal (#91[0], ci=0.333), the absence of gastralia (#109[1], ci=0.286), the well-defined distal tarsal IV/astragalus articulation (#150[1], ci=0.333), and the presence of a surangular lateral shelf (#166[1], ci=0.2).

Rhynchocephalians and squamates together form the Lepidosauria, and are unequivocally diagnosed by the presence of a coronoid process (#36[1], ci=0.333), the fusion of sacral (and caudal) ribs to their respective centra (#50[1], ci=0.429), the well-developed iliac blade (#67[0], ci=0.25), the prominent distal femoral condyles (#72[0], ci=0.4), the presence of a mineralized sternum (#81[1], ci=0.2), the marginal external nares position (#85[0], ci=0.125), the lack of slender and tapering cervical ribs (#102[0], ci=0.167), and the presence of a metatarsal V plantal tubercle (#172[1], ci=1). Implementation of ACCTRAN character optimization provides further support by the lack of a quadratojugal anterior process (#20[1], ci=0.167), the presence of a quadrate lateral conch (#29[1], ci=0.4), the presence of a zygosphene-zygantrum articulation (#44[1], ci=0.5), the slender subtemporal process of the jugal (#91[1], ci=0.333), the low caudal neural spines (#106[1], ci=0.312), the presence of an anterior process on the ilium (#113[1], ci=0.5), the presence of a gap between basioccipital and basisphenoid at the floor of the braincase (#137[0], ci=0.5), the well-developed olecranon (#147[0|, ci=0.333), and the comparatively short metatarsal I (#173[1], ci=0.286). DELTRAN character optimization adds support to the node by the superficial attachment of the teeth (#38[3], ci=0.429) and the presence of cervical intercentra (#43[0], ci=0.429).

Interestingly, *Helveticosaurus* is nested together with sauropterygians (*Placodus*, Pachypleurosaurs, *Simosaurus*, Pistosauridae). The node is supported by the following unequivocal synapomorphies: the insertional crest for the latissimus dorsi muscle is reduced (#62[1], ci=0.25), the total number of tarsal ossifications is less than four (#78[1], ci=0.5), metatarsal V is straight (#80[0], ci=0.333), and the holocephalous trunk ribs articulate with the neural arch only (#104[2], ci=0.333). ACCTRAN character optimization provides additional support by the absence of the lacrimal (#6[2], ci=0.8), the large upper temporal fenestra (#9[2], ci=0.3), the presence of a posterolateral frontal process (#10[1], ci=0.25), the akinetic palate (#30[1], ci=1), the absence of the suborbital fenestra (#31[0], ci=0.5), the absence of cervical intercentra (#43[1], ci=0.429), the elongated transverse processes (#46[1], ci=0.25), the reduced deltopectoral crest (#61[1], ci=0.2), the reduced internal trochanter (#120[1], ci=0.25), and the crescentic anterior border of the interpterygoid vacuity (#162[1], ci=1). There is no further support under DELTRAN character optimization.

Helveticosaurus is unequivocally diagnosed by the presence of caniniform teeth on the maxilla (#39[0], ci=0.333), the elongated radius (#66[1], ci=0.4), the absence of a thyroid fenestra (#68[0], ci=0.2), the stout femoral shaft (#70[0], ci=0.2), the reduced intertrochanteric fossa (#71[2], ci=0.429), the down-turned ventral margin of the premaxilla (#83[1], ci=0.4), the marginal location of the nares (#85[0], ci=0.125), the very tall proximal caudal neural spines (#106[3], ci=0.312), and the long caudal lateral projections (#107[0], ci=0.286). ACCTRAN character optimization provides further support by the small upper temporal openings (#9[3], ci=0.3), while DELTRAN character optimization also adds #9[3], as well as the elongated transverse processes (#46[1], ci=0.25), the reduced deltopectoral crest (#61[1], ci=0.2), the reduced internal trochanter (#120[1], ci=0.25), and the presence of a maxilla orbital exposure (#128[1], ci=0.444).

Placodus and the eosauropterygians (pachypleurosaurs, *Simosaurus*, pistosaurids) share the following unequivocal synapomorphies: tooth implantation is thecodont (#38[1], ci=0.429), the clavicle is applied to the medial surface of the scapula (#54[1], ci=1), the coracoid foramen is located between coracoid and scapula (#58[1], ci=0.75), a pectoral fenestration is present (#59[1], ci=1), the humerus is curved (#60[1], ci=1) and has reduced epicondyles (#63[1], ci=0.444), metatarsal V is long and slender (#79[0], ci=0.25), caudal lateral projections are absent beyond the fifth caudal (#169[0], ci=0.333), and the nares are positioned relatively far posteriorly (#180[1], ci=0.333). ACCTRAN character optimization adds support to the node by the increasing inclination of the posterior pre- and postzygapophyses (#47[1], ci=0.429), the short caudal stem of the interclavicle (#56[1], ci=1), the procumbent premaxillary and dentary teeth (#117[1], ci=0.5), and the absence of a maxilla orbital exposure (#128[0], ci=0.444). DELTRAN character optimization provides further support by the absence of the lacrimal (#6[2], ci=0.8), the large upper temporal fenestrae (#9[2], ci=0.3), the akinetic palate (#30[1], ci=1), the absence of the suborbital fenestra (#31[0], ci=0.5), and the crescentic anterior border of the interpterygoid vacuity (#162[1], ci=1).

The Eosauropterygia share the following unequivocal character states: the preorbital skull region is longer than the postorbital portion (#8[1], ci=0.462), a zygosphene-zygantrum articulation is present (#44[1], ci=0.5), the sutural facets on the dorsal side of the centrum are cruciform (#45[1], ci=0.2), the number of sacral ribs is three (#49[1], ci=0.5), a vomer/maxilla contact is present (#92[0], ci=0.333), the scapula is with a constriction separating a ventral glenoidal portion from a posteriorly directed dorsal wing (#119[2], ci=0.5), the fibula is bowed away from the tibia (#149[0], ci=0.4), and the surangular has a lateral shelf (#166[0], ci=0.2). When ACCTRAN character optimization is implemented, further synapomorphies are the separation of the nasals by a premaxilla/frontal contact (#5[1], ci=0.667), the lack of a quadratojugal anterior process (#20[1], ci=0.167), the reduction of the pterygoid flange (#32[1], ci=0.333), the short transverse processes (#46[0], ci=0.25), the medial expansion of the clavicles (#52[0], ci=0.333), the reduction of the posterior process of the interclavicle (#56[2], ci=1), the well-developed deltopectoral crest (#61[0], ci=0.2), the open ectepicondylar groove without an anterior notch (#64[1], ci=0.583), the absent subtemporal process of the jugal (#91[2], ci=0.333), the distally expanded haemal spines (#108[2], ci=0.462), the posterolateral deflection of the paroccipital processes (#158[1], ci=0.5), and the small lateral exposure of the angular (#167[1], ci=0.286). DELTRAN character optimization additionally lists the reduction of the interclavicle posterior process (#56[2], ci=1), the reduction of the internal trochanter (#120[1], ci=0.25), the strong posterior extension of the maxilla (#127[0], ci=0.286), the small lateral angular exposure (#167[1], ci=0.286), and the lack of a distinct posterior skull emargination (#177[0], ci=0.2).

Unequivocal autapomorphies of *Placodus* are the constriction of the snout (#3[1], ci=0.333), the presence of a prefrontal/postfrontal contact (#7[1], ci=0.6), the exclusion of the premaxilla from the internal naris (#33[1], ci=0.5), the presence of a distinct coronoid process (#36[1], ci=0.333), the contribution of the splenial to the formation of the symphysis (#37[0], ci=0.5), the notochordal vertebrae (#40[0], ci=0.75), the posteroventral elongation of the ectopterygoid/pterygoid suture without reaching the lateral corner of the transverse flange (#95[1], ci=0.4), the tall caudal neural spines (#106[2], ci=0.312), the presence of a processus lateralis (#114[0], ci=0.333), the presence of a diastema in the upper jaw (#116[1], ci=0.5), the presence of button-like teeth (#122[1], ci=0.667), the recurved dentary symphysis (#124[1], ci=0.5), the posteromedial deflection of the choanae (#125[1], ci=0.333), the short posterior postorbital extent (#131[0], ci=0.143), the transverse palatine/pterygoid suture (#139[2], ci=0.429), the distinct ventral extension of the pterygoid flange (#142[0], ci=0.25), the fused nasals (#153[1], ci=0.75), the relatively short frontals (#155[1], ci=0.333), and the dorsal facing of the Meckelian fossa (#165[1], ci=0.333). Further autapomorphies under ACCTRAN character optimization are the long nasals (#4[1], ci=0.143), the well-developed internal trochanter (#120[0], ci=0.25), the short posterior extent of the maxilla (#127[1], ci=0.286), and the distinct posterior emargination of the skull (#177[1], ci=0.2). DELTRAN character optimization additionally lists the long nasals (#4[1], ci=0.143), the presence of an anterior quadratojugal process (#20[0], ci=0.167), the distinctly elongated transverse processes (#46[1], ci=0.25), the increasing inclination of pre- and postzygapophyses (#47[1], ci=0.429), the short posterior process of the interclavicle (#56[1], ci=1), the reduced deltopectoral crest (#61[1], ci=0.2), the robust subtemporal process of the jugal (#91[0], ci=0.333), the procumbent anterior teeth (#117[2], ci=0.5), and the lateral direction of the paroccipital processes (#158[0], ci=0.5).

The Archosauromorpha include *Macrocnemus*, *Tanystropheus*, *Prolacerta*, *Trilophosaurus*, Rhynchosauria, and Archosauriformes, and are unequivocally diagnosed by the fusion of sacral (and caudal) ribs to their respective centra (#50[1], ci=0.429), the prominent distal femoral condyles (#72[0], ci=0.4), the distinct anterior notch of the interclavicle (#111[1], ci=0.25), the presence of an anterior process on the ilium (#113[1], ci=0.5), the presence of the processus lateralis (#114[0], ci=0.333), the short posterior extent of the postorbital (#131[0], ci=0.143), the presence of a hinge in the astragalus/calcaneum articulation (#171[2], ci=1), the very long mid-cervicals (#174[2], ci=0.286), and the large and ventrally turned pubic tubercle (#175[1], ci=1). ACCTRAN character optimization adds support to the node by the absence of the septomaxilla (#87[1], ci=0.5), the absence of a vomer/maxilla contact (#92[0], ci=0.333), the lateral orientation of the basipterygoid processes (#96[1], ci=0.2), and the narrow prefrontal/palatine antorbital contact (#130[0], ci=0.333). DELTRAN character optimization provides further support by the presence of a postnarial premaxilla process (#2[1], ci=0.333), the comparatively long nasals (#4[1], ci=0.143), the lateral orientation of the transverse flange (#140[0], ci=0.167), and the oblique naso-frontal suture (#154[1], ci=0.25).

Tanystropheus is unequivocally diagnosed by the fused parietals (#11[2], ci=0.75), the absence of a quadratojugal (#19[1], ci=0.286), the elongated radius (#66[1], ci=0.364), the presence of distal tarsal I (#76[1], ci=0.667), the holocephalous trunk ribs articulating with the neural arch (#104[2], ci=0.333), the non-tapering haemals spines (#108[0], ci=0.462), and the narrow basi/parasphenoid (#135[1], ci=0.25). Additional autapomorphies under ACCTRAN character optimization are the dorsal restriction of the squamosal (#18[2], ci=0.3), and the absence of palatine teeth (#99[1], ci=0.4). DELTRAN character optimization provides support by the lack of posterolateral frontal processes (#10[0], ci=0.273), the dorsal restriction of the squamosal (#18[2], ci=0.3), the lateral orientation of the basipterygoid processes (#96[1], ci=0.2), and the edentulous pterygoid flange (#163[2], ci=0.333).

The next node consists of a dichotomy between *Macrocnemus* and all remaining archosauromorphs, unequivocally characterized by the following synapomorphies: the pineal foramen is absent (#12[2], ci=0.538), the postorbital/parietal contact is absent (#89[0], ci=0.286), the second sacral rib is bifurcate (#105[1], ci=0.5), and metatarsal I is comparatively short (#173[1], ci=0.286). ACCTRAN character optimization adds support to the node by the presence of posterolateral frontal processes (#10[1], ci=0.25), the exclusion of the postfrontal from the upper temporal fenestra (#90[0], ci=0.375), the posteroventrally elongated ectopterygoid not reaching the lateral corner of the transverse flange (#95[1], ci=0.4), the deep excavation of the mid-dorsal neural arches (#103[1], ci=0.5), the comparatively long metacarpal IV (#148[0], ci=0.25), and the large distinct row of teeth along the posterior edge of the pterygoid transverse flange (#163[1], ci=0.333). DELTRAN character optimization provides further support by the presence of palatine teeth (#99[0], ci=0.4).

Macrocnemus is unequivocally diagnosed by the small upper temporal fossae (#9[3], ci=0.3), the strongly constricted parietal skull table (#13[1], ci=0.556), the lateral coverage of the quadrate (#27[0], ci=0.25), the presence of a lateral quadrate conch (#29[1], ci=0.4), and the elongated caudal lateral projections (#107[0], ci=0.286). ACCTRAN character optimization yields no further autapomorphies, while DELTRAN character optimization additionally presents the exclusion of the postfrontal from the upper temporal fenestra (#90[0], ci=0.375), the lateral orientation of the basipterygoid processes (#96[1], ci=0.2), and the elongated metacarpal IV (#148[0], ci=0.25).

Prolacerta and the remaining archosauromorphs share the following unequivocal synapomorphies: the premaxillae are small (#1[0], ci=0.2), dorsal intercentra are present (#42[0], ci=0.6), the thyroid fenestra is absent (#68[0], ci=0.2), the calcaneal tuber is present (#75[1], ci=0.333), the proximal caudal neural spines are tall (#106[2], ci=0.312), and the haemal spines are distally expanded (#108[2], ci=0.462). Under ACCTRAN character optimization, further support is given by the presence of a notch in the lateral premaxilla/maxilla suture (#88[1], ci=0.5), the anterolateral orientation of the basipterygoid processes (#96[0], ci=0.2), the presence of teeth on the palatine ramus of the pterygoid (#100[0], ci=0.375), the presence of an upturned retroarticular process (#101[1], ci=0.25), and the separation of maxilla and prefrontal due to a contact of lacrimal and nasal (179[0], ci=0.2). DELTRAN character optimization adds further support to the node by the posteroventrally elongated ectopterygoid not reaching the lateral corner of the transverse flange (#95[1], ci=0.4), and the deep excavation of the mid-dorsal neural arches (#103[1], ci=0.5).

Prolacerta is unequivocally diagnosed by the position of the pineal foramen in the middle of the skull table (#12[0], ci=0.538), the ventral extent of the squamosal (#18[0], ci=0.3), and the absence of a maxilla ascending process (#126[0], ci=0.4). ACCTRAN character optimization provides further support by the short metacarpal IV (#148[1], ci=0.25), and the unossified medial wall of the inner ear (#161[0], ci=0.667). Implementation of

DELTRAN character optimization additionally lists the presence of a notch in the premaxilla/maxilla suture (#88[1], ci=0.5), the exclusion of the prefrontal from the upper temporal fenestra (#90[0], ci=0.375), the presence of teeth on the palatine ramus of the pterygoid (#100[0|, ci=0.375), the presence of an upturned retroarticular process (#101[1], ci=0.25), and the lack of a contact between prefrontal and maxilla (#179[0], ci=0.2).

As already mentioned above, the relationships between *Trilophosaurus*, Rhynchosauria, and Archosauriformes are affected by a lack of resolution. Anyhow, their monophyletic status is unequivocally supported by the absence of a distinct coronoid process (#36[1], ci=0.333), the T-shaped interclavicle (#55[1], ci=0.375), the short radius (#66[0], ci=0.4), the short cultriform process (#141[1], ci=0.5), the expanded paroccipital processes (#159[1], ci=0.5), the short cervicals (#174[0], ci=0.286), and the narrow approach of the frontal to the upper temporal fenestra (#178[1], ci=0.4). ACCTRAN character optimization adds support to the node by the short nasals (#4[0], ci=0.143), the lack of a posterolateral frontal process (#10[0], ci=0.25), the presence of a sagittal parietal crest (#13[3], ci=0.556), the absence of supratemporals (#21[1], ci=0.556), the participation of the prefrontal in the formation of the upper temporal fenestra (#90[1], ci=0.375), the distinct expansion of the caudal stem of the interclavicle (#112[1], ci=0.333), the presence of a diastema between maxillary and premaxillary teeth (#116[1], ci=0.5), the long posterior extent of the maxilla (#127[0], ci=0.286), the long posterior extent of the postorbital (#131[1], ci=0.143), the absence of a premaxilla dentition (#152[1], ci=0.2), the edentulous transverse flange (#163[2], ci=0.375), and the dorsal facing of the Meckelian fossa (#165[1], ci=0.333). DELTRAN character optimization provides additional support by the lack of a posterolateral frontal process (#10[0], ci=0.25), the absence of the septomaxilla (#87[1], ci=0.5), the ossification of the medial wall of the inner ear (#161[1], ci=0.667), and the edentulous transverse flange (#163[2].

Due to the high numbers of characters and taxa it is not surprising that the consistency index is generally low and homoplasy is common, a phenomenon that has already been known for a long time (SANDERSON & DONOGHUE 1989). As a consequence, also bootstrap values are in many cases below 50%, and among neodiapsids, only lepidosaurs, sauropterygians, thalattosaurs, ichthyopterygians and *Hupehsuchus*, some archosauromorphs, and *Palaeagama*/*Saurosternon* have values equal or higher than 50% (fig. 51). The clade Neodiapsida, however, is statistically well supported.

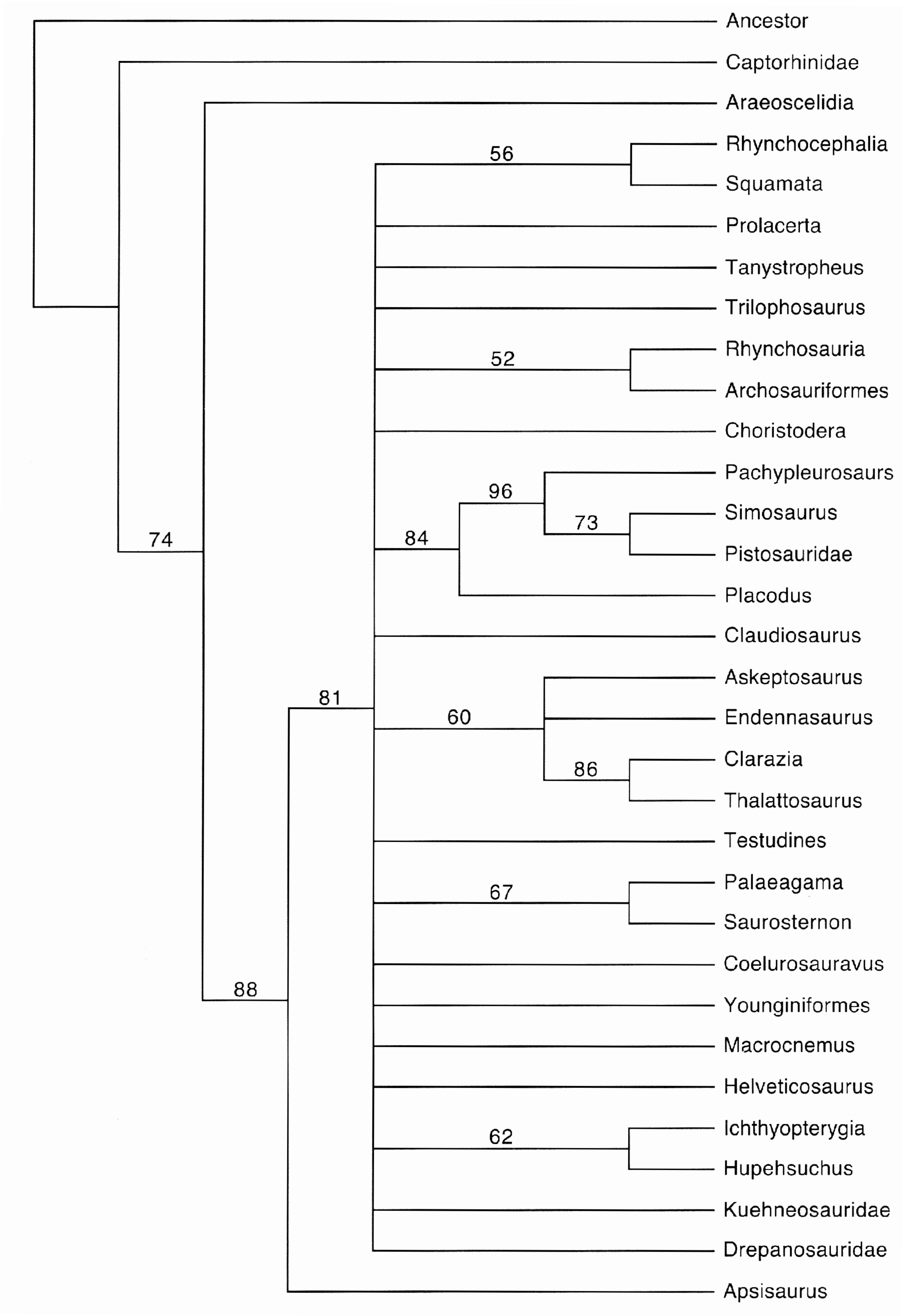


Fig. 51: 50% majority rule consensus of the bootstrap analysis (1000 replicates).

4.1.2. Discussion

In the following, several major groupings and problematic taxa will be discussed and compared with previous investigations. In the cases where specific character states are taken into consideration, it will only be referred to the unequivocal apomorphies, as they are independent of any optimization and also present in every relevant taxon. This consequence has been drawn because next to the ambivalent nature of synapomorphies restricted to ACCTRAN or DELTRAN character optimization, the character states justifiying those synapomorphies are sometimes missing in one of two sister-taxa. A thorough evaluation is difficult in these cases.

4.1.2.1. The early diapsids beyond araeoscelidians

The present investigation differs from other recent studies (e.g. DEBRAGA & RIEPPEL 1997, RIEPPEL et al.1999) in that younginiforms are placed basal to *Claudiosaurus*, and thus the latter is included within Neodiapsida (4 additional steps are needed until the basal position of younginiforms changes). As an interesting consequence, the loss of the lower temporal bar is regarded as an unequivocal synapomorphy for all diapsids above younginiforms, a feature that will be further discussed below.

LAURIN (1991) placed *Apsisaurus* above *Coelurosauravus*, a taxon that is here clearly nested within neodiapsids, as in other studies (e.g. GAUTHIER et al. 1988b, CALDWELL 1996). LAURIN, however, used only a comparatively small number of taxa for his investigation, and his result may be due to the unfortunate phenomenon that some taxa may shift the position of other clades to a notable extent (see below). But also when *Apsisaurus* is excluded, younginiforms are still basally positioned in 12 equally parsimonious trees, and only the relationships between *Claudiosaurus* and the node comprising *Palaeagama*, *Saurosternon*, and *Coelurosauravus* are weakened. *Apsisaurus* was not included in most of the more recent studies, possibly because of the incomplete preservation. On the other hand, this animal represents one of the earliest members of the whole clade, and it should therefore be seriously considered in an investigation on basal diapsid reptiles. The inclusion of this taxon has the same justification as the consideration of fossil taxa for phylogenetic investigations of modern organisms, since there may be character states that would otherwise be misinterpreted

(GAUTHIER et al. 1988b). The only difference here is that most of the other taxa are also extinct, but methodologically this remains the same.

It is not the first time that *Coelurosauravus*, *Palaeagama*, and *Saurosternon* are shown to be closely associated (see also CALDWELL 1996), even though the overall morphology of these forms looks superficially quite different. Unfortunately, there are no unambiguous synapomorphies (ci=1), and, as indicated above, the exclusion of *Apsisaurus* weakens the stability of the node. Personally, I think that the close affinity of the three taxa should not be considered to be equal to a relationship like, e.g., between rhynchocephalians and squamates. The reason is that the monophyletic grouping may reflect a widespread early radiation of some diapsid reptiles of which we know only a few members today, and that these forms, although still monophyletic, would turn out to be widely separate if additional taxa were known. As most convincing synapomorphy of the clade one may regard the superficial attachment of the teeth, a trait that is not widespread among diapsids and in the present analysis is only shared by lepidosaurs and *Clarazia*.

4.1.2.2. Kuehneosaurs and drepanosaurs

The monophyletic grouping of these two taxa is surely one of the most interesting results. While kuehneosaurs in the last years were increasingly regarded as lepidosauriform reptiles (e.g. CALDWELL 1996, DEBRAGA & RIEPPEL 1997, RIEPPEL et al. 1999), there was also some disagreement, especially in earlier studies (EVANS 1984, BENTON 1985, EVANS 1988). On the other hand, drepanosaurs were more or less viewed as archosauromorphs (DILKES 1998, RENESTO 2000), although the first known member of this taxon, *Drepanosaurus unguicaudatus*, was originally considered as aberrant lepidosaur (PINNA 1986).

The synapomorphies supporting the clade, especially the inclined pre- and postzygapophyses, are not widespread among diapsids (although none of them is unambiguous), and can therefore be regarded as comparatively reasonable. Interestingly, both taxa are also known from the late Triassic only, but this, of course, cannot be regarded as a firm additional support. The fact that a possible sister-group relationship has not been suggested earlier, is simply because there was hitherto no analysis in which both taxa were included. So the exclusion of drepanosaurids results in the “traditional“ grouping of kuehneosaurs as a member of lepidosauriforms, *Coelurosauravus* is not closely associated with *Palaeagama*/*Saurosternon*, and the ichthyosaur/*Hupehsuchus* clade is grouped with thalattosaurs. The exclusion of kuehneosaurs leaves drepanosaurs still outside saurians, *Coelurosauravus* still remains differently positioned, and thalattosaurs again form a monophyletic group with *Hupehsuchus* and ichthyopterygians.

A monophyletic origin of the two taxa suggests an interesting evolutionary scenario. While kuehneosaurs were obviously gliders (CARROLL 1988), drepanosaurs are currently regarded as chamaeleon-like climbers (RENESTO 2000), so a certain way of arboreal life style was present in both taxa. The monophyly of the two indicates that their common ancestor became adapted to arboreal life habits, and subsequently, drepanosaurs on the one hand and kuehneosaurs on the other developed their respective specializations.

The arguments illustrated above, however, do not apply to the fact that the clade is located outside the Sauria. Indeed, the two taxa are astonishingly basally positioned. Although the present result is based on the most parsimonious character distribution, many skeletal features, e.g. the pes in kuehneosaurs or the skull in drepanosaurs, are only poorly known, and thus the phylogenetic position presented here should be regarded rather as a new suggestion than a definite statement. Anyhow, there is a significant trait contradicting a placement of kuehneosaurs to lepidosauromorphs, the absence of a contact between maxilla and prefrontal due to the meeting of lacrimal and nasal, a plesiomorphic feature that does not occur in neither member of the latter clade. Moreover, the present analysis suggests that the exclusion of the lacrimal from the orbital margin is a typical feature of early neodiapsids, and the presence of this character state in kuehneosaurs provides further support for a low placement. Unfortunately, the antorbital region of drepanosaurs is not known. A better understanding of the latter taxon must therefore await additional fossil material.

4.1.2.3. The Choristodera

The placement of choristoderes as sister-group of lepidosauromorphs can surely only be seen as a very preliminary result, since knowledge of this group is still restricted. Unfortunately, there are no unambiguous character states. While some authors (e.g. DEBRAGA & RIEPPEL 1997, RIEPPEL et al. 1999) consider choristoderes as archosauromorphs, there are also serious doubts, favouring sometimes even a position outside the Sauria (EVANS 1988, EVANS & HECHT 1993, DILKES 1998, GAO & FOX 1998). Indeed, choristoderes present some features that one could also view as synapomorphies with derived archosauromorphs, such as the presence of a calcaneal tuber, the confluent nares, or the expansion of the caudal stem of the interclavicle. All these features were here interpreted as autapomorphies, however. On the other hand, morphological traits that reasonably support a more basal position are, in my opinion, not present, and it should be noted that the only recent cladistic analysis supporting such a low placement (DILKES 1998) did not include many non-archosauromorph taxa.

Even though the phylogenetic position obtained in the present analysis is by far not the final word, it indicates that choristoderes, if saurians, stand at the very base of the whole clade. The possible alternative, a placement outside “higher“ diapsids, should nonetheless be seriously considered in future research.

4.1.2.4. The Lepidosauromorpha and turtles

There are two noteworthy results concerning the relationships of lepidosauromorphs, one is the position of turtles, and the other is the assignment of sauropterygians to the clade, with *Helveticosaurus* as their sister-taxon.

The sister-group relationship of turtles and lepidosaurs is here relatively well-supported by even some unambiguous characters, like the astragalus/calcaneum fusion and the position of the clavicles relative to the interclavicle. The latter feature, however, requires a more thorough investigation in other diapsids, and may therefore be differently interpreted in future studies. The here presented grouping has not been suggested by earlier analyses, although the result of a more basal placement within the lepidosauromorph clade had already been obtained by several other workers (RIEPPEL 1994, CALDWELL 1996, DE BRAGA & RIEPPEL 1997). In this context, DEBRAGA & RIEPPEL (1997) discussed several indications beyond cladistic analysis, which should support a lepidosauromorph placement of turtles. Their arguments were the presence of a semi-lunate jugal in the early ontogeny of *Sphenodon*, squamates, and turtles, the identical topological replacement of the radiale by an enlarged centrale developed from budding of the intermedium, and the development of the tarsale proximale ossifying into astragalus and calcaneum. All these features are very distinct among amniotes, although one should keep in mind that developmental investigations on extinct animals can only rarely be conducted. Anyhow, there is obviously not only cladistic evidence supporting the assignment of turtles to the lepidosauromorph clade.

The above cited additional arguments of DEBRAGA & RIEPPEL (1997) were originally put forward in support of a sauropterygian/turtle relationship, and not to justify a monophyletic grouping of turtles and modern lepidosaurs. Their argumentation, however, applies even more to the present result. Additionally, although stratigraphy surely is a relatively weak argument (but has been used several times in recent years; LEE 1997, DEBRAGA & RIEPPEL 1997), the here suggested phylogeny reduces the stratigraphic gap between turtles and their supposed closest relatives much more than any previous alternative did, as both testudines and lepidosaurs are first known from the late Triassic.

Certainly, one may doubt the diapsid nature of turtles in general (see e.g. LEE 1997, 2001), and this is surely a problem which is currently not definitely resolved. However, there is also molecular support for a diapsid origin of turtles, although the clade is then placed to an archosauromorph position (see ZARDOYA & MEYER 2001 for a review), a result that is difficult to obtain by palaeontological studies since possible synapomorphies of turtles and archosaurs come from soft-part anatomy (RIEPPEL 2000b) and are therefore difficult, if not impossible, to code. The present analysis did not consider amniotes in general, and therefore a comparison of the different alternatives is difficult here. Anyhow, it should be mentioned that during the whole "development" of this analysis, turtles always nested with lepidosauromorphs, and that the inclusion of the parareptile *Procolophon* in the beginning of this study resulted in a polytomy of this taxon with captorhinids and araeoscelidians. Although not a firm empirical study, this at least indicates that the inclusion of turtles has a completely different effect on the outcome of the analysis than the consideration of other, definite non-diapsids.

Unlike in turtles, the diapsid status of sauropterygians is today widely accepted. There are, however, different opinions concerning the exact affinities of the clade. An assignment to the Lepidosauromorpha was favoured, for example, by CARROLL & CURRIE (1991), RIEPPEL (1994), CALDWELL (1996), and DEBRAGA & RIEPPEL (1997), but the contrary was suggested by MERCK (1997), who placed sauropterygians at the base of archosauromorphs, together with ichthyosaurs and thalattosaurs. The present result corroborates the former hypothesis, although there is unfortunately no unambiguous synapomorphy. Interestingly, the exclusion of turtles does not change the position of sauropterygians, but places choristoderes as sister-taxon of lepidosaurs. If sauropterygians are indeed lepidosauromorphs, they represent a very basal offshoot.

Surprisingly, *Helveticosaurus* turned out to be a sister-taxon of sauropterygians. Although there is no complete coincidence, the result supports more the opinion of PEYER (1955), who considered *Helveticosaurus* to be a primitive member of the Placodontia, than the view of RIEPPEL (1989b), who proposed that *Helveticosaurus* is not related to sauropterygians but possibly assignable to archosauromorphs. The here presented unequivocal synapomorphies supporting a monophyly of sauropterygians and *Helveticosaurus* are unfortunately not unambiguous and, additionally, can mostly be interpreted in the sense of aquatic specialization, such as the reduction of the insertional crest of the latissimus dorsi muscle or the low number of tarsal ossifications. There is, however, one exception: the high neural arches with which the holocephalous trunk ribs exclusively articulate. The configuration is identical to that seen in, e.g., *Placodus*, and the overall vertebral morphology was also one of PEYER´S (1955) major arguments for a closer relationship of the two taxa. On the contrary, RIEPPEL (1989b) considered the peculiar vertebral morphology as plesiomorphic, and thus uninformative for phylogenetic inferences. Outgroup comparison, however, indicates that such a vertebral structure is rarely distributed among amniotes and diapsids, and should therefore deserve serious consideration.

4.1.2.5. The Archosauromorpha

The most interesting result concerning archosauromorphs is the paraphyly of the Prolacertiformes. For a long time, prolacertiforms were considered as squamates (WILD 1973, 1980), and only in recent years, a consensus arose that the group should be included within archosauromorphs (BENTON 1985). The monophyly of prolacertiforms, however, was not completely out of question (EVANS 1988), and it was finally DILKES (1998), who for the first time obtained a result in which prolacertiforms were split and divided into several widely separated taxa, of which *Prolacerta* represented the sister-taxon of the Archosauriformes. The result of the present analysis is not completely similar, as *Macrocnemus* and *Tanystropheus* are not grouped together. Nevertheless, it corroborates the lack of evidence for monophyly, and *Prolacerta* again shows the closest affinity to archosauriforms, even though no character state is unambiguous.

RIEPPEL (1989c), although not questioning the monophyly of the Prolacertiformes, described fundamental differences in the tarsus of *Macrocnemus*, *Tanystropheus*, and *Prolacerta*. So the former two lack a lateral tuber on the calcaneum, an important character within archosauromorphs. While in the case of *Tanystropheus* one could argue that the absence of the tuber is secondary due to aquatic specialization and thus reduced ossification, this does not apply to *Macrocnemus*, which is doubtlessly terrestrial and also lacks the tuber.

If prolacertiforms were really monophyletic, the tuber must either have been lost in several taxa, or it must have been acquired indepentently in some others. In the present analysis, both scenarios are not the most parsimonious alternatives, and the obtained result rather suggests that the tuber was developed only once in archosauromorph evolution.

One major feature has always been considered as “key-character“ of prolacertiforms, the elongated mid-cervical vertebrae. This character was certainly included in the present analysis, but it did not support monophyly and instead resulted to be an early feature of archosauromorphs that had been lost in the more derived taxa. Hence, prolacertiform reptiles should currently at best be regarded as an early archosauromorph grade, and not as a monophyletic group. The reason why such a result had not been suggested earlier, may simply be due to the fact that prolacertiform reptiles were usually coded as one single taxon only.

4.1.2.6. Thalattosaurs and ichthyopterygians

In contrast to other computer-aided analyses (e.g. RIEPPEL 1998), the present investigation did not treat thalattosaurs *a priori* as a single taxon. This methodology was chosen with reference to the enigmatic Norian reptile *Endennasaurus*, for which a thalattosaur affinity has been doubted by RIEPPEL et al. (2000). Thalattosaurs clearly turned out to be monophyletic and show reasonable synapomorphies like the premaxilla/frontal contact or the elongated supratemporal, a feature that is even unambiguous and only equivocal due to the lack of preservation in *Endennasaurus*.

Ichthyosaurs and *Hupehsuchus* also form a well-supported monophyletic clade, although no character state is unambiguous. *Hupehsuchus* has not been included in recent studies on ichthyopterygian relationships (MOTANI 1999A, SANDER 2000, MAISCH & MATZKE 2000), probably because of its poor preservational status. Anyhow, it would be interesting for future research to include several different ichthyosaur taxa instead of only one single, composite taxon, in order to see whether *Hupehsuchus* still remains outside the clade. Within this context, a notable phenomenon is that the deletion of *Hupehsuchus* results in a monophyletic grouping of thalattosaurs and ichthyopterygians, which then is a relatively stable result, i.e., 3 additional steps are required for a collapse of the clade. Moreover, even when *Hupehsuchus* is retained, a run with only one step longer results in 12 additional trees in which 4 show a monophyletic grouping of *Hupehsuchus*/ichthyopterygia and thalattosaurs. Given that both thalattosaurs and ichthypterygians show an elongated, sharp snout formed almost exclusively by the premaxilla, an enlarged supratemporal (although differently developed), and slender and tall vertebrae whose rib articulation facets are often ventrolaterally positioned, the indication of a possible monophyly deserves serious consideration in future research.

Independent from the question whether the two taxa are monophyletic or not, it is interesting that they are positioned outside saurians. RIEPPEL (1998) suggested that thalattosaurs are the sister-group of sauropterygians, both nesting with lepidosauromorphs. CARROLL & CURRIE (1991) also tentatively assumed lepidosauromorph affinities of thalattosaurs. MERCK (1997), on the other hand, placed thalattosaurs to archosauromorphs, together with his monophyletic „Euryapsida“ (sauropterygians and ichthyopterygians). An archosauromorph placement was also suggested by EVANS (1988). In former times, however, thalattosaurs were simply considered as “Neodiapsida inc. sed.“ (BENTON 1985, RIEPPEL 1987). This opinion was also shared by NICHOLLS (1999), whereas the author clearly stated that thalattosaurs nonetheless belong to the Sauria.

Contrary to thalattosaurs, the diapsid affinity of ichthyopterygians was much more under debate (see e.g. MAISCH 1997), and therefore they have only rarely been included in recent analyses. A diapsid origin, however, will be accepted here on the basis of the arguments of MOTANI et al. (1998) and MOTANI (2000), who showed that the quadratojugal does not enter the upper temporal fenestra in basal ichthyosaurs, and the opening could therefore be seen as a modified version of the typical diapsid condition. Concerning the phylogenetic position within diapsids, MERCK (1997) suggested archosauromorph affinities (see above), while CALDWELL (1996) proposed relationships to sauropterygians, with both being either placed as sister-taxon to saurians or only to archosauromorphs, and finally MOTANI et al. (1998) placed them as sister-group to saurians, a result that is shared in the present analysis.

As in ichthyosaurs, the overall morphology of, e.g., *Askeptosaurus* is either plesiomorphic or taxon-specific, and there is no character that would doubtlessly indicate saurian affinities. It should be mentioned, however, that during the development of this analysis a certain signal towards archosauromorphs was recorded. However, typical features justifiying an archosauromorph placement, like, for example, a hinge in the tarsus or a notch in the interclavicle, are absent in thalattosaurs and ichthyopterygians.

A cautious conclusion may be that these two marine clades stand very close to the saurian dichotomy, but that a nesting within this assemblage cannot be excluded either. Then, however, they still would be very basally positioned.

4.1.2.7. The effect of “problematic“ taxa on the outcome of the phylogenetic analysis

Already previously it was recognized that the inclusion of certain taxa in a phylogenetic analysis may affect the result in a way that would not be predicted by cladistic theory (e.g. RIEPPEL 1994, or CALDWELL 1996). In other words, the relative relationships of three taxa should not be influenced by the inclusion of a fourth taxon, but indeed this influence occurs. For that reason, it was tried to exclude several “problematic“ taxa, and to test their effect on the outcome of the analysis (some examples have already been illustrated above). In the present context, “problematic“ taxa are those forms which, for different reasons, have only rarely been included in analyses of diapsid relationships (thalattosaurs, turtles, ichthyopterygians, *Apsisaurus*, *Palaeagama*, *Saurosternon*, *Coelurosauravus*, *Hupehsuchus*, drepanosaurids), or where difficulties concerning a firm phylogenetic placement exist (choristoderes, kuehneosaurs, sauropterygians).

In the present investigation, some of the “problematic“ taxa do not appear to be greatly influential. These are the thalattosaur clade, which has no influence at all, and, interestingly, ichthyopterygians, whose deletion only breaks the monophyly of drepanosaurs and kuehneosaurs. Also turtles appear to have only a minor effect (see above). When the clade comprising *Palaeagama*, *Saurosternon*, and *Coelurosauravus* is deleted, only the relationships between the clades kuehneosaurs/drepanosaurs and ichthyopterygians/*Hupehsuchus* remain unresolved. By contrast, the exclusion of sauropterygians has a dramatic effect, as then the node stability of many neodiapsid clades is weakened, the relationships within the Sauria collapse, and thalattosaurs are grouped with ichthyopterygians/*Hupehsuchus*. Also, the exclusion of *Helveticosaurus* groups ichthyopterygians/*Hupehsuchus* with thalattosaurs, and additionally shifts sauropterygians outside saurians. The effects of kuehneosaurs and drepanosaurs have already been described above, while the exclusion of choristoderes again suggests a monophyly of ichthyopterygians/*Hupehsuchus* and thalattosaurs, with a certain tendency to place the clade at the base of archosauromorphs.

The study shows that the effect of a taxon on the cladogram topology is highly depending on the other taxa that are entered in the analysis, and that this is possibly much more important than the number of included characters, or the number of characters for which a taxon can be coded. For example, RIEPPEL (2000a) states that especially turtles are responsible for a lepidosauromorph position of sauropterygians, but this is not the case in the present investigation. On the other hand, turtles indeed were strongly influential before I entered *Hupehsuchus* in the data matrix, while, e.g., *Helveticosaurus* then had no influence at all.

As already mentioned, many of the above taxa were not taken into consideration in previous studies. This way of ignoring, however, may bear the danger of a bias towards a topology that is only stable under a very special taxon selection. For that reason, the hypothesis of a phylogenetic affinity of a respective organism, or group of organisms, should not only be tested against one single taxon arrangement, but also against the influence of the deletion of one or more of the taxa considered, and certainly also against the inclusion of additional taxa. In the present study, for example, such a procedure indicates that thalattosaurs show a signal towards a closer relationship with ichthyopterygians, whereas a grouping of the clade with sauropterygians, as suggested by RIEPPEL (1998), appears less likely.

4.1.2.8. Two significant morphological features within diapsid evolution: the lower temporal arcade and the thyroid fenestra

In former times, the loss of the lower temporal arcade (figs. 52, 53) had always been considered as a typical feature of squamates, and thus many early diapsids like *Prolacerta*, *Tanystropheus*, or also *Askeptosaurus*, were assigned to the modern lizards (see e.g. VON HUENE 1956). Later, of course, this unnatural assemblage was split into widely separate clades (see above). As far as the lower temporal bar is concerned, most previous analyses suggested the independent loss of the contact between jugal and quadratojugal (see e.g. DEBRAGA & RIEPPEL 1997). The present analysis, however, supports the hypothesis that this loss was a major invention of all neodiapsids beyond younginiforms, a result that is congruent with the one obtained by MERCK (1997). Given the correctness of this interpretation, the re-acquisition of the lower temporal arcade must have occurred independently within several lineages. Such a reversal has, for example, already been postulated for modern *Sphenodon* (WHITESIDE 1986), but now it seems plausible that this took also place in archosauriforms. The hypothesis is additionally supported by the lack of the arcade in basal most rhynchosaurs (DILKES 1998), suggesting that a secondary closure occurred also in this clade, as well as in placodonts (RIEPPEL 2000c). A ventrally open lower temporal fenestra is therefore

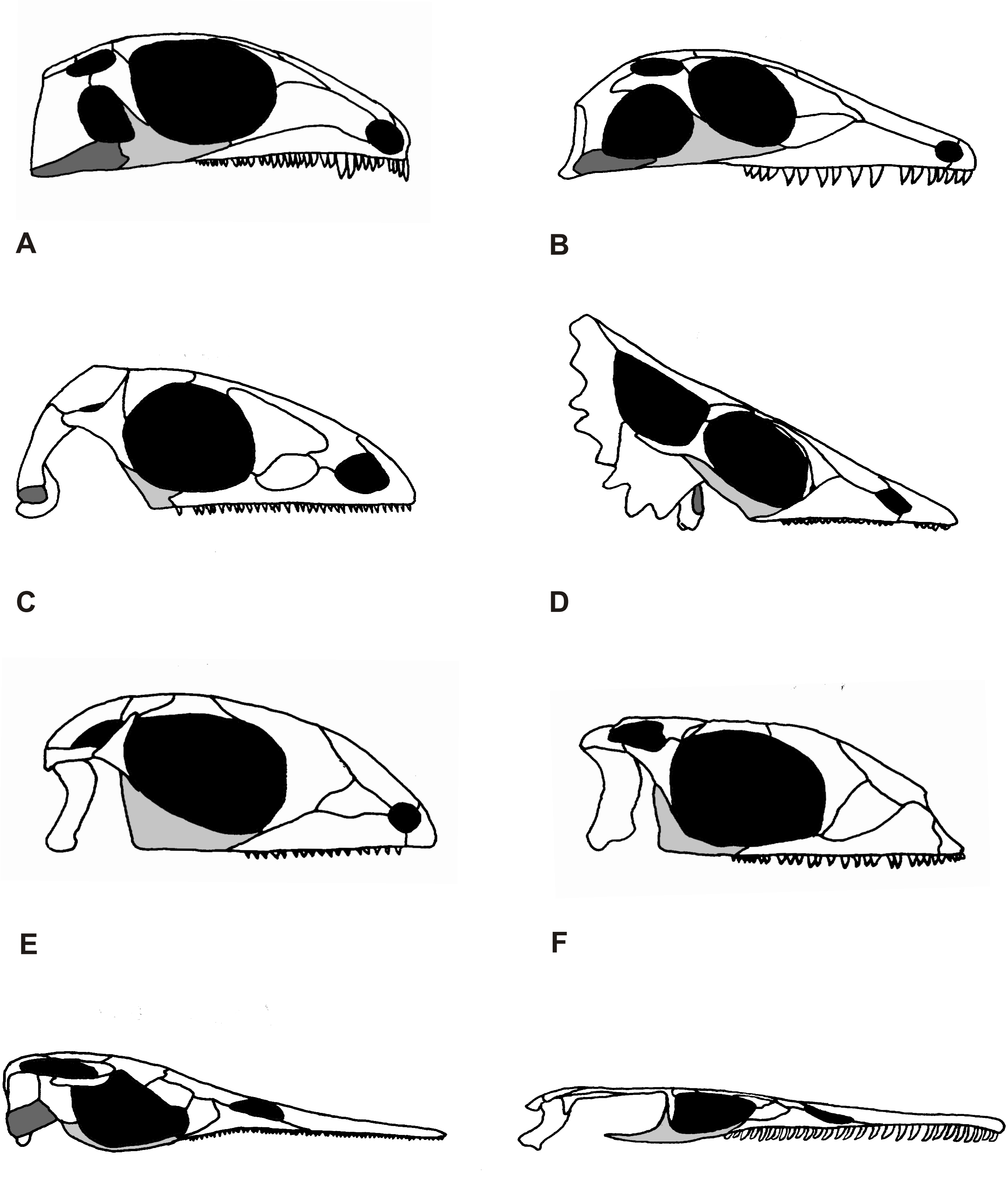


Fig. 52: Schematic diapsid skulls in lateral view to show the relationship between jugal (light grey) and quadratojugal (dark grey; after ROBINSON 1973, CARROLL 1975, 1981, GOW 1975, REISZ 1981 EVANS & HAUBOLD 1987, MOTANI et al. 1998). A) the early diapsid *Petrolacosaurus*, B) the younginiform *Youngina*, C) the basal diapsid *Claudiosaurus*, D) the Permian gliding reptile *Coelurosauravus*, E) the basal diapsid *Palaeagama*, F) the Triassic gliding reptile *Kuehneosaurus*, G) the early ichthyosaur *Utatsusaurus*, and H) *Askeptosaurus*. Not to scale.

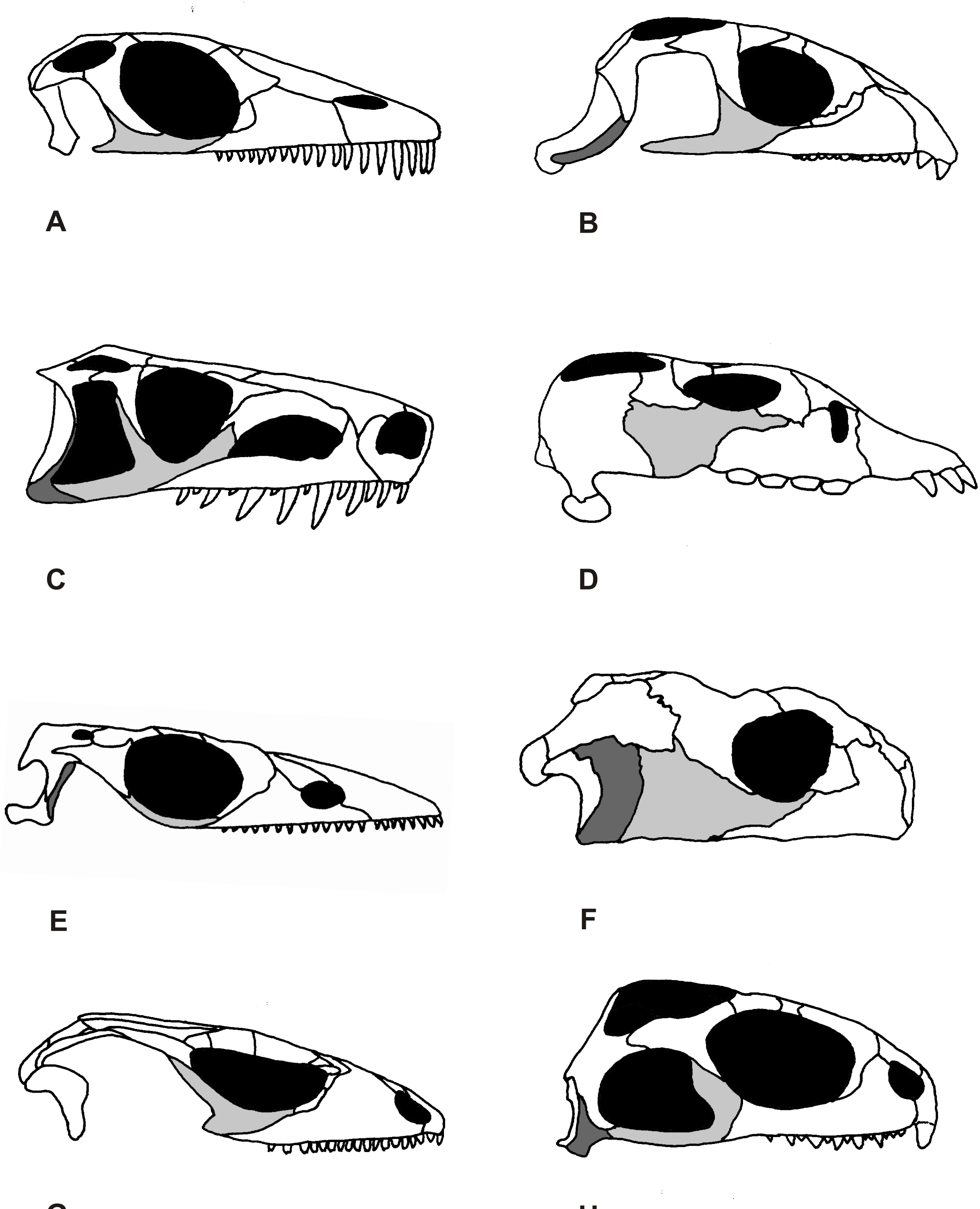


Fig. 53: Schematic diapsid skulls, continued (after BROILI 1912, WILD 1973, CARROLL 1988, RIEPPEL 1989a, GAFFNEY 1990, DILKES 1998, MÜLLER 2002). A) The archosauromorph *Tanystropheus*, B) the rhynchosaur *Mesosuchus,* C) the archosaur *Euparkeria*, D) the placodont *Placodus*, E) the pachypleurosaur *Serpianosaurus*, F) the Triassic turtle *Proganochelys*, G) the lacertid lizard *Parvilacerta*, and H) the tuatara, *Sphenodon.* Not to scale.

plesiomorphic for clades like squamates, “prolacertiforms“, or thalattosaurs. This view differs from RIEPPEL´s (2000c) assumption that the loss of the arch may be a synapomorphy of lepidosauromorphs.

Interestingly, the scenario suggested by cladistic analysis appears to be additionally supported by further anatomical evidence: The quadratojugal of all taxa in which the lower temporal bar is regarded as primary reaches far anteriorly, at least up to the mid-level of the lower temporal fossa (fig. 52A, B). By contrast, the quadratojugal of the taxa in which the closed lower temporal bar is interpreted to be secondary, e.g. the lepidosaur *Sphenodon* or the archosaur *Euparkeria* (figs. 53H, C, respectively) usually is very short, and the jugal forms the main part of the arcade (only in choristoderes the configuration is difficult to assess since the basal most representatives, *Cteniogenys* and *Lazarussuchus*, both lack preservation of the respective temporal region, and the remaining taxa show a cheek structure that is difficult to interpret due to the significant expansion of the posteriormost skull portion). Surprisingly, this difference has hitherto only been noted for *Sphenodon* (WHITESIDE 1986). It therefore seems plausible that the proposed secondary closure took place by an increasing posterior elongation of the jugal, which can also be seen in the ontogeny of both lepidosaurs and archosaurs (HOWES & SWINNERTON 1901, RIEPPEL 1992, 1993d). Given the correctness of this hypothesis, the ratio between jugal and quadratojugal may be indicative of a secondary or primary lower temporal arcade.

The present interpretation has also interesting implications for ichthyosaurs (fig. 52G). The peculiar cheek morphology of this clade would have resulted from an open lower temporal opening, where the contact between jugal and quadratojugal had already been lost and was therefore also absent in basal ichthyosaurs like *Utatsusaurus*, *Grippia*, or *Parvinatator* (MOTANI 2000). The expansions of most of the cheek bones in this group are possibly due to the original presence of tendinous fasciae, situated close to the ventral margin of the upper temporal arch. Such elements are present in the respective area of *Sphenodon* and squamates (see chapter 4.3.1), and especially the fasciae in the posterodorsal region of the lower temporal fenestra are topologically similar to the extent of the squamosal in, e.g., *Grippia* (MOTANI 2000, fig. 4).

The presence of an open lower temporal arch must not be confused with the phenomenon of streptostyly. So in many forms where the lower arcade is interrupted, e.g. in sauropterygians, the quadrate is still not movable. Furthermore, EVANS (1980) already supposed that streptostyly is not homologous within diapsids, and there is apparently no necessary functional correlation between loss of the bar and streptostyly (RIEPPEL & GRONOWSKI 1981). The possibility to move the quadrate is obviously a specific modification of the original configuration, and in several cases also accompanied by the loss of the quadratojugal (e.g. in squamates and thalattosaurs).

What reasons did the loss of the arcade have? This question can of course only tentatively be answered. RIEPPEL & GRONOWSKI (1981) suggested that the interruption of the lower temporal arch was caused by the strengthening of the superficialis layer of the adductor mandibulae externus muscle, which means that the muscle unit becomes thick and prominent, occupies most of the external temporal area and extensively inserts on the outer surface of the lower jaw. This interpretation requires that the posterior area of the arch would get interrupted, and thus mainly the quadratojugal would be affected by the reduction. Exactly this is observed in diapsids where the lower temporal bar is open. The suggested hypothesis seems therefore plausible, and no further stringent alternatives are currently known.

The problem of the thyroid fenestra is different (fig. 54). Crown-group diapsids usually have a well-developed thyroid fenestra, but an independent origin has already been assumed for a long time (CARROLL 1988), and this interpretation is also corroborated by the present analysis.

Obviously, there were different reasons for the establishment of this significant opening, and probably also different ways of development. In “Prolacertiformes“, there is either a well-developed thyroid fenestra that is ventrally open (e.g. *Tanystropheus*, fig. 54F), or there is still a pubo-ischiadic plate (*Prolacerta*, fig. 54D). Under the here presented tree topology, the taxa with a thyroid fenestra are positioned below *Prolacerta*, which suggests an independent origin of the opening, and, by the way, further supports the assumption that prolacertiform reptiles are paraphyletic. Among “higher“ archosaurs, however, there are several examples showing the reduction of the pubo-ischiadic plate proceeding from the lower portion of the pelvis (see e.g. the phytosaur *Parasuchus*, fig. 54E). Thus, the reduction must have originally started in the ventral most area. Probably the contact between pubis and ischium was slightly emarginated there, as in many reptiles with a pubo-ischiadic plate. Since the successive sister-taxa of lepidosaurs and turtles, in the here presented analysis choristoderes and *Helveticosaurus*, still have well-developed pubo-ischiadic plates and unfortunately do not show intermediate stages, it is difficult to present an interpretation for the ventrally open thyroid fenestra of lizards, rhynchocephalians, and turtles (fig. 54I). The

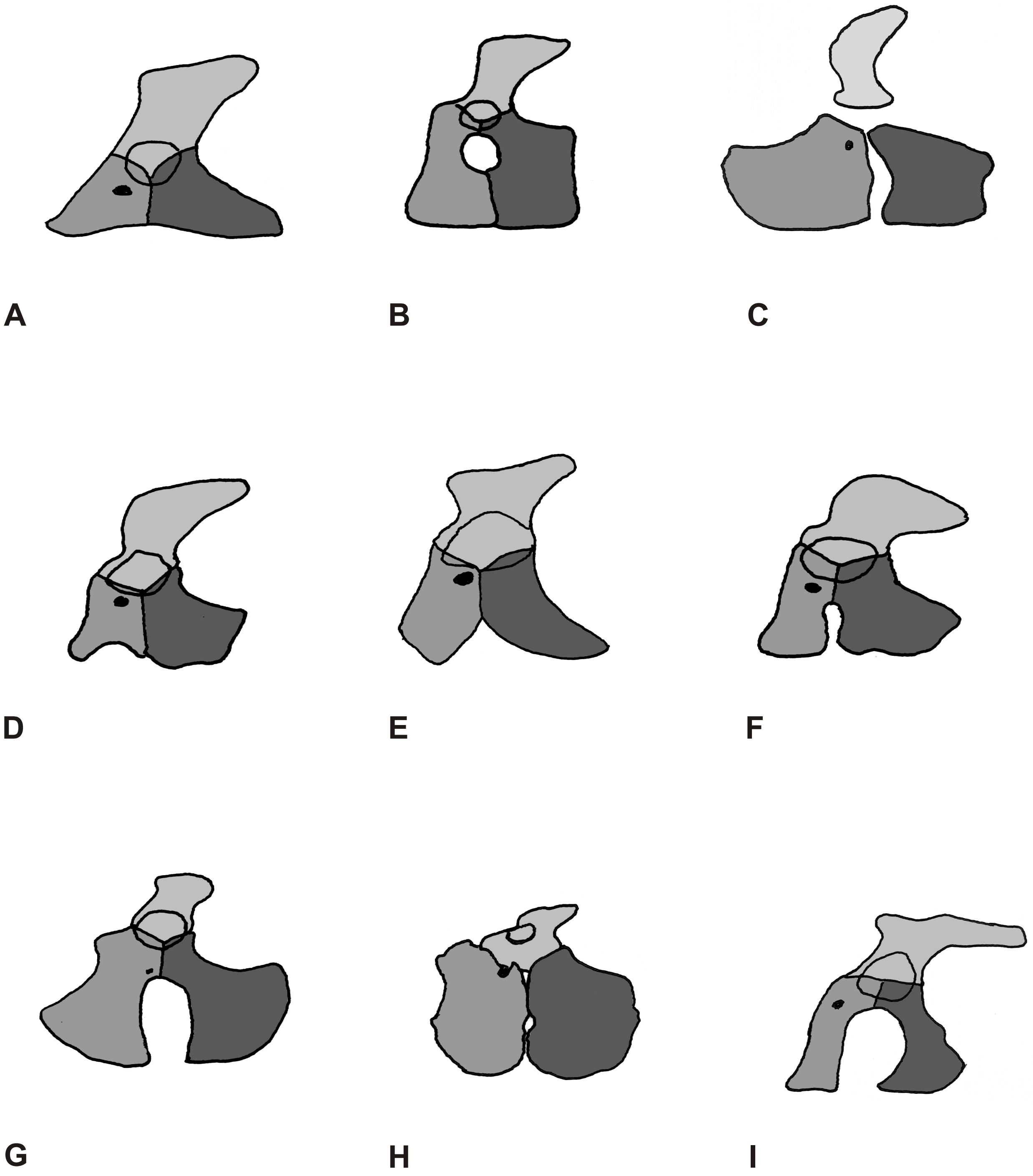


Fig. 54: The left pelvis of several diapsid reptiles in lateral view to show the different development of the thyroid fenestra (after ROMER 1956, WILD 1973, GOW 1975, BENTON 1985, CARROLL 1988, MOTANI et al. 1998). A) the younginiform *Hovasaurus*, B) the kuehneosaurid *Icarosaurus*, C) the early ichthyosaur *Utatsusaurus,* D) the archosauromorph *Prolacerta*, E) the archosaur *Parasuchus*, F) the archosauromorph *Tanystropheus*, G) the sauropterygian *Nothosaurus*, H) the placodont *Placodus*, and I) the monitor lizard *Varanus*. Not to scale.

general configuration, however, is very similar to archosauriforms, and it seems plausible that also here the reduction started with a ventral emargination.

On the other hand, not all diapsids with a fenestrated pelvis show the same kind of reduction. In kuehneosaurs, for example, the thyroid fenestra is not ventrally open (*Icarosaurus*, fig. 54B), but there is a small unossified area in the central part of the pubo-ischiadic plate. The same configuration is assumed for drepanosaurs (RENESTO 2000). In these cases, the reduction obviously started in the central portion and not at the ventral margin of the plate, which may be a further character supporting the above mentioned hypothesis of a monophyly of drepanosaurs and kuehneosaurs. A similar scenario may be proposed for the thalattosaur *Endennasaurus*, where the thyroid fenestra is ventrally closed, too (fig. 44). In the same area, *Askeptosaurus* specimen PIMUZ T 4831 shows a thinning of the pubo-ischiadic plate (fig. 20A), supporting the assumption that if there was a thyroid fenestra in some thalattosaurs, the reduction did not proceed from ventral to dorsal but began in the central portion instead. Interestingly, there is also a suite of synapsids where only in the central alrea of the pubo-ischiadic plate an opening occurs (ROMER 1956).

Ichthyosaurs present a further way of reduction. In one of the earliest members, *Utatsusaurus*, there is only a slight lack of ossification along the complete contact of pubis and ischium, resulting in a thyroid “gap“ rather than a fenestra (fig. 54C). In *Grippia*, this gap increasingly widens and becomes ventrally expanded (MAISCH & MATZKE 2000, fig. 30). The mechanism of reduction is therefore different from the other examples described above, as in none of the previous taxa the contact between ischium and pubis is completely absent.

Interestingly, *Placodus* shows some resemblances to this configuration. Although there is still a contact between ischium and pubis, this contact is loose and slightly interrupted in the dorsal most, central, and ventral area (fig. 54H). Eosauropterygians, on the other hand, have a large, ventrally open thyroid fenestra with a firm dorsal contact between pubis and ischium (fig. 54G). Due to the lack of a firm suture between the two elements in *Placodus*, it seems that the thyroid fenestra of eosauropterygians developed independently and most probably in the same way as in lepidosaurs and many archosauriforms, to which it shows a close resemblance.

In conclusion, it appears that there are at least three ways of how a thyroid fenestra can be established. One is by an increasing ventral emargination, the other is by a lack of ossification in the central area of the pubo-ischiadic plate, and the third possibility consists of a small, dorsoventrally directed absence of an ossified contact between ischium and pubis.

The first two possibilities are present both in aquatic and terrestrial diapsids, while the third way may be a result of reduced ossification due to aquatic life habits ("skeletal paedomorphosis", RIEPPEL 1989b). The here presented differences are of course difficult to code, as they are based more on interpretation than on observation, but a consideration in phylogenetic analyses will perhaps be possible in the future.

4.1.2.9. Stratigraphy and the present phylogeny

When the stratigraphic occurrence of early diapsid reptiles is compared with the here suggested phylogeny (fig. 55), there are several advantages over previous analyses (see the sections of kuehneosaurs/drepanosaurs and lepidosauromorphs/turtles), but also some problems.

The placement of *Apsisaurus* between araeoscelidians and younginiforms seems stratigraphically reasonable, as the taxon is younger than *Petrolacosaurus* but older than the first younginiforms. The placement of the latter below *Claudiosaurus* is not contradictory either, because both taxa are of roughly equal age. This is also true for the position of *Palaeagama*/*Saurosternon*/*Coelurosauravus* relative to the former two taxa.

The first major problem affects the clade comprising kuehneosaurs and drepanosaurs, as they are not known prior to the late Triassic, which requires a prominent "ghost lineage" due to the first occurrence of saurians already in the late Permian. A similar, but smaller problem are ichthyopterygians and thalattosaurs, which both are first known from the early Triassic. At least drepanosaurs/kuehneosaurs, however, live in an environment with a poor fossil documentation, and arboreal animals like these therefore have only a minor chance to fossilize. In the case of ichthyopterygians and thalattosaurs, it is evident that already at the beginning of the Triassic, ichthyosaurs and thalattosaurs were already well-defined groups, and possibly new, earlier fossils will provide more insights into the evolution of both clades.

Within the Sauria, there are principally not more contradictions than in other analyses. As long as no lepidosauromorphs are known from the late Permian - in contrast to archosaurs and their relatives -, a significant ghost lineage must be postulated for lepidosauromorph reptiles. The same is true for choristoderes, independent of the question whether the enigmatic Rhaetian reptile *Pachystropheus* indeed belongs to this clade (STORRS et al. 1996). Concerning archosauromorphs, a specific difficulty of this investigation is that *Tanystropheus* and *Macrocnemus* are positioned as sister-taxa to the remaining members of the clade, which

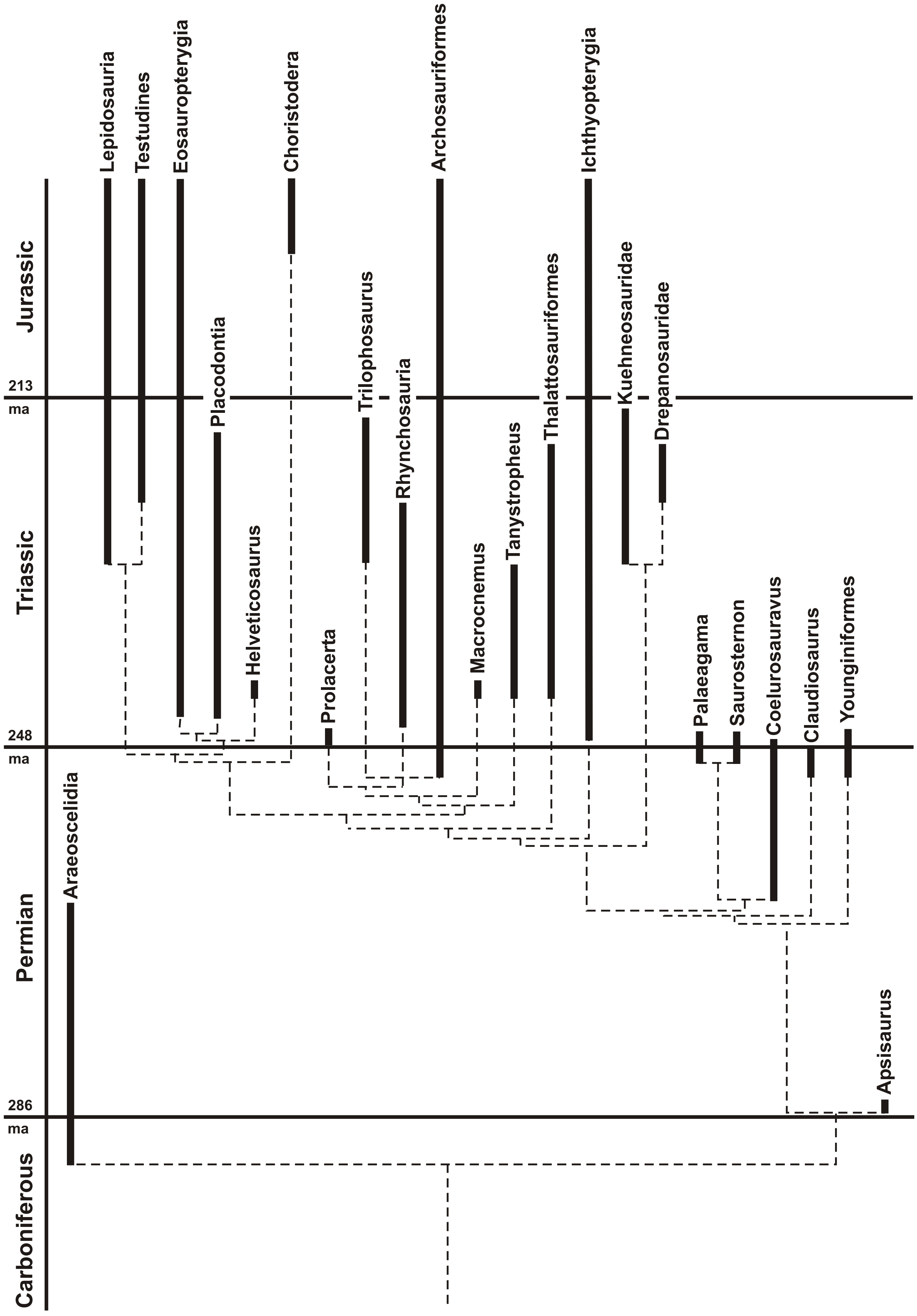


Fig. 55: The stratigraphic occurrence of diapsid reptiles, based on the phylogeny proposed by the present analysis. For a better understanding, eosauropterygians as well as *Hupehsuchus* and ichthyopterygians are treated as a single taxon, respectively.

causes a prominent ghost lineage due to the middle Triassic occurrence of the two forms. It should be added that if the Permian Kupferschiefer reptile *Protorosaurus* indeed is closely associated with *Prolacerta*, as has been suggested by, e.g., DILKES (1998), the problem that the latter is younger than one of its sister-taxa, Archosauriformes, would not be present any more, but instead other ghost-lineages would have to be postulated. *Protorosaurus* was not included in the present analysis because a re-investigation is currently being conducted by ANNALISA GOTTMANN (Universität Bonn).

Definite lepidosauriforms are still not known earlier than from the late Triassic. Anyhow, the here presented close association of rhynchocephalians, squamates, and turtles reduces the stratigraphic gap between Testudines and their proposed closest relatives to a significant extent (see above). The suggested sister-group of lepidosauriforms, the clade comprising *Helveticosaurus* and sauropterygians, is first documented in the lower Triassic. Hence, lepidosauriform reptiles should be expected to appear also in lower Triassic strata.

4.2. Ingroup relationships of thalattosaurs

4.2.1. Cladistic analysis

To evaluate the phylogenetic relationships within thalattosaurs, a separate analyis was conducted, including all valid thalattosaur genera (*Agkistrognathus, Anshunsaurus, Askeptosaurus, Clarazia, Endennasaurus, Hescheleria, Paralonectes, Thalattosaurus, Xinpusaurus*) as well as araeoscelidians and younginiforms as outgroups. The data matrix consists of 35 informative characters, many of them taken from NICHOLLS (1999) and LIU & RIEPPEL (2001). Several characters were modified or the polarity was changed due to outgroup comparison. The latter methodology resulted in the exclusion of #9 of LIU & RIEPPEL (2001; anteromedial processes of frontals that enter between nasal and premaxilla are shorter (0), or longer (1) than anterolateral processes of frontal), as state 1 is also present in araeoscelidians (REISZ 1981), while the whole character is not well-expressed in younginiforms; the necessary change of character polarity made the character uninformative. For a complete list of changes see Appendix IV, the matrix is listed in Appendix V. Furthermore, several characters that had previously not been considered in analyses of thalattosaur relationships were added (#3, #28, #29, #30, #31, #32, #33).

Using the branch-and-bound search option of PAUP* 4.0b8 (SWOFFORD 2001; all characters unordered; multiple character states interpreted as polymorphism), one single most parsimonious tree resulted (fig. 56A), with a length of 67 steps (CI=0.6716, HI=0.3433, RI=0.6857, RC=0.4606). *Endennasaurus, Askeptosaurus,* and *Anshunsaurus* represent a monophyletic group, whereas *Endennasaurus* is opposed to the latter two. The remaining thalattosaurs form the second major clade, with the monophyletic *Xinpusaurus* and *Nectosaurus* as sister-taxon of *Agkistrognathus, Paralonectes, Thalattosaurus,* and the monophyletic *Clarazia* and *Hescheleria.*

In the following, the respective dichotomies will be described more in detail. Since the monophyletic status of thalattosauriform reptiles has already been corroborated in the previous large-scale analysis, it will only be referred to the more inclusive nodes.

Askeptosaurus, Anshunsaurus, and *Endennasaurus* are unequivocally diagnosed by the absence of a pterygoid dentition (#11[1] & #12[1], ci=1), and the high number of cervical vertebrae (#27[1], ci=1). ACCTRAN character optimization adds support to the node by the

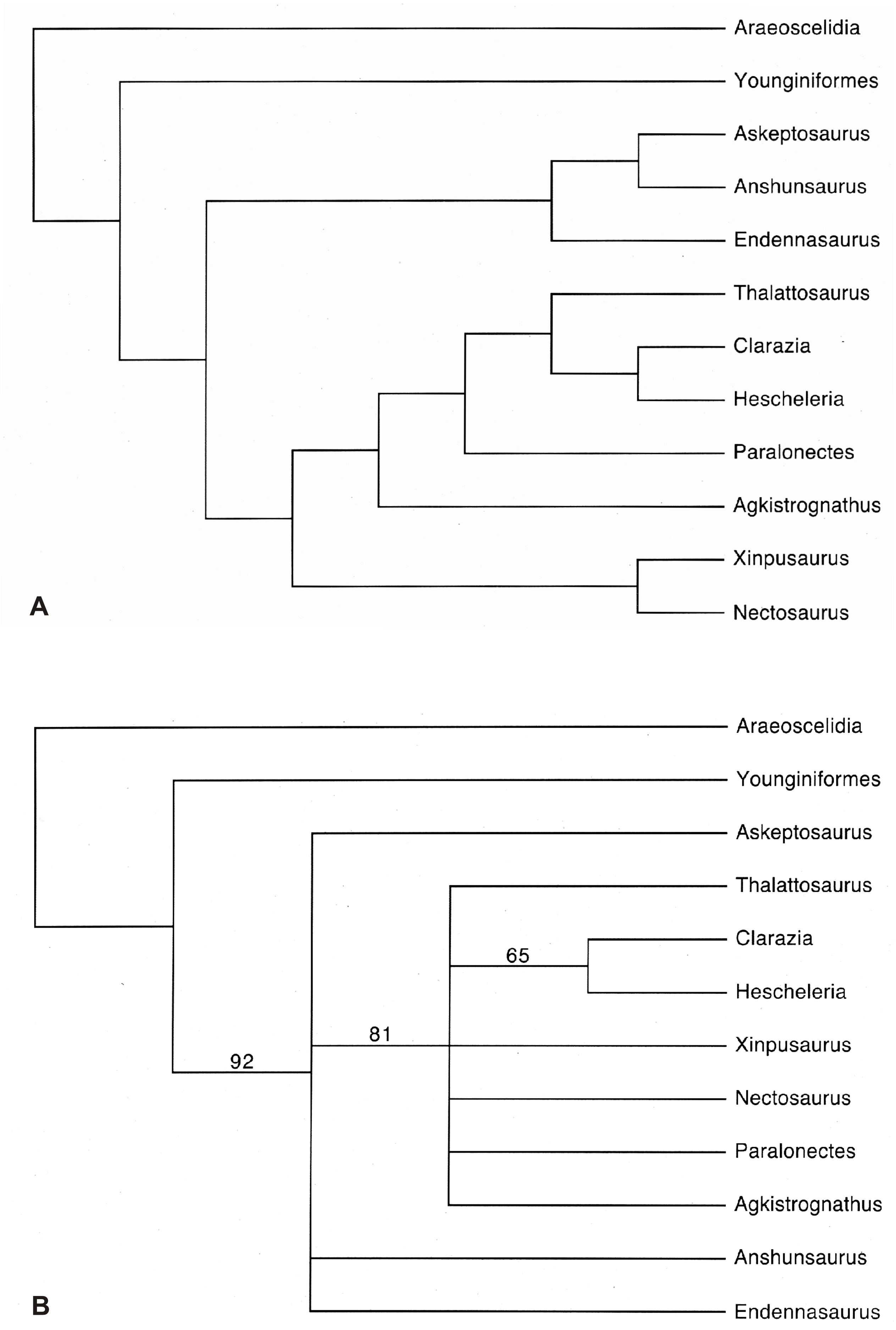


Fig. 56: A) most parsimonious tree showing the relationships among thalattosaurs (67 steps, CI: 0.6716, HI: 0.3433), B) 50% majority rule consensus of the bootstrap analysis (1000 replicates).

elongation of the preorbital region (#1[2], ci=0.667) and the relatively anteriorly positioned pineal foramen (#25[1], ci=1). DELTRAN character optimization also provides support by #1[2], but there are no further synapomorphies.

There is only one unequivocal autapomorphy of *Endennasaurus*, the absence of a premaxilla dentition (#6[1], ci=0.5). ACCTRAN character optimization furthermore lists the absence of an anterior process on the cervical ribs (#30[0], ci=0.5) and the long and slender humerus (#32[0], ci=0.5). DELTRAN character optimization adds no further autapomorphies.

Anshunsaurus and *Askeptosaurus* form the Askeptosauridae KUHN 1952 and are unequivocally diagnosed by the posterior extent of the nasals (#14[1], ci=0.333), while ACCTRAN character optimization provides further support by the absence of posterolateral frontal processes (17[0], ci=0.667) and the absence of a well-developed deltopectoral crest (#35[1], ci=0.5). DELTRAN character optimization additionally lists the anteriorly positioned pineal foramen (#25[1], ci=1).

Unequivocal autapomorphies of *Askeptosaurus* are the close approach of the anterolateral frontal processes to the external nares (#15[1], ci=0.5), the absence of a nasal/prefrontal contact (#16[1], ci=0.5), the lack of a frontal/supratemporal contact due to the short frontal (#18[0], ci=0.667), the separation of postfrontal and postorbital (#20[0], ci=0.5), the slit-like upper temporal fenestra (#21[1], ci=1), and the absence of a distinct retroarticular process (#26[0], ci=0.5). There are no specific autapomorphies under ACCTRAN character optimization, while DELTRAN character optimization additionally lists the absence of posterolateral frontal processes (#17[0|, ci=0.667), the presence of an anterior process on the cervical ribs (#30[1], ci=0.5), the comparatively stout humerus (#32[1], ci=0.5), and the reduced deltopectoral crest (#35[1], ci=0.5).

There are no unequivocal autapomorphies of *Anshunsaurus*, but ACCTRAN character optimization presents the far posteriorly extending posterolateral frontal process (#17[2], ci=0.667), as does DELTRAN character optimization.

The remaining thalattosaurs (the Thalattosauria sensu MERRIAM 1905) are unequivocally diagnosed by the ventral deflection of the snout (#2[1], ci=0.5), the short and high maxilla (#3[1], ci=0.5), the nasal is separated from the prefrontal (#16[1], ci=0.5), the high neural spines of the posterior cervical and trunk vertebrae (#28[1], ci=0.5), and the expanded, kidney-shaped radius (#33[2], ci=1). ACCTRAN character optimization adds support to the node by the thecodont tooth implantation (#5[1], ci=1), the broad posterolateral frontal process (#19[1], ci=0.5), the slender and elongated scapula (#31[1], ci=0.5), and the slightly expanded fibula (#34[1], ci=1). DELTRAN character optimization provides further support by the equal length of preorbital and postorbital skull portions (#1[1], ci=0.667) and the short and stout humerus (#32[1], ci=0.5).

The monophyly of *Xinpusaurus* and *Nectosaurus* is unequivocally supported by the distinct elongation of the caudal neural spines (#29[1], ci=1). ACCTRAN character optimization additionally lists the broadly expanded fibula (#34[2], ci=1), and DELTRAN character optimization presents the broad posterolateral frontal process (#19[1], ci=0.5) and the slender scapula (#31[1], ci=0.5).

Unequivocal autapomorphies of *Xinpusaurus* are the dorsally recurved anterior alveolar margin of the maxilla (#4[1], ci=0.5) and the presence of a pterygoid transverse flange dentition (#10[0], ci=0.5). There are no further autapomorphies under ACCTRAN character optimization, but DELTRAN character optimization additionally lists the broadly expanded fibula (#34[2], ci=1).

Only when DELTRAN character optimization is implemented, there are two autapomorphies of *Nectosaurus*, the distinctly ventrally recurved rostrum (#2[2], ci=0.5), and the thecodont tooth implantation (#5[1], ci=1).

Agkistrognathus is the sister-taxon of all remaining thalattosaurs. The dichotomy is unequivocally supported by the presence of a diastema in the upper jaw (#7[1], ci=1). ACCTRAN character optimization furthermore lists the ankylothecodont tooth implantation (#5[2], ci=1), the close approach of the frontal to the external naris (#15[1], ci=0.5), and the presence of a frontal/supratemporal contact (#18[2], ci=0.667). DELTRAN character optimization also adds support to the node by #5[2]. There are no autapomorphies of *Agkistrognathus* in the analysis.

Paralonectes and the remaining thalattosaurs are unequivocally diagnosed by the procumbent anterior most dentary teeth (#8[1], ci=1) as well as the blunt and bulbous posterior maxillary and dentary teeth (#9[1], ci=1). Neither ACCTRAN nor DELTRAN character optimization provide further support.

Unequivocal autapomorphies of *Paralonectes* are the dorsally recurved anterior alveolar margin of the maxilla (#4[1], ci=0.5) and the posterior extension of the nasals

(#14[1], ci=0.333). DELTRAN character optimization additionally lists the disctinctly ventrally recurved rostrum (#2[2], ci=0.5)

Thalattosaurus and *Clarazia/Hescheleria* are unequivocally supported by the lack of a ventral squamosal process (#22[1], ci=1). Only DELTRAN character optimization additionally lists the close approach of the frontal to the external naris (#15[1], ci=0.5) and the presence of a supratemporal/frontal contact (#18[2], ci=0.667).

Unequivocal autapomorphies of *Thalattosaurus* are the elongated preorbital skull portion (#1[2], ci=0.667), the long and low maxilla (#3[0], ci=0.5), the absence of a true premaxilla dentition (#6[1], ci=0.5) , and the presence of a medial lamina of the quadrate (#23[0], ci=0.5). Only DELTRAN character optimization provides further autapomorphies by the broad posterolateral frontal process (#19[1], ci=0.5) and the slender scapula (#31[1], ci=0.5).

Clarazia and *Hescheleria* form the Claraziidae sensu PEYER (1936a). Unequivocal support is given by the superficial tooth attachment (#5[3], ci=1), the only slightly expanded radius (#33[1], ci=1), and the reduced deltopectoral crest (#35[1], ci=0.5). ACCTRAN character optimization adds support to the node by the constricted posterolateral frontal process (#19[0], ci=0.5) and the broad scapula (#31[0], ci=0.5), while DELTRAN character optimization additionally lists the only slightly expanded fibula (#34[1], ci=1).

There is only one unequivocal autapomorphy of *Clarazia*, the low neural spines of the trunk (#28[0], ci=0.5). *Hescheleria* presents one autapomorphy under ACCTRAN character optimization, the distinctly ventrally recurved rostrum (#2[2], ci=0.5), while DELTRAN character optimization also lists #2[2], as well as the presence of an anterior process on the cervical ribs (#30[1], ci=0.5).

Due to the significant number of characters that could not be coded for every taxon, bootstrap support is not very high, and only a few nodes seem to be well-supported (fig. 56B). Furthermore, a search with only one step longer resulted in 16 trees (fig. 57A). Not all of them display the same dichotomies as above, although in a 50% majority rule consensus the here listed nodes are still represented (fig. 57B). A similar problem occurred in the thalattosaur analysis of LIU & RIEPPEL (2001).

In a different run, the Salzburg specimen was additionally included, even though it could be coded for only a few characters. The result consisted of 3 equally parsimonious trees

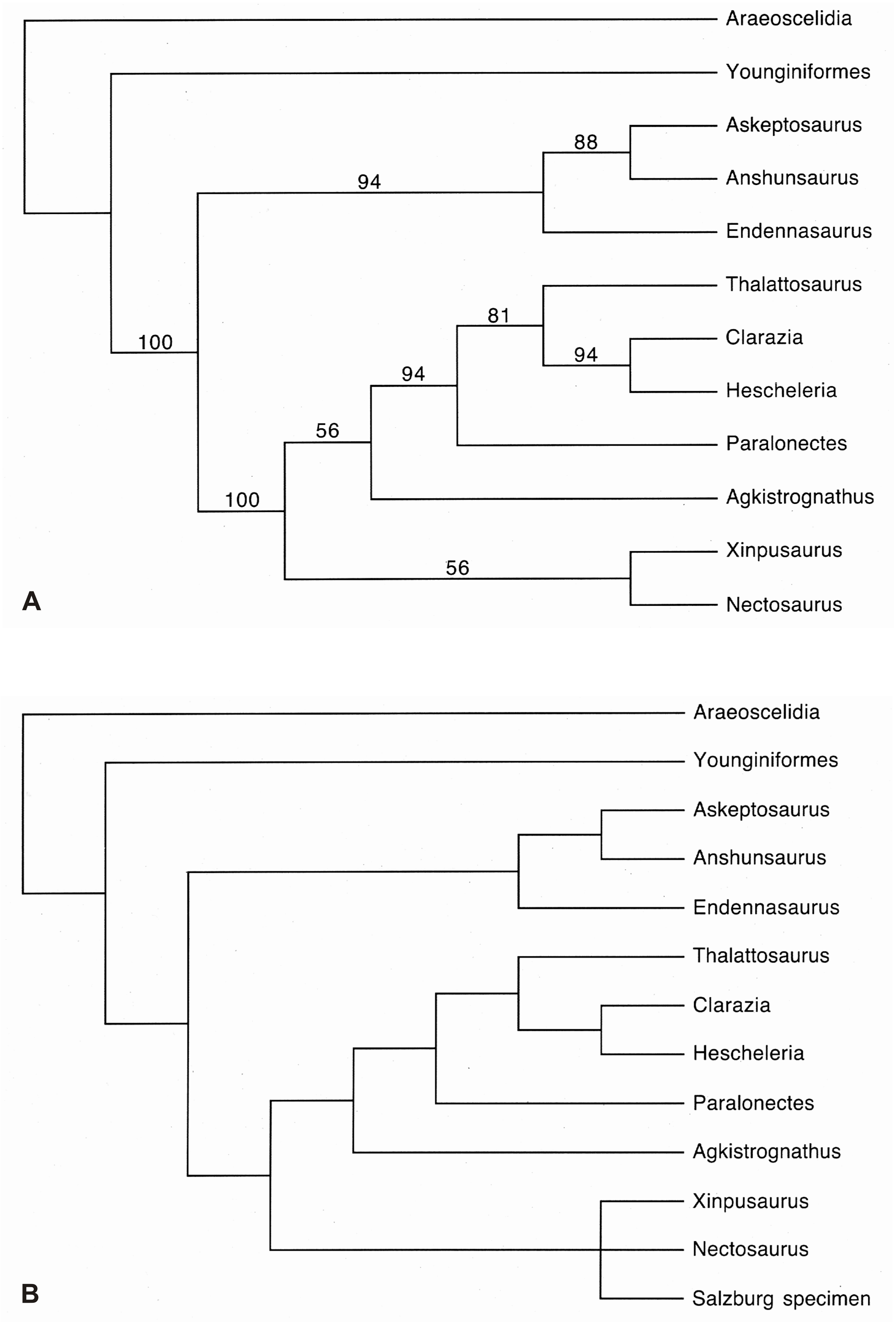


Fig. 57: A) 50% majority rule consensus of 16 equally parsimonious trees, resulted from a run being one step longer, B) strict consensus of three equally parsimonious trees (67 steps) when the Salzburg specimen is included.

(TL=64, CI=0.6875, HI=0.3281, RI=0.7260, RC=0.4991) in which the Salzburg specimen always nested within the clade comprising *Xinpusaurus* and *Nectosaurus*, while the remaining tree topology remained unchanged. Thus, the phylogenetic assumptions outlined in the description of the Salzburg specimen appear supported here.

Furthermore, it should be noted that the present topology still remains stable when the very poorly preserved taxa *Agkistrognathus* and *Paralonectes* are excluded.

4.2.2. Discussion

4.2.2.1. Comparison with previous analyses

In recent years, there were three computer-aided analyses of thalattosaur ingroup relationships, whereas none of them included all valid taxa known today.

When NICHOLLS (1999) conducted her analysis, the Chinese taxa were not described yet. Her result was mainly, but not exclusively based on cranial characters and consisted of an unresolved polytomy of *Endennasaurus*, *Askeptosaurus*, and all remaining thalattosaurs. Within the latter, *Hescheleria* was the sister-taxon of the others, successively followed by *Nectosaurus*, *Clarazia*, *Thalattosaurus*, *Paralonectes*, and *Agkistrognathus*. There are only a few similarities to the present result. The Thalattosauria are separated from *Askeptosaurus* and *Endennasaurus*, and *Clarazia* is relatively closely associated with *Thalattosaurus*. On the contrary, *Hescheleria* is widely separated from the latter two, and *Agkistrognathus* and *Paralonectes* are not that basally positioned.

RIEPPEL et al. (2000) excluded *Endennasaurus*, *Nectosaurus*, *Paralonectes*, and *Agkistrognathus*, but included *Anshunsaurus*. Furthermore, the data matrix only consisted of cranial characters. The result was a monophyletic group comprising *Anshunsaurus* and *Askeptosaurus*, opposed to the unresolved, but monophyletic clade of *Thalattosaurus*, *Clarazia*, and *Hescheleria*. The result is very similar to the one presented here, and may have suffered from the low number of included taxa.

The third analysis (LIU & RIEPPEL 2001) also included *Xinpusaurus*, *Agkistrognathus*, *Nectosaurus*, and *Paralonectes*, but still ignored *Endennasaurus*, and again only consisted of cranial characters. The result was *Askeptosaurus* as the sister-taxon of all other thalattosaurs, successively followed by *Anshunsaurus*, the monophyletic *Xinpusaurus* and *Nectosaurus*, *Agkistrognathus*, and finally the clade comprising *Clarazia*, *Hescheleria*, and the monophyletic *Thalattosaurus* and *Paralonectes*. Major differences to the present result are the lack of a monophyletic Askeptosauridae, the nesting of *Paralonectes* with *Thalattosaurus*, and the absence of a monophyletic *Clarazia* and *Hescheleria*. A notable similarity is the sistergroup relationship between *Xinpusaurus* and *Nectosaurus*.

In conclusion, the here presented analysis resurrects for the first time the previously suggested monophyly of *Clarazia* and *Hescheleria* (RIEPPEL 1987), and it also corroborates RENESTO´s (1992) assumption that *Endennasaurus* may be more closely related to *Askeptosaurus* than to other thalattosaurs. Furthermore, all analyses confirm the monophyly of the Thalattosauria, to which at least *Askeptosaurus* is always opposed.

The present result, however, slightly differs from the large-scale analysis in which the slit-like upper temporal fenestra of *Askeptosaurus* is considered as an autapomorphy of this taxon rather than a basal feature of thalattosaurs in general, a computational consequence of the poorly preserved cheek configuration of *Endennasaurus*. If more specimens of *Endennasaurus* become known, this problem may be clarified.

4.2.2.2. Biogeography and evolution of thalattosaurs (fig. 58)

Unfortunately, the fossil record of thalattosaurs is still very poor, and as LIU & RIEPPEL (2001) correctly stated, it is currently not possible to say much more than that thalattosaurs were obviously a widespread group during the Triassic period. Hence, only a tentative biogeographical interpretation can be given here.

At present, the clade comprising *Endennasaurus, Askeptosaurus,* and *Anshunsaurus* is only known from the Alpine Triassic and southern China, whereas the occurrence of *Askeptosaurus* in the middle Triassic represents the oldest record for the clade. *Anshunsaurus* stems from lower upper Triassic strata of the Chinese Guizhou Province (RIEPPEL et al. 2000), and *Endennasaurus* is of Norian age (RENESTO 1984). Since the latter is the sister-taxon of askeptosaurids and *Askeptosaurus* is the oldest known representative, there is a slight indication that the last common ancestor of the clade lived in the northwestern Tethyan area.

The next clade comprising *Xinpusaurus* and *Nectosaurus* shows a different distributional pattern. *Xinpusaurus* is known from the same age and locality as *Anshunsaurus* and currently represents the oldest member of this specific clade, but *Nectosaurus* comes from the upper Triassic of North America. LIU & RIEPPEL (2001) already assumed trans-Pacific (or trans-Panthalassan) relationships between *Xinpusaurus* and *Nectosaurus*, and their view

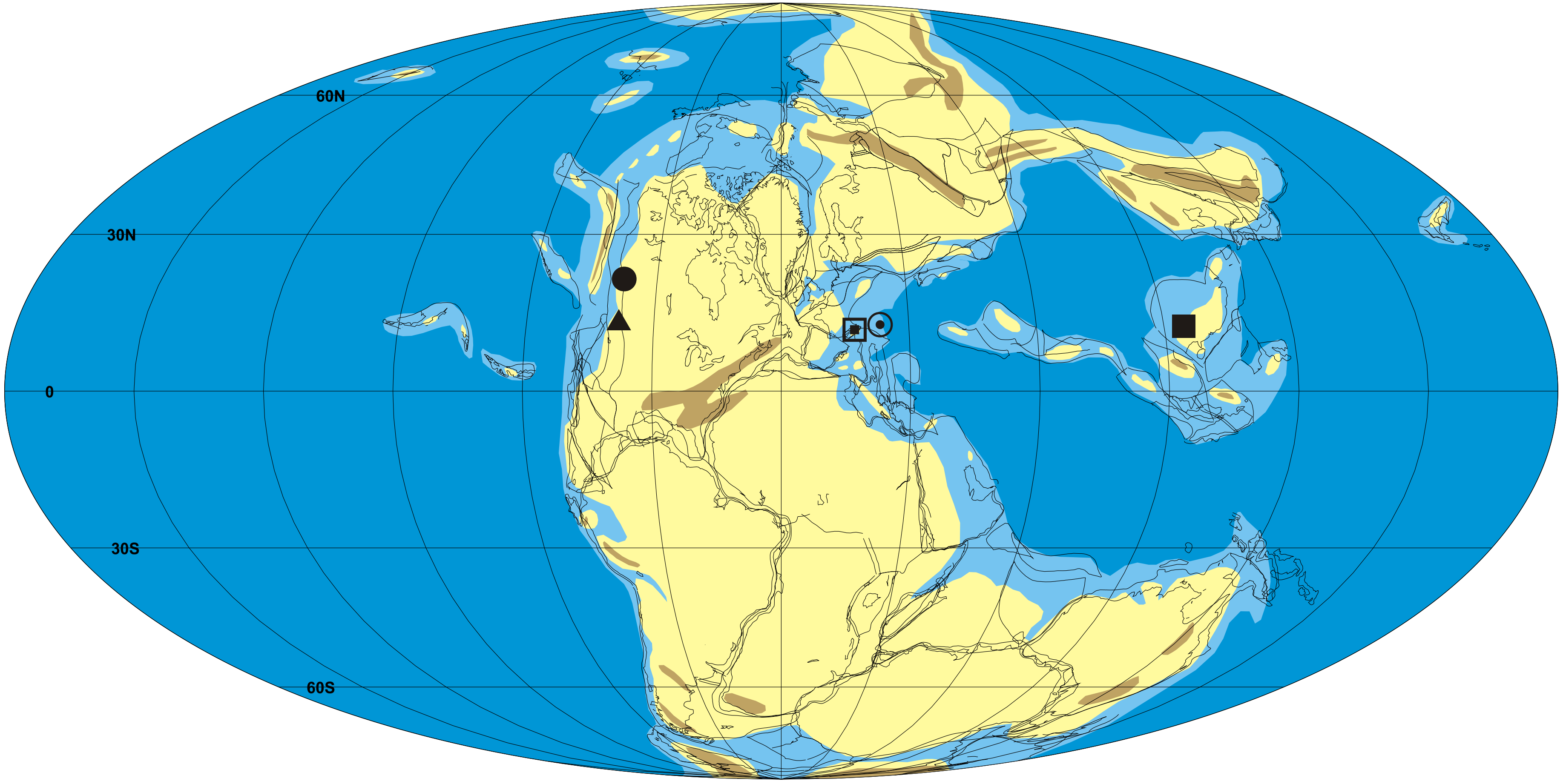


Fig. 58: World map of the late Middle Triassic (237 Ma) showing the localities where thalattosaurs have hitherto been found: ●, Lower/Middle Triassic of British Columbia (*Agkistrognathus, Paralonectes, Thalattosaurus*), ▲, Upper Triassic of California (*Thalattosaurus, Nectosaurus*), ⊡, Middle Triassic of Monte San Giorgio (*Askeptosaurus, Clarazia, Hescheleria*), ⊙, Norian of the Alpine Triassic (*Endennasaurus* and the Salzburg specimen), ■, Middle/Upper Triassic of the Guizhou Province, China (*Anshunsaurus, Xinpusaurus*). World map from KISSLING (unpublished).

appears to be corroborated in the present study. The fact that the Norian Salzburg specimen, however, also nests within the clade indicates that this assemblage was probably not as restricted as previously assumed, and rather showed a more widespread distribution.

The last major clade includes the oldest known thalattosaurs, *Paralonectes, Agkistrognathus,* and *Thalattosaurus* from the lower/middle Triassic of British Columbia (*Thalattosaurus* was obviously a long-existing taxon as it also occurs in the upper Triassic of California). These three taxa are relatively basally positioned, and it seems that the clade originated in North America and subsequently invaded the northwestern Tethys at latest in the middle Triassic, as then the monophyletic *Clarazia* and *Hescheleria* occurred at Monte San Giorgio. A problem of this interpretation is, however, that no representatives of this clade are currently known from China, but it should be mentioned that an undescribed, probably “claraziid“ thalattosaur from the Guizhou Province is housed in the Staatliches Museum für Naturkunde Stuttgart, which cannot be officially described due to its politically unresolved status. Another difficulty is that the remaining thalattosaur clades all include younger taxa, and therefore ghost-lineages must be postulated for the monophyletic groups comprising *Endennasaurus*/askeptosaurids and *Xinpusaurus/Nectosaurus*.

A tentative evolutionary scenario of thalattosaurs may be that the clade originated at latest in the early Triassic, and that the last common ancestor lived somewhere in the northern Tethys, i.e. at the southern margin of Laurasia. This assumption is corroborated by the above outlined interpretation that the clade comprising *Endennasaurus* and askeptosaurids probably originated in the northwestern Tethyan area and that the oldest-known member of the closest sistergroup, *Xinpusaurus,* comes from southern China, which, at Triassic time, was positioned within the transition from the eastern Tethyan to the Pacific ocean (RIEPPEL et al. 2000).

Generally, it seems that thalattosaurs usually lived in near-shore habitats with normal marine surface water and a rich faunal diversity. At least this can be stated for the thalattosaurs from Monte San Giorgio and Endenna, while the environment of the other taxa unfortunately is not so well investigated. However, the Chinese horizons as well as the North American localities also bear several other vertebrates, e.g. mixosaurid ichthyosaurs and different sauropterygians (NICHOLLS & BRINKMAN 1993, SANDER et al.1997, RIEPPEL et al. 2000), so the habitats were probably relatively similar to those of Europe. In the case of Monte San Giorgio, the fact that no thalattosaur is known from the younger Ladinian fossil-bearing horizons indicates that habitats with a depauperate fauna and partly hypersaline conditions were not preferred by these animals.

When the two major thalattosaur assemblages split from one another, the clade comprising *Endennasaurus* and askeptosaurids still retained some terrestrial features such as the relatively well ossified carpus and tarsus. Therefore one may assume that the animals still made excursions onto land. The development of long necks was perhaps related to the way of nutrition, as it seems that at least askeptosaurids mainly fed on movable prey, where a long, elastic neck might have been of advantage (see chapter 4.3.2). *Askeptosaurus* probably was a more generalized feeder, while *Endennasaurus* possibly preferred soft-bodied invertebrates and only occasionaly fed on small vertebrates. Additionally, both taxa developed different swimming styles, the former presented a laterally undulating movement, while the latter mainly swam by using its extremities (see chapter 4.3.4).

The remaining thalattosaurs show comparatively short limbs with broadly expanded zeugopodia, suggesting that they were more adapted to marine life. The high neural spines and the long tail, which are present in most of these taxa, additionally indicate that lateral undulation as a way of aquatic movement had been further improved. Moreover, all these forms present prominent and sometimes even blunt and bulbous teeth that are also often found in the palate, and many taxa additionally present a downturned rostrum of unknown function. A very specialized ecology was obviously a major feature of this clade and perhaps responsible for the separation of *Endennasaurus* and askeptosaurids, i.e. the respective taxa probably fed on hard-shelled, slow-moving or sessile invertebrates like bivalves or gastropods. The Thalattosauria may have invaded the North American shorelines via China and, as outlined below, Pacific islands, and later returned to Tethyan areas (see above). There were probably several re-invasions to the Tethys, indicated by the Salzburg specimen, which is relatively young and not closely related to *Clarazia* and *Hescheleria*.

As already noted by RIEPPEL et al. (2000), thalattosaur biogeography shows similarities to the pattern seen in stem-group sauropterygians. Also in this clade, there are monophyletic groups comprised of taxa from the western Tethys and China (pachypleurosaurs), but also taxa including representatives from the European Tethyan shoreline and North America (pistosaurids). Since the present phylogenetic analysis corroborates the result of RIEPPEL et al. (2000) and shows an even more detailed resolution, the authors´ arguments to explain such a distribution deserve serious consideration. RIEPPEL et al. (2000) and RIEPPEL (2000) suggest that the relatives of the today known clades may have lived in the surroundings of exotic terranes or volcanic arcs in the equatorial Pacific ocean, as in their opinion it is unlikely that forms without pelagic adaptations like stem-group sauropterygians or thalattosaurs crossed larger pelagic distances, and thus must have been restricted to epicontinental seas or intraplatform basins. A second possibility, a dispersal somewhere along the northern Laurasian coast, could be excluded due to the climatic differences between northern and more equatorial latitudes, which is indicated by ammonoids. The assumption seems reasonable because also today, ectotherm marine reptiles such as sea turtles are usually not able to stay in colder areas for a longer time (PRITCHARD 1979). By contrast, the fossil record of ichthyosaurs indicates that these animals indeed used the northern route (SANDER 2000). Ichthyosaurs, however, had probably a very different ecology due to their pelagic adaptations like, e.g., the thunniform body outline, and they are therefore not truly comparable.

Unfortunately, since thalattosaurs still show a very poor fossil record it is currently not possible to present a more detailed hypothesis, and an interpretation beyond the level outlined above would run the risk to consist of simple speculation.

4.3. Palaeoecological considerations

In this chapter, a restoration of the jaw muscles of *Askeptosaurus* will be presented, followed by a functional interpretation of the skull with regard to the supposed feeding strategy, and a discussion of the assumed way of aquatic locomotion. The results will then be used for a comparison with the inferred nutrition habits and swimming mode of *Endennasaurus*.

4.3.1. Restoration of the jaw muscles of *Askeptosaurus* (figs. 59, 60)

It is almost a trivial statement that without the knowledge of muscle anatomy, an interpretation of the functional morphology of an animal is extremely difficult and in some cases even impossible. While in extant taxa this problem can easily be resolved, soft parts of fossil forms are usually not preserved any more, and this is unfortunately also true for *Askeptosaurus*. For that reason, only a tentative restoration of the muscles rather than a real description is possible. The restoration of muscle anatomy in a fossil animal, however, has to follow a strong methodology, otherwise it could be considered to consist of simple speculation.

4.3.1.1. Ways of inference

As pointed out by BRYANT & SEYMOUR (1990), two general ways of inference are regularly be used when a muscle reconstruction is to be conducted. One is to restore the muscles as indicated by preserved muscle scars, and the other one is to infer the anatomy by using the closest living relative for comparison. BRYANT & SEYMOUR (1990) noted that an interpretation derived from muscle scars is problematical, because extant animals often show great differences in the development of the scars, even though shape and thickness of the respective muscle is equal. Hence, it is of course possible to use osteological traces for the inference of muscle anatomy, but one should not exclusively rely on this method. BRYANT & SEYMOUR (1990) suggest that the second attempt, an interpretation derived from phylogeny, should be favoured, but they also point out that this is only reliable when the relationship between the extant representative and the fossil animal is relatively close.

A third method, which, however, is doubtlessly depending on the above two attempts,

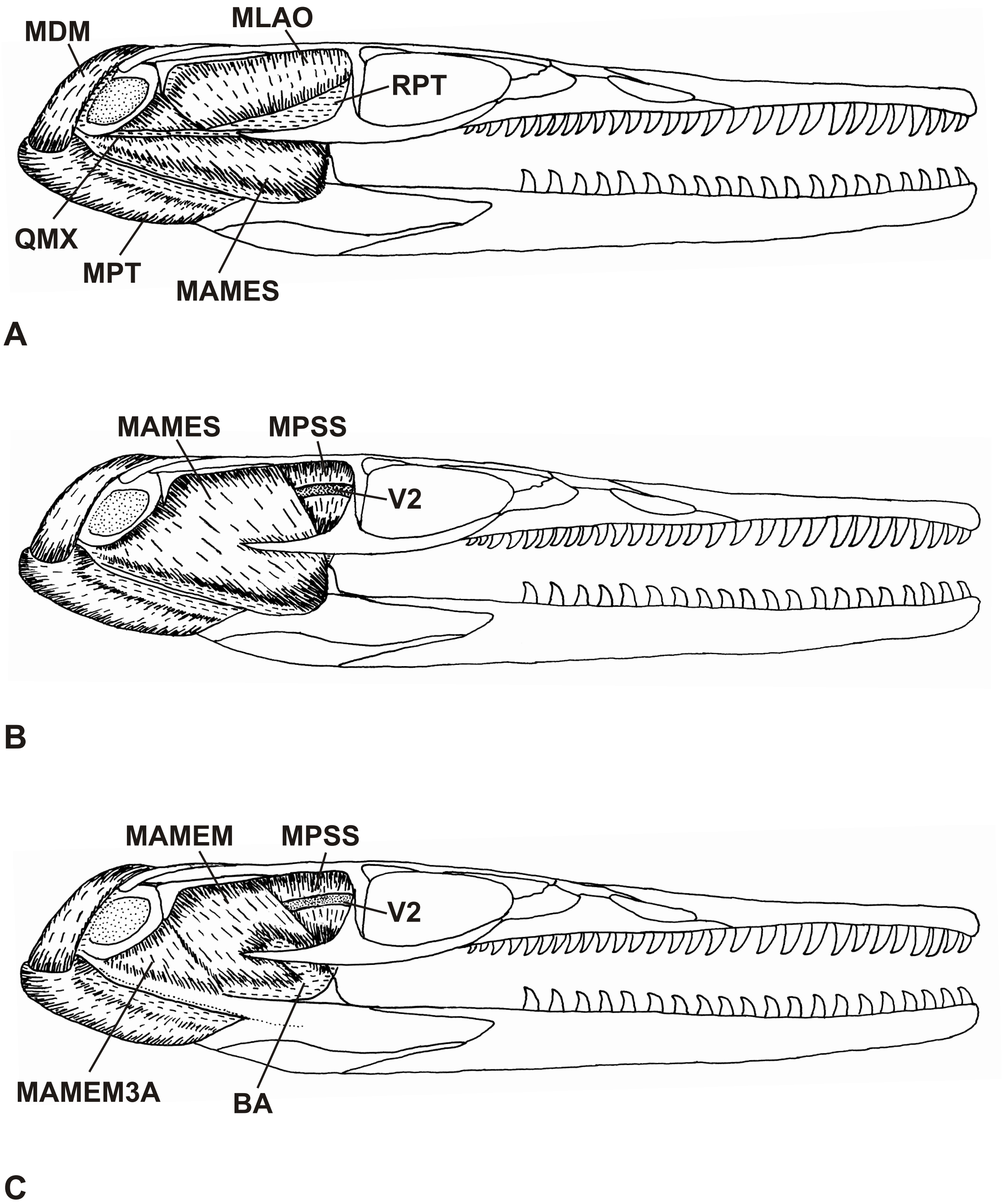


Fig 59: *Askeptosaurus italicus*, restoration of the jaw muscles, beginning with the external most part (A) and successively showing the deeper portions (B, C).

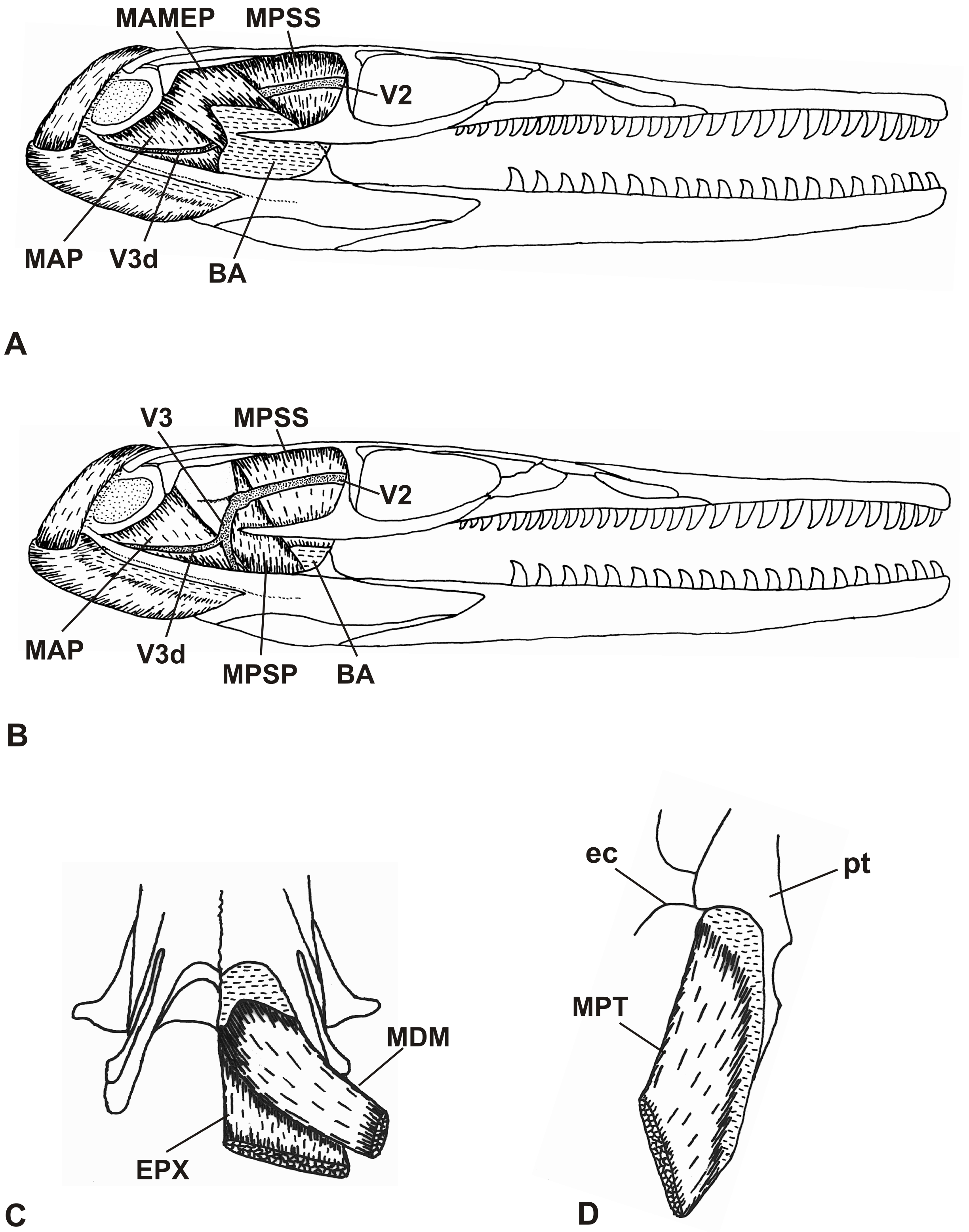


Fig. 60: *Askeptosaurus italicus*, restoration of the jaw muscles, continued. A) and B), deepest portions of the jaw muscles in the cheek region, C) the depressor mandibulae muscle in dorsal view, D) insertion of the pterygoideus muscle on the palate in ventral view. Not to scale.

is an inference of muscle anatomy as suggested by functional reasons (see e.g. RIEPPEL 1989a, 2000). Osteology of a fossil animal may, for example, prohibit that a muscle is trended in the same way as in an extant, possibly even closely related organism, because this would hamper efficient function due to an unusual arrangement of the muscle fibers.

In the following restoration of the jaw muscles of *Askeptosaurus* it is tried to combine all the three methods, as this is supposed to be the safest way of inference. Each attempt will be outlined below in a more detailed way.

4.3.1.1.1. Osteological indicators for muscle or tendon attachment (fig. 61A)

Personal dissections of extant lizard material (*Lacerta laevis*, *Darevskia rudis tristis*, *Parvilacerta parva*, *Timon pater*, *Varanus prasinus*) provided insights into the way of how muscles or tendons attach to a bone. Generally, the following major ways of attachment could be distinguished:

a) Sharp crests on the surface of a bone or sharpened bone margins. Those structures are usually coupled with the attachment of tendinous sheets. A typical example is the lateral crest often observed in the posterior part of the mandible of lacertid or teiid lizards. This crest does not function as point of insertion for a muscle itself, but serves as attachment area for a fascia of the superficial portion of the external jaw adductor as well as of the pterygoideus muscle (see e.g. MÜLLER 2002).

b) Distinctly flattened surfaces or slight depressions. Such structures also indicate muscle attachment, at least in some cases. For instance, on the smooth, ventrally orientated lateral facet of the parietal in *Varanus* originate parts of the adductor mandibulae muscle. Another example can be found in lacertids, where the posteriormost area of the mandibular fossa is usually roofed by a flattened, thin extension of the surangular, representing the insertion area of the 3a-head of the mandibulae externus muscle.

c) Irregular rugosities on the bone surface. Those structures are also indicators of fiber attachment. The coronoid apex in lacertids often shows a rugose surface, and indeed fibers of the externus superficialis portion insert into this point (MÜLLER 2002).

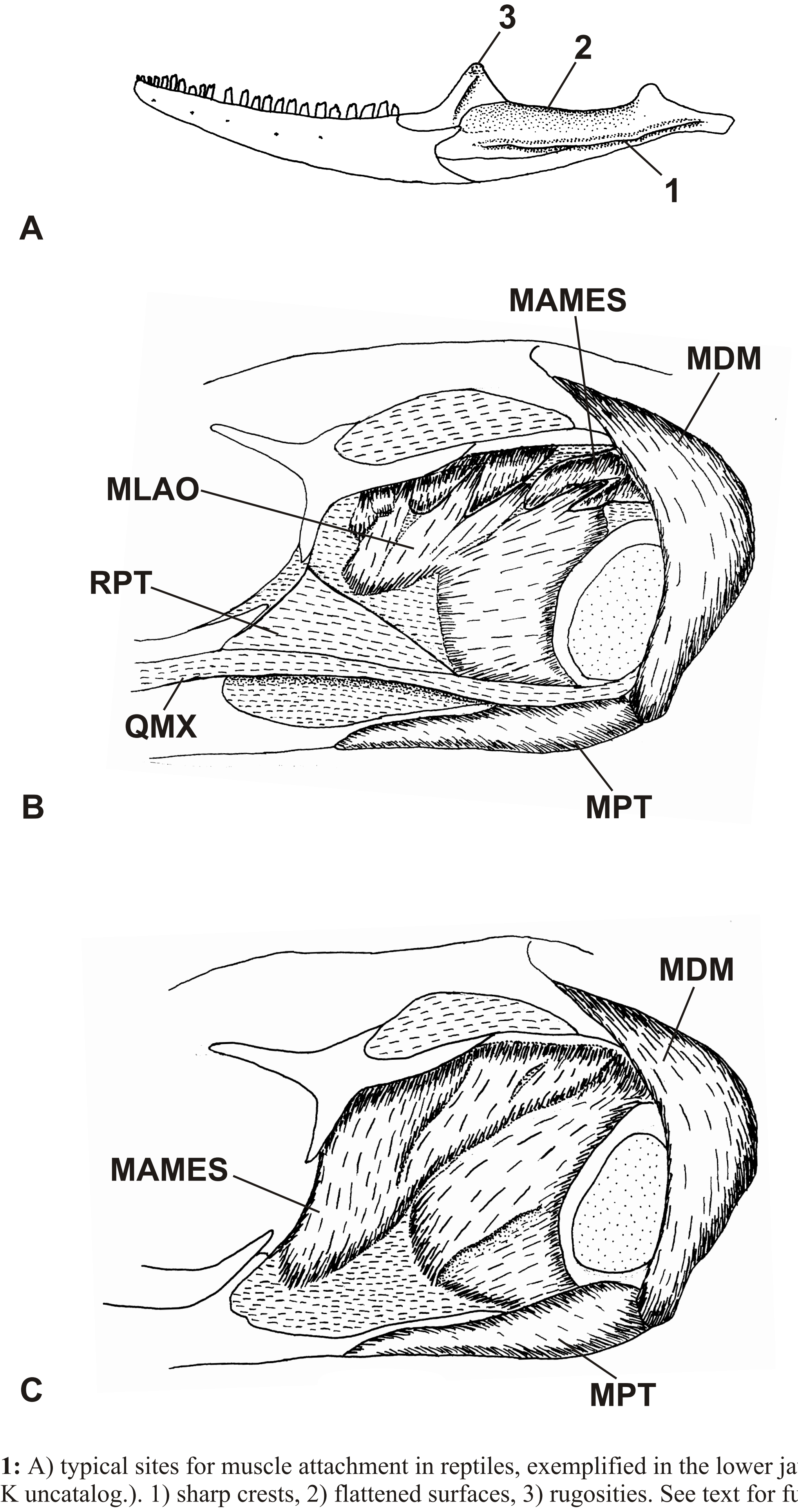


Fig. 61: A) typical sites for muscle attachment in reptiles, exemplified in the lower jaw of *Lacerta laevis* (ZFMK uncatalog.). 1) sharp crests, 2) flattened surfaces, 3) rugosities. See text for further details. B) and C) *Varanus prasinus*, trigeminal jaw muscles (GPIM uncatalog.). B) external most area, C) somewhat deeper portion. Not to scale.

4.3.1.1.2. Phylogenetic indicators

If a soft part restoration shall also be based on phylogenetic relationships, it should rely on a topological pattern resulting from cladistic analysis to provide a reasonable basis for the inference of muscle morphology by means of taking the closest extant relative into account. In the case of *Askeptosaurus*, the phylogenetic pattern proposes thalattosaurs to be the sister-group of saurians (see chapter 4.1), therefore archosaurs and lepidosaurs must be used as indicators. In the present study, crocodiles, *Sphenodon*, and squamates were therefore used as a reference. It should be noted that the morphology of lepidosaurs is personally supposed to be the most useful one, as cladistic analysis supports the view that the construction of the squamate skull is relatively plesiomorphic with regard to the kinetic palate and the reduced lower temporal bar, and suggests that the respective confíguration of *Sphenodon* and, especially, of crocodiles is derived (see chapter 4.1). The required neontological data were not only taken from the literature (LAKJER 1926, RADOVANOVIC 1935, SÄVE-SÖDERBERGH 1945, HAAS 1973, SCHUMACHER 1973, RIEPPEL 1980, 1984, YOUNG 1987, ZAHER 1994) but also stem from personally conducted dissections of lacertid and varanid lizards (see above). These two groups are very useful within this context, because lacertids present the morphology of a lizard with an almost completely closed upper temporal opening, and varanids, especially *Varanus prasinus*, have an elongated and relatively low head.

4.3.1.1.3. Functional indicators

There are several aspects that determine the functional potential of a muscle. The force output depends on the thickness of the compartment, i.e. the number of fibers, while the action range is related to the absolute length of the muscle (see e.g. RIEPPEL & GRONOWSKI 1981). The latter aspect has its reason in the fact that the overlap of actin and myosin filaments in a single sarcomere should not be reduced too dramatically during passive stretching, because in this case the force output would be too low in the initial phase of contraction. These determinants are very important, especially when small or, as in *Askeptosaurus*, low skulls are regarded, because in those cases it is often very difficult to achieve a jaw muscle length that provides an efficient function. The issue becomes especially problematic when an aspect like jaw opening is taken into consideration, as the danger of "over-stretching" may hamper a reasonable inference of anatomy. For these reasons, it may prove useful to additionally consider the concept of "functional equivalence" for a muscle restoration (see e.g. GANS et al. 1985, GANS & DEVREE 1987). This concept relates to the arrangement of sarcomeres in parallel-fibered or pinnate muscles. When "functional equivalent", the sarcomeres in those muscles should occupy the same position on the length-tension curve and possess equal properties. From this follows that muscle fiber length is depending on the distance to the center of rotation, which means that the distal most positioned fiber will be stretched to the highest degree in a rotational movement, as it occurs, e.g., during jaw opening. Additionally, the degree of stretching is also dependent on the angle of insertion, which has its reason in the fact that an insertion at low angle results in a lesser degree of stretching of the muscle fiber (RIEPPEL & GRONOWSKI 1981), an aspect of special importance in animals with small or very low skulls.

All these points shortly illustrated here are relevant when a muscle restoration is to be conducted, as especially the low skull of *Askeptosaurus* raises several problems concerning the functional effectivity of the respective muscles. Particularly in *Askeptosaurus*, however, one should also bear in mind that this animal had a relatively narrow skull table coupled with a prominent laterally extended position of the orbital rim and the jugal (fig. 8A). Thus, a muscle originating from the skull roof and inserting on the dorsal or lateral side of the mandible has, next to a ventral orientation, also a distinct lateral component in its alignment, which also "lengthens" the muscle to some extent. Furthermore, assuming that the degree of stretching amounted to 30% of the original muscle length, which corresponds to the average value for vertebrates (KARDONG 2002), a long-snouted animal like *Askeptosaurus* could thus achieve an appreciable gape despite a relatively low angle of opening.

4.3.1.2. Inferred muscle anatomy

4.3.1.2.1. The adductor mandibulae externus muscle of *Askeptosaurus* (figs. 59, 60A)

Following LAKJER´S (1926) definition, the adductor mandibulae externus muscle is that portion which is situated laterally to the trigeminal nerve. The external adductor is usually subdivided into different portions, the superficialis (MAMES), the medialis (MAMEM), and the profundus (MAMEP) portion. It is of course difficult todraw this distinction in a fossil animal, as even in some modern diapsids the respective separation of the different compartments cannot easily be observed. Anyhow, a tentative approach will be conducted in the following, whereas one should be aware that this only represents a very general interpretation.

In lepidosaurs, the superficial portion of the external adductor shows a small derivative on its lateral surface, the levator anguli oris muscle (MLAO; fig. 61B). This muscle, which is sometimes divided into several units (e.g. in *Sphenodon*, *Lanthanotus*, and amphisbaenians), is defined as to insert into the rictal plates (RPT), tendinous sheets that accompany the lower temporal arch of *Sphenodon* at its medial side. In squamates, where the lower arch is reduced, the rictal plates are associated with the quadrato-maxillary ligament (QMX) that extends from the posterior part of the upper jaw to the anteroventral margin of the quadrate (sometimes this ligament is modified and contacts the posterior part of the mandible instead of the quadrate (HERREL et al. 1998)). The rictal plates anteriorly originate at the posteroventral edge of the orbital rim. The levator anguli oris muscle has different points of origin within lepidosaurs. While in *Sphenodon*, where this muscle consists of a levator part and a retractor part, the main origin is situated on the medial surface of the lower temporal arch, the lizard configuration shows the fibers of this muscle to originate from the upper temporal arcade.

The superficialis portion *sensu stricto* covers almost the complete external area of the lower temporal fossa and inserts into the dorsal part of the posterolateral portion of the mandible, either by muscle fibers only or also by an additional tendinous fascia inserting on a mandibular crest (see above) as well as on a distinct lateral edge of the coronoid (fig. 61C). Anteroventrally, superficialis fibers may also insert into the lateral part of the coronoid apex. In *Sphenodon,* some fibers even insert into the lateral surface of the bodenaponeurosis, a tendinous sheet spanning the posterodorsal edge of the mandible in this animal. Dorsally, the superficialis portion originates from the ventral (medial) surfaces of the postorbital and squamosal. In *Sphenodon* and in some lizards as well (e.g. lacertids), the posterodorsal area of the superficialis portion shows a tendinous fascia, spanning both parts of the squamosal and the postorbital and serving also as insertion area for superficialis fibers. Posteriorly, also the anterolateral edge of the quadrate may serve as an area where fibers originate.

In crocodiles, the configuration is different, but less complex. The superficialis portion is a single compartment without any further subdivision, and originates from the broad lower temporal arch, i.e. from the ventral surface of the quadratojugal and sometimes also from the lateral part of the quadrate. The parallel fibers run along the anterior edge of the rictal plate and insert into the dorsal surface of the surangular.

In *Askeptosaurus*, the reduced lower temporal arch should have resulted in a configuration more or less similar to that in squamates (fig. 59A). Some sort of ligament persisted in the area where ancestrally the quadratojugal met the jugal, and the rictal plates originated at the posteroventral edge of the orbital rim, spanning the anteroventral portion of the lower temporal fossa. The levator anguli oris muscle should have lacked a *Sphenodon*-like retractor portion, as there is no bone where the fibres could have originated. Most probably, levator anguli oris fibers had their origin at least in the anterodorsal part of the postorbital, possibly they originated also more posteriorly, and insert into the rictal plates. The superficialis portion *sensu stricto* (also called "1b-head" by LAKJER 1926) is believed to have originated from the posterodorsal margin of the lower temporal fenestra, i.e. the squamosal and possibly also the ventrolateral margin of the quadrate (fig. 59B). Fibers that originated from this area would have inserted ventrally into the dorsal part of the posterolateral side of the mandible, i.e. into the lateral keel of the surangular, which served as attachment area for a tendinous fascia. More anteriorly, some muscle fibers may have inserted directly into the bone surface, which should then be expected to be slightly depressed in the area of insertion. A slight depression in the anterolateral part of the surangular is indicated in MSNM V456 (fig. 10), where the right mandible is exposed in dorsal view. Even though the impression that the respective area is depressed may have been increased by the lateral extension of the mandibular crest, the preserved alignment of the lateral margin still suggests that the surangular was indeed slightly depressed anterolaterally.

The described configuration would result in a strict posterodorsal-anteroventral trend, which would be in accordance with the above cited principle of functional equivalence, because the muscle would be sufficiently expanded and still coupled with a more or less parallel fiber arrangement. However, the overall superficialis-(1b)-portion would be very small, hampering a significant force output. Hence, it is assumed that some additional fibers originated from the dorsal edge of the lower temporal fossa, i.e. the squamosal and the postorbital, and trended relatively steeply into anteroventral direction, either intersecting with the ventral, more obliquely oriented fibers or inserting into a proposed lateral septum of the deeply situated bodenaponeurosis (BA; see below). The suggested configuration can today be observed, for instance, in *Varanus prasinus*, and would result in a more prominent development of the superficialis portion. Furthermore, it has already been suggested for other fossil reptiles like, e.g., *Macrocnemus* (RIEPPEL & GRONOWSKI 1981). Maybe these additional superficialis fibers covered the anterior temporal area completely, as it is suggested by modern diapsids as well as by distinct lateral depressions on the postorbital of *Thalattosaurus* and *Nectosaurus*. This, however, seems functionally problematic due to the flattened skull of *Askeptosaurus*, whose morphology is not mirrored in extant saurians nor in most other thalattosaurs.

The medialis portion of the external adductor of lepidosaurs is much more heterogenously developed than the superficialis layer (fig. 63). In *Sphenodon*, the medialis portion is subdivided into several different heads (at least five), originating from the posterior two-thirds of the upper temporal fossa including the parietal and squamosal. They all insert laterally of the bodenaponeurosis, a tendon situated in the posterior half of the lower jaw and attached on the posterior coronoid margin as well as on the posteromedian parts of the mandible. In squamates, the medialis layer is very different among the specific clades, and in many cases strongly intersected by several aponeuroses (fig. 63A). Generally, however, one can state that it always originates in the area of the posterior part of the upper temporal fossa, even if this is closed, but usually extends relatively far anteriorly as well. Contrary to *Sphenodon*, the bodenaponeurosis does not extend along the posterodorsal edge of the mandible, but it is restricted to the posterodorsal margin of the coronoid apex, hence the medialis portion not only inserts into the lateral side of this sheet but also, as a consequence, into the dorsomedian edge of the posterior part of the lower jaw, often directly beneath the lateral superficialis layer.

In crocodiles, as is often observed, some portions of the superficialis and medialis layers cannot easily be distinguished. Furthermore, in contrast to lepidosaurs and other diapsids, the lower jaw of archosaurs and thus crocodiles is peculiar in the sense that the coronoid is situated only on the medial surface of the lower jaw and lacks any dorsal projection that could serve as attachment for a bodenaponeurosis. The fibers of the medialis portion arise both from the ventral surface of the quadrate and from the anterior and lateral faces of the lateral and medial lamina of the cranial adductor tendon, situated on the lateral part of the skull roof. The medialis fibers show a roughly ventrolateral trend and run, for the most part, into the Meckelian fossa, thereby inserting into the medial surfaces of surangular and angular. The fibers originating from the medial lamina of the cranial adductor tendon insert into a leaf-like tendon lamina attached to the Cartilago transiliens.

Transferred to *Askeptosaurus*, again an arrangement resembling that of squamates is assumed (fig. 59C). The presence of a coronoid dorsal apex indicates that there was at least a

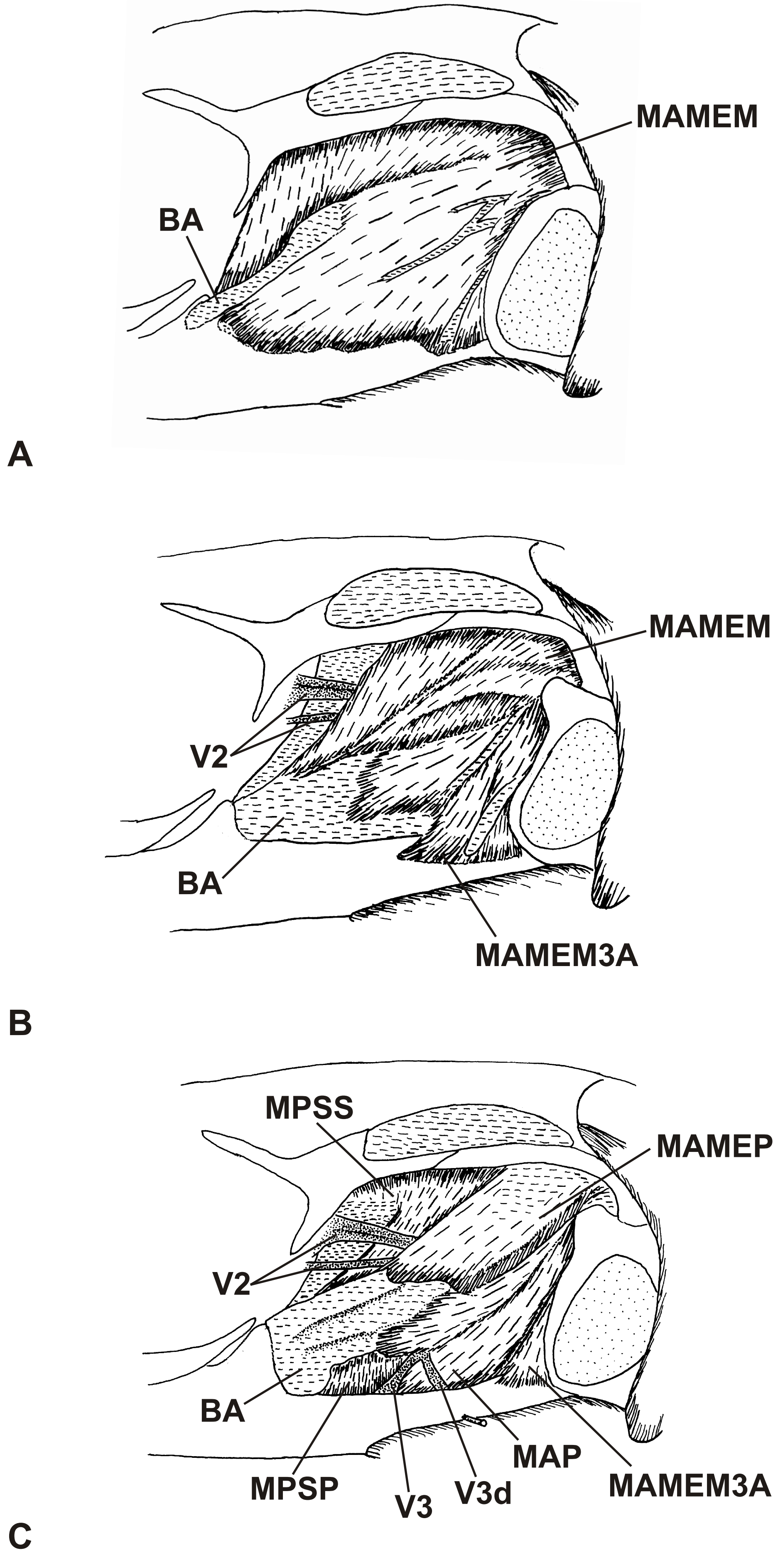


Fig. 62: *Varanus prasinus*, jaw muscles, continued. A), B), and C) showing successively deeper portions of the trigeminaladductor musculature.

small development of the bodenaponeurosis (see below for more details). The origin of the medialis layer is supposed to be situated on the ventral portion of the dorsal part of the squamosal, the posterior area of the postorbital, and possibly also of the posterolateral part of the parietal, i.e., that region where the upper temporal fossa is completely closed. Likewise, this region is equivalent with the posterior area of an ancestrally present upper temporal fenestra. Furthermore, also the anterior margin of the quadrate probably served as area of origin. The medialis portion inserted into the dorsomedian edge of the posterior part of the lower jaw. In the anterior portion of this area, a sharpened median ridge indicates that the bodenaponeurosis may also have had a certain posterior extent. The medialis layer must have inserted laterally, and the bodenaponeurosis is therefore inferred to have been obliquely oriented, slightly trending both dorsomedially and posterodorsally. More posteriorly on the mandible, the dorsal part of the surangular becomes rounded and smooth, and at the posteriormost level of the mandibular fossa even flattened and expanded, with a slender depression in the median area. In these portions the fibers of the medialis layer must have inserted more or less directly into the bone, most probably those originating from the quadrate, which presumably can be assigned to the so-called “3a-head“ (*sensu* LAKJER 1926; MAMEM3A; fig. 62B, C). This muscle was originally considered as part of the profundus layer, but has in the following been interpreted to belong to the medialis portion (RIEPPEL 1984).

The profundus layer of the adductor externus muscle in lepidosaurs is defined as to insert into the medial surface of the bodenaponeurosis (figs. 62C, 63A), even though some fibers sometimes also insert laterally (e.g. in teiids and lacertids; RIEPPEL 1984). In *Sphenodon*, fibers originate from the posterior wall of the upper temporal fenestra and from the posterodorsal process of the prootic (HAAS 1973), while in squamates, the profundus portion also bulges into the post-temporal fenestra, so that sometimes the paroccipital processes too serve as area of origin.

The profundus portion of crocodiles arises from the posterodorsal part of the temporal area, originating from parts of the cranial adductor tendon as well as from the ventral surface of the quadrate. The fibers insert into the medial wall of the Meckelian canal, into the dorsal side of Meckel´s cartilage, into the angular, and into the posterior part of the external adductor tendon.

Due to the poor preservation of the braincase and the internal part of the skull roof, it is much more difficult to restore the profundus layer of *Askeptosaurus* (fig. 60A). Anyhow, it is assumed that this muscle originated in the posterodorsal area of the skull, i.e. medially to the medialis portion and thus from the lateral wall of the braincase and the posterolateral portion of the parietal including the medial surface of the posterior projection leading to the paroccipital process. Presumably also the supratemporal and, due to the flattened nature of the skull, possibly also the post-temporal fenestra and the paroccipital process served as area of origin. As mentioned above, the bodenaponeurosis is assumed to have run posterodorsally. Into its medial surface the profundus fibers must have inserted. Whether they did also laterally, at least to a small extent, must remain open to question.

4.3.1.2.2. The adductor mandibulae posterior muscle of *Askeptosaurus* (fig. 60A, B)

This muscle (MAP) represents an embryological derivative of the externus portion and is always situated posteriorly to the main body of the mandibular (V3) branch of the trigeminal nerve. It is relatively simply developed in lepidosaurs, i.e. both in *Sphenodon* and in squamates its origin is usually situated on the pterygoid lamella of the quadrate or on the anteromedial surface of the same bone, respectively, sometimes also accompanied by a tendon (figs. 62C, 63A-C) . It always inserts into the medial surface of the mandibular fossa and sometimes extends far anteriorly within the lower jaw.

In crocodiles, the origin of the adductor posterior is situated on ventral parts of the quadrate. Furthermore, some fibers also arise from the posterior part of the medial lamina of the cranial adductor tendon. The adductor posterior muscle inserts posteriorly into the anterior surface of the articular, and more anteriorly on the caudal most portion of the Meckelian fossa. Moreover, the deepest parts of the posterior adductor, i.e. those fibers originating from the medial lamina of the cranual adductor tendon, insert into the posterior lamina of the mandibular adductor tendon.

In *Askeptosaurus*, the anteromedial portion of the quadrate can be supposed to have served as origin area (fig. 60A, B). The insertion was situated within the mandibular fossa. The mandibular branch of the trigeminal nerve must have entered the fossa anteriorly to the muscle, but, additionally, also presented a posterior, smaller offshoot (V3d) that passed through a foramen situated posteriorly to the mandibular fossa, ennervating the muscle portions lateral of the lower jaw. The inference of such a configuration is supported by its frequent occurrence in modern lepidosaurs.

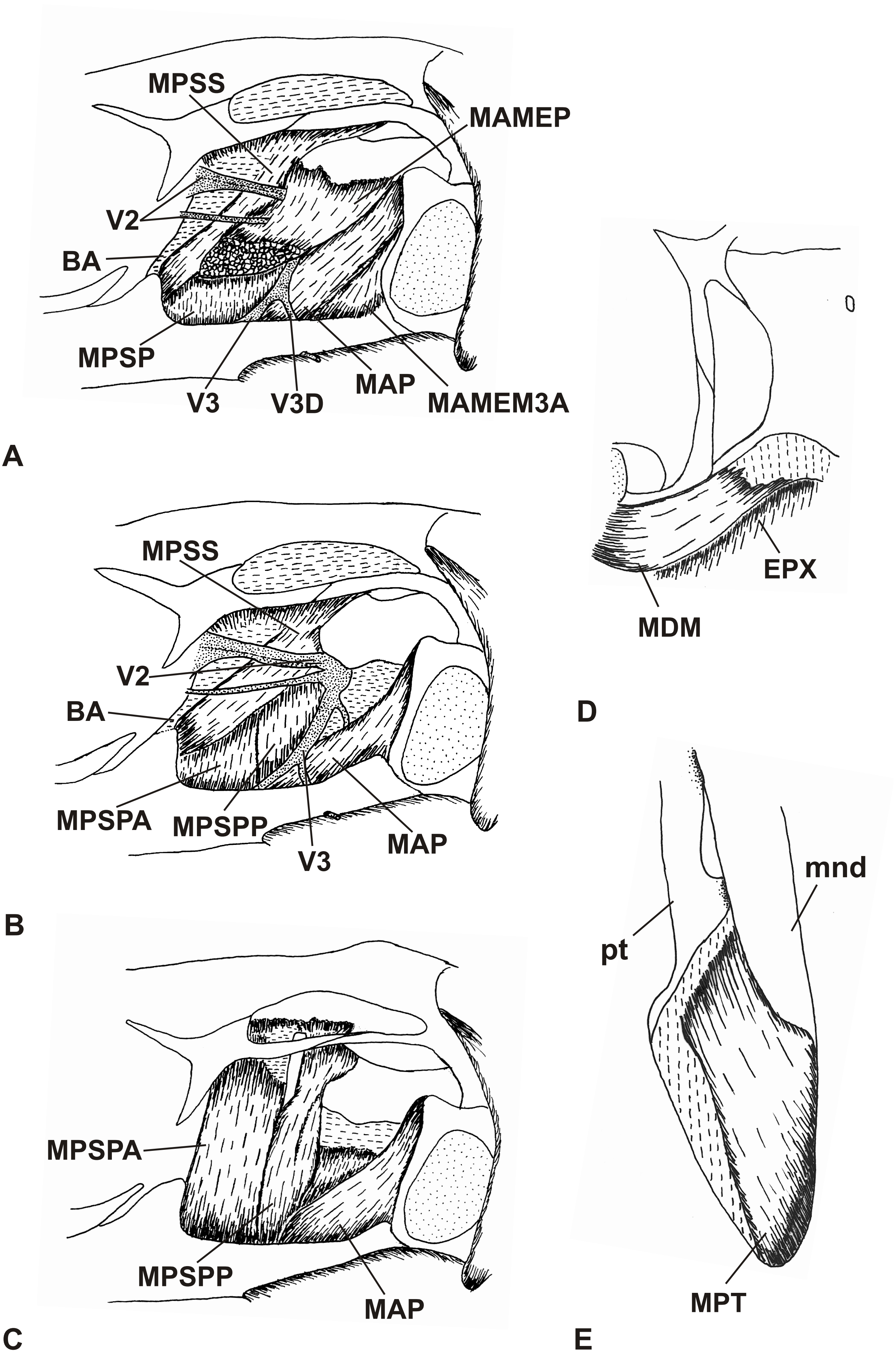


Fig. 63: *Varanus prasinus*, trigeminal musculature, continued. A), B), C), successively deeper muscle portions of the cheek region, D) depressor mandibulae muscle in dorsal view, E) pterygoideus muscle in ventral view. Not to scale.

4.3.1.2.3. The adductor mandibulae internus muscle of *Askeptosaurus* (fig. 60A, B, D)

This muscle is defined as to be situated between the mandibular and ophtalmic branches of the trigeminal nerve. It is subdivided into two major units, the pseudotemporalis and the pterygoideus muscle, both are further subdivided within lepidosaurs.

In *Sphenodon* and squamates, the pseudotemporalis muscle consists of two layers, a lateral superficialis (MPSS) and a medial profundus (MPSP) layer. The superficialis portion, which is lost in gekkotans and snakes, fills more or less that part of the upper temporal fenestra that is not occupied by the externus muscle, and the fibers originate at its medial wall, in lizards also incorporating parts of the descending process of the parietal, if present (fig. 63A, B). In cases where the upper temporal fenestra is closed, as, for instance, in lacertids, the fibers originate from the osteodermal layer occupying the ancestral medial margin of the fenestra, and from the remaining side of the posterior process of the parietal, thereby also contacting the supratemporal. The pseudotemporalis superficialis usually inserts into the anteroventral lateral area of the bodenaponeurosis, often close to the coronoid apex. The pseudotemporalis profundus is a heterogenous muscle. In *Sphenodon*, this layer is situated laterally and anteriorly to the epipterygoid, originating from the descending process of the parietal and the epipterygoid as well as from the membranous wall of the braincase, thereby subdivided into several heads (HAAS 1973). The pseudotemporalis profundus layer inserts into the lower jaw, extending from the anterior end of the coronoid to the articular. In squamates, the profundus portion usually originates from the epipterygoid, the descending process of the parietal, the alar process of the prootic, and sometimes also from the membranous wall of the braincase and the postfrontal (fig. 63A-C), whereas it is usually subdivided into an anterior (MPSPA) and a posterior part (MPSPP). It directly inserts into the ventromedial edge of the mandible comprising the area from the coronoid until to the articular, in a few cases some fibers may also be attached to the bodenaponeurosis.

In crocodiles, the pseudotemporalis portion cannot be subdivided into two distinctive layers. The fibers originate from the upper temporal fossa and the surrounding bones, i.e. parietal, squamosal, and supraoccipital, as well as from the alisphenoid. They have a dorsomedial to ventrolateral alignment and are attached to the Cartilago transiliens, sometimes via narrow tendinous laminae. The most deeply situated fibers insert into the dorsal surface of the mandibular adductor tendon.

In *Askeptosaurus*, the deeper region of the skull unfortunately is not sufficiently preserved, therefore only a very tentative interpretation can be given for the morphology of the pseudotemporalis muscle. It is assumed that there were two pseudotemporalis layers, as the overall configuration of lepidosaurs is interpreted to be more plesiomorphic (see above; fig. 60B). The superficialis portion must have originated from the remaining area of the closed upper temporal fenestra, i.e. those parts which are not occupied by layers of the external adductor. In this case, this would mean that the pseudotemporalis superficialis portion arose anteriorly to the externus portions and probably extended rostrally along the lateral area of the parietal until to the anterior end of the slit-like rest of the upper temporal fenestra, which supposedly was roofed by a fascia that also served as origin area for superficialis fibers. The portion inserted into medial parts of the bodenaponeurosis relatively far anteriorly. The pseudotemporalis profundus layer must have originated around the epipterygoid and the anterolateral wall of the braincase, possibly on its membranous wall as well, and inserted ventromedially to the mandibular fossa. A more definite determination is not possible.

The pterygoideus muscle (MPT) is differently developed among lepidosaurs. So *Sphenodon* presents a unique muscle, the so-called pterygoideus atypicus (HAAS 1973), situated relatively far anteriorly and originating from the dorsal surface of the palatine and the ventral area of the interorbital septum. It inserts into the medial side of the lower jaw close to the coronoid. The pterygoideus typicus muscle of *Sphenodon* is more posteriorly situated. It arises from the ectopterygoid and ventral parts of the pterygoid, from the lower portion of the epipterygoid and the lateral part of the pterygoid extension of the quadrate. It inserts as a great masticatory cushion into the posterventral part of the mandible, but it also extends medially up to the ventromedial edge of the splenial to which it is attached by a tendon. Another tendinous fascia covers the anteroventral portion of the layer. In squamates, the pterygoideus muscle is roughly similar to the typicus portion of *Sphenodon*. In many cases, however, it is subdivided into a deeper and a superficial (ventral) layer. The former, called pterygoideus profundus *sensu* LAKJER (1926), originates from the lateral surface of the quadrate ramus of the pterygoid and inserts into the medial part of the posteriormost area of the lower jaw. The pterygoideus superficialis layer is sometimes clearly separated from the former by a horizontal aponeurosis. It forms the “typical“ pterygoideus muscle and arises from a tendinous sheet situated at the posteroventral edge of the ectopterygoid and the transverse expansion of the pterygoid, as well as from its quadrate ramus. It inserts into the posterior and ventral edge of the mandible and forms the characteristical masticatory cushion (figs. 61B, C, 63E). In some lizards, e.g. lacertids, the lateral insertion of the pterygoideus superficialis portion is formed by a tendon ventrally attached to the above mentioned lateral mandibular crest.

The pterygoideus muscle of crocodiles are usually subdivided into an anterior and posterior portion, although both have strong connections with each other. The anterior part originates from the quadrate, the dorsomedial part of the pterygoid, the praesphenoid, the cartilaginous part of the interorbital septum, the pilar process of the prefrontal, the maxilla, and the ventrolateral part of the palatine, filling the palatal opening completely. The posterior fibers insert into the angular, the articular, and into the posterior lamina of the mandibular adductor tendon. The more anterior fibers are attached to the dorsal surface and the anterior lamina of the tendon. The posterior part of the pterygoideus muscle reaches behind the retroarticular process and also covers lateral parts of the neck. It can be further subdivided into a medial and a lateral layer, and six aponeuroses form the origin and insertion of the fibers: Superficial fibers originate from the medial surface of a tendon attached to the lower jaw and insert into a tendon connected to the pterygoid. From the ventral surface of the pterygoid, further fibers originate and insert into a tendinous sheet that is also attached to the lower jaw. A fourth aponeurosis, connected to the pterygoid and to the posterior lamina of the mandibular adductor tendon - which represents the fifth aponeurosis -, serves as a further point of origin and insertion, along with a sixth tendon attached to the lower jaw.

It is impossible to subdivide the pterygoideus muscle of *Askeptosaurus* as strongly as it can be done for modern diapsids. Nevertheless, origin and insertion of the pterygoideus muscle can relatively easily be determined. So, there is a sharp keel extending along the posterior edge of the transverse flange and the anterolateral portion of the quadrate ramus of the pterygoid, suggesting a tendinous origin of the pterygoideus muscle in this area (fig. 60D). Possibly the muscle originated also from parts of the ectopterygoid and from the more posterior area of the quadrate ramus, but this inference must remain somewhat speculative. The insertion of the pterygoideus muscle is also clearly determinable. The above mentioned crest on the posterolateral surface of the mandible served not only as attachment zone for a tendon of the externus superficialis layer (e.g. fig. 59), but also for a fascia into which pterygoideus fibers must have inserted. Hence, the pterygoideus muscle is assumed to have comprised the ventrolateral and posterior area of the lower jaw, probably it formed also a significant masticatory cushion. It should be added, however, that *Askeptosaurus* shows no retroarticular process, whose posterior portion usually serves as insertion area for the pterygoideus muscle. The absence of this process is a notable peculiarity for a neodiapsid reptile.

4.3.1.2.4. The depressor mandibulae muscle of *Askeptosaurus* (fig. 60)

The lack of a true retroarticular process is also interesting in relation to the depressor mandibulae muscle (MDM). *Sphenodon* presents a depressor mandibulae that originates from the posterior area of the parietal and the squamosal, from the post-temporal arch and from a median tendon posteriorly to the skull roof ("ligamentum nuchae"; HAAS 1973). The muscle trends ventrally and inserts into the retroarticular process. In squamates, the depressor mandibulae muscle is subdivided into an anterior portion, the "true" depressor mandibulae (figs. 61B, C 63D; sometimes this portion is also further subdivided, e.g. in the agamid *Laudakia stellio*; HAAS 1973), and into a posterolateral layer named cervico-mandibularis muscle. The former arises from the posterior edge of the skull roof, the latter from the above mentioned ligamentum nuchae and both insert into the retroarticular process, sometimes not directly on the bone but on the external surface of the posteriormost part of the pterygoideus muscle (e.g. in the lacertid *Parvilacerta parva*; MÜLLER 2002). The depressor mandibulae furthermore serves as attachment area for a tendon spanning the posterior edge of the tympanum (pers. obs.).

In crocodiles, the depressor mandibular is not further subdivided. Fibers arise from the posterior edge of the skull roof, i.e. parietal, squamosal, and supraocciptal, and trend ventrally to insert into the retroarticular process.

The arrangement of this muscle compartment in *Askeptosaurus* was surely determined by the deep posterior excavation of the skull table. Due to the absence of osteological indicators, it is generally problematical to divide the depressor mandibulae into possible separate units, therefore it will be treated here as a single muscle. Assuming that the ligamentum nuchae was well-developed, which is at least indicated by the occipital crest on the posterodorsal surface of the supraoccipital, it can be inferred that some fibers of depressor mandibulae originated at this fascia (fig. 60C). Furthermore, the posteromedial edge of the parietal shows a distinct concavity, which also must have served as area of muscle origin. Although it is supposed that from this point also epaxial neck muscles (EPX) originated, fibers of the depressor mandibulae probably were attached there as well. Presumably the dorsal edge of the concavity served as area for a tendinous attachment of the depressor mandibulae, while the concavity itself represented the origin area of epaxial neck muscles, a similar arrangement can at least be observed in *Varanus prasinus*. The depressor mandibulae trended obliquely into posteroventral direction and must have inserted either into the outer surface of the pterygoideus muscle or into the lateral side of the very short posterior end of the mandible. Thereby the depressor mandibulae must also have contributed to the formation of the posterior edge of a tympanum, whose presence is indicated by the posteriorly excavated morphology of the quadrate. Hence the muscle is supposed to have laterally overlapped the caudalmost portion of the posteroventrally sloping posterolateral process of the parietal (figs. 59, 60).

4.3.1.3. Jaw muscle systems

The general arrangement of the jaw adductor musculature in tetrapods was subdivided by OLSON (1961) into the “kinetic inertial system“ (KI-system) and the“static pressure system“ (SP-system).

The first term is attributed to forms where maximum force is exerted on the lower jaw at wide gape, and the general alignment of the jaw adductors trends from an anterodorsal to a posteroventral direction. Typical anatomical features of animals with a KI-system are a more or less drop-shaped subtemporal fenestra, i.e. its anterior region is distinctly narrowed and the posterior part ovoid-shaped, a flat skull with enlarged interpterygoid vacuities, and reduced kinesis of palate and braincase. The mandible is often relatively elongated, sometimes also deep and heavy, and only in a few cases a retroarticular process is present. Insertion of the adductors is regularly restricted to the immediate surroundings of the mandibular fossa. The KI-system is usually found in amphibians, and, following OLSON (1961), some modified arrangements of the same type can also be detected in crocodiles and a few other reptiles (e.g. some mosasaurs).

The pattern of the SP-system results in a development of maximum force output when the jaws are not in motion and close to the occlusal position. Jaw muscle inclination is posterodorsal or vertical, typical anatomical features are an increasing depth of the skull and the adductor chamber, the development of temporal fenestrae, the presence of a pterygoid flange, kinesis of palate and braincase, additional support of the suspensorium by paroccipital processes and temporal elements, a well-developed coronoid apex and a retroarticular process, and the insertion of the adductor muscles not only around the mandibular fossa but also on the lateral surface of the lower jaw. The SP-system is found in most reptiles and is viewed as a basal feature of diapsids (RIEPPEL 1989a).

One notable exception of these two general patterns were described for nothosaurian sauropterygians by RIEPPEL (1989a, 2000a) on the basis of jaw muscle restorations. In these animals, the upper temporal fenestra is positioned distinctly anteriorly to the mandibular fossa. This unusual configuration obviously resulted in a functional partitioning of the adductor muscles, i.e. the deeper layers arising from the upper temporal opening were anteriorly situated and must have trended posteroventrally, while the superficial portion of the external adductor showed a posterodorsal direction and was situated well posteriorly. This “dual jaw adductor system“ is unique among tetrapods, allowing on the one hand the imparting of maximum force on the lower jaw at wide gape by the arrangement of the deeper muscles, and on the other hand effective pressure when the jaws are near to closure due to the alignment of the superficial layer of the external adductor.

In *Askeptosaurus*, the general configuration was obviously not that specialized. On the basis of the above description, the arrangement of the muscles seems to correspond roughly to the SP-system. This is mainly indicated by the the vertical or posterodorsal alignment of the adductor muscles both inserting on the medial and lateral side of the lower jaw well outside the mandibular fossa, having a line of action pointing into a posterodorsal direction that is characteristic of the SP-pattern. Furthermore, also the ventrolateral insertion on the mandible by the pterygoideus muscle is frequently observed in tetrapods with an SP-system. There are, however, some anatomical differences to animals with the “typical“ SP-expression. As mentioned above, a retroarticular process is ususally present as a result of a well-developed depressor mandibulae muscle. Its absence in *Askeptosaurus,* therefore, is a notable phenomenon. However, it seems that a caudal elongation of the mandible was obviously not necessary due to the distinct posterior excavation of the skull roof to which the anterior portion of the depressor mandibulae was attached, thus forming an obliquely oriented and sufficiently elongated muscle compartment. Another difference is the distinct flattening of the skull of *Askeptosaurus*, reducing the depth of the adductor chamber. However, as can be seen in the dorsal view of the skull, the temporal area is notably laterally expanded in relation to the relatively narrow skull table, hence there should be enough place for well-developed adductor muscles.

4.3.2. Functional interpretation of the *Askeptosaurus* skull

On the basis of the assumption that *Askeptosaurus* displayed an SP-pattern, its functional properties will now be discussed in more detail.

Next to muscle anatomy, also cranial kinesis has to be considered when conducting a functional interpretation. The skull roof of *Askeptosaurus* was obviously akinetic, which is indicated by the complex outline of most of the bones and especially by the strongly interdigitating border between frontals and parietals. According to RIEPPEL (1978), a mesokinetic movement can thus be excluded.

A problematical issue is the question whether *Askeptosaurus* also lacked a metakinetic movement, as the dorsal portion of the braincase as well as the ventral part of the skull roof, which both are essential for a confident inference of metakinesis, are not preserved. A thorough statement is therefore impossible and would only consist of simple speculation. It can be confirmed, however, that the palate and obviously also the quadrate were kinetic. This is suggested by the presence of a basipterygoid articulation and the lack of a sutured contact between pterygoid and quadrate, as well as the absence of a closed lower temporal bar. All of these features are also found in extant lizards, which are typical representatives of tetrapods with a streptostylic jaw articulation, even though it should be admitted that a kinetic palate is not directly related to streptostyly and may simply be viewed as a basal feature of tetrapods (see e.g. RIEPPEL 1978). It is of course difficult to say whether *Askeptosaurus* had an identical way of jaw articulation, but it seems at least probable that there was a certain way of kinesis in the temporal and palatal area, and this assumption will also be taken into consideration in the following interpretation.

An impressing feature of *Askeptosaurus* is the generally low skull and the comparatively long snout, although the rostrum is not similar to the extremely long and narrow snouts of, e.g., gavialid crocodiles. According to TAYLOR (1987), a flat skull minimizes the drag exerted by the surrounding water during movement of the head, and the small cross-sectional area of a slender, elongated rostrum reduces the resistance against water during swimming. The cranial shape of *Askeptosaurus* is therefore rather typical for a marine reptile, but may also have been useful for a specialized predatory strategy (see below).

The distinct elongation of the snout causes the tooth-bearing portion of the mandible to be comparatively long in relation to the part where muscles must have inserted. When such a configuration is present in streptostylic lizards, as, for example, pygopodids (PATCHELL &

SHINE 1986), it is usually related to feeding on vertebrates, allowing a relatively fast but not very strong bite (RIEPPEL & LABHARDT 1979). It can thus be inferred that also *Askeptosaurus* was able to close the jaw relatively fast. The reasons for the elongation of the tooth-bearing portion, however, are surely not the same as in terrestrial lizards. Next to the hydrodynamical demands cited above and the problem that water resistance usually hampers fast movement of a "normally" developed, i.e. relatively short and expanded jaw, the displayed morphology can also be interpreted in the sense of an adaptation to lateral strike movements for prey capture: aquatic vertebrates using this predatory strategy usually have a long tooth-bearing part and a generally low skull, whose flat morphology reduces water resistance and thus facilitates fast movement, and the long tooth-bearing portion increases the probability of a successful strike. This way of prey capture seems likely for *Askeptosaurus*, especially when also the long, movable neck is taken into consideration.

Another point to be considered is the dentition. The teeth of *Askeptosaurus* are relatively homogenously developed, being roughly conical with slightly recurved, sharp apices and only minor differences in size, furthermore they have a relatively robust impression. They greatly differ from other, probably explicitly piscivorous marine reptiles like nothosaurs, which have a distinctly heterodont dentition and relatively slender and elongated teeth (RIEPPEL 2000a). To some extent, the displayed tooth morphology of *Askeptosaurus* resembles the one of modern dolphins (MASSARE 1987, fig. 1A), which usually catch the prey by piercing the body of the animal. The latter author also established several "guilds" in which she placed different marine reptiles from the Jurassic and the Cretaceous. *Askeptosaurus* would roughly fall into the category "Pierce I", which means that the tooth does not show cutting edges but has a sharply pointed apex. On the other hand, the taxon differs from this category in that the teeth are relatively robust and not as slender as it is typical for this "guild" (MASSARE 1987, fig. 4). One should bear in mind, however, that the larger the preferred prey is, the larger and stouter tooth shape becomes (TAYLOR 1987). The fact that the dentition of *Askeptosaurus* is difficult to place into a special category suggests that the spectrum of prey preference was probably relatively broad.

The above notions now make it possible to draw a picture of the feeding ecology of *Askeptosaurus*. This reptile obviously preferred relatively small to medium-sized prey, but it was not exclusively piscivorous, which is indicated by the generalized teeth. *Askeptosaurus* most probably fed on any prey that it was capable to catch and swallow, presumably small to medium-sized fish and maybe also small or young sauropterygians. Prey was putatively caught by lateral sweeps and thereby pierced (see above), while the way of swallowing probably ranged from “ratchet feeding“, where the prey, like it is observed in the modern, streptostylic water snake *Nerodia* (TAYLOR 1987), is forced into the gullet by alternating movements of the unfused mandibles, to “inertial feeding“, which means that the food is momentarily released by the jaw while the head is newly positioned, causing the prey to be finished further back in the mouth.

4.3.3. Aquatic locomotion of *Askeptosaurus*

As can be seen in the skeletal restoration (fig. 64), *Askeptosaurus* had a long neck, a modestly elongated trunk, and a very long tail, coupled with relatively short and stout fore- and hindlimbs. Although the tail was not very tall, the lack of transverse processes indicates that it was not very broad either, but rather laterally constricted. This overall morphology certainly has implications for the locomotory habits of the animal.

Most probably, *Askeptosaurus* did not use underwater flight as mode of locomotion, as it is displayed, for instance, by modern sea turtles (REIF 1984), in which the anterior extremities are significantly enlarged. The trunk morphology displayed by *Askeptosaurus* does not allow to assume that the legs significantly contributed to aquatic locomotion and rather suggests that this animal swam mainly by using the body axis, with the legs being held at the sides of the trunk. Thus, different ways of axial propulsion must rather be taken into consideration.

In a large-scaled survey, BRAUN & REIF (1982, 1985) presented an extensive terminology for different ways of aquatic locomotion, and four of their categories deserve attention in the present case: undulatory locomotion, in which the complete body is strongly laterally undulated with an increasing amplitude towards the end of the tail; subundulatory locomotion, in which movement is restricted to the posterior half of the trunk; suboscillatory locomotion, which means that only the posterior third of the body is undulated; and suboscillatory locomotion, in which only the caudal most area of the trunk is used for propulsion, e.g. the semilunate tail in tuna. An undulatory way of locomotion can be observed in eels (REIF 1984, BRAUN & REIF 1982, 1985, GILLIS 1996), while the subundulatory mode is found in crocodiles (personal field observation on *Crocodylus acutus* in Jamaica) or swimming lizards (pers. obs.). Suboscillatory and oscillatory habits are assumed for many ichthyosaurs (BRAUN & REIF 1982, 1985; MASSARE 1988; but see RIESS 1986 for a

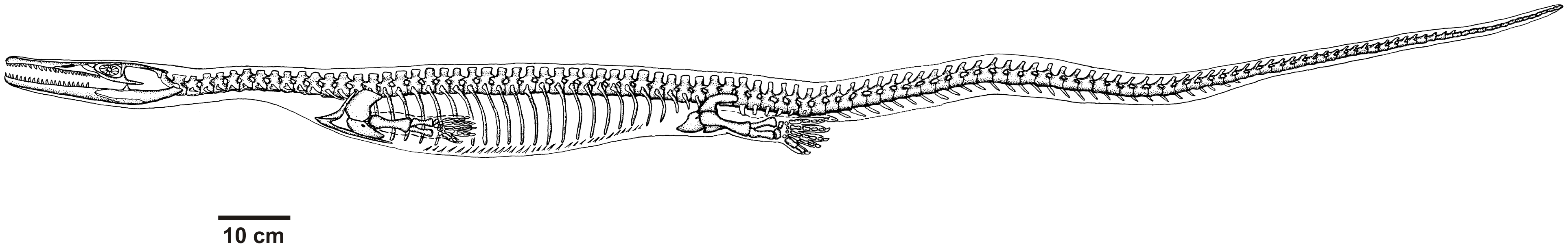


Fig. 64: *Askeptosaurus italicus*, skeletal restoration, shown in the supposed mode of swimming.

contradictory view).

Oscillatory and suboscillatory modes of propulsion are usually restricted to fast swimmers with thunniform body outlines (MASSARE 1988), which necessarily implies that the tail is very short and often tall. For that reason, these very specialized ways of locomotion can most probably be excluded for *Askeptosaurus*, as the morphology of this animal shows no resemblances to typical representatives of these two categories.

An explicitly undulatory mode is often found in vertebrates that lack limbs, such as the above cited eels, but also aquatic snakes (pers. obs.), while subundulatory habits are probably the least specialized way, since this mode is frequently found in semiaquatic or even terrestrial modern reptiles that only occasionally enter the water (pers. obs.). In the case of *Askeptosaurus*, the way of aquatic locomotion possibly was intermediate between the undulatory and the subundulatory mode. An argument for undulatory habits is the elongate trunk with the very long neck, a body outline that has no identical counterpart in modern reptiles with four legs (only some varanids slightly resemble this condition). Snakes, however, are much more suitable for a comparison and, as mentioned above, use an undulatory mode of aquatic propulsion. On the other hand, the fact that the limbs of *Askeptosaurus* are still well-developed - although comparatively short - shows similarities to the condition found in crocodiles, which, as already illustrated, present subundulatory habits when swimming. A (sub)undulatory mode of aquatic propulsion is therefore the most reasonable assumption for *Askeptosaurus*.

On the basis of hydrodynamical grounds, MASSARE (1988) argues that an axial (sub)undulatory swimming mode is not as fast as a thunniform locomotion, and indeed this is also mirrored in modern aquatic vertebrates. Hence, the author concludes that mesosuchian crocodiles, for example, would not have pursued constantly fast-moving prey, but would have caught food by using an ambush mode, i.e. the animal used only a very short period of rapid movement to approach and capture the prey, while prior to the attack it behaved very carefully so that the pursued animal was not aware of being observed. Possibly the same behaviour can also be assumed for *Askeptosaurus*, coupled with the feeding mode illustrated previously. Thus, the inferred ecology of *Askeptosaurus* well fits with an animal that lives close to shorelines, where reef structures or rocks favour such a strategy of prey capture. It may also be assumed that *Askeptosaurus* was still able to enter the land, e.g. for sun basking or egg deposition (under the premise that this animal was oviparous), which is indicated by the only slightly reduced ossification in the feet.

4.3.4. Feeding and locomotion of *Endennasaurus*

As already illustrated in chapter 3.4, *Endennasaurus* is not as well preserved as *Askeptosaurus*, therefore the palaeoecological considerations must remain more restricted in this case.

A significant feature of the skull of *Endennasaurus* is the complete absence of teeth, both in the jaws and on the palate. It seems highly probable that keratinous structures may have functionally replaced the teeth, like in turtles. Given that the animal was not an explicitly terrestrial reptile that only accidentally came to preservation in the Norian marine sediments of Northern Italy (like some other tetrapods, e.g. the arboreal taxa *Drepanosaurus* and *Megalancosaurus*; PINNA 1986, CALZAVARA et al. 1980) but was indeed at least semi-aquatic, which appears to be supported by the retracted nares, the elongated and sharp skull with the eyes positioned dorsally, the relatively stout autopodia, and the rigid gastral basket, an aquatic feeding strategy must be assumed.

Due to the lack of preservation of many parts of the posterior skull portion, it is difficult to evaluate whether the skull of *Endennsaurus* was kinetic or not. It seems, however, that the mandibles were firmly fused in the symphyseal area, contrary to *Askeptosaurus*. Additionally, if the lower temporal bar was (secondarily) closed, which is at least indicated by the strong development of the posterior jugal process, then a more or less akinetic skull should be assumed, like in modern *Sphenodon*.

Modern sea turtles, which definitely have an akinetic skull and also lack teeth in the jaws, can possibly be used as analogy. Sea turtles feed on a variety of organisms, mainly fish, echinoderms, crustaceans, jellyfish, and plants (PRITCHARD 1979). Whether *Endennasaurus* also fed on plants is surely difficult to determine, but it seems plausible that the prey spectrum ranged from small decapod crustaceans to soft-bodied invertebrates. At least the former group was very abundant in the Norian sediments of Northern Italy (PINNA 1993), while the presence of the latter group is certainly difficult to confirm. Possibly, *Endennasaurus* also fed on echinoderms, but these were obviously not that common. It has furthermore been suggested that the prey of *Endennasaurus* additionally consisted of small vertebrates (fish and tetrapods; PINNA 1993). Although this cannot be definitely excluded, the small skull makes a preferred predation on vertebrates unlikely. If at all, *Endennasaurus* could only have caught juvenile vertebrates. Given the different prey spectrum in comparison to *Askeptosaurus*, the long neck, which obviously represents a synapomorphy of this thalattosaur lineage (see chapter 4.2), was maybe not explicitly used to support lateral sweeps of the head for prey capture. Anyhow, the neck was surely advantageous for rapid movements that are necessary for a successful strike. This can be observed, e.g., in the modern pleurodire freshwater turtle *Chelodina*, which has a very elongated neck (pers. obs.).

As in the case of nutrition, also the mode of aquatic locomotion was probably very different from the one proposed for *Askeptosaurus*. Even though the overall proportions of the stylopodia relative to the zeugopodia appear to be roughly equal in the two taxa (*Endennasaurus* has a humerus length : radius length ratio of 1.85, and a femur length : fibula length ratio of 1.87, which both lie in the spectrum of *Askeptosaurus*; see chapter 3.2), *Endennasaurus* had much longer limbs in relation to the trunk (the humerus length : glenoid-acetabulum length ratio is 0.32, as compared to values between 0.15 and 0.18 in *Askeptosaurus*). The difference becomes additionally apparent when the number of thoracal vertebrae is compared: *Askeptosaurus* possessed at least 25 thoracals, while *Endennasaurus* had only 16.

As a consequence, the comparatively elongated limbs suggest that the animal used mainly its extremities for propulsion instead of a lateral undulation of the body axis, and thus displayed a certain degree of paraxial locomotion (REIF 1984). The rigid gastral rib cage possibly served for a stabilization of the trunk during swimming. However, the mode of locomotion was surely still different from tetrapods that show underwater flight, and also from other aquatic reptiles like the pachypleurosaur *Keichousaurus* (LIN & RIEPPEL 1998), which, although not considered as subaquatic flyer, probably used its greatly enlarged forelimbs for a prominent power stroke. Putatively, the locomotory habits of *Endennasaurus* were a relatively undifferentiated version of paraxial locomotion and corresponded to the so-called “pectoropelvical rowing”, as it is displayed by many freshwater turtles (BRAUN & REIF 1982, 1985). Like these animals, *Endennsaurus* presumably still made excursions onto land, which is indicated by the relatively well ossified autopodia. Thus, the here proposed, rather unspecialized mode of swimming may be a consequence of a certain degree of semi-terrestriality.

5. Acknowledgements

The present work greatly benefited from the support of a variety of persons. First of all, I wish to thank my supervisors, Prof. Dr. JÜRGEN A. XXX, Johannes-Gutenberg-Universität Mainz, and PD Dr. P. MARTIN XXX, Rheinische Friedrich-Wilhelms-Universität Bonn, for their useful advice and technical support they gave me throughout my study.

Prof. Dr. HANS XXX, Paläontologisches Institut and Museum Zürich, generously allowed me to investigate the thalattosaur material housed in the PIMUZ. PD Dr. WINAND XXX, Dr. HEINZ XXX, and HEINZ XXX offered helpful technical support and hospitality during several stays in Zürich.

Drs. CRISTIANO XXX, STEFANIA XXX, and GIORGIO XXX, Museo Civico di Storia Naturale di Milano, provided access to the *Askeptosaurus* material in their care, and friendly gave me every support I needed. To all of them my sincere thanks.

Dr. ANNA XXX and the complete, very friendly staff of the Museo Civico di Scienze Naturali “Enrico Caffi“, Bergamo, let me study the *Endennasaurus* type material and made my stay in Bergamo very pleasant.

Dr. RUPERT XXX, Staatliches Museum für Naturkunde Stuttgart, generously allowed me to loan parts of the *Blezingeria* material of the SMNS, as well as to study the thalattosaur specimen from the Norian of Austria.

I am also indebted to Dr. HANS XXX, Muschelkalkmuseum Ingelfingen, who loaned me important parts of his *Blezingeria* collection.

Further *Blezingeria* material was provided to me by Dr. MICHAEL XXX, Eberhard-Karls-Universität Tübingen. Additional thanks to him for several useful and pleasant discussions on marine reptiles in general (and not only about that...).

Prof. Dr. KEVIN XXX and Dr. PATRICIA XXX, University of California at Berkeley, allowed me to study the Californian thalattosaur material in their care, and made it possible that I received financial support by the SAMUEL P. WELLES Fund. I also wish to thank Dr. SIMONE XXX and Dr. AXEL XXX for their hospitality during my stay in Berkeley, and for the pleasant touristic trip to San Francisco.

WOLFGANG XXX and Prof. Dr. WOLFGANG XXX, Zoologisches Forschungsinsitut & Museum Koenig Bonn, generously provided extant lizard material for dissection and comparative studies.

Dr. OLIVIER XXX, Field Museum of Natural History Chicago, was a great intellectual help throughout my study, and he always offered generous advice. I also wish to thank him and his wife, MYRIAM XXX, for their hospitality during my stay in Chicago.

A lot of people additionally helped me with technical support and/or useful discussions. These include Prof. Dr. ROBERT L. XXX, McGill University Montréal, Dr. SUSAN E. XXX, University College London, Dipl.-Geol. ANNALISA XXX, Universität Bonn, Dr. RAINER XXX, Humboldt-Museum für Naturkunde Berlin, and Prof. Dr. HANS-DIETER XXX, Royal Ontario Museum Toronto.

My “Vertrauensdozent“ of the Studienstiftung des deutschen Volkes, Prof. Dr. ANDREAS XXX, Universität Mainz, generously helped me for several times with problems like financial travel support or the continuation of my doctoral scholarship.

As during the work on my diploma thesis, the members of the “Kaffeerunde“ of the palaeontological department of the Universität Mainz provided useful technical help and entertainment, and certainly deserve to be named: PD. Dr. THOMAS XXX, Dipl.-Geol. MICHAEL XXX, Dipl.-Geol. MARKUS XXX, Dr. KIRSTEN XXX, Dipl.-Geol. UWE XXX, Dipl.-Geol. KARSTEN XXX, Dipl.-Geol. MICHAEL XXX, Dr. CLEMENS XXX, Dipl.-Geol. MARKUS XXX, and Dipl.-Geol. BEATRIX XXX. Additionally, also Dipl.-Phys. THORSTEN XXX provided technical assistance.

My very special thanks to Dipl.-Geol. INKEN XXX, formerly Bonn, now Mainz: it is a fact that without her valuable help this thesis could not have been completed.

Special thanks also goes to my father, JOACHIM XXX, Madrid, who, in the last weeks, spent much of his few free time to lingually correct many parts of this study.

Finally, I wish to thank my mother, GERTRUD XXX, Schwalbach, for the support she gave me and my interests throughout my life, beginning with the innumerable visits in the Zoo Frankfurt and the Senckenberg Museum when I was 5 (or 4?) years old.

During completion of my diploma thesis, my favourite and highly adored football club, EINTRACHT FRANKFURT, managed to get back into the highest division of German football, a success I then considered worth to be mentioned in the acknowledgements, due to its strong connection with my personal identity. Unfortunately, the second descent in club history occurred when I was carrying out the present work, causing much sneer in the department from which I strongly had to suffer. It is a hard life to be in the second division again, but I hope that if I ever write a habilitation thesis, I will be able to mention the glorious return into one of the *belétages* of European football (☺)!

6. References

BENTON, M. J. (1984): The relationships and early evolution of the Diapsida. – Symp. Zool. Soc. Lond. **52:** 575-596, London.

- (1985): Classification and phylogeny of the diapsid reptiles. – Zool. J. Linn. Soc. **84:** 97-164, London.

BERMAN, D. S., & REISZ, R. R. (1992): *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. – J. Paleont. **66:** 1001-1009, Lawrence.

BEUTLER, G., & SZULC, J. (1999): Die paläogeographische Entwicklung des Germanischen Beckens in der Trias und die Verbindung zur Tethys. – [In:] HAUSCHKE, N. & WILDE, V. [eds.]: Trias, eine ganz andere Welt: Mitteleuropa im frühen Erdmittelalter: 71-80, München (Pfeil).

BRAUN, J., & REIF, W.-E. (1982): A new terminology of aquatic propulsion in vertebrates. – N. Jb. Geol. Paläont., Abh. **164:** 162-167, Stuttgart.

- , & - (1985): A survey of aquatic locomotion in fishes and tetrapods. – N. Jb. Geol. Paläont., Abh. **169:** 307-332, Stuttgart.

BRINKMANN, W. (1994): Paläontologisches Museum der Universität Zürich. Führer durch die Ausstellung. – 108 pp., Zürich (Paläontologisches Institut und Museum der Universität Zürich).

BROILI, F. (1912): Zur Osteologie des Schädels von *Placodus*. – Palaeontographica, **59:** 147-155, Stuttgart.

BRYANT, H. N., & SEYMOUR, K. L. (1990): Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. – J. Morph. **206:** 109-117, New York.

BÜRGIN, T., RIEPPEL, O., SANDER, P. M., & TSCHANZ, K. (1989): The fossils of Monte San Giorgio. – Scientific American **260:** 74-81, New York.

CALDWELL, M. W. (1996): Ichthyosauria: A preliminary phylogenetic analysis of diapsid affinities. – N. Jb. Geol. Paläont., Abh. **200:** 361-386, Stuttgart.

- (1997): Limb osteology and ossification patterns in *Crypoclidus* (Reptilia: Plesiosauroidea) wit a review of sauropterygian limbs. – J. Vert. Paleont. **17:** 295-307, Lawrence.

CALZAVARA, M. MUSCIO, G., & WILD, R. (1980): *Megalancosaurus preonensis* n. g. n. sp., a new reptile from the Norian of Friuli. Gortania **2:** 59-64, Udine.

CARROLL, R. L. (1975): Permo-Triassic “Lizards” from the Karroo. – Palaeont. afr. **18:** 71-87, Johannesburg.

- (1978): Permo-Triassic “Lizards” from the Karoo System. Part II: A gliding reptile from the Upper Permian of Madagascar. – Palaeont. afr. **21:** 143-159, Johannesburg.

- (1981): Plesiosaur ancestors from the Upper Permian of Madagascar. – Phil. Trans. R. Soc. Lond. B **293:** 315-383, London.

- (1988): Vertebrate Paleontology and Evolution. – 668 pp., New York (W.H. Freeman).

- , & GASKILL, P. (1985): The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. – Phil. Trans. R. Soc. Lond. B **309:** 343-393, London.

- , & CURRIE, P. J. (1991): The Early Radiation of Diapsid Reptiles. – [In:] SCHULTZE, H.-P., & TRUEB, L. [eds.]: Origins of the Higher Groups of Tetrapods: Controversy and Consensus: 354-424, Ithaca (Cornell University Press).

- , & ZHI-MING, D. (1991): *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. – Phil. Trans. R. Soc. Lond. B **331:** 131-153, London.

CHATTERJEE, S. (1974): A rhynchosaur from the Upper Triassic Maleri Formation of India. – Phil. Trans. R. Soc. Lond. B **267:** 209-261, London.

CLARK, J, & CARROLL, R. L. (1973): Romeriid reptiles from the Lower Permian. – Bull. Mus. Comp. Zool. **147:** 353-407, Harvard.

DALLA VECCHIA, F. M. (1993): Reptile remains from the Middle-Upper Triassic of the Carnic and Julian Alps (Friuli-Venezia Giulia, northeastern Italy). – Gortania-Atti Mus. Friul. St. Nat. **15:** 49-66, Udine.

DEBRAGA, M., & RIEPPEL, O. (1997): Reptile phylogeny and the interrelationships of turtles. – Zool. J. Linn. Soc. **120:** 281-354, London.

DILKES, D. W. (1998): The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. – Phil. Trans. R. Soc. Lond. B **353:** 501-541., London.

EDMUND, G. (1969): Dentition. – [In:] GANS, C. & PARSONS, T. [eds.]: Biology of the Reptilia Vol. 1: 117-200, London (Academic Press).

EVANS, S. E. (1980): The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. – Zool. J. Linn. Soc. **70:** 203-264.

- (1982): The gliding reptiles of the Upper Permian. – Zool. J. Linn. Soc. **76:** 97-123, London.

- (1984): The classification of the Lepidosauria. – Zool. J. Linn. Soc. **82:** 87-100, London.

- (1986): The braincase of *Prolacerta broomi* (Reptilia, Triassic). – N. Jb. Geol. Paläont., Abh. **173:** 181-200, Stuttgart.

- (1987): The braincase of *Youngina capensis* (Reptilia: Diapsida; Permian). – N. Jb. Geol. Paläont., Mh. **1986:** 181-200, Stuttgart.

- (1988): The early history and relationships of the Diapsida. – [In:] BENTON, M. J. [ed.]: The Phylogeny and Classification of the Tetrapods. Volume 1: Amphibians, Reptiles, Birds: 221-260, Oxford (Clarendon Press).

- , & HAUBOLD, H. (1987): A review of the Upper Permian genera *Coelurosauravus*, *Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). – Zool. J. Linn. Soc. **90:** 275-303, London.

- , & HECHT, M. K. (1993): A history of an extinct reptilian clade, the Choristodera: longevity, Lazarus-taxa, and the fossil record. – Evol. Biol. **27:** 323-338, New York.

FOX, R. C., & BOWMAN, M. C. (1966): Osteology and relationships of *Captorhinus aguti* (COPE) (Reptilia: Captorhinomorpha). – Univ. Kans., Paleont. Contr. **41:** 1-79, Lawrence.

FRAAS, E. (1896): Die schwäbischen Trias-Saurier. – 15 pp., Stuttgart (Schweizerbart).

FURRER, H. (1995): The Kalkschieferzone (Upper Meride Limestone; Ladinian) near Meride (Canton Ticino, Southern Switzerland) and the evolution of a Middle Triassic intraplatform basin. – Eclogae geol. Helv. **88:** 827-852, Basel.

FURRER, H. (1999): New excavations in marine Middle Triassic fossil-Lagerstätten at Monte San Giorgio (Canton Ticino, Southern Switzerland) and the Ducan Mountains near Davos (Canton Graubünden, Eastern Switzerland). – Riv. Mus. civ. Sc. Nat. “E. Caffi” **20:** 85-88, Bergamo.

GAFFNEY, E. S. (1990): The comparative osteology of the Triassic turtle *Proganochelys*. – Bull. Am. Mus. Nat. Hist. **194:** 1-263, New York.

GANS, C., & DEVREE, F. (1987): Functional Basis of Fiber Length and Angulation in Muscle. – J. Morph. **192:** 63-85, New York.

- , - , & CARRIER, D. (1985): Usage pattern of the complex masticatory muscles in the shingle-back lizard, *Trachydosaurus rugosus*: A model for muscle placement. – Am. J. Anat. **173:** 219-240, New York.

GAO, K., & FOX, R. C. (1998): New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Palaeocene, Alberta and Saskatchewan, Canada, and phylogenetic relationships of Choristodera. – Zool. J. Linn. Soc. **124:** 303-353, London.

- , EVANS, S., QIANG, J., NORELL, M. & SHU´AN, J. (2000): Exceptional fossil material of a semi-aquatic reptile from China: the resolution of an enigma. – J. Vert. Paleont. **20:** 417-421, Lawrence.

GAUTHIER, J., ESTES, R., & DEQUEIROZ, K. (1988a): A phylogenetic analysis of Lepidosauromorpha. – [In:] ESTES, R., & PREGILL, G. [eds.]: Phylogenetic relationships of the lizards families: 15-98, Stanford (Stanford University Press).

- , KLUGE, A. G., & ROWE, T. (1988b): Amniote phylogeny and the importance of fossils. – Cladistics, **4:** 105-209, London.

GILLIS, G. B. (1996): Undulatory Locomotion in Elongate Aquatic Vertebrates: Anguilliform Swimming since SIR JAMES GRAY. – Amer. Zool. **36:** 656-665, Lawrence.

GOW, C. E. (1975): The morphology and relationships of *Youngina capensis* BROOM and *Prolacerta broomi* PARRINGTON. – Palaeont. afr. **18:** 89-131, Johannesburg.

GOWER, D. J. (1997): The braincase of the early archosaurian reptile *Erythrosuchus africanus*. – J. Zool. **242:** 557-576, London.

-, & SENNIKOV, A. G. (1996): Morphology and phylogenetic informativeness of early archosaur braincases. – Palaeontology **39:** 883-906, Durham.

- , & WEBER, E. (1998): The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. – Biol. Rev. **73:** 367-411, Cambridge.

HAAS, G. (1973): Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. – [In:] GANS, C. & PARSONS, T. [eds.]: Biology of the Reptilia Vol. 4: 285-483, London (Academic Press).

HEATON, M. J., & REISZ, R. R. (1980): A skeletal reconstruction of the early Permian captorhinid reptile *Eocaptorhinus laticeps* (WILLISTON). – J. Paleont. **54:** 136-143, Lawrence.

HERREL, A., AERTS, P., & DEVREE, F. (1998): Static biting in lizards: functional morphology of the temporal ligaments. – J. Zool. **244:** 135-143, London.

HOWES, G. B., & SWINNERTON, H. H. (1901): On the development of the tuatara, *Sphenodon punctatus*. – Trans. Zool. Soc. Lond., **16:** 1-86, London.

HUENE, F. VON (1951): Eine neue Ichthyosaurier-Gattung der mittleren Trias. – N. Jb. Geol. Paläont., Abh. **94:** 80-92, Stuttgart.

- (1956): Paläontologie und Phylogenie der Niederen Tetrapoden. – 716 pp., Jena (Gustav Fischer).

KARDONG, K. V. (2002): Vertebrates: comparative anatomy, function, evolution. – 762 pp., Boston (McGraw Hill)

KUHN, E. (1952): Die Triasfauna der Tessiner Kalkalpen. XVII: *Askeptosaurus italicus* NOPSCA. – Schweiz. Paläont. Abh. **69:** 1-73, Basel.

KUHN-SCHNYDER, E. (1960): Über einen Schultergürtel von *Askeptosaurus italicus* NOPSCA aus der anisischen Stufe der Trias des Monte San Giorgio (Kt. Tessin, Schweiz). – Eclogae geol. Helv. **53:** 805-810, Basel.

- (1971): Über einen Schädel von *Askeptosaurus italicus* NOPSCA aus der mittleren Trias des Monte San Giorgio (Kt. Tessin, Schweiz). – Abh. Hess. L.-Amt Bodenforsch. **60:** 89-98, Wiesbaden.

- (1988): Bemerkungen zur Ordnung der Thalattosauria (Reptilia). – Eclogae geol. Helv. **81:** 879-886, Basel.

LAKJER, T. (1926): Studien über die Trigeminus-versorgte Kaumuskulatur der Sauropsiden. – 154 pp., Copenhagen (C. A. Reitzel).

LAURIN, M. (1991): The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. – Zool. J. Linn. Soc. **101:** 59-95, London.

LEE, M. S. Y. (1997): Pareiasaur phylogeny and the origin of turtles. – Zool. J. Linn. Soc. **120:** 197-280, London.

- (2001): Molecules, morphology, and the monophyly of diapsid reptiles. – Contr. Zool. **70:** 1-22, Amsterdam.

LIN, K. & RIEPPEL, O. (1998): Functional morphology and ontogeny of *Keichosaurus hui* (Reptilia, Sauropterygia). – Fieldiana (Geology), n.s. **39:** 1-35, Chicago.

LIU, J. (1999): New discovery of sauropterygian from Triassic of Guizhou, China. – Chin. Sc. Bull. **44:** 1312-1315, Bejing.

-, & RIEPPEL, O. (2001): A second thalattosaur species from the Triassic of Guizhou, China. – Vert. Palasiat. **39:** 77-87, Bejing.

LOMBARDO, C., TINTORI, A., FELBER, M., DANINI, G., MORATTO, D., PACOR, G., & TENTOR, M. (1999): Faunal assemblages in the Kalkschieferzone (Meride Limestone, Upper Ladinian) of Meride (Canton Ticino, Switzerland). – Riv. Mus. civ. Sc. Nat. "E. Caffi" **20:** 101-104, Bergamo.

MAISCH, M. W. (1997): A case against a diapsid origin of the Ichthyosauria. – N. Jb. Geol. Paläont, Abh. **205:** 111-127, Stuttgart.

- , & MATZKE, A. T: (2000): The Ichthyosauria. – Stuttgarter Beitr. Naturk. B **298:** 1-159, Stuttgart.

MASSARE, J. A. (1987): Tooth morphology and prey preference of Mesozoic marine reptiles. – J. Vert. Paleont. **7:** 121-137, Lawrence.

- (1988): Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. – Paleobiology **14:** 187-205, Lawrence.

MERCK, J. W. (1997): A Phylogenetic Analysis of the Euryapsid Reptiles. – Unpublished Ph.D. Thesis, University of Texas at Austin, XVI+785 pp.

MERRIAM, J. C. (1904): A new marine reptile from the Triassic of California. – Bull. Dept. Geol. Univ. Calif. **3:** 419-421, Berkeley.

- (1905): The Thalattosauria: A group of marine reptiles from the Triassic of California. – Mem. Cal. Acad. Sci. **5:** 1-52, Berkeley.

- (1908): Notes on the osteology of the thalattosaurian genus *Nectosaurus*. – Bull. Dept. Geol. Univ. Calif. **5:** 217-223, Berkeley.

MOTANI, R. (1999a): Phylogeny of the Ichthyopterygia. – J. Vert. Paleont. **19:** 472-495, Lawrence.

- (1999b): The skull and taxonomy of *Mixosaurus* (Ichthyopterygia). – J. Paleont. 73: 924-935, Lawrence.

- (2000): Skull of *Grippia longirostris*: no contradiction with a diapsid affinity for the Ichthyopterygia. – Palaeontology **43:** 1-14, Durham.

-, MINOURA, N., & ANDO, T. (1998): Ichthyosaurian relationships illuminated by new primitive skeletons from Japan. – Nature **393:** 255-257, London.

MÜLLER, J. (2002): Skull Osteology of *Parvilacerta parva*, a Small-Sized Lacertid Lizard from Asia Minor. – J. Morph., New York [in press].

NICHOLLS, E. L. (1999): A reexamination of *Thalattosaurus* and *Nectosaurus* and the relationships of the Thalattosauria (Reptilia: Diapsida). – PaleoBios **19:** 1-29, Berkeley.

- , & BRINKMAN, D. (1993): New thalattosaurs (Reptilia: Diapsida) from the Triassic Sulphur formation of Wapiti Lake, British Columbia. – J. Paleont. **67:** 263-278, Lawrence.

NOPSCA, F. VON (1925): *Askeptosaurus*, ein neues Reptil aus der Trias von Besano. – Cbl. Min. Geol. Pal. **B:** 265-267, Stuttgart.

OLSON, E. C. (1961): Jaw mechanisms: rhipidistians, amphibians, reptiles. – Amer. Zool. **1:** 205-215, Lawrence.

PARRISH, J. T. (1999): Pangaea und das Klima der Trias. – [In:] HAUSCHKE, N. & WILDE, V. [eds.]: Trias, eine ganz andere Welt: Mitteleuropa im frühen Erdmittelalter: 37-42, München (Pfeil).

PATCHELL, F. C: & SHINE, R. (1986): Feeding mechanisms in pygopodid lizards: How can *Lialis* swallow such large prey? – J. Herpetol., **20:** 59-64, St. Louis.

PEYER, B. (1936a): Die Triasfauna der Tessiner Kalkalpen. X. *Clarazia schinzi* nov. gen. nov. sp. – Abh. schweiz. Paläont. Ges. **57:** 1-61, Basel.

- (1936b): Die Triasfauna der Tessiner Kalkalpen. XI. *Hescheleria rübeli* nov. gen. nov. sp. – Abh. schweiz. Paläont. Ges. **58:** 1-48, Basel.

- (1955): Die Triasfauna der Tessiner Kalkalpen. XVII: *Helveticosaurus zollingeri* n. g. n. sp. – Abh. Schweiz. Paläont. Ges. **72:** 1-50, Basel.

PINNA, G. (1986): On *Drepanosaurus unguicaudatus*, an Upper Triassic Lepidosaurian from the Ialian Alps. – J. Paleont. **60:** 1127-1132.

- (1993): The norian reptiles of northern Italy. – Paleontologia Lombarda, n.s. **109:** 115-124, Milano.

PRITCHARD, P. C. H. (1979): Encyclopedia of turtles. – 895 pp., New Jersey (T. F. H. Publications).

RADOVANOVIC, M. (1935): Anatomische Studien am Schlangenkopf. – Jena. Z. Naturw. **69:** 321-421, Jena.

REIF, W.-E. (1984): Biophysik & Morphologie schneller Schwimmer. – [In:] REIF, W.-E. [ed.]: Paläontologische Kursbücher, Band 1: Funktionsmorphologie: 233-259, München (Paläontologische Gesellschaft).

REISZ, R. R. (1981): A diapsid reptile from the Pennsylvanian of Kansas. – Spec. Pap. Mus. Nat. Hist. Univ. Kans. **7:** 1-74, Lawrence.

- , BERMAN, D. S., & SCOTT, D. (1984): The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. – J. Vert. Paleont. **4:** 57-67, Lawrence.

RENESTO, S. (1984): A new lepidosaur (Reptilia) from the Norian beds of the Bergamo Prealps. Preliminary note. – Riv. It. Paleont. Strat. **90:** 165-176, Milano.

- (1992): The anatomy and relationships of *Endennasaurus acutirostris* (Reptilia, Neodiapsida) from the Norian (Late Triassic) of Lombardy. – Riv. It. Paleont. Strat. **97:** 409-430, Milano.

- (1994a): A reinterpretation of the shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Diapsida). – Zool. J. Linn. Soc. **111:** 247-264, London.

- (1994b): *Megalancosaurus preonensis*, a possibly arboreal archosauromorph from the Norian (Late Triassic) of Northern Italy. – J. Vert. Paleont. **14:** 38-52, Lawrence.

- (2000): Bird-like head on a chameleon body: new specimens of the enigmatic diapsid reptile

Megalancosaurus from the Late Triassic of Northern Italy. – Riv. It. Paleont. Strat. **106:** 157-180, Milano.

- , & PAGANONI, A. (1995): A new *Drepanosaurus* (Reptilia, Neodiapsida) from the Upper Triassic of Northern Italy. – N. Jb. Geol. Paläont., Abh. **197:** 87-99, Stuttgart.

RIEBER, H. (1973): Ergebnisse paläontologisch-stratigraphischer Untersuchungen in der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kanton Tessin, Schweiz). – Ecolgae geol. Helv. **66:** 667-685, Basel.

RIEPPEL, O. (1978): The phylogeny of cranial kinesis in lower vertebrates, with special reference to the Lacertilia. – N. Jb. Geol. Paläont., Abh. **156:** 353-370, Stuttgart.

- (1979): The skull of the Upper Jurassic cryptodire turtle *Thalassemys*, with a reconsideration of the chelonian braincase. – Palaeontographica A **171:** 105-140, Stuttgart.

- (1980): The trigeminal jaw adductor musculature of *Tupinambis*, with comments on the phylogenetic relationships of the Teiidae (Reptilia, Lacertilia). – Zool. J. Linn. Soc. **69:** 1-29, London.

- (1984): The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). – Zool. J. Linn. Soc. **82:** 291-318, London.

- (1987): *Clarazia* and *Hescheleria*: a re-investigation of two problematical reptiles from the Middle Triassic of Monte San Giorgio (Switzerland). – Palaeontographica A **195:** 101-129, Stuttgart.

- (1989a): A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. – Phil. Trans. R. Soc. Lond. B **323:** 1-73, London.

- (1989b): *Helveticosaurus zollingeri* PEYER (Reptilia, Diapsida): skeletal paedomorphosis, functional anatomy and systematic affinities. – Palaeontographica A **208:** 123-152, Stuttgart.

- (1989c): The hindlimb of *Macrocnemus bassani* (Reptilia, Diapsida): development and functional anatomy. – J. Vert. Paleont. **9:** 373-387, Lawrence.

- (1992): The skull in a hatchling of *Sphenodon punctatus*. – J. Herpetol. **26:** 80-84, St. Louis.

- (1993a): Middle Triassic reptiles from Monte San Giorgio: recent results and future potential of analysis. – Paleontologia Lombarda, n.s. **109:** 301-325, Milano.

- (1993b): Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. – J. Vert. Paleont. **13:** 31-47, Lawrence.

- (1993c): Euryapsid relationships: a preliminary analysis. – N. Jb. Geol. Paläont., Abh. **188:** 241-264, Stuttgart.

- (1993d): Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* DAUDIN (Reptilia, Crocodylia). – Zool. J. Linn. Soc. **109:** 301-325, London.

- (1994): Osteology of *Simosaurus gaillardoti*, and the phylogenetic interrelationships of stem-group Sauropterygia. – Fieldiana (Geology), n.s. **28:** 9-23, Chicago.

- (1998): The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. – J. Vert. Paleont. **18:** 545-557, Lawrence.

- (2000a): Sauropterygia 1. Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. – [In:] WELLNHOFER, P. [ed.]: Handbuch der Paläoherpetologie; Teil 12 A: 1-134, München (Pfeil).

- (2000b): Turtles as diapsid reptiles. – Zool. Scripta **29:** 199-212, Oslo.

- (2000c): *Paraplacodus* and the phylogeny of the Placodontia (Reptilia: Sauropterygia). – Zool. J. Linn. Soc. **130:** 635-659, London.

- , & LABHARDT, L. (1979): Mandibular mechachanics in *Varanus niloticus* (Reptilia: Lacertilia). – Herpetologica **35:** 158-163, Lawrence.

- , & GRONOWSKI, R. W. (1981): The loss of the lower temporal arcade in diapsid reptiles. – Zool. J. Linn. Soc. **72:** 203-217, London.

- , & WILD, R. (1996): A revision of the genus *Nothosaurus* (Reptilia, Sauropterygia) from the Germanic Triassic, with comments on the status of *Conchiosaurus clavatus*. – Fieldiana (Geology), n.s.: **34:** 1-82, Chicago.

- , & HAGDORN, H. (1998): Fossil reptiles from the Spanish Muschelkalk (Montral and Alcover, Province Tarragona). – Hist. Biol. **13:** 77-97, London.

- , & REISZ, R. R. (1999): The origin and early evolution of turtles. – Ann. Rev. Ecol. Syst. **30:** 1-22, Palo Alto.

- , LIU, J., & BUCHER, H. (2000): The first record of a thalattosaur reptile from the Late Triassic of Southern China (Guizhou Province, PR China). – J. Vert. Paleont. **20:** 507-515, Lawrence.

- , MAZIN, M., & TCHERNOV, E. (1999): Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. – Fieldiana (Geology), n.s. **40:** 1-85, Chicago.

RIESS, J. (1986): Fortbewegunsweise, schwimmbiophysik und phylogenie der Ichthyosaurier. – Palaeontographica A **192:** 93-155, Stuttgart.

ROBINSON, P. L. (1973) : A problematic reptile from the British Upper Trias. – J. geol. Soc. Lond. **129:** 457-479, London.

ROMER, A. S. (1956): Osteology of the Reptiles. – 772 pp., Chicago (University of Chicago Press).

RÜFFER, T. (1999): Exkurs: Sedimentation und Faziesräume in der nordalpinen Trias. – [In:] HAUSCHKE, N. & WILDE, V. [eds.]: Trias, eine ganz andere Welt: Mitteleuropa im frühen Erdmittelalter: 175-204, München (Pfeil).

SANDER, P. M. (1989a): The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland), with the description of a new species. – Phil. Trans. R. Soc. Lond. B **325:** 561-670, London.

- (1989b): The large ichthyosaur *Cymbospondylus buchseri* sp. nov. from the Middle Triassic of Monte San Giorgio (Switzerland) with a survey of the genus in Europe. – J. Vert. Paleont. **9:** 163-173, Lawrence.

- (2000): Ichthyosauria: their diversity, distribution, and phylogeny. – Paläont. Z. **74:** 1-35, Stuttgart.

-, RIEPPEL, O. C., & BUCHER, H. (1994): New marine vertebrate fauna from the Middle Triassic of Nevada. – J. Paleont. **68:** 676-680, Lawrence.

-, -, & - (1997): A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. – J. Vert. Paleont. **17:** 526-533, Lawrence.

SANDERSON, M. J., & DONOGHUE, M. J. (1989): Patterns of variation in levels of homoplasy. – Evolution **43:** 1781-1795, Lawrence.

SÄVE-SÖDERBERGH, G. (1945): Notes on the trigeminal musculature in non-mammalian tetrapods. – Nova Acta Reg. Soc. Sci. Upsaliensis **13:** 1-59, Uppsala.

SCHOCH, R., & WILD, R. (1999): Die Wirbeltier-Fauna im Keuper von Süddeutschland. . – [In:] HAUSCHKE, N. & WILDE, V. [eds.]: Trias, eine ganz andere Welt: Mitteleuropa im frühen Erdmittelalter: 395-408, München (Pfeil).

SCHUMACHER, G.-H. (1973): The head muscles and hyolaryngeal skeleton of turtles and crocodiles. – [In:] GANS, C. & PARSONS, T. [eds.]: Biology of the Reptilia Vol. 4: 101-199, New York (Academic Press).

SIGOGNEAU-RUSSELL, D. (1979): Les champsosaures Européens : Mise au point sur le Champsosaure d´Erquelinnes (Landénien Inferieur, Belgique). – Ann. Paléont., Vert. **65:** 93-154, Paris.

STORRS, G. W. (1991): Note on a second occurrence of thalattosaur remains (Reptilia: Neodiapsida) in British Columbia. – Can. J. Earth Sci. 28: 2065-2068, Ottawa.

- , GOWER, D. J., & LARGE, N. F. (1996): The diapsid reptile, *Pachystropheus rhaeticus*, a probable choristodere from the Rhaetian of Europe. – Palaeontology **39:** 323-349, Durham.

SWOFFORD, D. L. (2001): Phylogenetic Analysis Using Parsimony* 40b8. – Sinauer Associates Inc., Sunderland.

TAYLOR, M. A. (1987): How tetrapods feed in water: a functional analysis by paradigm. – Zool. J. Linn. Soc. **91:** 171-195, London.

TICKLE, C. (2002): Vertebrate Limb Development and Possible Clues to Diversity in Limb Form. – J. Morph. **252:** 29-37, New York.

TINTORI, A. (1992): Fish Taphonomy and Triassic anoxic basins from the Alps: a case history. – Riv. It. Paleont. Strat. **97:** 393-408, Milano.

- (1995): The Norian (late Triassic) Calcare die Zorzino Fauna from Lombardy (N. Italy): the state of the art. – Ext. Abstr. 2nd Int. Symp. Lithographic Limestones: 139-142, Cuenca.

WHITESIDE, D. I. (1986): The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. – Phil. Trans. R. Soc. Lond. B **312:** 379-430, London.

WILD, R. (1973). Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus langobardicus* (BASSANI) (Neue Ergebnisse). – Schweiz. Paläont. Abh. **95:** 1-162, Basel.

- (1980): Neue Funde von *Tanystropheus* (Reptilia, Squamata). – Schweiz. Paläont. Abh. **102:** 1-43, Basel.

WUTTKE, M. (1988a): Tod und Einbettung Messeler Wirbeltiere. – [In:] SCHAAL, S. & ZIEGLER, W. [eds.]: Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens: 259-262, Frankfurt a. M. (Waldemar Kramer).

- (1988b): Erhaltung – Lösung – Umbau. Zum Verhalten biogener Stoffe bei der Fossilisation. – [In:] SCHAAL, S. & ZIEGLER, W. [eds.]: Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens: 265-275, Frankfurt a. M. (Waldemar Kramer).

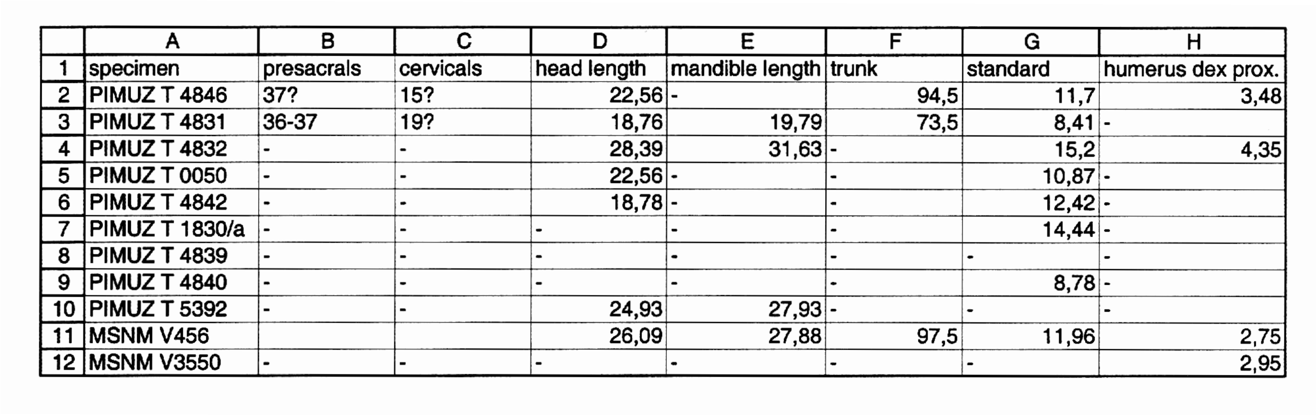
YIN, G., ZHOU, X., CAO, Z. YU, Y., & LUO, Y. (2000): A preliminary study on the early late Triassic marine reptiles from Guanling, Guizhou, China. – Geol. Geochemistry **28:** 1-23, Bejing [in Chinese with English summary].

YOUNG, B. A. (1987): The comparative cephalic osteology and myology of three species of sea snakes. – Zool. Jb., Abt. Anat. Ont. **116:** 421-452, Jena.

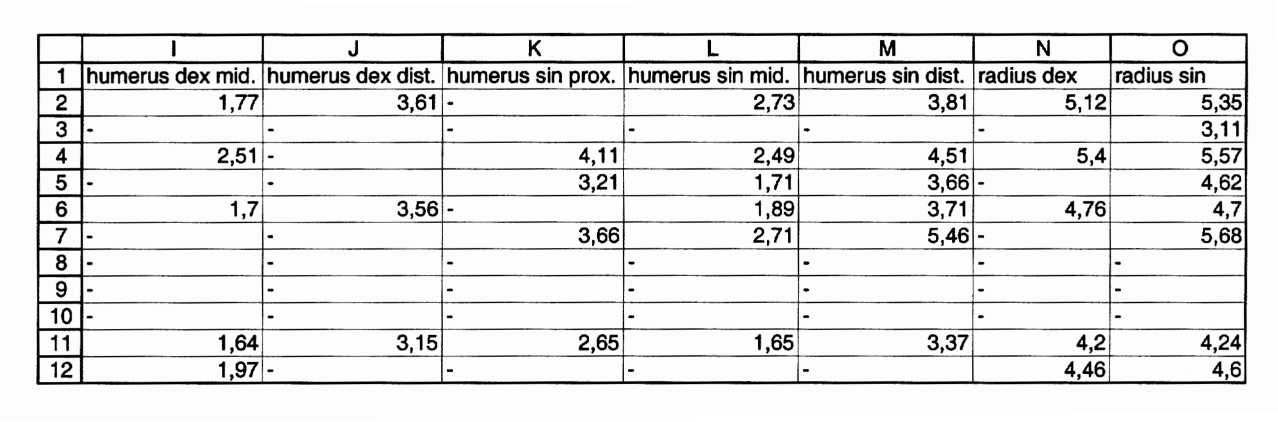
ZAHER, H. (1994): Comments on the evolution of the jaw adductor musculature of snakes. – Zool. J. Linn. Soc. **111:** 339-384, London.

ZARDOYA, R., & MEYER, A. (2001): The evolutionary position of turtles revised. – Naturwissenschaften **88:** 193-200, Heidelberg.

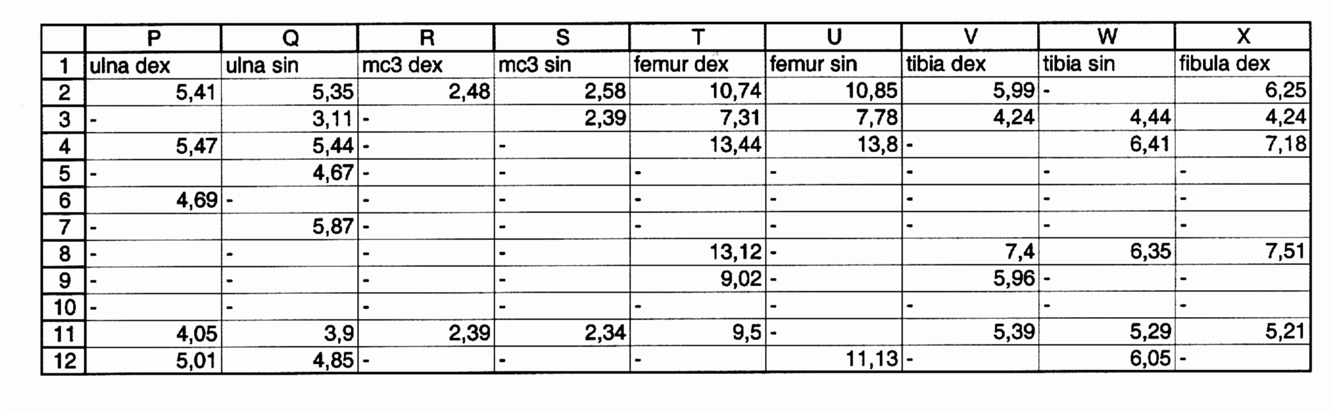
Appendix I: Biometric values of the different *Askeptosaurus italicus* specimens (measurements in cm).(sin = left; dex = right; mid = middle; med = average value; #WERT! = incalculable value).



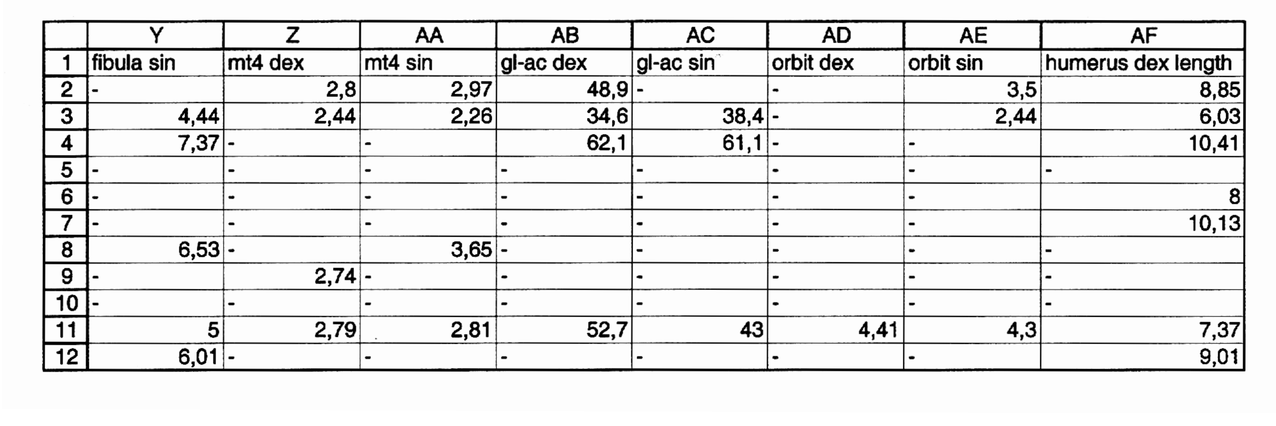
	A	B	C	D	E	F	G	H
1	specimen	presacrals	cervicals	head length	mandible length	trunk	standard	humerus dex prox.
2	PIMUZ T 4846	37?	15?	22,56	-	94,5	11,7	3,48
3	PIMUZ T 4831	36-37	19?	18,76	19,79	73,5	8,41	-
4	PIMUZ T 4832	-	-	28,39	31,63	-	15,2	4,35
5	PIMUZ T 0050	-	-	22,56	-	-	10,87	-
6	PIMUZ T 4842	-	-	18,78	-	-	12,42	-
7	PIMUZ T 1830/a	-	-	-	-	-	14,44	-
8	PIMUZ T 4839	-	-	-	-	-	-	-
9	PIMUZ T 4840	-	-	-	-	-	8,78	-
10	PIMUZ T 5392	-	-	24,93	27,93	-	-	-
11	MSNM V456			26,09	27,88	97,5	11,96	2,75
12	MSNM V3550	-	-	-	-	-	-	2,95



	I	J	K	L	M	N	O
1	humerus dex mid.	humerus dex dist.	humerus sin prox.	humerus sin mid.	humerus sin dist.	radius dex	radius sin
2	1,77	3,61	-	2,73	3,81	5,12	5,35
3	-	-	-	-	-	-	3,11
4	2,51	-	4,11	2,49	4,51	5,4	5,57
5	-	-	3,21	1,71	3,66	-	4,62
6	1,7	3,56	-	1,89	3,71	4,76	4,7
7	-	-	3,66	2,71	5,46	-	5,68
8	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-
11	1,64	3,15	2,65	1,65	3,37	4,2	4,24
12	1,97	-	-	-	-	4,46	4,6

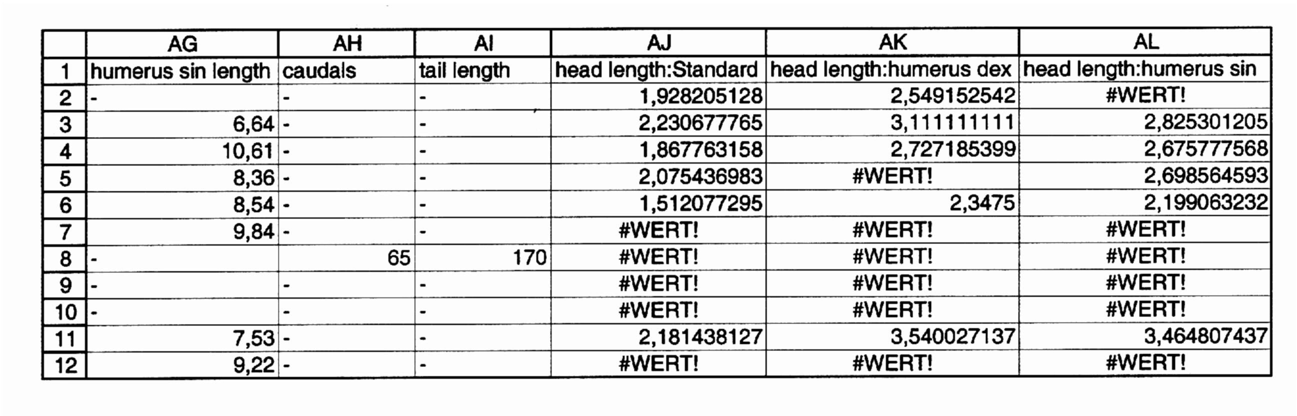


	P	Q	R	S	T	U	V	W	X
1	ulna dex	ulna sin	mc3 dex	mc3 sin	femur dex	femur sin	tibia dex	tibia sin	fibula dex
2	5,41	5,35	2,48	2,58	10,74	10,85	5,99	-	6,25
3	-	3,11	-	2,39	7,31	7,78	4,24	4,44	4,24
4	5,47	5,44	-	-	13,44	13,8	-	6,41	7,18
5	-	4,67	-	-	-	-	-	-	-
6	4,69	-	-	-	-	-	-	-	-
7	-	5,87	-	-	-	-	-	-	-
8	-	-	-	-	13,12	-	7,4	6,35	7,51
9	-	-	-	-	9,02	-	5,96	-	-
10	-	-	-	-	-	-	-	-	-
11	4,05	3,9	2,39	2,34	9,5	-	5,39	5,29	5,21
12	5,01	4,85	-	-	-	11,13	-	6,05	-

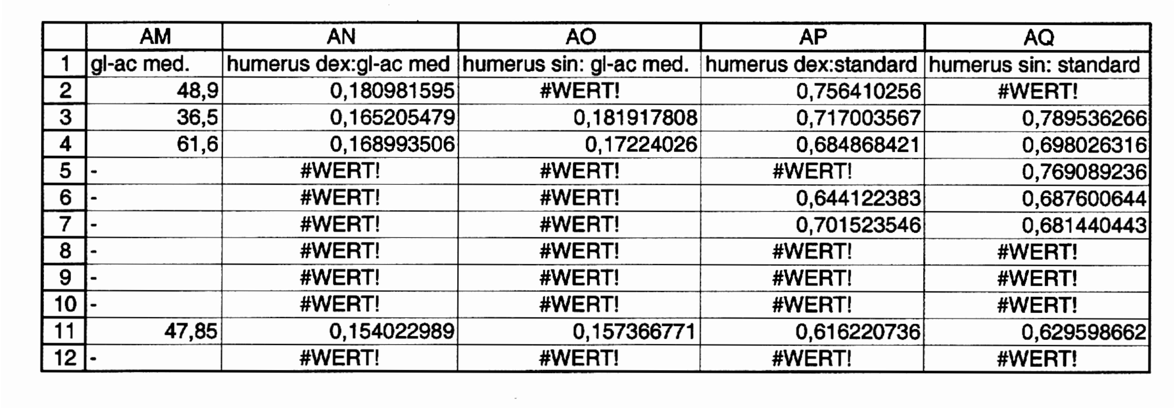


	Y	Z	AA	AB	AC	AD	AE	AF
1	fibula sin	mt4 dex	mt4 sin	gl-ac dex	gl-ac sin	orbit dex	orbit sin	humerus dex length
2	-	2,8	2,97	48,9	-	-	3,5	8,85
3	4,44	2,44	2,26	34,6	38,4	-	2,44	6,03
4	7,37	-	-	62,1	61,1	-	-	10,41
5	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	8
7	-	-	-	-	-	-	-	10,13
8	6,53	-	3,65	-	-	-	-	-
9	-	2,74	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-
11	5	2,79	2,81	52,7	43	4,41	4,3	7,37
12	6,01	-	-	-	-	-	-	9,01

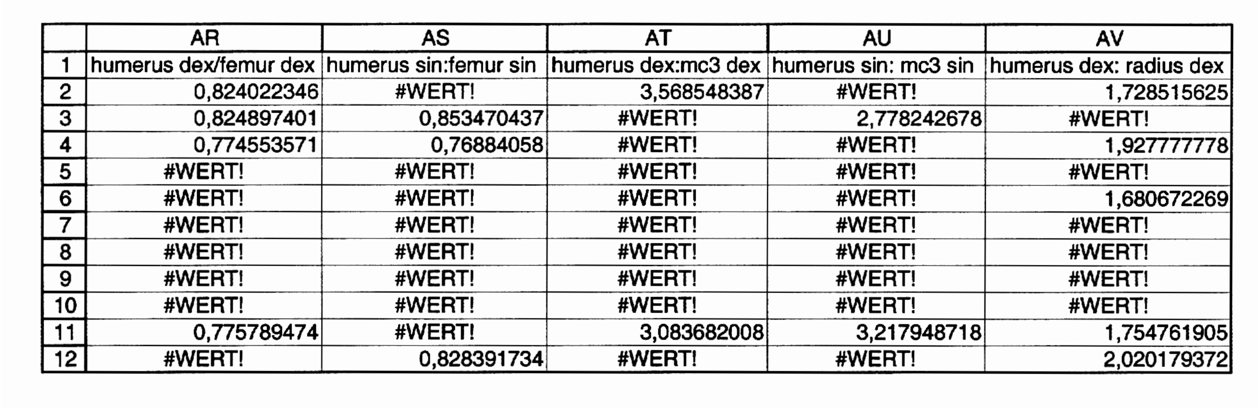
Appendix I: Biometrics of *Askeptosaurus*, continued.



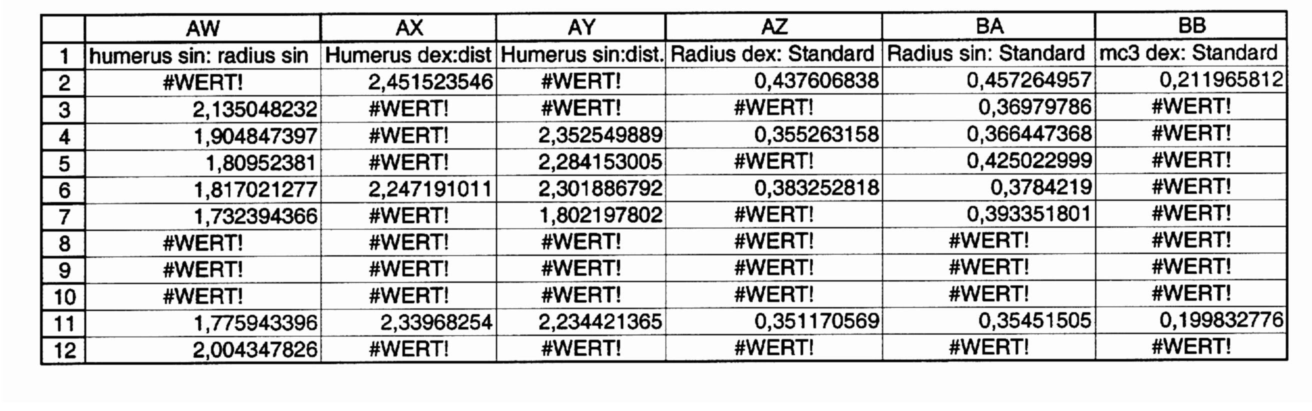
	AG	AH	AI	AJ	AK	AL
1	humerus sin length	caudals	tail length	head length:Standard	head length:humerus dex	head length:humerus sin
2	-	-	-	1,928205128	2,549152542	#WERT!
3	6,64	-	-	2,230677765	3,111111111	2,825301205
4	10,61	-	-	1,867763158	2,727185399	2,675777568
5	8,36	-	-	2,075436983	#WERT!	2,698564593
6	8,54	-	-	1,512077295	2,3475	2,199063232
7	9,84	-	-	#WERT!	#WERT!	#WERT!
8	-	65	170	#WERT!	#WERT!	#WERT!
9	-	-	-	#WERT!	#WERT!	#WERT!
10	-	-	-	#WERT!	#WERT!	#WERT!
11	7,53	-	-	2,181438127	3,540027137	3,464807437
12	9,22	-	-	#WERT!	#WERT!	#WERT!



	AM	AN	AO	AP	AQ
1	gl-ac med.	humerus dex:gl-ac med	humerus sin: gl-ac med.	humerus dex:standard	humerus sin: standard
2	48,9	0,180981595	#WERT!	0,756410256	#WERT!
3	36,5	0,165205479	0,181917808	0,717003567	0,789536266
4	61,6	0,168993506	0,17224026	0,684868421	0,698026316
5	-	#WERT!	#WERT!	#WERT!	0,769089236
6	-	#WERT!	#WERT!	0,644122383	0,687600644
7	-	#WERT!	#WERT!	0,701523546	0,681440443
8	-	#WERT!	#WERT!	#WERT!	#WERT!
9	-	#WERT!	#WERT!	#WERT!	#WERT!
10	-	#WERT!	#WERT!	#WERT!	#WERT!
11	47,85	0,154022989	0,157366771	0,616220736	0,629598662
12	-	#WERT!	#WERT!	#WERT!	#WERT!

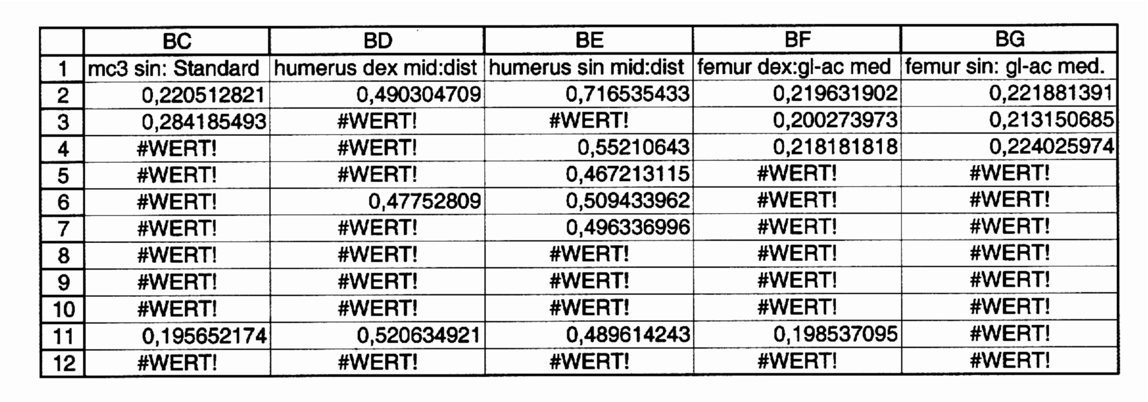


	AR	AS	AT	AU	AV
1	humerus dex/femur dex	humerus sin:femur sin	humerus dex:mc3 dex	humerus sin: mc3 sin	humerus dex: radius dex
2	0,824022346	#WERT!	3,568548387	#WERT!	1,728515625
3	0,824897401	0,853470437	#WERT!	2,778242678	#WERT!
4	0,774553571	0,76884058	#WERT!	#WERT!	1,927777778
5	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
6	#WERT!	#WERT!	#WERT!	#WERT!	1,680672269
7	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
8	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
9	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
10	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
11	0,775789474	#WERT!	3,083682008	3,217948718	1,754761905
12	#WERT!	0,828391734	#WERT!	#WERT!	2,020179372

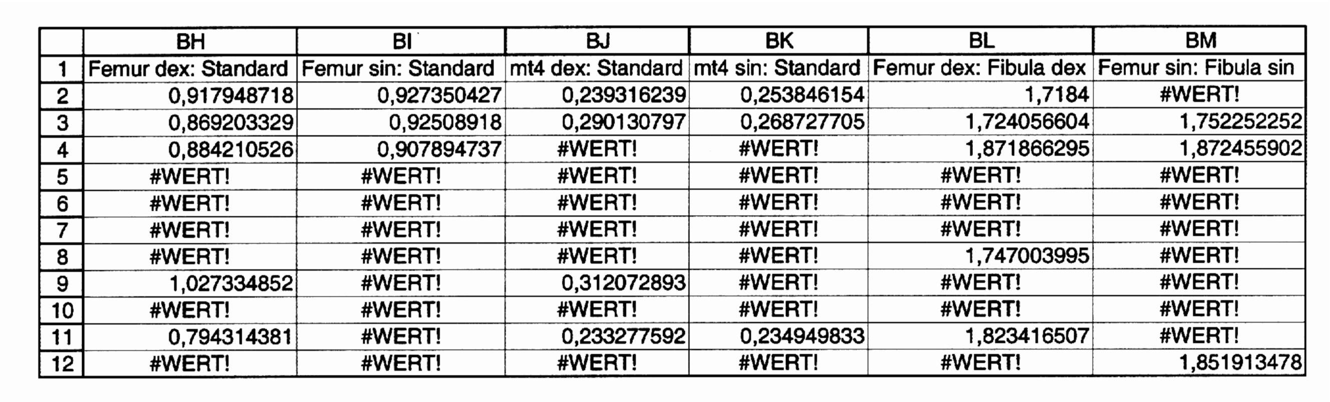


	AW	AX	AY	AZ	BA	BB
1	humerus sin: radius sin	Humerus dex:dist	Humerus sin:dist.	Radius dex: Standard	Radius sin: Standard	mc3 dex: Standard
2	#WERT!	2,451523546	#WERT!	0,437606838	0,457264957	0,211965812
3	2,135048232	#WERT!	#WERT!	#WERT!	0,36979786	#WERT!
4	1,904847397	#WERT!	2,352549889	0,355263158	0,366447368	#WERT!
5	1,80952381	#WERT!	2,284153005	#WERT!	0,425022999	#WERT!
6	1,817021277	2,247191011	2,301886792	0,383252818	0,3784219	#WERT!
7	1,732394366	#WERT!	1,802197802	#WERT!	0,393351801	#WERT!
8	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
9	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
10	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
11	1,775943396	2,33968254	2,234421365	0,351170569	0,35451505	0,199832776
12	2,004347826	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!

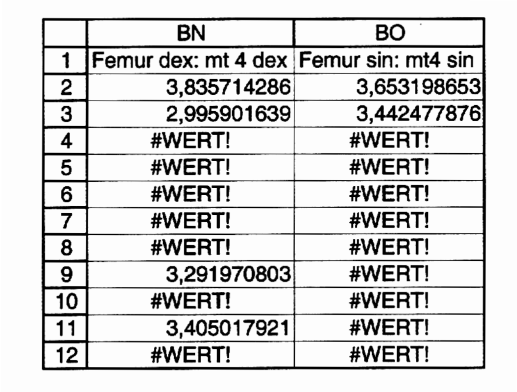
Appendix I: Biometrics of *Askeptosaurus*, continued.



	BC	BD	BE	BF	BG
1	mc3 sin: Standard	humerus dex mid:dist	humerus sin mid:dist	femur dex:gl-ac med	femur sin: gl-ac med.
2	0,220512821	0,490304709	0,716535433	0,219631902	0,221881391
3	0,284185493	#WERT!	#WERT!	0,200273973	0,213150685
4	#WERT!	#WERT!	0,55210643	0,218181818	0,224025974
5	#WERT!	#WERT!	0,467213115	#WERT!	#WERT!
6	#WERT!	0,47752809	0,509433962	#WERT!	#WERT!
7	#WERT!	#WERT!	0,496336996	#WERT!	#WERT!
8	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
9	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
10	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
11	0,195652174	0,520634921	0,489614243	0,198537095	#WERT!
12	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!



	BH	BI	BJ	BK	BL	BM
1	Femur dex: Standard	Femur sin: Standard	mt4 dex: Standard	mt4 sin: Standard	Femur dex: Fibula dex	Femur sin: Fibula sin
2	0,917948718	0,927350427	0,239316239	0,253846154	1,7184	#WERT!
3	0,869203329	0,92508918	0,290130797	0,268727705	1,724056604	1,752252252
4	0,884210526	0,907894737	#WERT!	#WERT!	1,871866295	1,872455902
5	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
6	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
7	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
8	#WERT!	#WERT!	#WERT!	#WERT!	1,747003995	#WERT!
9	1,027334852	#WERT!	0,312072893	#WERT!	#WERT!	#WERT!
10	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!
11	0,794314381	#WERT!	0,233277592	0,234949833	1,823416507	#WERT!
12	#WERT!	#WERT!	#WERT!	#WERT!	#WERT!	1,851913478



	BN	BO
1	Femur dex: mt 4 dex	Femur sin: mt4 sin
2	3,835714286	3,653198653
3	2,995901639	3,442477876
4	#WERT!	#WERT!
5	#WERT!	#WERT!
6	#WERT!	#WERT!
7	#WERT!	#WERT!
8	#WERT!	#WERT!
9	3,291970803	#WERT!
10	#WERT!	#WERT!
11	3,405017921	#WERT!
12	#WERT!	#WERT!

Appendix II: Character list for the phylogenetic analysis of the Diapsida (chapter 4.1)

1. Premaxillae are small (0) or large (1), forming most of snout in front of external nares.
2. Premaxilla is without (0) or with (1) postnarial process, restricting the contact of the maxilla to the external nares or even excluding maxilla. (Character definition modified in the interest of informativeness).
3. Snout is unconstricted (0) or constricted (1).
4. Nasals are shorter (0) or longer (1) than frontals.
5. Nasals meet in dorsomedial suture (0) or are separated from one another by nasal processes of the premaxillae extending back to the frontal bone(s) (1).
6. The lacrimal is present and enters the external naris (0), or it is present but remains excluded from the external naris by a contact of maxilla and nasal (1), or it is absent (2).
7. The prefrontal and postfrontal are separated by the frontal along the dorsal margin of the orbit (0), or a contact of prefrontal and postfrontal excludes the frontal from the dorsal margin of the orbit (1).
8. Preorbital and postorbital regions of skull are of subequal length (0); preorbital region is distinctly longer than postorbital region (1); postorbital region is distinctly longer (2).
9. Upper temporal fossae are absent (0), present and subequal in size or slightly larger than the orbit (1), present and distinctly larger than the orbit (2), or present and distinctly smaller than the orbit (3).
10. Frontal(s) are without (0) or with (1) distinct posterolateral processes.
11. Parietal(s) are paired (0), fused in their posterior part only (1), or fully fused (2) in the adult.
12. Pineal foramen is close to the middle of the skull table (0), displaced anteriorly (1), or absent (2). (Character definition modified in the interest of informativeness).
13. Parietal skull table is broad (0), weakly constricted (1), strongly constricted (at least posteriorly) (2), or forms a sagittal crest (3).
14. Postparietals are present (0) or absent (1).
15. Tabulars are present (0) or absent (1).
16. The jugal extends backward no farther than to the middle of the cheek region (0) or nearly to the posterior end of the skull (1).
17. Lower temporal fossa is absent (0), present and closed ventrally (1), or present but open ventrally (2). (Modified in Rhynchosauria).
18. Squamosal descends to ventral margin of skull (0), reaches only the approximate mid level of the lower temporal fossa (1), or remains distinctly restricted to the dorsal region of the cheek (2). (Character definition modified in the interest of informativeness).
19. Quadratojugal is present (0) or absent (1).
20. Quadratojugal has (0) or lacks (1) anterior process.
21. Supratemporals are present (0) or absent (1).
22. Mandibular articulations are approximately on a level with occipital condyle (0) or displaced to a level distinctly behind occipital condyle (1), or they are positioned anterior to the occipital condyle (2).
23. Exoccipitals do (0) or do not (1) meet dorsal to the basioccipital condyle.
24. Supraoccipital is exposed more or less vertically on occiput (0) or more or less horizontally at posterior end of parietal skull table (1).
25. Occipital crest is absent (0) or present (1).

26. Quadrate has straight posterior margin (0) or the quadrate shaft is deeply excavated (concave) posteriorly (1).
27. Quadrate is covered by squamosal and quadratojugal in lateral view (0) or exposed in lateral view (1).
28. Dorsal wing of epipterygoid is broad (0) or narrow (1).
29. Lateral conch on quadrate is absent (0) or present (1).
30. Palate is kinetic (0) or akinetic (1).
31. Suborbital fenestra is absent (0) or present (1).
32. Pterygoid flanges are well developed (0) or strongly reduced (1).
33. Premaxillae enter internal naris (0) or are excluded (1).
34. Ectopterygoid is present (0) or absent (1).
35. Retroarticular process of lower jaw is absent (0) or present (1).
36. Distinct dorsal process of lower jaw formed by the coronoid only is absent (0) or present (1). (Character definition modified in the interest of informativeness).
37. Splenial bone enters the mandibular symphysis (0) or remains excluded therefrom (1).
38. Tooth implantation is subthecodont (0), thecodont (1), ankylothecodont (2), or teeth are superficially attached to bone (3).
39. One or two caniniform teeth are present (0) or absent (1) on maxilla.
40. Vertebrae are notochordal (0) or nonnotochordal (1).
41. Vertebrae are amphicoelous (0), platycoelous (1), or other (2).
42. Dorsal intercentra are present (0) or absent (1).
43. Cervical intercentra are present (0) or absent (1).
44. Zygosphene-zygantrum articulation is absent (0) or present (1).
45. Sutural facets receiving the pedicels of the neural arch on the dorsal surface of the centrum in the dorsal region are narrow (0) or expanded into a cruciform or butterfly-shaped platform (1).
46. Transverse processes of neural arches of the dorsal region are relatively short (0) or distinctly elongated (1).
47. Pre- and postzygapophyses do not (0) or do (1) show an anteroposterior trend of increasing inclination within the dorsal and sacral region.
48. Cervical ribs are without (0) or with (1) a distinct free anterior process.
49. The number of sacral ribs is two (0), three (1), or four or more (2).
50. Sacral (and caudal) ribs of transverse processes are sutured (0) or fused (1) to their respective centrum.
51. Cleithrum is present (0) or absent (1).
52. Clavicles are broad (0) or narrow (1) medially.
53. Clavicles are positioned anteroventrally (0) or dorsally (1) to the interclavicle. (Modified in many taxa, see chapter 4.1 for details).
54. Clavicle is applied to the anterior (lateral) (0) or to the medial (1) surface of scapula.
55. Interclavicle is rhomboidal (0) or T-shaped (1).
56. Posterior process on interclavicle is elongate (0), short (1), or rudimentary or absent (2). (Character definition modified in the interest of informativeness).
57. Supraglenoid buttress is present (0) or absent (1).
58. Coracoid foramen is enclosed by coracoid ossification (0), or lies between coracoid and scapula (1).
59. Pectoral fenestration is absent (0) or present (1).
60. Humerus is rather straight (0) or “curved“ (1).
61. Deltopectoral crest is well developed (0) or reduced (1).
62. Insertional crest for latissimus dorsi muscle is prominent (0) or reduced (1).
63. Humerus has prominent (0) or reduced (1) epicondyles.

64. The ectepicondylar groove is open and notched anteriorly (0), open without anterior notch (1), or closed (i.e. ectepicondylar foramen is present) (2).
65. Entepicondylar foramen is present (0) or absent (1).
66. Radius is shorter than ulna (0), longer than ulna (1), or approximately the same length (2).
67. Iliac blade is well developed (0) or reduced. (Character definition modified in the interest of informativeness, together with new codings for Choristodera & Younginiformes).
68. Thyroid fenestra is absent (0) or present (1).
69. Acetabulum is oval (0) or circular (1).
70. Femoral shaft is stout and straight (0) or slender and sigmoidally curved (1).
71. Intertrochanteric fossa is deep (0), distinct but reduced (1), or rudimentary or absent (2).
72. Distal femoral condyles are prominent (0) or do not project markedly beyond shaft (1).
73. Anterior femoral condyle relative to posterior condyle is larger and extends further distally (0) or is smaller/equisized and of subequal extent distally (1).
74. Foramen for the supposed passage of the pes artery is present (0) or absent between astragalus and calcaneum (1). (Character definition modified in the interest of informativeness).
75. Calcaneal tuber is absent (0) or present (1).
76. Distal tarsal 1 is present (0) or absent (1).
77. Distal tarsal 5 is present (0) or absent (1).
78. Total number of tarsal ossifications is four or more (0), or less than four (1). (Character definition modified in the interest of informativeness).
79. Metatarsal 5 is long and slender (0) or distinctly shorter than the other metatarsals and with a broad base (1).
80. Metatarsal 5 is straight (0) or “hooked“ (1).
81. Mineralized sternum is absent (0) or present (1).
82. Upper temporal fenestra. Oval in outline and not elongated caudally (0) or elongated caudally with inner surface of parietal and squamosal facing dorsally (1).
83. Shape of premaxilla. Horizontal ventral margin (0) or down-turned ventral margin (1).
84. External nares. Separate (0) or single, medial naris (1).
85. External nares location. Marginal (0) or close to midline (1).
86. External nares shape. Rounded (0) or elongate (1).
87. Septomaxilla is present (0) or absent (1).
88. Form of suture between premaxilla and maxilla above dentigerous margin. Simple vertical or diagonal contact (0) or notch present in maxilla (1).
89. Postorbital and parietal contact is absent (0) or present (1).
90. Postfrontal is excluded from upper temporal fenestra (0) or enters upper temporal fenestra (1).
91. Subtemporal process of jugal is robust with height >50% of length (0), slender with height <50% of length (1), or absent (2). (Character definition modified in the interest of informativeness).
92. The contact between vomer and maxilla is absent (0) or present (1).
93. Contact between ectopterygoid and jugal. Restricted area of contact approximately equal or less than contact between ectopterygoid and pterygoid (0) or ectopterygoid expanded caudally (1).
94. Contact between ectopterygoid and maxilla is absent (0) or present (1).
95. Shape of ectopterygoid along suture with pterygoid. Transversely broad (0),

posteroventrally elongate and does not reach lateral corner of transverse flange (1), or posteroventrally elongate and reaches corner of transverse flange (2).

96. Orientation of basipterygoid processes is anterolateral (0) or lateral (1).
97. Parasphenoid teeth are present (0) or absent (1).
98. Paroccipital process ends freely (0) or reaches suspensorium (1).
99. Palatine teeth are present (0) or absent (1).
100. Teeth on palatine ramus of pterygoid are present (0) or absent (1). (Character definition modified in the interest of informativeness).
101. Upturned retroarticular process is absent (0) or present (1).
102. Slender and tapering cervical ribs at low angle to vertebrae are absent (0) or present (1).
103. Neural arches of mid-dorsals are shallowly excavated (0) or deeply excavated (1).
104. Most trunk ribs are dichocephalous (0), holocephalous but not clearly articulating with the neural arch only (1), or holocephalous and only articulating with the neural arch (2). (Character definition modified in the interest of informativeness).
105. Second sacral rib is not bifurcate (0), or bifurcate (1). (Character definition modified in the interest of informativeness).
106. Proximal caudal neural spine height. Moderately tall with height/length >1.0 and <2.0 (0), low with height/length <1.0 (1), tall with height/length >2.0 and <3.0 (2), or very tall with height/length >3.0 (3).
107. Ratio of lengths of caudal transverse processes and centra > 1.0 (0) or < /=1.0 (1). (Character definition modified in the interest of informativeness).
108. Distal width of haemal spine is equivalent to proximal width (0), tapering (1), or wider than proximal width (2).
109. Gastralia are present (0) or absent (1).
110. Coracoid process is small (0) or large (1).
111. Cranial margin of interclavicle lacks (0) or has distinct notch (1).
112. Caudal stem of interclavicle lacks (0) or has distinct expansion (1).
113. Dorsal margin of ilium is without (0) or with (1) anterior process.
114. Processus lateralis is present (0) or absent (1).
115. Supratemporal stout and short (0), long and slender, projecting far anteriorly (1), or same as (1) but also contacting the frontal (2).
116. Diastema between maxillary and premaxillary teeth absent (0) or present (1).
117. Anterior (premaxillary and dentary) teeth are upright (0) or strongly procumbent (1).
118. The maxillary tooth row is restricted to a level in front of the posterior margin of the orbit (0), or it extends backward (1). (Character definition modified in the interest of informativeness).
119. Scapula is represented by a broad blade of bone (0), is slender, high, and narrow (1), or with a constriction separating a ventral glenoidal portion from a posteriorly directed dorsal wing (2). (Character definition modified in the interest of informativeness).
120. Internal trochanter is well-developed (0) or reduced (1).
121. Heavy, conical teeth on vomer are absent (0) or present (1). (Character definition modified in the interest of informativeness).
122. Button-like, durophagous teeth are absent (0) or present (1).
123. One (0) or two (1) coracoid ossifications are present.
124. Dentary symphysis is straight (0) or recurved (1). (Character definition modified in the interest of informativeness).
125. Choana palatal exposure: parallel medial border of maxilla (0); deflected posteromedially (1); hidden in palatal view (2).

126. Maxilla ascending process between naris and orbit is absent (0) or present (1).
127. Maxilla extends to posterior orbital margin (0) or not (1).
128. Maxilla orbital exposure is absent (0) or present (1).
129. Lacrimal duct: enclosed by lacrimal only (0); lateral border formed by maxilla (1).
130. Prefrontal/palatine antorbital contact is narrow forming less than one third the transverse distance between the orbits (0), or forming at least one half the distance (1).
131. Postorbital posterior extent: terminates prior to reaching posterior limit of parietal (0); extends to at least the posterior limit of the parietal (1).
132. Squamosal occipital flange is absent or poorly developed forming only a thin ridge (0), or it is well developed forming a broadly exposed lappet (1).
133. Stapes morphology: robust with its greatest depth exceeding one third of its total length (0); slender with the length at least four times the depth (1).
134. Stapedial dorsal process: present as ossified process (0); absent (1).
135. Basi/parasphenoid ratio: narrowest transverse width no more than 60% of the maximum length measured from basipterygoid process to posteriormost limit (0); narrowest part (waist) exceeds 80% of the length (1).
136. Ventral braincase tubera: absent (0); present and restricted to basioccipital (1); present, very large, and restricted to basisphenoid (2).
137. Basioccipital/basisphenoid relationship: floor of braincase with gap between both elements (0); elements fused to floor brain cavity (1).
138. Sphenethmoid is present (0) or absent (1).
139. Palatal process of pterygoid: extends anterior to the anterior limit of the palatine (0); forms oblique suture with palatine but process ends before reaching anterior limit of palatine (1); forms transverse suture with palatine (2).
140. Orientation of transverse flange of pterygoid: directed predominantly laterally (0) or anterolaterally (1).
141. Cultriform process: long exceeding length of parasphenoid body and reaching forward to the level of the posterior limit of the internal nares (0); short not reaching the level of the internal nares (1).
142. Pterygoid transverse flange extends ventrally below the level of the maxillary tooth row (0) or not (1).
143. Surangular extends anterior to coronoid eminence (0) or terminates prior to reaching eminence (1).
144. Atlantal ribs are ossified (0) or not (1).
145. Humeral torsion: proximal and distal ends of humerus are set off at 45° angles from one another (0); angle between opposing ends reduced to not more than 20° (1).
146. Humeral distal articulations: distinct trochlea and capitellum (0); low double condyle (1).
147. Olecranon is well developed (0) or small or absent (1).
148. Metacarpal IV is longer than metacarpal III (0), or equal or shorter (1).
149. Fibula is bowed away from tibia (0) or straight and not bowed away (1).
150. Astragalus/distal tarsal IV articulation: articulation poorly defined (0), well defined (1), or absent (2).
151. Number of pedal centralia: both lateral and medial centrali present (0); medial pedal centrale lost (1); both centralia lost (2).
152. Premaxilla dentition is present (0) or absent (1).
153. Nasals are paired (0), fused (1), or lost.
154 . Frontal anterior margins: frontal suture with nasal transverse (0); oblique forming an angle of at least 30 ° with long axis of the skull (1).
155. Frontal proportions: length exceeds width by at least four times (0); length no greater

than twice the width (1).

156. Quadrate anterior process: long, extending forward along its sutural contact with the quadrate process of the pterygoid to nearly reach the level of the transverse flange (0); short, not extending anteriorly beyond 55% the length of the quadrate process of the pterygoid (1).
157. Parietal shelf for adductor musculature is absent (0) or present as shallow excavations on the lateral parietal margin (1).
158. Paroccipital processes extend laterally forming 90° with parasagittal plane (0), or are deflected posterolaterally at an angle of about 20° from the transverse width of the skull (1), or are deflected dorsolaterally at an angle of nealry 45° (2).
159. Paroccipital processes are slender (0) or heavy with anteroposterior dimension at least one third greater than dorsoventral dimension (1).
160. Prootic/parietal contact is absent (0) or present (1).
161. Medial wall of inner ear is unossified (0) or ossified (1).
162. Interpterygoid vacuity: anterior end tapers sharply (0); anterior border crescentic (1); absent (2).
163. Dentition on transverse flange of pterygoid: present as shagreen of teeth (0); present but with one large distinct row of teeth along the posterior edge of the transverse flange (1); edentulous (2).
164. Transverse flange lateral margin: posterolateral margin forms sharp edge with anteromedial margin (0); posterolateral margin merges smoothly into anteromedial margin forming a smoothly convex lateral outline (1).
165. Meckelian fossa faces mediodorsally (0) or dorsally due to greatly expanded prearticular (1).
166. Surangular lateral shelf is absent (0) or present (1).
167. Angular lateral exposure: exposed along one third the lateral face of the mandible (0); exposed only as a small sliver along the lateral face (1); absent from lateral aspect (2).
168. Prearticular extends anterior to coronoid eminence (0) or terminates prior reaching eminence (1).
169. Caudal lateral projections (transverse processes) are absent (0) or present (1) beyond fifth caudal.
170. Tibia/astragalus articulation: loose fitting (0); tightly fitting with well developed articulation (1). (Modified in Choristodera).
171. Astragalus and calcaneum: never fused in adult (0); fused (1); hinge present (2).
172. Metatarsal V plantal tubercle is absent (0) or present (1).
173. Metatarsal I / IV ratio: I greater than 50% the length of IV (0); I less than 50% the length of IV (1). (Modified in Choristodera).
174. Ratio of length of centra of mid-cervical and mid-dorsal vertebrae: < or = 1.0 (0); > 1.0 (1); > 1.5 (2).
175. Pubic tubercle: if present small and and directed anteroventrally (0); large and strongly turned ventrally (1).
176. Supinator process: large angled away from humeral shaft (0); large confluent with shaft (1); small or absent (2).
177. Skull roof is without (0) or with (1) distinct posterior emargination.
178. Frontal widely separated from the upper temporal fossa (0), or narrowly approaches or enters the anteromedial margin margin of the upper temporal fossa (1). (Character definition modified in the interest of informativeness).
179. Prefrontal and maxilla do not meet due to a contact of lacrimal and nasal (0), or prefrontal contacts maxilla and thereby separates lacrimal and nasal from one another (1).

180. Nares are positioned anteriorly (0) or are situated in the central or posterior area of the antorbital skull portion (1).
181. Lacrimal enters the orbital margin (0), or remains excluded therefrom due to an external contact between the posteroventral part of the prefrontal and the posterodorsal margin of the maxilla (1).
182. Quadratojugal remains restricted to the ventral margin of the cheek (0), or shows a distinct dorsal extension (1).

Appendix III: Data matrix of the phylogenetic analysis of the Diapsida.

```
Input data matrix:

                           111111111122222222223333333333444444444455555555556666666666777
Taxon/Node        123456789012345678901234567890123456789012345678901234567890123456789012
------------------------------------------------------------------------------------------
Ancestor          000000000000000000000000000000000000000000000000000000000000000000000000
Captorhinidae     00000000000000100000000?000000000010000000000?00000?000000000000000000000
                             1
Araeoscelidia     000000011100000000000010000?00100000100000000?000000000100000000000000000
                                  1
Rhynchocephalia   000001001000011110010010011100100011131000010000011110101000000200011110
                       2   1112   2   1   1   1          1 1
Squamata          0000010010000110221?0000011110100011131101000000011010101000000010011110
                       211  112       11111       1       2  1  1    1   1       2
                         2   2         2
Prolacerta        010101011100011020010010011?0010001010110010?001011100001000000012001110
Tanystropheus     1101010110210110221?0010011?0010001010110110?001011100001000000011011110
Trilophosaurus    01000?11100231100?0??2?0?1100010001110111010?0010111001010000?0000001110
                                                          2
Rhynchosauria     01000100101231112101100001110010101112110010?001011100101?00000010001110
Archosauriformes  010101001000001011000010011?00100010111110000010100110010100000010001110
                         1 11221   2  11  1    1  11 1    111   1 21       1    1       21
                                       2                  2
Choristodera      110101021002111010001110111?0?101010101111001001101100101000000012101111
                                    1                                            2
Pachypleurosaurs  1000020131000110200110?1011101010110?11101111001101001021111010001111111
                      1                                                 1       11 2
Simosaurus        100012022021111020011110001001010010111111111011101001121111011122111121
Placodus          101102102101011020001010011101001011011001100111001101111111111012111111
                            2
Pistosauridae     1000120121113110201?11?010110100?0???1011??110?1??1101??11111111120??1??
Claudiosaurus     0000010111000110200110?0000?00110000101?0000?001011100101000111100001111
Askeptosaurus     1010110130000110211?011?111?10100001101101101001001000001000011011001111
Endennasaurus     10001?01?1?????1?????1???????010?01???1?01?0?0100011001010000?1211010111
Clarazia          10001?0001000110221?00??111?10101011131?0110000?00110?001?0?0????20??111
Thalattosaurus    10001?0131000110221?01??111?1?10101112110?001000?0????????0001???????011
Testudines        0000010000020110020000000110001001001?1001000000101010?10000000010110001
                        12            12       1  1 1    12 1                   12
Palaeagama        0?000?0110000110221?0???11?00????????31?00??00?000?1??10??0000000?0?1101
Saurosternon      0???????????????????????????????????????00?1000??1110?101000000002001101
Coelurosauravus   10010??0100?011021010???11?0??????10?31?0110000001?????????000000000?1?1
Younginiformes    000001011100000001000010011?00100011?01000000000000100001000000000101110
                                1                                  11   1        2 1
Macrocnemus       110101013102111021???0??01011010001010110110?001011100001000??0?12011110
Helveticosaurus   100???003????????????0?????????????0?00?0110?101?01100101000110?11101021
Apsisaurus        ???????????????01000?0????010010?000?0?00010?00?001000000?00001101???100
Ichthyopterygia   101101013101011 00?01001?001?00?01110?011111010000011000010001111120100 21
                                                                           1
Kuehneosauridae   010001001101011022111010111?1010??10?0110?11?01?????10000000212011110
Drepanosauridae   110???010002011?????11?1011???????10?0112110?01?1111?0???000001?1201?111
Hupehsuchus       1?01021130?10110010010?0?00?00101010??1?11100010?011?????00111?120??021

Input data matrix (continued):

                                             111111111111111111111111111111111111111111111
                  777777788888888889999999999000000000011111111112222222222333333333344444
Taxon/Node        345678901234567890123456789012345678901234567890123456789012345678901234
------------------------------------------------------------------------------------------
Ancestor          000000000000000000000000000000000000000000000000000000000000000000000000
Captorhinidae     000000000?1000000?21???01010?000021010100000000010100010000100000000000
Araeoscelidia     000000001000000000000000000001001111110000000000010001 0?0010000??010000
Rhynchocephalia   1100101110000000011100020110100010011000000000000000010111111101?110111?
                     1               1 1           1 2    1
Squamata          110110111000000001111111100000101111100100000000000000001110110101011001
                                  112       11       2                 1 1          1
Prolacerta        10101011000011?10010?11011001111121200101000000000000010?000110111000011?
Tanystropheus     10011011000011?0111001211111010200100010100000000000011??00011111100011?
Trilophosaurus    10101011?100011001100??011110111011000?111???0000000????????10111011101
Rhynchosauria     11101011001111110111111011001111130201111001000000001100?110110011001111
Archosauriformes  101010111000111100111011110011121201001010000010000010000101111?1110111?
                   1 1      1          1             2     1 1          111
Choristodera      10101011?1011000001101001100000101010001010000000000?0101?1?1100111010?1
                               1   1                1     1
Pachypleurosaurs  110111000000010?01120????1?0100020012001?01?00021000001001?11????11?11??
                                                   1
Simosaurus        110111000000010?01120012?111111020?1?000001?01121100001011?11????10?11??
```

Appendix III: Diapsid data matrix, continued.

```
Placodus          11011100000010?01101?110110101020211000000?11000010111101101???1?121101?
Pistosauridae     ????????000011?01110?1??1111?102?01?00??1??01121000001011?11?????11?11??
Claudiosaurus     10000000?00010?01120002011000101011000000000000000000?11??11??10??010111
Askeptosaurus     100010110000010000101020111101010210000001100000000001100?101101?1?10?00
Endennasaurus     110?10100?001100??10?0?11?1101010011000000????00000?011???1???01?10????0
Clarazia          1?0111100?1001?01?11?0?011110101001100000121000011010110??1??????111??0?
Thalattosaurus    1????????01011?01?11?0???1100?01?????0???121001011010110?110?????1?1??0?
Testudines        110010110?0010100?00???011000101000?1000000???00000?11000101111111111111
                     1               1      11                            11
Palaeagama        100???10100000?0112???????????00?010?0??00?0??0?0?0???010??00???????????
Saurosternon      100000101??????????????????????0??1011?0000????00??0????????????????????
Coelurosauravus   00000000000000?0112??????????10001?11???00??00?0?0???111??0?11???1??????
Younginiformes    10000010100000?01010000011000001001000000000000000000000000111100?00001?1
                                                      1
Macrocnemus       100010110?0?11?0001????11?0101?11001001010?000000000?11???001101?1?00?1?
Helveticosaurus   1??111100?1000?011??????????0102?301000001?00001?000?1?1????????????????
Apsisaurus        1???????0?????????1????01?11??00?01???00??????01?00??00???????0?0100000?
Ichthyopterygia   1100100?000011?011?0???01?01000100?000000100000100000110?00001??1111010?
                                            1                       1
Kuehneosauridae   1????????00110?00121002001111?02011010??00?0001000000111??1???01??????0?
Drepanosauridae   101010000?0011???????????????1?01031010??1??0001??000?1???????????????0?
                                                     2
Hupehsuchus       1?00100000000???1021??2?1?110101?3110???01????0100000?????00??0??1010???

Input data matrix (continued):

                  11111111111111111111111111111111111111
                  44444555555555566666666667777777777888
Taxon/Node        56789012345678901234567890123456789012
--------------------------------------------------------
Ancestor          00000000000000000000000000000000000000
Captorhinidae     00000000001000000100000000000020?0000
Araeoscelidia     000000100001000??010000000001101000000
                                                   2
Rhynchocephalia   00001000000110010020001111110001001 0?1
                   1    1      1  1           1
Squamata          1101012000011001102101101111100100100?
                    1 1   1           1  1
                          2
Prolacerta        01111010010111010010000110201212100001
Tanystropheus     011110100101110 1?0200001102002121 0100?
Trilophosaurus    01001011010?1111102110?1?020101211?0??
Rhynchosauria     0110101100011110?020011111201111111001
Archosauriformes  00111010000?10111010100?11200011?00001
                   1           1    2              1
Choristodera      01111?1010011101?01100?110001001101000
Pachypleurosaurs  11110020000111011121011?0000000100?1?1
Simosaurus        11110020000111011121011?0000000100?1?1
Placodus          111110?010111001112110010000000110?1??
Pistosauridae     11110020000111011121011?0000000101?1??
Claudiosaurus     011100100?01100??010?00000000102000010
Askeptosaurus     011110200101110??020011?0000000211010?
Endennasaurus     011110?10101????????????00000001???1??
Clarazia          ??101??00101?1????00?00?0000000?1??1??
Thalattosaurus    ??1????00101?1????200011?????0??1??1??
Testudines        11101121001000111?211111111000010?1001
                     1
Palaeagama        ?0101???000110??????????0000?00100?01?
Saurosternon      0010111?????????????????0000??01??????
Coelurosauravus   0000101?000111??????????00000002101 0?0
Younginiformes    011110100001100??010?00?10001001001000
Macrocnemus       011010100?0111????1??0011020121210100?
Helveticosaurus   ?1111?20?????????????00?10?00001??100?
Apsisaurus        011????????1?????01??00??????1?200?000
Ichthyopterygia   11110?2001111??000101000?0000002110101
                                        1
Kuehneosauridae   00?1??10000110???000??1???00?00100001?
Drepanosauridae   ?1010010??0?000?????00??000002?20??0??
                                            1
Hupehsuchus       11110011001100???021?0??000000?200?1?1
```

Appendix IV: Character list for the phylogenetic analysis of thalattosaurs (chapter 4.2)

1. Rostrum absent (0); rostrum present but preorbital region of skull not distinctly longer than postorbital region of skull (1) (distance from tip of the snout to anterior margin of orbit shorter than distance from anterior margin of orbit to posterior tip of supratemporal), and rostrum tapering to pointed tip, i.e., with convergent lateral margins in front of external nares); rostrum present but preorbital region of skull distinctly longer than postorbital region of skull (2) (distance from tip of the snout to anterior margin of orbit longer than distance from anterior margin of orbit to posterior tip of supratemporal), and rostrum tapering to blunt tip, i.e., with parallel lateral margins in front of external nares.
2. Tip of snout (rostrum) straight (0), tip of snout (rostrum) slightly deflected ventrally (1), or strongly deflected ventrally (2). Character definition has been expanded due to the addition of state (2).
3. Maxilla is elongate and low (0) or short and high, with a well-developed ascending process (1).
4. Anterior part of alveolar margin of maxilla straight (0), or distinctly curved upwards (1). Coding for this character has been changed for *Nectosaurus* (1).
5. Tooth implantation is subthecodont (0), thecodont (1), ankylothecodont (2), or teeth are superficially attached to the bone (3).
6. Premaxilla dentition is present (0) or absent (1) (state 1 includes also pseudodont projections).
7. Diastema between premaxillary and maxillary teeth absent (0), present (1).
8. Anterior most dentary teeth upright (0), procumbent as their implantation curves around anterior end of dentary (1). Character coding has been changed for *Clarazia* and *Hescheleria* (both 1).
9. Posterior dentary and maxillary teeth conical and pointed (0), bulbous and blunt (1).
10. Pterygoid transverse flange dentition is present (0) or absent (1).
11. Pterygoid palatal ramus dentition is present (1) or absent (1).
12. Vomerine dentition is present (0) or absent (1).
13. Nasals meet each other medially (0) or are separated due to the posterior extent of the premaxilla (1).
14. Nasals do not (0), or do (1) extend backwards to level behind anterior margin of orbit. Character coding has been changed for *Paralonectes* (1).
15. Anterolateral processes of frontal remain broadly separated form external naris (0), or anterolateral processes of frontal closely approach or even enter the posterior margin of external naris (1).
16. Nasal in contact with prefrontal (0), nasal separated from prefrontal (1).
17. Posterolateral processes of frontal absent (0), present and not extending far beyond anterior margin of lower temporal fossa (1), present but extending far beyond anterior margin of lower temporal fossa (2).
18. Posterolateral processes of frontal absent (0), present but separate from supratemporal (1), or present and in contact with supratemporal (2).
19. Posterolateral process of frontal constricted (0) or broad (1) at its base (i.e., fronto-parietal suture interdigitating, oriented transversely for most of its part [0], or deeply embayed in the shape of a broad V, the apex pointing forwards [1]).
20. Postfrontal and postorbital separate (0), or fused (1).
21. Upper temporal fenestra present and large (0), reduced and slit-like (1), absent (2). Coding for this character has been changed for *Thalattosaurus* (0).
22. Posterior end of squamosal with (0), or without ventral process (1). Character polarity has

been changed, as well as the coding for *Paralonectes* (0).

23. Quadrate with (0), or without (1) distinct medial lamina. Character definition and polarity has been changed. Orignally it was defined as “quadrate without or with distinct anterior flange.”
24. The quadratojugal is present (0) or absent (1).
25. Pineal foramen small and located at center or somewhat behind of parietal skull table (0), or large and located in front of midpoint of parietal skull table (1).
26. Retroarticular process is small or absent (0) or present and distinct (1).
27. Number of cervical vertebrae is less than 10 (0) or higher than 10 (1).
28. Neural spines of posterior cervicals and thoracals are relatively low (0) or at least two times higher than broad (1).
29. Proximal caudal neural spines are relatively low (0) or distinctly elongated and at least three times higher than broad (1).
30. Cervical ribs are without (0) or with (1) anterior process.
31. Scapula is broad and rounded (0), or slender and elongate (1).
32. Humerus is long and slender (0) or stout and short (1), as compared to the trunk.
33. Radius is slender (0), slightly expanded (1), or strongly expanded and roughly kidney-shaped (2).
34. Fibula is slender (0), slightly expanded (1), or broadly expanded (2).
35. Deltopectoral crest is well developed (0) or reduced (1).

Appendix V: Data matrix of the phylogenetic analysis of thalattosaurs.

```
Input data matrix:

                           11111111112222222222333333
Taxon/Node        12345678901234567890123456789012345
-----------------------------------------------------
Araeoscelidia     00000000000000000000000000000000000
Younginiformes    00000000000001001100000000000000000
Askeptosaurus     20000000011111110000101110100101001
Thalattosaurus    21002111110010111211210 10??1??112?0
Anshunsaurus      2000?0??????1100210120?111?????????
Clarazia          11103011110010l?120121110100 0?0?111
Hescheleria       12103011110?1??????12????1010101111
Xinpusaurus       1111?0000000100111112011?1011?11220
                          1
Nectosaurus       ?21010??010010?11?112?11?1?11?112?0
Paralonectes      12112011110011???????0?1?1?????????
Agkistrognathus   ????2?100??0???????????????????????
Endennasaurus     200??1???11110?01?01??1??1100000000
Salzburg specime  ????????????????????????????1???22?
```

Lebenslauf

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Geburtsdatum: 16.06.1973
Geburtsort: Frankfurt am Main
Staatsangehörigkeit: deutsch

Schulbildung:

1979 bis 1983: Besuch der Geschwister-Scholl-Schule in Schwalbach am Taunus

1983 bis 1992: Besuch der Bischof-Neumann-Schule in Königstein/Ts., wo auch die Abiturprüfung abgelegt wurde

Zivildienst:

August 1992
bis Oktober 1993: Zivildienstleistender im Kinderhaus Höchst/Ffm.

Studium:

ab WS 1993/94: Studium der Geologie/Paläontologie an der Universität Mainz

im SS 96: Vordiplom

im März 1999: Diplom in Geologie/Paläontologie, Thema der Diplomarbeit: „Osteologie und phylogenetische Beziehungen von *Eolacerta robusta*, einer großwüchsigen Eidechse aus dem Mitteleozän von Messel und dem Geiseltal“

Januar 2000
bis April 2002: Doktorarbeit am Fachbereich Geowissenschaften der Universität Mainz