PHYLOGENY AND EVOLUTION OF THE GORGONOPSIA WITH A SPECIAL REFERENCE TO THE SKULL AND SKELETON OF GPIT/RE/7113 (‘*AELUROGNATHUS*?’ *PARRINGTONI*)

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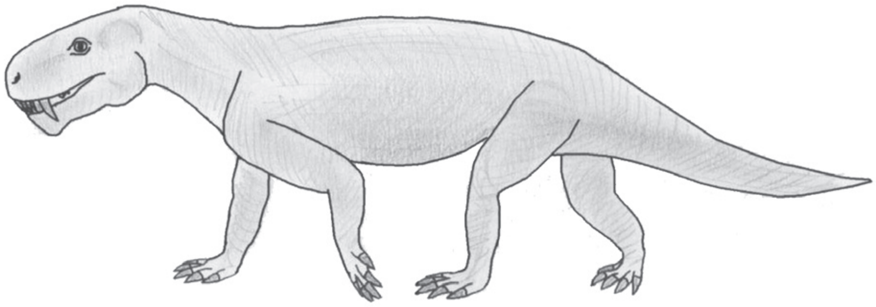

„Suchen heißt: ein Ziel haben.
Finden aber heißt: frei sein, offen sein, kein Ziel haben.“

Hermann Hesse, Siddhartha

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ABSTRACT

The Gorgonopsia, a group of carnivorous therapsids from the Upper Permian, is revised. The basis for this re-assessment is the gorgonopsian material from the NOWACK-Collection, which is housed at the Geologisch-Paläontologisches Institut Tübingen. The collection was founded by VON HUENE and consists of finds from the Ruhuhu- Valley in Tanzania that were discovered by NOWACK in the 1930s. It includes eight well-preserved gorgonopsian specimens and nine incomplete and eroded skulls, which do not show the diagnostic characters well enough to determine their taxonomic position. One of the best preserved specimens is an almost complete skeleton, GPIT/RE/7113. It was allocated to the genus '*Scymnognathus'* by VON HUENE (1950) but was later assigned to the taxon *Aelurognathus*? *parringtoni* by SIGOGNEAU (1970). A renewed investigation of the skull revealed that the specimen could not be allocated to any South or East African taxon, but rather to the Russian genus *Sauroctonus*. Thus, a true connection between the African and Russian biozones is established for the first time.

The alpha-level taxonomy of the other specimens in the NOWACK-Collection is resolved as a result of a re-assessment of the complete Gorgonopsia. This reassessment made it possible to carry out phylogenetic analyses, and present the first computer-based cladogram of the Gorgonopsia. It is shown that the family Gorgonopsidae does not include the genera *Aloposaurus*, *Cyonosaurus* and *Aelurosaurus*. Instead these taxa form the stem-group representatives of the remaining taxa. Within the Gorgonopsidae only the subfamily Rubidgeinae could be recognised whereas the other taxa constitute a gradual evolutionary pattern.

The second part deals with functional aspects of the Gorgonopsia, focusing on jaw mechanics and limb movements. Here GPIT/RE/7113 was used again as a basis for comparative research because its well-preserved postcranial skeleton enabled a thorough and detailed anatomical investigation

It is proposed that gorgonopsians were not only able to move in a dual gait fashion with the hindlimbs, as stated by KEMP (1982), but also with their forelimbs. The shape of the humeral head and the glenoid, which allow for a variety of positions, provide morphologic evidence for this hypothesis. In addition it is postulated that the animal was able to move faster when the humerus was placed at a sloping angle, because the humeral rotation would be more extensive, which in turn would increase the stride length.

The main interest, however, was the possibility that the enlarged canines of gorgonopsians and saber tooth cats might portend to further similarities in their skulls and postcranial skeletons. In order to investigate this idea, specimen GPIT/RE/7113 was closely compared with a specimen of *Smilodon fatalis*. In addition, both GPIT/RE/7113 and *Smilodon fatalis* were compared with their closest relatives, therocephalians and cynodonts, and *Panthera leo*, respectively. It is shown that the skull morphology is highly modified to be able to accommodate the high root of the caninus, that the incisivi are arranged in a parabolic arch to serve as an additional gripping device, and that a specialised jaw mechanism allows for a wide gape. In the postcranial skeleton, the massive humeri display well-developed muscle attachment areas and the necks are elongated with a stable posterior region, possibly to enable them to carry out a precise throat bite.

With this new information on phylogeny and functional morphology gorgonopsian evolution can be re-evaluated, which is essential for future studies on the group. However, more research and especially more material is needed to make additional contributions to the knowledge of these saber-toothed predators.

ZUSAMMENFASSUNG

In der vorliegenden Arbeit wurden die Gorgonopsia, eine Gruppe karnivorer Therapsiden aus dem Oberen Perm revidiert. Den Ausgangspunkt für diese neue Überarbeitung bildet das Gorgonopsidenmaterial der NOVACK-Kollektion, die sich am Geologisch-Paläontologischen Institut in Tübingen befindet. Diese Sammlung wurde in den 50er Jahren von VON HUENE begründet und besteht aus fossilen Tetrapoden, die in den 30er Jahren von NOVACK im Ruhuhu-Tal von Tansania ausgegraben wurden. Unter den Gorgonopsiden der NOVACK-Kollektion befinden sich acht gut erhaltene Stücke und neun Schädel oder Schädelfragmente, die zu unvollständig und/ oder zu verwittert sind, um diagnostische Merkmale zu zeigen. Da ihre Alphataxonomie nicht geklärt werden kann, wird das Material als Gorgonopsia indet. betrachtet. Eines der sehr gut erhaltenen Exponate ist GPIT/ RE/7113, das aus einem Schädel mit Unterkiefer und dem nahezu vollständigen Postcranialskelett besteht. In der Erstbeschreibung wurde das Tier als neue Art zur Gattung ‚*Scymnognathus*' gestellt (VON HUENE, 1950). SIGOGNEAU (1970) löste dieses Taxon jedoch auf und stellte GPIT/RE/7113 als Art *A.*? *parringtoni* zur Gattung *Aelurognathus*. Die genaue taxonomische Stellung blieb jedoch weiterhin unklar.

Eine neue detaillierte Untersuchung des Schädels ergab, dass das Stück keiner Süd-oder Ostafrikanischen Gattung zugeordnet werden kann. Dagegen ist eine deutliche Ähnlichkeit mit der Russischen Gattung *Sauroctonus* erkennbar, so dass GPIT/RE/7113 diesem Taxon als Art *S. parringtoni* zugeteilt wird. Damit konnte zum ersten Mal eine Verbindung zwischen der Afrikanischen und Russischen Biozone festgestellt werden.

Die Alphataxonomie der restlichen Stücke aus der NOVACK-Kollektion wurde im Zuge der Neubearbeitung der Gorgonopsia ebenfalls geklärt. Diese neue Untersuchung hat das Ziel anhand von morphologischen Strukturen bestimmte Taxa zu kombinieren, die ich als nicht genügend gegeneinander abgegrenzt betrachte. Diese Klassifikation ermöglichte schließlich eine phylogenetische Analyse und zum ersten Mal ein modernes computergestützes Kladogramm. Die phylogenetische Untersuchung zeigt, dass die drei Gattungen *Aloposaurus*, *Cyonosaurus* und *Aelurosaurus* nicht in der Familie Gorgonopsidae mit eingeschlossen sind, sondern als Stammgruppenvertreter der restlichen Taxa angesehen werden müssen. Innerhalb der Gorgonopsidae konnte nur eine monophyletische Gruppe festgestellt werden, die der Subfamilie Rubidgeinae. Alle übrigen Taxa hingegen weisen ein kontinuierliches Entwicklungsmuster auf ohne weitere monophyletische Gruppen zu bilden. Jedes Taxon verdeutlicht eine eigene Entwicklungsstufe, und das jeweils höher abgeleitete ging sehr wahrscheinlich aus dem primitiveren hervor, ohne weitere monophyletische Gruppen zu bilden.

Der zweite Teil der Arbeit beschäftigt sich mit funktionsmorphologischen Aspekten wie dem Kieferapparat und der Funktionsweise der Extremitäten und Gürtel. Als Ausgangspunkt für diese Studien diente wiederum GPIT/ RE/7113, da das Postcranialskelett in guten Zustand ist und detaillierte Untersuchungen erlaubt. In Gegensatz zu KEMP (1982) postuliere ich, dass Gorgonopsiden nicht nur mit dem Hinterbein zu dem so genannten ‚dual-gait' fähig waren, sondern auch mit dem Vorderbein. Diese Hypothese wird durch die Morphologie des Humeruskopfes und der Artikulationsfläche der Schulter bestärkt. Die Artikulation ermöglicht durchaus eine Anzahl von Stellungen des Humerus. War der Humerus nicht horizontal, sondern schräg artikuliert, konnte er sich in höherem Ausmaß drehen. Dies wiederum erzeugte eine größere Schrittlänge, welche schließlich bei schnellerer Geschwindigkeit von Nutzen war.

Das Hauptaugenmerk lag jedoch bei der Lösung der Frage, ob der verlängerte Caninus in einem Gorgonopsiden und einer Säbelzahnkatze noch andere Gemeinsamkeiten im Schädel und Postcranialskelett mit sich bringt. Hierzu stellte ich einen Vergleich mit der Säbelzahnkatze *Smilodon fatalis* an. Beide Arten, GPIT/RE/7113 und

Smilodon fatalis wurden darüber hinaus noch mit ihren jeweils nächsten Verwandten Gruppen, Therocephalen und Cynodontier, beziehungsweise Großkatzen, verglichen. Es zeigte sich, dass beide Tierarten verblüffende Ähnlichkeiten aufweisen, die jedoch zumindest im Schädel zum Großteil mit der Form des Caninen zusammenhängen. So ist der vordere Teil des Schädels relativ hoch, damit die lange Wurzel des Caninus untergebracht werden konnte. Die Incisivi sind bogenförmig angeordnet, um das Fleisch der Beute zusätzlich greifen zu können und außerdem gewährleistet eine solche Form mehr Stabilität für die Caninen während des Bisses. Schließlich ist das Kiefergelenk dahingehend modifiziert, so dass das Maul weit geöffnet werden konnte, damit die Beute zwischen die langen Caninen passte. Auch im Postcranialskelett gibt es Parallelen: Der Humerus ist kräftig mit gut entwickelten Muskelansatzstellen, um die Beute packen und festhalten zu können und die Halswirbelsäule ist vergleichsweise lang mit jedoch kräftigem Hinterabschnitt. Dies stabilisierte den Hals optimal und war sehr nützlich wenn das Tier seine zappelnde Beute vorne mit dem Maul packte.

Mit diesen neuen Informationen habe ich die Evolution und Funktionsmorphologie der Gorgonopsia weiter erhellt und Grundlagen für künftige Forschungen geschaffen. Weitere Untersuchungen und vor allem zusätzliches Material wären daher wünschenswert, um diese interessanten Säbelzahnräuber des Perm noch besser kennen zu lernen.

1 Introduction

1.1 Prelude

The therapsid group Gorgonopsia includes the dominant carnivores of the Upper Permian. They are exclusively restricted to this period, and, at least as far as it is known at present, all became extinct by the end of the Permian (fig.1). Within the Therapsida the gorgonopsians constitute the most basal group of the Theriodontia, which are, characterised by an enlargement of the temporal opening in association with modifications in the lower jaw, including the jaw articulation and jaw musculature. Figure 2 provides a cladogram that reflects the current majority view of therapsid interrelationships and the phylogenetic position of the Gorgonopsia as proposed by Rubidge & Sidor (2001).

The teeth and postcranial skeleton of the gorgonopsians, suggest that all forms were exclusively carnivorous predators, probably feeding on contemporaneous dicynodonts, dinocephalians or pareiasaurs. The individual gorgonopsian taxa are comparatively homogenous in their

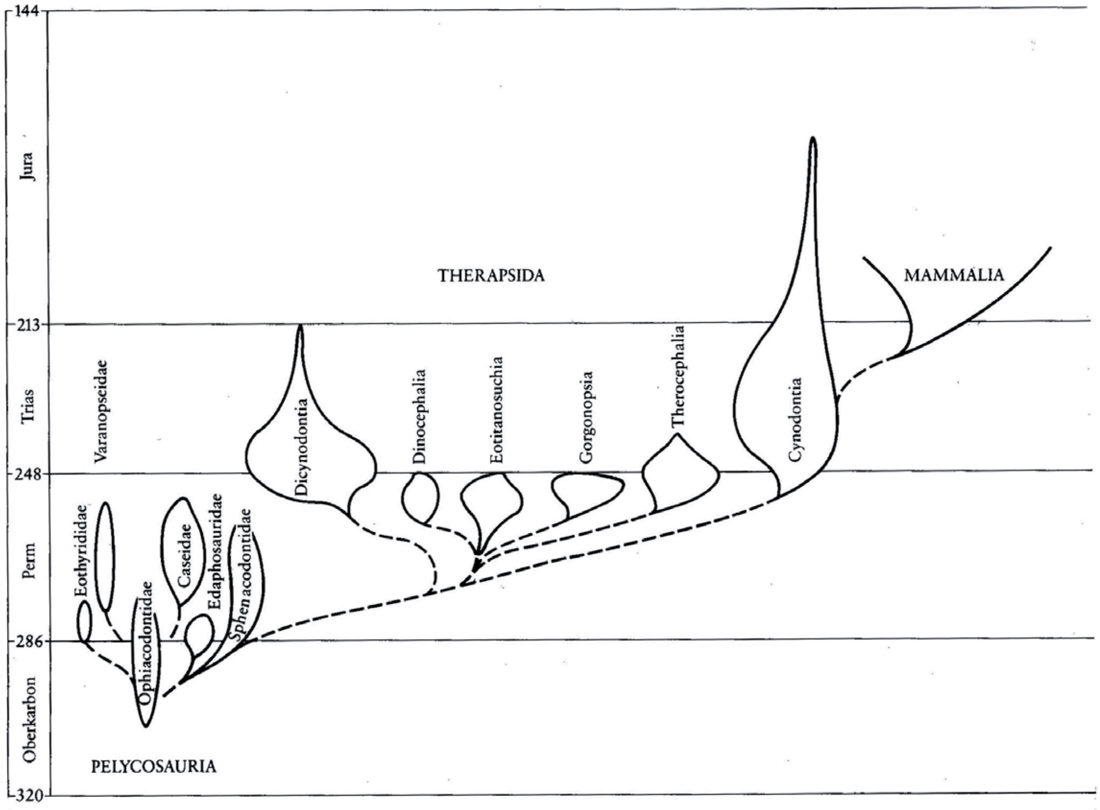


Figure 1. Phylogenetic relationships of the Synapsida and their stratigraphic distribution (from Carroll 1993).

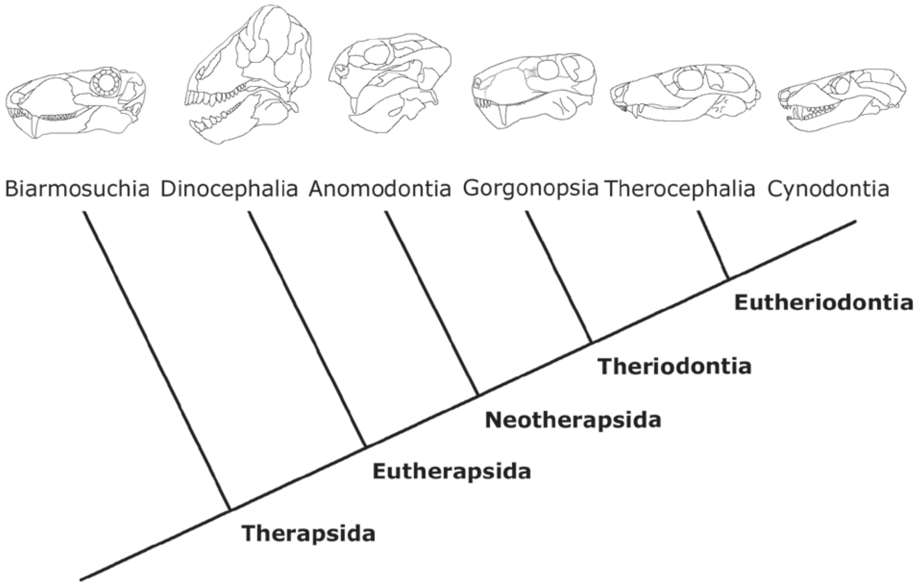
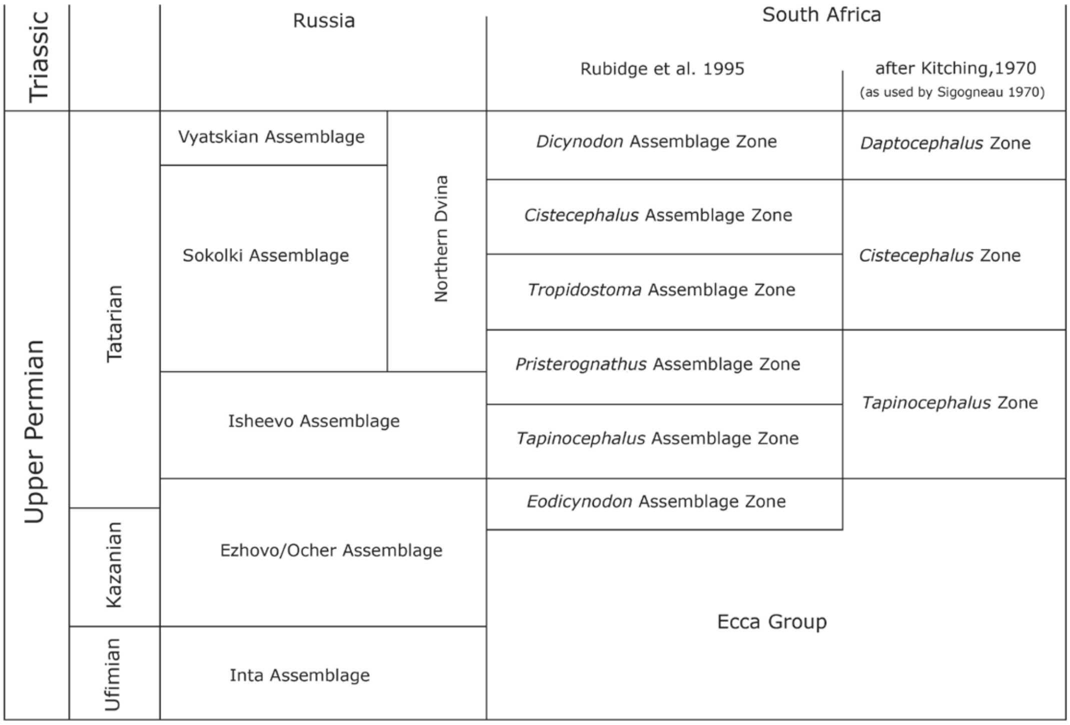


Figure 2. Cladogram of the principal therapsid groups (modified from RUBIDGE & SIDOR 2001).

overall appearance, but they do differ in size (even if ontogenetic variation, which most probably occurs in some cases, is taken into account). Some forms are only cat-sized, whereas the largest animals can reach a size that may be somewhat larger than a lion or bear.

The origin of the gorgonopsians is rather unclear since the Late Permian radiation had already resulted in the existence of several carnivorous therapsid groups that show certain similarities but at the same time display a number of specialisations. The most basal and pelycosaur-like forms are *Biarmosuchus* and *Eotitanosuchus* from the Ezhovo (Ocher) locality in Russia, whereas the South African biarmosuchian genera such as *Lemurosaurus*, *Ictidorhinus* and *Rubidgina* all date from the *Cistecephalus* and *Dicynodon* Assemblage Zones. Only *Hipposaurus* occurs as early as the *Tapinocephalus* Assemblage Zone (RUBIDGE et al. 1995). However, none of these forms is likely to present a direct ancestor to the gorgonopsians since they are either already contemporaneous with the gorgonopsians and/or have developed some autapomorphies of their own. In addition, the fossil material of *Eotitanosuchus* is too incomplete for a sound phylogenetic analysis.

A chart of Late Permian stratigraphy is shown in figure 3, however, it must be noted that the correlations of the Russian and South African zones are only approximate as well as the time-classification of the latter.



Triassic		Russia		South Africa	
				Rubidge et al. 1995	after Kitching,1970 (as used by Sigogneau 1970)
Upper Permian	Tatarian	Vyatskian Assemblage	Northern Dvina	*Dicynodon* Assemblage Zone	*Daptocephalus* Zone
		Sokolki Assemblage		*Cistecephalus* Assemblage Zone	*Cistecephalus* Zone
				Tropidostoma Assemblage Zone	
		Isheevo Assemblage		*Pristerognathus* Assemblage Zone	*Tapinocephalus* Zone
				Tapinocephalus Assemblage Zone	
	Kazanian	Ezhovo/Ocher Assemblage		*Eodicynodon* Assemblage Zone	
				Ecca Group	
	Ufimian	Inta Assemblage			

Figure 3. Upper Permian Correlations, mostly after GOLUBEV (2000) and RUBIDGE et al. (1995).

The first gorgonopsians already show all synapomorphic characters of the group, such as a well developed squamosal wing, the presence of a preparietal, a high symphysis with a chin and a coronoid process of the dentary (SIGOGNEAU-RUSSELL, 1989).

1.2 The history of gorgonopsian investigation

Gorgonopsians were amongst the earliest finds of mammal-like reptiles in the Great Karoo of South Africa. However, most of those specimens such as '*Lycosaurus pardalis'* or '*Cynodraco serridens'* should be classified as Gorgonopsia indet. or even Gorgonopsia?, since they are too poorly preserved and/or incomplete. On the other hand, taxa such as *Gorgonops torvus*, '*Lycosaurus' curvimola* (= *Arctognathus curvimola*) and *Aelurosaurus felinus* remain valid.

The specimens were first described by Owen (1876), who divided them, into three groups: 'Binarialia', 'Mononarialia' and 'Tectinarialia'. At this time the gorgonopsian specimens were not distinguished from other known carnivorous therapsids, but lumped together in the order Theriodontia. This was also done by Lydekker (1890), who established the two families Galesauridae and Gorgonopsidae. Only Seeley (1895) emphasised *Gorgonops torvus* but on a rather misinterpreted character: he believed that the specimen had no temporal opening and thus erected the new suborder Gorgonopsia for this form, as opposed to the suborder Theriodonta. Although Broom (1910) recognised the temporal opening in *Gorgonops torvus* he still regarded *G. torvus* as being distinct, whereas he interpreted *Aelurosaurus* and '*Lycosaurus'* as typical therocephalians. In 1913, however, Broom established the Gorgonopsia as a distinct group from the Therocephalia and placed a number of genera and species, including '*Scymnognathus' tigriceps*, *Scylacops capensis* and *Scylacognathus parvus,* into this taxon.

During the first half of the 20th Century, various authors carried out extensive work on gorgonopsians. One of the most diligent among those was Broom, who contributed most to the knowledge of gorgonopsian alphataxonomy in a long series of publications (e.g. 1925, 1930, 1932, 1936, 1940). Other workers were the South African palaeontologists Haughton and Boonstra. Haughton described such forms as '*Gorgonognathus' longifrons* (= *Gorgonops longifrons*) and '*Scymnognathus' serratidens* (= *Aelurognathus serratidens*) in 1915, *Sycosaurus laticeps* (1924), *Eoarctops vanderbyli* (1929) and specimens from Malawi (1927). Boonstra (1934) was the first to discuss postcranial material in detail and with a number of figures (*Aelurognathus tigriceps*, *Aelurognathus mircrodon*, *Arctognathus breviceps*). In addition he reported on specimens from the Ruhuhu-valley in Tanzania (1953). Other East African forms were mainly described by von Huene and Parrington. Von Huene (1950) examined a number of specimens from Tanzania, which form a part of the Nowack-Collection that is housed at the University of Tübingen (including GPIT/RE/7113). Parrington (1955, 1974) was among the first authors to deal with functional aspects of gorgonopsian morphology, a subject continued by his student Kemp (1969, 1982 and 2005). This author investigated the functional morphology of a gorgonopsian skull and compared gorgonopsian limb movements with those of other synapsid groups.

With respect to the alpha-level taxonomy and systematics of gorgonopsians, the contributions of a number of additional authors are of interest. From 1934 to 1936 Broili & Schröder produced four comprehensive and reliable publications concerning gorgonopsians, one of which concerning *Gorgonops* cf. *whaitsi*, another almost complete postcranial skeleton but with a rather incomplete skull. Olson (1937) comprehensively described a small and somewhat immature skull and established the genus *Cyonosaurus*; Colbert (1948) re-described *Lycaenops ornatus* in a detailed account, which established this taxon as one of the best known and easily recognisable gorgonopsian. Brink and Kitching (1953) and Manten (1958) contributed much to the knowledge of the rubidgeid genera *Clelandina*, *Prorubidgea* and *Rubidgea*.

This extensive work resulted in the creation of a large number of new genera and species. The inevitable taxonomic revision of the Gorgonopsia that followed was produced by Sigogneau (1970).

Sigogneau's and Sigogneau-Russell's (1989) great efforts culminated in a comprehensive revision of the South and East African material including the Russian taxa in 1989. Since then there were few authors looking at aspects other than the taxonomy. Laurin (1998) described a skull of *Lycaenops angusticeps* and discussed the possibility of streptostyly. Kemp (1982 and 2005) contributed much to the knowledge of functional morphology and considered gorgonopsians mainly in comparison with other therapsid groups.

The Russian taxa were predominantly described by Russian paleontologists where current scientific work is still in process. Following Amalitzky (1922, *Inostrancevia*), Hartmann-Weinberg (1938, '*Arctognathus' progressus*), Vjuschkov (1953, *Pravoslavlevia*) and Bystrow (1955, *Sauroctonus*), it was Tatarinov and Ivakhnenko who made important and various contributions to the knowledge of Russian gorgonopsians. Tatarinov (1972) discussed the holotype of *Sauroctonus progressus* at length, and established the two new genera: *Viatkogorgon* (1999) and *Suchogorgon* (2000). Ivakhnenko provided a phylogeny developed in a number of accounts, which also deal with paleobiological and functional aspects (1990, 2001, 2002, 2003, 2005).

1.3 Gorgonopsian occurrence

1.3.1 The Karoo-Basin

The best-known region for therapsid finds is undoubtedly the Great Karoo of South Africa, and gorgonopsians were amongst the earliest fossils to be found in the deposits there.

The main Karoo-Basin is a Late Carboniferous - Middle Jurassic retroarc foreland fill, developed in front of the Cape Fold Belt (Catuneanu et al 1998). It reflects sedimentary successions from glacial to deep marine, deltaic, fluvial and aeolian environments and is subdivided in different groups and formations (e.g. Smith, 1990 and 1993).

Figure 4. **A**, Map of South Africa with the location of the main Karoo-Basin marked. **B**, enlarged map of the Great Karoo where the most abundant gorgonopsian finds were made. Maps modified from Expediamaps.com.

The Permian-Triassic Beaufort Group is most relevant for this study since its Upper Permian deposits yield rich gorgonopsian fossil material. The sequence is composed predominantly of mudstones and shales, interbedded with subordinate siltsones and sandstones, deposited by a variety of fluvial depositional systems. The abundance and variety of the rich fossil material made it possible to subdivide this succession biostratigraphically into a number of fossil Assemblage Zones (Rubidge et al. 1995).

Although the first gorgonopsian finds were known from the *Eodicynodon* Assemblage Zone, the material is sparse, poorly preserved and incomplete and of no taxonomic value (Rubidge 1999). The earliest clearly identifiable specimens are from the overlying *Tapinocephalus* and *Tropidostoma* Assemblage Zones and can mainly be assigned to the genera *Galesuchus*, *Eoarctops* and *Gorgonops*. However, the greatest abundance occurred in the *Cistecephalus* and *Dicynodon* Assemblage Zones. At the same time a decrease in diversity of genera at the end of the *Dicynodon* Assemlage Zone foreshadowed the complete extinction of the Gorgonopsia at the Permo-Triassic boundary. Thus only *Cyonosaurus*, *Prorubidgea* and *Rubidgea* are common in the uppermost Permian deposits (Rubidge et al. 1995).

1.3.2 East Africa

Gorgonopsian specimens were additionally found in the three East African Countries Tanzania (Ruhuhu-Valley), Zambia (Upper Luangwa Valley) and Malawi (Chiweta), which all have Karoo deposits.

The Ruhuhu-Valley in the southwest of Tanzania is a prominent sedimentary basin with Permo-Triassic deposits. The deposits are divided into eight formations (Stockley 1932, Kreuser, 1990), but all gorgonopsians date from the K 6-Formation or Kawinga Formation (Charig 1963). The fossil remains in the Ruhuhu-Valley were collected mostly in the 1930s by the British geologist Stockley and the German engineer Nowack who were sent to map and exploit the coal measures in this area by their governments. The gorgonopsians found by Stockley were described by Haughton (1932) - they are, however, Gorgonopsia indet. now - and Boonstra (1953, '*Tangagorgon' teniurostris = Lycaenops tenuirostris*).

In 1934 and 1936 Nowack collected a large number of well-preserved therapsid and other reptile specimens at various localities in the Ruhuhu-Valley. The majority of them now constitute the Nowack-Collection of the Tübingen Museum, which includes numerous gorgonopsians originally described by von Huene (1950). Amongst these fossils was a rare, almost complete postcranial skeleton (GPIT/RE7113). In the 1950s the Cambridge palaeontologist Parrington made another expedition. He was able to collect additional

Figure 5. Map of the East African Countries Zambia, Malawi and Tanzania with the Locations of gorgonopsian finds marked and illustrated at the enlargements above. Maps modified from Expediamaps.com.

gorgonopsian specimens from the Ruhuhu-area and as a consequence the material became fairly numerous.

The taxa from Malawi are *Aelurognathus nyassaensis*, *Aelurognathus quadrata* and *Gorgonops*? *dixeyi* which were found in the Chiweta region by the geologist Dixey during the field season of 1925. Dixey left his collection of vertebrate remains to Haughton who described them in 1927.

A comparatively large number of specimens came from the Upper Luangwa Valley of Zambia, which were collected by Kitching in 1960 and 1961. However, the majority of the material is badly preserved and incomplete. It was never published except for three specimens, which were referred to the taxon *Aelurognathus quadrata* by Sigogneau (1970). In 1974 Kemp collected several gorgonopsian specimens but again they were poorly preserved and remain unpublished.

1.3.3 Russia

Permian deposits in Russia cover a large area between Moscow in the west and the Ural mountains in the east. Ivakhnenko (2001) used the term East European Placket, which was introduced by Vysotskii (1927) for the deposits of these strata to address an ecosystem constituted by deltoidal, ephemeral and lacustrine environments (Tverdokhlebova et al. 1989).

Fossil finds of the rich fauna date back to the middle of the 19th century, but it were 20th Century authors such as Pravoslavev (1927), Efremov (1954) and Tatarinov (1974) who made important contributions to the knowledge of the Russian gorgonopsian fauna. Ivakhnenko (e.g. 2002, 2003 and 2005) has subsequently revised the East European gorgonopsians in a series of papers.

Similar to the South African Karoo, the Permian of Russia is divided into different faunal assemblage Zones (e.g., Efremov, 1937; Ivakhnenko, 1990; Golubev, 2000).

The first Russian excavation was headed by Amalitzky in 1899, who collected the so-called Northern Dvina Gallery, named after the location at the Northern Dvina River. Amongst the therapsid fossils found there, were also two skeletons of the large gorgonopsian *Inostrancevia*. Other important localities are Semin Ovrag in Tartastan, Kotelnich and Ust'e Strel'ny where *Sauroctonus progressus*, *Viatkogorgon* and *Suchogorgon* were found. Although *Inostrancevia* comes from the Vyatkian horizon and the other taxa from the Severdovinian, both belong to the Sokolki Assemlage.

Figure 6. Map of Russia with the location of the south-western Ural region marked and illustrated at the enlargement. Maps modified from Expediamaps.com.

1.4 Outline and aim of this study

This study of gorgonopsian phylogeny and evolution has two major purposes. The first aim is to provide a re-assessment of the taxonomy of the Gorgonopsia and to produce a modern computer based cladogram.

Secondly I investigated different functional aspects of a gorgonopsian to create a basis for a functional comparison with the saber-toothed cat *Smilodon*. Consequently the study is divided in two parts, which, however, are connected, especially when concerning the skeleton GPIT/RE/7113. This specimen is one of the rare, almost complete skeletons that provides a major resource for scientific research and is therefore of great importance.

The configuration of the first part is to solve the alphataxonomic problems first, which still remain despite SIGOGNEAU's work. In particular the gorgonopsian specimens of the NOWACK-Collection show uncertain taxonomic positions, as shown at the list below:

Aelurognathus? *parringtoni*
Aloposaurus sp.
Dinogorgon quinquemolaris
Arctognathus? *nasuta*
cf. *Arctognathus*? *nasuta*
Leontocephalus haughtoni
Sycosaurus? *kingoriensis*

This record elucidates that only two of the recognisable forms have a definite taxonomic position. In addition there is a specimen from South Africa in the Tübingen Collection, which was allocated to the genus *Aelurosaurus* by SIGOGNEAU-RUSSELL (1989), but again has a doubtful taxonomic position. Therefore the starting point was to thoroughly re-examine these specimens in the context of developing a reliable phylogeny. Recognition of structural types made it possible to combine certain genera or species and thus I was able to reduce the number of genera and to establish clearly delimited generic diagnoses. Only with this achievement was it possible to manage the high degree of homoplastic character distribution throughout the group. This in turn allowed a phylogenetic analysis at the final stage and the construction of a cladogram.

The second part aims to solve the question if the presence of the saber tooth in a gorgonopsian and a saber-toothed cat implies other morphologic similarities in the skull and postcranial skeleton of both taxa. Again the main source here was the specimen GPIT/RE/7113 and especially its postcranial bones. On the basis of this mostly well-preserved material it was possible to study aspects of the functional morphology such as limb movements and jaw mechanics. This finally enabled me to make a comparison not only with *Smilodon,* but also with other theriodont groups.

1.5 Material & methods

As already stated above, the basis for this thesis was the gorgonopsian material held in the Tübingen Museum, which mostly belong to the Nowack-Collection. See the list below; the specimens are listed with their names and numbers as used by Sigogneau-Russell (1989) to facilitate recognition. The modernised list will be shown in chapter 2.2.

Aelurognathus? *parringtoni* (IGP U 28)	almost complete skeleton
Aloposaurus sp. (IGP K51)	skull
Dinogorgon quinquemolaris (IGP K 12)	snout
Dinogorgon quinquemolaris (IGP K 16)	skull
Arctognathus? *nasuta* (IGP K 52)	skull
Arctognathus? *nasuta* (IGP K 96)	skull
cf. *Arctognathus*? *nasuta* (IGP K 41)	skull and few postcranial elements
cf. *Arctognathus*? *nasuta* (IGP K 107)	eroded skull
cf. *Arctognathus*? *nasuta* (IGP K 115)	eroded skull
Leontocephalus haughtoni (IGP K 46B)	skull
Sycosaurus? *kingoriensis* (IGP K 47)	skull
Aelurosaurus? (IGP 7412);South Africa	skull

Gorgonopsia indet.

IGP K 13	strongly weathered skull
IGP K 35	snout
IGPK40	anterior part of snout
IGPK46	incomplete right half of the skull
IGP K 58	incomplete snout
IGP K 68	unprepared snout

The Tübingen specimens, however, only constitute a small part of the material investigated during this study. In order to obtain a broad knowledge of the group it was necessary to examine a wide range of specimens and especially the holotypes. The list below shows all collections with gorgonopsian specimens relevant for this study (please note that the institutions depicted in blue could not be visited personally).

AMNH	American Museum of Natural History, New York, USA
AMG	Albany Museum, Grahamstown, South Africa
BMNH	British Museum of Natural History, London, Great Britain
BPI	Bernard Price Institute for Paleontological Research, Johannesburg, South Africa
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
IGP/GPIT	Institut und Museum für Geologie und Paläontologie, Tübingen, Germany
MMK	McGregor Museum, Kimberly, South Africa
MZC	University Museum of Zoology, Cambridge, Great Britain
NASMUS	National Museum, Bloemfontein, South Africa
PIN	Paleontological Institute, Moscow, Russia
RC	Rubidge Collection, Wellwood, South Africa
SAM	South African Museum, Capetown, South Africa
SZ	Zoologische Schausammlung, Tübingen, Germany
TMP	Transvaal Museum, Pretoria, South Africa
WMUC	Walker Museum, Chicago, USA

From all specimens investigated, I made drawings and took those measurements that I considered useful for the phylogenetic analyses. They are, however, not listed in the text since a large number of comprehensive measurements are already provided by Sigogneau (1970). Thus I only give the length of each skull at the beginning of each genus discussion in chapter 2.2. The same applies for the photographs, which are comprehensively arranged and presented in very good quality by Sigogneau, and therefore do not need any repetition. Nevertheless I consider it appropriate to provide a selection of photographs of the Tübingen specimens and particularly of GPIT/RE/7113 as well as from the specimen of *Smilodon fatalis*. Concerning the drawings I also refer to Sigogneau (1970) for the single specimens; however, in order to elucidate the differences between the respective genera in my study, which were used for the phylogenetic analysis, I give a standardised figure for each. Detailed drawings for GPIT/RE/7113 and the other Tübingen specimens as well as for all taxa discussed in part 2 are provided.

2 PART I: SYSTEMATICS AND PHYLOGENY

2.1 The systematic position of the specimen GPIT/RE/7113 (‘*Aelurognathus*? *parringtoni*’)

2.1.1 Introduction

The specimen GPIT/RE/7113 (former IGP U 28), which is housed in the collection of the Institut für Geowissenschaften in Tübingen, is one of only a few nearly complete gorgonopsian skeletons in the world. As made obvious by the question mark, the generic allocation of the species is still uncertain. GPIT/RE/7113 does not seem to fit well into the genus *Aelurognathus*, and it is difficult to allocate it to any other South African genus. However, a close resemblance to the Russian taxon *Sauroctonus progressus* was noticed and for this reason GPIT/RE/7113 was allocated to this genus as the species *S. parringtoni*.

In order to solve this alpha-taxonomic problem it was essential to study the specimen closely, although the skull and skeleton have been described extensively by VON HUENE (1950). There are, however, no comparative comments in VON HUENE’s account and I therefore consider it justified to provide a short re-description combined with a comprehensive comparison with other taxa. The re-description will refer to both the skull and the skeleton; however, since complete postcranial material is rare in gorgonopsians in general, its use for phylogenetic analyses is limited. Thus, concerning the postcranial material, the comparison only superficially enlightens the relationships of GPIT/RE7113 with other taxa. Furthermore, only postcranial material which I could observe personally was taken into consideration.

Another comprehensive and detailed description of postcranial material is given by SIGOGNEAU (1970) and SIGOGNEAU-RUSSELL (1989) and I therefore limit my description to essential details or points that are obviously different from other taxa. In general it can be stated that the differences in the postcranial material are even smaller between the different taxa than they are in the skull.

Concerning the skull, I only describe characters that are important for the phylogenetic analyses and if appropriate I refer to *Aelurognathus* for comparison. After that I discuss the history of the specimen in the literature and make a comprehensive comparison with the taxon *Aelurognathus*. Finally, I discuss the taxon *Sauroctonus progressus* and explain why GPIT/RE/7113 is allocated to this genus as *Sauroctonus parringtoni*. In contrast to most other specimens, I was unable to study the specimen of *Sauroctonus* personally. Thus the comparison is based on the literature, which is however extensive and includes a number of good figures.

2.1.2 Comparative re-description of GPIT/RE/7113

2.1.2.1 General remarks

The skull and mandible are nearly complete, but the skull in particular has experienced some distortion. It is compressed laterally and the right side is displaced posteriorly with respect to the left. Additionally the left dorsal skull roof is considerably depressed. This condition makes an exact determination of the proportions somewhat difficult but, nevertheless, this was possible after thorough restoration. Although the lower jaw is less deformed than the skull, the right side is again compressed laterally and somewhat displaced posteriorly. The list below gives an overview over the most important measurements (all in mm).

Skull length (from tip of snout to occipital condyle):	250
Snout length (from tip of snout to anterior margin of orbit):	135
Length of posterior skull part (from anterior margin of orbit to occipital condyle):	115
Length of palatine (from tip of snout to interpterygoid vacuity):	150
Length of cranial basis (from interpterygoid vacuity to occipital condyle):	100
Height of snout (from anterior margin of canine to dorsal margin of snout):	70
Width of snout (measured between the two canines):	45
Orbital width:	65
Temporal width:	75
Width of occiput (measured between the tips of the squamosals):	140
Height of the occiput (from occipital condyle to occipital crest):	85
Length of a mandibular ramus:	240
Height of symphysis of lower jaw:	55
Length of symphysis of lower jaw:	25
Width of symphysis of lower jaw:	43
Height of dentary (at the level of the second postcanine tooth):	37

The missing parts are: the zygomatic arch, squamosal, tabular, quadrate and the posterior parts of the postorbital and parietal (all on the left side), both epipterygoids, stapes and rami quadrates and the sphenethmoid region. Although the vomer was described by VON HUENE (1950) it is now missing, which might have been the result of inadequate cast production. In the mandible the left posterior ramus is missing except for small parts of the processus coronoideus and the articular. The lower parts of the right lamina reflecta are missing as well.

Restoration shows that the skull is rather low and the snout is almost as wide as high. The dorsal profile of the snout is slightly sloping whereas the dorsal skull roof is straight. The curvature of the ventral margin of the maxilla and that of the zygomatic arch is only slight. All three skull arches are comparatively slender with the suborbital arch being the thickest. The orbit is round and medium-sized and the temporal opening long. The palate shows a narrow palatine and palatal fossa and the transverse apophyses are situated posteriorly. Although the occiput appears strongly concave, this is mostly due to deformation. Thus the occiput might originally have been only slightly concave but somewhat sloping antero-posteriorly. The median ridge is narrow, but well developed, and terminates in a bulbous thickening above the foramen magnum. In dorsal direction the occipital surface is considerably concave, forming two round depressions on both sides of the median ridge.

In the mandible, the dentary is stronger than in *Aloposaurus* but more slender than in *Aelurognathus*. The same applies for the symphysis which is of medium heaviness and slopes to a lesser degree than in *Aloposaurus* but is not as straight as in *Aelurognathus*.

For comparison the measurements (all in mm) for the mandible in *Aloposaurus* and *Aelurognathus* are given below.

	Aloposaurus	***Aelurognathus***
Length of skull:	150	290
Height of symphysis of lower jaw:	26	85
Length of symphysis of lower jaw:	14	35
Width of symphysis of lower jaw:	30	60
Height of dentary:	20	55

2.1.2.2 Dentition

The dentition is almost complete though most tips of the incisors are broken off. In the upper jaw the comparatively strong incisors are somewhat displaced and damaged but their serrations and wear facets are clearly visible. The first three incisors have the same length, whereas the fourth is the longest and the fifth the shortest. This is a condition found in many gorgonopsian specimens. Both canines are well preserved and show serrations on the posterior margin and wear facets antero-ventrally. The postcanine dentition is rather difficult to determine, since the maxilla is damaged in this area on both sides. Nevertheless there are at least four to five moderately sized teeth observable on the right side; however, the fifth might be a replacement tooth since it is situated medially to the fourth.

The lower jaw has the usual four incisors, which are, however, somewhat squeezed on the left side. Nevertheless the serrations on both margins and the wear facets are recognisable. The first incisor is the largest whereas the remaining ones have approximately the same length. The canine directly follows the last incisor. It is less crescent-shaped than the upper canine but also shows serrations on both margins and wear facets on the ventral half of the anterior margin.

The determination of the postcanines is again difficult. On the right side three postcanine teeth are visible, although the tips are broken off. In front of the first postcanine tooth and between the first and second tooth, there remains an empty space 5 mm in width, but no alveolus is visible. On the right side, two basal parts of postcanine teeth are present and three alveolar roots are also visible. Thus it is possible that the number of postcanines in the lower jaw was five.

2.1.2.3 Skull (figs. 7 - 11)

2.1.2.3.1 Premaxilla/septomaxilla

The premaxilla is relatively low, since the external nares are situated comparatively ventrally. Posteriorly the bone is overlapped by the maxilla on the external surface of the skull, but on the internal face the premaxilla persists slightly further posteriorly, thus forming a scarf joint. Dorsally the premaxilla meets the septomaxilla and nasal. The suture with the latter is unclear because the ascending internarial process of the premaxilla is missing, except for the ventral-most 6 mm.

The septomaxilla extends comparatively far posteriorly as a narrow process, it is, however, relatively low. There is no recess in the area of the septomaxilla foramen and thus the suture with the maxilla is regularly bow-shaped. The septomaxillary foramen perforates the bone at the dorsal end of a distinct oval fossa.

2.1.2.3.2 Maxilla

The maxilla is strongly sculptured with radiate grooves, pits and elevations. Its dorsal and posterior suture establishes a straight contact with the nasal, prefrontal, lacrimal and jugal. Postero-ventrally it forms a scarf joint with the jugal, sending a narrow process posteriorly on its external surface.

On the internal face the maxilla constitutes the steep internal wall of the snout. Medial to the canine the bone is strongly convex to accommodate the massive and long canine root. Posteriorly, the maxilla meets the palatine at the level of the first postcanine. Posterolaterally the maxilla contains the postcanine tooth row and continues caudally to terminate between the pterygoid and the jugal as a narrow process.

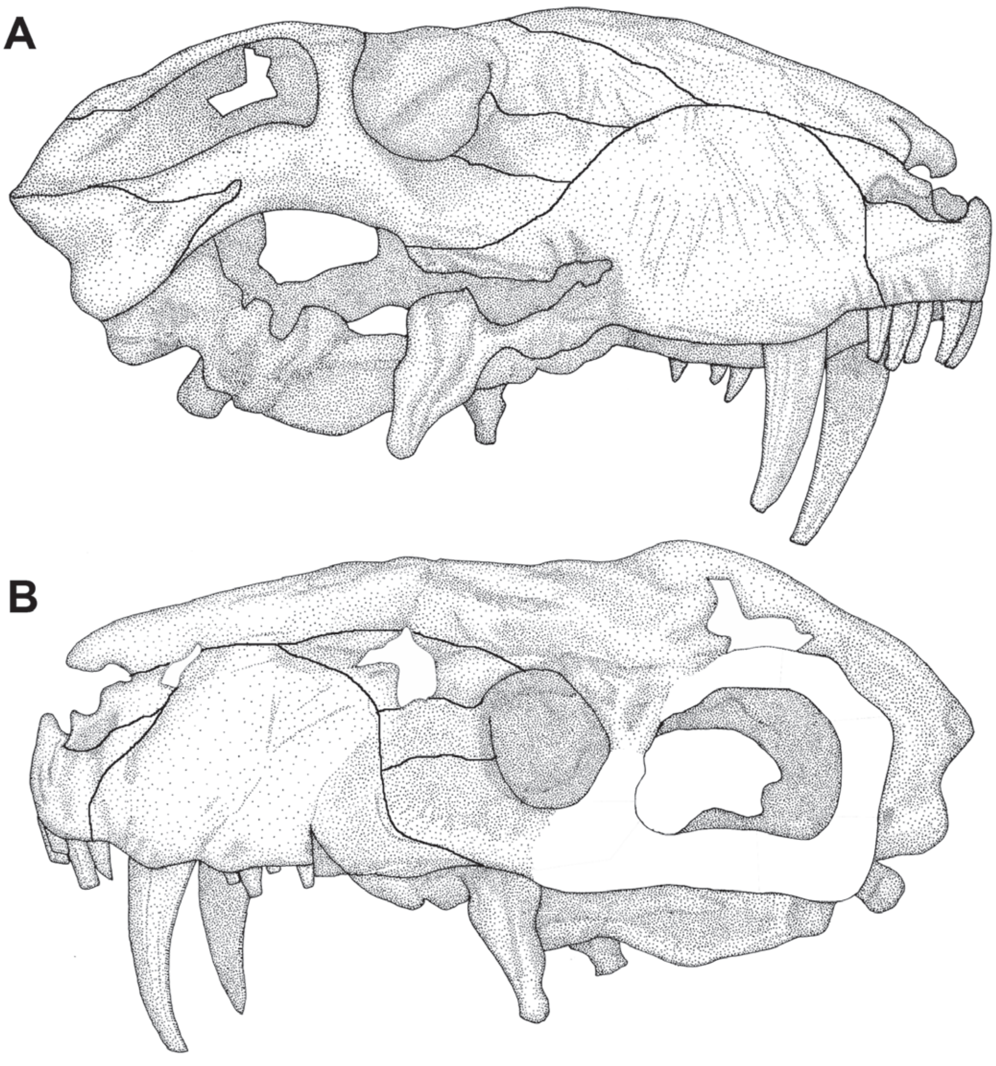


Figure 7. GPIT/RE/7113; drawings of the skull in **A**, rightlateral view; **B**, leftlateral view. Scale bar 50 mm.

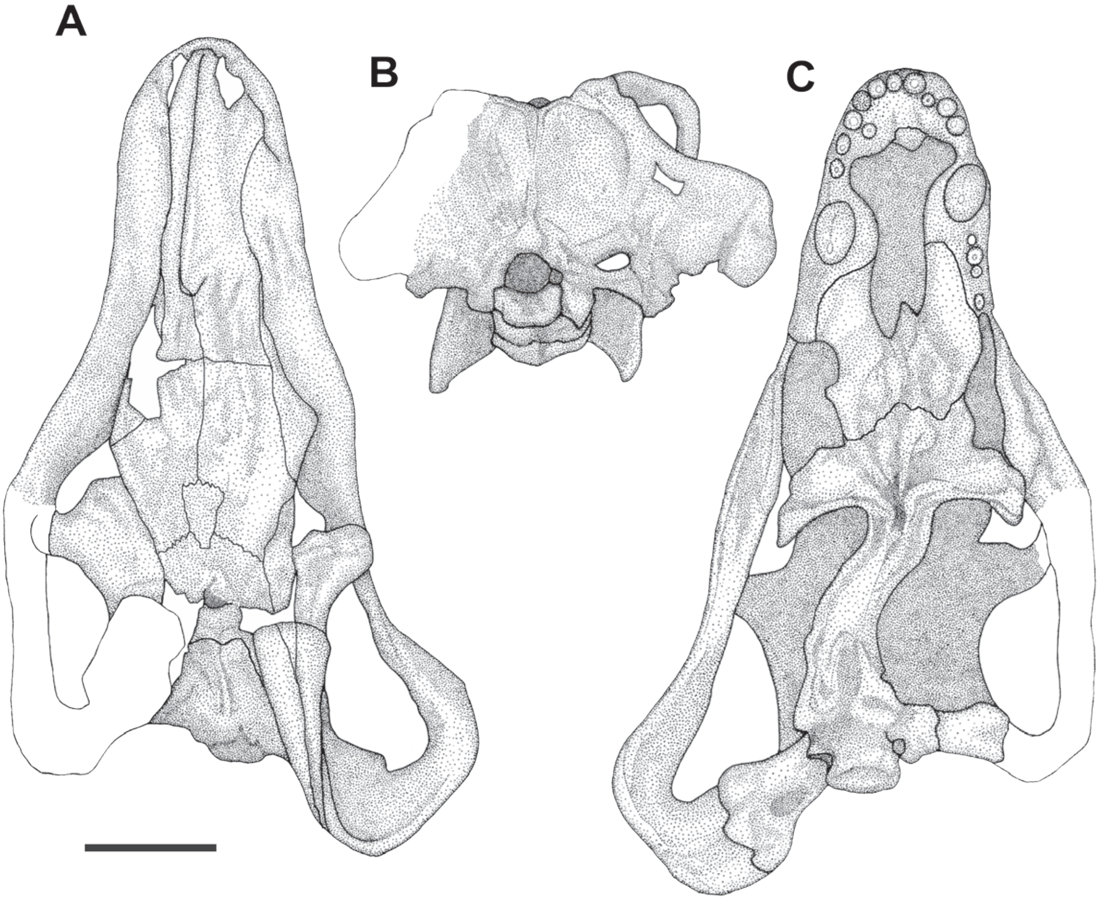


Figure 8. GPIT/RE/7113; drawings of the skull in **A**, dorsal; **B**, occipital; **C**, ventral view. Scale bar 50 mm.

2.1.2.3.3 Lacrimal/jugal

The lacrimal is a small bone, which is clearly longer than high and somewhat sculptured with grooves and pits. It shows no antorbital depression and only the orbital margin is slightly set off from the rest of the bone. The suture with the jugal is straight but the lacrimal-prefrontal suture is somewhat undulating in front of the orbit. On the internal rim of the orbit two small lacrimal foramina are visible that are situated more on the lateral side of the orbital wall.

The jugal forms a moderately thick suborbital bar. Posteriorly it forms an extensive double scarf joint with the squamosal. Thus on the external face the squamosal reaches far anteriorly by means of a narrow process that overlaps the jugal and on the internal face the jugal overlaps the squamosal ventrally and dorsally.

Figure 9. GPIT/RE/7113; photographs of the skull in **A**, rightlateral; **B**, leftlateral and **C**, occipital view; Scale bar 50 mm.

2.1.2.3.4 Nasal

The anterior extension of the nasal is unclear because the internarial bar is missing and the premaxilla/nasal suture is beyond recognition. The nasal is strongly sculptured with oblong furrows anteriorly that get somewhat thinner and shorter posteriorly. It is hardly constricted in the middle, in contrast to *Aelurognathus*. Posteriorly the naso-frontal suture is situated just in front of a boss-like elevation. It is somewhat bow-shaped and strongly serrated.

On the internal side of the skull roof two smooth parallel ridges extend over the entire length of both nasals.

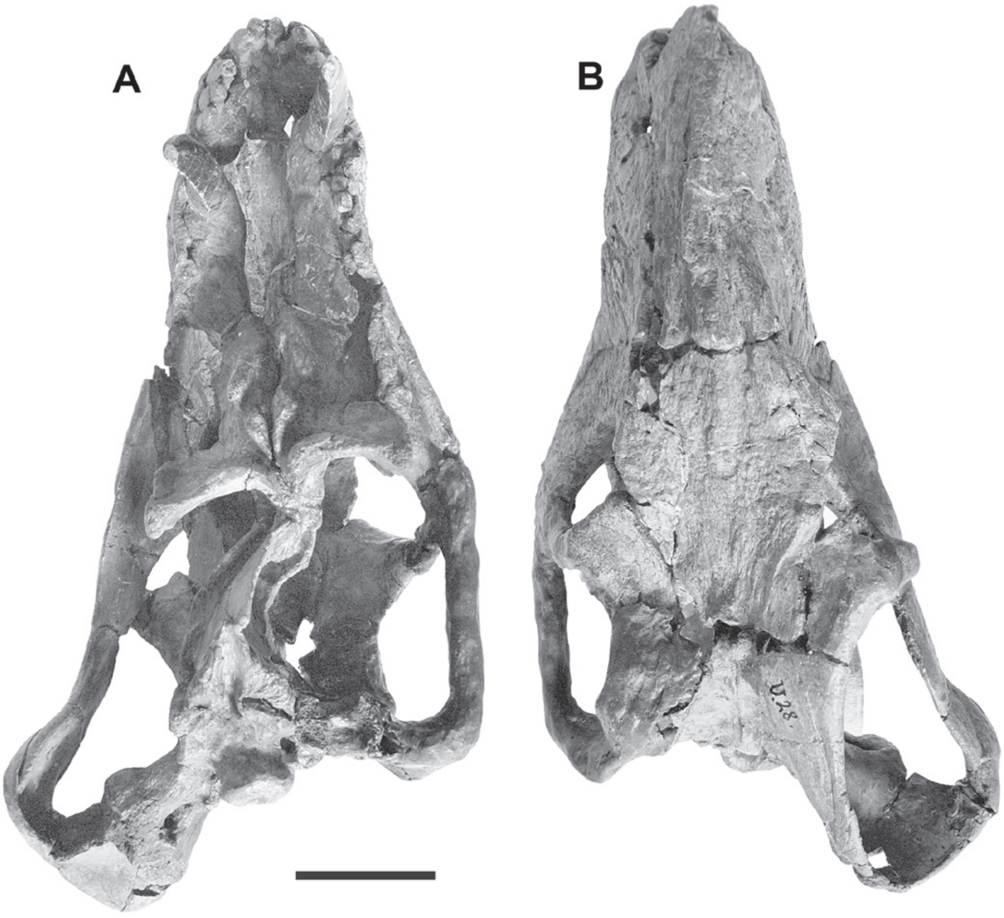


Figure 10. GPIT/RE/7113; photographs of the skull in **A**, ventral; **B**, dorsal view; Scale bar 50 mm.

2.1.2.3.5 Prefrontal/frontal

The prefrontal is a relatively large bone that reaches far anteriorly compared to the situation in other gorgonopsians. The contribution of the prefrontal to the dorsal margin of the orbit is rather small since it is largely bordered by the frontal posteriorly. In front of the orbit the prefrontal forms a slight elevation which is, however, not as pronounced as in *Aelurognathus*. The surface of the prefrontal is covered with grooves and knots but less sculptured than the maxilla and nasal.

The frontal is rather long since the suture with the nasal is situated far anteriorly. In the area of the naso-frontal contact an elongate median elevation is established that is bordered by shallow grooves laterally, which terminate at the level of the orbit. The frontal forms a considerable part of the orbital margin, but the latter it is bordered by the postfrontal posteriorly.

A serrate suture with the parietal runs transversely from the medial margin of the frontal in a posterolateral direction up to the level of the anterior margin of the temporal fossa. Posteromedially the two frontals are separated by the preparietal. On the internal side of the skull roof two strong 40 mm long turbinal ridges are established, which slightly diverge at an angle of 20°. The anterodorsal median ossification is situated between these ridges.

2.1.2.3.6 Preparietal/parietal

The fan-shaped and moderately sized preparietal does not reach the parietal foramen but is situated almost 10 mm in front of it. The anterior suture with the frontal and the posterior suture with the parietal are strongly serrated, whereas the lateral suture is straight. The surface of the preparietal is covered with narrow striations.

The parietal is narrow anteriorly but widens posteriorly to give it a wing-shaped appearance. The surface is only slightly sculptured and thus the intertemporal space is relatively smooth. The foramen parietale is surrounded by a narrow ridge and situated on a slight elevation, which is, however, deformed. It is well separated from the preparietal, as mentioned, above and lies also well in front of the occipital crest. The parietal does not contribute to the occipital surface and thus the suture with the interparietal directly forms the margin of the occipital crest. On the internal side of the skull roof the suspension for the orbitosphenoid is established as two narrow but strong ridges that reach anteriorly into the frontal. Lateral to the foramen parietale the dorsal-most remains of the epipterygoid are visible.

2.1.2.3.7 Postfrontal/ postorbital

The postfrontal is rather narrow compared to other gorgonopsians and retains the same width throughout its entire length. The posterior margin is straight but its lateral margin is somewhat extended posteriorly.

The ventral extension of the postorbital on the postorbital bar is beyond recognition since this part is missing on both sides of the skull. However, the preserved parts indicate a rather slender postorbital arch. Dorsally on the skull roof the postorbital extends with a long narrow process that extends posteriorly before it forms a scarf joint with the squamosal laterally. Medially, the suture with the parietal is situated in a shallow groove.

2.1.2.3.8 Squamosal

The squamosal forms the posterolateral part of the skull and the posterior margin of the temporal fossa. Anterodorsally it is overlapped by the posterior process of the postorbital and the parietal on the external side. On the internal side, however, the squamosal reaches anteriorly with a small process, meeting the postorbital and parietal again but almost 35 mm farther anteriorly. On the lateral face the squamosal sends a pointed process into the jugal and reaches anteriorly up to the middle of the temporal fossa. In posterior view the squamosal constitutes the lateral boundary of the occiput. It shares a long suture with the tabular and meets the paroccipital process of the opisthotic ventrally. Anteriorly, on its internal face lateral to the paroccipital process, a concave, 20 mm wide recess for the quadrate is established. This recess is roofed dorsally by a crista of the squamosal and has a smooth surface.

2.1.2.3.9 Quadrate/ quadratojugal (fig. 11)

Only the right, disarticulated quadrate with parts of the quadratojugal are preserved. The quadrate is elongated in a dorsal direction and measures 40 mm in height. The posterior face is convex whereas the anterior face is slightly concave. Medioventrally the posterior face shows two pronounced fossae, which are separated from each other by a thin ridge. The lower fossa is more elongated and served for the insertion of the stapes. The upper fossa is shallower and might have housed the ramus quadratus of the pterygoid and the epipterygoid. The ventral margin of the quadrate exhibits a rounded facet for the articulation with the articular. It is concave in the middle and convex anteriorly and posteriorly. Posterolaterally a small part of the quadratojugal is preserved. The recess on the ventrolateral margin might be the medial border of the foramen quadratojugalis.

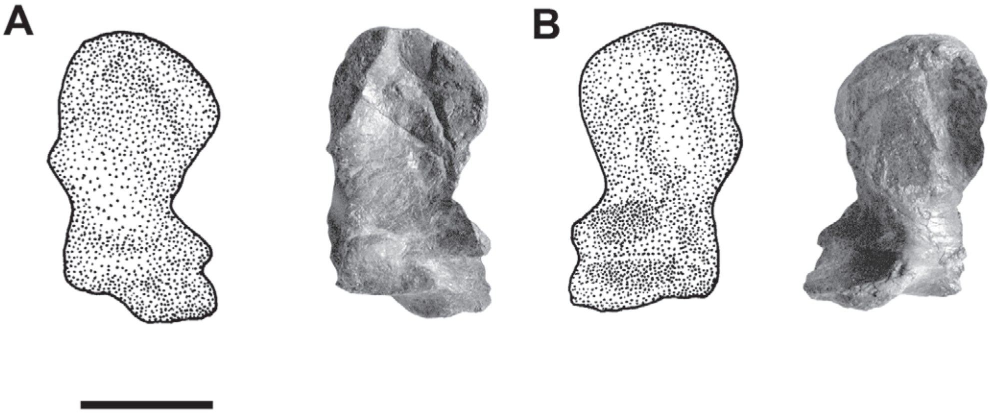


Figure 11. Drawings and photographs of the right quadrate of GPIT/RE/7113. **A**, anterior; **B**, posterior view. Scale bar 20 mm.

2.1.2.3.10 Vomer

Most parts of the vomer are missing although von Huene (1950) described and figured it as complete. Today, however, only the anteriormost and posteriormost portions of the vomer are preserved. The entire vertical blade is missing and thus no information on its width can be given. However, the posterior portion is narrower than the anterior portion. The latter borders the premaxilla with a strongly serrated suture. Posteriorly the vomer continues between the palatines and extends posteriorly for almost 25 mm, separating the palatines and forming a deep groove between them.

2.1.2.3.11 Palatine/ectopterygoid/pterygoid

The rather narrow and elongate palatine overlaps the maxilla anteriorly. Laterally it is bordered by the ectopterygoid. No information can be given about the anterior extension of this bone since the skull is damaged in this area on both sides. Hoverer, laterally, the suture with the maxilla lies in a deep groove that extends anteriorly. The ectopterygoid does not reach far ventrally on the transverse apophyses of the pterygoid and thus seems to be wider than long. Posteriorly, the palatine is connected with the pterygoid by a strongly serrated suture. The latter bone is composed of the horizontal palatal part, the vertical standing transverse apophyses and the ramus quadratus, which is, however, missing. Medially on the palatine and pterygoid the palatal fossa is situated, which is deep but rather narrow. It is bordered by the palatal tuberosities. The ones on the palatine are larger, more elongate and broader than those on the pterygoid. The latter are only broad on their anterior extremities but considerably narrower and pointed posteriorly. Both tuberosities are separated from each other by a groove. They bear numerous small teeth. The interpterygoid vacuity is situated posteriorly and is oval and deep. Lateral to it are the transverse apophyses of the pterygoid. They are mostly directed ventrally and only somewhat posteriorly. The ventral margin forms a broad rim medially, which contains a few teeth. It becomes a sharp ridge laterally that terminates in a rounded tip. Here the otherwise smooth bone surface is rugose. The lateral face of the transverse process, which abuts the lower jaw, has the shape of an elongate triangle and also exhibits a smooth surface.

2.1.2.3.12 Para-basisphenoid complex

Posterior to the transverse apophyses is the vertical sheet of the parasphenoid. It is bordered laterally by the horizontal ramus quadratus of the pterygoid, which bears a sharp ridge on its lateral margin. Dorsally only the ventralmost parts of the thin parasphenoid rostrum are preserved. Because of the deformation in this area (the bone is stretched and bent heavily) the usually hardly visible suture with the basisphenoid is recognisable as an oblique line. Dorsally the basisphenoid forms the anteroventral margin of the foramen magnum and the posterior border of the hypophyseal fossa. Here the bone reaches dorsally with a rounded tip. Ventrally the basisphenoidal tuberosities are narrow, elongate and strongly rugose. Between them the long para-basisphenoid fossa is situated, which is also narrow. Posteriorly, the fossa merges into a broader and shallower area that forms the middle parts of the basioccipital tubera. The basisphenoidal tuberosities and the basioccipital tubera are separated by a narrow trench. The fenestra ovalis is only visible on the right side: it is, however, well developed and bordered by a narrow wall. Posteriorly the occipital condyle is somewhat detached from the rest of the basioccipital body. It is undivided and kidney-shaped with a smoothly rounded lower margin. Dorsally there is no sutural separation from the exoccipital but this bone is distinguishable by its knobbly and tuberous appearance.

2.1.2.3.13 Prootic/opisthotic

The prootic forms the mid-parts of the anterior wall of the occiput. Laterally it is fused with the paroccipital process of the opisthotic. Dorsally the prootic establishes the upper margin of the foramen posttemporalis whose posterolateral edge is, however, bordered by the squamosal, that forms a somewhat overhanging sheet. Anteriorly the prootic forms the anterolateral wall of the foramen magnum. Between the squamosal sheet and the edge of the foramen magnum an oval depression is established. Dorsally the two prootics are separated by the supraoccipital, which constitutes the dorsal rim of the foramen magnum.

The prootic is fused with the opisthotic ventrally. This bone is mainly composed of the paroccipital process, which is shifted somewhat anteriorly. It is comparatively low medially but widens laterally where it abuts against the tabular and squamosal with a massive facet.

2.1.2.3.14 Supraoccipital/interparietal/tabular

The supraoccipital forms extremely serrated sutures with the interparietal and the tabular. It is rather high but is also very narrow and only constitutes the medial half of the upper margin of the fenestra posttemporalis. The surface of the supraoccipital is dominated by faint ridges that radiate from the medial thickening.

The interparietal is somewhat larger than the supraoccipital and exhibits strongly serrated sutures as well. It is slightly wider than high with a quadrate outline and meets the parietal dorsally.

The tabular is only visible on the occipital plate where it flanks the interparietal and the supraoccipital laterally. It reaches the paroccipital process of the opisthotic ventrally, the posterior extensions of the parietal and postorbital dorsally and the squamosal ventrolaterally. Here the tabular forms a protruding flange, which borders the lateral margin of the foramen posttemporalis, and which extends further ventrally for about 7 mm where it overlaps the paroccipital process of the opisthotic.

2.1.2.4 Lower jaw (figs. 12-14)

2.1.2.4.1 Dentary/splenial

As mentioned above, the symphyseal part of the dentary, which is covered with numerous small foramina, is relatively massive in comparison to the rest of the bone. Posterior to the level of the canine there is a marked depression for the reception of the upper canine.

It reaches ventrally almost up to the lower margin of the bone and is separated from the symphyseal part by a sharp edge. Posteriorly, the dentary retains its height up to the level of the angular, then narrows slowly and terminates in the processus coronoideus, which forms its dorsalmost extremity. This process is rather slender and is oriented more posteriorly than dorsally. Its tip is strongly rugose. On the internal face the dentary only forms the upper two-thirds of the symphyseal part because it is internally covered by the splenial ventrally. Posteriorly, the dentary narrows rapidly with a somewhat undulating suture and only forms

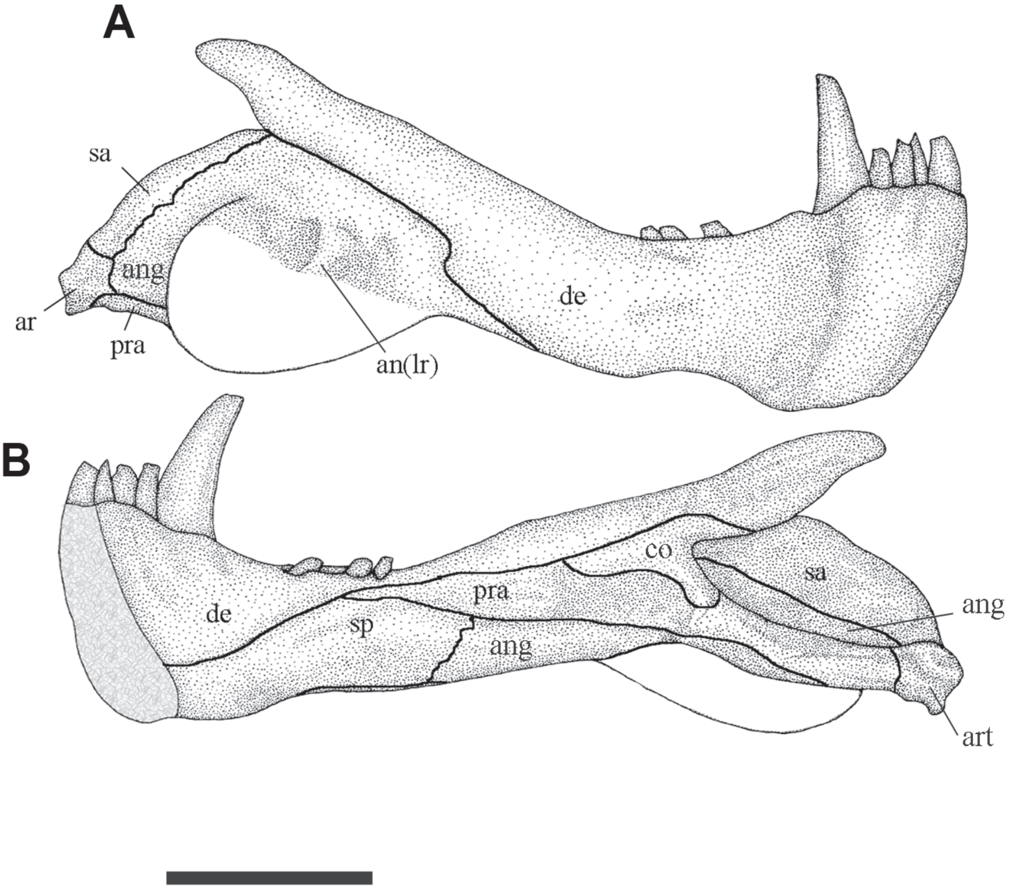


Figure 12. GPIT/RE/7113; drawings of the lower jaw in **A**, rightlateral; **B**, internal view. Scale bar 50 mm.

the alveolar border and the processus coronoideus, since it is overlapped by the splenial, coronoid and prearticular ventrally.

The splenial is visible on the internal and ventral side of the lower jaw. It forms the ventral parts of the symphysis and is situated between the dentary dorsally and ventrally and the prearticular and angular posteriorly. In the area of the postcanines it extends dorsally before it again bends ventrally to send a broad triangular process to contact the prearticular and the angular, covering these two bones. At the ventral margin it is again bordered by the dentary as described above. The splenial/dentary contact on the symphysis is marked by a depression that is oriented postero-laterally.

2.1.2.4.2 Angular

The angular mainly forms the lamina reflecta but also a small part of the mandibular ramus and of the area postero-dorsal to the lamina reflecta. On the external face, the angular borders the dentary anteriorly with a narrow process that gets wider in posterior direction and forms the lamina reflecta. The lower extension of the sheet is beyond recognition, as described above, but the upper parts of the ridge of the lamina reflecta, which runs anterodorsally to posteroventrally, are preserved. It is well developed with a rounded contour and with an elongate depression in front and behind. Posteriorly, the suture with the surangular runs bow-shaped in a posteroventral direction until the angular reaches the prearticular ventrally. On the internal face the lamina reflecta is covered medially by a rod-like element that is mainly composed of the prearticular.

2.1.2.4.3 Prearticular/coronoid

The prearticular reaches anteriorly up to the level of the last postcanine tooth until it is covered by the dentary and splenial. Posteriorly, it widens to meet the angular ventrally. In this area a relatively broad groove is established which separates these two bones for almost 25 mm. At the level of the anterior margin of the lamina reflecta, but on the internal face, the prearticular is covered by the coronoid dorsally. This comparatively small bone has a triradiate shape and forms the angle where the rod shaped part of the prearticular and the processus coronoideus diverge.

2.1.2.4.4 Surangular/ Articular (fig. 14)

The surangular forms the dorsal margin of the posteroventrally directed posterior portion of the upper jaw. It is visible both on the external and internal face, however the internal part is larger. Posteroventrally it reaches the articular, but both bones are highly intergrown and thus no suture is visible.

The articular has two articulating surfaces for the quadrate. The anterior fossa is smaller and almost round in shape. It is situated entirely on the same level and is surrounded by a distinct ridge. The second fossa is elongated mediolaterally and declines steeply posteroventrally. The dorsal and ventral margins as well as the lateral and medial ones bear ridges.

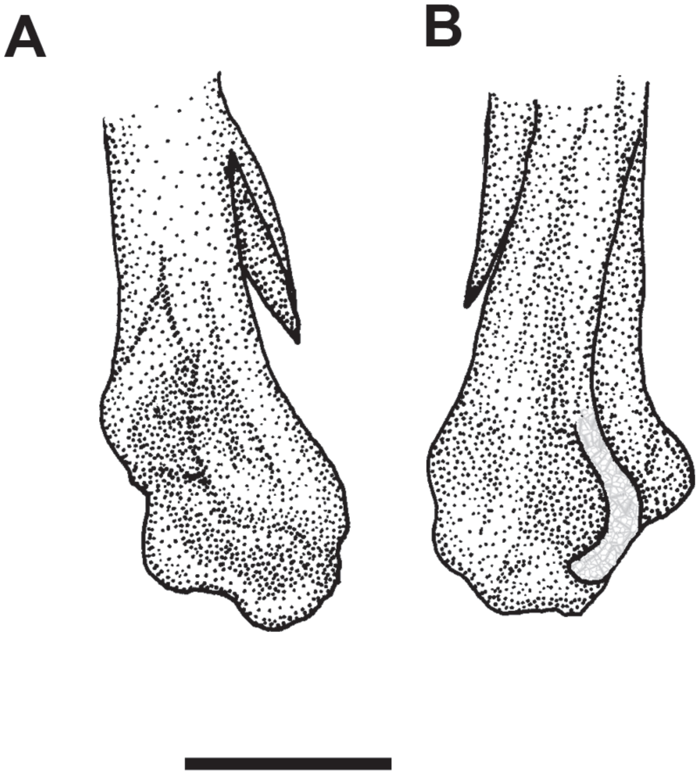


Figure 13. GPIT/RE/7113; right articular in **A**, dorsal and; **B**, ventral view. Scale bar 20 mm.

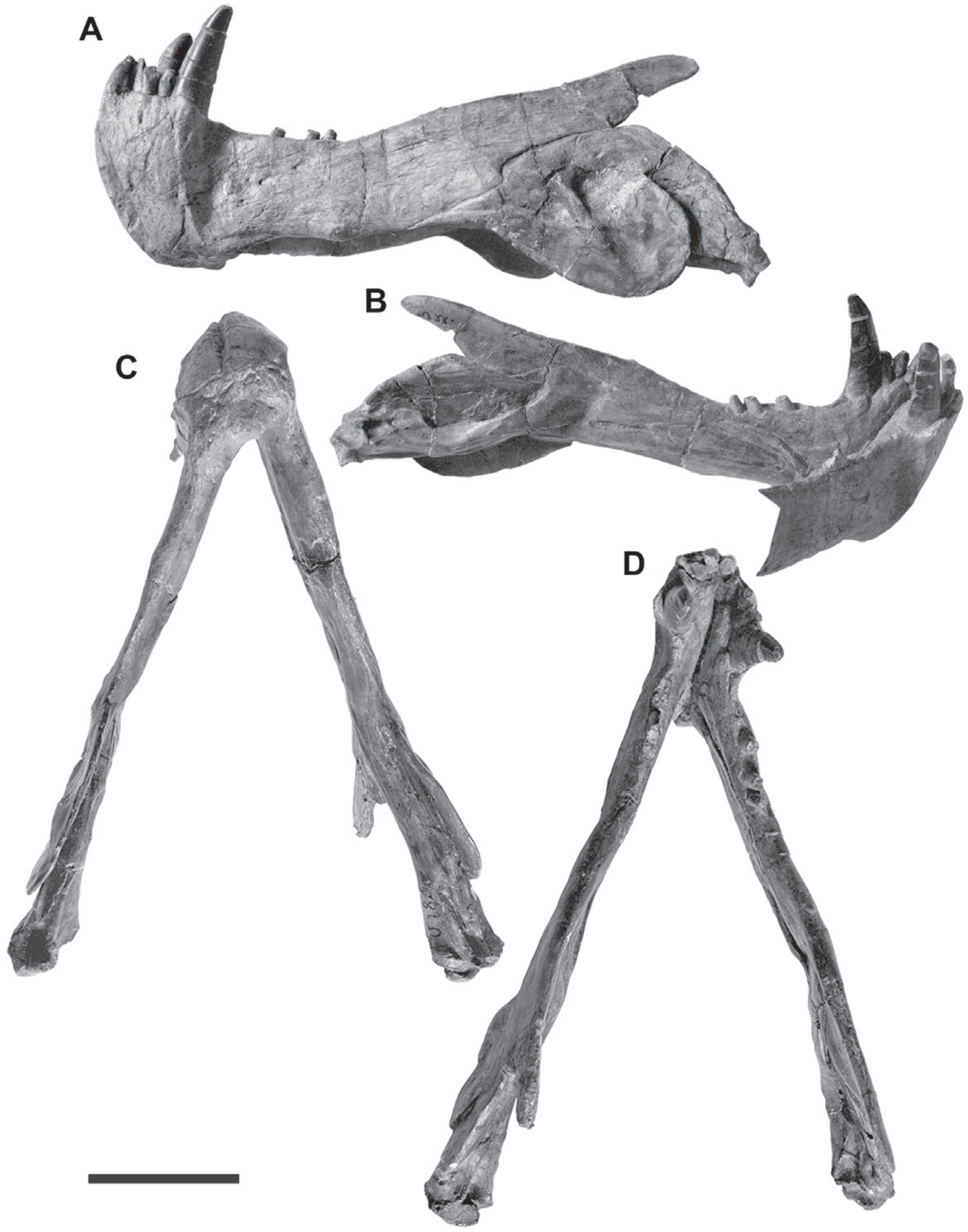


Figure 14. GPIT/RE/7113; photographs of the lower jaw in **A**, leftlateral; **B**, internal; **C**, ventral; and, **D**, dorsal view. Scale bar 50 mm.

2.1.2.5 Postcranial skeleton

2.1.2.5.1 Pectoral girdle (fig. 15)

The pectoral girdle is almost complete: only the cleithrum and sternum are missing.

The three endochondral bones, the scapula, coracoid and procoracoid, are fused, whereas the interclavicle and the two clavicles are disarticulated.

The list below gives an overview over the most important measurement (all in mm) of the different elements.

Height of scapular blade:	70 (deformed)
Width of posterior margin of scapular blade:	65 (deformed)
Width of articulation facet of glenoid:	25
Length of interclavicle:	105

The dorsal blade of the scapula is strongly compressed ventro-medially on both sides. This gives the impression of a short, broad and strongly medially curved blade with a markedly expanded upper extremity. However, when restored, the blade is of medium thickness and is only slightly curved medially.

Since the anterior and ventral parts of the pectoral girdle are missing, no information can be given about the margins of the precoracoid and coracoid. The glenoid is well preserved and forms two articulating facets that meet each other almost perpendicularly. The dorsal facet is higher than wide and mostly formed by the scapula. Only the ventralmost parts are formed by the precoracoid. The lower facet is wider than high with a rounded ventral margin and exclusively formed by the coracoid. The precoracoid foramen is exclusively situated on the precoracoid. On the mesial side it is prolonged in dorsal direction forming a narrow channel. The mesial face of the girdle is somewhat convex but posteriorly to the precoracoid foramen a broad elevation is established.

Only the anterior part of the interclavicle is preserved. The median keel is well developed whereas the lateral parts, which are covered by the curved clavicles, are strongly rugose. The ventral face of the proximal extremity is covered with numerous ridges and grooves whereas the dorsal face is smooth.

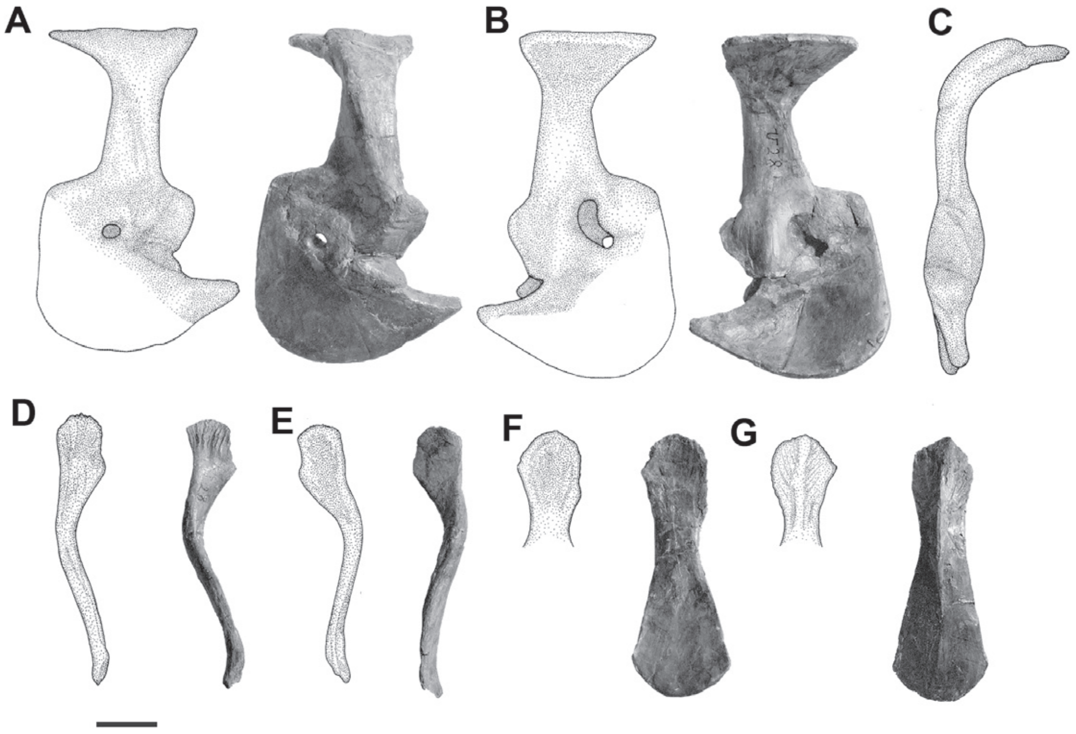


Figure 15. Drawings and photographs of the left pectoral girdle of GPIT/RE/7113. **A**, lateral; **B**, mesial and **C**, posterior view; left clavicle in **D**, ventral; **E**, dorsal view; interclavicle in **F**, ventral; **G**, dorsal view. Scale bar 25 mm.

2.1.2.5.2 Anterior limb (fig. 16)

The anterior limb is completely preserved, at least on the left side. Only some components of the manus are missing on both sides. The list below gives an overview over the most important measurement (all in mm) of the different elements.

Length of humerus:	170
Width of diaphysis of humerus:	27
Length of ulna:	138
Length of radius:	125

Humerus. The humerus is rather slender with the proximal and distal extremities only moderately expanded. Both extremities are rotated at an angle of about 40°. The diaphysis has an anteroposteriorly oval cross-section and is thus somewhat flattened dorsoventrally. The humeral head is convex, narrow and declines slightly posterodistally. Anteroventrally the deltopectoral crest is strongly rugose but comparatively weakly developed. Distally, the entepicondyle is flattened whereas the ectepicondyle is well rounded. Between both, the intercondylar fossa is rather shallow, but extends comparatively far medially.

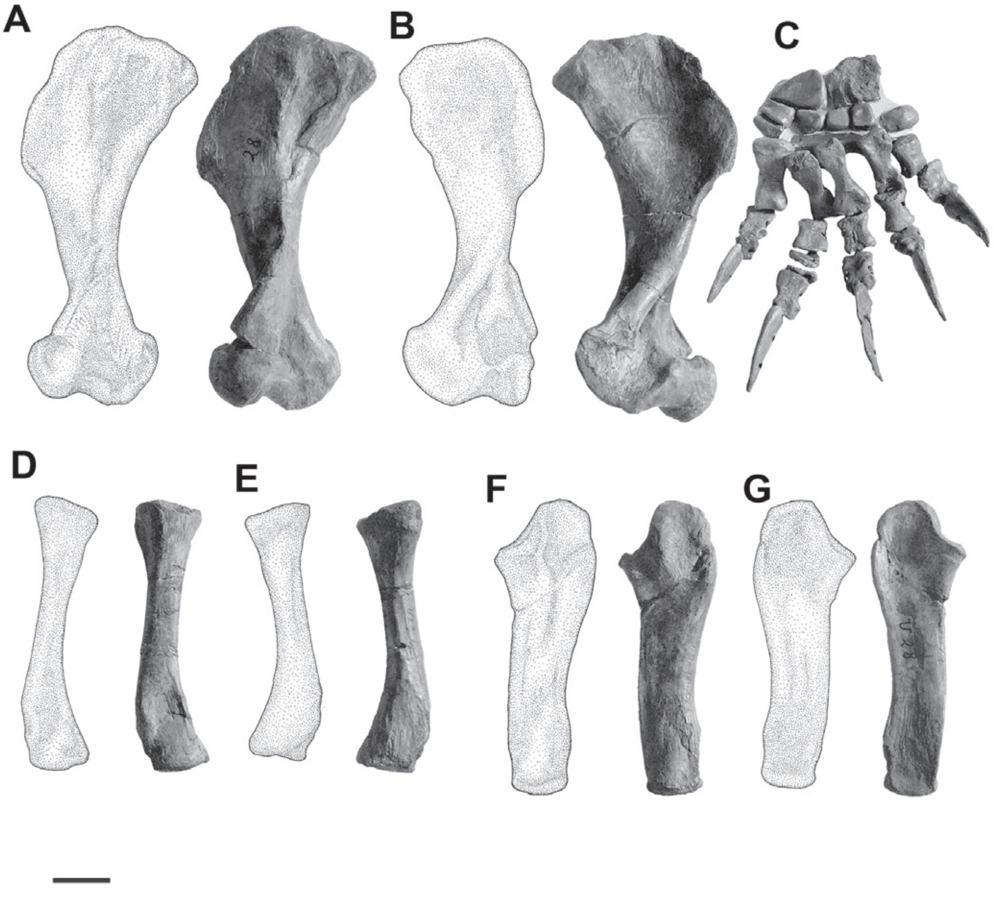


Figure 16. Drawings and photographs of the anterior limb of GPIT/RE/7113. left humerus in **A**, dorsal; **B**, ventral view; **C**, left manus in dorsal view; left radius in **D**, mesial; **E**, lateral view; left ulna in **F**, mesial; **G**, lateral view. Scale bar 25 mm.

Ulna/Radius. Ulna and radius are of moderate thickness. The anterior surface of the ulna is slightly concave whereas the posterior surface is slightly convex. Laterally the margin is smoothly rounded, but medially a keel is established. Dorsally, the articulation facet with the humerus is only slightly convex whereas the olecranon is broad but rather low. The ventral extremity is strongly rugose and less expanded.

The radius curves towards the ulna, especially in its ventral part. It is comparatively stout with massive proximal and distal extremities. The proximal extremity has an oval cross-section whereas the distal one is more flattened.

Manus. The bones of the right hand are well-represented (with the exception of the claws). The ulnare is rather elongated and slightly constricted in the middle, whereas the radiale is quadrate in shape. Centrale 2 is situated between these two bones and has pointed proximal and distal ends. The intermedium is missing. Centrale 1 is situated ventral to the radiale and is flat and wider than high. Ventral to this bone follows the mediolaterally oriented row of distal carpals. The fused fourth and fifth distal carpals are only slightly wider than the others. The metacarpals measure between 15mm and 35 mm in length with the fourth and fifth being the longest. The first metacarpal is short and stout, the second longer and less constricted in the middle, the third and fourth are elongated, constricted in the middle and have expanded extremities, whereas the fifth, though also long, is relatively broad and flattened in the middle. The phalanges (as far as they are preserved) have the numbers: 1-2-3-4-2. Only the third claw is preserved: it is mediolaterally compressed and thus less distinctive.

2.1.2.5.3 Pelvic girdle (fig. 17)

The pelvic girdle is almost complete. Only the right pubis, the anteroventral and posteroventral parts of the left pubis, the ventral margin of the right ischium, and the dorsal, posterior and ventral margins of the left ischium are missing. The list below gives an overview over the most important measurement (all in mm) of the different elements.

Length of dorsal margin of iliac blade:	100
Height of ilium:	90
Length of pubis:	55
Length of ischium:	100

Ilium. The ilium is composed of the flattened iliac blade and the acetabular part. The dorsal margin of the iliac blade slopes posteroventrally and terminates in a broad posterior expansion. The acetabular crest is weakly developed. The acetabulum is large and the posterior and anterior margins, which are the contact areas for the ischium and pubis, have the same length and form a broad triangle.

On the medial side, the iliac blade is slightly convex with strong scars for contact with the sacral ribs. A prominent ridge runs transversely in an anterodorsal - posteroventral direction from the anterior extension of the iliac blade to the middle of the bone. Here it terminates in a pointed elevation which is situated in front of an elongate depression that is again bordered

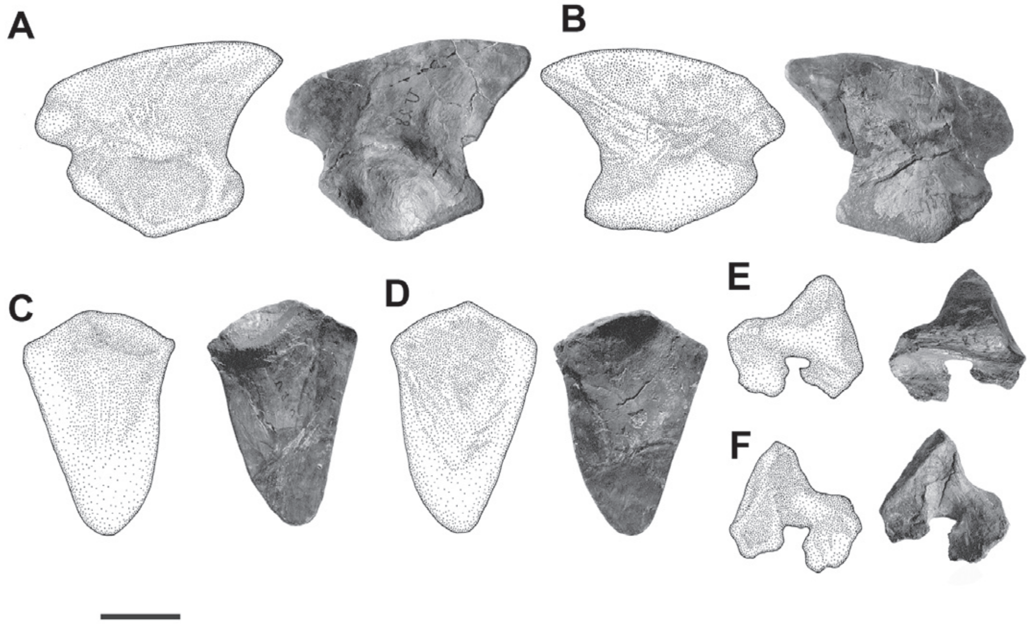


Figure 17. Drawings and photographs of the pelvic girdle of GPIT/RE/7113. right ilium **A**, lateral; **B**, mesial view; left ischium in **C**, lateral; **D**, mesial view; left pubis in **E**, lateral; **F**, mesial view. Scale bar 35 mm.

by a ridge. The acetabular part is convex and rather smooth except for the strongly rugose contact areas with the ischium and pubis.

Pubis. Since the pubis is only fragmentarily preserved in most specimens, comparison is limited. In GPIT/RE/7113 the pubis constitutes only a small part of the acetabulum whereas in MZC 883 the acetabular part is comparatively larger. The posteroventral contact with the ischium is only half as long as the one with the ischium.

Ischium. The ischium is the most flattened of the three pelvic bones and only the acetabular part is slightly expanded. The blade narrows distinctly in postero-ventral direction. Again, the actetabular part is comparatively small and the ventral elevation is less well developed.

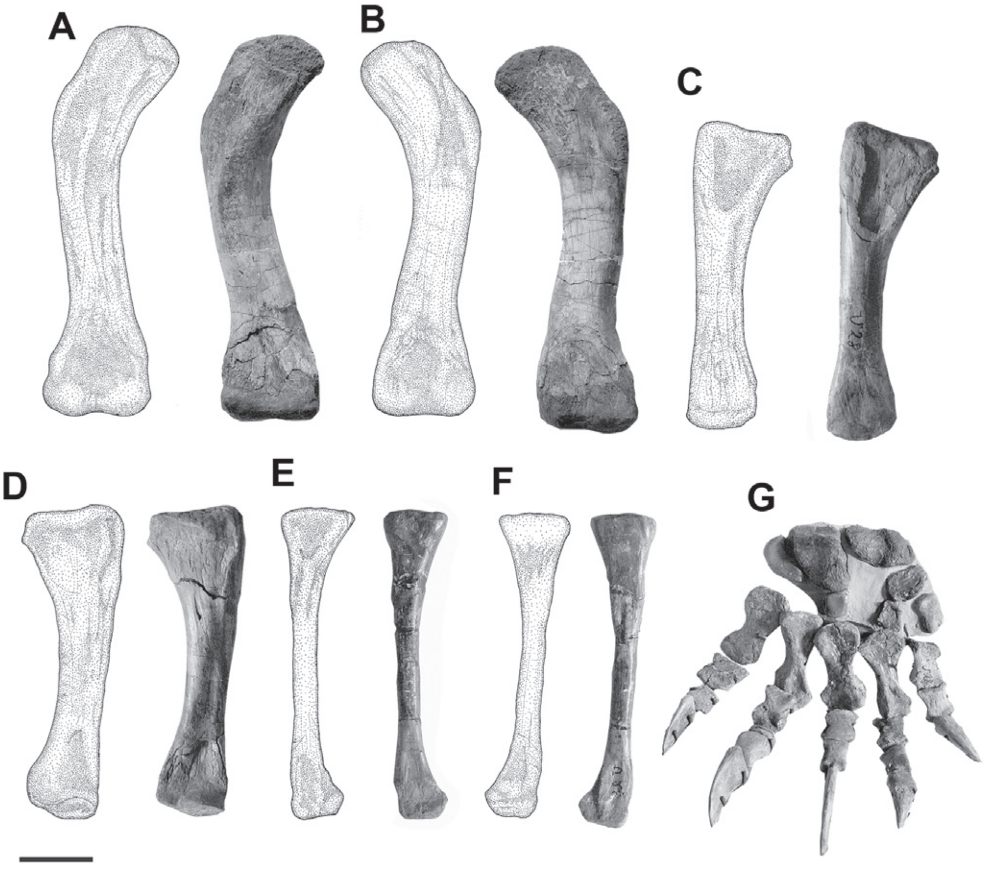


Figure 18. Drawings and photographs of the posterior limb of GPIT/RE/7113. left femur **A**, posterior; **B**, anterior view; left tibia in **C**, anterior; **D**, posterior view; right fibula in **E**, anterior; **F**, posterior view, **G**. left pes in dorsal view. Scale bar 35 mm.

2.1.2.5.4 Posterior limb (fig. 18)

Both femora are completely preserved, as well as the right tibia, the proximal part of the left fibula and the distal part of the right fibula. The bones of the foot are incomplete, with only a few elements of the right one are preserved; these are, however, strongly weathered. The list below gives an overview over the most important measurement (all in mm) of the different elements.

Length of femur:	185
Width of diaphysis of femur:	32
Length of tibia:	142
Length of fibula:	148

Femur. As in all other taxa the curved femur is longer and more slender than the humerus. The strongly rugose femoral head is only slightly expanded and rather flat, which may be due to preservation. The diaphysis is strongly curved and terminates in the two distal condyles, which are again rather flat. Both condyles have nearly the same size which is in contrast to all other gorgonopsians where the medial condyle is usually somewhat larger.

Tibia/fibula. The tibia and fibula are again rather flattened. The tibia is curved towards the fibula only with its dorsal part whereas the lower part is rather straight. Corresponding to this, the fibula is curved toward the tibia only with its distal extremity. However, the proximal extremity is incompletely preserved. Nevertheless, this is in contrast to the other taxa, where both bones are more strongly curved towards each other.

Pes. The components of the tarsus are also embedded in plaster and their arrangement is questionable. However, the bones are strongly weathered and as von Huene (1950) stated, all bones were found disarticulated so that he only could guess at their correct arrangement. The largest bone which has a concave dorsal surface might be the calcaneum, medially another larger bone which is expanded more in a mediolateral direction is probably the astragalus. Ventral to this, a smaller bone is situated which is wider than high and might be the centrale. None of the other elements of the tarsus are preserved. However, the metatarsalia are complete. The first is short and wide, the second is narrower and has an expanded proximal extremity, the third has expanded proximal and distal extremities, and the fourth is long and slim whereas the fifth is wide and not constricted in the middle. They are between 20mm and 45mm long with the fourth being the longest. The phalanges (as far as they are preserved) have the numbers: 1-2-3 -4 -2. The claws are not preserved.

2.1.2.5.5 Vertebrae (figs. 19 – 22)

The vertebrae are more or less completely preserved except for certain parts of some dorsals, and the caudals from the eighth caudal onwards.

Atlas/Axis-complex and cervicals. The atlas-axis-complex is composed of two intercentra, two pleurocentra and two neural arches of the atlas, all of which are disarticulated. A proatlas is not preserved. The atlas intercentrum is a small and narrow crescent shaped element, which is, however, somewhat more compact than the axis intercentrum. The atlas centrum is comparatively short but also low in comparison to other taxa. It is, however, somewhat compressed dorsoventrally. The anterior face slopes postero-ventrally and thus the ventral face is rather short. The dorsal surface is broadened and concave with the two oval articulation facets for the neural arches situated laterally. Between them is another round and protruding knob. Ventrally the broad articulation facet with the ventral parts of the basioccipital condyle is established. The neural arch is somewhat t-shaped, with the horizontal bar that forms the postzygapophysis expanded more in posterior direction. On the internal side a concave

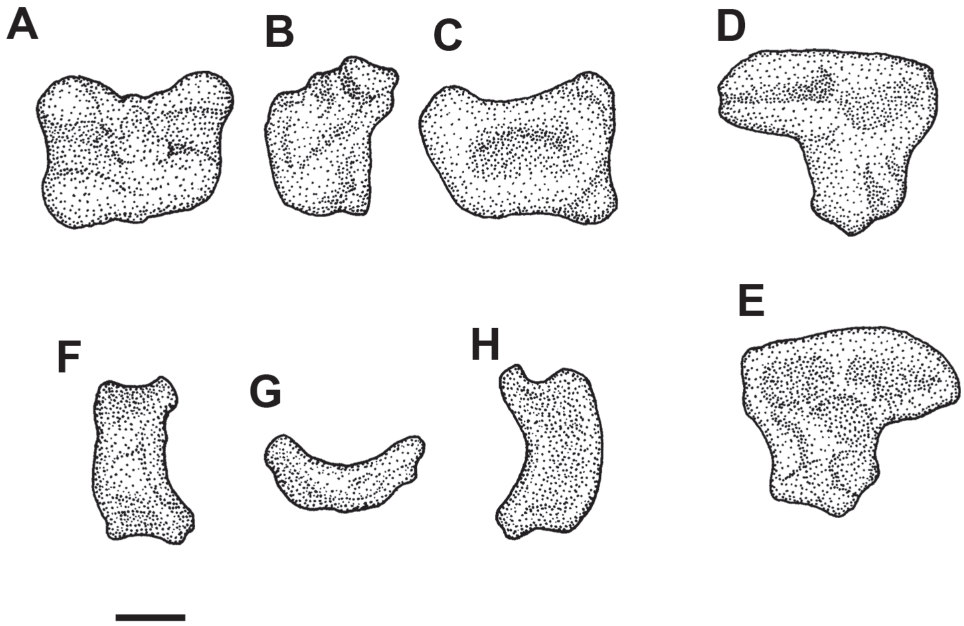


Figure 19. GPIT/RE/7113; Atlas pleurocentrum in **A**, anterior; **B**, left lateral; **C**, posterior view; Atlas neural arch in **D**, lateral; **E**, mesial view; Axis intercentrum in **F**, ventral; **G**, anterior, **H**, dorsal view. Scale bar 10 mm.

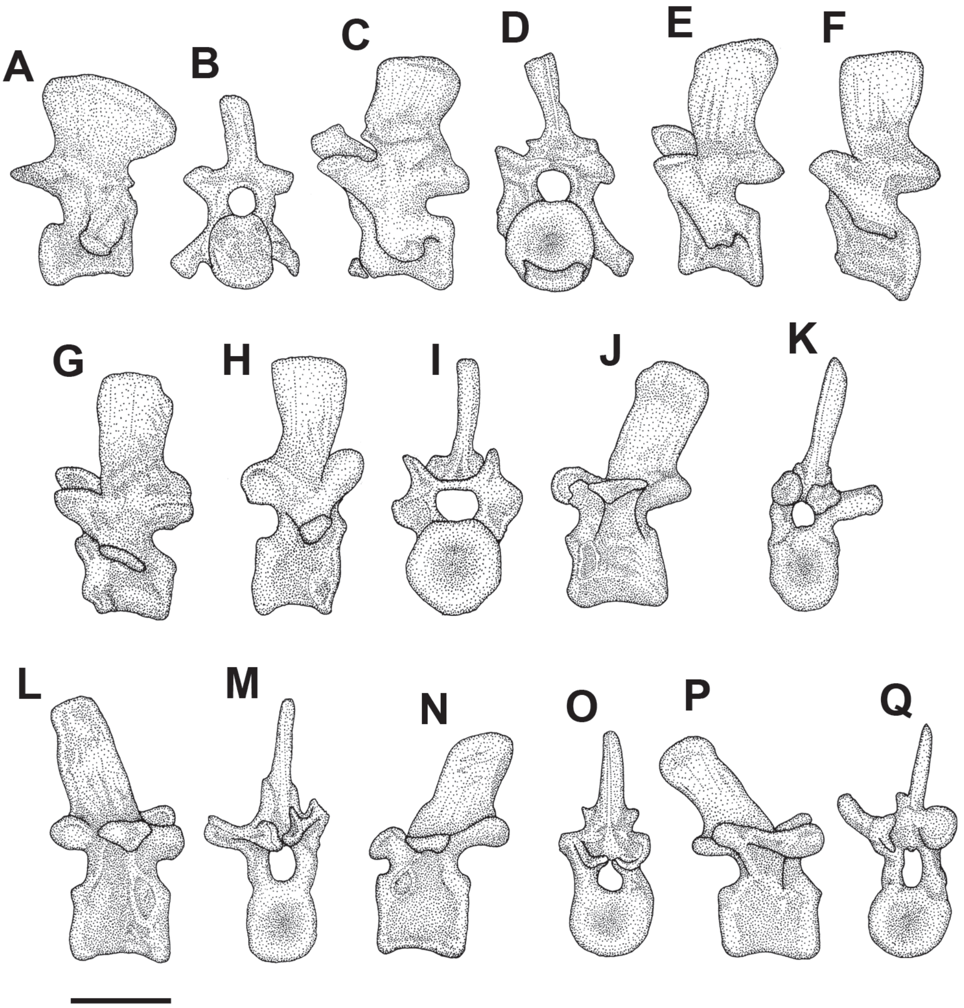


Figure 20. GPIT/RE/7113; cervical vertebrae; axis in **A**, rightlateral; **B**, anterior view; third in **C**, leftlateral; **D**, anterior view; **E**, fourth in leftlateral view; **F**, fifth in leftlateral view; **G**, sixth in leftlateral view; seventh in **H**, rightlateral; **I**, anterior view. Dorsal vertebrae; second in **J**, leftlateral and; **K**, anterior view; sixth in **L**, rightlateral and; **M**, anterior view; eleventh in **N**, leftlateral and; **O**, anterior view; sixthteenth in **P**, rightlateral and; **Q**, anterior view. Scale bar 30 mm.

depression is situated, which faces antero-medially. This facet might have embraced the dorsal parts of the basioccipital condyle. Postero-ventrally the articulation for the atlantal rib is visible; the rib, however, is not preserved.

The cervicals do not differ much in their morphology, except for the axis and the seventh cervical. The axis shows some characters of its own, whereas the latter more resembles the following dorsal vertebrae.

All cervicals, except for the seventh, are 25 mm long and 20 mm high, the seventh cervical is somewhat shorter and lower. These relations are observable in all other taxa. The anteriorly-posteriorly sloping centra are strongly amphicoelous. The lateral face of the axis is least

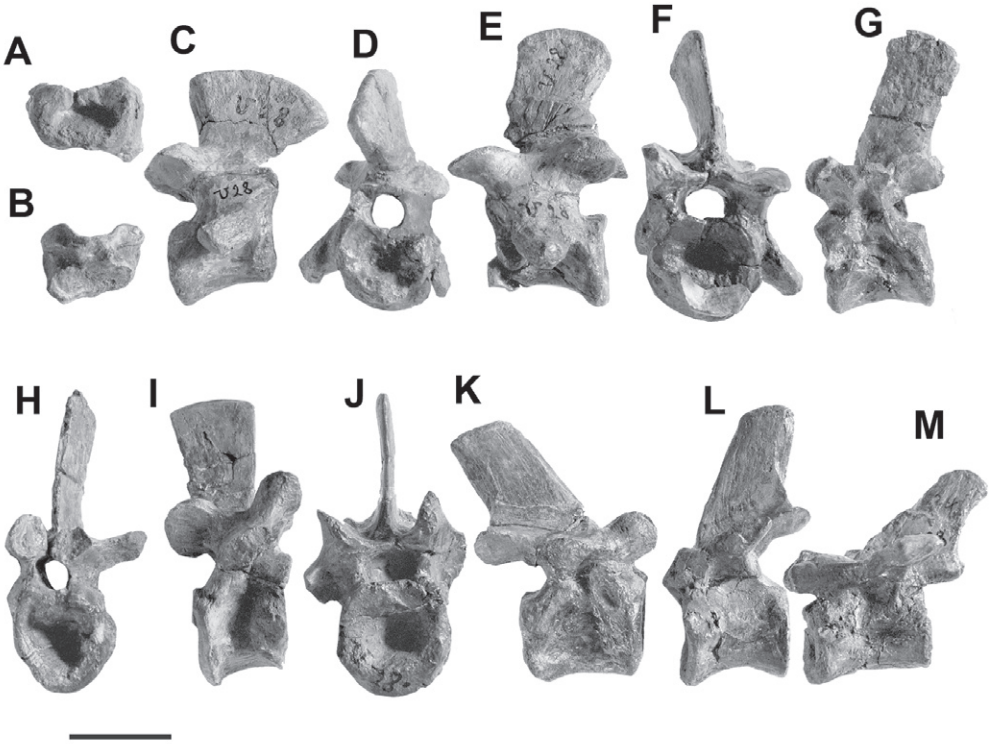


Figure 21. Photographs of the cervical and dorsal vertebrae of GPIT/RE/7113. Atlas in **A**, posterior; **B**, anterior view; Axis in **C**, rightlateral; **D**, anterior view; third cervical in **E**, leftlateral; **F**, anterior view; seventh cervical in **G**, leftlateral; **H**, anterior view; second dorsal in **I**, rightlateral; **J**, anterior view; **K**, tenth dorsal in rightlateral view; **L**, fourteenth dorsal in leftlateral view; **M**, seventeenth dorsal in leftlateral view. Scale bar 30 mm.

depressed whereas the anterior cervicals have an elongate depression on their ventral half which becomes deeper and more rectangular in the posterior cervicals. In the last cervical, which already shares many features with the dorsals, this depression is oriented in dorsoventral direction.

The zygapopyses are different in the anterior and posterior cervicals. The prezygapophyses are oval in an anterior-posterior direction in all cervicals and do not meet each other in the middle. The articulating facets are almost horizontal in all cervicals but get slightly steeper in posterior direction. The postzygapophyses of the first five cervicals are more massive since they are intergrown in the midline. Their posterior margin is rounded with a short recess in the middle.

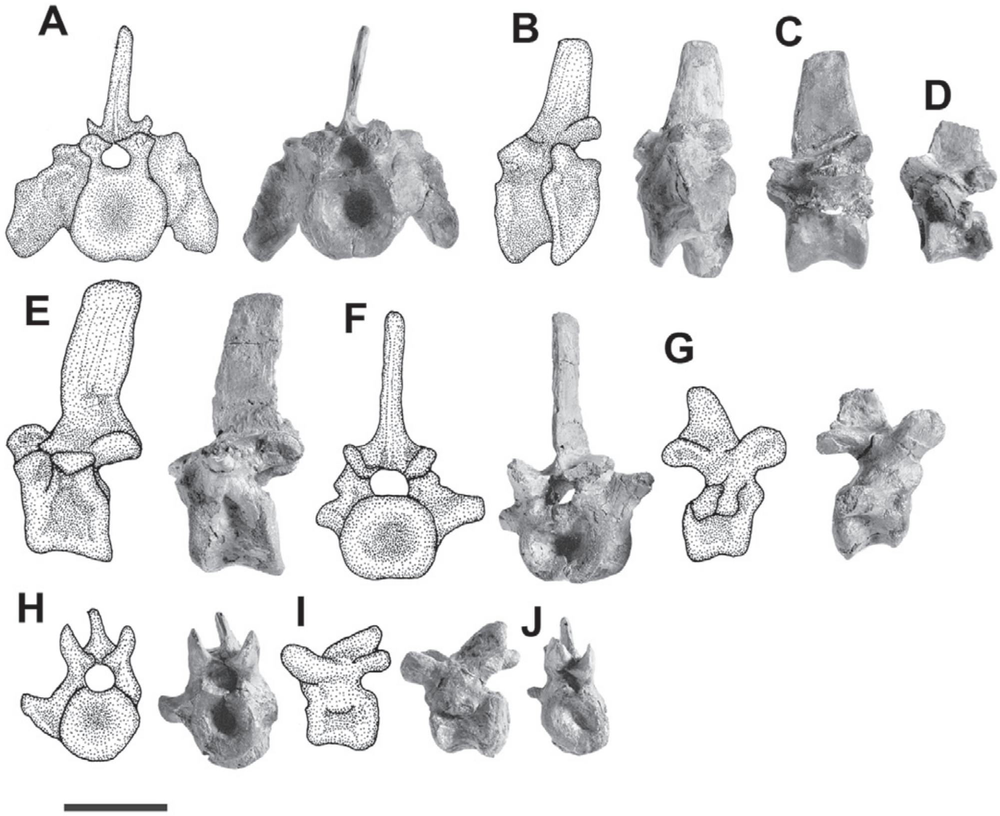


Figure 22. Photographs and drawings of the sacral and caudal vertebrae of GPIT/RE/7113. First sacral in **A**, anterior and **B**, leftlateral view; **C**, second sacral in leftlateral view; **D**, third sacral in leftlateral view; first caudal in **E**, leftlateral and **F**, anterior view; third caudal in **G**, rightlateral and **H**, anterior view; sixth caudal in **I**, leftlateral and **J**, anterior view. Scale bar 30 mm.

The diapophysis merges into the ventral part of the prezygapophysis anterodorsally. It has a broad dorsal insertion area but narrows laterally and terminates in a round articulation facet for the tuberculum. The parapopyhsis is visible on the ventralmost edge of the centrum in the sixth cervical but presumably already existed in the fifth. The articulation facet is surrounded by a low ridge which leaves a slightly depressed area in the middle.

The neural spine is of medium height. It measures 25 mm in the axis and gets somewhat higher in the following cervicals (30-35 mm). The neural spine of the axis is the most massive of the cervical spines. It is fan-shaped with a curved dorsal margin that is slightly more expanded in anterior than in posterior direction.

The neural spines of the following cervicals are steeply inclined in dorsal and posterior direction. In the third cervical it is shorter and more massive than in the following. All cervicals have a more or less sharp keel on the anterior and posterior margins of their neural spines and the dorsal margin of the neural spine is slightly broadened. Compared to other taxa the spines in GPIT/RE/7113 seem to be rather short.

Dorsals. The dorsals again do not differ much from each other. The length of the centrum varies between 20 mm and 27 mm with most being 23 mm or 25 mm long; the height of the centrum varies between 20 mm and 25 mm and the neural spine measures between 30 mm and 40 mm in height.

The deeply concave anterior and posterior articulation surfaces are thickened which gives the centrum its characteristic spool-shaped appearance. This is even more accentuated by an elongated depression on its lateral face which is more pronounced than in the cervicals. In dorsal direction this concavity merges into a deep fossa which is situated right under the diapophysis. The zygapophyses are steep and both, the pre- and postzygapophyses, are oval in an anterior-posterior direction, the posterior ones being slightly more enlarged. The prezygapophyses reach freely in anterodorsal direction whereas the postzygapophyses are attached directly laterally to the neural spine which emerges in the middle. The insertion area of the diapophysis is smaller than in the cervicals. The transverse apophysis mainly reaches laterally and extends more or less markedly in posterior and dorsal direction. The dorsal face of the diapophysis is smooth and flattened, whereas the ventral has a triangular shape. The parapophysis which inserts in the first dorsal approximately at mid-height of the vertebral body has reached the dorsal margin of the centrum in the fifth dorsal and reaches beyond the dorsal margin of the body at latest at the tenth. In the seventeenth dorsal it is still visible but it is not clear if the next (and last) two dorsals have a parapophysis since these two vertebrae are heavily weathered.

The neural spine is slender and measures approximately 40 mm in the first nine dorsals. It is relatively steeply inclined in postero-dorsal direction but does not taper. The dorsal margin is rounded and not thickened as in the cervicals. From the tenth dorsal onwards the neural spine broadens ventrally since the anterior margin is less steeply inclined. This results in a more anterior origin of the spine and in a tapering in dorsal direction. The anterior and posterior margins of all neural spines show a keel. Again, the spines of GPIT/RE/7113 are rather short but also comparatively massive.

Sacral vertebrae. There are three sacrals which fit remarkably well into the insertion area of the ilium. The first sacral vertebra is the largest of the three. The massive centrum measures 25 mm in length and 20 mm in height. It is flattened ventrally and dorsally and displays a rectangular outline if seen in anterior or posterior view. The anterior margin is strongly thickened and reaches 5 mm beyond the posterior margin which terminates at the same level as the ventral margin of the centrum. The anterior and posterior articulation surfaces are strongly concave but the depression narrows towards the middle of the centrum. The prezygapophyses are less steep than in the dorsals whereas the oval postzygapopyses are again rather steep and considerably far apart from each other. The processus transversus is strongly expanded laterally and forms a massive sacral rib. The insertion area covers almost the entire centrum and the ventral part of the neural arch between the zygapopyses. Dorsally almost at the same levels as the zygapophyses but more laterally the processus transversus terminates in a knob-like process, which might have served as muscle attachment area. The neural spine is 30 mm high and comparatively narrow. Its anterior margin inclines less steeply than the almost vertical posterior margin but has the same shape as in the last dorsals.

The centrum of the second sacral vertebra is as large as the first but the transverse processus is remarkably smaller, less massive and exclusively oriented in lateral direction. The insertion area covers only the dorsal part of the centrum and the ventralmost part of the neural arch. Dorsally the pronounced knob is established again but it is more medially situated. In a ventral direction, the surface slopes rapidly before it terminates in the low articulation surface, which has a rectangular section. The oval zygapophyses are oriented at an angle of nearly 45°.

The third sacral vertebra is considerably smaller than the other two. The anterior and posterior articulation surfaces are concave but less than in the first sacral vertebra. Though the processus transversus is considerably less massive and large than in the first sacral it resembles the shape of the latter almost perfectly. However the insertion area is steeply inclined from anterodorsal in posteroventral direction, the dorsal knob is more rectangular shaped and the ventral tip is directed more posteriorly. The neural spine is missing.

Caudals. Only the first seven caudals are preserved and they are partly incomplete. The first caudal differs noticeable from the others. The centrum is square-shaped as the centra of the sacrals, and it is larger and more massive than the following caudals. The neural spine is again as high and slender as in the anterior dorsals whereas the zygapophyses are less steep and the processus transversus is massive but already short and still has a triangular section. The second caudal is almost completely restored in plaster, the third is fairly weathered but the centrum is smaller and more flattened, however the latter could be due to deformation. The transverse process remains massive but short. The following caudals are remarkably smaller. The anterior and posterior articulation surfaces of the centrum are strongly concave but only in the middle of the body. Thus the articulation surfaces are pinched by a small round and deep depression which is surrounded by a broad and smooth elevation which at the same time forms the anterior and posterior thickenings that are responsible for the constriction of the centrum.

The zygapophyses remain oval but get more steeply oriented further posteriorly. The postzygapophyses reach beyond the level of the posterior margin of the neural spine.

The oval processus transversi get more slender and shorter until they only form small knots before they disappear completely at the tenth caudal. The pointed neural spine rapidly decreases in height.

Ribs. Although the skeleton of *Aelurognathus*? *parringtoni* was mounted with ribs it is difficult to tell if these are attached on the right places since they were probably found disarticulated. Furthermore they are often broken and incomplete. Nevertheless the cervical and the anterior dorsal ribs are more complete; they all have two heads. The posterior dorsal ribs are restored in plaster so that there is no information about the point when they become single headed. All ribs are strongly curved medially and markedly shorter in the cervical region (see fig. 23). Since they are broken off in the lumbar region no information can be given about their length here.

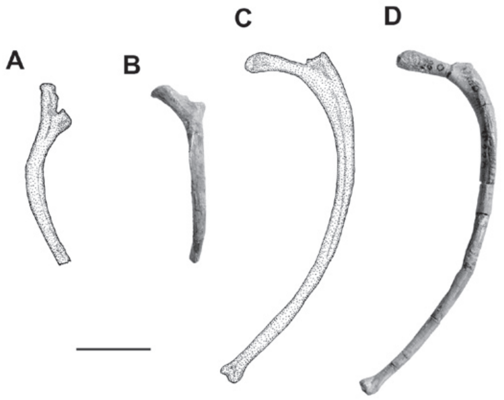


Figure 23. Ribs of GPIT/RE/7113. **A**, drawing and **B**, photograph of a left cervical rib in posterolateral and lateral view; **C**, drawing and **B**, photograph of a left mid-dorsal rib in anterolateral view. Scale bar 30 mm.

2.1.3 Comparison of Postcranial material of GPIT/RE/7113 with other taxa

As already mentioned above, this comparison only briefly states the most significant aspects in which GPIT/RE/7113 differs from the other specimens taken into consideration. A list of this material is given below:

Aelurognathus tigriceps (SAM 2342) – pectoral girdle, humerus, hand
Arctognathus breviceps (SAM 9345) – pectoral girdle, forelimb, vertebrae
Inostrancevia alexandri (PIN 1758) – almost complete postcranial skeleton
SAM 9334 (*Lycaenops*? *microdon*) – humerus, pelvic girdle, hindlimb, vertebrae
Lycaenops ornatus (AMNH 2240) – almost complete postcranial skeleton
Scylacops capensis (SAM 2343) – pectoral girdle, humerus, anterior caudals
BSP 1934 VIII – almost complete postcranial skeleton
MZC 883 – almost complete postcranial skeleton

Figure 24 shows the three mounted gorgonopsian skeletons *Inostrancevia alexandri*, *Lycaenops ornatus* and GPIT/RE/7113 for comparison.

The scapular blade of the pectoral girdle in GPIT/RE/7113 is somewhat comparable with that in *Lycaenops ornatus*. Thus it is broader than in *Scylacops capensis* or *Arctognathus breviceps* but narrower than in *Aelurognathus tigriceps* or *Inostrancevia*. The glenoid is larger than in *Scylacops capensis* but not as large as in *Lycaenops ornatus*. The length of the posterior extension of the coracoid is intermediate between *Arctognathus breviceps* and BSP 1934 VIII. The curved clavicle is more slender than in *Lycaenops ornatus* and *Inostrancevia*. Because of the lack of material in other taxa it is, however, not possible to make a sound comparison. The humerus is less stout than in other gorgonopsians, except *Scylacops capensis*, *Lycaenops ornatus* and SAM 9334. The expansion of the dorsal extremity is intermediate between SAM 9334 and *Lycaenops ornatus* on the one hand and *Inostrancevia alexandri* and *Aelurognathus tigriceps* on the other hand. The diaphysis, which has an anteroposterior oval cross-section, is again comparable with SAM 9334 and *Lycaenops ornatus*. The distal condyles are less developed than in other taxa except for *Scylacops capensis*. The ulna and radius do not differ greatly from other taxa. They are stouter than in *Lycaenops ornatus* but less massive than in *Arctognathus breviceps*.

The dorsal margin of the iliac blade slopes to a greater extent than in MZC 883 or SAM 9334, its posterior expansion is, however, broader and less restricted ventrally than in the latter taxon. The blade of the ischium narrows distinctly in postero-ventral direction which is in contrast to *Lycaenops ornatus* and MZC 883 but comparable to SAM 9334.

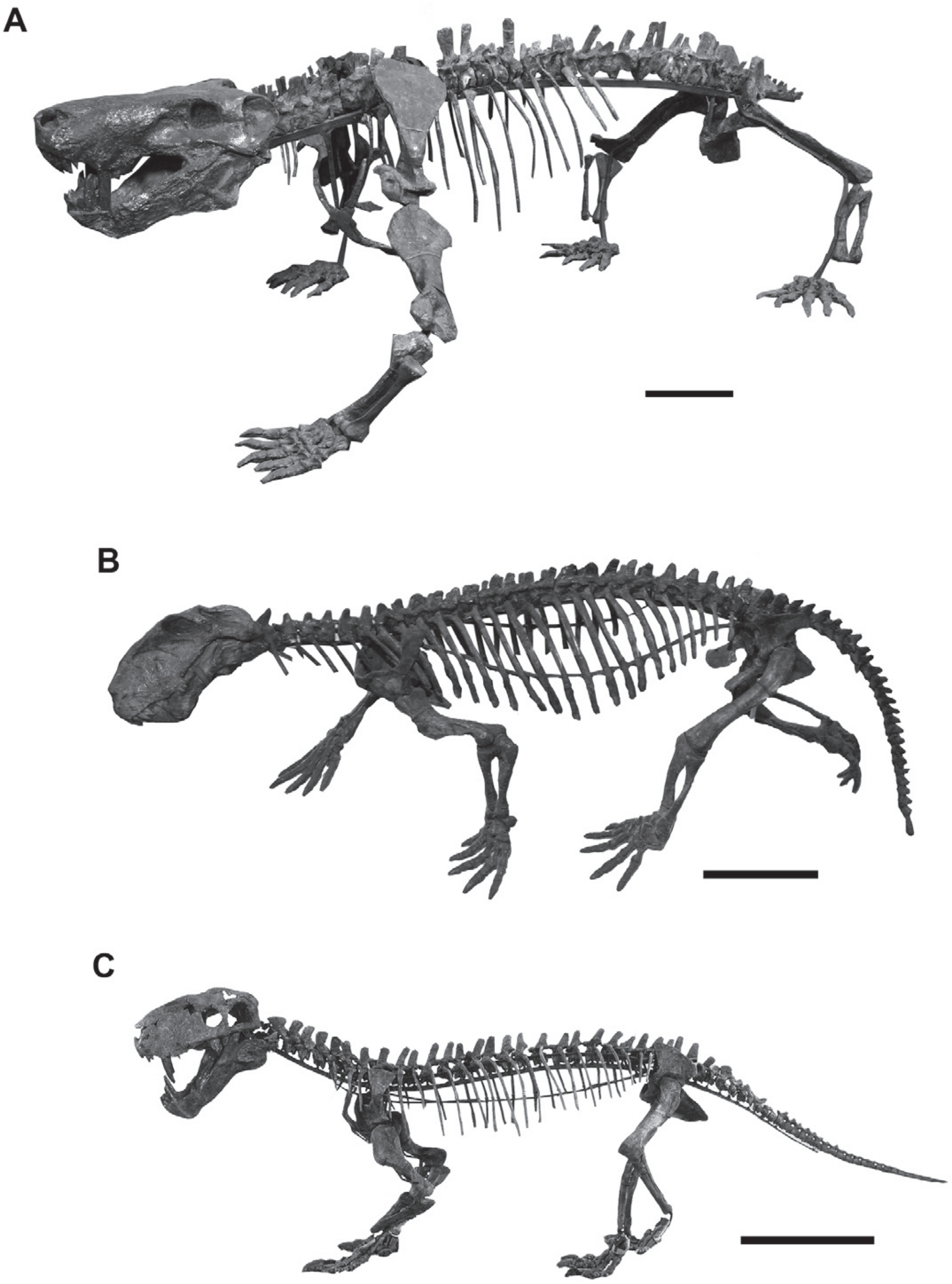


Figure 24. Photographs of mounted gorgonopsian skeletons. **A**, *Inostrancevia alexandri* (PIN 1758), scale bar 200 mm; **B**, *Lycaenops ornatus* (AMNH 2240), scale bar 150 mm; **C**, *Sauroctonus parringtoni* (GPIT/RE/7113).Scale bar 250 mm.

The femur is broader than in *Lycaenops ornatus* and SAM 9334 but not as massive as in MZC 883, BSP 1934 VIII or *Inostrancevia alexandri*. The greater trochanter is only slightly set off from the rest of the bone and thus it is only comparable with BSP 1934 VIII. The tibia and fibula do not differ much from the other taxa in general shape except for the tibia in SAM 9334 and *Inostrancevia alexandri*. In the first the tibia is somewhat more slender, and in the latter the proximal and distal extremities are extremely massive.

The shape of the atlas-axis complex is comparable with that in MZC 883 whereas the spine is lower and more expanded posteriorly in *Arctognathus breviceps* and higher in SAM 9334. The centra of all vertebrae do not differ much in the various taxa, but the length and orientation of the spine seems to vary throughout the taxa. However, one has to keep in mind that particularly the spine is often broken off and damaged. In GPIT/RE/7113 the spine is of intermediate height and the direction changes from vertical to posterodorsal. In *Arctognathus breviceps* and MZC 883 the spine is rather short and sloping. SAM 9334 and *Inostrancevia alexandri* on the other hand have a long and slender spine which is directed more dorsally than posterodorsally. In BSP 1934 VIII and MZC 883 the centrum of the first sacral is also larger and more massive than the following caudals, whereas the broadness of the sacral rib is even more accentuated in those two specimens than in GPIT/RE/7113.

The comparison shows that GPIT/RE/7113 holds an intermediate position between the available taxa concerning the postcranial skeleton. It is obvious that its postcranial skeleton is more slender in its overall appearance than in the large taxa *Aelurognathus tigriceps* and *Inostrancevia alexandri*. Concerning the other taxa, however, there is no clear distinction possible. At best, if considered only postcranial material, GPIT/RE/7113 can be allocated to the near relationship of SAM 9334 and *Lycaenops ornatus*.

2.1.4 History of GPIT/RE/7113 and discussion of literature

The specimen was first described by von Huene (1950) in a rather detailed account which is however of only little comparative value as mentioned above.

Von Huene allocated the specimen to the genus '*Scymnognathus'* as the new species *parringtoni* and mentioned a close relationship with the taxa *Aelurognathus* and '*Pachyrhinos'* (= *Gorgonops kaiseri*). He saw the 'shape of a typical *Scymnognathus'* because of the convex and ascending snout profile. However the genus '*Scymnognathus'* never was clearly defined with respect to other similar forms, which is revealed by the fact that Sigogneau (1970) saw the type species as representing the genus *Gorgonops* and distributed the remaining species between the genera *Lycaenops* and *Aelurognathus*. Furthermore von Huene's allocation was based on a rather common character and thus is exchangeable to a great extent.

In his overall description von Huene remarked that the anterior margin of the orbit was situated in the middle of the skull length, the maxilla was high, the canine long and slender and the five to six postcanines were only slightly smaller than the incisors. Further he was of the opinion that the frontal did not reach the orbit which is however not the case. Indeed the contribution of the frontal to the suborbital rim is comparatively large. Von Huene stated that there was no step in the ventral maxilla border, the maxilla, frontals and prefrontals were intensely sculptured, the orbits were not covered with tuberosities, the postorbital bar and suborbital arch were slender and the transverse process of the pterygoid was long. In the following detailed account of the single bones he mentioned the large and steeply oriented basioccipital tubera, the high interparietal, the posteriorly long parietal, the small foramen parietale which was surrounded by a ridge and well separated from both, the occipital crest and the preparietale. Furthermore, he stated that the postorbital was long posteriorly, the septomaxilla narrow, the choanae elongate, the vomer narrow and the symphysis relatively massive with a chin.

Sigogneau (1970) allocated GPIT/RE/7113 to the genus *Aelurognathus*, although with a dubious position. Since the type specimen of the genus '*Scymnognathus' whaitsi'* was made the holotype of the taxon *Gorgonops whaitsi* by her, the genus '*Scymnognathus'* became redundant as mentioned above. Sigogneau however did not see a close connection of GPIT/RE7113 with the genus *Gorgonops* because of the lower snout and the heavier skull arches in that genus and thus discussed a possible relationship with the genera *Aelurognathus* and *Lycaenops*. With the latter GPIT/RE/7113 shared, according to her, the slender skull arches and the convex profile of the snout but the interorbital and intertemporal widths were the same as in *Aelurognathus* as well as the small size of the orbits and the shape of the dentary. Although Sigogneau admitted that the temporal fossa was rather elongate, which would be in contrast to the definition for the genus *Aelurognathus*, she especially saw a close resemblance in the postcranial material with *Aelurognathus tigriceps*. Thus the cervicals had high neural arches in both cases and the anterior limbs were similar in proportions. However postcranial material is rather limited in gorgonopsians in general and it is therefore questionable if the material at hand covers a range of taxa large enough to provide a sound basis for comparison. Besides, the available postcranial material shows that the differences are even smaller between the various taxa than they are in the skull.

2.1.5. Comparison with Aelurognathus Haughton*, 1924*

In order to clarify the unresolved taxonomic position of GPIT/RE/7113 it is necessary to consider the taxon *Aelurognathus* more precisely (see fig. 42 in chapter 2.2 for comparison). The type species of this genus is *Aelurognathus tigriceps* with SAM 3342 as the holotype. Compared to this specimen, GPIT/RE/7113 displays many characters which distinguish it clearly from this form, and therefore from the taxon *Aelurognathus*. This is explained especially clearly by Sigogneau's diagnosis for the genus *Aelurognathus* which does not apply for GPIT/RE/7113 in many points, including: heavy skull, high temporal fossa, wide interorbital space, thick suborbital and postorbital bar, narrow supraorbital frontal, high occiput, massive and thick dentary.

The holotype SAM 3342 differs significantly from GPIT/RE/7113. The skull in SAM 3342 is more massive and higher, the snout is heavier and the posterior part is more enlarged compared to GPIT/RE/7113. Almost all diagnostic bones differ as well. Thus in *A. tigriceps* the posterior process of the maxilla is markedly elongate, the prefrontal is short, high and situated on an elevation, the naso-frontal suture is situated posteriorly and straight, the supraorbital frontal is small, the postfrontal is broad and large, the vomer is broad anteriorly, as well as the palatal fossa, the palatal tuberosities are confluent and the posterior para-basisphenoidal area is broad. Furthermore, the teeth are larger and more massive, the symphysis of the lower jaw is straighter and heavier, and the lamina reflecta is stronger and situated more anteriorly than in GPIT/RE/7113. Additionally the taxon *Aelurognathus* shows some characters such as the highly convex ventral margin of the maxilla, the ridge on the maxilla postero-dorsal to the postcanine teeth and the dorso-laterally constricted snout which are completely absent in GPIT/RE/7113.

All these comparative notes show that GPIT/RE/7113 does not belong to the genus *Aelurognathus*. However there is great difficulty in making an allocation to any other South African taxon. The rubidgeinid genera are excluded for reasons such as the downturned zygomatic arch and the other characters that constitute this family. *Sycosaurus* is heavier in its overall appearance and is furthermore distinguished by the absence of a preparietal and the frontal does not contribute to the orbits in most of its species. The small sized genera such as *Aelurosaurus*, *Aloposaurus* and *Cyonosaurus* differ in size and proportion. In *Scylacognathus* the shape of the snout is different and the interorbital-and intertemporal widths are greater. The skull in *Gorgonops* is lower, the palatal tuberosities have a dissimilar shape and the supraorbital portion of the frontal is much narrower. *Eoarctops* has a shorter snout and a broader temporal region and *Lycaenops* differs by its quadrangular temporal opening and the preparietal which is closer situated to the parietal foramen than in GPIT/RE/7113.

Thus an allocation to the South African genera fails because GPIT/RE/7113 shares an insufficient number of characters with any described genus. However the Russian genus *Sauroctonus* provides a character set which is matched perfectly well by GPIT/RE/7113. Unfortunately there is little information about the geographic distribution of the Russian and East African forms which is however to some extent certainly a result of the rare terrestrial Permian deposits in this part of the world. Further a close relationship between a Russian form and a taxon from the eastern part of Africa or even one from South Africa has never been reported except for the dinocephalian genera *Ulemosaurus* and *Moschops*. But the reason for this could be the fact that both, the Russian and the 'western' authors might not have examined the material under this aspect and mostly did not consider the respective specimens of the other region.

2.1.6 Comparison with Sauroctonus progressus (Hartmann-Weinberg, 1938)

In order to make a sound comparison it is necessary to consider the history of the taxon *Sauroctonus progressus*. The holotype PIN 156/5 was first described by Hartmann-Weinberg (1938). She allocated the taxon to the genus *Arctognathus*, however, as a new species *A. progressus*. Bystrow (1955) gave another description after re-preparation. He mentioned the strongly concave occiput with a strong median keel and a small contribution of the parietal, the high maxilla, small prefrontal, the massive paroccipital process, the small ectopterygoid, the teeth on the palatal tuberosities, the broad and long splenial and the triangular coronoid. Tatarinov (1974) worked on the taxon again and contributed a particularly detailed account in his monograph on 'Theriodonts of the USSR'. He, however, sometimes gets lost in extremely detailed descriptions of nerve openings, canals and other foramina and thus a large part of the account is currently of little comparative value. Nevertheless Tatarinov made some important new contributions; he mentioned a preparietal which was not discovered by Hartmann-Weinberg and Bystrow. Further, he stated that the supraorbital portion of the frontal was comparatively large, the prefrontal was longer at the orbit than figured by Bystrow, the vomer was long and narrow, the palatal fossa was rather narrow, the supraoccipital was broad and the interparietal was broader ventrally than dorsally. Finally he gave some measurements of the skull: Length 225 mm, preorbital length 110 mm, broadest width (in the temporal region) 150 mm, snout height 68 mm.

Sigogneau-Russell (1989) listed the genus and species as *Sauroctonus progressus* and noted the posteriorly narrow skull, the elongate temporal fossa, the small orbits and narrow skull arches, the very narrow interorbital and intertemporal spaces and the moderately high

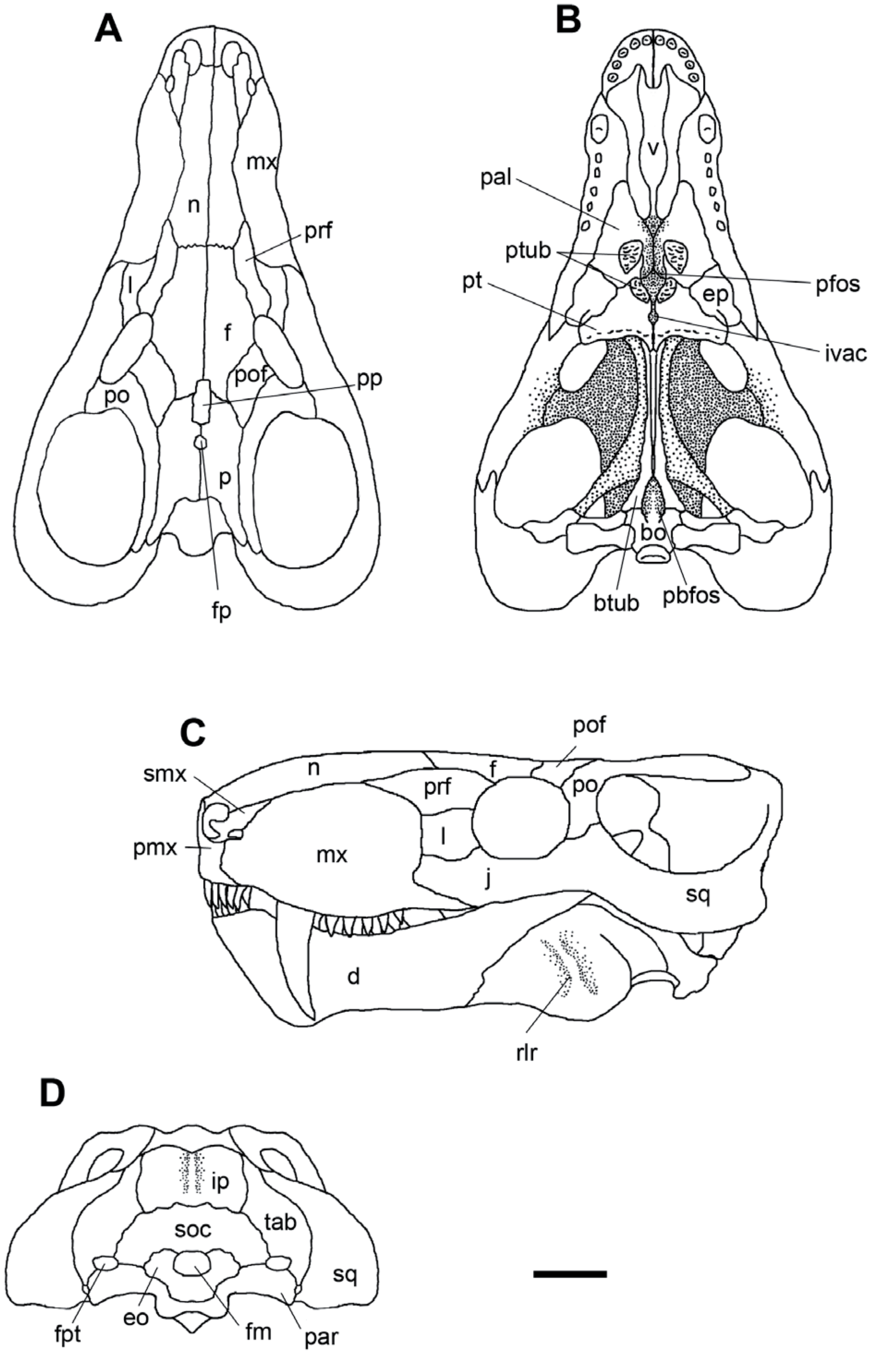


Figure 25. Skull of *Sauroctonus progressus* (PIN 156/5) in **A**, dorsal; **B**, ventral; **C**, leftlateral; **D**, occipital view. Scale bar 30 mm (from TATARINOV, 1974, and IVAKNENKO, 2001).

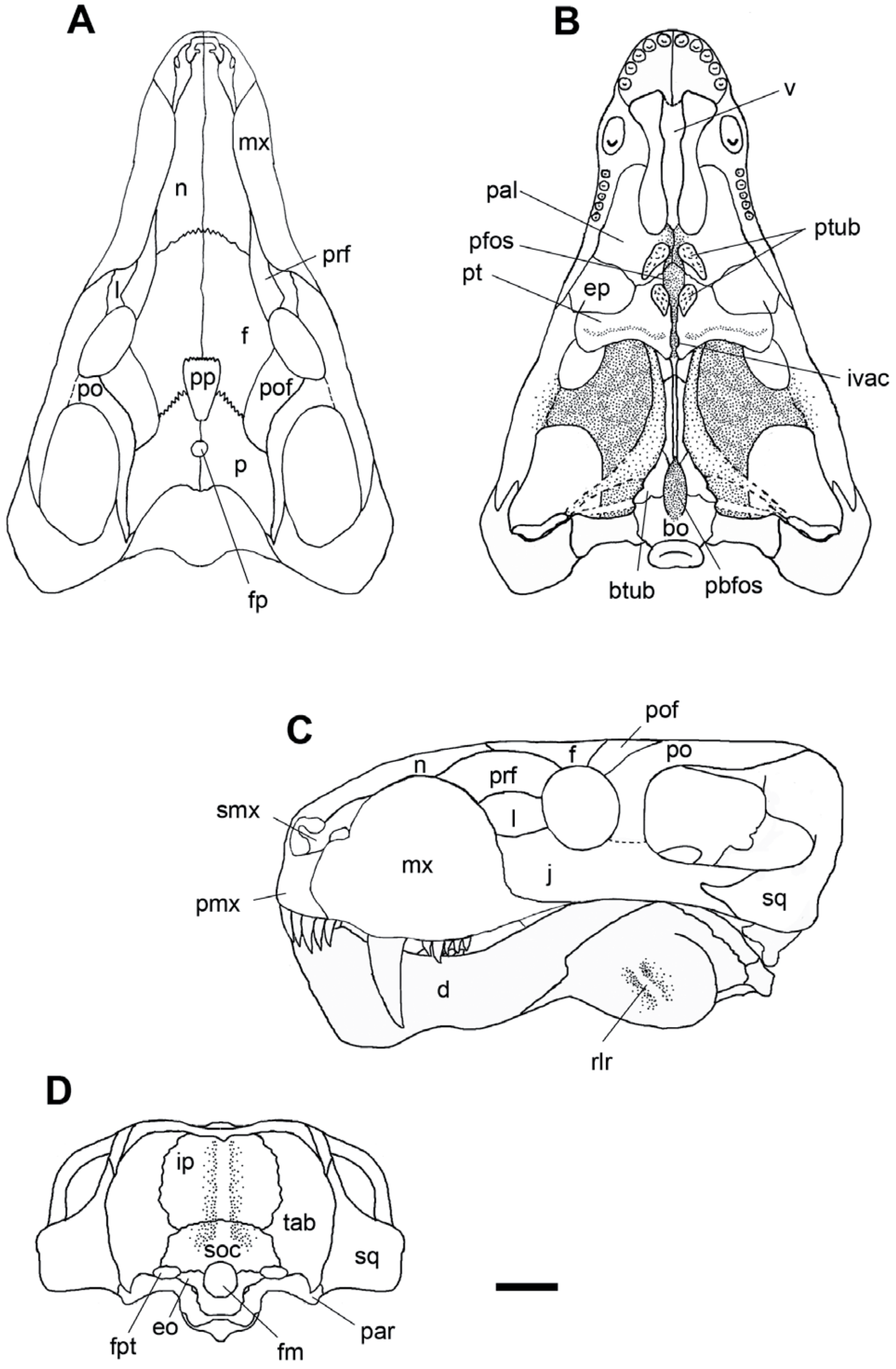


Figure 26. GPIT/RE/7113; reconstruction of the skull of in **A**, dorsal; **B**, ventral; **C**, leftlateral; **D**, occipital view. Scale bar 30 mm.

dentary. Finally IVAKHNENKO (2003) remarked on the high palatal tuberosities which had numerous teeth, the only slightly sculptured bones and incisors that were only slightly larger than the postcanine teeth. Each author additionally provided a number of illustrations which are shown here as a composite in figure 25.

After thorough study of the literature and figures I have come to the conclusion that the genus *Sauroctonus* is the gorgonopsian genus with the most similarities to GPIT/RE/7113 (fig. 26). In both forms the skull is slender and the posterior part of skull is only moderately enlarged, which means that the squamosal is less flaring laterally than in *Aelurognathus*. The sloping snout is narrow and somewhat higher than wide with the external nares situated ventrally. Posteriorly the skull roof is straight. The round orbit is rather small but well visible in dorsal view and the temporal fossa is clearly elongate. In GPIT/RE/7113 the interorbital and intertemporal spaces are wider than in *Sauroctonus progressus*. They are, however, unusually narrow in this taxon, which may well be subject to deformation. Nevertheless the difference in the width exists but this might be specific. In both forms the ventral border of the maxilla is only slightly convex and the septomaxilla is rather narrow. The nasal is somewhat constricted in the middle with the naso-frontal suture situated anteriorly and slightly bow-shaped. The prefrontal is distinctly elongate and low and terminates anteriorly in a narrow process. The elongate lacrimal has no antorbital depression. On the dorsal skull roof the contribution of the frontal to the supraorbital margin is rather large whereas the preparietal is of medium size. In *Sauroctonus progressus* it is figured as extremely small and narrow by TATARINOV (1974) but somewhat larger in IVAKHNENKO (2002). It seems, however, that the skull surface is rather weathered in this area and thus the delimitation of the bone might be rather difficult and/or beyond recognition. The postfrontal is narrow in both forms but seems to be shorter in *Sauroctonus progressus*; its posterior margin is straight. Laterally the anterior squamosal process on the zygomatic arch reaches only to the middle of the temporal opening. All three skull arches are comparatively slender with the suborbital and zygomatic arch only slightly curved. The palate exhibits considerable similarities as well. The vomer is slender throughout its entire length, a character that is shared only with *Aloposaurus*, *Cyonosaurus* and *Aelurognathus* and therefore indicates a rather plesiomorphic condition. The palatine is small and the ectopterygoid is wider than long. The moderately broad palatal fossa is bordered by well developed tuberosities which are separated from each other. Both tuberosities have numerous teeth and the palatal ones are much larger than the pterygoid ones. The tooth-bearing transverse apophyses of the pterygoid are posteriorly situated, somewhat more in GPIT/RE/7113 than in *Sauroctonus progressus*. The basisphenoid tubera are elongate and narrow as well as the basisphenoid fossa. The quadrangular occiput is rather convex with a well developed median ridge and a massive paroccipital process. The lower jaw differs somewhat in the two forms since the symphysis is more massive in GPIT/RE/7113 than in *Sauroctonus progressus*. Nevertheless it is somewhat sloping in both taxa.

2.1.7 Conclusion

In conclusion it can be confidently stated that despite the geographic separation of the genus *Sauroctonus* and GPIT/RE/7113 the similarity between the specimens is overwhelming:

Posterior part of skull somewhat enlarged but zygomatic arch does not flare laterally to a great extend; dorsal profile of snout slightly sloping but posterior dorsal skull part straight, snout narrow, slightly higher than wide, orbits of medium size and well visible in dorsal view, temporal opening oblong, interorbital and intertemporal spaces nearly of the same width, both rather narrow; ventral margin of maxilla straight, nasal broad but slightly constricted in the middle, naso-frontal suture anteriorly situated and somewhat bow-shaped, prefrontal long and extremely low, lacrimal oblong, contribution of frontal to supraorbital rim large, preparietal medium sized and well separated from parietal foramen, postfrontal rather narrow and of the same width throughout its length, posterior margin extended in a narrow process, postorbital reaches not far ventral on the postorbital bar, squamosal reaches up to the mid-level on the zygomatic arch; skull arches rather slender, but suborbital arch somewhat enlarged; palatine narrow and small, choanae long, vomer of nearly the same width throughout its length, palatal fossa oval but relatively narrow, palatal tuberosities well developed and separated by a trench, both with numerous teeth, the tuberosities on the palatine are larger than the pterygoid ones and their anterior tips are pointing towards each other, interpterygoid vacuity large, parabasisphenoid fossa deep but narrow, basisphenoidal tubera rather slender, basioccipital rather long; occiput slightly wider than high, only slightly concave, interparietal large, supraoccipital low, paroccipital process low, parietal contributes to occipital rim; teeth comparatively massive, five postcanine teeth; symphysis sloping but relatively massive, dentary high, ridge on lamina reflecta moderately developed.

As it is made clear by the list above, *Sauroctonus* and GPIT/RE/7113 can be regarded as congeneric and thus the latter will be allocated to the genus *Sauroctonus* as the species *S. parringtoni*.

Systematic Palaeontology

Genus: ***Sauroctonus*** Bystrow, 1955

Type species: *S. progressus* (Hartmann-Weinberg, 1938) in Bystrow, 1955

Revised generic diagnosis: snout narrow with sloping dorsal profile, prefrontal long, low and terminating in a narrow process anteriorly, bone surface of maxilla and nasal strongly sculptured, skull arches rather slender, vomer narrow throughout its entire length, palatine tuberosities well developed and separated from each other, both with numerous teeth, symphysis somewhat sloping.

Sauroctonus progressus (Hartmann-Weinberg, 1938) in Bystrow, 1955

(=*Arctognathus progressus*, Hartmann-Weinberg, 1938, = *Inostrancevia progressa* Efremov, 1940)

Holotype: PIN 156/5

Referred Material: PIN 156/6, PIN 156/51, PIN 156/57, PIN 156/7, PIN 156/8, PIN 156/58, PIN 156/59, PIN 156/65, PIN 156/9, PIN 156/52, PIN 156/53, PIN 156/54, PIN 156/55, PIN 156/56, PIN 156/60.

Specific diagnosis: preparietal small, transverse apophyses with teeth, basioccipital narrow, skull bones sculptured.

Bibliography: Hartmann-Weinberg 1938, pp. 47-123
Bystrow 1955, pp. 7-18, fig. 1-6
Tatarinov 1974, pp. 30-50, fig. 11-17
Sigogneau-Russell 1989, pp. 97-98, fig. 236-239

Sauroctonus parringtoni (von Huene, 1950) new comb.

(= *Scymnognathus parringtoni* von Huene, 1950, = *Aelurognathus*? *parringtoni* in Sigogneau, 1970)

Holotype: GPIT/RE/7113

Specific diagnosis: interorbital and intertemporal spaces wider than in the type species, symphysis massive, supraoccipital low, paroccipital process massive.

Bibliography: von Huene 1950, pp. 48-79, fig. 1-30
Sigogneau 1970, pp. 185, fig. 102-104, pl. 43
Sigogneau-Russell 1989, p. 70, fig. 175-176

2.2 Re-assessment of the Gorgonopsia

2.2.1 Introduction

As already stated by previous authors, the genera and species of the Gorgonopsia differ not much from each other osteologically, at least as far as it is known from the available material.

Nevertheless many earlier workers rather tended to erect a new genus or species when describing a new specimen than to allocate it to an already existing taxon. This resulted in a large number of genera and species and in an almost intricate systmatics. Despite Sigogneau's effort to disentangle the relationships of the group there are still many uncertainties left, especially concerning alphataxonomic problems. This is especially shown by the fact that seven out of nine recognisable genera and species from the Kawinga Formation still have an uncertain taxonomic position. Although Sigogneau was able to reduce the number of gorgonopsian genera to 23 and recognise three subfamilies, the delimitation of the different genera against each other still remained problematic. Therefore I was of the opinion that further combination of taxa should be necessary, since I regard well defined generic diagnosis as an essential requirement for any phylogenetic analyses. Many of the characters used to distinguish between taxa are probably ontogenetically variable, and others only show such slight variation that their taxonomic value is limited. Nevertheless, the general shape of the skull and its proportions, as well as the morphology of several cranial elements, have proven useful for taxonomic proposes during my investigation. Indeed I was able to group the main South and East African specimens into well defined genera on the basis of the general skull shape and proportions. Thus the number of genera previously recognised could be further reduced to thirteen. In a second step I investigated the morphological details and sutures of the skulls. As a result I was able to develop a new approach to the alphataxonomy of the African gorgonopsians. Furthermore, I emerged with 43 characters that I used for phylogenetic analyses to present a computer-based cladogram and to provide a revised phylogeny of the Gorgonopsia.

The following re-assessment of the Gorgonopsia has the aim to discuss each valid genus (sensu Sigogneau-Russell 1989) subsequently and to show whether and why I grouped it together with another taxon. All secondary chapters have the same conception. For each of the new 'groups'(genus level), investigation starts with the genus that was established first; then the newly included species are discussed, especially pointing out contradictions or misinterpretations of previous authors. Since I observed all specimens directly, except for three or four skulls, I am able to present personal observations and interpretations.

Each secondary chapter concludes with the modified generic and specific diagnosis of the respective taxa. For each specimen, number, size and bibliography are given additionally. The assessment concludes with the in-group phylogeny of the Gorgonopsia in chapter 2.3. For obvious reasons the Russian genus *Sauroctonus* is included here as well as the genus *Inostrancevia*, which is another well defined taxon from Russia that forms a well illustrated sister-taxon to the rubidgeines.

2.2.2 The genera from the Tapinocephalus Zone

2.2.2.1 Introduction

This chapter is about the stratigraphically oldest gorgonopsian genera *Broomisaurus*, *Eoarctops* and *Galesuchus*, which are all monospecific. The material is noticeably sparse and the specimens are mostly poorly preserved. This makes it extremely difficult to establish diagnostic characters and to carry out a sound comparison. Sigogneau kept all three taxa, since gorgonopsian finds were, according to her, remarkably rare in the *Tapinocephalus* Zone. This is certainly true but it is questionable whether a specimen which does show so few diagnostic characters should be kept as a valid genus or species for stratigraphic reasons only or if it might be more useful to expect the discovery of better preserved material.

In this context it is necessary to consider the biostratigraphic subdivision of the Karoo Supergroup to obtain an overview over the different classifications. Sigogneau (1970) and Sigogneau-Russell (1989) used the classification of Kitching (1970, 1977). Rubidge (1990) and Rubidge et al. (1995) presented a somewhat modified and supplemented classification of the Assemblage zones after discovering a new fossil reptilian fauna below the *Dinocephalian* (after SACS 1980) Assemblage zone. This Zone was named *Eodicynodon* Assemblage Zone and contains mostly the primitive dicynodont *Eodicynodon oosthuizeni*, a few pristerognathid therocpehalians and two rather poorly preserved gorgonopsian parts of uncertain generic relationship (Rubidge 1988).

I follow the classification presented by Rubidge et al. (1995) which is shown in figure 1.

2.2.2.2 *Galesuchus* Haughton, 1915

The first genus to be considered is *Galesuchus* with the type species *G. gracilis*. The holotype SAM 2754 was first described by Haughton (1915) and then again in 1924. The skull is very poorly preserved lacking the snout completely, the postero-ventral part of the skull and the arches except for the postorbital bar. The bone surface is partly eroded and it is impossible to trace any sutures precisely apart from the ones on the dorsal skull roof. Furthermore, it is compressed somewhat dorso-laterally. On the whole the specimen is in such a poorly preserved state that it should not constitute the holotype of a type species.

HAUGHTON (1915) described the skull as having outward looking orbits, a sloping occiput, a fairly large canine, four small postcanine teeth, teeth on the palate and a large prefrontal, jugal, frontal and parietal (but in fact as far as one can trace the sutures those bones are of normal gorgonopsian condition). HAUGHTON (1924) added a few points like the form which was rather narrow and elongate, the snout being square shaped in cross section and the small contribution of the frontal to the orbita. At the end he stated that this specimen shared primitive and advanced characters and should therefore not be seen as possible ancestor to the later Gorgonopsians. He gave a list of primitive characters which were: ‘the high, square shaped section of the snout, the laterally directed orbits, the posterior position of the pterygoid flanges, the sloping occiput and the deep basioccipital and basisphenoidal tubera. As more advanced features he mentioned ‘the lack of an antorbital depression, the reduction in size of the lacrimal (contra 1915) and the small part played by the frontals in the formation of the supraorbital border.’

SIGOGNEAU (1970) added that this specimen might be immature. The diagnosis for the genus which she gives in 1986 reads as follows: Skull wide posteriorly (the posterior part is not completely preserved and her reconstruction appears a little bit exaggerated), snout moderately wide and relatively high (the anterior part of the snout is missing), temporal fossa as high as long (there are some other genera with this character, e.g. *Arctops*), intertemporal width slightly superior to interorbital width (dito), postorbital bar narrow (see e.g. *Cyonsaurus*, *Aelurosaurus*, *Aloposaurus*), large preparietal anteriorly situated, lacrimal rather short (from personal observation I can state that the lacrimal is hardly discernable), pterygoid transverse apophyses rather posteriorly situated (HAUGHTON, 1924 stated the contrary).

The diagnosis is therefore rather generally which is not surprising at all considering the state of the specimen. After thorough examination I came to the conclusion that it is rather impossible to determine a reasonable set of characters and thus SAM 2754 is regarded as Gorgonopsia gen. et sp. indet.

SIGOGNEAU-RUSSELL (1989) added another four specimens to the genus as *Galesuchus* sp. (SAM 11846, SAM K 230, SAM K 208 and SAM 11849). They are, however not much better preserved or even worse and thus are equally considered as Gorgonopsia gen. et sp. indet. Consequently the taxa *Galesuchus* and *G. gracilis* become nomina dubia at least as long as no better material is at hand from this early Zone.

2.2.2.3 *Broomisaurus* JOLEAUD, 1920

The next genus is *Broomisaurus* with the type species *B. planiceps* and its holotype AMG 3752. This specimen however consists only of a snout which is in addition heavily weatherd so that no sutures are traceable at all.

SIGOGNEAU (1970) mentioned the very broad snout, the flat skull roof and the strong and anteriorly sloping caninus. These features are however the only 'characters' that can be observed at this skull. From the condition of the specimen it es even uncertain if this is a gorgonopsian at all, as already mentioned by BROOM (1913). He was not sure whether to allocate the specimen to the therocephalians or gorgonopsians but allocated it to the latter in 1932.

SIGOGNEAU-RUSSELL (1986) again mentioned the uncertain association within the Gorgonopsians but stated that the skull could be most likely be compared with *Eoarctops*. This is certainly true since the snouts of both taxa are remarkably broad. But since the specimen of *Broomisaurus* is only composed of a snout, other similarities can not be established. That is also one of the reasons why SIGOGNEAU refrained from assigning *Broomisaurus* to the genus *Eoarctops* but the main problem was the name priority of *Broomisaurus* over *Eoarctops*. This would result in a poorly preserved holotype of the type species which she tried to avoid.

Considering the extremely incomplete and weathered state of AMG 3752 this specimen is regarded as Gorgonopsia gen. et sp. indet. Consequently the genus *Broomisaurus* and the species *B. planiceps* become nomina dubia.

2.2.2.4 *Eoarctops* HAUGHTON, 1929 (fig. 27)

The last *Tapinocephalus* Zone genus is *Eoarctops*. The type species, *Eoarctops vanderbyli* with the holotype SAM 5598, was first described by HAUGHTON (1929). This 120 mm long skull and mandible is only slightly better preserved than the preceding ones but it shows more and clearer characters.

Although the specimen has some features in common with *Arctops* and *Scylacognathus* it clearly and mostly displays characters of its own. The skull is broad in all respects, but the arches are remarkably slender. The preparietal is large and almost perfectly rounded, a form that is truly unique, but the supraorbital portion of the frontal is comparatively small. The lacrimal is slightly elongated but gets wider when it meets the maxilla. The latter is rather high, which makes the nasals narrow. The postfrontal is very broad at the orbital margin but

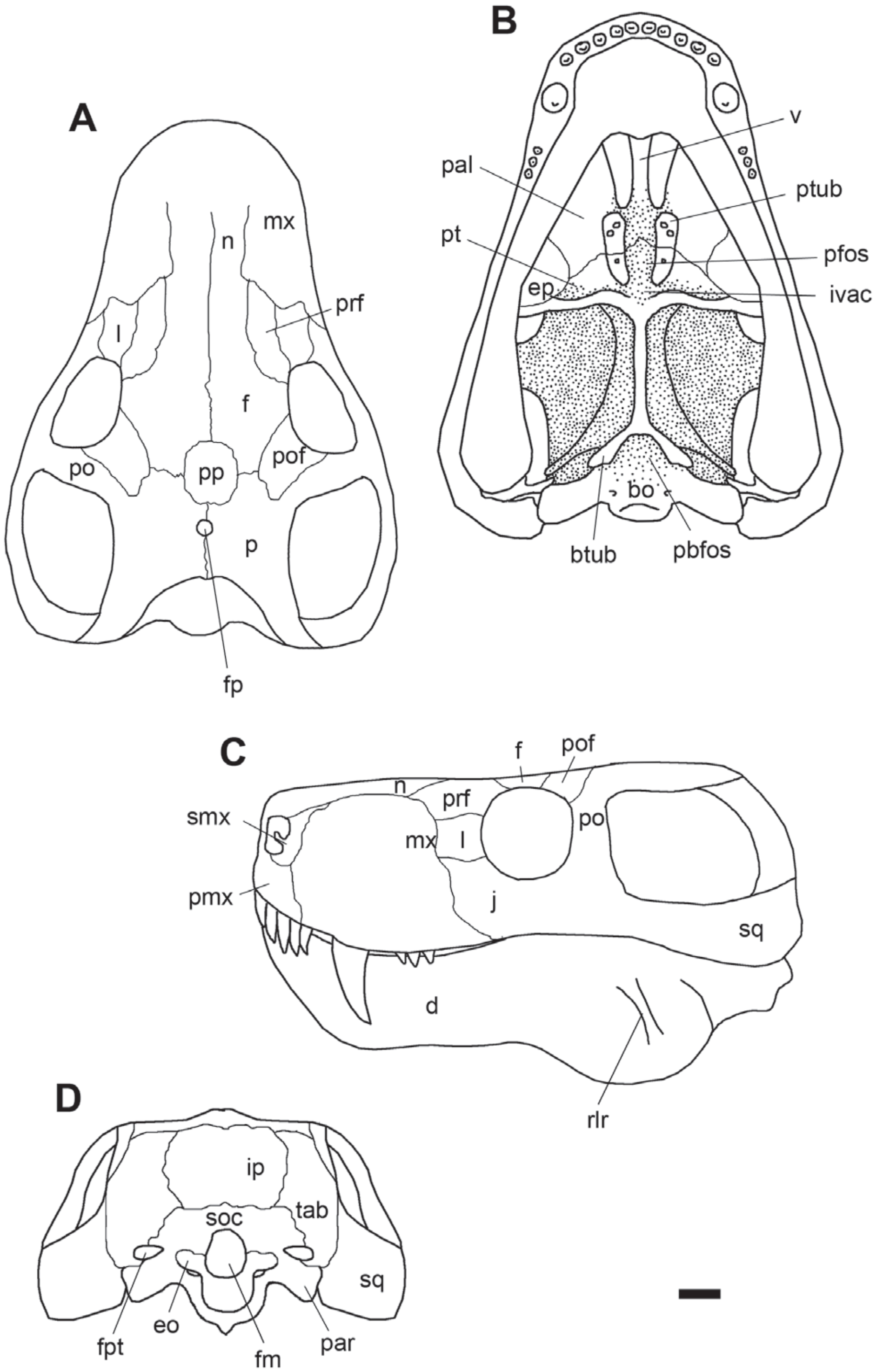


Figure 27. Illustration of the characters in the genus *Eoarctops* Haughton, 1929 based on the holotype of the type species, *Eoarctops vanderbyli* (SAM 5598). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

narrows rapidly in posterior direction. The number of incisors remains uncertain, since the upper jaw is too incompletely preserved in this area. HAUGHTON and SIGOGNEAU both saw three incisors in the lower jaw, however SIGOGNEAU admits that there also could be a fourth. Unfortunately even after thorough personal observation I was not able to solve the question satisfactorily. However the evidence might well indicate a genus that has only four upper incisors. The number of postcanine teeth is, however, three.

Systematic Paleontology

Genus: ***Eoarctops*** HAUGHTON, 1929
Type species: *Eoarctops vanderbyli* HAUGHTON, 1929

Revised generic diagnosis: small size, skull short altogether and broad posteriorly, snout as high as wide and well rounded anteriorly, orbit large, preparietal large and almost circular, supraorbital frontal large, skull arches rather slender, interorbital and intertemporal width relatively narrow compared to the width of the skull, palatal fossa narrow but tuberosities well developed, para-basisphenoidal tubera slender, interparietal large, dentary massive and short.

Eoarctops vanderbyli HAUGHTON, 1929
Holotype: SAM 5598
Diagnosis: as for genus, as this is the only species.

Bibliography: HAUGHTON 1929, pp.68-70, fig.12-13
BROOM 1932, p. 110, fig. 34B; 35A
BOONSTRA 1963, p. 178
SIGOGNEAU 1970, pp. 9-12, fig. 2-3, pl. 1c; 2a
SIGOGNEAU-RUSSELL 1989, pp. 85-86, fig. 206-211

2.2.3 The small sized genera Aelurosaurus, Aloposaurus, Cerdorhinus, Cyonosaurus, Paragalerhinus and Scylacognathus

2.2.3.1 Introduction

This chapter is, on the one hand, about the problem of identifying probably immature specimens and the difficulty of allocating them to a particular genus. From this originates, on the other hand, the question whether most of the existing taxa with small sized individuals are valid and furthermore, if they probably can be attributed to another taxon as immature ontogenetic stage.

There exists a large amount of ‘small’ gorgonopsians in the fossil record. First of all, however, it is uncertain whether these forms were all young individuals and, if so, whether they constitute one or more genera. Then there is the (most likely) possibility that some of them are young and some are the adult stage of one or more different taxa. The ideal situation to solve this problem would be to find a presumably young specimen next to an adult, which would provide the possibility for a direct comparison. But unfortunately this case has never happened concerning gorgonopsians or at least, if such an ensemble ever existed it was never recognised by the finders. Therefore one has to rely on the skulls that are provided and examine the structure and appearance of the bones. Moreover, study of the ontogeny of Recent mammals and reptiles can be helpful as well as the reports on fossil material from which a juvenile stage is confirmed. In the following paragraph I will briefly refer to the assertions of some authors to illustrate the historic background of therapsid ontogeny.

Almost all early authors who wrote about gorgonopsians did not pay great attention to the fact that certain specimens could be young individuals. Thus they rather erected a new genus and/or species if these did not fit into an already established taxon. Sometimes they gave a short note which would indicate that this particular specimen might not have been fully grown, but they never listed any features why they believed that this was the case, except for the small size and the probable large eyes (e.g., Broom & George 1948 for ‘*Galerhinus rubidgei*’ Broom, 1936 = *Paragalerhinus rubidgei* Sigogneau, 1970; Broom 1948 for ‘*Cyniscops kitchingi*’ = *Cyonosaurus kitchingi* Sigogneau, 1970).

Brink (1955) described a slab that was composed of an evidently mature female cynodont *Thrinaxodon liorhinus* specimen associated very closely together with a tiny specimen of the same taxon. This was one of the rare possibilities to study juvenile and adult characters in a direct comparison with the almost definite certainty that it concerns a mother with its young. Brink was sure that the adult specimen was female since he had been able to make a distinction between male and female specimens, because of their sizes, in earlier finds. However, the main focus in Brink’s description was drawn at the typical mammalian arrangement of dental succession. This and the fact that the specimens were incomplete posteriorly and the palate hardly accessible resulted in an account of rather little comparative value for this study. However, Brink noted the large frontals in the young specimen, which almost contributed to the orbital margin, the small prefrontal and the slender postorbital bar.

Van Heerden (1972) considered growth changes but also intraspecific variation in *Thrinaxodon liorhinus* on the basis of three new finds of which two were regarded as definitely immature. He came to the conclusion that such characters as open sutures, a large septomaxilla foramen, an anteriorly situated naso-frontal suture, a short postorbital, a large and round parietal foramen, a well developed parietal crest, a low zygomatic arch, the occurrence of two separated interparietals, an inclined occiput, the presence of an interpterygoid vacuity, the small diastema between the canine and postcanine teeth and tooth replacement indicated an immature individual.

Abdala et al. (2001) describe relative modifications in cranial structure in the postweaning ontogeny of *Didelphis albiventris*. They stated that the postorbital was constricted in the adult but straight in the juvenile, the petrosal, promontorium, tympanic process of the petrosal, and the internal acoustic meatus were relatively small in the adult but relatively large in the juvenile and the exoccipitals were only partially fused with the basicocipital in the latter but entirely fused in the adult form. They figured the juvenile form with a broader cranial skull roof, a shorter snout, a less flaring zygomatic arch, a larger foramen magnum and a shorter lower jaw compared to the adult.

Concerning gorgonopsians an attempt with more detailed reference to ontogeny was first made by Sigogneau (1970). By discussing the matter she, however, admits that it is always possible that differences between specimens are not related to growth changes but still to specific or generic variation even if it concerns an explicitly small form. She listed the following specimens as being presumably immature: BPI 3 *Cyonosaurus* sp., MMK 2046 cf. *Aloposaurus tenuis*, AMG 3751 *Scylacognathus parvus*, RC 2 *Paragalerhinus rubidgei*, RC 4 *Cerdorhinus*? *rubidgei*, WMUC 1515 and BPI 295 *Cyonosaurus longiceps*, MMK 5028 *Cyonosaurus kitchingi* and probably RC 101 *Broomicephalus laticeps*.

Sigogneau brings up a number of characters, however, on the proviso that they also occurred in presumed adult forms such as *Aelurosaurus*? *watermeyeri*, *Aloposaurus*? *tenuis* or some *Cyonosaurus* forms and therefore some might as well be rather basal: small size, short snout, large orbit, high supraoccipital, large frontals, small postfrontals, short distance from canine to postcanine tooth row. She also mentions the relative interorbital and intertemporal widths but is not able to make a definite statement, whether the cranial skull roof widened or narrowed during ontogeny, because of the various conditions that are found throughout the small taxa. The same applies for the size of the preparietal and its distance to the parietal foramen, as well as for the position of the transverse apophyses.

As seen from the discussion above there are certain characters which occur in each account and therefore are regarded here as evident indicators of an immature state. In order to complete the list it is necessary to consider the reason why certain areas of the skull change during ontogeny.

One reason is the growth of muscle mass and hence the enlargement of muscle attachment areas. This would primarily affect all parts which are related to jaw musculature but also the regions that serve as attachment areas for the neck muscles. At least in mammals, young carnivore individuals do not need powerful jaw or neck muscles, since they are cared for by their mother (or father) for a certain time period and do not need to hunt by themselves. Therapsids have a somewhat intermediate status since they do not lactate their young and therefore one could state that there was no need for parental care after hatching. However, birds nurse their offspring and even some dinosaurs did (Norell et al. 1995, Meng et al. 2004). Brink (1955) already suggested the possibility that *Thrinaxodon liorhinus* might have nursed its young. Although cynodonts are regarded as more advanced than gorgonopsians, it is well possible that gorgonpsids nursed their offspring, too. Evidence for this would be the rather weakly developed muscle attachment areas such as the zygomatic arch, the coronoid process or the median ridge on the occiput in presumed young gorgonopsian individuals.

Concerning the temporal width, one could assume that in gorgonopsians, where the temporalis musculature had not yet invaded the external skull roof, this space widened during ontogeny to give more room for musculature. However as already indicated by Sigogneau (1970) there is no clear pattern developed throughout the specimens to verify this presumption. But probably the change of the rather small and narrow postfrontal and the usually narrow postorbital in presumed immature specimens to larger and broader bones in the temporal skull roof in adults indicates a more stable structure and hence a sound muscle attachment area.

According to Emerson & Bramble (1993), in nearly all vertebrates accelerated differentiation of the central nervous system and sensory capsules produces embryos and neonates with large braincases, eyes and auditory regions relative to trophic components of the skull. Concerning the orbit, this certainly applies for gorgonopsians, too, but it is more problematic to make a clear statement about the braincase and the auditory regions because they are often obscured by matrix. However, in some presumed young specimens such as BPI 3 and AMG 3751 at least the ventral part of the braincase, i.e., the para-basishpenoid complex with the para-basisphenoidal tubera and the basisphenoid fossa is somewhat broadened.

Another part of the skull that changes during ontogeny is the preorbital region. The snout is usually about as high as it is wide and shortened in the young individual. This affects the septomaxilla, the prefrontal and lacrimal which are therefore rather short, too. However, the degree of the lengthening of these bones in the adult form obviously depends on the genus and species. The same applies for the supraorbital part of the frontal and the preparietal which are considered as relatively large in the juvenile but smaller in the adult form. The shape of the snout itself, however, does not change during ontogeny which thus appears as a good diagnostic character to generically diagnose an immature specimen.

The taxa which contain exceptionally small specimens with a distinctive set of characters are *Aelurosaurus*, *Aloposaurus*, *Cerdorhinus*, *Cyonosaurus*, *Paragalerhinus* and *Scylacognathus*. In the following section I will discuss the different species of those genera and will give an overview of their history and classification. As one will notice, the relationships are usually dubious and one gets the impression that all those specimens are more or less easily exchangeable between the different genera. In fact, the systematic characters given by the authors occur variedly across all genera. The main problem is to distinguish whether the characters which define a certain genus are valid or whether these characters in one way or another indicate an immature state.

The list below illustrates the modifications that were made and gives an overview of the generic names as used by Sigogneau-Russell (1989) and the new proposal:

Cerdorhinus parvidens
TMP282……Gorgonopsia indet.
Cerdorhinus ? *rubidgei*
RC 4……*Cyonosaurus kitchingi*
Paragalerhinus rubidgei
RC 2……*Lycaenops* sp.
Aloposaurus gracilis
AMHN 5317……*Aloposaurus gracilis*
Aloposaurus? *tenuis*
BPI 256……*Aloposaurus tenuis*
BPI 257……*Aloposaurus tenuis*
cf. *Aloposaurus tenuis*
MMK 2046……cf. *Aloposaurus tenuis*
BSP 1932 I 57 ……*Lycaenops* sp.
Aloposaurus sp.
GPIT/RE/7123……*Cyonosaurus broomianus*
Cyonosaurus longiceps
WMUC 1515……*Cyonosaurus longiceps*
RC 75, BPI 254, BPI 253, BPI 294……*Cyonosaurus longiceps*
Cyonosaurus rubidgei
RC 74……*Cyonosaurus rubidgei*

Cyonosaurus cf. *rubidgei*

BPI251...*Cyonosaurus rubidgei*

BPI387...*Cyonosaurus rubidgei*

TMP2040...Gorgonopsia indet.

Cyonosaurus kitchingi

MMK 5028...*Cyonosaurus kitchingi*

RC51...*Cyonosaurus kitchingi*

SAM 8790...Gorgonopsia indet.

Cyonosaurus sp.

BPI3...*Cyonosaurus* sp.

Aelurosaurus felinus

BMNH R 339 ....*Aelurosaurus felinus*

BMNH R 885...Gorgonopsia indet.

AMNH5506...Gorgonopsia indet.

Aelurosaurus cf. *felinus*

AMNH5504...Gorgonopsia indet.

Aelurosaurus whaitsi

AMNH5528...Gorgonopsia indet.

AMNH 5514...*Aelurosaurus felinus*

BMNH R 885a...*Aelurosaurus felinus*

Aelurosaurus polyodon

TMP341...Gorgonopsia indet.

Aelurosaurus wilmanae

MMK 4667...*Aelurosaurus wilmanae*

Aelurosaurus? *watermeyeri*

RC21...*Aloposaurus watermeyeri*

Aelurosaurus sp.

RC7...*Aelurosaurus felinus*

Aelurosaurus?

GPIT/RE/7124...*Aelurosaurus wilmanae*

Scylacognathus parvus

AMG 3751...*Scylacognathus parvus*

TMP 256...*Scylacognathus robustus*

BPI 399...*Scylacognathus parvus*

Scylacognathus robustus

BMNH R 5743...*Scylacognathus robustus*

Scylacognathus grimbeeki

TMP 245...*Scylacognathus parvus*

TMP 246...*Scylacognathus parvus*

Arctops willistoni

BMNH 4099...*Scylacognathus parvus*

Arctops watsoni

BPI 263...*Scylacognathus parvus*

Arctops cf.watsoni

BPI 395..*Scylacognathus robustus*

Arctops? *minor*

RC 110...Gorgonopsia indet.

Arctops? *kitchingi*

BPI 265...*Scylacognathus*? *kitchingi*

Arctops? *ferox*

RC 62...*Aelurognathus ferox*

RC 81, RC 82, BPI 226, TMP 132..*Aelurognathus ferox*

Before turning to the history of the taxa I shall give a general list of features which are considered here to suggest an early ontogenetic stadium. The characters are based on personal observations and the assertions of the authors discussed above: small size with slender appearance, squamosals do not flare far laterally if seen in dorsal view; snout short, as high as wide, pointed?; dorsal margin of snout and skull rather straight, at best slightly convex, skull arches extremely slender, orbit large, temporal opening square-shaped; septomaxilla short, nasal small, supraorbital portion of frontal large (but depends on genus), postfrontal exceptionally small and narrow, preparietal large (however, depends on genus) and close to parietal foramen, nasofrontal suture anteriorly situated and pointed, lacrimal rather short, postorbital on postorbital-arch far ventrally reaching, squamosal on zygomatic arch reaching far anteriorly; ectopterygoid elongated and/or large, choanae long, palatal groove broad but shallow, palatal tuberosities well separated from each other; the tuberosities on the palate are often nearly closed anteriorly whereas the posterior ends of the pterygoid ones are always pointing towards each other; numerous teeth on the tuberosities and on the transverse flanges, basisphenoid fossa deep and broad, para-basisphenoidal tubera diverge at a great angle; occiput only slightly inclined, interparietal wide, supraoccipital high, foramina large; symphysis may be open; dentary slender, coronoid process low, lamina reflecta weak; tooth-replacement, teeth slender, numerous postcanines.

2.2.3.2 *Cerdorhinus* Broom, 1936

The genus *Cerdorhinus* contains the two species *C. parvidens* and *C.*? *rubidgei*.

C. parvidens

Broom (1936) described a poorly preserved and weathered skull (TMP 282) which lacks the anterior part of the snout and measures appr. 150 mm in length. He erected the new genus and species *Cerdorhinus parvidens* for it and described it as nearly complete. But personal observation showed me that the skull is not in a good condition since the lateral and posterior parts are badly weathered and the palate is only visible in parts. Only the bones of the skull roof are relatively well preserved. Broom mentioned the narrowness of the head, the very slender lower jaw and the small size of the five molars. He figured only the dorsal view with broad and long prefrontals, short and narrow postfrontals, the long and narrow frontal which widely contributes to the orbital margin and a small preparietal. He mentioned the shortness of the parietals but they were probably of normal length since the surface of the skull roof is broken in this area. No attempt was made at a comparison with other genera.

Sigogneau (1970) added to the list of the characters of this specimen the slenderness of the skull arches, the very long temporal opening, but in fact, the posterior extent can not be determined. In the palate she mentioned that the palatal tuberosities of the palatine and pterygoid were separated by a profound and narrow groove, while I observed that the tuberosities are confluent and only separated by the suture. Furthermore, she suggested a comparison with *Cyonosaurus* and *Aloposaurus* but was unable to do so with the latter because of the lack of a direct examination. However, she saw a good concordance with *Cyonosaurus* and especially *C. longiceps*, but because of the name priority of *Cerdorhinus* over *Cyonosaurus*, which is by far better preserved, she did not allocate TMP 282 to the genus *Cyonosaurus*.

This specimen badly illustrates its characters and therefore should not constitute a taxon. The genus *Cerdorhinus* would be based on a dorsoventrally flattened, heavily weathered and incomplete specimem that lacks the snout, most parts of the skull arches and occiput and only shows small parts of the palate.

C.? *rubidgei*

Sigogneau (1970) allocated another species to the genus *Cerdorhinus*, though with a questionmark (RC 4). This specimen was first described by Broom (1937) as *Galerhynchus rubidgei* gen. et spec. nov. This skull is better preserved than TMP 282 but somewhat squeezed dorsoventrally and was the hitherto smallest known gorgonopsian (80 mm skull length). Broom mentioned the relative large size of the parietals, the small postfrontal, the large supraorbital frontal, the small incisors and slender canine, nine small postcanine teeth and the slender stapes.

Sigogneau (1970) added the particularly short and rounded snout, the large orbits, the elongated temporal opening, the thin skull arches, the wide interparietal, the short septomaxilla, the quadrate-shaped lacrymal, the large foramina magnum and jugulare, the short paroccipital process, the long basioccipital, the posteriorly situated transverse apophyses of the pterygoids with teeth and the long ectopterygoid. She suggested that the specimen was immature but was not sure if all these characters: short snout, large orbita, the dimension of some foramina, the composition of the occiput, the replacement of the dentition, a long squamosal on the zygomatic arch, extreme posteriorly situated transverse apophyses of the pterygoid and a long ectopterygoid were juvenile or diagnostic for a certain genus. She compared the skull with the following genera: It shared with *Paragalerhinus* most of the characters which would indicate immaturity; with *Aelurosaurus* it shared the short snout (which is however longer in *Cerdorhinus*? *rubidgei*) and the dimension of the interorbital space, but the long temporal openings, the position of the transverse apophyses and the tooth sequence were different. She finally suggested the specimen to be the young form of *Aloposaurus* or *Scylacognathus*. The closest relationship she saw, however, is with *Cyonosaurus*, but once more the same problem arises as for the type species, concerning a union of those two taxa.

Discussion

The type specimen TMP 282 could be a young specimen for many reasons: large orbits, teeth on transverse apophyses, long lateral postfrontal on postorbital arch and squamosal reaching anteriorly on zygomatic arch, were it not for the relatively long snout which is already elongated, even without the part that is missing. It was probably a sub-adult specimen which certainly would belong to the genus *Cyonosaurus* if fully grown. However, TMP 282 is too badly preserved and rather insatisfactorily individualized to be a type species so that it will become Gorgonopsia gen. et. sp. indet. *Cerdorhinus rubidgei* (RC 4) will be allocated as referred specimen to the species *Cyonosaurus kitchingi* since it shares many features with this taxon: very small size, large orbits, relatively broad interorbital and intertemporal widths, extremely slender skull arches, zygomatic arch not flaring laterally, small postfrontal, narrow dorsal postorbital, anteriorly situated preparietal, large parietal foramen which is situated close to the preparietal, large ectopterygoid, well developed and large palatal tuberosities with teeth, presence of teeth on the transverse apophyses which are posteriorly situated, stout basisphenoidal tubera, wide and large supraoccipital, slender paroccipital process, large foramen magnum and postemporal fenestra, slender and small canine, small and numerous postcanine teeth, slender dentary and the weak lamina reflecta on the angular. Although all these characters certainly indicate a young individual the similarity between RC 4 and *Cyonosaurus kitchingi* are real.

With TMP 282 as Gorgonopsia gen. et. sp. indet. and RC 4 allocated to the genus *Cyonosaurus kitchingi*, the genus *Cerdorhinus* becomes a nomen dubium.

2.2.3.3 *Paragalerhinus* Sigogneau, 1970

The genus *Paragalerhinus* is only monospecific.

P. rubidgei

In the same account as that describing TMP 282 Broom (1936) mentioned another small specimen (RC 2) which he allocated to the genus '*Galerhinus*' Broom 1935, however he gave no explanation for his decision. (The type species of '*Galerhinus*' was *G. polyodon* which was allocated to the genus *Aelurosaurus polyodon* by Sigogneau 1970, but is now Gorgonopsia gen. et. sp. indet., see below).

RC 2 is, again, a very small skull (105 mm skull lenght) and rather badly preserved. Broom pointed out that the specimen had eight molars, long nasals, large prefrontals, long frontals, small lacrymals, a well developed preparietal, a narrow postfrontal and a well-developed interparietal. The mandible had a slender dentary but a deep symphysis.

'Galerhinus rubidgei' was referred to by Broom & Robinson in 1948 in a comparison with *Nanogorgon gracilis* (BPI 3 = *Aelurosaurus*? *watermeyeri* Sigogneau 1970; =*Cyonosaurus* sp. Sigogneau-Russell 1989). Although these authors mentioned that '*G. rubidgei'* was probably a young individual, they considered it not closely allied to BPI 3 because of the long canine and the well developed incisors of RC 2, which are, however, of the same size as in BPI 3.

Concerning RC 2, Sigogneau (1970) added to Broom's description the stocky snout, slender skull arches, the narrow skull roof, the short prefrontal, the high supraoccipital, the thickened tuberosities of the palate, the anteriorly situated transverse apophyses and, contra Broom, saw seven postcanine teeth. Once again, Sigogneau considered this specimen to be immature because of the same charateristics as those of *Cerdorhinus rubidgei* and suggested it to be a juvenile form of *Aloposaurus* or *Cyonosaurus rubidgei*, but she again was not sure whether, e.g., the short snout or the relative wideness of the interorbital space were charaters of immaturity or generic.

SIGOGNEAU also mentioned a possible reference for RC 2 to the taxa *Lycaenops*, *Arctognathus* and *Scylacognathus* but rejects a close relationship mainly because of the narrow interorbital width of *Paragalerhinus*. With *Cerdorhinus* ? *rubidgei* (RC 4) she saw a generic barrier because of the proportions, the interorbital dimension, the position of the transverse apophyses and the arrangement of the palatal tuberosities. She ends with mentioning *Aelurosaurus* but states that with the present condition of knowledge, she will leave the specimen provisionally in its present taxon. She continued to do so in 1989, but mentioned that it might be a young form of *Cyonosaurus* but the transverse apophyses were more anterior in *Paragalerhinus*.

Discussion

Again, in my opinion, this is a young individual, which shows many of the typical characters that are confirmed by personal observation of the skull. These are: the small size, the large orbits, the short snout which is as wide as high, the slender skull arches, the narrow and short postfrontal, the large supraorbital portion of the frontal, the anteriorly situated preparietal and foramen parietale, the postorbital which reaches ventrally on the postorbital arch but is rather narrow dorsally, the anteriorly reaching squamosal on the zygomatic arch, the well-developed palatal tuberosities with numerous teeth, the large parabasisphenoid fossa, the large interparietal, the slender canine, the small and numerous postcanine teeth, the tooth replacement, the slender lower jaw with a weak lamina reflecta. With this conclusion the genus *Paragalerhinus* becomes doubtful and the possible allocation of RC 2 to another genus must be discussed. The rather narrow cranial skull roof, the short temporal opening, the anteriorly situated transverse apophyses and the already somewhat laterally flaring zygomatic arch restrict the number of possibilities. From *Gorgonops*, *Scylacops*, *Arctops*, *Arctognathus* and *Aelurognathus* it is distinguished by the narrow cranial skull roof. From *Cyonosaurus* it is separated by the last three characters, but these together with the first would match a genus such as *Lycaenops* perfectly well. Therefore I propose the genus *Paragalerhinus* to be obsolete and allocate the specimen RC 2 to the genus *Lycaenops* BROOM, 1925 as *Lycaenops* sp. (see Chapter 2.2.6.5).

2.2.3.4 *Aloposaurus* Broom, 1910

The genus *Aloposaurus* contains the two species *A. gracilis* and *A.*? *tenuis*. Additionally there are two specimens which were allocated to the taxon as cf. *Aloposaurus tenuis* and one as *Aloposaurus* sp.

A. gracilis

The poorly preserved, weathered and laterally compressed holotype of the type species AMNH 5317 was first described by Broom (1910). He mentioned the small size (120 mm in length), the narrowness of the skull, the large septomaxilla, the small lacrimal, the narrow nasal, the long frontal, the broad parietal region, the long and slender lower jaw and the probable five postcanine teeth. In 1932 he pointed out that the specimen was immature and added that the canines were in the state of replacing each other, the frontals did not contribute to the orbital margin, the preparietal was large but the parietal foramen rather small and there were six postcanine teeth. Boonstra (1935) stated that there was a large supraorbital portion of the frontal and that there were probably only four postcanine teeth. Sigogneau (1970) did not examine the specimen personally, but in her account she emphasized the long and low snout, the slender skull arches, the rhombic preparietal which was close to the foramen parietale and the slightly higher than long lacrimal. She mentioned that AMNH 5317 was close to *Aelurosaurus* but provisionally keeps the genus, attributing, however, the following species with a questionmark.

I had the opportunity to examine the specimen personally. Though it is considerably compressed laterally, which gives it a narrow appearance, the snout still remains remarkably slender and pointed after restoration, whereas the posterior part of the skull shows a ‘normal’ width. Here, however, the relatively large cranial skull roof is to be noted, which distinguishes the specimen from *Cyonosaurus* as well as the quadrangular temporal opening. Because of the first character, a probable immature state could be supposed but the long snout, the small orbits, small parietal foramen, large postfrontal and the relatively high dentary are opposed to this suggestion. From *Aelurosaurus* it is distinguished by the shorter snout, dorsally situated nares and broader palatal tuberosities of the latter.

A.? *tenuis*

The holotype of this species was first described by Brink & Kitching (1953) as *Aloposauroides tenuis* gen.et sp. nov. They mentioned two skulls; BPI 256, which is better preserved and was made the holotype, and BPI 257 as referred material. Brink & Kitching pointed out that the skull was slender and delicate, the preparietal was diamond-shaped and did not reach the parietal foramen, the supraorbital portion of the frontal was large, the postorbital slender and there were seven molars. SIGOGNEAU (1970) remarked on the long snout, small orbits, narrow interorbital region, triangular occiput, quadrate lacrimal, deep basisphenoidal fossa and the palatal tuberosites that were well developed and had teeth as well as the transverse apophyses. In the final discussion she mentioned a possible relationship with *Aelurosaurus*, *Gorgonops*, *Scylacops* or *Cyonosaurus* but concluded in seeing the most accordance with *Aloposaurus*. Concerning BPI 257, which is far more poorly preserved than the type, SIGOGNEAU saw some differences with BPI 256 in the proportions and considered the allocation to the genus doubtful, but nevertheless left it as a possible referred specimen to *Aloposaurus tenuis*.

The species *A. tenuis* will be retained here since the specimens illustrate well the characters of the genus.

cf. *Aloposaurus tenuis*

Two more specimens were allocated to the species as cf. *Aloposaurus tenuis* by SIGOGNEAU (1970). The first skull is MMK 2046, which was first described by BROOM (1925) as *Cynarioides tenuis* gen. et sp. nov., concerns a badly crushed and fractured skull and mandible that measures 106 mm in length. BROOM mentioned that it was an immature individual, there was tooth replacement and that it had five molars. SIGOGNEAU (1970) pointed out that the specimen had a rather long and anteriorly narrow snout, the arches were slender, the orbits large, the nasofrontal suture was anteriorly situated, the supraorbital portion of the frontal was large, the large preparietal reached the parietal foramen, the postfrontal was short, the postorbital narrow dorsally, the foramen magnum large, the transverse aopophyses had teeth and the dentary was slender. She also mentioned the probable immature state and admits that the systematic position of the specimen remains uncertain. Since I could not observe this specimen personally, SIGOGNEAU's allocation is retained in this account.

The second specimen is BSP 1932 I 57 which was first described as *Aelurognathus* cf. *serratidens* by BROILI and SCHRÖDER (1934). SIGOGNEAU sees the same proportions and thus a probable immature state, as in the preceeding specimen. She rejects a relationship with *Aelurognathus* because of its much more slender and delicate features but at the same time concedes the uncertain systematic position of this specimen. The systematic position of this specimen is indeed problematical since the probable immature state and the poor condition especially at the posterior part of the skull do not allow a precise diagnostic analysis. However, an allocation to the genus *Aloposaurus* is rejected here because of the different snout shape with a strongly concave ventral border, the narrow nasals, the prefrontal elevation and the stronger symphysis. As a result of these characters, an allocation with the genus *Lycaenops* is conceivable (see. chapter 2.2.6.5).

Aloposaurus sp. (figs. 28 & 29)

Another specimen with a rather uncertain systematic position is GPIT/RE/7123 (formerly IGP K 51) from Kingori/Tanzania. It concerns a well-preserved skull without mandible that measures 120 mm in length. The specimen was first described by von Huene (1950), who allocated it to the genus '*Cyniscops'* as the new species *broomianus*. Von Huene gave a rather general description but already mentioned the broad postfrontal on the orbital margin, the small teeth, the short temporal opening and the markedly ventrally situated palatal tuberosities. Sigogneau (1970) placed the specimen into the taxon *Aelurosaurus*? *watermeyeri* but did not justify her decision, although her short description listed many important characters. At the end of the account she only mentioned that GPIT/RE/7123, on the one hand, resembled the genus *Aelurosaurus* better than the type specimen of *Aelurosaurus*? *watermeyeri* (RC 21), but both also shared certain characters with the genus *Cyonosaurus*. Thus the taxon *Aelurosaurus*? *watermeyeri* would be a rather elusive one. Sigogneau-Russell (1989) allocated the specimen to the genus *Aloposaurus* as *Aloposaurus* sp. Again, she gave no explanation for her decision but only mentioned that the size of the orbits was comparable to *Aloposaurus*? *tenuis* MMK 2046. The statements summarized above elucidate the difficult systematic position of GPIT/RE/7123. Although none of the previous authors mentioned the probable immature state, there are many characters that would draw attention to this possibility. In the following passage I will give a short description to establish a sound basis for further discussion concerning the specimen.

With 120 mm in length the skull is relatively small. It is undistorted but the somewhat weathered and broken surface impedes the observation of the sutures in places. The snout region is remarkably narrow and widens only slightly in posterior direction. The snout is as high as wide, though, because its dorsal profile is slightly inclined in posterior direction. The lateral face of the snout is almost vertically oriented, which produces an angular transition on its back. At the orbital region the skull widens suddenly, being 60 mm broad from the left to the right suborbital arch. The posterior part of the skull is only slightly wider, measuring 70 mm from the left to the right zygomatic arch. This gives the specimen its typical appearance with its unusual extremely narrow snout and the rather bulky posterior skull region.

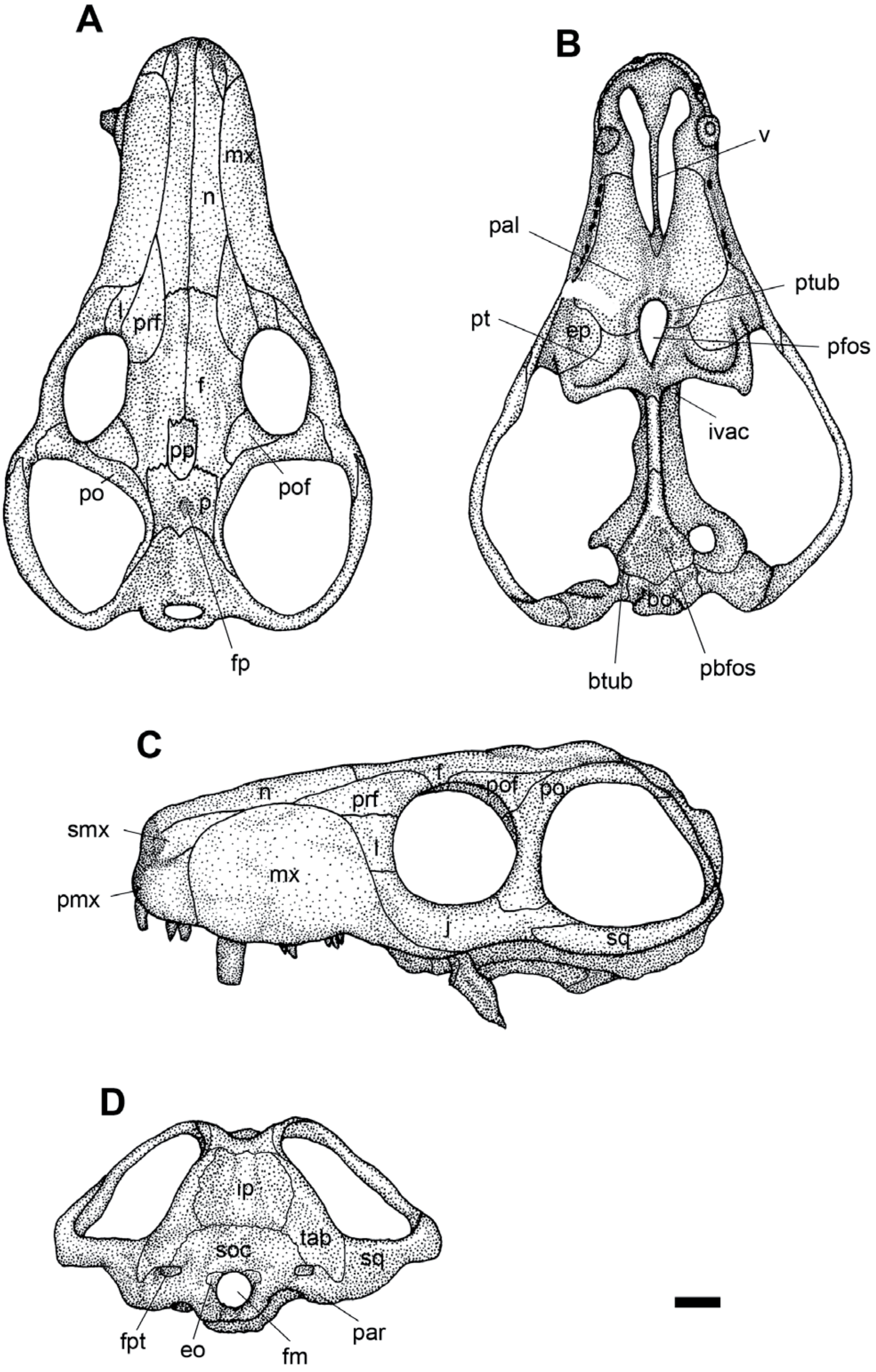


Figure 28. Drawings of GPIT/RE/7123 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

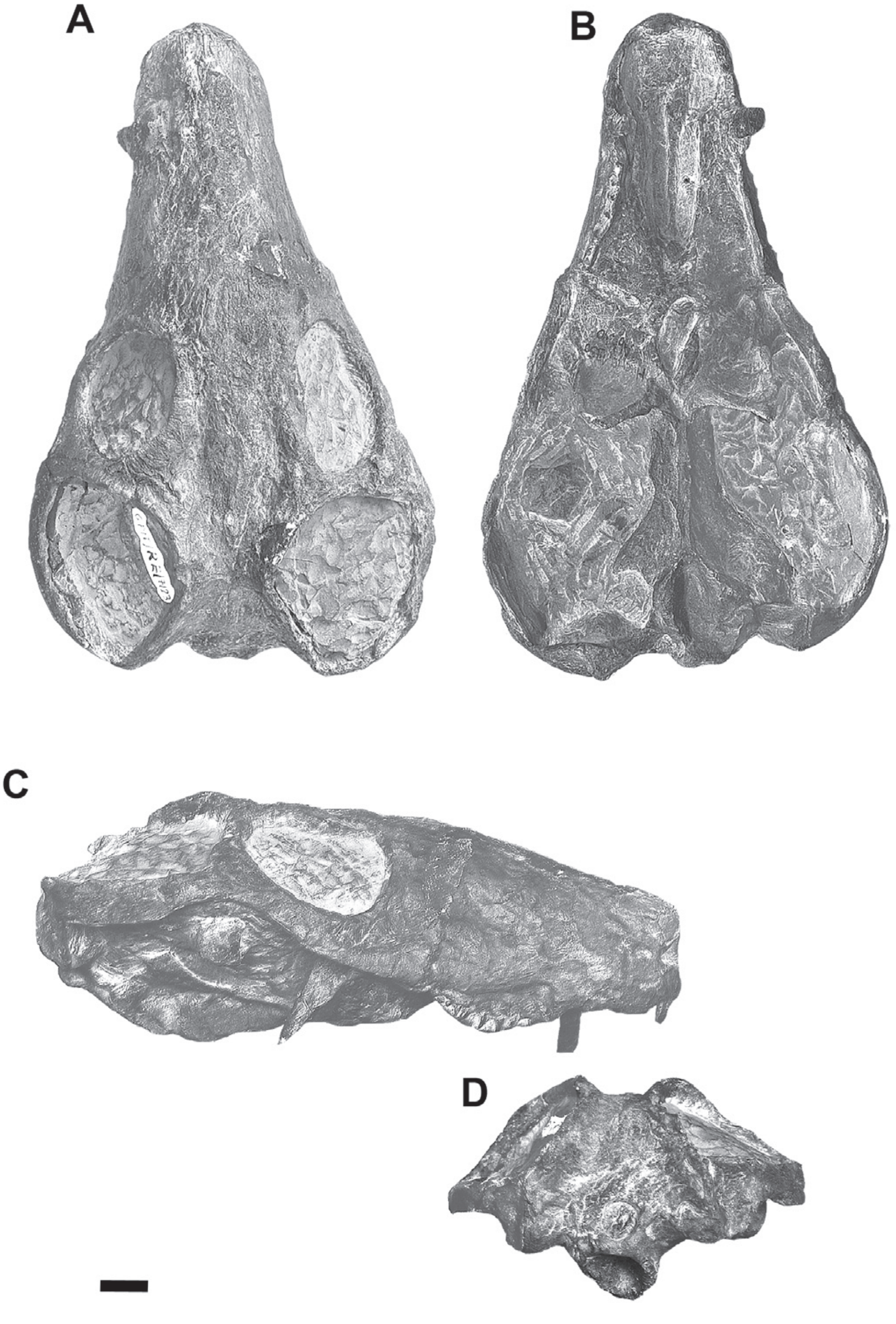


Figure 29. Photographs of GPIT/RE/7123 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

The orbit is rather large and almost circular. The interorbital space measures 23 mm and is hence larger than the intertemporal space, which measures 19 mm. Both spaces are remarkably narrow and, although a part of the dorso-lateral margin of the temporal opening is missing, the intertemporal width is still extremely narrow. The temporal fossa is as high as wide; however, the ventral margin is wider than the dorsal one. The entire area is less steeply oriented than in other Gorgonopsians so that the temporal opening appears to lie almost horizontal if seen in dorsal view.

The premaxilla is low but forms an angle with the nasal dorsally, which means that the nares are situated relatively far dorsalwards. This is unusual for a gorgonopsian with an inclining dorsal snout profile. The septomaxilla is narrow but elongated and reaches almost as far as the anterior tip of the prefrontal. The ventral border of the maxilla has no step and is only slightly sinuous. Posteriorly, the process of the maxilla reaches into the jugal almost as far as the mid-level of the orbit. Because of the peculiarly shaped snout, the nasal is extremely narrow, too. The nasofrontal suture is uncertain because of the state of the surface in this part but it is most likely situated rather anteriorly. The prefrontal is low and short without an anterior elevation. The lacrimal is quadrangular and shows no depression. On the dorsal skull roof the supraorbital portion of the frontal is medium sized, whereas the preparietal is narrow and rhombic. It, however, reaches the foramen parietale, which is situated closely to the occipital crest. Another remarkable bone is the postfrontal, which is exceptionally short but comparatively broad at the orbit. The postorbital reaches notably far ventral on the postorbital bar; dorsally, it is obviously rather narrow. On the zygomatic arch the squamosal reaches up to the mid-level of the postorbital bar, which is particularly far anteriorly. As it is rather common for a gorgonopsian of such a small size, the skull arches are considerably slender. However, the postorbital bar, which is extremely delicate posteriorly, widens noticeably in ventral direction. The zygomatic- and suborbital arches are of the same width throughout their length but curve dorsally at the level of the postorbital bar.

Concerning the palate, the specimen shows another peculiarity. The palatal fossa is situated remarkably far ventral on a steeply inclining elevation. The position is also comparatively far posterior. Anteriorly, the bone surface slopes steeply to meet a slender vomer, which widens only moderately in anterior direction. The internal nares are elongated, whereas the palatine is short and appears, despite the narrowness of the snout, rather wide. The palatal fossa has an oval form. No information can be given about its depth since it is completely filled with matrix. The tuberosities are comparatively weakly developed but form a conspicuous ring around the fossa. Even the anterior margin of the fossa is bordered by a feeble ridge. Both the palatal and pterygoid tuberosities are equally developed and only slightly separated by the palate/pterygoid suture. They have a number of very small teeth on them. The posteriorly situated and delicate transverse apophyses direct postero-ventrally but are also expanded relatively far in ventral direction. They are equipped with a few diminutive teeth. The interpterygoid vacuity between the transverse apophyses is oval and rather large. The ventral braincase region is somewhat deformed and obscured with matrix; however, the ventral parts of the parabasisphenoid and basisphenoid are well visible. The parabasisphenoid fossa is elongated and narrow but comparatively deep, whereas the basisphenoidal tubera are slender and small as expected in a small gorgonopsian. Finally, the basioccipital is rather short with a small condyle. As mentioned above, no information can be given about the quadratojugal, stapes, ramus quadratus or periotic area.

The occiput, again, is very distinctive for this specimen since it is exceptionally narrow, especially the dorsal margin, thus giving it a noticeably triangular outline. Additionally, it is hardly concave but strongly slopes posteroventrally. The median ridge is only faintly developed dorsally but terminates in a comparatively distinct elevation just above the interparietal/supraoccipital suture. Because of the narrow occiput, the interparietal is slightly higher than wide but nevertheless rather small, since the parietal reaches considerably far ventrally on the occipital face. The supraoccipital is low and of normal width since the lateral extension terminates at mid-level of the fenestra posttemporalis. The latter is small and almost round. The paroccipital process is short and low. The dentition is exclusively slender. Especially the incisors are remarkably small and the space between the individual teeth is particularly wide in comparison to other forms. The anterior postcanine teeth are only minimally smaller than the incisors but become even smaller in posterior direction. Because of the large space between them and the incomplete state of dentition, their amount is doubtful but comes to at least seven. In my opinion, GPIT/RE/7123 is neither an *Aelurosaurus* nor an *Aloposaurus*. The relationship with the first taxon is hindered by the overall appearance of the skull with a snout that is much narrower compared to the posterior part of the skull in GPIT/RE/7123. Furthermore, the cranial skull roof is much narrower, the preparietal smaller and the squamosal reaches further anteriorly on the zygomatic arch in this specimen. Concerning the genus *Aloposaurus*, the snout, again, is narrower, the palatal tuberosities are less elongate and the preparietal is too small in GPIT/RE/7123. However, the overall shape of the skull, the slender cranial skull roof, the triangular occiput, the small and narrow preparietal and the less wide supraorbital frontal indicate a close relationship with the genus *Cyonosaurus*. Although there are some similarities with the species *C. kitchingi* such as the extremely narrow snout, the large and sloping temporal opening, the inclined occiput, the high supraoccipital and the markedly narrow intertemporal width, GPIT/RE/7123 clearly constituts a separate species, *Cyonosaurus broomianus*. A significant indication for this assertion might be its East African provenience. Additionally, the peculiar snout form and the ventrally situated palatal fossa of GPIT/RE/7123 illustrate its specific separation well enough.

Discussion of genus Aloposaurus

The genus *Aloposaurus* remains one of the poorer defined genera, which is mostly subject to the imperfect state of the holotype. Nevertheless the specimens which are now included in the genus have a number of characters in common which allows retaining a separate genus and which delimits it from others:

individuals rather small sized, outline of skull as an elongate triangle, posterior part of skull moderately widened, zygomatic arches hardly flaring laterally; dorsal profile of skull slightly convex, snout longer than in *Aelurosaurus* as high as wide, external nares ventrally situated, orbits small, well visible in dorsal view, temporal openings quadrangular, almost of the same width, both narrow; septomaxilla short and narrow, ventral margin of maxilla without step, nasalia narrow, nasofrontal suture bow-shaped, prefrontal low with slight elevation in front of the orbit, lacrimal elongate, with slight preorbital depression, supraorbital portion of frontal of moderate size, preparietal rhombic to diamond shaped, comparatively large, well separated from the foramen parietale, postfrontal with a straight posterior margin; all three skull arches rather slender, posterior margin of postorbital bar straight; internal nares elongate, palatal fossa elongate and narrow, palatal tuberosities elongate and situated parallel to each other, confluent, both tuberosities have numerous teeth, ectopterygoid elongate, transverse apophyses posteriorly situated and without teeth in the adult form, interpterygoid vacuity less developed (can, however, be due to the poor state of the specimens in this area), parabasisphenoid broad and short, basisphenoid tubera markedly slender, basioccipital of moderate size; occiput somewhat concave, slightly sloping, interparietal of normal size, only slightly wider than high, supraoccipital low, parietal contributes slightly to the occipital face, paroccipital process short and stout; incisors of usual size, caninus slender, postcanine teeth small (five to six); mandible slender, symphysis sloping, dentary low, ridge on lamina reflecta rather weakly developed. See figure 30 for illustration.

Systematic Palaeontology

Genus: ***Aloposaurus*** Broom, 1910
Type species: *A. gracilis* Broom, 1910

Revised generic diagnosis: small size, posterior part of skull moderately widened, snout longer than in *Aelurosaurus* but shorter than in *Cyonosaurus*, orbit small and well visible in dorsal view, temporal opening quadrangular, interorbital and intertemporal spaces almost of the same width, both narrow; septomaxilla short, preparietal large, palatal tuberosities situated almost parallel to each other, paroccipital process short and stout, dentary low.

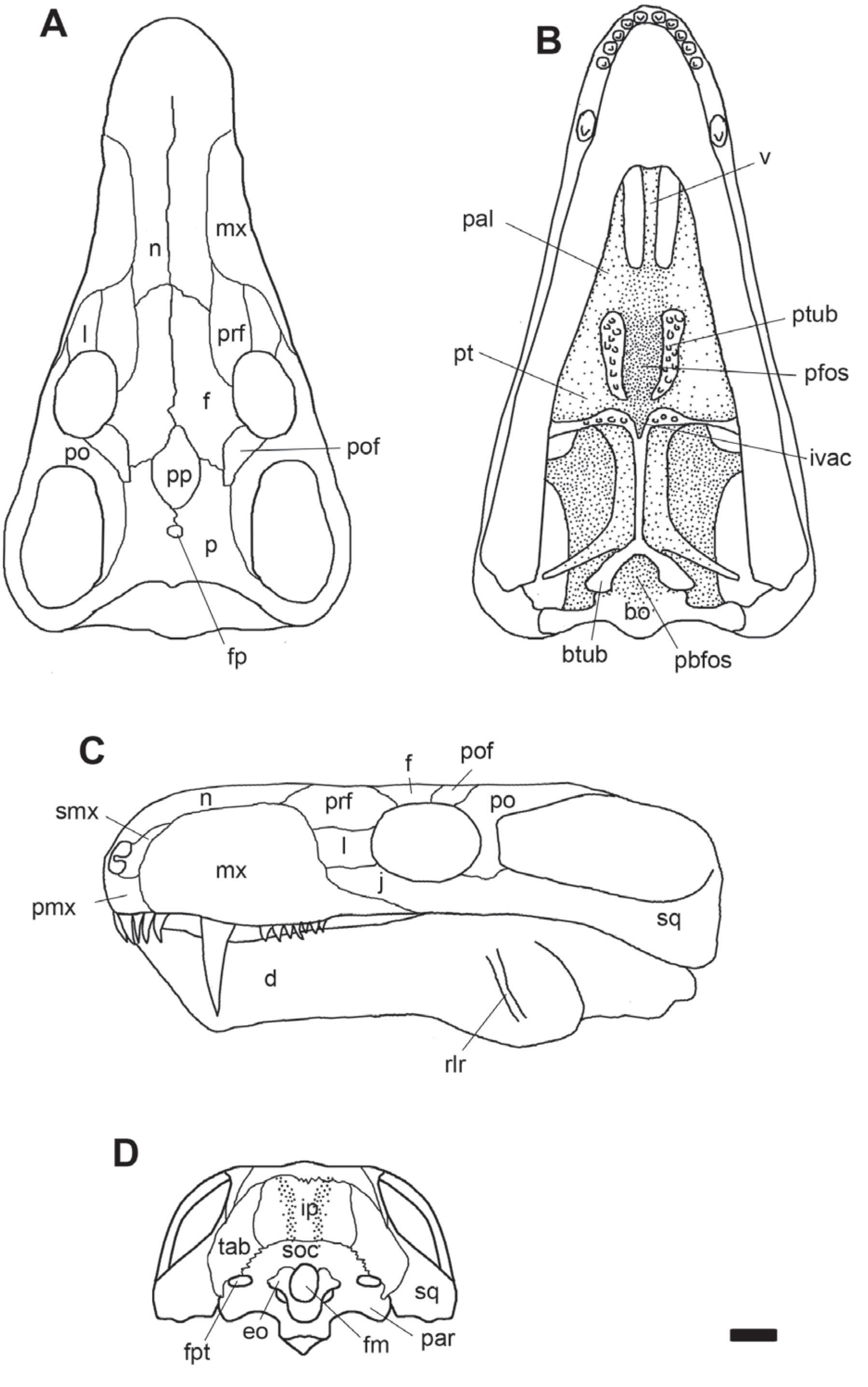


Figure 30. Illustration of the characters in the genus *Aloposaurus* Broom, 1910 based on the holotype of the type species, *Aloposaurus gracilis* (AMNH 5317). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

Aloposaurus gracilis BROOM, 1910

Holotype: AMNH 5317

Specific diagnosis: skull narrowest of genus, postfrontal short, transverse apophyses without teeth

Bibliography: BROOM 1910a, pp. 208-209, fig.7
BROOM 1932, p. 126, fig.35c; 40e
BOONSTRA 1935b, pp. 7-8
SIGOGNEAU 1970, pp. 105-106, pl.15c
SIGOGNEAU-RUSSELL 1989, pp. 73-74

Aloposaurus tenuis (BRINK & KITCHING) in SIGOGNEAU, 1970

(= *Aloposauroides tenuis* BRINK & KITCHING, 1953)

Holotype: BPI 256

Referred material: BPI 257

Specific diagnosis: snout broadest of genus, transverse apophyses with teeth, basisphenoidal tubera slender, ridge on lamina reflecta anteriorly situated.

Bibliography: BRINK & KITCHING 1953, pp19-20, fig. 22
SIGOGNEAU 1970, pp. 106-109, fig. 61, 14a-b
SIGOGNEAU-RUSSELL 1989, p. 74, fig. 183

cf. *Aloposaurus tenuis:* MMK 2046

(=*Cynarioides tenuis* BROOM, 1925, = cf. *Aloposaurus tenuis* SIGOGNEAU, 1970)

Bibliography: BROOM 1925a, pp. 324-325
BROOM 1930a, p. 356, pl. XXIX 22
BROOM 1932, p. 130, fig.43c
SIGOGNEAU 1970, pp. 109-111, fig. 62, pl.13c
SIGOGNEAU-RUSSELL 1989, p. 75

Aloposaurus watermeyeri (BROOM, 1940) nov comb.

(= *Scylaococephalus watermeyeri* BROOM, 1940, = *Aelurosaurus*? *watermeyeri* (BROOM, 1940) in SIGOGNEAU, 1970)

Holotype: RC 21

Specific diagnosis: large postfrontal, preparietal more rhombic than in the other species, dentary short.

Bibliography: BROOM 1940a, pp. 79-80, fig. 8-9
SIGOGNEAU 1970, pp. 70-72, fig. 39, pl.11a-b
SIGOGNEAU-RUSSELL 1989, p. 72

***Aloposaurus* sp.**
(= *Cyniscops cookei* BROOM, 1948, =*Arctognathu*s ? *cookei* (BROOM, 1948) in SIGOGNEAU, 1970)
BPI 648

Bibliography: BROOM 1948a, p. 597, fig. 15 B
SIGOGNEAU 1970, pp. 95-96, fig. 55 a-b,
SIGOGNEAU-RUSSELL 1989, p. 77

2.2.3.5 *Cyonosaurus* OLSON, 1937

The genus *Cyonosaurus* OLSON, 1937 contains the three species *C. longiceps* (with cf. *longiceps*), *C. rubidgei* (with cf. *rubidgei*) and *C. kitchingi*, as well as the taxon *Cyonosaurus* sp.

C. longiceps

OLSON (1937) presented a detailed description and drawings of a specimen which he named *Cyonosaurus longiceps* gen. et sp. nov. (WMUC 1515). It is a fairly well preserved skull which measures 155 mm in length. OLSON mentioned the broad frontals which contributed widely to the supraorbital rim, the diamond shaped, relatively large preparietal, the small and rectangular lacrymal, the low supraoccipital, the teeth on the transverse apophyses of the pterygoids and on the palatal tuberosities and the long and narrow palatines. Furthermore, he gave the number of incisors in the upper jaw as four and of postcanines as seven.

BROOM & ROBINSON (1948) referred to the specimen in the course of a comparison with *Nanogorgon gracilis* (= *Cyonosaurus* sp. in SIGOGNEAU-RUSSELL 1989) and mentioned that it was closely allied to BROOM'S *Cyniscops,* 1937 (=*Cyonosaurus longiceps*) but, because of the four incisors, should remain in a different genus.

SIGOGNEAU (1970) believed that the snout was less high and more rounded than indicated in OLSON'S figures. Apart from that, she pointed out that the specimen was very slender with large orbits and narrow interorbital and intertemporal widths. She mentioned further the short and large postfrontal, the short distance from the preparietal to the parietal foramen, the posterodorsally narrow postorbital, the elongated lacrimal (contra OLSON), the inclined and depressed occiput with the large interparietal, the long choanae, the broad but shallow palatal groove, the long dentary with its short coronoid process and the short lamina reflecta on the angular. Also, contra Olson, she gave the number of incisors as five. At the end she suggested that this specimen was immature because of the same reasons as discussed above.

Referred material

Sigogneau allocated four other specimens to the taxon *Cyonosaurus longiceps*, three of them belonging, until then, to the genus *Cyniscops* (RC 75, BPI 254, BPI 253). The fourth (BPI 294) is longitudinally sectioned now and was unpublished until Sigogneau (1970).

RC 75, which is a rather poorly preserved but complete specimen, was first described by Broom (1941) and measures 180 mm in length. It was allocated to the genus *Cyniscops* as the new species *longiceps*. Broom described the specimen as having 'a long and narrow preparietal, long and narrow frontals which form an appreciable part of the orbital margin, a long and narrow lacrimal, seven molars and a very long and slender dentary.' He states that it differed from the type species *Cyniscops rubidgei* Broom 1937 (=*Cyonosaurus rubidgei*) by its differently shaped parietals and much wider nasals.

BPI 254, BPI 253 and BPI 294 were first mentioned by Brink & Kitching (1953). According to them, the three specimens agreed 'perfectly with the type of *Cyniscops longiceps'* and only differed slightly in size. Sigogneau (1970) declared that Broom & George (1948) had already mentioned the close relationship of *Cyniscops* and *Cyonosaurus,* and the only reason for keeping two different genera was the presumed number of four incisors of *Cyonosaurus*. Since this assumption was disproved by her and can also be rejected by myself after personal observation, the two taxa can be reunited into one genus.

The specimens, which constitute the taxon *Cyonosaurus longiceps,* show indeed many characters which can be attributed to an immature state. However, the size of the specimens is not that small; the snout is extremely long, the lacrimal elongated, the postfrontal rather large, the parabasisphenoid fossa small, the supraoccipital low and the incisors are stronger. On the other hand, the arches are slender, the orbit is large, the ectopterygoid large, the choanae elongated, the postcanine teeth small and numerous and the lower jaw slender. But these features can also indicate primitive characters, which are shared with young individuals during their growing process.

C. rubidgei

Broom (1937) described a somewhat weathered and incomplete skull (RC 74) that measures 180 mm in length. It became the type specimen of the genus '*Cyniscops'*, *Cynicops rubidgei*. Broom stated that it was 'in its general appearance not unlike such typical gorgonopsians like *Scylacognahus* or *Aelurosaurus*, but it differed from these and from almost all other known genera in having seven molars. Furthermore he mentioned the small parietal foramen, the narrow parietals and the long frontals.

Sigogneau (1970) added the rather long and triangular snout, the oval orbits and elongated temporal fossa, the narrow interorbital space and the very slender skull arches. She also sees these characters in *C. longiceps,* but distinguishes both species because of the slightly shorter snout, the slightly wider interorbital and intertemporal width and the slightly thicker skull arches of *C. rubidgei*. She also mentioned the large contribution of the frontal to the supraorbital rim, the triangular preparietal and the rectangular lacrimal.

Cyonosaurus cf. *rubidgei*

Sigogneau added three other specimens to this taxon (BPI 251, BPI 387, TMP 2040), though, as *Cyonosaurus* cf. *rubidgei*. The first was described by Brink & Kitching (1953) as '*Cyniscopoides' broomi* gen. et. sp. nov. because they thought it had only four incisors and six molars. This assumption was based on the supposed three incisors in the lower jaw since the anterior part of the snout was missing. They did not mention *Cyonosaurus* at all (which was then supposed to also have only four incisors in the upper jaw) but recognised the close resemblance with *Cyniscops longiceps*. They would have neglected the difference in the amount of the teeth (five incisors and seven molars in *C. longiceps*) if not for the lower dentary, the larger orbits, the broader skull and the wider interorbital and intertemporal space of their specimen. Sigogneau (1970) mentioned the large and broad postfrontals and the long squamosal on the zygomatic arch. Also, she stated that there were four incisors in the lower jaw and hence there must have been five in the upper jaw. At the end she admitted that this specimen was intermediate between *C. longiceps* and *C. rubidgei*.

The other two specimens of *Cyonosaurus* cf. *rubidgei* were unpublished until Sigogneau 1970. BPI 387 is an eroded and deformed skull with mandible that measures 162 mm in length. Sigogneau states that the snout is typical of this species, but the narrowness of the interorbital and intertemporal space and the extreme slenderness of the skull arches would rather evoke *C. longiceps*. Nevertheless she allocated this specimen to C. cf. *rubidgei* because of the size, the snout, the form of the postfrontal and the position of the transverse apophyses.

But again she admitted that this specimen, too, was intermediate between *C. longiceps* and *C. rubidgei*.

The species *rubidgei* is most probably based on an immature individual. Although RC 74 shows the generic characters such as a narrow snout, narrow posterior part of skull, slender skull arches, it is doubtful whether such a specimen really can be indicative for a separate species or whether it rather grows into *C. longiceps* when it reaches the adult stage. However, two of the specimens which are attributed to the taxon as cf. *rubidgei* (BPI 251 and BPI 387) are more advanced ontogenetically than RC 74. Therefore the species will be retained here and the two specimens BPI 251 and BPI 387 will be entirely allocated to the species *C. rubidgei*.

The allocation of TMP 2040 as second to cf. *rubidgei* referred specimen is fairly uncertain, although it is labelled as *C. rubidgei*. Sigogneau leaves it in this species because of the shorter and larger snout than in *C. longiceps*, but also recognises the narrow interorbital space and the small orbits which are more like the type-species. After personal observation the question arises whether this specimen is a *Cyonosaurus* at all because of its comparatively large size (220 mm in length). But it is too poorly preserved and shows most of the characters insufficiently to solve this question satisfactorily and therefore becomes Gorgonopsia gen. et sp. indet. in this account.

C. kitchingi

The holotype (MMK 5028) is a poorly preserved and dorsoventrally flattened skull with a mandible that measures 89 mm in length. It was first described by Broom (1948) as a new species of *Cyniscops*. Broom mentioned the small preparietal, which reached the large parietal foramen, the small postfrontal, the narrow temporal region, the narrow snout, the six postcanine teeth and the broad intertemporal. According to him, it differed from *Cyniscops rubidgei* by the much larger parietal foramen, the smaller postfrontal and in having seven molars, and from *Cyniscops longiceps* by the much smaller size, the smaller postfrontals and the narrower snout. However, he stated that this specimen might be immature and might also have seven postcanine teeth when fully grown.

Sigogneau added to this relatively detailed description the large size of the orbits, the slender arches, the elongate temporal opening, the largely open median suture of the parietals, the elongated lacrimal, the ventrally reaching postorbital on the postorbital arch, the inclined occiput, the high supraoccipital, the presence of teeth on the transverse apophyses, the large ectopterygoid, the long choanae, the long basioccipital, the deep parasphenoid fossa, the eruption of the incisors, the large foramina and large supraorbital portion of the frontal. At the end she concludes that this specimen was without doubt a young individual. Although I have not observed it personally, I am of the same opinion because of the many features that this specimen shares with the list above.

Referred material

Brink & Kitching (1953) described another small specimen (RC 51) which was already given the name '*Alopecorhynchus' rubidgei* by Broom, who, however, never published an account. They mentioned that they did not know on which characters Broom established this new genus but they accepted his decision. According to them the skull was long and slender, the arches were slender, the parietal foramen large and anteriorly situated, the preparietal small, reaching the foramen parietale, the number of incisors and postcanine teeth was four in each case. Concerning the supposed four incisors, I can state from personal observation that there are undoubtely five but the fifth is very small on both sides and was mistakenly seen as a replacement tooth by the authors. The number of postcanine teeth is hardly determinable, because of the preservation; Sigogneau sees five on the left side, but there is still space left between them.

Sigogneau-Russell (1989) allocated this specimen to the species *Cyonosaurus kitchingi* and suggested that RC 51 might be a grown up form of *C. kitchingi*. Evidence for this was the longer snout, the smaller orbits the narrower interorbital and intertemporal space and the higher dentary. The jugal was elongated, the supraoccipital relatively high (which I however cannot confirm from personal observation), the basisphenoid fossa was more shallow, there were no teeth on the transverse apophyses, the ectopterygoid was narrow (but I can state that it is still elongated) and the dentary was slender.

In this case the same applies as for the species *C. rubidgei*: The holotype of the species *C. kitchingi* is without doubt immature, and therefore the grown up form can only be estimated. However RC 51 indicates the species rather well with the still markedly narrow snout, the sloping temporal openings and the particularly long and slender basisphenoid tubera. The three specimens MMK 5028, RC 51, RC 74 ('*Cerdorhinus*? *rubidgei*') are therefore united in the species *C. kitchingi*.

Sigogneau-Russell (1989) allocated another specimen (SAM 8790) to *C. kitchingi*, but it is too poorly preserved and is regarded here as Gorgonopsia gen.et sp. indet.

Cyonosaurus sp.

BROOM & ROBINSON (1948) described a very small specimen which they already suggested to be a young indiviual (BPI 3). They stated that it was closely related to *Cyniscops* but that 'the very small size of the canine and a number of other characters justify us in placing it in a new genus' (i. e. '*Nanogorgon' gracilis*). They also mentioned the rather large parietal foramen, the large preparietal, the short postfrontals, the long frontals, the short lacrimal and septomaxilla and the small teeth with six postcanines. SIGOGNEAU (1970) adds the large orbits, the square shaped temporal openings, the slender arches, the v-shaped nasofrontal suture, the large supraorbital frontal, the ventrally reaching postorbital on the postorbital bar, the anteriorly reaching squamosal on the zygomatic arch, the high supraoccipital and wide interparietal, the large foramen magnum, the v-shaped tuberosities on the palatine, the large ectopterygoid and the teeth on the transverse apophyses and the less ossified braincase. She allocated the specimen to the genus *Aelurosaurus* because of its short snout and the teeth on the transverse apophyses. But she also admits that the attribution remains doubtful, especially since it is a young specimen. SIGOGNEAU-RUSSELL (1989) finally allocated the specimen to the genus *Cyonosaurus* as *C*. sp. She explains her opinion with the observation that 'growth produces a lenghtening of the snout, a diminution in size of the orbits and the interorbital roof and an increase in height of the interparietal.' After growing, the specimen would perfectly evoke *Cyonosaurus*. Considering this suggestion and after personal observation, I agree with the opinion that the specimen most likely belongs to the genus *Cyonosaurus*.

Discussion of genus Cyonosaurus

The genus *Cyonosaurus* will be retained and only the generic diagnosis will be modified and updated in some points. The taxon contains several specimens which are certainly young individuals. However, most of the material also shows characters that are attributed to adult forms such as the long snout, the narrow cranial skull roof, a small orbit, a relatively long or large postfrontal and a comparatively wide dorsal portion of the postorbital. Other characters such as the numerous teeth on the palate, the posteriorly situated transverse apophyses or the slender skull arches are shared with young individuals but indicate only the rather basal systematic position of this taxon. Therefore the genus *Cyonosaurus* is clearly defined by the following characters:

skull narrow and slender, snout considerably long, posterior part of skull rather narrow; dorsal profile of skull straight with anterior part of snout slightly rounded, external nares dorsally situated, snout sightly higher than wide with a rounded contour, orbits middle sized and oval, temporal opening elongated and dorsal margin at the same level as the dorsal margin of the orbit, intertemporal skull roof slightly wider than interorbital one, both rather narrow; septomaxilla narrow and small, ventral margin of maxilla without step, nasalia broad, nasofrontal suture V-shaped and anteriorly situated, prefrontal broad and without elevation in front of the orbit, lacrimal elongated and without preorbital depression, supraorbital portion of the frontal considerably large, preparietal rhombic, foramen parietale situated well in front of the occipital crest, postorbital narrow but elongated with a straight posterior margin, postorbital reaches extremely far ventrally on the postorbital bar, squamosal reaches with narrow process almost up to the midlevel of the postorbital bar; all three skull arches remarkably slender, posterior margin of postorbital bar straight, suborbital bar widens slightly in anterior direction, zygomatic arch widens somewhat in posterior direction; vomer relatively slender throughout its length, choanae elongated, palatines of normal length and width, palatal fossa broad and shallow, oval in shape and open anteriorly, palatal tuberosities well developed, separated from each other by a small groove, both tuberosities have numerous teeth, ectopterygoid large, transverse apophyses posteriorly situated and without teeth, interpterygoid vacuity well developed and oval, parabasisphenoid fossa elongated, basisphenoid tubera slender and small, basioccipital long; occiput only slightly concave, sloping, large interparietal slightly wider than high, supraoccipital relatively high, parietal contributes slightly to the occipital face, paroccipital process short; incisors and caninus slender, postcanine teeth small and numerous (four to seven); mandible slender, symphysis sloping, dentary low, ridge on lamina reflecta weak. See figure 31 for illustration.

Systematic palaeontology

Genus: ***Cyonosaurus*** OLSON, 1937
Type species: *Cyonosaurus longiceps* OLSON, 1937

Revised generic diagnosis: skull narrow and slender, posterior part of skull hardly enlarged, snout remarkably long, temporal opening elongated, narrow interorbital and intertemporal widths, nasalia broad and not constricted in the middle, lacrimal elongated, postorbital reaches remarkable far ventrally on the postorbital bar, vomer comparatively slender throughout its entire length, palatal fossa broad, interparietal large and slightly wider than high, dentary low, ridge on lamina reflecta weak.

Cyonosaurus longiceps OLSON, 1937
(= *Cyniscops longiceps* BROOM, 1941)
Holotype: WMUC 1515 (immature)
Referred material: RC 75, BPI 254, BPI 254, BPI 294

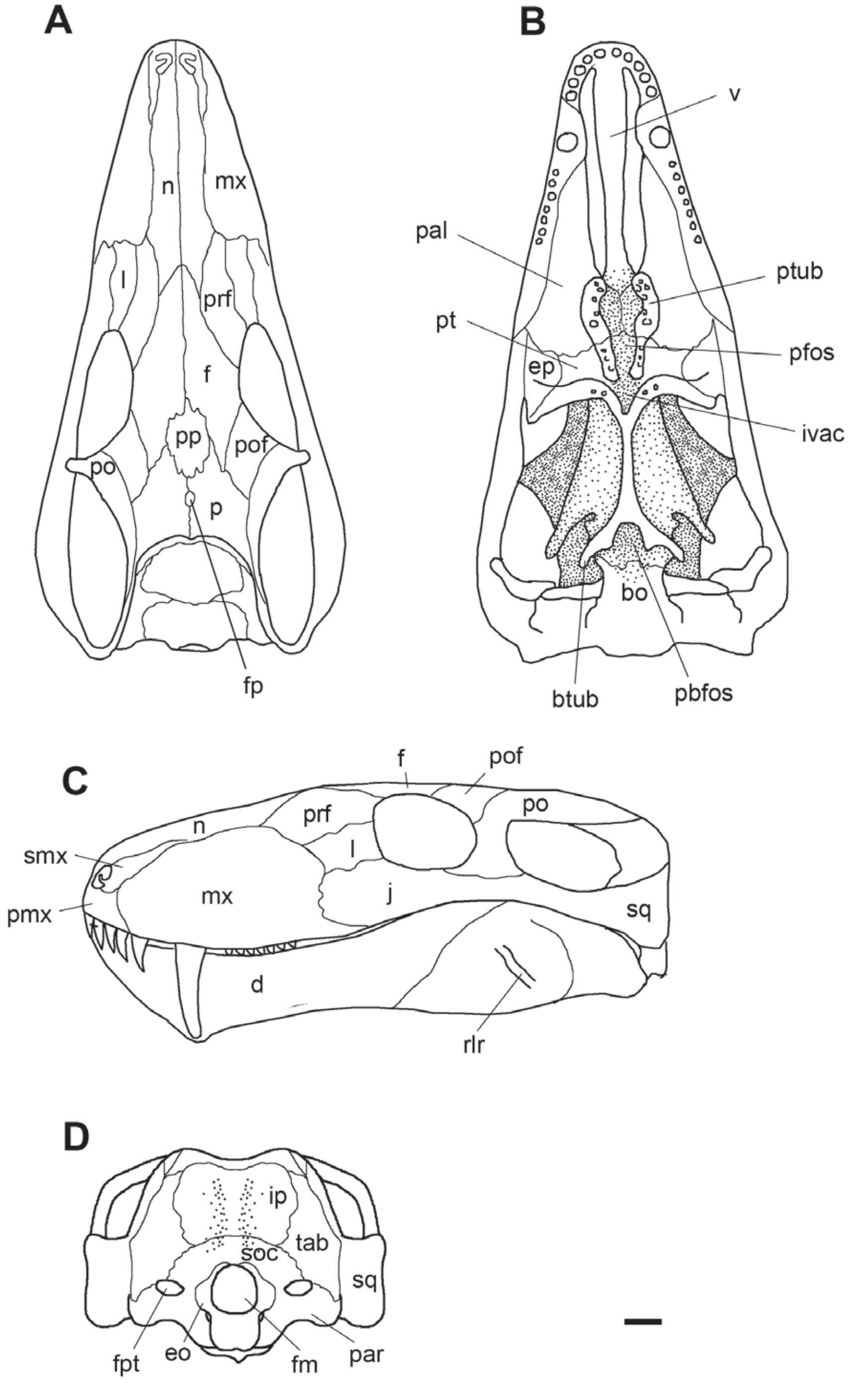


Figure 31. Illustration of the characters in the genus *Cyonosaurus* OLSON, 1937 based on the holotype of the type species, *Cyonosaurus longiceps* (WMUC 1515). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

Specific diagnosis: snout long, as high as wide, interparietal much larger than supraoccipital, palatal fossa wide, septomaxilla largest of genus.

Bibliography: Olson 1937, pp. 511-524, fig. 1-6
Broom 1941, pp. 197-198, fig.1B, 2B
Olson 1944, pp. 1-131, fig. 3B, 6B, 10A, 12B, 13F-H,15D, 18C, 19C, 25B
Broom & Robinson 1948, p.400
Brink & Kitching 1953, pp. 17-18
Sigogneau 1970, pp. 218-231, fig.123-132, pl. LII – LVb,c
Sigogneau-Russell 1989, p 83, fig. 202-203

Cyonosaurus rubidgei Sigogneau, 1970

(= *Cyniscops rubidgei* Broom, 1937, = *Cyniscopoides broomi* Brink & Kitching, 1953, = *Cyniscops* cf. *rubidgei* Sigogneau, 1970)

Holotype: RC 74 (probably immature)

Referred material: BPI 251, BPI 387

Specific diagnosis: snout relatively shorter and more stout, skull arches thicker, supraoccipital high, lacrimal large.

Bibliography: Broom 1937, p. 143, fig. 4
Broom 1941, p. 198
Broom & Robinson 1948, p.400
Brink & Kitching 1953, pp. 16-17, fig. 19A-B
Sigogneau 1970, pp. 232-238, fig.134-137, pl. LV – LVIIIa-b
Sigogneau-Russell 1989, pp 83-84, fig. 204

Cyonosaurus kitchingi Sigogneau, 1970

(= *Galerhynchus rubidgei* Broom 1936, =*Cyniscops kitchinigi* Broom 1948, = *Alopecorhynchus rubidgei* Brink & Kitching 1953, = *Cerdorhinus*? *rubidgei* Sigogneau 1970, = *Cyonosaurus* cf. *kitchingi* Sigogneau 1970)

Holotype: MMK 5028 (immature)

Referred material: RC 51, RC 4

Specific diagnosis: snout extremely slender and pointed anteriorly, ventral margin of maxilla slightly convex, supraoccipital as high as interparietal, palatal fossa relatively narrow.

Bibliography: Broom 1937, p. 303-304, fig. 4
Broom 1948, pp. 595-596, fig.16
Broom & Robinson 1948, p.400
Brink & Kitching 1953, pp. 8-10, fig. 9
Sigogneau 1970, pp. 216-218, 238-244, fig. 122, 138-141, pl.58c,d - 59a,c
Sigogneau-Russell 1989, pp 82, 84 fig. 205

Cyonosaurus broomianus (VON HUENE, 1950) nov comb.

(= *Aelurosaurus*? *watermeyeri* in SIGOGNEAU, 1970, = *Aloposaurus* sp. in SIGOGNEAU-RUSSELL 1989)

Holotype: GPIT/RE/7123

Specific diagnosis: snout extremely narrow, temporal fossa less steeply oriented than in other forms, posterior process of maxilla reaches far posteriorly, palatine fossa far ventrally situated, occipu narrow.

Bibliography: VON HUENE 1950, pp. 96-99, fig. 40
SIGOGNEAU 1970, pp. 72-74, fig. 40-41, pl. 12b, c
SIGOGNEAU-RUSSELL 1989, p. 75, fig 185

Cyonosaurus tenuirostris (BOONSTRA, 1953) nov. comb. (discussion see chapter 2.2.6.)

(= *Tangagorgon tenuirostris* BOONSTRA, 1953, = *Lycaenops*? *tenuirostris* (BOONSTRA, 1953) in SIGOGNEAU, 1970)

Holotype: SAM 1174

specific diagnosis: interorbital space comparatively wide, pterygoid transverse apophyses without teeth, preparietal large

Bibliography: BOONSTRA 1953, pp. 8-9, fig. 2-3
SIGOGNEAU 1970, pp. 209-211, fig.118-119, pl. 50 a
SIGOGNEAU-RUSSELL 1989, pp. 95-96, fig. 232

***Cyonosaurus* sp.:** RC 3 (immature)

(= *Nanogorgon gracilis* BROOM & ROBINSON, 1948, = cf. *Aelurosaurus watermeyeri* SIGOGNEAU, 1970)

Bibliography: BROOM & ROBINSON 1948, pp. 398-400,fig. 3-4
SIGOGNEAU 1970, pp. 77-79, fig. 43-45, pl. XIIIa,b
SIGOGNEAU-RUSSELL 1989, p.84

2.2.3.6 *Aelurosaurus* Owen, 1881

The genus *Aelurosaurus* contains the five species *A. felinus* (with cf. *felinus*, *A. whaitsi, A. polyodon*, *A. wilmanae* and *A.*? *watermeyeri*. Additionally two specimens were allocated to the taxon as *Aelurosaurus* sp. and one as *Aelurosaurus*?.

A. felinus

Owen (1881) described a small specimen (BMNH R 339) that consisted only of the anterior part of the skull. He named it *Aelurosaurus felinus* and allocated it to the 'Mononarialia'. Owen (1881, p. 262) stated that: 'From the degree in which the sutures are obliterated, I conclude it to have come from a fullgrown and probably old individual, the state of the dentition supporting that inference.' From then the specimen was referred to by Lydekker (1890), Seeley (1895), Broom (1910) and Watson (1921). Broom (1932) listed some characters such as the fairly large nostril, the rather large septomaxillary foramen, the wide nasals, the large portion of the supraorbital frontal, the large oval and anteriorly situated preparietal, the large parietal foramen and the five postcanine teeth. Boonstra (1934) listed as primitive features the higher than wide snout, the laterally directed orbits, the slight preorbital depression, and, as advanced features, the rounded snout, the anteriorly situated transverse apophyses, the deep maxilla and the absence of a step in the alveolar border. Sigogneau (1970) added some points: the slender shape of the skull, the convex interorbital skull roof with two grooves at the orbit, the pointed nasofrontal suture, the short septomaxilla, the rectangular lacrimal with the two well visible foramina, the teeth on the transverse apophyses, the low dentary, the sloping and open symphysis and occurrence of tooth replacement. The latter character together with the largely open symphysis and the large supraorbital portion of the frontal led her to the assumption that this specimen was probably a young individual and not an old one as indicated by Owen. I concur with that view because the specimen shows many features which indicate immaturity: short snout, large orbits, slender postcanine teeth, tooth replacement, numerous small postcanine teeth, well developed foramina, large supraorbital portion of the frontal, anteriorly situated preparietal, slender skull arches, narrow vomer, well developed palatal tuberosities, teeth on transverse apophyses, large ectopterygoids, slender mandible, open symphysis.

Sigogneau-Russell (1989) allocated two other specimens to the taxon. The first is BMNH R 855 (='*Aelurosauroides' watsoni* Boonstra, 1934c). It consists of a small snout which is crushed and deformed. Lydekker (1890) and Broom (1910) both regarded the specimen as *Aelurosaurus felinus* but Boonstra (1934) erected a new genus and species because of differences in the palate. Watson (1921) pointed out that this specimen was an advanced form and already mentioned that it might differ from the holotype. He remarked on the deep and rounded cross-section of the snout, the surpression of a step in the maxilla and the slight overhang of the anterior border of the nasal. He further stated that the septomaxilla as well as the septomaxilla foramen were large, the palatal tuberosities were well developed and had teeth and the ectopterygoid was long. Boonstra listed as primitive features the laterally directed orbits, the slightly higher than wide snout, the slight preorbital depression, large portion of the supraorbital frontal, and, as advanced features the short and rounded snout, the anteriorly situated transverse apophyses, the slightly curved tooth row and the deep maxilla without a step in the alveolar border. This diagnosis, however, almost literally is a repetition of the list given by Boonstra for the species *felinus*. Sigogneau (1970) attributed the differences stated by Watson and Boonstra to the incomplete and deformed condition of the specimens and regards a generic and specific distinction as unjustified. The specimen R 855 is regarded here, however, as Gorgonopsia gen. et sp. indet. because of its incomplete state which allows no satisfactory diagnosis. The few characters which are discernable and listed by the authors above apply to almost every gorgonopsian and are not sufficient to make a sound allocation. Besides, the ontogenetic stage of this specimen is dubious and it is well conceivable that R 855 also is a young individual.

The second referred specimen is AMNH 5506, which consists of a small deformed and very poorly preserved snout. It was first described by Broom (1912) as *A. striatidens* because of its smaller size but was already allocated to the species *A. felinus* by Boonstra (1935). This specimen is regarded as Gorgonopsia gen. et sp. indet., too, because of the same reasons as given for BMNH R 855.

Sigogneau (1970) designated AMNH 5504 as *A.* cf. *felinus*. It was first described by Broom (1911) as the new species *A. tenuirostris* because of its slender snout and larger size. Again, Boonstra (1935) considered it to be *A. felinus*. This specimen is even more incomplete and weathered and thus becomes Gorgonopsia gen. et sp. indet., as well.

A. whaitsi

The holotype (AMNH 5528), a fragmentary and extremely poorly preserved snout with a part of the skull roof, was first described by Broom (1911). He distinguished it from *A. felinus* only by the less sloping symphysis and the more rounded cross-section of the incisors. Boonstra (1934) saw no real difference with the type species, nor did Sigogneau (1970). She however saw a closer affinity with *A. breviceps*, a species still valid at that time, but refrained from uniting both taxa because of the poor condition of AMNH 5528. 1989, however, she allocated the two better preserved specimens of the former species *A. breviceps* (AMNH 5514 and BMNH R 855a) to the species *A. whaitsi*, thus omitting the species *A. breviceps*. AMNH 5514 was first described by Broom (1910) as a referred specimen of the species *A. felinus*. He remarked on the comparatively large size, the short and high snout and the large orbits. In 1931, however, he established the new species *A. breviceps* because of the characters he had already listed 1910 which would in his opinion justify a separate species. Boonstra (1935) maintained his view that the specimen AMNH 5514 belonged to the species *A. felinus*. Sigogneau (1970) re-established the species *A. breviceps* but in 1989 removed it definitively in favour of the species *A. whaitsi* as mentioned above. AMNH 5514 is indeed very close to BMNH R 339 (*A. felinus*) with respect to the sutures; only the snout is somewhat shorter and more pointed; however, this is regarded here as intraspecific variation. Besides, this specimen is also definitely immature, which also applies for the next specimen, BMNH R 855a, first described by Lydekker (1890) as *Aelurosaurus* sp. Broom (1911) attributed it to the species *A. whaitsi*, however, with a questionmark. Boonstra (1934) regarded it as gen. indet. and Kermack (1956) finally allocated the specimen to the species *A. felinus*. Sigogneau (1970) listed the following characters: short and high snout, teeth on the transverse apophyses, palatal groove narrow and deep, and five postcanine teeth.

The species *A. whaitsi* is problematic. All three specimens are poorly preserved and/or rather incomplete. They only consist of snouts or even only parts thereof. The allocation to the presumable genus *Aelurosaurus* was rather obvious since it concerns only small, delicate and short snouted specimens. However, all show the characters of immature individuals and could also belong to different genera. The situation is further complicated by the fact that the holotype of the type species of *Aelurosaurus*, BMNH 339 is most likely a young individual itself. However, the historical record with the shifting of species names shows that the authors were never secure about the real relationships. Therefore, the species *A. whaitsi* is regarded as a nomen dubium in this account. The former holotype AMNH 5528 is regarded as Gorgonopsia gen. et sp. indet., whereas the two referred specimens AMNH 5514 and BMNH R 855a are allocated to the species *A. felinus*.

A. polyodon

The holotype TMP 244, which is a crushed snout, was first described by Broom (1935) as *Galerhinus polyodon* gen. et sp. nov. He already mentioned a close resemblance to *Aelurosaurus* and distinguished it only by the number of eight postcanine teeth. Sigogneau (1970) considers a generic separation not justified but retains the species. Again, this incomplete specimen is here regarded as Gorgonopsia gen. et sp. indet., the genus *Galerhinus* and the species *G. polyodon* becoming nomina dubia.

A. wilmanae

The species *Aelurosaurus wilmanae* is only represented by its holotype MMK 4667, which is a small skull that measures 110 mm in length and is somewhat incomplete and compressed. It was first described by Broom (1940) as *Aelurosauroides wilmanae* gen.et sp. nov. Broom mentioned the long frontals, which formed a considerable part of the orbital rim, the narrow and small postfrontal, the small postorbital, the well developed parietal foramen which was close to the large preparietal, the well developed parietals, the large interparietal, the large prefrontal, the small lacrimal, the short and broad nasal and the five small postcanine teeth. Sigogneau (1970) allocated the specimen to the genus *Aelurosaurus* and added the following characters: frontonasal suture anteriorly situated, short prefrontal anteriorly, parietal foramen anteriorly situated, occiput less inclined, first postcanine tooth close to the canine. In the following discussion she remarked that this form resembles *Aelurosaurus* in most ways, which, however, also could be a case of a parallel evolution, since the specimen was regarded by her as most probably a young individual. This opinion is shared by me because of the most obvious characters listed above. However, because of the incomplete state of all *A. felinus* specimens and the longer and broader snout of MMK 4667, the species *A. wilmanae* will be retained here.

Aelurosaurus ? *watermeyeri*

The specimen RC 21 is a slightly weathered skull with a mandible that lacks the anterior part of the snout and measures appr. 120 mm in length. It was first described by Broom in (1940) as '*Scylacocephalus' watermeyeri* gen. et sp. nov. He pointed out that the snout was relatively short, the orbit fairly large, the parietal foramen small, the preparietal moderately large, the postorbital long and slender, the postfrontal rather large, the lacrimal moderately large, the canine slender, there were six molars and the dentary was slender.

Sigogneau (1970) sees a close resemblance with the genera *Aloposaurus*, *Aelurosaurus* and *Cyonosaurus* and thus questioned the independence of these genera.

As already indicated by Sigogneau (1970) and Sigogneau-Russell (1989), the systematic of RC 21 is problematical. However, an allocation to the genus *Cyonosaurus* fails because of the comparatively larger cranial skull roof, the larger preparietal and postfrontal and longer lacrimal. With *Aelurosaurus* it shares the large orbit, the relatively short snout (however, the anterior part is missing) and the slightly elongate temporal opening. In contrast, the preparietal and postfrontal are larger, the naso-frontal suture is bow-shaped, the prefrontal is lower, the cranial skull roof is narrower and the occiput is more concave in RC 21, thus suggesting a closer relationship to the genus *Aloposaurus*. Therefore the specimen RC 21 will be allocated to the genus *Aloposaurus* as the species *watermeyeri* thus the taxon *Aelurosaurus*? *watermeyeri* becoming a junior synonym.

Aelurosaurus sp.

In the Rubidge collection exists another small specimen which was undescribed until Sigogneau (1970). RC 7 measures 130 mm in length, is rather well preserved but lacks the mandible. Sigogneau (1970) allocated the skull to *Aelurosaurus*? *watermeyeri* and remarked on the triangular shape, the high and pointed snout, the wide dorsal cranial skull roof, the short pterygoid, the large ectopterygoid, the replacement of the teeth and the seven small postcanine teeth. She pointed out that the specimen, though not published, had been identified as '*Cyniscops' rubidgei* by Broom who did not notice that it resembled RC 21, '*Scylacocephalus' watermeyeri* (= *Aelurosaurus*? *watermeyeri*) in many ways: the high snout and teeth on the transverse apophyses. Sigogneau-Russell (1989), however, called the specimen *Aelurosaurus* sp. and pointed out that a definite allocation to a species of *Aelurosaurus* was difficult because of the 'insufficient knowledge of the posterior region of the skull of *Aelurosaurus felinus* and *polyodon'*. She also mentioned the possibility of the specimen being a young individual of *Cyonosaurus* but sees this uncertainty as more evidence for a close relationship of the two genera *Aelurosaurus* and *Cyonosaurus*.

This specimen, however, resembles, in my opinion, the species *A. felinus* perfectly. Although it shows some characters of immaturity such as the large orbit, the numerous small teeth or the presence of teeth on the transverse apophyses, the shape of the sutures is modified in such a way that at least a sub-adult stage for *A. felinus* is well conceivable. This assumption would also be supported by the fact that the specimen shows 'derived' characters parallel to the ones indicating an immature state: larger prefrontal, straight naso-frontal suture, narrower ventral braincase area. An allocation to the problematical species *Aelurosaurus*? *watermeyeri* (now *Aloposaurus watermeyeri*) is rejected because of the larger postfrontal and the more concave occiput of the latter.

Aelurosaurus? (figs. 32 & 33)

One specimen which I will emphasise in this context is GPIT/RE/7124 (formerly IGP 7412). It was first described by VON HUENE (1937) in a detailed account which is, however, also rather general on the other hand. He allocated the specimen to the genus and species *Aloposaurus gracilis* on the presumption of the presence of two canines in both this taxon and his specimen. Besides, VON HUENE made no comparison with other taxa at all and thus his allocation is somewhat astonishing, particularly if one has the actually poorly preserved and therefore unfavourable holotype of *Aloposaurus gracilis* in mind. VON HUENE did not regard the second smaller caninus as a replacement tooth because it was, according to him, situated anterior to the functioning one and not medially to it.

SIGOGNEAU (1970) considered VON HUENE's allocation to be doubtful and because she could not assign this specimen to any genus at all, she finally listed it as Gorgonopsia incertae sedis. However, she gave a rather detailed account, mentioning among other things the small orbits, the triangular snout (which is, however, not markedly more pronounced than in other taxa but only appears so because of the deformation), the elongate palatine (which is however of normal length compared with such forms as, e.g., *Cyonosaurus*) and the short dentary. In the discussion afterwards she rejects VON HUENE's allocation and stated that the presumed second canine certainly was a replacement tooth and the interorbital and intertemporal spaces were wider than in *Aloposaurus gracilis*. Because she already had included forms with even narrower spaces into this taxon, she could not leave GPIT/RE/7124 in it. A relationship with *Cyonosaurus* fails, according to her, because of snout and skull roof proportions and a larger suborbital portion of the frontal of this taxon. Also with *Paragalerhinus*, *Aelurosaurus* and *Scylacognathus* there would be too much dissimilarity in the end. She refrains from erecting a new genus, though, because of the already close relationship of GPIT/RE/7124 and the taxa *Aelurosaurus*, *Aloposaurus* and *Cyonosaurus*. SIGOGNEAU-RUSSELL (1989), however, allocated the specimen to the genus *Aelurosaurus*, although not without doubt. She admitted that GPIT/RE/7124 was not a typical aelurosaurid because of its wider cranial skull roof, the pointed snout, the smaller orbit, the smaller suborbital portion of the frontal and the longer lacrimal. However, all these characters are of a typical ontogenetic nature and are therefore no hindrance from including GPIT/RE/7124 in the genus *Aelurosaurus*.

Description of GPIT/RE/7124

The short description of the specimen given in the next paragraph follows the principle that mostly peculiarities and characters are described which help to distinguish a taxon as precisely as possible. It will explain why I think an allocation to the genus *Aelurosaurus* is justified and which species of this genus is most appropriate.

GPIT/RE/7124 is, with a skull length of 140 mm, still one of the small-sized specimens. It is somewhat flattened dorso-ventrally and, in addition, compressed asymmetrically; however, most sutures are well visible. The skull shape is a rather unremarkable form since there are no conspicuous peculiarities that would distinguish it immediately. If seen in dorsal view the skull displays a well proportioned triangle with a smoothly rounded snout. The latter is slightly wider than high and its dorsal profile smoothly inclines up to the level of the orbits. Thus the external nares are ventrally situated and the premaxilla is low anteriorly. The oval orbits are medium sized and the temporal openings are slightly wider than high. Their dorsal margin is situated at the same level as the dorsal margin of the orbits. The interorbital and intertemporal spaces are rather wide, the latter being slightly wider than the first. The skull roof is only slightly ornamented but there is a shallow elongate depression medial to the orbit, and in front of the parietal foramen a knob-like elevation is situated. No ridges or tuberosities are present on the dorsal margin of the orbit.

Anteriorly, the extension of the septomaxilla is obscured by the damaged and deformed surface. The maxilla is of usual height but is sinuous on its ventral margin and displays a step in front of the canine. The nasals are remarkably narrow posteriorly, which is due to the wide prefrontal, and the straight naso-frontal suture is situated posteriorly. The prefrontal is high but short, as already mentioned, with a clear elevation in front of the orbit. On the lateral face of the skull the lacrimal is a rather small bone being somewhat longer than high. The foramina are no longer visible on both sides of the skull. There is, however, a moderate depression in front of the orbit. On the skull roof the supraorbital portion of the frontal is of medium size, whereas the rhombic preparietal is comparatively small. It reaches the foramen parietale with its posterior tip and is therefore situated on the above-mentioned elevation with its posterior half. The parietal foramen itself is not elevated and only surrounded by a faint ridge. It is situated somewhat in front of the occipital crest. The postfrontal is again of a rather common shape which means that it is neither remarkably large or broad nor particularly short or narrow. However, the extension at the orbital margin is rather large and thus the ventral margin of the postfrontal bends more or less abruptly in dorsal direction when leaving the orbit. The posterior margin of the bone is straight. As long as it is situated laterally to the postfrontal, the adjacent postorbital is rather broad; however, as soon as it borders the parietal the postorbital narrows rapidly. Laterally, the ventral extension of the postorbital on the postorbital bar is almost beyond recognition since the postorbital bar is obscured by the lower jaw on the left side, and on the right side the surface is damaged and covered with a number of matrix-filled tiny fissures. However, since this applies only for

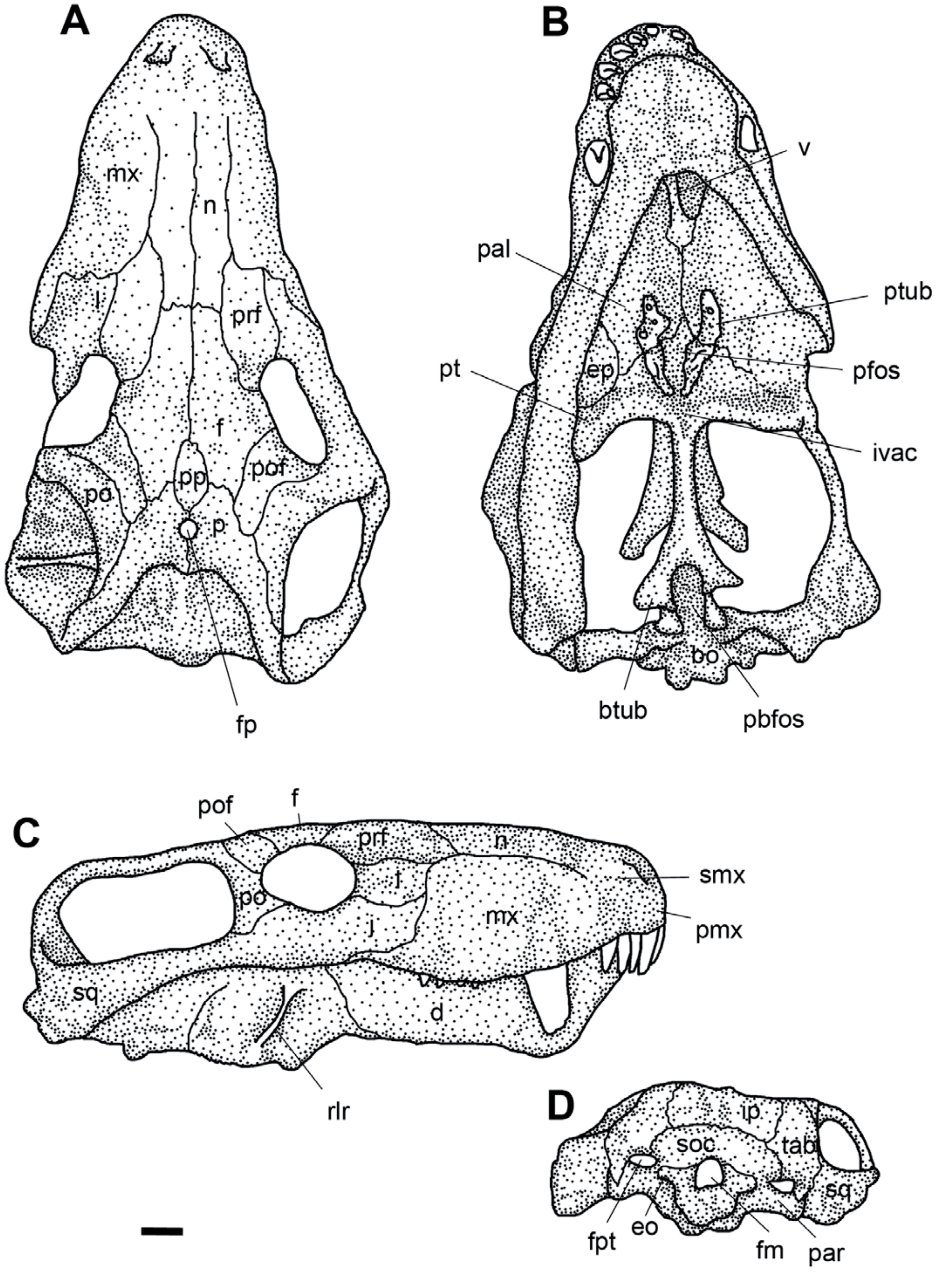


Figure 32. Drawings of GPIT/RE/7124 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

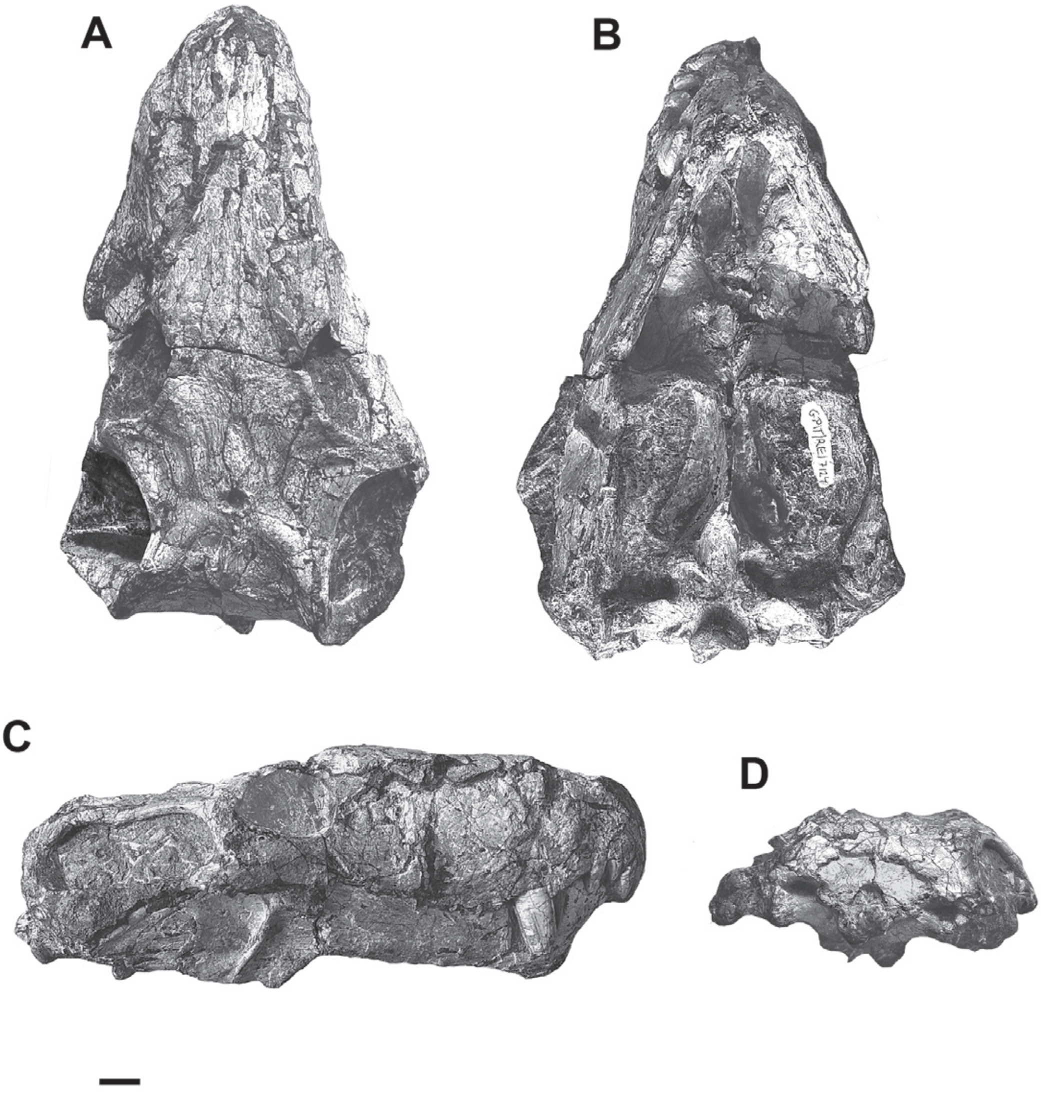


Figure 33. Photographs of GPIT/RE/7124 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

the posterior part of the ventral postorbital bar and further in ventral direction there is no suture visible, it can be presumed that the extension of the lateral postorbital was not all too far ventrally on the postorbital bar. No information can be given about the extension of the squamosal on the zygomatic arch, since both arches are more or less missing. The three skull arches are rather slender with the suborbital arch presumably being the thickest. The postorbital bar widens considerably in ventral direction; however, this might, at least in parts, be the result of the dorso-ventral compression. The posterior margin of the postorbital bar appears to be straight. Judging from the few preserved parts of the zygomatic arch it was considerably slender and not curved.

In the palate the posterior part of the vomer is extremely narrow. In fact, this part almost appears to be composed of only a thin sheet of bone. Anteriorly, the vomer, however, widens to a usual shape with a median and two lateral ridges well visible. No information can be given on the anterior-most part of the snout since this area is obscured by the lower jaw. The choanae are rather short, as well as the palatine. The broad and shallow palatal fossa is situated posteriorly and thus leaves a considerably broad and comparatively long fan-shaped area anteriorly that is situated on a slightly deeper level than the surrounding parts of the palatine. Such an area is present in all gorgonopsians; however, it is mostly smaller and narrower. The palatal ridges are of medium size but equipped with a few small teeth that are somewhat larger on the tuberosities of the palatine. These are more bulbous and parallel to each other, which implies that the palatal fossa is widely open anteriorly. The more elongate and narrower tuberosities on the pterygoid taper posteriorly. Both tuberosities are confluent and are only separated by their different form and the palatine-pterygoid suture. Laterally, the ectopterygoid is of the usual size, its ventral expansion on the transverse process is, however, minimal. The palatal surface slopes only slightly from the palatal fossa in lateral direction. Posterior to the palatal fossa a narrow but elongate and deep interpterygoid vacuity is developed. Lateral to it the edentulous and posteriorly situated transverse apophyses are rather short dorsoventrally but show, nevertheless, a fairly massive appearance. Further in posterior direction the sheet-like parabasisphenoid complex is of the usual height. The parabasisphenoid fossa is rather shallow, whereas the basisphenoidal tubera are thin anteriorly but considerably massive on their posterior end. Additionally, they diverge in a comparatively great angle. The basisphenoid is short and the condyle of the usual size and shape.

The occiput is remarkably straight concerning both the usual concavity and the dorso-ventral inclination. However, this feature might, at least in parts, be the result of deformation. This incidence also restricts the determination of the sutures in this part of the skull since the surface is damaged and compressed. Medially, the ridge is well developed but narrow, being less accentuated on its ventral half. As far as can be judged despite the deformed surface, the parietal does not contribute to the occiput. The size and extension of the interparietal is beyond recognition, since the surface is covered with several matrix-filled grooves in this part of the occiput. However, the supraoccipital is well discernable. It is low and its lateral extension is comparatively modest. The paroccipital process is short and stout, especially on its lateral extremity.

The dentition, again, is of the usual sort. The incisors are, however, comparatively large or at least they appear to be large since the canine is rather short but quite strong. The postcanine teeth are hardly visible because they are obscured by the lower jaw, on the one hand, but are also fairly small. At least four teeth are visible on the right side.

The mandible is slender; however, the symphysis is rather strong and only slightly sloping. The dentary is low but the ridge on the lamina reflecta is well accentuated and long. Further details concerning the lower jaw are not given because of the deformed condition of the specimen.

As stated above, GPIT/RE/7124 can well be considered to be an adult form of the genus *Aelurosaurus*. Within this taxon it is best placed in the species *wilmanae* since both share a number of characters: relatively broad snout, prefrontal large but short anteriorly, broad intertemporal space, transverse apophyses without teeth, occiput less inclined than in the other species.

Conclusion on the genus Aelurosaurus

Although certainly most of the specimens are immature or sub-adult, the genus *Aelurosaurus* is retained. It will only contain two species. After these slight modifications the taxon is better established and the species show a number of characters now that define this genus clearly:

small size, outline of skull as a short triangle, posterior part of skull not much widened, zygomatic arches hardly flaring laterally; dorsal profile of skull almost straight, snout short and somewhat pointed, about as high as wide, external nares dorsally situated, orbits of medium to large size, well visible in dorsal view, temporal openings slightly wider than high, interorbital and intertemporal spaces of moderate width, the latter only being slightly wider; septomaxilla short, ventral margin of maxilla with slight step, nasalia narrow, nasofrontal suture V-shaped and anteriorly situated in the young form but rather straight in the adult, prefrontal broad and short with slight elevation in front of the orbit, lacrimal slightly elongated and without preorbital depression, supraorbital portion of frontal considerably large, preparietal rhombic and moderately sized, situated close to the foramen parietale, postfrontal small and rather narrow with a straight posterior margin, postorbital reaches moderately far ventral on the postorbital bar, squamosal reaches up to the mid-level of the temporal opening; all three skull arches rather slender, the suborbital bar being the thickest, postorbital bar widens somewhat ventrally, posterior margin straight; vomer rather slender posteriorly but widens moderately in anterior direction, choanae short and broad, palatal fossa broad and shallow, considerably broad anteriorly, palatal tuberosities well developed, separated from each other by a groove, both tuberosities have numerous teeth, transverse apophyses posteriorly situated and without teeth in the adult form, interpterygoid vacuity well developed and oval, parabasisphenoid fossa oval and broad, basisphenoid tubera small and short, basioccipital short; occiput hardly concave, hardly sloping, interparietal of normal size, only slightly wider than high, supraoccipital low, parietal contributes slightly to the occipital face, paroccipital process short an stout; incisors relatively large, caninus short and massive, postcanine teeth small (five to six); mandible slender, symphysis only somewhat sloping, dentary low and short, ridge on lamina reflecta well developed. See figure 34 for character illustration.

Systematic Paleontology

Genus: ***Aelurosaurus*** Owen, 1881

Type species: *Aelurosaurus felinus* Owen, 1881

Revised generic diagnosis: small size, snout short and about as high as wide, dorsal profile of skull straight, temporal opening only slightly wider than high, interorbital and intertemporal spaces of moderate width, nasalia narrow, lacrimal only slightly longer than high, supraorbital portion of frontal large, preparietal situated closely to parietal foramen, choanae short and broad, palatal fossa broad anteriorly, occiput hardly concave, incisors relatively large, symphysis only somewhat sloping, ridge on lamina reflecta well developed.

Aelurosaurus felinus Owen, 1881

(=*Aelurosaurus breviceps* Broom, 1931 and Sigogneau, 1970; =*Aelurosaurus whaitsi* Sigogneau-Russell, 1989; = *Aelurosaurus* sp. Lydekker, 1890; = *Aelurosaurus whaitsi* Broom, 1911; = *Aelurosaurus*? *watermeyeri* Sigogneau, 1970; = *Aelurosaurus* sp. Sigogneau-Russell, 1989)

Holotype: BMNH R 339

Referred material: AMNH 5514, BMNH R 855a, RC 7

Specific diagnosis: snout as high as wide, supraorbital portion of frontal large, nasalia narrow, palatal tuberosities and transverse apophyses with numerous teeth.

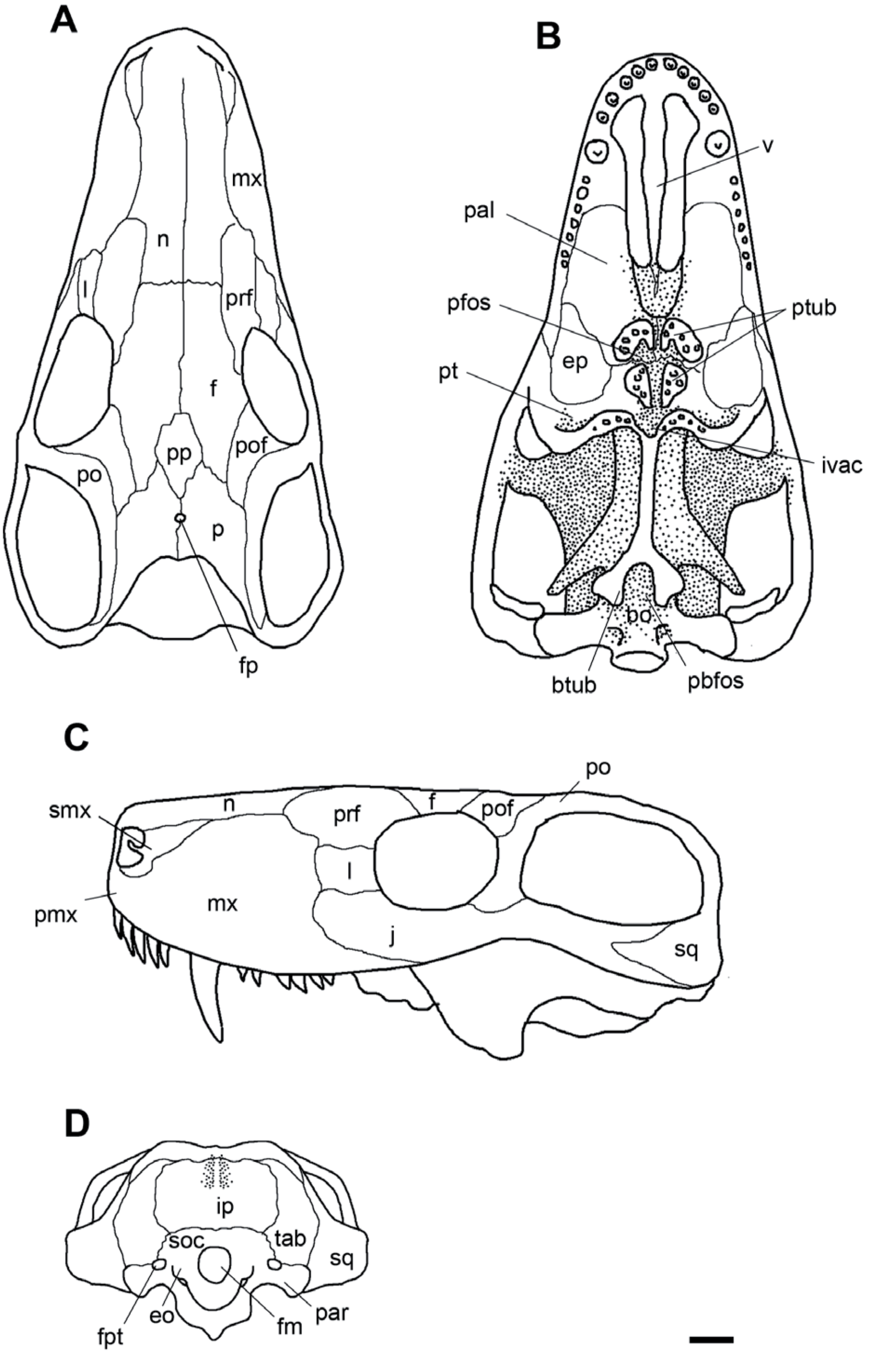


Figure 34. Illustration of the characters in the genus *Aelurosaurus* OWEN, 1881 based on the holotype of the type species, *Aelurosaurus breviceps* (BMNH R 339). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

Bibliography: OWEN 1881, pp. 261-166, pl. IX 1-3
LYDEKKER1890, pp. 74-75; 77, fig. 16
SEELEY 1895, pp. 991-993, fig. 2, pl. 88 (2)
BROOM 1910, p. 473
BROOM 1911, p. 1077
WATSON 1921, p. 86
BROOM 1931, p. 165
BROOM 1932, pp. 120-122, fig. 35b, 40a,b
BOONSTRA 1934, pp. 189-191, fig. 8a
BOONSTRA 1935, p. 6
SIGOGNEAU 1970, pp. 59-61; 64-66; 75-76, fig. 32-33; 34; 42-42b, pl. 8a,b; 9e, f; 11c; 12a
SIGOGNEAU-RUSSELL 1989, pp. 70-71, fig. 177; 180-181

Aelurosaurus wilmanae (BROOM, 1940) in SIGOGNEAU, 1970

(=*Aelurosauroides wilmanae* BROOM, 1940; = *Aloposaurus gracilis* VON HUENE, 1937, = Gorgonopsidae inc. sedis in SIGOGNEAU, 1970; = *Aelurosaurus*? in SIGOGNEAU-RUSSELL, 1989)

Holotype: MMK 4667

Referred Material: GPIT/RE/7124

Specific diagnosis: snout slightly wider than high, prefrontal high but short anteriorly, postfrontal largest of genus, occiput less inclined, no teeth on transverse apophyses.

Bibliography: BROOM 1940b, pp. 171-173
BROOM 1941, pp. 212-213
VON HUENE 1937, pp. 302-307, pl. 22
SIGOGNEAU 1970, pp. 67-70; 72-74, fig. 36-38; 40-41, pl. 10a,b; 24a
SIGOGNEAU-RUSSELL 1989, pp. 72, fig. 179; 182

2.2.3.7 *Scylacognathus* BROOM, 1913 and *Arctops* WATSON, 1914

2.2.3.7.1 Introduction

The last genera considered in this chapter are *Scylacognathus* which contains the three species *Scy. parvus*, *Scy. robustus* and *Scy. grimbeeki* and *Arctops* WATSON, 1914, which contains the five species *A. willistoni*, *A.watsoni*, *A.*? *kitchingi*, *A.*? *minor* and *A.*? *ferox*. Although *Arctops* is mostly represented by medium sized forms, whereas *Scylacognathus* is clearly composed of small specimens, both taxa are discussed here together since they are considered to be congeneric and thus *Scylacognathus* is regarded as the immature state of *Arctops*.

2.2.3.7.2 History of *Scylacognathus* BROOM, 1913

S. parvus

The type species of *Scylacognathus* is *S. parvus* BROOM, 1913. The holotype AMG 3751 is a rather incomplete and deformed skull which measures appr. 120 mm in length and was first described by BROOM (1913) in a short account. He mentioned the five postcanine teeth, the relatively short snout and the orbits being near the middle of the skull. In 1932 he added that the supraorbital portion of the frontal was very small.

SIGOGNEAU (1970) pointed out that the snout was indeed very short, but the posterior enlargement and the ventral sinuosity was not as marked as indicated in BROOM'S figures but must be due to deformation. However, she noted that the interorbital and intertemporal spaces were wide and the skull arches slender. The nasals were wide and less constricted in the middle, the nasofrontal suture was anteriorly situated, the supraorbital portion of the frontal was large, the preparietal was large and anteriorly situated, the parietal foramen was situated right in the middle between the preparietal and the occipital crest, the lacrimal was particularly short, the maxilla extended far posteriorly, the septomaxilla was short, the interparietal and supraoccipital had the same height, the parietal did not contribute to the occipital face, the paroccipital process was short and low and the position of the transverse apophyses was very far posterior. Since the palate is badly preserved, no information concerning the presence of teeth on the transverse apophyses can be given, but according to SIGOGNEAU, there were certainly some on the palatal tuberosities. In the following discussion SIGOGNEAU supposed that this specimen was a young individual because of its short snout, the large orbits and the postcanine teeth which directly follow the canine. She also compared the specimen with *Scylacops* because of the snout that narrowed anteriorly, but thought that the ventral sinuosity in the latter was not that accentuated, in her opinion. According to SIGOGNEAU, AMG 3751 shared the short snout, the short lacrimal and the anterior position of the preparietal with *Galesuchus* and *Aelurosaurus* but these were however probable juvenile characters.

This specimen is certainly immature. In addition to the features already mentioned, the small size, the slender skull arches, the pointed naso-frontal suture, the small postfrontal and narrow dorsal postorbital, the posteriorly situated transverse apophyses, and replacement of teeth, can also be added.

Referred material

One referred specimen is BPI 399, which was undescribed until Sigogneau (1970). It concerns a deformed and incomplete skull which measures appr. 144 mm in length. Sigogneau stated that the snout was short and higher than in the preceding specimen, the ventral border was sinuous, the nasofrontal suture more posteriorly situated, the lacrimal short, the occiput inclined, the supraoccipital low, the transverse apophyses were posteriorly situated and had teeth, the dentary was low and the five postcanine teeth followed right after the canine. All these characters show that the specimen certainly is another young individual.

Another referred specimen is TMP 256, which was named *Scylacognathus major* by Broom (1935). It concerns a somewhat incomplete and weathered skull which measures 160 mm in length. Broom stated that the frontal formed a considerable part of the supraorbital rim, the prefrontal was large, the preparietal rhombic and large, the postfrontal unusually large, the parietals short and wide, the parietal foramen well developed and the interparietal very large. Sigogneau (1970) allocated the specimen to the species *parvus* because she saw the same proportions as in the holotype except for the slightly longer snout and the slightly broader skull arches. The ventral sinuosity of the maxillo-jugal area was the same, the large frontal as well; so were the anteriorly situated nasofrontal suture, the short and large postfrontal and the large preparietal which does not reach the parietal foramen. The latter is, however, situated closer to the occipital crest. The occiput was said to be inclined, the interparietal higher than the supraoccipital, the paroccipital process was short, the transverse apophyses had teeth and the five postcanine teeth also followed the canine closely.

Although TMP 256 is somewhat larger than the holotype I presume that it still represents a young individual or at least a sub-adult because of the large eyes, the slender skull arches, quadratic temporal openings and the numerous teeth on the palatal tuberosities and transverse apophyses. On the other hand it also displays some ‘advanced’ characters such as the large postfrontal and the longer snout, which is additionally somewhat wider and more rounded anteriorly than in *S. parvus*. The latter character, however, links TMP 256 rather well with the next species and thus the specimen will be allocated to the species *S. robustus*.

S. robustus

The holotype of this species is BMNH 5743, which was first described by Broom (1925) as *Cynariops robustus* gen. et sp. nov. The skull is heavily weathered and deformed and measures 125 mm in length. Broom mentioned the sub-rhombic preparietal but otherwise only referred to the dentition where he saw four postcanine teeth. In 1930 he pointed out that the frontals reached the orbital margin and the postfrontal was long and narrow. Boonstra (1934) gave a more detailed account after further preparation. However, it mostly concerns the palate and braincase region: The palate had well developed palatal ridges bearing teeth, the foramen magnum was considerably large and the basioccipital condyle small. As primitive features Boonstra listed the sloping occiput, the slender epipterygoid and the preorbital depression, whereas he mentioned as advanced features the snout being as broad as high and rounded, the absence of a step in the maxillary border, the slightly anteriorly directed orbit, the somewhat dorsally directed temporal opening, the undeveloped basioccipital, the small supraorbital portion of the frontal, the deep maxilla, the short but straight tooth row and the slender paroccipital process.

Sigogneau (1970) allocated the specimen to the genus *Scylacognathus* and pointed out that it was another small form with a wide, rounded and high snout. She stated that the nasals were wide and only slightly constricted in the middle, the septomaxilla was short, the prefrontal situated on a boss, the supraorbital portion of the frontal rather small, the parietal foramen situated well in front of the occipital crest, the lacrimal short, the occiput slightly inclined, the supraoccipital particularly low and wide, the foramen magnum rather large, the transverse apophyses had teeth (which I can not confirm) and were situated posteriorly. In conclusion she remarked that the differences to the preceding species were hardly discernable and thus considered an allocation of the specimen to the genus *Scylacognathus* as justified, although she also saw some similarities with *Aelurosaurus* and *Arctognathus*. Sigogneau briefly referred to three other specimens, two of which were mentioned by Broom (1925) but could not be observed neither by her nor by myself, and one sectioned skull mentioned by Olson (1936).

S. grimbeeki

The holotype of this species is TMP 245, which was first described by Broom (1935) as *Cynarioides grimbeeki*. In this account he, however, mentioned another specimen which he named *Cynarioides laticeps* (TMP 246). Sigogneau (1970) allocated both specimens to the genus *Scylacognathus*, but mistakenly listed TMP 246 as the holotype of the taxon *Scylacognathus grimbeeki* because she thought that Haughton & Brink (1954) had reversed both numbers in their classification. However, I personally examined the specimen TMP 245 and could verify that it carried the label ‘*Cynarioides grimbeeki’,* while TMP 246 carried the label ‘*Cynarioides laticeps’*. Unfortunately, Broom 1935 gave no numbers, but the specimen he figured as *Cynarioides laticeps* is clearly TMP 246 since the anterior part of the snout is missing. However, he mentioned another specimen, which he called the topotype, but it could be found neither by Sigogneau nor by myself.

TMP 245 is somewhat weathered and badly compressed antero-posteriorly. Therefore its measurements are hard to determine, but the length was appr. 80 mm. Broom mentioned the wide frontal, the relatively small postfrontal, the preparietal extending forwards, the relatively short and broad parietal and the long and slender canine. Sigogneau (1970) remarked that this specimen was 'la réplique du précédent', referring to TMP 246, which she thought was the type, that will be dealt with later in this text. She added that the transverse apophyses were posteriorly situated and had teeth, the palatal tuberosities had numerous teeth, the mandible was thick, the dentary was long and high and there were, however, three spaced postcanine teeth.

The referred specimen is therefore TMP 246, which measures appr. 80 mm but is also heavily deformed and incomplete. Broom (1935) mentioned that the frontals were narrower than in *grimbeeki*, the postfrontals larger, the preparietal was broad and oval and the parietal short and wide. Sigogneau (1970) pointed out that the specimen had approximately the same proportions as the ones of the preceding species *S. parvus* and *S. robustus* but the snout was more pointed (however, if she refers to TMP 246, the anterior part of the snout is missing and in TMP 245 it is heavily deformed). Furthermore, she noted that the snout was short, the interorbital space was the largest of the genus, the postorbital bar widened ventrally, the nasofrontal suture was anteriorly situated, the supraorbital portion of the frontal was slightly larger than in the preceding species, the preparietal large and slightly more anteriorly situated than in *S. parvus*, the postfrontal was triangular, the lacrimal short, the parietal did not contribute to the occiput, which was inclined, the supraoccipital was large, the paroccipital process short, the foramen magnum large. In conclusion she mentioned that this specimen, again, was possibly a young individual. From personal observation it can be confirmed that TMP 245 and TMP 246 are both young individuals, since the set of characters perfectly matches the list given in the text above. However I do not see a specific separation between the species *S. parvus* and *S. grimbeeki*. Already Sigogneau listed a number of identical characters for both taxa in her specific diagnosis. This fact and the very close overall resemblance: same snout form, same structures of palate and in the bones of the skull roof, leads to the assumption, that both taxa are conspecific.

2.2.3.7.3 History of *Arctops* Watson, 1914

A. willistoni

The holotype of the type species *Arctops willistoni* is BMNH 4099. It is, however, a very badly preserved specimen which lacks the snout and the skull arches. Watson (1914) gave the first description, which was restricted to the occipital and brain case characters. But in 1921 he mentioned the rectilinear section of the snout, the small and laterally directed orbit, the flat and wide cranial skull roof, the shallow palatal fossa and the small palatal tuberosities. Broom (1932) mentioned the specimen and stated that it would be impossible to tell the relationships of this skull because of its incompleteness. Boonstra (1934) provided an additional description after further preparation of the specimen and, again, figured it in dorsal and ventral view. However, Sigogneau (1970) and Sigogneau-Russell (1989) and my own observation differ in parts from his drawings. In Boonstra's account, however, the braincase, again, is the main subject of his description. Moreover, he mentioned the short frontal and the posteriorly situated ectopterygoid; he could see no teeth on the palatal tuberosities but assumes that there were some, as in other forms; he mentioned the broad and deep basisphenoid fossa and added that a considerable part of the otic region was not ossified. Finally, he listed the primitive (1) and advanced features (2); (1): square section of the snout, laterally directed orbits, small lateral temporal openings (which is not a primitive feature because their dorsal margin is situated on the same level as the dorsal margin of the orbits and not ventrally as in pelycosaurs), large basioccipital, strong paroccipital, parietal foramen situated posteriorly, preorbital depression, frontal forming large part of orbital border, little ossification of the sidewalls of the brain case, wide parietal region; (2): pterygoid flanges not far posteriorly (Sigogneau, 1970, however, saw them rather posteriorly), skull slightly wider than high, maxilla apparently fairly deep (in comparison with other forms the snout is, however, low and, besides, the exact extent of the maxilla is beyond recognition since this part of the skull is missing), occiput fairly upright but not concave. Boonstra concluded that *Arctops* would be a rather primitive form.

Sigogneau (1970) figured the preparietal as narrow and the postfrontal as rather long, which I can confirm. She saw the extent of the supraorbital portion of the frontal as uncertain but doubted Boonstra's interpretation. The sutures of the occiput are disputable but in my opinion, Boonstra's wide and Sigogneau's mushroom-shaped interparietal, is, in fact, of normal quadratic shape and the supraoccipital is low. The species *A. willistoni* will be allocated to the taxon *Scylacognathus*, the reasons are discussed below.

A. watsoni

Until 1953 *Arctops willistoni* was the only species but then BRINK & KITCHING (1953) introduced the species *watsoni* (BPI 263). It concerns a rather complete specimen which measures 260 mm in length. However, BRINK & KITCHING admitted that the allocation of their specimen to the genus *Arctops* was questionable because of the incomplete condition of the holotype which they could not even observe personally. According to them, the only difference was the longer and narrower postfrontal of A. *watsoni*. The other listed differences were due to the inadequate drawings of BOONSTRA (1934) (the round preparietal, the short postfrontal, the wide interparietal) and are therefore regarded as invalid here. In the palate they mentioned the long and narrow palatal tuberosities that surrounded an oval palatal fossa and were almost closed anteriorly and posteriorly.

SIGOGNEAU (1970) added some more important characters to the rather short description of BRINK & KITCHING which complete the list of characters of the genus *Arctops*: the rather heavy snout, which was long, high and widened in posterior direction; the small orbit and the round temporal opening, the wide interorbital and intertemporal spaces and the flat skull roof. The postorbital bar is described as narrow dorsally but widened slightly in ventral direction and the zygomatic arch was rather slender. The concave ventral profile of the ventral margin of the postorbital bar reminded her of *Scylacognathus*. Furthermore, SIGOGNEAU stated that the participation of the frontal at the supraorbital rim was important, the bulged prefrontals were short, the nasals wide, the nasofrontal suture straight, the maxilla high and the course of the suture was rectangular posteriorly. The jugal was high and the lacrimal short, but from personal observation I can state that it is longer than high and narrows anteriorly, as also indicated by BRINK & KITCHING (1953). The occiput was wide, high and concave, the interparietal high, the low paroccipital process was shifted forward, the basisphenoid fossa was wide and deep and the tubera were strong and round. The palate was flat, the palatal fossa was shallow but wide; however, from personal observation I can state that it is rather narrow. The tuberosities were slender and with a few small teeth. The choanae were elongated and the vomer was at the same level as the palatines. At the end SIGOGNEAU mentioned that *A. willistoni* and *A. watsoni* were probably monospecific and discussed the supposed differences. She comes to the same conclusion as I did, namely, that the establishment of two species results from the imprecise drawings of BOONSTRA (1934). Thus the only real difference remains the age, because *A. willistoni* is supposed to come from the *Tapinocephalus* Zone, whereas *A. watsoni* is from the *Cistecephalus* Zone. But since the exact provenience of the type is uncertain and the similarities are striking, I consider *A. watsoni* to be conspecific with *A. willistoni*.

Hence BPI 263 becomes *Scylacognathus parvus* as well.

A. cf *watsoni*

Sigogneau (1970) additionally introduced another specimen as *A*. cf. *watsoni* (BPI 395). It concerns another rather complete skull, which is, however, slightly more weathered than the type and measures 215 mm in length. Sigogneau saw this skull as only very slightly different from that of the preceding species and explained the most important discrepancies by their different age and individual variation. The most striking differences, she saw in the shorter paroccipital process, the proportions of the basioccipital and basisphenoid and perhaps in the transverse apophyses.

Indeed BPI 395 differs in some ways from BMHN 4099 and BPI 263, however, the resemblance with the referred specimen of *Scylacognathus parvus,* TMP 256, is striking: same shape of the skull, same pattern and position of naso-frontal suture, same extent of supraorbital portion of the frontal, same size and shape of preparietal, same shape of palatal tuberosities. Thus, this skull links the two genera *Scylacognathus* and *Arctops* more closely together, a fact that was already noted by Sigogneau in 1970: She saw a close resemblance of BPI 395 with the type specimen of *Scylacognathus* but to a certain extent hesitated to regard *Scylacognathus parvus* as a young form of *A*. *willistoni* or *A*. *watsoni* or *Scylacognathus* as the immature form of *Arctops*. Mostly, she was reluctant to eliminate the historical genus *Arctops* in favor of *Scylacognathus*, which was poorly defined, in her opinion. However, BPI 395 could well represent the adult form of BMHN 5743 (*Scyl*. *robustus*) with TMP 256 linking the two forms together. Thus I consider that all three taxa can be united into one genus and species.

The following three species were allocated to the genus *Arctops* with a questionmark by Sigogneau-Russell (1989):

1.) *A*? *minor*:

Arctops? *minor* (RC 110) was first described by Broom (1948) as '*Gorgonorhinus' minor* sp. nov. He considered it being close to '*Gorgonorhinus luckhoffi'* because of the dental formula. The latter specimen, however, consists only of a snout and is now Gorgonopsia? (Sigogneau-Russell 1989). RC 110 is also rather badly preserved with a large part of the skull restored in plaster, the sutures are hardly traceable if preserved at all, the occiput is damaged and the palate not visible. Broom stated that there was no preparietal, the frontals were short and formed only a small portion of the orbital rim, the postfrontal was large, the temporal arch rather slender, the lacrimal relatively small, the prefrontal rather large but not much raised, and that it had five well-developed postcanine teeth. At the end, he discussed the relationship with other taxa and suggested that RC 110 might be closely related to '*Tigricephalus' kingwilli* (=*Lycaenops kingwilli* Sigogneau 1970).

Sigogneau (1970) noted the long and high snout with the convex ventral border, although she considered this convexity as figured by Broom (1948) as somewhat exaggerated. But this is difficult to judge since most parts are now restored in plaster. Furthermore, she stated that the interorbital and intertemporal spaces were rather wide, and from the absence of the skull arches she concluded that they must have been rather slender. She discussed the probable absence of a preparietal and supraorbital portion of the frontal but left the question unsolved because of the weathered skull roof. Finally she allocated the specimen to the genus *Arctops* 'avec lequel la correspondance nous paraît le plus satisfaisante' (Sigogneau 1970, p. 147).

This specimen is too incompletely preserved to tell its relationships appropriately. Thus it will become Gorgonopsia indet.

2.) *A*? *kitchingi*:

Arctops.? *kitchingi* (BPI 265) was first described by Brink & Kitching (1953) as a referred specimen of '*Aelurognathus minor*' (= *Lycaenops*? *minor*). They mentioned Three additional skulls (BPI 262, which is now the type specimen of *Lycaenops*? *minor*, RC119 and BPI 264 as referred specimens of this taxon). The authors, however, mainly discussed the relationship between the two genera *Aelurognathus* and *Lycaenops,* since they considered that both genera were closely allied. Though Brink & Kitching provided two figures (lateral and dorsal view), they gave no description of the specimen BPI 265.

Sigogneau (1970) mentioned the long snout with its square section, the wide and flat skull roof, the relatively large orbits, the large preparietal and supraorbital portion of the frontal, the straight nasofrontal suture, the quadratic lacrimal (which is, however, in my opinion slightly longer than high), the wide and vertical occiput with a large supraoccipital and a slightly anteriorly shifted paroccipital process, the long basioccipital with a deep basisphenoid fossa, the backwards pointing transverse apophyses with only one tooth and the five small postcanine teeth. In the following discussion she stated that the skull shows signs of immaturity such as the large orbits, the large foramina parietale and magnum and the teeth in replacement. Furthermore, she did not leave BPI 265 with the three other specimens as proposed by Brink & Kitching because she was of the opinion that the proportions were different: transverse apophyses more posteriorly situated, shorter palatal tuberosities, longer basioccipital. As already noted by Sigogneau, BPI 265 shows some characters of immaturity but is with 160 mm rather large for a young individual, though smaller than the other *Arctops* specimens. Besides, the shape of the bones would indicate an adult form and thus this individual was probably sub-adult.

The specimen is indeed somewhat different from the other *Arctops* specimens but nevertheless an allocation to this taxon seems justified by the well rounded snout, the narrow and oblong preparietal, the narrow and oval palatal fossa, the narrow and oblong palatal tuberosities with a few teeth, the oblong choanae and the concave occiput. It differs by the narrower and less convex snout and the less enlarged posterior skull part but these characters are considered as specific here.

3.) *A.*? *ferox*:

This species is, in my opinion, the most doubtful of the three in question. Sigogneau (1970) combined five specimens in the species *A.*? *ferox*. Three of them were given different names by Broom, who described them first in 1948, whereas the other two were undescribed until Sigogneau (1970). Although I do confirm the homogeneity of the five specimens, the allocation to the genus *Arctops* is rejected, but the matter will be discussed in with *Aelurognathus* and *Lycaenops* in chapter 2.2.6.

2.2.3.7.4 Discussion

The genera *Arctops* and *Scylacognathus* were never considered that closely allied by most of the authors. Only Sigogneau mentioned the possibility that *Scylacognathus* might be the young form of the genus *Arctops*. Unfortunately, the genus *Arctops* is not satisfactorily established since the holotype is badly and incompletely preserved. Moreover, the holotype and the other species of *Scylacognathus* are most probably immature, but this only confirms the assumption that some of the *Scylacognathus* species are young individuals of *Arctops*.

Sigogneau listed a number of characters in her diagnoses that were shared by *Scylacognathus* and *Arctops*: skull rather wide posteriorly, interorbital and intertemporal width great, zygomatic arch slender, lacrimal short, paroccipital anteriorly shifted, transverse apophyses posteriorly situated, palatal tuberosities short, dentary slender and low. The characters in her diagnosis that were different in both genera relate to ontogenetic changes, in my opinion: short snout, extremely slender skull arches, anteriorly situated preparietal, parietal foramen far away from occipital crest, short postfrontal, inclined occiput, wide interparietal and small postcanine teeth in *Scylacognathus*; long snout, broader skull arches, reduced preparietal, parietal foramen situated near the occipital crest, less inclined occiput, powerful symphysis, long canine and large postcanine teeth in *Arctops*. Additionally, she listed for *Scylacognathus* the sinuous ventral profile and the concave ventral profile of the postorbital bar, but these features also apply to *Arctops*. For *Arctops* she additionally listed: heavy snout which was slightly higher than wide, long basioccipital, anteriorly short prefrontal, wide occiput, palate flat, prootic little ossified. The first two characters are the result of ontogenetic changes, whereas the prefrontal is indeed longer in *Scylacognathus*. But this feature could also be of ontogenetic origin, and the prefrontal might get shorter anteriorly as the maxilla gets larger. The last characters apply to *Scylacognathus* as well.

In this account it is assumed that most specimens of the genus *Scylacognathus* are young individuals. Thus, if it is supposed that growth changes certain structures in the skull (length of snout, cranial skull roof, proportions of some bones) as mentioned above in this account, the adult form of a *Scylacognathus* individual would perfectly resemble an *Arctops*-like form. In fact, the shape of the snout is very characteristic since it is, in all specimens, inclining with a distinct concave 'bend' dorsally at the level of the anterior margin of the prefrontals, whereas the ventral margin is highly convex. Furthermore the cranial skull roof is remarkably wide in the *Scylacognathus* specimens but also still wide in *Arctops*. The supraorbital portion of the frontal, however, is rather small in *Scylacognathus* and smallest in TMP 256 but this specimen is regarded as being an adult or at least a sub-adult individual. The preparietal is anteriorly situated and large in the young form (*Scylacognathus*) but rather small in the adult (*Arctops*). In the same way, the nasofrontal suture shifts from a V-shaped posteriorly situated form to a more anteriorly situated, rectangular and interdigitating shape, the interparietal narrows, the nasal gets more constricted in the middle, the orbita gets smaller and the snout longer.

These ontogenetic changes together with the similarities in the snout, the cranial skull roof and the palate indicate a close relationship, and therefore it is proposed here that the genera *Scylacognathus* and *Arctops* become congeneric, sharing the following characters:

Skull with the outline of an elongated triangle in dorsal view, posterior part of skull moderately wide, zygomatic arches slightly flaring laterally; dorsal profile of skull sloping from the snout to the level of the orbit with a distinct 'bend' at the level of the anterior part of the prefrontal and slightly sloping posteriorly; snout bulky, rounded, slightly higher than wide, external nares ventrally situated, orbits of medium size round, visible in dorsal view, however, more or less only as slits, temporal openings roughly rectangular, interorbital and intertemporal spaces wide, the latter slightly wider; ventral margin of the maxilla strongly sinuous, septomaxilla rather long and high with a pronounced recess dorsal to the septomaxilla foramen, maxilla high, posterior suture with the prefrontal, lacrimal and jugal runs completely straight in ventral direction so that the posterior process has a rectangular border with the jugal, nasal long, naso-frontal suture posteriorly situated, rectangular and interdigidating, prefrontal short but high and situated on an elevation, lacrimal slightly elongated but also high with antorbital depression and convex dorsal suture, supraorbital portion of frontal narrow, preparietal rhombic and small, well separated from the parietal foramen, the latter being situated closer to the occipital crest; postfrontal long but narrow and of the same width throughout its length, posterior margin somewhat extended in postero-lateral direction, postorbital broad dorsally and reaching the level of the ventral margin of the orbit on the postorbital bar, squamosal reaches not far in anterior direction on zygomatic arch; skull arches rather slender, with the suborbital arch being the broadest, postorbital bar narrow dorsally but widens somewhat in ventral direction with the posterior margin, however, more or less straight, its ventral margin concave, zygomatic arch gets wider in posterior direction with a slightly convex ventral margin; palate flat, choanae elongated, vomer lying roughly on the same level as the palatines and widened in the middle but constricted anteriorly, palatal fossa elongated, narrow and deep, palatal tuberosities rather narrow and elongated, the ones on the palate being open anteriorly and only slightly longer than the pterygoid ones, both confluent and only separated by the suture, teeth on both tuberosities present, interpterygoid vacuity is rather large, deep and oval in shape, ectopterygoid large and reaching far posteriorly on the transverse apophyses, which are somewhat directed posteriorly, bearing few teeth, parabasisphenoid fossa deep and wide, basisphenoidal tubera rather massive, basioccipital long; occiput wide with a rectangular outline, only slightly concave, interparietal quadratic or slightly higher than wide, supraoccipital low but only slightly wider than the interparietal, paroccipital process short, posttemporal fenestra slit-like, parietal contributes very slightly to the occiput; teeth of normal size, three to four postcanine teeth. See figure 35 for illustration.

The type species will become *Scylacognathus parvus* and thus the holotype is a young individual. However the referred material illustrates the features of the adult form adequately. This will contain BMNH 4099 (‘*A. willistoni*’), BPI 263 (‘*A. watsoni*’) as well as the specimens of *Scyl. grimbeeki*. The second species is *Scyl. robustus* with BMNH 5743 as holotype and TMP 256 (former referred specimen of *Scyl. parvus*) and BPI 395 (‘*A.* cf *watsoni*’) as referred material. *A. kitchingi* will become *Scyl. kitchingi*, however, its relationship to the genus *Scylacognathus* still remains doubtful.

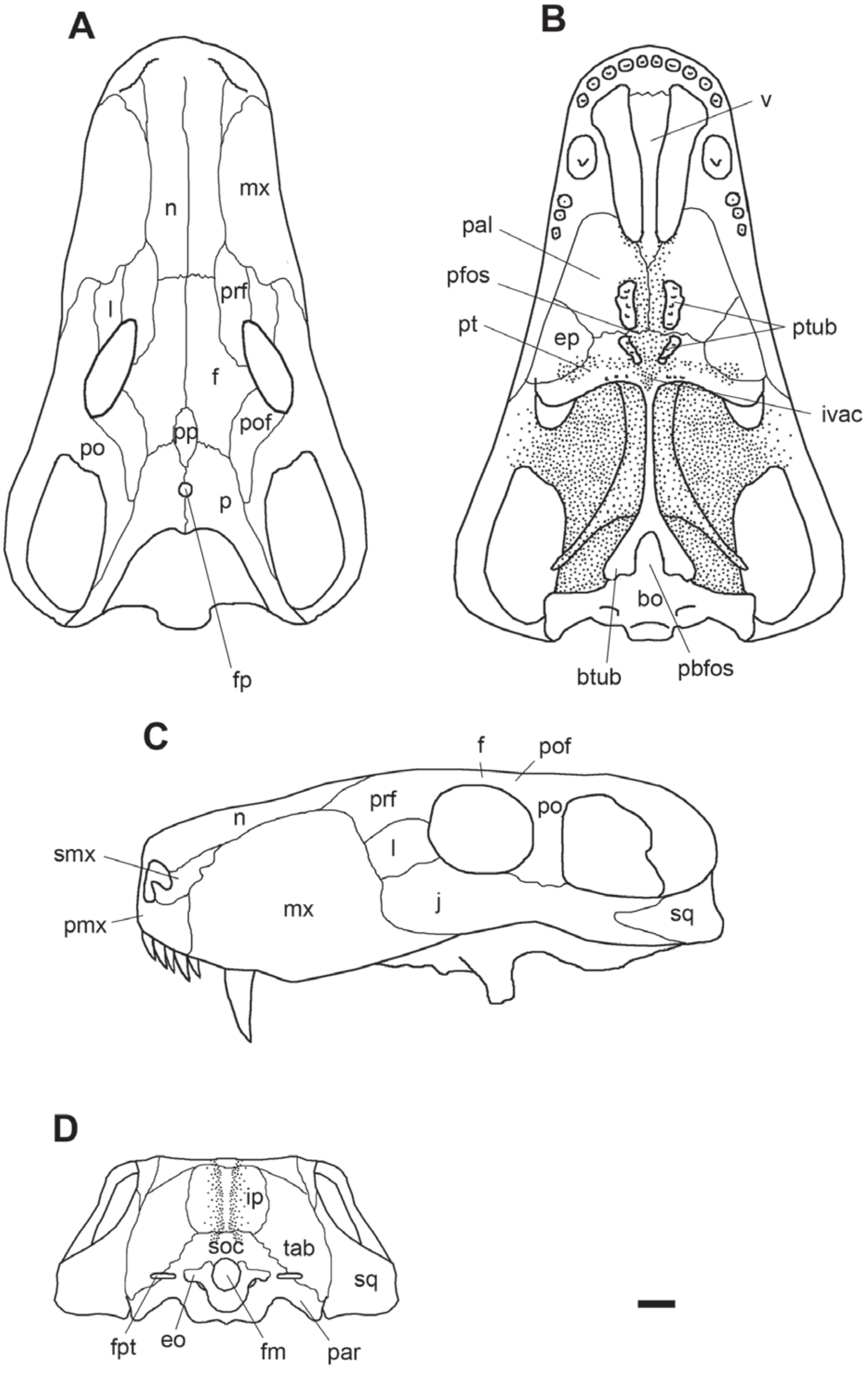


Figure 35. Illustration of the characters in the genus *Scylacognathus* Broom, 1913 based on the holotype of the type species, *Scylacognathus parvus* (AMG 3751). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

Systematic Paleontology

Genus: ***Scylacognathus*** Broom, 1913
Type species: *Scylacognathus parvus* Broom, 1913

Revised generic diagnosis: snout sloping with distinct 'bend' at the level of the anterior margin of the prefrontal, temporal opening quadratic, interorbital and intertemporal spaces wide, ventral margin of maxilla strongly sinuous, posterior maxillary process long and with rectilinear dorsal border, lacrimal with a convex dorsal margin, preparietal narrow and oblong, skull arches rather slender, palate flat, choanae long, palatal fossa and palatal tuberosities narrow, postcanines rather large.

Scylacognathus parvus Broom, 1913
(= *Arctops willistoni* Watson, 1914, = *Cynarioides grimbeeki* Broom, 1935, = *Cynarioides laticeps* Broom, 1935, = *Arctops watsoni* Brink and Kitching, 1953, = *Arctops* cf. *watsoni* (Brink & Kitching, 1953) Sigogneau, 1970, = *Scylacognathus grimbeeki* (Broom, 1935) Sigogneau, 1970)
Holotype: AMG 3751
Referred material: BPI 399, TMP 245, TMP 246, BMNH 4099, BPI 263
Specific diagnosis: skull wide posteriorly, preparietal small and narrow, interparietal higher than wide, no teeth on transverse apophyses.
Bibliography: Broom 1913, pp. 398-399
Watson 1914, pp. 1026-1033, fig. 3c, 4b
Watson 1921, pp.36-39, fig. 1-3
Broom 1930, p. 125, pl. 20, fig. 21
Broom 1932, p. 110, fig. 43b
Boonstra 1934, pp. 176-181, fig. 1-3
Broom 1935, pp. 2-5, fig. 2-3
Brink & Kitching 1953, pp. 25-27, fig.26
Sigogneau 1970, pp 123-126; 133-146, fig. 70-71; 76-83, pl. 23a; 25a-b; 26-27; 29b.
Sigogneau-Russell 1989, pp. 78; 98, fig. 194; 240-241

Scylacognathus robustus (Broom, 1925) in Sigogneau, 1970
(= *Cynariops robustus* Broom, 1925, = *Scylacognathus major* Broom, 1935)
Holotype: BMNH 5743
Referred material: TMP 256, BPI 395
Specific diagnosis: lacrimal oblong, teeth on transverse apophyses, preparietal larger than in *Scyl. parvus*, very small supraorbital frontal.

Bibliography: Broom 1925, pp. 323-324
Broom 1930, pl. 29, fig. 26
Broom 1932, p. 130, fig. 43e
Boonstra 1934, pp. 197-202, fig. 11-14
Broom 1935, pp. 60-62, fig. 3
Sigogneau 1970, pp 126-132, fig. 72-75, pl. 24b,c; 25c.
Sigogneau-Russell 1989, p. 98,

Scylacognathus kitchingi (Sigogneau, 1970) new comb.

(= *Aelurognathus minor*, = *Arctops kitchingi* Sigogneau, 1970, = *Arctops*? *kitchingi* Sigogneau-Russell, 1989)

Holotype: BPI 265

Specific diagnosis: snout rather straight dorsally, very few teeth on transverse apophyses, contribution of frontal to supraorbital rim relatively large, supraoccipital high, five postcanine teeth.

Bibliography: Brink & Kitching 1953, pp. 23-25, fig. 25
Sigogneau 1970, pp 155-158, pl. 28b; 29c
Sigogneau-Russell 1989, p. 80; fig. 198.

2.2.4 Gorgonops Owen, 1876 and Scylacops Broom, 1913

2.2.4.1 Introduction

This chapter is about the two taxa *Gorgonops* Owen, 1876 with the six species *G. torvus*, *G. whaitsi*, *G. longifrons*, *G. eupachygnathus*, *G.*? *dixeyi* and *G.*? *kaiseri* as well as *Scylacops* Broom, 1913 with the two species *S. capensis* and *S. bigendens*.

The genus *Gorgonops* is among the earliest gorgonopsian taxa established. Owen (1876) introduced the holotype of the type species, BMNH R 1647, as the only specimen of his new family ‘Tectinarialia’. He gave a rather comprehensive account which is however of less comparative value because the material was only sparse at the time of Owen’s writing.

The holotype of the type species *Scylacops* is of historical interest as well, since it is on this skull, that Broom (1913) recognised the gorgonopsian structure and separated the gorgonopsians from the therocephalians.

The list below opposes the former classification (after Sigogneau-Russell, 1989) and the revision as proposed in this account:

Gorgonops torvus	
BMNH 1647	*Gorgonops torvus*
AMNH 5515	*Gorgonops torvus*
BPI 277, 386, 385	*Gorgonops torvus*
Gorgonops whaitsi	
AMNH 5530	*Gorgonops* ?*whaitsi*
AMNH 5531	*Gorgonops* ?*whaitsi*
5544, 5546, 5568	Gorgonopsia indet.
BMNH 4052, 4053	Gorgonopsia indet.
Gorgonops cf. *whaitsi*	
BSP 1934 VIII 28	Gorgonopsia indet.
BPI 290.	*Gorgonops torvus*
Gorgonops longifrons	
SAM 2671	*Gorgonops torvus*
Gorgonops eupachygnathus	
BMNH 4051	*Gorgonops* ?*eupachygnathus*
Gorgonops? *dixeyi*	
SAM 7846	*Gorgonops dixeyi*
Gorgonops? *kaiseri*	
BSP 1934 VIII 10	*Gorgonops*? *kaiseri*
Scylacops capensis	
SAM 2343	*Scylacops capensis*
SAM 10188, 3444	*Scylacops capensis*
MZC 885	*Njalila insigna* nov. sp.
Scylacops bigendens	
BPI 266	*Scylacops capensis*

2.2.4.2 History of the genus *Gorgonops* Owen, 1876

G. torvus

As already mentioned in the introducion the genus *Gorgonops* and especially the holotype BMNH R 1647 of the type species *Gorgonpos torvus* is of great historical interest. Although this specimen is not the best preserved of this species it was often described, figured and mentioned; it will thus only be shortly discussed here.

OWEN (1876) thought that his specimen was not closely related to the gorgonopsians although he grouped them together in the Theriodontia. LYDEKKER (1890, p.111) gave a generic and specific diagnosis which is however somewhat outdated: 'Skull depressed, long and narrow, with the orbits small and lateral, approximated to the occiput, and far removed from the muzzle. Nares forming small horizontal slits, overhung by large nasals. Upper incisives five in number.' SEELEY (1895) who believed, that the temporal region was roofed, erected the sub-order Gorgonopsia. BROOM (1910, p. 20) noted shortly: 'On re-examinating the skull it appears that though the parietal region is broad there is a distinct temporal fossa…' WATSON (1921) again gave a detailed account and mentioned the flat skull, the large and laterally directed orbit, the square-shaped cross-section of the snout, the preorbital thickening, the depression in the lacrimal region, the broad interorbital and intertemporal regions, the wide interparietal and low supraoccipital, the parietal foramen which was situated on an elevation, the narrow vomer and the small ectopterygoid. BOONSTRA (1934) agreed with WATSON's (1921) figures of the dorsal and lateral surfaces but added the presence of a preparietal. In the palate he disagreed with WATSON's relations of the palatines, pterygoids and ectopterygoids and stated that the palate was rather in agreement with other gorgonopsians. As primitive features, he listed the square cross-section of the snout, the laterally directed orbits, the slightly sloping occiput, the straight tooth row and a step in the alveolar border, the very small lateral temporal openings (which are however of usual gorgonopsian condition), the large basioccipital, the posterior position of the parietal foramen, the preorbital depression, the frontals forming a large part of the orbital border and the large (long) postfrontals. As advanced feature he sees the rather anteriorly situated transveres apophyses (SIGOGNEAU, 1970, stated that they were posteriorly situated), the slightly cupped occiput, the sloping sides of the skull, the snout which is wider than high (contradicting with his above statement), the deep maxilla and the flat basipterygoid process which was laterally placed.

SIGOGNEAU (1970) also gave a rather detailed account but only additional points are mentioned here. She saw the snout as long and probably slightly wider than high, the orbits rather small but the temporal opening elongated, the postorbital bar widening somewhat ventrally, the frontal participating only slightly in the orbital rim (contra BOONSTRA), the size of the preparietal uncertain but situated on a boss, the palatal fossa wide and shallow, the size of the ectopterygoids again uncertain but, according to her, they did not reach as far ventrally on the transverse apophyses as indicated by BOONSTRA.

Referred material

The first referred specimen is AMNH 5515 which is in a better state than the type. Broom (1915) only listed it very briefly, emphasizing the presence of a temporal opening. Boonstra (1935) gave an informative account with three good drawings. He figured the preparietal as middle sized and round and well in front of the foramen parietale, which was surrounded by a ridge. The palatal tuberosities were described as widely separated from each other and rather wider than long.

Sigogneau (1970) stated that the snout was somewhat wider posteriorly and the interorbital width narrower than in the type but she admitted that it very closely resembled it in the general proportions and sutures of the bones. The paroccipital process was described as situated anteriorly, low and slanting; the choanae short and the transverse apophyses posteriorly situated and she found at least three postcanine teeth.

The next three specimens were undescribed until Sigogneau (1970). They are housed in the collection of the Bernard Price Institute and have the numbers BPI 277, BPI 386 and BPI 385. The first one is serially sectioned now and could not be observed personally. According to Sigogneau (1970), it was slightly smaller than the type with a triangular outline, the lacrimal was elongated, the postorbital reached far ventral on the postorbital bar, the postorbital was as long as in the type but got wider at the orbit, the squamosal reached anteriorly up to the level of the posterior border of the postorbital bar, the occiput was low, wide and triangular, there were teeth on the transverse apophyses and the tuberosities of the palatine had the shape of an inversed V anteriorly. The dentary was of medium height, the lamina reflecta was situated at the level of the mid-orbit and the specimen had five postcanine teeth.

BPI 386 also confirmed the diagnosis of the genus and species *Gorgonops torvus*. BPI 385 lay according to Sigogneau (1970) somewhat between *G. torvus* and *G. whaitsi*. The orbit was smaller, the postorbital bar wider dorsally, the zygomatic arch did not show the same contraction towards the suborbital arch, the interorbital space was narrower, the preparietal smaller as well as the supraoccipital portion of the frontal. Finally she considered this specimen to be a young, or a late form, of the species *G. torvus* and suggested a comparison with *Scylacops*.

G. whaitsi

The species *whaitsi* is very poorly defined being based on largely incomplete, compressed and damaged material.

The holotype of *G. whaitsi* (AMNH 5530) could not be observed personally at the Natural History Museum in New York because it was loaned several years ago but never returned. The same applies to the referred specimen AMNH 5531. I was able to study other referred material from the AMNH but these largely incomplete, compressed and damaged skull parts do not show their characters sufficiently for allowing an allocation to a certain genus or species and are therefore regarded here as Gorgonopsia gen. et sp. indet.

The material was first mentioned by BROOM (1912) and named '*Scymnognathus' whaitsi* gen. et sp. nov. BROOM already noted the close relationship with *G. torvus* but then decided to place this new specimen in another genus. 1932 he justified his decision by stating that one marked difference between the two was the large parietal foramen in *G. torvus* whereas it was relatively small in '*Scymnognathus*'. In 1912 gorgonopsians were still grouped together with the therocephalians and so BROOM makes his comparison mostly with this group. He mentioned that the intertemporal space was about as wide as the interorbital, the snout was long, the orbits small, the temporal region fairly wide, the parietal foramen situated well back, the septomaxilla, postfrontal and postorbital relatively large, the symphysis deep and that there were three or four postcanine teeth. 1932 he added that the frontals of this large specimen formed small parts of the orbital margins, the preparietal was large and the squamosal reached up to the mid length of the temporal fossa.

SIGOGNEAU (1970) allocated the species *whaitsi* to the genus *Gorgonops* although she did not observe the American specimens. She relied on the description and figures given by BROOM (1912 and 1932). However these must be regarded with caution as noted by BOONSTRA (1935) who stated that:' WATSON's figures, based on a specimen in the British Museum, are more nearly correct than those of BROOM.' Although SIGOGNEAU-RUSSELL (1989) somewhat disputed the allocation of '*Scymnognathus' whaitsi* to the taxon *Gorgonops* she considered this species as a more evolved form of *G. torvus*, mainly because of its larger size, the broader posterior part of the skull, the thicker arches and the smaller orbits. SIGOGNEAU (1970) listed BMNH 4053 and BMNH 4052 (both attributed to *Scymnognathus whaitsi* by WATSON 1921) as additional referred material. However it concerns very poorly preserved and incomplete snouts and skull fragments. Although WATSON (1921) described the specimens and presented figures which are composed of both individuals, their reconstructed shape and course of the sutures is doubted here. Therefore the specimens are regarded as Gorgonopsia indet. in this account.

The existence of the species *G. whaitsi* is doubtful but as long as the type specimen AMNH 5530 is not available it will be retained, although with a dubious position.

G. cf *whaitsi*

The same problem as for BMNH 4053 and BMNH 4052 appears for two other specimens: MS 1934 VIII 28 and BPI 290. The first was described by Broili & Schröder (1935) and allocated to the taxon *Scymnognathus* as cf. *whaitsi*. Although the specimen shows a nearly complete postcranial skeleton the skull is rather incomplete, consisting only of a partial snout and rather uncharacteristic fragments of the posterior part of the skull. Because an adequate number of postcranial material for comparison is not given, the phylogenetic relationship of MS 1934 VIII 28 can not be determined since the skull fragments alone do not allow an appropriate allocation. Hence the specimen is regarded here as Gorgonopsia gen. et sp. indet.

The second specimen, BPI 290, was first described by Manten (1958) in an extensive account. He allocated it to *Gorgonops torvus* although noticing some differences with this taxon such as the larger size, the smaller postfrontal and supraorbital portion of the frontal and the larger ectopterygoid in BPI 290. Sigogneau (1970) and Sigogneau-Russell (1989) clearly saw a specific barrier between BPI 290 and *G. torvus* because of the smaller size, the wider interorbital and intertemporal spaces and the more posteriorly situated transverse apophyses in the latter. She indicated that BPI 290 rather evoked the species *G. whaitsi*. However I regard the differences as only a matter of degree, and especially compared to BPI 277 (referred specimen of *G. torvus*) the similarity is remarkable: same flat skull, oval orbit, elongate temporal opening, same proportions of the skull arches as well as of most of the bones. Even the size of the supraorbital portion of the frontal is comparable. As for the smaller intertemporal width in BPI 290 this might be caused by deformation. Remains only its larger size, however compared to BPI 385 (another referred specimen of *G. torvus*) the difference amounts to only 50 mm. Thus this species ranges from 205 mm to 286 mm in skull length and it can be quite possible that BPI 290 ranges at the top end of the scale with 340 mm. For that reason I will re-allocate this specimen to the species *G. torvus*.

G. longifrons

The holotype (SAM 2671) was first described by Haughton (1915) as ‘*Gorgonognathus*’ *longifrons* gen. et sp.nov. The weathered skull measures appr. 340 mm in length and the left side of the posterior part of the skull is compressed anterodorsally. Haughton himself stated that in the general features it resembled *G. torvus*. The septomaxilla is described as large (however it is hardly determinable since the bone surface is badly weathered in this region), four postcanine teeth were present, the incisors were rather large, the nasals and prefrontals large, the frontal contributed only slightly to the supraorbital rim, the orbit was small and faced forwards and outwards, the temporal fenestra was slightly larger than the orbit (it appears to be higher than wide, which is however due to compression, but nevertheless it is quadratic in shape), the postfrontal contributed largely to the orbital rim, the intertemporal region was wide (about as wide as the interorbital width), the parietal foramen was situated near the occipital crest, the preparietal was small (it is indeed of moderate size) and did not reach the parietal foramen, the occiput was broader than high, concave and vertical (in fact it is slightly sloping), the interparietal was slightly broader than deep, the paroccipital process was short and low but massive and the vomer was comparatively broad anteriorly. To this detailed account Haughton (1918) only added some points concerning the braincase and gave three figures in 1924. However in my opinion he exaggerated the broadness of the posterior part of the skull, the ventral expansion of the zygomatic arch and the transverse apophyses. Thus the shape is more like that given by Broom (1932). This is also suggested by Sigogneau in 1970. Haughton (1924) stated that there were teeth on the palatal ridges, that the transverse apophyses were situated anteriorly, that the palatines were large (they are of normal size) and that the step in the dentigerous border was weak.

Sigogneau (1970) added only a few points to Haughton's account. She is of the opinion that the snout only appears to be that extremely long because of deformation and that it was only slightly longer than in *torvus* and *whaitsi*. According to her, it was low and rounded in cross-section with parallel lateral borders, the proportions of the arches had the same relations as in the preceding species, the lacrimal was rectangular, the postorbital reached far ventrally on the postorbital bar and the supraoccipital was low and comparatively small. She concluded, that '*Gorgonognathus' longifrons* showed great similarities with *G. torvus* and *G. whaitsi* in the sutures of the bones and in the proportions and that the differences were only a matter of degree (slightly longer snout, slightly larger orbit, slightly wider posterior part of skull, teeth slightly stronger, transverse apophyses slightly more anteriorly situated). However she did not go as far as to allocate this specimen to the species *whaitsi* but rather agreed with Haughton's opinion that *G. longifrons* was an advanced form of *G. whaitsi*.

Considering the incomplete state of the holotype of the species *G. whaitsi* and the unsatisfactory developed species diagnosis it seems difficult to make references to the species *whaitsi* at all. However SAM 2671 shows all the distinct characters of the species *torvus*: interorbital width as wide as intertemporal, preparietal slightly smaller than in the other species, tuberosities on the palatine of inversed V-shape anteriorly, interpterygoid vacuity large and presence of teeth on the transverse apophyses. With the length of 340 mm it is one of the larger specimens of the species *G. torvus* but corresponds well with BPI 290. With the allocation of SAM 2671 to the species *G. torvus* the species *G. longifrons* becomes a junior synonym of *G. torvus*.

G. eupachygnathus

The rather poorly preserved holotype (BMNH R 4051) which does not show any features of the palate, was first introduced by Watson (1912) as '*Scymnosuchus' whaitsi*. However in this account Watson only considered the lower jaw. In 1914 he referred the specimen to '*Scymnognathus' whaitsi* but admitted, that he was not certain of the identification. In 1921 Watson again changed the name of the specimen in '*Leptotrachelus' eupachygnathus* because of its more evolved braincase. Broom (1932) noted that the form might have been allied to '*Scymnognathus' whaitsi*. Thus the frontal formed a considerable part of the orbita, the preparietal was large and the parietal foramen fairly well developed. Boonstra (1934) gave a short re-description and refigured the dorsal view with some small corrections of Watson's drawing. He listed the primitive (1) and advanced characters (2) as follows: (1) preorbital depression, frontals forming large part of the orbital border, apparent step in the alveolar border, large postfrontal, large quadrate. (2) rounded snout, fairly depressed; deeply cupped but upright occiput; curiously small basioccipital; basisphenoid far forward; prootic fairly large and deep maxilla. Finally he remarks that '*Leptotrachelus*' was closely related to '*Scymnognathus*.' Manten (1958) mentioned some differences between *G. torvus* and '*Leptotrachelus*' *eupachygnathus*. The latter had a deeper jugal in front of the orbita, larger frontals, a more anteriorly situated parietal foramen, a more concave occiput and a smaller basioccipital.

Sigogneau (1970), however, allocated the species to the genus *Gorgonops*. In the size and width of the supraoccipital portion of the frontal it was judged comparable to *G. torvus* whereas the posterior part of the skull, the long temporal openings and the strongly concave occiput rather evoked *G. whaitsi*. She also suggested this specimen to be a young form but refrained from a definite statement because of its incomplete state.

The species *eupachygnathus* is retained here because of its wider intertemporal and interorbital widths than in *G. torvus* although it is very close to this species and both might as well be conspecific. However the incomplete state of the specimen BMNH R 4051 allows no definite allocation and therefore its relationships are considered as dubious.

G. dixeyi

The specimen (SAM 7846) comes from Chiweta/Malawi. It was first described by HAUGHTON (1927) and named *Chiwetasaurus dixeyi* gen. et sp. nov. The skull measures 330 mm in length and is somewhat incomplete and deformed. HAUGHTON was of the opinion that it was close to *'Lycaenoides' angusticeps* (= *Lycaenops angusticeps*) because of its proportions and the orbits, which were situated in the posterior half of the skull. He mentioned that the snout was higher than wide, the lacrimal was large, the supraorbital portion of the frontal small, the preparietal was of moderate size and did not touch the parietal foramen and there were no teeth on the palate.

SIGOGNEAU's (1970) reconstruction differs somewhat from HAUGHTON's in the proportions. In fact she only gave the palatal and occipital view whereas HAUGHTON gave the lateral and dorsal views. However SIGOGNEAU stated that the snout was probably wider, the broadness of the skull not that accentuated and the temporal fenestra slightly higher than indicated by HAUGHTON. In fact it is rather difficult to say what the exact proportions might be since the skull is laterally compressed and displaced in a right ventral direction. SIGOGNEAU also mentioned the small orbits, the relatively slender postorbital and suborbital arches (which are however not complete), the large septomaxilla, the inclined occiput, the anteriorly shifted paroccipital processes, the long basioccipital, the wide but shallow palatal fossa and the relatively strong teeth. She concluded in considering this form as a geographic variation of *G. whaitsi*.

G. dixeyi corresponds well with the characters diagnostic for the genus *Gorgonops*: flat skull, straight dorsal skull roof, oval orbit, moderate width of the posterior part of the skull, medium sized preparietal, anteriorly situated and strongly interdigitating naso-frontal suture, large pre- and postfrontal, palatine tuberosities situated near to the internal choanae, interparietal only slightly wider than high, supraoccipital low. Therefore I retain this species however with an unambiguous state. The species *G. dixeyi* is well delimited from the other species by the more square shaped snout, the rather small supraorbital frontal, the round preparietal and wider palatal fossa.

G.? kaiseri

The holotype of this species (BSP 1934 VIII) was first descibed by BROILI & SCHRÖDER (1934) as '*Pachyrhinos' kaiseri* nov. gen. et sp. It concerns a large but incomplete and somewhat deformed skull which measures 340 mm in length. BROILI & SCHRÖDER gave a very detailed description but I will only refer to the points which are of comparative value. They stated that the maxilla was large and high, the septomaxilla reached relatively far posteriorly (which I cannot confirm), the nasal was narrow and the suture with the frontal was postriorly situated and pointed, the supraorbital portion of the frontal was moderately large, the postfrontal relatively small, the preparietal small (indeed it is relatively large) and situated on a marked boss, the parietal foramen was surrounded by a ridge and lay just in front of the occipital crest (and also close to the parietal foramen), the palatal tuberosities were inversed V shaped and with teeth (the more posteriorly situated components of the palate are however missing), the vomer was situated more dorsally than the rest of the palate and there were four postcanine teeth. In the following discussion the authors compared their specimen with various other gorgonopsians known at the time and came to the conclusion, that it was closely related to *Gorgonops torvus* and ‘*Scymnognathus*’ *whaitsi*, differing from these however by a number of important characters which would justify a new genus: larger size than *G. torvus*, preparietal in ‘*Pachyrhinos*’ *kaiseri* situated on a marked boss and the foramen parietale smaller (which is not true indeed). Further *G. torvus* and *G. whaitsi* had a distinct step in the alveolar border which was missing in *kaiseri* (it is however indicated in the specimen).

Sigogneau (1970) only added a few more points, mentioning that the external nares were large (they are however damaged) and the interparietal was high (it is also broad). Further she discussed the intraspecific relationships: *G. torvus* was of a smaller size, *G. longifrons* had the same large postcanine teeth but the orbit was bigger, *G. dixeyi* differed in its dentition and *G. whaitsi* in having smaller postcanine teeth and a smaller supraoccipital portion of the frontal. Since important characteristics such as the dimensions of the posterior part of the skull or the position of the transverse apophyses cannot be determined she placed this specimen in a different species of *Gorgonops*.

The dubious state of the species *G.* ? *kaiseri* is retained here because of the incomplete condition of the holotype BSP 1934 VIII as already stated by Sigogneau and mentioned above.

2.2.4.3 History of the genus *Scylacops* Broom, 1913

Having discussed all *Gorgonops* species it is necessary to turn the attention to the genus *Scylacops,* which resembles in my opinion the genus *Gorgonops* to such a great degree that a generic separation is unjustified. In the following paragraph I will discuss the genus *Scylacops* successively and explain why I will allocate this genus to *Gorgonops*.

S. capensis

The holotype of the type species is SAM 2343, a rather well preserved, 165 mm long skull and mandible that was repeatedly mentioned by Broom. He gave a first but short description in 1913 whereas in 1925 he provided a more detailed account but referred mostly to the pre-vomer and vomer. 1930 and 1932 he figured and very shortly mentioned *Scylacops capensis* again. Broom (1932) wrote that the skull was rather flat and that there was a large preparietal, large prefrontals and postfrontals. In the palate the ectopterygoid was large and the anterior part of the pterygoid comparatively smaller. Boonstra (1934) partly agreed with the drawings of the palate given by Broom (1932) but stated that the palatal fossa was wider and more oval and the vomer tapered posteriorly instead of getting wider.

Sigogneau (1970) described SAM 2343 as having a rather heavy snout which was wider than high as in *Gorgonops*. She stated that the interorbital space was rather wide (narrower in *Gorgonops*) and the intertemporal space only slightly wider, the postorbital bar was slightly wider ventrally and the posterior margin convex, the zygomatic arch hardly more slender than the suborbital arch which was of medium thickness. The preparietal was rather large but there was no supraorbital frontal contribution, the foramen parietale did not reach the preparietal nor the occipital crest, the postorbital narrowed extremely in posterior direction, the prefrontal was large, the lacrimal short (elongated in *Gorgonops* but according to my own observations also elongated in *Scylacops*) and the squamosal did not reach far ventrally on the postorbital bar as in *Gorgonops torvus*; the occiput was only slightly inclined and the shape of the interparietal and the supraoccipital were the same as in *Gorgonops*, however the slender paroccipital process was not shifted in anterior direction. The basioccipital was slightly shorter and the basisphenoid fossa less deep than in *Gogonops torvus*. Finally she counted five small postcanine teeth but mentioned that the alveolar border was damaged. In the following discussion Sigogneau stated that she had the intention to unite *Scylacops* with *Gogonops* and wondered why other authors did not see the resemblances that were already mentioned by Broom (1913). Indeed Haughton and Brink (1954) did not group them together although their genus diagnosis for both is roughly the same and Watson and Romer (1956) allocated them eve to different families. However finally Sigogneau refrained from grouping *Gorgonops* and *Scylacops* together beause of the more evolved state of the latter and certain differences which she calls ‘subtile’ and which seemed to point to another morphological type. Thus she namely suggested a common origin but proposed a different evolution for both genera.

Referred material

The first referred specimen is SAM 10188 which was already allocated to *Scylacops capensis* by Boonstra (1934). He described his specimen as having a palatine that stretches far forward, a smaller preparietal than the type and an only slightly inclined occiput. Sigogneau (1970) saw the specimen as more lightly built than the type but with the same shape, proportions and details of the bones.

The second referred specimen, SAM 3444 was first described by Haughton (1918). In 1924 he gave a somewhat more detailed account. Thus he states that SAM 3444 was slightly smaller, the snout slightly shorter and the parietal region somewhat narrower than in the holotype SAM 2343, but these differences he considered to be due to individual variation. He also mentioned that the occiput was fairly concave and the paroccipital process placed well forward. Sigogneau (1970) and Sigogneau-Russell (1989) added no new facts to this description; since I could not observe this specimen personally I need to rely on Haughton and his rather incomplete figures.

The last referred specimen, MZC 885 is from Tanzania and was first described by Parrington (1955). In his fairly detailed account he refers to almost all aspects of the skull but only those with comparative value will be mentioned here. Parrington pointed out, that MZC 885 had a rather slender snout which was not constricted behind the canines. In transverse section the snout was rounded anteriorly. The diamond-shaped preparietal was situated closely to the parietal foramen which was surrounded by a boss. The occiput sloped steeply and the interparietal was wide as well as the supraoccipital. In lateral view the orbits faced laterally, the ventral border of the maxilla had a step anterior to the canine. In the palate there were only a few teeth on both tuberosities, the ventral borders of the transverse apophyses were thickened and turned backwards, the parabasipshenoid fossa wass deep, the paroccipital process faced somewhat anteriorly and there were four postcanine teeth. In the following discussion Parrington stated that he saw a close similarity between his specimen and the drawings of Broom for *Scylacops*. However the differences were: the narrower interorbital space, the larger size, the more posterior position of the preparietal, the somewhat different shape of the zygomatic arch, the squamosal/jugal contact and the occipital condyle being directed more downwards than backwards in MZC 885. Parrington considered the position and size of the preparietal as minor, the differences in the squamosal/jugal contact and occipital condyle, he attributes to the incorrect drawings of Broom and refers to Boonstra's (1934) account. Concerning the occiput he saw a close accordance with Haughton's (1924) figure of SAM 3444. The only real difference he noticed in the narrower interorbital region of MZC 885 but nevertheless considered an allocation to another genus or species as not justified.

SIGOGNEAU (1970) admitted that there were certain similarites in proportions and shape of the bones between this specimen and the other specimens of *Scylacops capensis*. She mentioned the form of the postorbital arch, the wide nasals, the short lacrimal and the position of the transverse apophyses. On the other hand she sees the postcanine teeth as larger and indicated, that the exact course of the sutures of the preparietal and the postfrontal could not be easily traced. Finally she mentioned the narrower interorbital space which she always considered to be a diagnostic generic character. However she left the specimen in this genus and species, though provisionally, since at that time a student of PARRINGTON was supposed to revise the gorgonopsian material in the Cambridge Collection. But it appears that this work was not aimed at resolving gorgonopsian alphataxonomy.

In my opinion this specimen clearly does not belong to the genus *Scylacops* since it differs significantly from this genus: the form of the skull is widely dissimilar since it does not show the low skull with the wide snout and the straight contour of the dorsal profile. If seen in dorsal view the orbits are well visible in comparison to the more narrow appearance in the other *Scylacops* specimens. Besides the orbit is too large, the interorbital and intertemporal widths are too narrow, and the postfrontal and the preparietal are too small. Further the palatal tuberosities and the palatal fossa are situated more posteriorly in MZC 885, the ectopterygoid is wider and the parabasisphenoid fossa is narrower. Although PARRINGTON saw no supraorbital frontal contribution I consider it as even comparatively large.

Concluding it should be noted that all these characters and the overall appearance recall strongly the new genus *Njalila* which is discussed in the next chapter: dorsally pointed snout, quadrate shaped in cross-section, slender and anteriorly bent postorbital arch, presence of a depression in front of the palatal fossa, long squamosal on zygomatic arch, triangular, rather high and strongly concave occiput with large interparietal, large orbit. Therefore the specimen will be allocated to the genus *Njalila* as the new species *N. insigna*. For discussion of this new genus and species see chapter 2.2.5.3.

S. bigendens

This specimen (BPI 266) was first described by BRINK & KITCHING (1953) and named ‘*Sycocephalus’ bigendens*. Although the specimens of *Scylacops capensis* were well known at this point of time they compared BPI 266 only with *Cyniscops longiceps* and ‘*Cyniscopoides’ broomi*. They mentioned the posteriorly wide skull, the large preparietal and parietal foramen, the small supraorbital portion of the frontal, the fairly large incisors and the two postcanine teeth.

Sigogneau (1970) pointed out that the skull was rather flat, with a triangular outline since the snout narrowed continuously in anterior direction. The interorbital and intertemporal spaces were as wide as in the type-species, the shape of the postorbital bar was identical as well as the suborbital and zygomatic arch, the temporal opening, the parietals and the postorbital. The nasals were wide and slightly constricted in the middle, the prefrontal was large as well as the preparietal which was situated near the foramen parietale, the contribution of the frontals to the supraorbital rim was minimal, the lacrimal was short and high. Further she stated that the postorbital/jugal contact was the same as in SAM 10188 and the squamoso-jugal covering as in SAM 2343. The occiput was more inclined than in the type-species, almost as in *Gorgonops torvus*, the interparietal larger and wider than the supraoccipital, the paroccipital process slightly higher and slightly shifted anteriorly, the basioccipital longer but the parabasisphenoid fossa as deep as in the holotype, the transverse apophyses had teeth, the ectopterygids were long, the palatal fossa was narrow and deep and the specimen had four postcanine teeth (contra Brink & Kitching 1953, but confirmed by my observation). Finally Sigogneau mentioned that this species 'confirms the relationship of *Scylacops* and *Gorgonops* between those it is in certain respects intermediate'.

Discussion of genera Gorgonops and Scylacognathus

Of all authors only Sigogneau recognised the close relationship between *Gorgonops* and *Scylacops*. The resemblance between *Gorgonops torvus* and *Scylacops* is, however striking and both taxa share a number of characters:

medium sized with low skull, outline seen from above in the form of an elongated triangle, zygomatic arch slightly flaring laterally, intertemporal skull roof slightly concave; snout about as high as wide with a straight or slightly convex dorsal contour, not constricted laterally, external nares situated dorsally, orbits medium sized with an oval shape, visible in dorsal view and facing laterally, not covered, temporal opening quadrate-shaped or slightly elongated, dorsal margin situated at the same level as the dorsal margin of the orbits, intertemporal space only slightly wider or as wide as interorbital space, both beeing wide; septomaxilla low and extending far posteriorly with a narrow process, no ridge on maxilla above the postcanine teeth, nasals rather broad but constricted in the middle, naso-frontal suture anteriorly situated, slightly curved and interdigidating, prefrontal with no elevation at the orbita and large, lacrimal elongated and large as well, preorbital depression present, supraorbital portion of the frontal small, preparietal rather large and rhombic, postfrontal wide at the orbit, with a slight constriction in the middle and long posteriorly, posterior margin rounded, foramen parietale anteriorly situated but not reaching the preparietal, postorbital reaches very far ventrally on the postorbital bar, squamosal reaches with broad process up to the level of the anterior margin of the temporal opening; skull arches rather slender, suborbital arch slender and straight, postorbital bar slender dorsally but widens slightly in ventral direction, posterior margin convex, zygomatic arch widens somewhat in posterior direction; palatine elongated and narrow, palatine fossa narrow and shallow, palatine tuberosities situated near the choanae, both tuberosites rather narrow and elongated, with teeth, ectopterygoid broad, short anteriorly but reaching far ventral on the transverse apophyses which are anteriorly situated and can have teeth, interpterygoid vacuity well developed and deep, parabasisphenoid fossa broad and deep, basisphenoidal tubera slender and elongated, basioccipital long; occiput triangular, slightly inclined and strongly concave, parietal contributes slightly to the occipital face, interparietal only slightly wider than high, supraoccipital low, paroccipital process slender; incisors and canine of intermediate size, four to five postcanine teeth; symphysis of lower jaw sloping, dentary slender, ridge on lamina reflecta rather weak. For character illustration see figure 36.

Sigogneau listed in her diagnosis a number of characters that apply to both genera: skull rather wide posteriorly (however it is of moderate width in both taxa); suborbital arch of medium thickness, zygomatic arch more slender; frontal participates slightly to the supraorbital rim (for *Gorgonops*) and 'frontal contributes only slightly or not at all to the supraorbital rim'(for *Scylacops*). From personal observation however I can state that the orbit is reached by the frontal at least in a small area in each species; 'preparietal well developed, postfrontal long and narrow, V. nerve enclosed by the prootic.'

As differences, she listed: 'snout with parallel margins, about as high as wide' for *Gorgonops* and 'snout narrows steadily in anterior direction' for *Scylacops*. The difference is however only very slight. *Scylacops capensis* also has parallel borders whereas the snout narrows somewhat in *Gorgonops kaiseri* and *G. eupachgnathus*. In both taxa the snout is about as high as wide. 'temporal fossa elongated (*G.*) and temporal opening nearly as high as wide' (*S.*). Again the differences are very slight the situation is variable in both genera. 'postorbital bar widens ventrally' (*G.*) and ' postorbital bar with a more constant width throughout its length' (*S.*). This is indeed a character that distinguishes certain specimens from each other but again applies to both genera. 'lacrimal elongated' (*G.*), 'lacrimal rather short'(*S.*). The lacrimal is however also elongated in *Scylacops*. 'occiput triangular, rather low and inclined towards the bottom and the back' (G.), 'occiput wide, few inclined and concave' (S.). In both taxa it is triangular, somewhat inclined and rather concave; ' palatal tuberosties long in *Gorgonops*, shorter in *Scylacops*. This is indeed a difference, at least between *Scylacops* and *G. torvus* as well as *G. dixeyi* but it does not apply to *G. kaiseri*. This variation is however considered as specific. Additional characters only listed for the genus *Gorgonops* were: 'orbit of middle size and paroccipital process situated somewhat anteriorly.' The orbit is

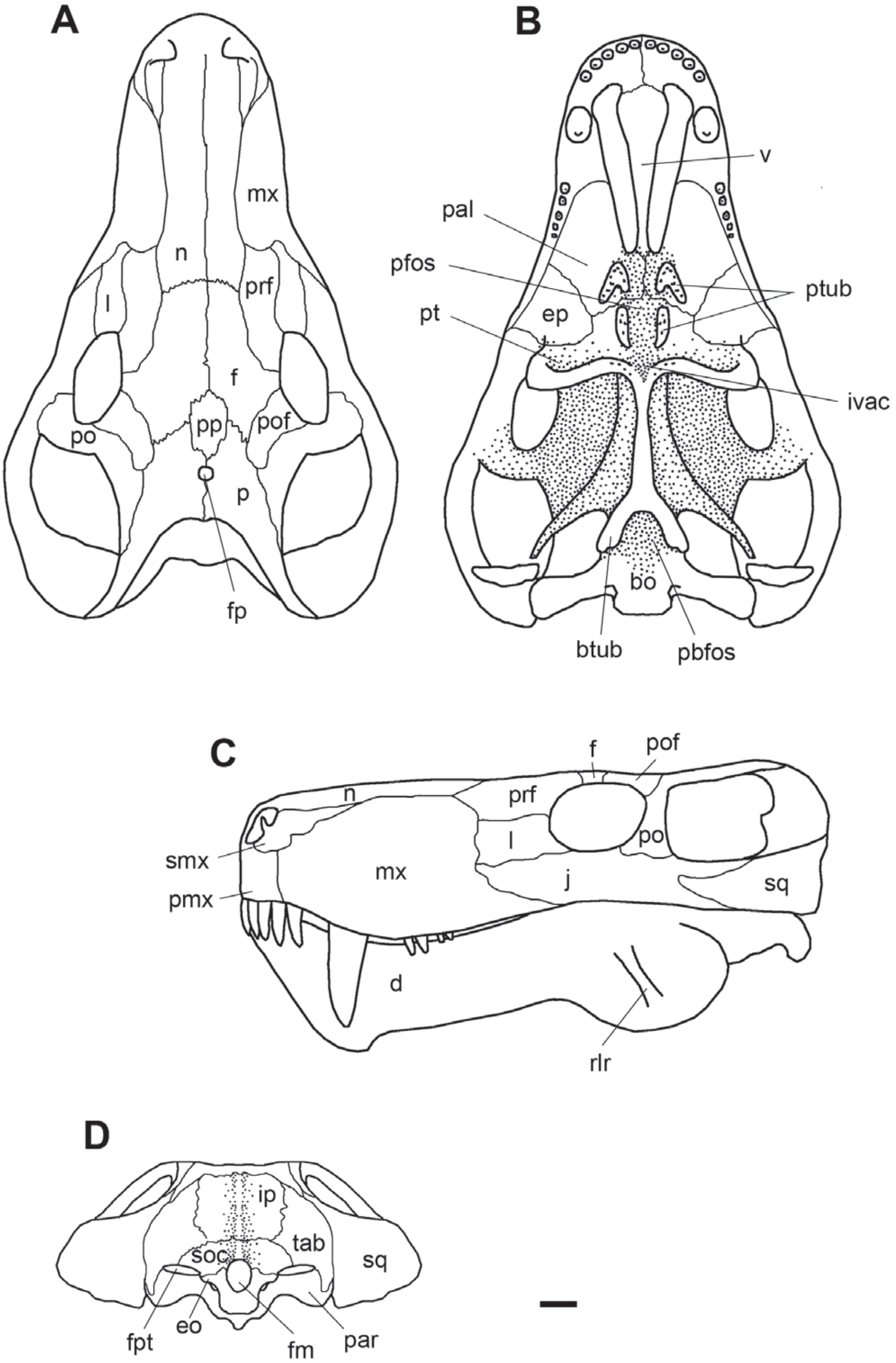


Figure 36. Illustration of the characters in the genus *Gorgonops* Owen, 1876 based on the holotype of the type species, *Gorgonops torvus* (BMNH 1647). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

slightly larger in *Scylacops* but the paroccipital process is also somewhat shifted in anterior direction. For the genus *Scylacops* Sigogneau additionally listed: 'transverse process rather posteriorly situated.' However it is rather anteriorly situated in *Scylacops* as well as in most specimens of *G. torvus* and in the other species where the palate is known, but slightly more posteriorly in *G. longifrons* and AMNH 5515 (*G. torvus*).

As the character analysis above shows that the differences that occur are of minor importance or can be regarded as only a matter of degree it is concluded here that the two genera *Gorgonops* and *Scylacops* must be united. The valid genus name is *Gorgonops* Owen, 1876 with the type species *G. torvus* Owen, 1876. The other five species are: *G. whaitsi* (Broom 1912) in Sigogneau 1970, *G. eupachygnathus* (Watson 1912) in Sigogneau 1970, *G. capensis* (Broom 1913), *G. dixeyi* (Haughton 1927) and *G. kaiseri* (Broili & Schröder 1934). The species *torvus* contains, apart from the holotype (BMNH R 1647), all the referred material listed by Sigogneau (1989) but also the specimen BPI 290 which was referred to the species cf. *whaitsi*: This specimen resembles in its general form, measurements and the shape of the bones the species *torvus* and especially the specimen BPI 277; an allocation to the poorly defined species *whaitsi* does not appear justified. The last referred specimen is SAM 2671 (= *Gorgonognathus longifrons*, = *G. longifrons*).

In the species *capensis* the taxa *Scylacops capensis* and *Scylacops bigendens* are united. The specimen MZC 885 is, however, excluded but its relationships will be discussed later in the text. Sigogneau (1970) already listed a number of characters that apply to both species: In her specific diagnosis she wrote that both species were of medium size, the foramen parietale lay slightly in front of the occipital crest and the frontal contributed only very slightly to the orbital rim. As differences, she listed the higher paroccipital process and the larger postcanine teeth in *bigendens*. These very slight dissimilarities are however regarded as individual variations.

The species *dixeyi* and *kaiseri* will be retained because of the incomplete state of the specimens which does not allow any further assumption concerning the specific relationships. However the allocation to the genus *Gorgonops* is not doubted.

Gorgonops Owen, 1876
Type species: *G. torvus* Owen, 1876

Revised generic diagnosis: snout narrows slightly in anterior direction and is about as high as wide, dorsal skull roof flat and low, skull arches are slender, postorbital bar tends to widen ventrally, pre- and postfrontal large, preparietal medium sized and round, palatal fossa narrow, palatal tuberosities closely situated to the choanae and conspiciously pointed on their anterior ends, basisphenoidal fossa wide, occiput rather wide and only somewhat concave.

Gorgonops torvus Owen, 1876

(= *Gorgonops* cf. *whaitsi* Sigogneau, 1970, = *Gorgonognathus longifrons* Haughton, 1915, = *Gorgonops longifrons* Haughton, 1915 in Sigogneau, 1970)

Holotype: BMNH 1647

Referred material: AMNH 5510, BPI 277, BPI 386, BPI 385, BPI 290, SAM 2671.

Specific diagnosis: interorbital width as wide as intertemporal width, preparietal slightly smaller as in the other species, tuberosities on the palatine inversed V-shaped anteriorly, teeth on the transverse apophyses.

Bibliography: Owen 1876, pp. 27-29, pl. XXI-XXII
Lydekker 1890, p. 111
Seeley 1895, p.1014
Watson 1912, p. 861
Broom 1915, p. 126
Haughton 1915, pp 84-88, fig. 11 (3), pl. XIII (1-3)
Watson 1921, pp. 39-44, fig. 4-6
Haughton 1924, pp. 505-507, fig. 4
Broom1930, pp. 347-348
Boonstra 1934, pp. 181-183, fig. 4
Boonstra 1935, pp. 2-5, fig. 1-3
Manten 1958, pp. 51-67, fig. 22-25 and 28
Sigogneau 1970, pp. 23-38 and 45-51, fig. 11-21 and 24-28, pl. IV (b,c), V, VI (a)
Sigogneau-Russell 1989, pp. 87-90, fig. 216-218 and 220-222

Gorgonops capensis (Broom, 1913) nov.comb.

(= *Sycalacops capensis* Sigogneau 1970, = *Sycocephalus bigendens* Brink & Kitching, 1953, = *Scylacops bigendens* Sigogneau, 1970)

Holotype: SAM 2343

Referred material: SAM 10188, SAM 3444, BPI 266

Specific diagnosis: intertemporal space slightly wider than interorbital space, supraorbital portion of frontal extremely small, preparietal larger as in *G. torvus*, palatal tuberosities confluent.

Bibliography: Broom 1913, pp. 8-12, pl. 6, fig. 5
Broom 1913, pp. 226-227, pl. 36
Haughton 1918, p. 210
Haughton 1924, pp. 501-503, fig. 2
Broom 1925, pp. 312-314, fig. 1

Broom 1930, pl. 28, fig. 16; pl. 29, fig. 24; pl. 34, fig. 44;
Broom 1932, pp. 118, fig 34D, 39A
Boonstra 1934, pp. 142, fig. 1
Brink & Kitching 1953, pp. 27-28, fig. 27A-B
Sigogneau 1970, pp. 112-123, fig. 63-69, pl. XXI-XXII
Sigogneau 1989, pp. 99-101, fig. 242-245

Gorgonops dixeyi Sigogneau-Russell, 1989

(= *Chiwetasaurus dixeyi* Haughton, 1927, = *Gorgonops* ? *dixeyi* Sigogneau 1970)

Holotype: SAM 7846

Specific diagnosis: orbit smaller than in the other species, preparietal round, interparietal square shaped, three postcanine teeth.

Bibliography: Haughton 1927, pp. 71-73, fig. 3-4
Sigogneau 1970, pp. 53-55, fig. 29-30, pl. XIIc
Sigogneau-Russell 1989, pp. 90-91, fig. 223

Gorgonops? eupachygnathus (Watson, 1921)

(= *Scymnosuchus whaitsi* Watson, 1912, = *Scymnognathus whaitsi* Watson, 1912 and 1914, = *Leptotrachelus eupachygnathus* Watson, 1921, = *Leptotracheliscops eupachygnathus* Kuhn, 1965)

Holotype: BMNH R 4051

Specific diagnosis: large supraorbital portion of frontal, preparietal large, basioccipital small, occiput rather concave, four to five postcanine teeth.

Bibliography: Watson 1912, p. 578, fig. 3
Watson 1914, pp. 1027-1032, fig. 3-5
Watson 1921, pp. 55-58, fig. 14-16
Broom 1932, p. 125, fig 41d
Boonstra 1934, pp. 186-188, fig. 6-7
Manten 1958, pp. 66-67
Sigogneau 1970, pp. 51-51, pl. VIb
Sigogneau-Russell 1989, p. 90

Gorgonops*? *kaiseri Sigogneau-Russell, 1989

(=*Pachyrhinos kaiseri* Broili & Schröder, 1934, *Gorgonops kaiseri* Sigogneau, 1970)

Holotype: BSP 1934 VIII 10

Specific diagnosis: prefrontal long and low, interorbital and intertemporal width narrowest of genus, preparietal situated on a boss, postfrontal rather short.

Bibliograpy: Broili & Schröder 1934, pp. 209-223, fig. 1-5, pl. 1
Sigogneau 1970, pp. 55-58, fig. 31, pl. XIIa
Sigogneau-Russell 1989, p. 91, fig. 224

Gorgonops*? *whaitsi Broom, 1912
(= *Scymnognathus whaitsi* Broom, 1912, =*Gorgonops whaitsi* in Sigogneau, 1970)
Holotype: AMNH 5530
Referred material: AMNH 5531
Specific diagnosis (from Sigogneau-Russell, 1989, p.89): Larger than *G. torvus*. Posterior widening of the skull more accentuated. Snout higher? Thicker arches. Smaller orbit. The supraorbital frontal is slightly narrower, the transverse apophyses less posteriorly situated. Finally, the mandibular symphysis is less sloping, and the dentary higher. 4 to 5 postcanines.
Bibliography: Broom 1912, pp. 861-863, pl. Xc, fig. 4-5
Watson 1921, pp. 44-55
Broom 1932, pp. 116, fig 37b-c
Boonstra 1935, p. 8
Sigogneau 1970, pp. 38-44, fig. 22-23, pl. IIIc
Sigogneau-Russell 1989, p. 89, fig. 219

2.2.5 Arctognathus Broom, 1911 and the new genus Njalila

2.2.5.1 Introduction

The genus *Arctognathus* Broom, 1911 contains four species at present: *A. curvimola*, *A. breviceps*, *A. cookei* and *A. nasuta*. However the last two species were allocated by Sigogneau with doubt.

Although the genus *Arctognathus* will be retained here, it is necessary to make some modifications.

First the species *cookei* is omitted and the specimen is allocated to the genus *Aloposaurus* as *Aloposaurus* sp. Further the allocation of the species *A. nasuta* to the genus *Arctognathus* is rejected since many of the characters stand in conflict with Sigogneau's diagnosis and with the new genus diagnosis erected in this account. The species *A. nasuta* with its referred specimens constitutes a genus of its own since I consider the differences between these specimens and any other species as occurring on a generic level. Since the holotype of the invalid genus '*Dixeya*' became holotype of the species *Aelurognathus quadrata*, it is impossible to use the old generic name *Dixeya*. Therefore the genus is named *Njalila* nov. gen. It will be discussed later in the chapter.

Thus only two definite species, *A. curvimola* and *A. breviceps*, remain. They share a number of characters and retain the genus *Arctognathus* as a rather well characterised form:

skull short and compact, broad anteriorly and moderately enlarged posteriorly, outline in dorsal view a short and broad triangle; snout short, as high as wide with a slightly convex dorsal profile, external nares dorsally situated, premaxilla high anteriorly, orbit rather large, interorbital space wide, dorsal profile of skull straight, temporal opening quadratic with dorsal margin somewhat directed dorsally, intertemporal space only slightly wider than interorbital width; septomaxilla short and low, maxillary ridge present, ventral border of maxilla strongly convex, nasal broad and only slightly constricted in the middle, nasofrontal suture roundly pointed and strongly serrated, prefrontal short and high, no elevation in front of the orbita, lacrimal quadratic, no antorbital depression, supraorbital portion of frontal and preparietal small, the latter well separated from the parietal foramen, postfrontal of normal length but rather broad at the orbita, posterior margin straight, postorbital broad dorsally and reaching not far ventrally on the postorbital bar, squamosal reaches almost up to the mid-level of the postorbital bar on the zygomatic arch; postorbital bar slender dorsally but widens in ventral direction, posterior margin straight, zygomatic arch of medium thickness, widens somewhat in posterior direction, no ventral curvature; palatine broad and short, palatine fossa broad and deep, palatine tuberosities confluent and well developed, both have teeth, ectopterygoid rather small but expanded in medial direction, transverse apophyses without teeth and posteriorly situated, interpterygoid vacuity well developed, parabasisphenoid fossa considerably enlarged and broad, basisphenoid tubera long and slender, basioccipital short and massive; occiput slightly more rectangular than quadrate, somewhat concave but not sloping, interparietal quadratic, supraoccipital low, parietal contributes to occipital face, paroccipital process low medially but gets wider laterally, posttemporal fenestra rather large; incisivi well developed, caninus slender but long, four to five medium sized potscanine teeth; lower jaw compact, symphysis high but slightly sloping, dentary high and short, ridge on lamina reflecta moderately developed. For character illustration see figure 37.

First it is necessary to give an historical overview to show the differences between *A. nasuta* and the other species of *Arctognathus*.

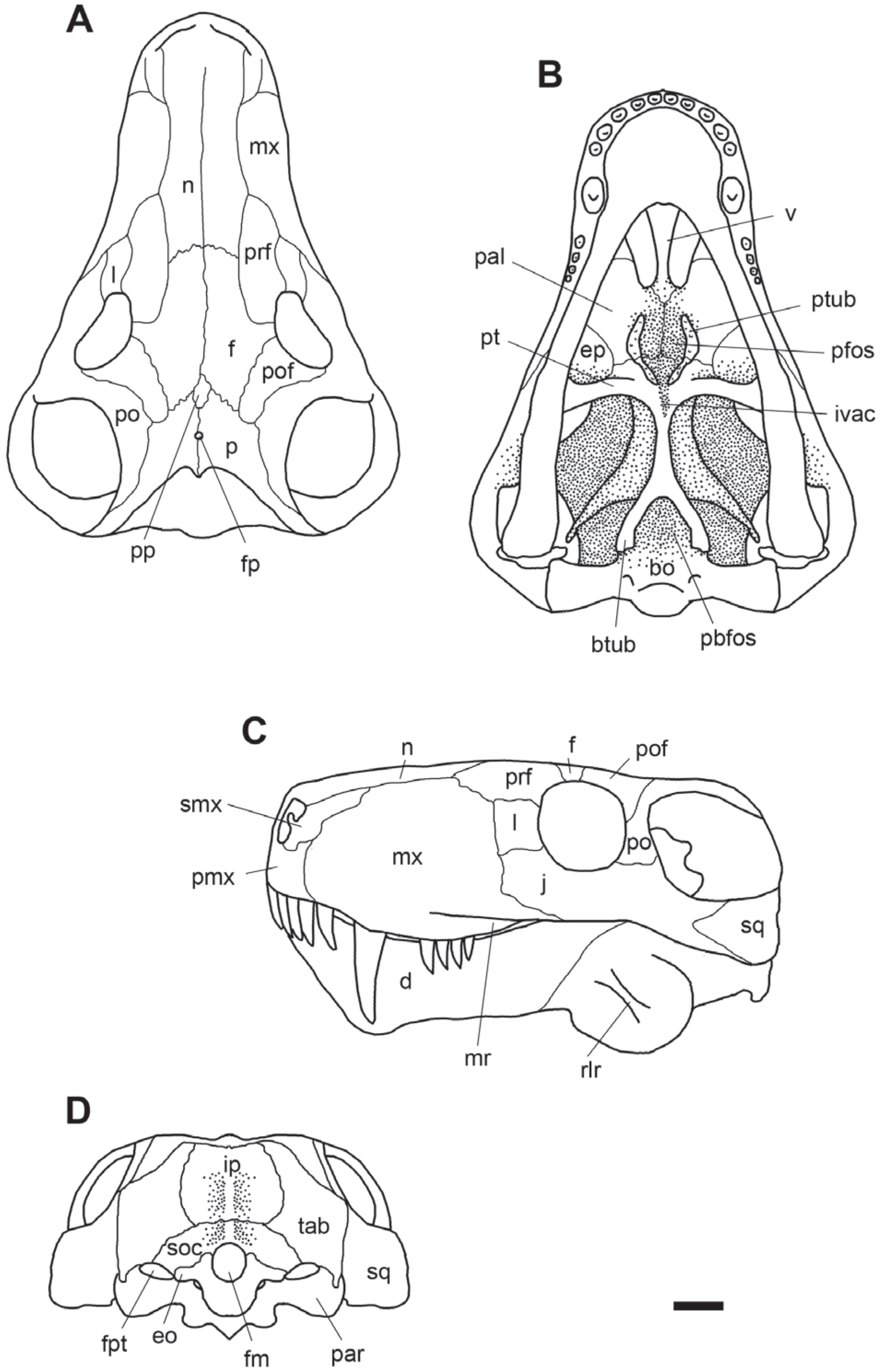


Figure 37. Illustration of the characters in the genus *Arctognathus* Broom, 1911 based on the holotype of the type species, *Arctognathus curvimola* (BMNH 47339). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

2.2.5.2 History of the genus *Arctognathus*

A. curvimola

The type species of *Arctognathus*, *A. curvimola* (BMNH 47339) belongs to the historically earliest known gorgonopsians but is, however, badly preserved, incomplete and weathered. It was first mentioned by OWEN (1876a) as a species of '*Lycosaurus'* (= Theriodontia incertae sedis). In 1876b OWEN gave a more comprehensive account which is however mostly restriced to the description of the teeth. LYDEKKER (1890) allocated the specimen to the genus *Aelurosaurus* because of its general shape as the 'oblique upward inclination' of the symphysis, the backwards inclination of the postorbital bar and the serration of the posterior margin of the postcanine teeth. This allocation however was not accepted by the following authors.

BROOM (1910) stated that BMNH 47339 might certainly belong to a different genus than *Lycosaurus* and thus suggested the new generic name *Arctognathus* (BROOM 1911). WATSON (1913 and 1921) mentioned the broad and short skull, the rounded snout with a small septomaxilla and the short and deep maxilla with a convex ventral margin.

BOONSTRA (1934) gave another detailed account in which he commented on WATSON's description. As primitive characters he saw: the preorbital depression (which is however weak), the large septomaxilla with a large foramen, the rod-like epipterygoid and the wide space between the fenestrae ovales. As advanced characters he stated: the short and rounded snout, the not exclusively laterally directed orbits, the small postfrontal, the small preparietal, the short and deep maxilla, the convex ventral dentigerous border without a step, the anteriorly situated transverese apophyses, the reduced interorbital and intertemporal widths, the fairly large temporal openings and the reduced basisphenoidal tubera.

SIGOGNEAU (1970) again referred to WATSON's and BOONSTRA's descriptions. She stated that the occiput was rather vertical, the vomer deep, the palatine and pterygoid remarkably sloping, the palatal fossa was wide but shallow, the high and slender transverse apophyses had no teeth and where situated posteriorly (contra BOONSTRA) and that there were five incisors instead of four (the fifth is reduced which I can confirm from personal observation). Further she mentioned a probable relationship with *Aelurosaurus*, seeing *Arctognathus* as a more evolved species of the latter but because of other forms that were also similar to *Arctognathus* but not as much to *Aelurosaurus* she refrained from combining both taxa.

Referred material

SIGOGNEAU (1970) referred another specimen, SAM 3329 to the genus. It concerns an anterior part of a skull and mandible and was first described by HAUGHTON (1929) as '*Lycaenodontoides' bathyrhinus*. He compared it to *Aelurosaurus felinus*, but according to him SAM 3329 differed from this taxon by a larger size, the details of its structure and the marked convex border of the maxilla without a step. Furthermore, he stated that the parietal region was probably as wide as the interorbital, the peparital was very small, the orbit round, the lacrimal small, the prefrontal large and that there where six postcanine teeth. BROOM (1932) added the large contribution of the frontal to the supraorbital rim and the long and slender caninus. BOONSTRA (1934) mentioned some aspects of the palate as the short ectopterygoid and suggested that the palate on the whole was very similar to that of *Arctognathus curvimola*.

SIGOGNEAU (1970) emphasised the distinct convex border without the step in front of the canine, already mentioned by HAUGHTON, as the generic definition of the genus *Arctognathus*. Further she saw the allocation of SAM 3329 to the genus and species *Arctognathus curvimola* confirmed by the following characters that are shared with the holotype: the same short and massive snout with a rounded section, the short lacrimal and septomaxilla, the small preparietal and supraorbital portion of the frontal, the fifth incisivus shorter than the others and the powerful symphysis.

Arctognathus cf. *curvimola*

Besides, SIGOGNEAU (1970) assigned two specimens with some reservation to the species as cf. *curvimola*. The first is a well preserved skull (BPI 174) which was first decribed by BROOM & ROBINSON (1948) as *Lycaenops pricei*. They mentioned the rounded snout, the moderately large and round orbits, the very small parietal foramen, the small supraorbital portion of the frontal, the large prefrontal, the narrow and long nasal, the short septomaxilla, the long canine, the four postcanine teeth and the deep sympysis. They considered it as a species of *Lycaenops* though the skull was considerably broader and shorter and the preparietal was smaller.

SIGOGNEAU (1970) recognised many affinities to the preceeding specimens in the specimen such as the rounded snout which was as high as wide, the temporal fossa being higher than long, the slender postorbital bar and broader suborbital arch, the small preparietal and supraorbital frontal, the short prefrontal, lacrimal and septomaxilla, the vertical occiput, the slender and posteriorly situated transverse apophyses, the shallow palatal fossa and the reduced palatine tuberosities, the deep vomer, the powerful symphysis and the five strong postcanine teeth. On the other hand this specimen differed, according to her, in the following characters from the preceeding ones: the intertemporal width was larger in relation to the interorbital width, the dentary was rather slender, the snout slightly longer, the skull base more massive. But Sigogneau was of the opinion that the agreements with *Arctognathus* were more convincing than with *Lycaenops*. Further she described BPI 174 as having a long posterior maxilla process, a short postorbital on the postorbital bar, a posteriorly situated foramen parietale, a long postfrontal, a rather small interparietal and supraoccipital, a slender paroccipital process and a short lamina reflecta.

Despite the existing differences I consider the allocation of BPI 174 to the genus *Arctognathus* as justified. Furthermore, I am of the opinion that those differences occur on an individual level and thus regard the specimen as referred to the species *A. curvimola*.

The second referred specimen is SAM 11490 which was undescribed until Sigogneau (1970) but consists only of a snout and will therefore regarded here as Gorgonopsia indet.

A. breviceps

The holotype SAM 9345 was first described by Boonstra (1934) as '*Arctognathoides' breviceps* gen. et sp. nov. It concerns a skull and mandible that are rather complete but somewhat eroded. Boonstra already mentioned the close resemblance between SAM 9345 and '*Lycaenodontoides'* as well as *Arctognathus* which are both combined in the species *A. curvimola* now. Boonstra stated that the snout was broad, short and relatively high. However, according to him, it differed from *Arctognathus* by having the interorbital region wider than the parietal region and the transverse apophyses situated more anteriorly. Further he described the palate as highly vaulted, the occiput as nearly vertical, the orbits as facing more outwards than upwards, the snout as having a square cross-section, the arches as strong, the preparietal as small, the supraobital portion of the frontal as rather large, the parietal foramen as small and situated posteriorly, the temporal fenestra as large and the six postcanine teeth as rather large.

Sigogneau (1970) remarked that the specimen was somewhat unusual because of the exceptionally short and square snout. Further she added only few extra points to Boonstra's description: the postfrontal was rather long but narrow, the septomaxilla and prefrontal short, the nasal wide, the parietal participated in the occiput, the paroccipital process was shifted anteriorly to a great extent, the base of the skull was massive and the mandible stocky and heavy. She concluded in regarding the species *breviceps* as a more specialized form than *curvimola*.

A.?cookei

The holotype (BPI 648) which lacks the posterior part of the skull was first described by Broom (1948) as '*Cyniscops' cookei* sp.nov. He mentioned the small preparietal, the narrow postfrontal, the small supraorbital portion of the frontal (which is however of medium size), the temporal region only slightly wider than the interorbital region, the large prefrontals, seven molars and teeth on the transverse apophyses. He did not specify his allocation and only stated that the new species differed from the other forms of '*Cyniscops'* by the very small size of the preparietal.

Sigogneau (1970) pointed out that the snout of this small specimen narrowed in anterior direction. Further she remarked on the small orbits (which are indeed rather large), the rather large interorbital with, the slender skull arches, the large supraorbital portion of the frontal (contra Broom), the V-shaped naso-frontal suture, the quadratic lacrimal and the posteriorly situated transverse apophyses. In her opinion the attribution to the genus '*Cyniscops'*, which is now a synonym of *Cyonosaurus*, is doubtful because of the different proportions of the kull roof and the lacrimal. These conditions would rather evoke *Aelurosaurus* or *Arctognathus* but because of the small preparietal and the position of the transverse apophyses she rather chose the latter. In 1989 she, however, stated that this specimen could be more closely related to *Aloposaurus* than to *Arctognathus*.

Although the specimen is incomplete it clearly shows a number of characters which point to an immature state: small size, large orbit, relatively short snout, slender skull arches, v-shaped and anteriorly situated naso-frontal suture, narrow postfrontal, the narrow palatal fossa with parallel tuberosities, teeth on the transverse apophyses and the seven postcanine teeth. With the assumption that it represents a young individual it is, however, difficult to state which genus BPI 648 belongs to. However if such characters as a short snout become longer during growth the specimen would have a longer snout than any adult *Arctognathus* specimen. Further the anteriorly pointed and rather narrow snout itself differs from the heavy and rather broad snout in the *Arctognathus* specimens. Therefore I reject a relationship with the genus *Arctognathus* and propose an allocation to the genus *Aloposaurus* as already suggested by Sigogneau-Russell (1989). With this taxon BPI 648 shares the small size, the ventrally situated external nares, the straight ventral margin of the maxilla, the elongate choanae and ectopterygoid and the narrow palatal fossa. However, a specific allocation is not possible since the incomplete state of the specimen does not allow any statements about the posterior part of the skull. Thus I regard BPI 648 as *Aloposaurus* sp.

2.2.5.3 History of *Njalila* nov. gen.

Introduction

All specimens which constitute the species *Arctognathus*? *nasuta* and cf. *Arctognathus*? *nasuta* formerly belonged to the genus and species '*Dixeya' nasuta* and '*Dixeya*' *quadrata*, beeing now a nomen dubium (Sigogneau, 1970).

The holotype of the type species '*Dixeya*' *quadrata* Haughton, 1927 was SAM 7856. This specimen, however, is now the type of *Aelurognathus quadrata* (Sigogneau, 1970) and is discussed in the *Aelurognathus* section

The other specimens referred to the taxon '*Dixeya*' were allocated to the genus *Arctognathus*, thus omitting the genus '*Dixeya*' completely. Since the species *quadrata* was already occupied, Sigogneau combined all referred specimens in the taxon *Arctognathus nasuta*, although with a dubious position. Indeed it would be doubtful to retain the genus '*Dixeya*' established on SAM 7856 which lacks the snout and thus the most distinctive part of a number of animals which could be easily grouped together. These specimens might well belong to a genus of their own and should not be allocated to the genus *Arctognathus* because of a number of differences which will be discussed later in the text. On the other hand all the specimens in question are from the eastern part of Africa, either Malawi or Tanzania and it might only be a geographic variation of one of the known genera. In the following text all options will be discussed but first I will provide a short overview over their history. For a better overview the list below shows the different specimens with their numbers and synonyms:

'*Dixeya*' *quadrata* Haughton, 1927
SAM 7856; holotype; Chiweta/Malawi…….……………………...*Aelurognathus quadrata*; holotype
BPI 390 (unpublished); Luangwa/Zambia…………..…………………….*Aelurognathus quadrata*
BPI 389 (unpublished); Luangwa/Zambia…………..…………………….*Aelurognathus quadrata*
BPI 3303 (unpublished); Luangwa/Zambia………..……………………...*Aelurognathus quadrata*

'*Dixeya*' *quadrata* det. von Huene 1950
GPIT/RE/7120; holotype; Ruhuhu/Tanzania……………………………….*Arctognathus*? cf. *nasuta*
GPIT/RE/7121; Ruhuhu/Tanzania………………………………………….*Arctognathus*? cf. *nasuta*

'*Dixeya*' *quadrata* det. Parrington, 1955
MZC886;Ruhuhu/Tanzania………………………………………………….*Arctognathus*?cf.*nasuta*
MZC876;Ruhuhu/Tanzania………………………………………………….*Arctognathus*?cf.*nasuta*

MZC887;Ruhuhu/Tanzania……………………………………………… *Arctognathus*?cf.*nasuta*

'*Dixeya*' *nasuta* VON HUENE, 1950
GPIT/RE/7118; holotype; Ruhuhu/Tanzania……………………… *Arctognathus*? *nasuta*; holotype
GPIT/RE/7119; Ruhuhu/Tanzania…………………………………………… *Arctognathus*? *nasuta*

GPIT/RE/7120 and GPIT/RE/7121

VON HUENE (1950) allocated two specimens GPIT/RE/7120 (former IGP K 41) and GPIT/RE/7121 (former IGP K 115) to HAUGHTON's (1927) genus and species *Dixeya quadrata*. It concerns two skulls that are somewhat incomplete and which lack the skull arches, however, GPIT/RE/7120 is the better preserved. VON HUENE described it as having a narrow and streched skull, with the occiput beeing narrow and strongly concave. The foramen parietale, which was situated just in front of the occipital crest, was small, surrounded by a ridge and close to the anteriorly pointed preparietal. The postfrontal was broad, the transverse apophyses had teeth and there were four postcanine teeth. Further he stated that the orbit and the preserved parts of the temporal openings would correspond to HAUGHTON's figures. He did not mention the restriction on the nasal/maxilla border behind the septomaxilla which gives the snout its characteristic shape but indicated this feature in his figure.

SIGOGNEAU (1970) allocated GPIT/RE/7120 GPIT/RE/7121 to the genus *Arctognathus* as *A*.cf. *nasuta* however with a dubious position. Concerning the first specimen she wrote that the skull appeared to be narrower posteriorly than in the preceeding specimens but this might be due to compression. However, the interorbital space was comparatively slightly wider as in the holotype, the temporal fossa was extended, the snout short, the parietal foramen was large, the septomaxilla, maxilla and lacrimal had the same shape as GPIT/RE/7119, the occiput was high and only slightly inclined, the interparietal was large, the vomer wide, the choanae long, the palatal fossa shallow, the palate flat, the transverse apophyses had teeth, the basisphenoid fossa was narrow and deep, the skull base was massive and there were also four postcanine teeth.

GPIT/RE/7118 and GPIT/RE/7119

In VON HUENE's collection were two additional specimens (GPIT/RE/7118 = IGP K 52 and GPIT/RE/7119 = IGP K 96) which resembled GPIT/RE/7120 and GPIT/RE/7121 rather well, however he erected the new species *nasuta*. GPIT/RE/7118 is the better preserved (see figs 38 & 39) VON HUENE saw the snout broader as in the species *quadrata*, the foramen parietale as situated more anteriorly and the preparietal as smaller. Although he also admitted that it was situated near the occipital crest in GPIT/RE/7119. Further he described the skull as having a small supraorbital portion of the frontal, a broad postfrontal with a blunt posterior margin, a square lacrimal, no step in the maxillary border (but slightly more accentuated as in *quadrata*) and having four postcanine teeth. Although he does not mention it for GPIT/RE/7118, he pointed out that GPIT/RE/7119 had teeth on the transvere apophyses.

Sigogneau (1970) allocated GPIT/RE/7118 and GPIT/RE/7119 to the genus *Arctognathus* as species *nasuta* although with a dubious position. She saw the same heavy appearance in the skull as in the other *Arctognathus* species and especially the snout was shorter than in *breviceps*. According to her, the intertemporal space was wider than the interorbital one, the septomaxilla was short, the palate flat, the palatal fossa wide and shallow, the vomer short, the skull basis massive but the parabasispenoid fossa shallower than in *A. curvimola*. Concerning *Aelurognathus quadrata*, she stated that the snout was probably higher and longer and the transverse apophyses were more anteriorly situated. Especially the latter character suggests, according to her, a close relationship to *Arctognathus curvimola*, but here she also recognised differences such as the lower and wider snout, the narrower interorbital space, the flat palate and the less convex ventral maxillary border of GPIT/RE/7118.

MZC 886, MZC 887 and MZC 876

Parrington (1955) described a well preserved skull and mandible which he assigned to the species *quadrata*. Parrington stated that the skull was ‘remarkably straight sided with the zygomatic arches showing no lateral expansions.’ The snout got its distinct appearance because it was markedly hollowed on each side in the region of the posterior parts of the septomaxilla. This gave it ‘a curious pinched appearance which appears to be quite characteristic.’ Furthermore, the borders of the orbits were raised above the main level of the frontals, the parietal was well developed, the postfrontal broad posteriorly, the parietal foramen was situated on a boss, the nasofrontal suture was straight, the supraorbita frontal was of medium size, there was a moderate step in the ventral border of the maxilla in front of the caninus, there was a maxillary ridge, the choanae were broad, the palate was vaulted and wide and there were five postcanine teeth.

Since MZC 886 was already described in detail by Parrington, Sigogneau (1970) only added a few points: the orbits were larger than in the preceeding specimen and the relation of the interorbital and intertemporal width smaller than in the holotype but larger than in GPIT/RE/7120. The parietal contributed to the occiput and the mandible was low as in the other species of *Arctognathus*.

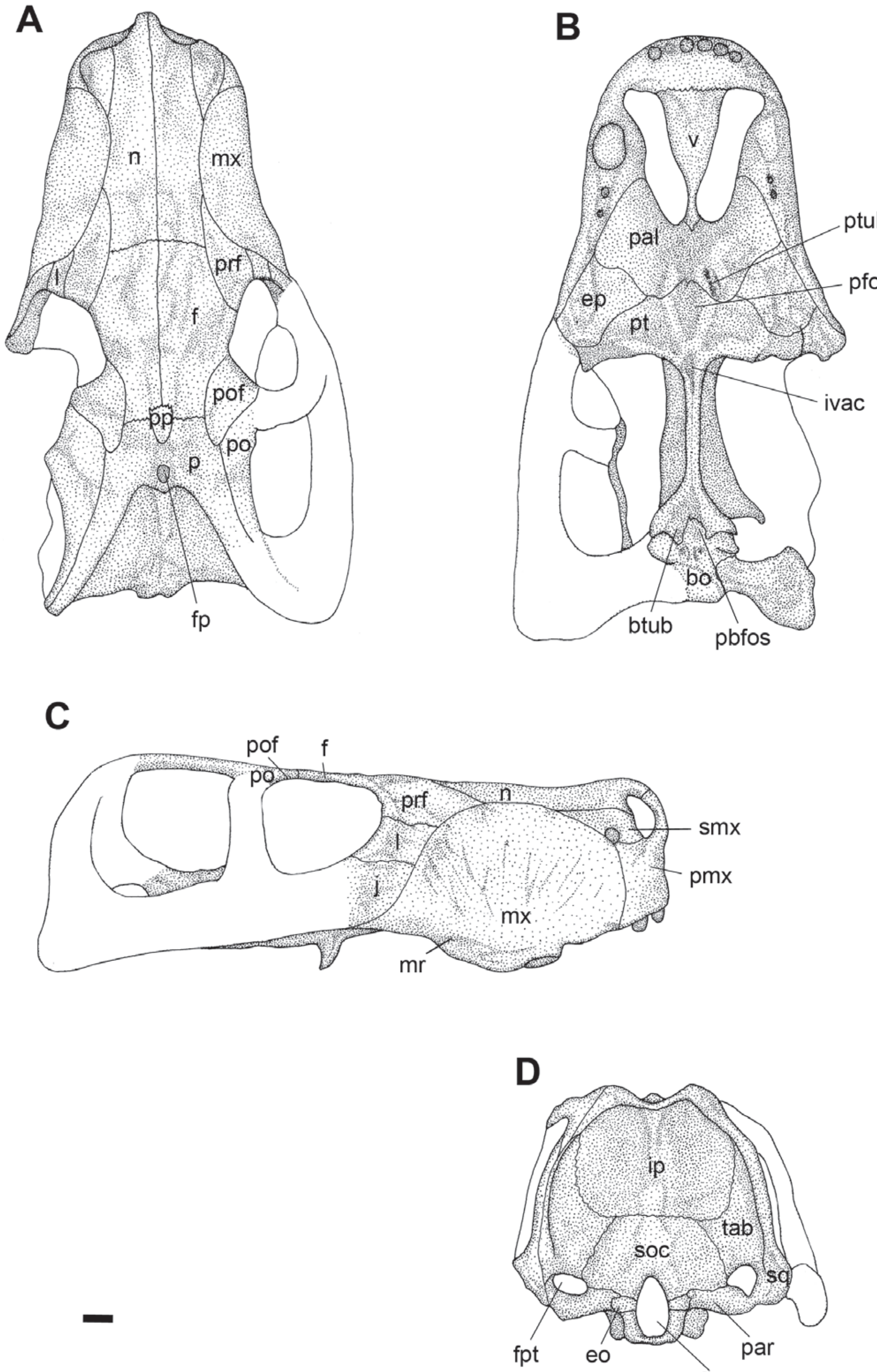


Figure 38. Drawings of GPIT/RE/7118 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

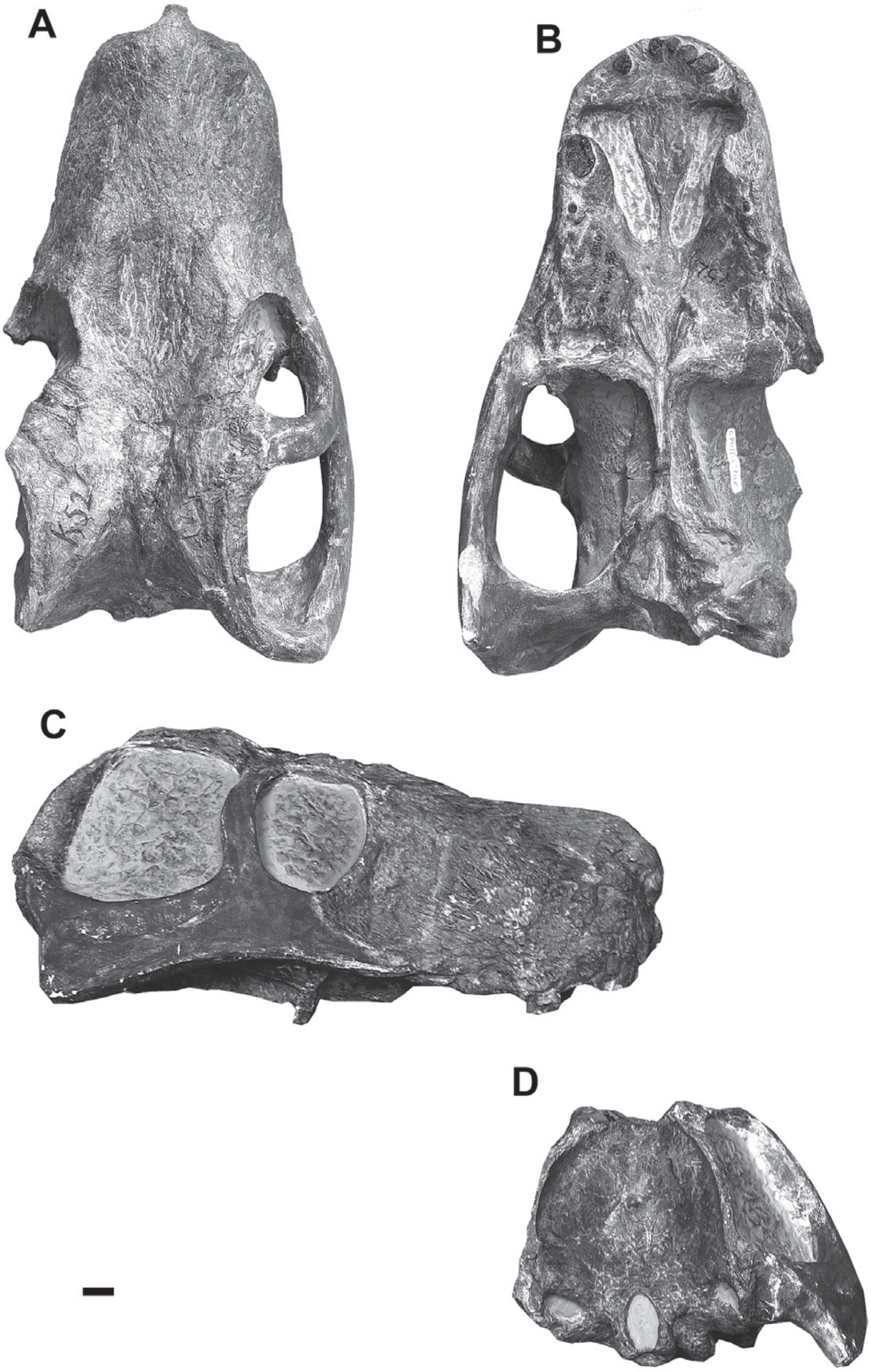


Figure 39. Photographs of GPIT/RE/7118 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

Discussion

The fact that almost all specimens which constituted the species '*Dixeya' quadrata* and '*Dixeya' nasuta* were allocated with a dubious position to the genus *Arctognathus* by SIGOGNEAU indicates their differences and peculiarities quite well. Furthermore, previous authors such as VON HUENE and PARRINGTON did not doubt their generic independence. Although this account aims to make gorgonopsian systematic more transparent by reducing the number of taxa, in this case it is necessary to combine certain specimens in a taxon of their own. An allocation to the genus *Arctognathus* for these specimens is hampered by many points in my opinion.

Although the skull is short and compact in both genera, it is less wide posteriorly in '*Dixeya'*. Further, since the snout is already broad and not as high as in *Arctognathus*, the difference in width between the anterior and posterior parts of the skull is less marked in '*Dixeya'*. The appearance of the snout is rather distinctive in '*Dixeya'* with its dorsally pointed tip and the bulged septomaxilla where it forms the border of the external nares. This feature is most conspicuously developed in GPIT/RE/7118 but can also be distinguished in all other specimens, whereas it is not found in any other taxon. Therefore I consider this peculiar formed snout as a truly unique character. The snout is also somewhat longer than in *Arctognathus*. Posteriorly the dorsal skull roof is somewhat concave in '*Dixeya*' whereas it is straight in *Arctognathus*. Furthermore, the temporal opening is more elongate, the supraorbital portion of the frontal and the preparietal are larger, the alveolar border is less convex and the skull base and the dentary are more slender in '*Dixeya'*. Although both taxa have short and broad palatines and wide ectopterygoids, the palatal fossa is situated more posteriorly in '*Dixeya'*. This taxon additionally shows a well developed depression anteriorly to the palatal fossa, which is comparatively broad and deep and slopes anteriorly.

Furthermore, the two taxa are different in the following points: In '*Dixeya'* the nasal is narrower, the prefrontal is situated on a more distinctive elevation, the preparietal is situated closer to the parietal foramen, the postorbital reaches further ventrally on the postorbital bar, the skull arches are more slender, the palatal fossa is narrower, the palatal tuberosities are less developed, especially the palatine ones, the parabasisphenoid fossa is shorter, the occiput is more quadratic, the parietal does not contribute to the occipital face, the supraoccipital is lower and the incisors are smaller.

This comparison shows that the differences are too many and besides do clearly not occur on a specific level, since the taxon '*Dixeya'* illustrates some characters which separate it not only from the genus *Arctognathus* but also from any other known genus. Apart from these characters the specimens of the genus '*Dixeya'* share all following characters:

skull already broad anteriorly but only slightly enlarged posteriorly, distinct groove mesially and parallel to the prefrontal elevation, zygomatic arch straight and not flaring much laterally; dorsal profile curved, snout with distinctive appearance: dorsally pointed and constricted laterally dorsal to the septomaxilla foramen, wider than high, dorsal skull roof somewhat concave, posterior part of skull dorsally directed, orbit rather large, interorbital width narrow, orbits visible in dorsal view as large triangles, temporal opening quadratic, temporal space only slightly wider than interorbital width; septomaxilla short and low, maxilla comparatively low with slight convex ventral border, maxillary ridge present, nasal broad but constricted in the middle, nasofrontal suture straight and anteriorly situated, prefrontal short, situated on a distinct elevation, lacrimal quadratic without antorbital depression, supraorbital portion of the frontal and preparietal medium sized, the latter situated close to the parietal foramen, postfrontal broad and short with a rounded posterior margin, dorsal postorbital narrow, lateral postorbital reaches far ventrally on the postorbital bar, squamosal reaches up to the anterior margin of the temporal fenstra on the zygomatic arch; suborbital arch slender, postorbital bar particularly slender with posterior margin curved anteriorly, zygomatic arch rather slender and straight; vomer broad and only narrow for a short distance posteriorly, palatine broad and short, palatine fossa comparatively narrow and shallow, tuberosities less developed and rather confluent, anterior edges of palatine tuberosities pointing towards each other, teeth present on both tuberosities, ectopterygoid large and expanded mesially, transverse apophyses centrally situated, with a few teeth, interpterygoid vacuity well developed but elongated and narrow, parabasisphenoid fossa narrow, elongated and deep, basisphenoid tubera moderately developed, basioccipital long and slender; occiput high to quadratic, concave and sloping, parietal does not contribute to occipital surface, interparietal only slightly wider than high, supraoccipital low, paroccipital process short and stout; incisivi comparatively small, caninus ordinarily developed, four to five small postcanine teeth; lower jaw slender, symphysis sloping, dentary with chin, ridge on lamina reflecta moderately developed. (see figure 40 for illustration.)

Therefore I propose that the specimens which constitute the taxa *A.*? *nasuta* and *A.*? cf. *nasuta* form a genus of their own. This genus is named *Njalila* and contains the two species *nasuta* and *insigna* nov. sp. In the species *nasuta* all specimens which constituted the taxa *A.*? *nasuta* and *A.*? cf. *nasuta* are combined, whereas the species *insigna* consists of MZC 885 which was originally described by PARRINGTON (1955) as a referred specimen of *Scylacops capensis*. The specimen has already been discussed in the chapter 2.2.4.

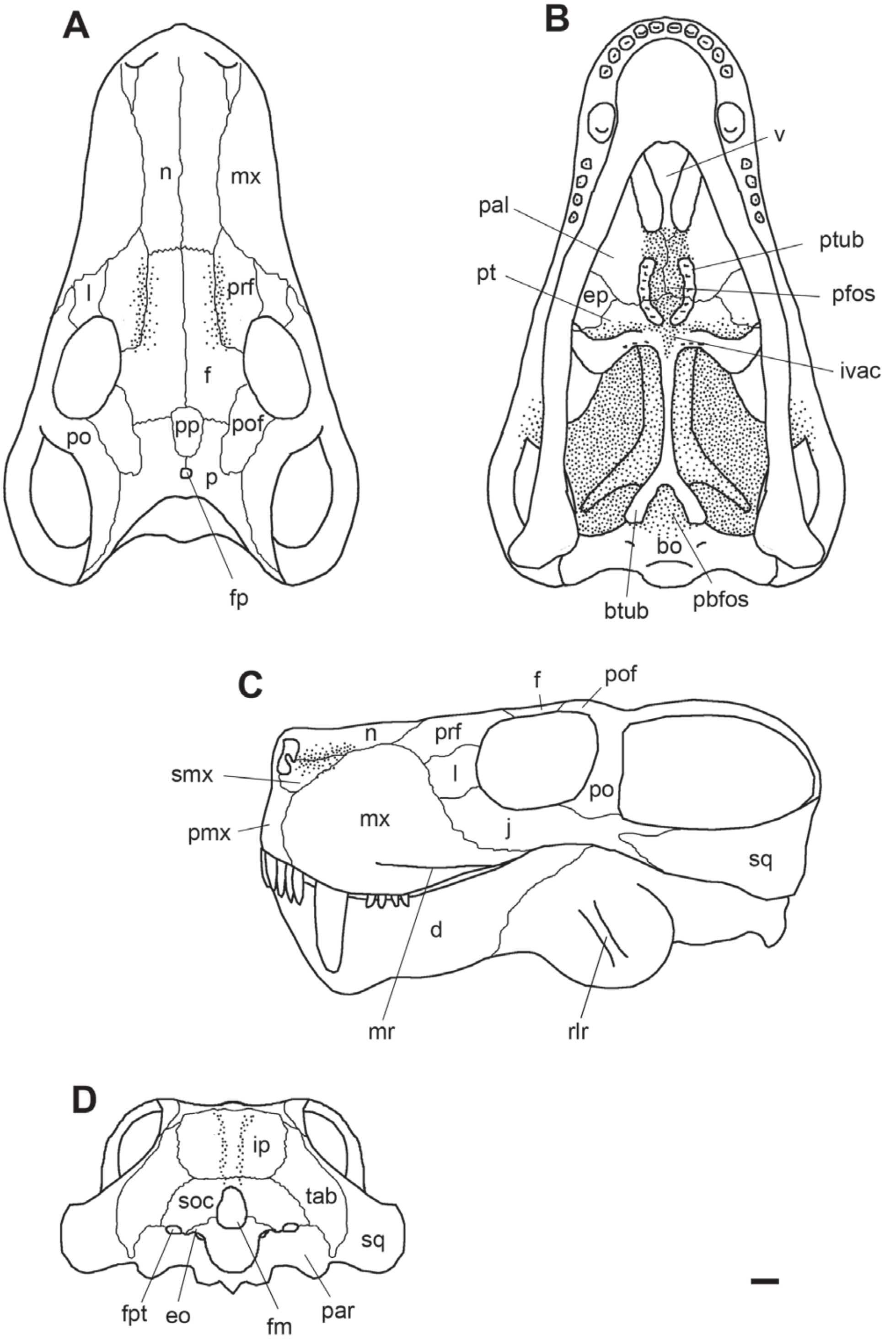


Figure 40. Illustration of the characters in the genus *Njalila* nov.gen. based on the holotype of the type species, *Njalila nasuta* (GPIT/RE/7118) and MZC 885 (*Njalila insigna*). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 10 mm.

Systematic Paleontology

Genus: ***Arctognathus*** BROOM, 1911

Type species: *Lycosaurus curvimola* OWEN, 1876

Revised generic diagnosis: skull short and compact wit a straight dorsal profile, snout short and heavy, posterior part of skull moderately enlarged, ventral border of maxilla strongly sinuous, lacrimal short, skull arches moderately enlarged, preparietal very small, supraorbital frontal moderately large, teeth comparatively strong, temporal opening quadrate, maxillary ridge present, prefrontal short and high, palatine broad and short, palatal fossa wide and oval, para-basisphenoid fossa considerably large, basisphenoid tubera long and slender, interparietal quadrate, symphysis somewhat sloping but high, dentary short, five to six postcanine teeth.

Arctognathus curvimola (OWEN, 1876)

(= *Lycosaurus curvimola* OWEN, 1876, = SEELEY, 1895, =*Aelurosaurus curvimola* LYDEKKER, 1890, =*Lycaenodontoides bathyrhinus* BOONSTRA, 1934)

Holotype: BMNH 47339

Referred material: SAM 3329

Specific diagnosis: palatal fossa oval, orbit large and round, dentary exceptionally short, posterior part of skull markedly short.

Bibliography: OWEN 1876a, pp. 357-359, fig. 8
OWEN 1876b, pp. 71-73, pl. LX8
LYDEKKER 1890, pp.77-78
BROOM 1910c, p. 20
BROOM 1911, p. 1079
WATSON 1913, p. 77, fig.6-7
WATSON 1921, pp. 60-64, fig.18-20
BOONSTRA 1934c, pp. 203-209, fig. 15-17
SIGOGNEAU 1970, pp. 82-86, fig. 47-48, pl. 17c
SIGOGNEAU-RUSSELL 1989, pp. 75-76

Arctognathus cf. ***curvimola***

1. BPI 174 (= *Lycaenops pricei* BROOM & ROBINSON, 1948)

Bibliography: BROOM &ROBINSON 1948, pp. 400-401, fig. 5-6
SIGOGNEAU 1970, pp. 87-91, fig. 49-51, pl. 16a,b
SIGOGNEAU-RUSSELL 1989, pp. 75-76, fig. 186-188

2. SAM 11490

Bibliography: SIGOGNEAU 1970, p. 91
SIGOGNEAU-RUSSELL 1989, p. 76, fig. 189

Arctognathus breviceps (Boonstra, 1934) in Sigogneau, 1970

(= *Arctognathoides breviceps* Boonstra, 1934)

Holotype: SAM 9345

Specific diagnosis: snout short and massive, skull arches thicker than in *A. curvimola*, posterior part of skull more enlarged, occiput concave and wider.

Bibliography: Boonstra 1934b, pp. 143-146, fig. 4 a-d; 5 c-d; 6 f-h; 8 d-e
Sigogneau 1970, pp. 61-95, fig. 52-54, pl. 18a-b
Sigogneau-Russell 1989, pp. 76-77, fig. 190-191

Genus: *Njalila* nov. gen.

Derivatio nominis: after the tributary Njalila of the Ruhuhu River in South-western Tanzania, the region where most of the specimens come from.

Type species: *Dixeya nasuta* von Huene, 1950

Locus typicus: Kingori, Ruhuhu-Valley, Tanzania

Generic diagnosis: tip of snout pointing dorsally, septomaxilla bulged anteriorly while forming the lateral margin of the external nares, dorsal skull roof concave between the orbits, prefrontal short and situated on a marked elevation, posterior part of skull barely enlarged, skull arches slender, preparietal small and situated closely to the parietal foramen, palate with pre-fossa, palatal tuberosities little developed, basicranium slender, occiput quadrate, interparietal small, symphysis sloping, dentary slender.

Njalila nasuta (von Huene, 1950)

(= *Dixeya quadrata* von Huene, 1950, = *Dixeya nasuta* von Huene, 1950, = *Arctognathus*? *nasuta* Sigogneau, 1970, = *Arctognathus*? cf. *nasuta* Sigogneau, 1970)

Holotype: GPIT/RE/7118

Referred material: GPIT/RE/7119, GPIT/RE/7120, GPIT/RE/7121, MZC 886, MZC 887,
MZC 876

Specific diagnosis: tip of the snout strongly pointed dorsally, dorsal profile straight, orbit round, postfrontal small, prefrontal situated on pronounced elevation; vomer broad anteriorly, narrows only at the posterior-most part.

Bibliography: von Huene 1950, pp. 91-96, fig. 36-38
Parrington 1955, pp. 15-20, fig. 9-10
Sigogneau 1970, pp. 97-104, fig. 56-60, pl. 19-20
Sigogneau-Russell 1989, pp. 77-78, fig. 192

Njalila insigna nov. sp.
(= *Scylacops capensis* (Broom, 1913) in Parrington, 1955)
Holotype: MZC 885
Derivatio nominis: from the latin word 'insigna' which means remarkable or conspicuous.

Specific diagnosis: dorsal profile of snout somewhat sloping, skull arches somewhat stronger than in *N. nasuta*, palatal fossa narrow, intertemporal space as wide as interorbital, posterior part of skull more enlarged

Bibliography: Parrington 1955, pp. 9-15, fig. 5-8
Sigogneau 1970, p. 118, fig. 67
Sigogneau-Russell 1989, p. 100

2.2.6 Lycaenops Broom, 1925, Aelurognathus Haughton, 1924 and Prorubidgea Broom, 1940

2.2.6.1 Introduction

The genera *Lycaenops*, *Aelurognathus* and *Prorubidgea* were always hardly distinguishable since they share a number of characters. The history of the taxa in the literature clearly illustrates their insecure taxonomy. This is shown first by the fact that some of the species that today form the genera *Lycaenops* and *Aelurognathus* were united together in the genus '*Scymnognathus',* which is however no longer valid, its species are now distributed between the genera *Lycaenops*, *Aelurognathus* and *Gorgonops* (the latter including the type–species of *G. whaitsi*). The taxa which formerly were attributed to *Scymnognathus* are *Lycaenops angusticeps*, *Lycaenops* cf. *angusticeps*, *Aelurognathus sollasi* and *Aelurognathus parringtoni*. These new allocations were made by Sigogneau (1970) and at the same time she made some other changes within those three genera. Thus *Aelurognathus minor* and *A. microdon* became *Lycaenops*? *minor* and *L. microdon,* whereas '*Lycaeniodes angusticeps*' (BPI 259) was allocated to *Aelurognathus* as cf. *serratidens*. Finally *Lycaenops alticeps* was made *Prorubidgea alticeps*. The distinction between the specimens of these three taxa is indeed very slight but exists and is somewhat overlapping from one to the other.

In this account it is considered that the species that form the three genera *Lycaenops*, *Aelurognathus* and *Prorubidgea* can be grouped together in two genera. This implies two important achievements: Firstly I was able to present a diagnosis which separates the two taxa *Lycaenops* and *Aelurognathus* definitely. In order to achieve this I had to make some re-arrangements of the taxonomic position of different specimens that constitute the two genera. Secondly I attributed all specimens of the genus *Prorubidgea* to the genus *Aelurognathus*,

thus omitting the taxon *Prorubidgea* completely. The list below provides an overview over the former and new systematic positions of the taxa considered.

Lycaenops ornatus
AMNH 2240; holotype…………*Lycaenops ornatus*
BPI 260, BPI 334, RC 147, RC148…………*Lycaenops ornatus*
Lycaenops angusticeps
AMNH 5537; holotype…………*Lycaenops angusticeps*
AMNH 5535…………*Lycaenops angusticeps*
Lycaenops cf. *angusticeps*
WMUC 1513…………*Lycaenops* cf. *angusticeps*
Lycaenops kingwilli
RC 60; holotype…………*Aelurognathus kingwilli*
Lycaenops? *minor*
BPI 262; holotype…………*Lycaenops sollasi*
RC 119, BPI 264, BPI 281…………*Lycaenops sollasi*
Lycaenops? *microdon*
SAM 9344; holotype…………*Lycaenops* sp.
Lycaenops? tenuirostris
SAM 11744; holotype…………C*yonosaurus tenuirostris*
Aelurognathus tigriceps
SAM 3342; holotype…………*Aelurognathus tigriceps*
SAM 4334, SAM 10071…………*Aelurognathus tigriceps*
Aelurognathus serratidens
SAM 2792; holotype…………*Aelurognathus tigriceps*
Aelurognathus cf. *serratidens*
BPI 259…………*Lycaenops attenuatus* nov. sp.
Aelurognathus nyassaensis
SAM 7847; holotype…………*Aelurognathus tigriceps*
Aelurognathus quadrata
SAM 7856; holotype…………*Lycaenops quadrata*
BPI 390, BPI 389; BPI (FN) 3303…………*Lycaenops quadrata*
Aelurognathus sollasi
BSP 1934 VIII 29, holotype…………*Lycaenops sollasi*
RC 61…………*Lycaenops sollasi*
Aelurognathus? *parringtoni*

GPIT/RE/7113……………………………………………………………*Sauroctonus parringtoni*

Prorubidgea maccabei

RC 34; holotype……………………………………………………….……*Aelurognathus maccabei*

Prorubidgea alticeps

BPI 261; holotype………………………………………….…………*Aelurognathus alticpes*

Prorubidgea brinki

BPI 289; holotype……………………………………….……………*Aelurognathus alticpes*

Prorubidgea broodiei

TMP 1493; holotype……………………………………………………*Aelurognathus broodiei*

Prorubidgea robusta

BPI 249; holotype………………………………………………………*Aelurognathus broodiei*

Arctops? ferox ………………………………………………………..*Aelurognathus ferox*

In the text below I will provide an explanation and discuss the different species of the respective genera successively. By doing this I will also sum up the bibliographic history since knowledge of the record of some specimens is important to comprehend the modifications I made.

The genus *Lycaenops* Broom, 1925 with its six species *L. ornatus*, *L. angusticeps*, *L. kingwilli*, *L.*? *minor*, *L.*? *microdon* and *L.*? *tenuirostris* is discussed first, followed by *Aelurognathus* Haughton 1924 with its six species *A. tigriceps*, *A. serratidens*, *A. nyassaensis*, *A. quadrata*, *A. sollasi* and *A.*? *parringtoni* and last *Prorubidgea* Broom, 1940 with its five species *P. maccabei*, *P. laticeps*, *P. brinki*, *P. broodiei* and *P. robusta*.

2.2.6.2 History of the genus *Lycaenops* Broom, 1925

L. ornatus

The holotype of the type species *Lycaenops ornatus* is AMNH 2240, which was first described by Broom (1925) in a short account. He mentioned the long, narrow and deep skull, the large and subrectangular preparietal and the four small molars. In 1930 he described the postcranial skeleton in detail and gave figures in lateral and dorsal views. In 1932 Broom listed the charcaters as: canine powerful, four postcanine teeth, septomaxilla unusually large, frontals long and forming a little bit of the supraorbital margin, parietal extremely wide, parietal foramen wider than long, preparietal large and wider in front than behind. The most detailed and comprehensive description was however provided by Colbert (1948). This author stated that the skull was of medium size (206 mm) with a great depth and narrowness especially in the snout region. The septomaxilla was indicated as large and prominent, the lacrimal as quadratic, the nasals as large bones which however did not reach as far posteriorly as indicated by Broom (1930), the canine as large; four postcanine teeth were present, the prefrontal was large and elongated, the frontal long and contributing slightly to the oribital rim, the large preparietal was situated just in front of the parietal foramen and formed a long rectangle, the parietals were broad in comparison to their length, the postfrontal was large, the occiput was sloping and concave, the interparietal large, the supraoccipital broad and high and the symphysis deep.

Sigogneau (1970) did not observe the specimen personally but proposed some additonal points. She considered that the relations of the interorbital and intertemporal width were the same as in *Aelurognathus tigriceps* but altogether they were slightly narrower in AMNH 2240. In her opinion, the great width of the intertemporal region, mentioned by Broom, was wide only in relation to the narrowness of the snout, but was of normal gorgonopsian type if compared with other forms. Further she stated, that the nasofrontal suture was V-shaped and the postfrontal did not reach far ventrally on the postorbital bar. At the end she indicated the resemblance with *Aelurognathus* but considered *Lycaenops* as somewhat more basal. Indeed she saw it as one of the most primitive genera because of the small temporal openings, the narrow interorbital width, the convex dorsal profile, the inclined occiput, the slender arches and dentary, the short postorbital, the large preparietal and supraorbital portion of the frontal.

Referred material

Brink & Kitching (1953) referred three other specimens to the taxon: BPI 260, RC 147 and RC 148. The authors stated that all specimens resembled the type so well that, given the detailed account of Colbert, they were not worth a description.

Sigogneau (1970) saw some slight but minor differences but did not doubt their allocation to the taxon *L. ornatus*. Further she referred a fourth specimen to *L. ornatus*, BPI 334, which was hitherto undescribed. Sigogneau's attribution is accepted here.

L. angusticeps

The holotype of the species *L. angusticeps* is AMNH 5537 which was first described by Broom (1913) as *Scymnognathus angusticeps*. It is an incomplete and weathered skull that measures appr. 300 mm in length. Broom mentioned that the specimen was a close ally of '*Scymnognathus' tigriceps* (= *Aelurognathus tigriceps*) although it differed by being of a smaller size and having a relatively longer and more slender skull. Further he stated that the snout was extremely long, the orbit large, the temporal fossa small, the squamosal did not reach far anteriorly on the zygomatic arch, the frontal region was narrow, the supraorbital portion of the frontal relatively large, the preparietal small, the sympysis deep but the rest of the jaw was slender. In 1925 Broom changed the name to '*Lycaenoides' angusticeps* being of the opinion that it did not belong to the genus '*Scymnognathus'* because of the presence of a preparietal. Boonstra (1935) doubted the strong dorsal curvature as indicated in Broom's figures by referring to the photo which was added by Broom (1915).

Sigogneau (1970) finally allocated this specimen to the genus *Lycaenops*, but apart from that could not give additional relevant points since she was not able to examine the specimen personally. However she regarded the species *L. angusticeps* as a more evolved one of the genus.

The species *L. angusticeps* is indeed distinguished from all other *Lycaenops* species by its distinctly elongated snout, the accentuated slenderness of the skull arches and its narrow posterior skull part. On the other hand the slightly convex dorsal profile of the snout, the sloping posterior skull part and the curved zygomatic arch obviously characterise it as a member of the genus *Lycaenops*. However, in contrast to Sigogneau I consider this species as a rather basal form within the genus *Lycaenops* namely because of the above listed characters.

L. cf. *angusticeps*:

Sigogneau (1970) also allocated the specimen WMUC 1513 to the genus as cf. *angusticeps*. It was first described by Olson and Broom (1937) as '*Scymnognathus*' *major*. Sigogneau could not examine the specimen personally but she remarked on the long snout, the slender skull arches, the small preparietal, the supraorbital portion of the frontal and the four postcanine teeth. She stated that it might also belong to the species *L. kingwilli*. Since I was not able to observe this specimen, too, its systematic position will remain still uncertain in future.

L. kingwilli

The holotype of the species *kingwilli*, RC 60 was first described by Broom (1948) as '*Tigricephalus' kingwilli* gen. et spec. nov. He stated that the fairly complete specimen measured 320 mm in length and was therefore quite large. It had no preparietal, the parietal foramen was comparably small, the parietals were short but wide, the postfrontals were large and broad, the supraorbital portion of the frontal was small, the snout powerful and deep and the suborbital and postorbital arches were strong. Further he wrongly supposed, that there were only three postcanine teeth, but there clearly are four. In the following text Broom discussed the probable relationships, but excluded *Aelurognathus tigriceps* because it had a preparietal and four postcanine teeth. Thus he suggested '*Gorgonorhinus minor'* (= *Arctops*? *minor*) as probable closest ally because of its three postcanine teeth.

Sigogneau (1970) allocated the specimen to the genus *Lycaenops*. She mentioned the rounded snout which was however shorter and not as wide as in *L. ornatus*, the large orbit, the slightly wider skull arches, the anteriorly short prefrontal, the long and wide postfrontal, the short lacrimal, the long basioccipital, the shallow para-basispehoid fossa, the anteriorly situated transverse apophyses, the high dentary, the powerful lamina reflecta, the strong incisivi, the long caninus; the intertemporal space was only slightly wider than the interorbital space but both being larger than in the type specimen. Concluding she stated that the short and high dentary, the broad suborbital bar, the wider interorbital and intertemporal space and the form of the zygomatic arch strongly resembled *Arctops*? *ferox*. However, since the holotype of *Lycaenops kingwilli* belonged, according to her, to the genus *Lycaenops* without doubt, whereas she thought that *A.*? *ferox* might rather not, she did not unite both taxa.

Discussion

In this account the specimen RC 60 is attributed to *Aelurognathus* as a separate species *A. kingwilli*. Sigogneau (1970) listed in her diagnosis for the species '*L. kingwilli'* the following characters: large size, skull wider, arches tend to be thicker and dentary more massive than in *L. ornatus* and *L. angusticeps*, no preparietal. These characters are, however, considered as generic in this account and clearly point to the genus *Aeluognathus*, as well as the following: heavy skull with well enlarged posterior part, heavy snout, clearly higher than wide, with a strong dorso-lateral constriction, dorsal profile of the snout strongly convex and posterior part of skull sloping, orbit only visible as a slit in dorsal view, maxillary ridge present, nasofrontal suture slightly pointed, serrated and posteriorly situated, lacrimal quadratic, small supraorbital portion of frontal, postorbital reaches far ventral on the postorbital bar, skull arches rather broad, posterior margin of postorbital bar slightly convex, palate broad, palatal tuberosities confluent, interpterygoid vacuity less developed, parabasisphenoidal fossa broad, basioccipital long, occiput wide and concave, supraoccipital wide and low, paroccipital process strong, incisors and canine strong, lower jaw heavy, ridge on lamina reflecta strong. Finally there is hardly any character that is shared with *Lycaenops* except for those few that apply to both taxa, *Lycaenops* and *Aelurognathus*.

L. ? *minor*

The holotype, BPI 262, was first described by Brink & Kitching (1953) as *Aelurognathus minor*. It is a somewhat incomplete and deformed skull which measures 175 mm in length. Brink & Kitching already mentioned its resemblance to *Lycaenops* but allocated the specimen finally to the genus *Aelurognathus* because of the preparietal that was situated close to the parietal foramen, the relatively small postcanine teeth and the sloping symphysis. They considered it closely related to *Aelurognathus sollasi* and also mentioned three referred skulls. One is RC 119, the other two are BPI 264 and 265. The latter was however made the holotype of *Arctops*? *kitchingi* by Sigogneau (1970).

Sigogneau (1970) stated that the snout of BPI 262 had the same rather wide and rounded form as in *Arctognathus* cf. *curvimola* (BPI 174), but was too long. The temporal openings were short and high, the postorbital bar was of moderate thickness troughout its length, the suborbital arch was rather broad anteriorly but narrowed abruptly at the level of the middle of the orbit as in *L. ornatus*, the preorbital bosses were accentuated, there was a preorbital fossa present, the nasofrontal suture was serrated, the lacrimal was slightly longer than high, the supraorbital portion of the frontal small, the preparietal rhombic, the dentary slender and long, the symphysis sloping and there were most probably five postcanine teeth. In the following text she discussed the allocation of Brink & Kitching but stated that the characters upon which they separated *Lycaenops* from *Aelurognathus* were partly due to age, and partly no real distinctions between the two genera since they were present in some species of both genera. But she admitted that BPI 262 might provide a link between the two taxa which were without doubt closely related. However in her opinion the general appearance of BPI 262 more closely resembled the *Lycaenops* type than the heavier built *Aelurognathus* type.

Sigogneau stated that the first referred specimen, RC 119, resembled the holotype closely, except for the presumably narrower interorbital and intertemporal width. BPI 264 differed somewhat in the proportions. The snout was slightly shorter and wider, the suborbital arch slightly broader and did not show the pronounced narrowing at the level of the orbit, the postfrontal and postorbital were wider, the occiput was more vertical, the parabasisphenoid fossa more shallow and the transverse apophyses were situated slightly more anteriorly.

Sigogneau (1970) also referred a third specimen to the species which had been undescribed. In her opinion BPI 281 resembled the general appearance well and differed only slightly in proportions.

The new allocation of this species is discussed in the *Aelurognathus sollasi* section.

L. ? *microdon*

The holotype of this species, SAM 9344, was first described by Boonstra (1934) as a new species of *Aelurognathus*. The author gave a very short account of this weathered skull with its inaccessible palate and provided two figures of the lateral and dorsal views. Boonstra saw the specimen as being without doubt congeneric with *A. tigriceps* and *A. serratidens*, since the shape of the bones was very similar, there was an antorbital depression, too, the snout was high and rounded and the intertemporal space was much wider than the interorbital one. He saw the specific delimitation in the three (instead of four) comparatively small postcanine teeth and in the larger supraorbital portion of the frontal. Sigogneau (1970) allocated the specimen to the genus *Lycaenops* and considered it as intermediate between *L.*? *minor* and *L. ornatus*. The relation of the interorbital and intertemporal spaces and the high and narrow snout were the same as in L. *ornatus* but the orbits were as large as in *L.*?*minor*. She mentioned a slight preorbital fossa, the postorbital bar which was narrow dorsally and wide ventrally, the well developed preparietal, the postorbital which narrowed rapidly in posterior direction, the rectangular nasofrontal suture, the short septomaxilla, the slightly longer than high lacrimal, the more posteriorly situated transverse apophyses with teeth and the dentary which was long and slender as in ?*minor*. Finally she stated that she regarded this specimen closer to *Lycaenops* than to *Aelurognathus* because of its relatively large orbits and slender skull arches. She refrained however from allocating it to either the species *L. ornatus* or *L.*? *minor* because of the presence of teeth on the transverse apophyses.

I see the specimen SAM 9344 also definitely closer to *Lycaenops* than to *Aelurognathus*. However, this heavily weathered and incomplete skull allows no conclusion concerning its specific allocation and is therefore considered as *Lycaenops* sp.

L. ?*tenuirostris*

The holotype of the species SAM 11744, which comes from Tanzania, measures 190 mm in length and was first described by Boonstra (1953) as '*Tangagorgon*' *tenuirostris* gen. et sp. nov. Boonstra mentioned that the snout was higher than wide, narrow and long, the temporal openings were of medium size and oval, the parietal foramen small and posteriorly situated, the supraorbital portion of the frontal was small, the incisivi were medium-sized and the four postcanine teeth small.

Sigogneau (1970) described the specimen as having a high and pointed snout which narrowed anteriorly. The interorbital and intertemporal space was rather wide compared to this otherwise lightly built skull, the large and rhombic preparietal reached the parietal foramen, the postorbital was narrow, the nasal wide, the lacrimal elongated, the basioccipital long, the parabasisphenoid fossa short and deep, the transverse apophyses were situated anteriorly, the palatal tuberosities were long and the ones on the pterygoid were separated from the palatine ones by a pronounced trench, the choanae and the vomer were long as well and the dentary short.

In the following discussion Sigogneau pointed out that the slender form of the specimen rather recalls the image of *Cyonosaurus*, but the interorbital and intertemporal width were too large. She considered that *Aelurognathus* differed in the shorter snout and higher lacrimal and so the only genus remained *Lycaenops*. However she saw in SAM 11744 the most primitive species because of its comparatively low snout.

Discussion

SAM 11744 resembles the characters of the genus *Lycaenops* rather poorly. On the other hand, it recalls more the genus *Cyonosaurus* with its overall slenderness of the skull, long and pointed snout, markedly slender skull arches, elongate temporal opening, narrow postfrontal, rhombic and medium sized preparietal, narrow vomer and palatal fossa and the slender mandible with extremely sloping symphysis and long dentary. Although Sigogneau saw the interorbital and intertemporal widths as too large for *Cyonosaurus* in SAM 11744, I regard this character as only specific and thus the specimen is allocated to the genus *Cyonosaurus* as species *tenuirostris*. Indeed, especially the interorbital space is considerably wider than in the other *Cyonosaurus* species but the intertemporal width does not differ that much. The retaining of the separate species is justified by the Tanzanian provenance of the specimen.

2.2.6.3 History of the genus *Aelurognathus* Haughton, 1924

A. tigriceps

The type species of the genus *Aelurognathus* is *A. tigriceps* with SAM 2342 as holotype. It is a somewhat incomplete and crushed skull which measures 305 mm in length and was first described by Broom & Haughton (1913) as a new species of '*Scymnognathus*'. They mentioned that it was more powerful than '*Scymnognathus*' *whaitsi* (= *Gorgonops whaitsi*), the septomaxilla was large, it had four postcanine teeth, the incisors were large, the lacrimal and prefrontals large, the suborbital bar was thick, the preparietal close to the parietal foramen, the postfrontal well developed, the interparietal well developed and deep and the symphysis powerful and deep. Broom (1913) described the palate and lower jaw in detail and added that the basisphenoid was very large. Haughton (1924) established the new genus *Aelurognathus,* making *A. tigriceps* the type species with SAM 2342 as holotype, but however he did not justify his decision. He only explains that the snout was not so rounded as that in '*Scy. whaitsi'*. Further he stated that there was no step in front of the canine, the septomaxilla, ectopterygoids and palatines were large and there was a weak antorbital depression. In 1932 Broom shortly listed *A. tigriceps* in his classification and gave an additional figure in dorsal view.

Sigogneau (1970) pointed out that this skull was rather characteristic with its heavy appearance. She mentioned that the snout was long and high with a rounded contour, the temporal opening was high, the orbit small, the suborbital arch thick but the zygomatic arch rather slender, the postorbital bar was somewhat incomplete but seemed to be of moderate thickness and with a constant width troughout its length, the intertemporal width was moderate, the preparietal large, the postfrontal long and narrow, the postorbital narrowed rapidly in posterior direction, the prefrontal was long, the nasofrontal suture was posteriorly situated, the supraorbital portion of the frontal was small, the septomaxilla wide, the lacrimal as high as long, the occiput was vertical and concave, the interparietal high, the paroccipital process was slanting, the basisphenoid fossa was rather long and deep, the transverse apophyses were anteriorly situated and had no teeth and the ectopterygoid was narrow.

Referred material

The first to *A. tigriceps* referred specimen is SAM 4334 which was already allocated to the taxon by Haughton (1918) who supposed that this somewhat compressed skull which he called large (225 mm in length) might be closely allied to SAM 2342.

Sigogneau (1970) confirmed this suggestion and pointed out that it resembled the type in most characters. In 1970 she referred another specimen to the taxon which was hitherto undescribed. SAM 10071 is however rather poorly preserved especially the snout. With 210 mm it is also smaller than the type but resembled it otherwise perfectly.

A. nyassaensis

The holotype of the species, SAM 7847 from Malawi, was first described by Haughton (1927) as *Aelurognathus nyassaensis*. This rather large specimen is weathered and lacks the posterior part of the skull. Haughton saw a close resemblance with *Aelurognathus* but mentioned that it differed from the species *tigriceps* by the number of postcanine teeth, which he presumed was one in SAM 7847. Further he stated that the snout was higher than wide, the lacrimal elongated, there was a preorbital fossa, the orbit was slightly overhung by the prefrontal, the nasal was narrow, the frontal reached the orbit, the preparietal was small and rhombic and the lower jaw massive with a deep symphysis. SIGOGNEAU (1970) considered the specimen as closely comparable to the species *tigriceps* and referred it to this species as *Aelurognathus* cf. *tigriceps*. However, she refrains from allocating it completely to this taxon since SAM 7847 had a broader postorbital bar and snout as *A. tigriceps*. This and its overall more massive appearance was the reason why she re-established the species *nyassaensis* in 1989.

A. serratidens

The holotype of *A. serratidens*, SAM 2792, was first described by HAUGHTON (1915). He allocated this specimen, which lacks the posterior part of the skull to the genus '*Scymnognathus'* as a new species *serratidens*. HAUGHTON pointed out that it was smaller than '*Scy.' whaitsi* or '*Scy.' tigriceps* (snout length 125 mm). Further it had four postcanines, a very small supraorbital portion of the frontal, an oval and large preparietal which was well separated from the parietal foramen, a preorbital fossa, long nasals, a weaker symphysis which was sloping and a ridge on top of the snout. In 1924 HAUGHTON provided figures in lateral, dorsal and ventral views and added a description of the palate which had been recently prepared. Thus he stated that the palatal fossa was narrow and deep, the palatines and pterygoid tuberosities had teeth, the choanae were long and the transverse apophyses massive. The snout was higher than wide, with a rounded cross-section, there was no step in the maxillary border and the septomaxilla was large. Further he declared that this specimen also belonged to the genus *Aelurognathus* as well as the species *tigriceps*, since they both were different from '*Scy.' whaitsi*.

BROOM (1932) mentioned in his classification, that the species *tigriceps* and *serratidens* were closely related, the latter probably beeing a young individual of the first taxon. However they differed in the size of the parietal foramen (large in *serratidens*, small in *tigriceps*).

SIGOGNEAU (1970) additionally mentioned that SAM 2792 was very similar to the preceeding species but also differed in some ways. The snout was high, the orbit larger than in *tigriceps*, the preorbital fossa, although according to her, oversizedly drawn by HAUGHTON, was nevertheless present, the nasofrontal suture was V-shaped as in *tigriceps*, the prefrontal particularly long the septomaxilla short but high, the transverse apophyses were however situated more posteriorly. At the end she concluded that this specimen indeed could be synonymous with *tigriceps*, of which it would be a young form as already suggested by Broom (1932) but refrained from uniting the species *tigriceps* and *serratidens* because SAM 2792 did not correspond well with SAM 4334 (referred specimen of *A. tigriceps*).

Discussion

As already indicated, most of the above mentioned authors already saw a close relationship between the three species *A. tigriceps*, *A. serratidens* and *A. nyassaensis*. Sigogneau only hesitated to unite *A. tigriceps* and *A. serratidens* since the preparietal of the latter was larger. It is nonetheless only somewhat larger but shows otherwise the same round form with the indented margin. Both taxa have further a number of characters in common: short septomaxilla, high maxilla with conspicuously long posterior process, slightly elongate lacrimal, very narrow supraorbital portion of the frontal, short dentary. Besides the overall appearance with the heavy snout and the almost straight symphysis does not justify a specific separation between *A. tigriceps* and *A. serratidens*. *A. nyassaensis* is referred to the species *A. tigriceps* because of the same characters listed above. Although Sigogneau saw a more massive form with a wider snout and heavier skull arches these differences are very slight and are considered as individual variation. Thus the specimens of the species *A. nyassaensis* and *A. serratidens* will be attributed to the species *A. tigriceps* and thus the taxa *A. nyassaensis* and *A. serratidens* become redundant.

Aelurognathus cf. *serratidens*

Sigogneau (1970) allocated BPI 259 as *Aelurognathus* cf. *serratidens* to the genus and species. This extremely laterally compressed specimen was first described by Brink & Kitching (1953) as a referred specimen of '*Lycaenoides*' *angusticeps* (= *Lycaenops angusticeps*). They mentioned that the skull was with 265 mm slightly smaller than the type and although they admit that there were some differences between it and the type they 'consider them not to be of specific importance.' They stated that the preparietal was larger in their specimen, the parietal foramen large and situated on a boss, the supraorbital portion of the frontal was very small, the zygomatic arch was more slender than in the type and it had five postcanine teeth.

Sigogneau (1970) saw the specimen still as high and narrow, even after correction of the lateral depression. The snout was however not rounded anteriorly, the interorbital space only slightly wider than the interorbital one, the suborbital bar broad, the zygomatic arch missing, the orbit small, the delimitation of the preparietal uncertain (contra BRINK & KITCHING), the postorbital narrow posterodorsally, the frontal nearly excluded from the orbital rim, the lacrimal elongated, the supraoccipital was as high as the interparietal but not as wide, the paroccipital process was low and slightly shifted anteriorly, the parabasispenoid fossa relatively short, the transverse apophyses were slightly more anteriorly situated than in the preceding specimens, the dentary was short and high and the symphysis powerful. Further she considered the differences between BPI 259 and the type of '*Lycaenoides*' that were listed by BRINK & KITCHING as generic but as she stated in 1989, p. 68: 'The incompleteness of the type of *Aelurognathus serratidens* however, prevents a complete assimilation of BPI 259 to this species.'

Discussion

BPI 259 clearly can not be attributed to the species *serratidens*. In comparison with SAM 2792 (*A. serratidens*) the snout is lower, sloping, pointed anteriorly and only very slightly constricted dorsolaterally, the premaxilla is low, the ventral border of the maxilla more convex, there is no ridge on the maxilla, the nasofrontal suture is anteriorly situated and straight, the lacrimal is elongated, the preparietal is situated close to the foramen parietale, the palate is elongated, the tuberosities on the palate are well separated from each other, the interpterygoid vacuity is well developed, the caninus is more slender and the postcanine teeth are smaller. Referring to other characters concerning the posterior part of the skull no comparison can be made since this part is missing in the holotype. Mostly because of the above mentioned characters this specimen is attributed to the genus *Lycaenops* since it shares most of the characters in the posterior part of the skull with this genus: the temporal opening is slighly elongated, the posterior part of the skull is only slightly enlarged and the dorsal profile is straight, the postfrontal is narrow with a straight posterior margin, the skull arches are moderately thick, the basisphenoidal tubera are slender, the supraoccipital high and the paroccipital process low. Although the orbit is comparatively small, the interparietal rather wide and the supraorbital frontal small, these resemblances with *Aelurognathus* are considered as specific peculiarities and thus the specimen is allocated to the genus *Lycaenops* as the new species *L. attentuatus*.

A. quadrata

Haughton (1927) erected his new genus and species *Dixeya quadrata* from Malawi upon a skull (SAM 7856) that lacks the anterior parts of the snout but did not give an explanation concerning the distinctions of this specimen with other forms. He described it as having four rather small postcanine teeth, the snout being rather higher than wide at the level of the canini but becoming more square in cross-section in front of the orbits with a flatter surface, the orbits as looking almost entirely outwards, the parietal foramen as situated on a small boss, the occiput as almost vertical, the jugal as being a large bone (hence the processes of the maxilla and squamosal were not very pronounced), the lacrimal, prefrontal and supraorbital portion of the frontal as being large, the front part of the palate as beeing vaulted and the transverse apophyses as having teeth.

Sigogneau (1970) saw the square section of the snout as artificial, the temporal openings as higher than wide, the orbits large, the interorbital space as only slightly narrower than the intertemporal width, both being large, the postorbital bar widened ventrally; there was no preorbital fossa, the parietal foramen was small and situated near to the long and narrow preparietal, the supraorbital frontal was moderate, the postorbital narrows considerably alongside the temporal fossa, the lacrimal was elongated, the occiput was vertical and concave, the slender paroccipital process was slightly shifted anteriorly, the palatal fossa was narrow and deep, there were teeth on the transverse processes, the basisphenoid fossa was short and deep and the basioccipital was long. In the following discussion she excluded the taxa *Gorgonops*, *Scylacops* and *Arctognathus* because of the proportions of the snout, but rather mentioned *Arctops* and *Aelurognathus* for comparison. However she also excluded *Arctops* for the difference in the interorbital and intertemporal widths and the position of the transverse apophyses. With *Aelurognathus,* finally, she saw accordance in the proportions, the snout, the skull roof and the palate. Further she attributed three other specimens to the taxon which were collected by Kitching during an expedition to the Upper Luangwa valley in Zambia in the early 1960ies and were undescribed hitherto (BPI 390, BPI 389 and BPI FN 3309).

Sigogneau (1970) mentioned that they all correspond fairly well to the holotype, and if different in proportions or sutures, this was only to a slight degree. However, she also admitted that they ‘are more similar to each other than any one is to the type’.

Discussion

Sigogneau and Haughton had mentioned the square section of the snout which differentiated this species from *Lycaenops* however this feature would distinguish the taxon *quadrata* also from *Aelurognathus*. The species *L. microdon* on the other hand also shows a snout which is almost as wide as high and therefore links the two taxa together. Nevertheless this feature is clearly specific for *quadrata* and be due to geographic variation as already pointed out by Sigogneau (1970). Another character that would correspond imperfectly with the genus *Lycaenops* is the temporal opening that seems to be higher than wide in the holotype. This feature however is due to compression and after correction it would have the normal quadratic shape as in the referred specimens.

Sigogneau (1970) listed as species diagnosis for *A. quadrata* already some characters that apply for the diagnosis of the genus *Lycaenops* in my sense. Thus, according to her, the size was medium, the snout was wider, the suborbital and postorbital bars thinner, the orbits larger, the supraorbital frontal larger and the dentary more slender than in the other species, the lacrimal was longer than high and there were teeth on the transverse apophyses. She did not mention the genus *Lycaenops* in her discussion and indeed the holotype of *A. quadrata* shows a somewhat more blunt appearance than the comparatively more gracile *Lycaenops ornatus*. However the referred specimens and especially BPI FN 3303 link this species reasonably to the genus *Lycaenops*. Moreover the species *quadrata* shares a great number of other characters with this genus and thus the allocation is more than justified: posterior part of skull moderately enlarged, snout pointed anteriorly, dorsal profile of snout straight, dorsal profile of posterior part of skull straight respecively slightly declining, ventral border of maxilla strongly convex, orbit large and well visible in dorsal view, maxilla without ridge, nasofrontal suture anteriorly situated and straight, postfrontal rather narrow, preparietal close to parietal foramen, postorbital gets wider ventrally, palatal fossa narrow, tuberosities rounded and separated by a trench, few teeth on transverse apophyses, basisphenoidal tubera slender, paroccipital process low, slender lower jaw.

Aelurognathus on the other hand is clearly distinguished by its heavier skull, the higher and narrower snout, broader skull arches, broader palatines, confluent tuberosities of the palate, stronger canine and the heavier lower jaw with the straight symphysis.

A. sollasi

The type specimen of this species (MS 1934 VIII 29) was first described by Broili &Schröder (1935). They admitted that the skull was very incomplete since it consisted only of a snout which is strongly weathered. *A. sollasi* had a preorbital fossa, the maxilla was only slightly longer than high, the nasalia were narrow and long, the palatal fossa deep, the transverse apophyses had teeth and were comparatively anteriorly situated, the ectopterygoid was large, the symphysis powerful and slightly sloping and there were three comparatively small postcanine teeth in the upper and four in the lower jaw. In the following discussion they stated that the specimen had the strongest resemblance with the genera '*Scymnognathus*'and *Aelurognathus* since the general form and the proportions were the same (rounded snout, preorbital fossa, no step in the maxilla border, form of the symphysis). They concluded that the specimen, although showing some slight differences with the respective species of *Aelurognathus*, definitely belonged to this genus and erected the new species *A. sollasi*.

Sigogneau (1970) was of the opinion that the snout was not as flattened as indicated by Broili & Schröder and the suborbital arch might not have been that broad (but this part of the skull is missing nonetheless). She noticed that the nasals were slightly constricted in the middle, the maxilla reached not far posteriorly under the orbit, the lacrimal was quadratic, the jugal of moderate height and the palatal fossa was wide (contra Broili & Schröder). In the following discussion she stated that most points Broili & Schröder listed for their specimen could be used to define the genus *Aelurognathus* (for example: snout higher than wide, with vertical lateral faces and a rounded contour). However she saw the specific distinctions (number of postcanine teeth, teeth on the tuberosites of the palate and other slight variations) as somewhat doubtful and admitted that she would not have retained this species if there was not a specimen (RC 61) which recalls MS 1934 VIII 29.

This slightly weathered and also incomplete specimen measures appr. 160 mm in length and was first described by Broom (1948) as '*Scymnognathus' holmesi* sp. nov. Broom mentioned the very large preparietal, the relatively large postorbital which formed most of the orbital margin, the large postfrontal, the slightly sloping occiput, the large incisors and the four postcanine teeth. Sigogneau (1970) mentioned the stocky appearance of the specimen, the high and rounded snout, the large orbits, the rather slender suborbital bar, the absence of a preorbital fossa, the large preparietal and parietal foramen, the straight posteriorly situated naso-frontal suture, the short septomaxilla and lacrimal, the interparietal of normal size and the four or five postcanine teeth. In the following discussion she also mentioned *Lycaenops* as a closely related form especially with regard to the skull arches. Within the genus *Aelurognathus* she saw some similarities with *A. serratidens* but this species differed by the smaller size of the orbits, the smaller supraorbital portion of the frontal and the form of the lacrimal for example. She concluded that the concordance between RC 61 and MS 1934 VIII 29 would justify the maintenance of the species *sollasi*.

Discussion

Aelurognathus sollasi is assigned to the genus *Lycaenops* mostly because of the same reasons as the species *quadrata*. Sigogneau already mentioned in her species diagnosis the medium size, the larger orbits, larger supraorbital portion of the frontal and more slender dentary than in the other species of *Aelurognathus* and the teeth on the transverse apophyses. Here again the more slender appearance with the sloping dorsal profile of the snout and the rather low premaxilla as well as the sloping symphysis with its 'chin' is reminiscent of the genus *Lycaenops*. The snout is pointed anteriorly, only slightly higher than wide and only very slightly constricted dorsolaterally, the nasofrontal suture is anteriorly situated and straight, the preparietal is situated closely to the parietal foramen, the canine is slender and the orbit large and well visible in dorsal view. The posterior part of the skull is slightly more enlarged as in the other species but this part is incomplete and deformed in the referred specimen RC 61 whereas the holotype only consists of a snout. However the heavier posterior skull part is considered as specific and links the taxon with the genus *Aelurognathus* as the most evolved species of the genus *Lycaenops*.

Within the new combination *Lycaenops sollasi* is placed also the taxon *L. minor*. Brink and Kitching (1953) already mentioned a close relationship with *Aelurognathus sollasi* and Sigogneau (1970) saw the species *L. minor* as a link between the two genera *Lycaenops* and *Aelurognathus*. Indeed both taxa show the same convex and slightly sloping dorsal profile of the snout, the sloping symphysis with the relatively shorter dentary (if compared to the other *Lycaenops* species) and the broad palatal fossa. Therefore I consider both taxa as conspecific. All specimens of the previous taxa *Lycaenops minor* will be allocated to the species *L. sollasi* and thus the species *L. minor* becomes a nomen dubium.

Arctops? *ferox*

The last species which will be attributed to the genus *Aelurognathus* is *Arctops? ferox*. It is however the least certain since Sigogneau (1970) already mentioned the somewhat particular characters which would almost constitute a separate genus. The species is composed of its holotype RC 62 and four referred specimens.

Sigogneau allocated them to the genus *Arctops* since she sees most resemblances with this taxon. Indeed the specimens possess a few characters cited in her generic diagnosis for *Arctops*: wide posterior part of the skull, heavy and high snout, small orbit, broad suborbital bar, long postfrontal, wide occiput, long basioccipital, powerful symphysis and long canine. But these characters also apply to the genus *Aelurognathus*, and besides, the species *ferox* does not fit well into the new diagnosis of the genus *Scylacognathus*. There were already some characters in Sigogneau's diagnosis that clearly separate the species *ferox* from the other species of the genus *Arctops*: very large size, very wider intertemporal region, postorbital wide dorsally, no teeth on transverse apophyses, which are slightly more anteriorly situated than in the other species. The species *ferox* here again shows the characteristics of the genus *Aelurognathus* (in my sense). Moreover the snout is convex and constricted dorso-laterally, the dorsal profile of the posterior part of the skull is slightly sloping, the premaxilla is high anteriorly, the orbit is only visible as a slit in dorsal view, the septomaxilla is constricted above the septomaxilla foramen, the maxillary ridge is present, the nasofrontal suture is anteriorly situated and slightly pointed and the postorbital reaches far ventrally on the postorbital bar. Especially the palate resembles that of *Aelurognathus* perfectly with a short and broad palatine, the elongated and confluent palatal tuberosities, the large ectopterygoid, the less developed interpterygoid vacuity, the broad para-basisphenoid fossa, the slender and elongated basisphenoidal tubera and the long basioccipital. Also the occiput is wide and concave, the interparietal wider than high, the supraoccipital is comparatively narrow. The greatest difference is, however, found in the postorbital bar which is extremely narrow for such an otherwise rather heavy skull. Furthermore the snout is somewhat broader and longer in comparison to the posterior part of the skull. Although these features would rather point to the genus *Arctops*, respectively, indicate a separate genus. However, the similarities which are shared with the genus *Aelurognathus* are considered here to be sufficient to allocate the species *ferox* to this genus. The broader snout and the narrow postorbital bar are regarded as specific peculiarities.

Prorubidgea Broom, 1940

P. maccabei

The holotype of the type species (RC 34) is a well preserved skull and mandible that measures 310 mm in length and was first described by Broom (1940). In this account he also gave two figures in lateral and dorsal views, (however, the figure captions mistakenly read '*Prorubidgea pugnax')*. Broom mentioned that the well developed parietal foramen was situated near the occiput and surrounded by a ridge, the temporal fenestra was large, the postorbital bar strong, the postfrontal rather broad, the preparietal well developed (it is small indeed), the supraorbital portion of the frontal small, the prefrontal long and narrow, the lacrimal short, the snout narrow, the maxilla deep and that there were five postcanine teeth.

Sigogneau (1970) added that the skull was notably widened posteriorly, the temporal opening was as high as wide, the posterior margin of the postorbital bar strongly convex, the zygomatic arch only a little less wider than the suborbital arch and also only slightly expanded in ventral direction, there was no preorbital fossa, the preparietal and supraorbital portions of the frontal were small, the postfrontal long and narrow, the nasal constricted in the middle, the lacrimal short, the jugal slightly expanded in lateral direction, the squamosal wing particularly wide, the occiput vertical and strongly concave, the interparietal large, the transverse apophyses were anteriorly situated, without teeth and stood vertically, the teeth on the palatal tuberosities of the palatine were larger than the ones on the pterygoid tuberosities; she noted that the palatal fossa might have been shallower than it appears now, the dentary was relatively low, the lamina reflecta well developed, the incisivi were strong and there were probably six postcanine teeth.

In the following discussion Sigogneau stated that the genus *Prorubidgea* was close to *Aelurognathus* on the one side and to *Sycosaurus* on the other. With the first taxon it shared the high and narrrow skull and the rounded snout, but the intertemporal space was too narrow in *Aelurognathus*, the postorbital and zygomatic arches were less broad and had a different form and the incisors were less strong.

P. alticeps

The holotype of this species, BPI 261 was first described by Brink & Kitching (1953) as *Lycaenops alticeps*. It concerns a somewhat weathered skull with the anterior part of the mandible, which measures 230 mm in length. Brink & Kitching were of the opinion that the skull closely resembled *L. pricei* and *L. ornatus* in its general form but differed in proportions from those taxa. They remarked on the high and rounded snout, the narrow and high skull, the nasals being slightly constricted in the middle, the four large molars, the broad postorbital arch and the postorbital that reaches far ventral on the arch, the straight symphysis and the tooth replacement.

Sigogneau (1970) additionally mentioned that the specimen had the same heavy, high and rounded snout as *Aelurognathus tigriceps* SAM 4334. The orbit was slightly smaller, the suborbital and zygomatic (restored) arches not as broad and the interorbital space narrower. Moreover the temporal openings were short and high, the preparietal and supraorbital portion of the frontal small, the lacrimal short and high, the occiput high and less inclined with a well developed supraoccipital, the dentary more massive and higher than in *P. maccabei*, the symphysis almost straight, the incisivi large, the caninus strong and there were five postcanine teeth. In the final discussion she stated that the proposed relationship of this specimen with the genus *Lycaenops* was not tenable because of the more slender form and the more primitive features of the latter. However she also saw a close resemblance with BPI 174 '*Lycaenops pricei'* (= *Arctognathus* cf. *curvimola*) because of the heavy and high snout, the narrow interorbital space, identical preparietal, frontal and lacrimal, the strong postcanine teeth and the expanded coronoid process. On the other side BPI 261 also evoked *Aelurognathus* in many respects like the preceding species.

P. brinki

The holotype BPI 289 was first described by Manten (1958) as *Prorubidgea brinki*. Sigogneau (1970) allocated it to the species *P. alticeps* with a questionmark but re-established the species *brinki* 1989. Manten gave the following diagnosis of the 280 mm long skull: medium size, five postcanine teeth, canines large, snout narow and deep, orbit small, interorbital space wider than intertemporal, supraorbital frontal and preparietal small, parietal foramen rather posteriorly situated, postorbital extending far backwards, transverse process situated about mid-way in the skull length and not very massive, ectopterygoid and palatine relatively large, mandible massive, symphysis sloping. He further stated that the lacrimal was as high as long, the occiput inclined forward with the interparietal higher than broad and the supraoccipital narrow and high, the paroccipital process was massive, the palatal tuberosities were well developed and had teeth, there was no clear step in the alveolar border between the incisors and the canine and the lamina reflecta was well developed. In the final discussion Manten compared BPI 289 with *P. maccabei* and *P. robusta*. According to him the first differed by the shorter nasals, the longer frontals, the larger lacrimal, the larger preparietal and supraorbital portion of the frontal and the more massive postorbital bar. *P. robusta* had a rather different general appearance. (frontal excluded?, post-and suborbital bar more massive, postfrontals larger, praparietal large, temporal openings small.)

Sigogneau (1970) added the following points: temporal fossa wide (contra Manten) and high, posterior margin of postorbital bar convex, postfrontal narrow posteriorly but wide at the orbit, supraorbital portion of the frontal uncertain, naso-frontal suture posteriorly situated, large septomaxilla (contra Manten), occiput concave, long basioccipital, deep para-basisphenoid fossa and transverse apophyses anteriorly situated with teeth. She saw in BPI 289 the same proportions and the same details of the bones as in BPI 261 (*P. alticeps*) and allocated BPI 289 to the species *P. laticeps*.

In 1989 she re-estabslished the species *P. brinki* but did not justify her decision and only pointed out that this was the species with the narrowest intertemporal skull roof.

P. robusta

The holotype BPI 249 was first described by BRINK & KITCHING (1953) as a new species of the taxon *Prorubidgea*. These authors stated that although their specimen agreed perfectly in proportions with the type species of the genus *Prorubidgea*, there were some differences wich separated the two species. In BPI 249 the preparietal was situated more posteriorly and reached the parietal foramen. Furthermore the pre-and postfrontals were differently shaped, the frontals were excluded from the orbital margin and there were some proportional differences especially in the temporal and orbital region.

SIGOGNEAU (1970) pointed out that the postorbital bar was quite massive and the intertemporal widening notable, but that the orbits were still visible in dorsal view. Contra BRINK & KITCHING she saw no preparietal, regarded the postfrontals as rather wide, the lacrimal as short, the occiput as not inclined, the high interparietal as wide as the supraoccipital, the skull basis as massive and long, the transverse apophyses as quite posteriorly situated, the palatal tuberosities of the pterygoid as reduced, the choanae elongated, the sympysis powerful and not sloping and she counted four to five postcanine teeth.

Concluding she mentioned that the species *robusta* most resembled the species *maccabei*. Thus, although the specimen was stratigraphically older than the type specimen, it showed more advanced characters in the posterior part of the skull, whereas the position of the transverse apophyses was more primitive. Finally she concluded that the ancestral form for both would be *Aelurognathus*.

P. brodiei

The holotype TMP 1493 is somewhat weathered and incomplete with an unprepared palatal and occipital region. It measures 340 mm in length and was first described by BROOM (1941) as a new species of *Sycosaurus*. Although BROOM saw the close resemblance with *Prorubidgea maccabei* he refrained from allocating TMP 1493 to this genus because of the loss of the preparietal and the exclusion of the frontal from the supraorbital rim. He saw these two characters in *Sycosaurus* and thus placed the specimen in his genus. He stated further that the parietals were large, the parietal foramen was small and surrounded by a ridge, the postorbital well developed, the postfrontal small, the prefrontal long and narrow, the canine long and slender, the lacrimal quadratic, there were five postcanine teeth and the symphysis was very deep and strong.

SIGOGNEAU (1970) added that the snout was high with a convex dorsal profile, the orbit was small and the temporal openings ample, the suborbital bar was as massive as in *P. maccabei* whereas the zygomatic arch was comparatively slender as in *P. alticeps* with a more slight ventral curvature, the intertemporal space was much wider than the interorbital one (contra BROOM). She further stated that the shape of the postorbital was reminiscent of *Arctops*? *ferox*, whereas the straight naso-frontal suture was posteriorly situated as in *P. alticeps*, the lacrimal was short and low, the squamosal did not reach far anteriorly on the zygomatic arch and the dentary was high and massive. In the final discussion she again mentioned *Arctops*? *ferox* because of the small interorbital width and the shape of the postorbital, but after a direct comparison with one of the *Arctops*? *ferox* specimens (TMP 132), she refrained from allocating TMP 1493 to this genus. Finally, she concluded that the specimen belonged without doubt to the genus *Prorubidgea* but differed from the one or the other species in such a way that she needed to maintain this species.

2.2.6.5 Conclusion

With all three genera discussed successively, the chapter is concluded with the extended diagnosis and systematic palaeontology of the revised genus *Lycaenops* first. This is followed by the discussion of the combined genera *Aelurognathus* and *Prorubidgea* and their systematic palaeontology.

Conclusion Lycaenops

As worked out in the discussions and considerations above the genus *Lycaenops* is now clearly delimited against the genus *Aelurognathus*. It is constituted by a number of species, which all share the following characters:

skull slender, posterior part of skull moderately enlarged, outline in dorsal view forms an elongate and narrow triangle; snout narrow and higher than wide, with a longish and slim appearance, pointed anteriorly and with a slight constriction dorsolaterally, dorsal profile of snout straight or slightly sloping, dorsal profile of posterior part of skull straight or slightly sloping, external nares situated dorsally but premaxilla low, ventral border of maxilla however strongly convex, orbit rather large and round, well visible in dorsal view, interorbital width broad, temporal opening quadratic, intertemporal width only slightly wider than interorbital width; septomaxilla short and low, ridge on maxilla modestly pronounced, nasal only slightly constricted in the middle, nasofrontal suture anteriorly situated and straight, prefrontal short but high with a slight elevation in front of the orbit, lacrimal somewhat elongated with depression, supraorbital portion of frontal medium to small, postfrontal rather narrow with a straight posterior margin, preparietal small to medium-sized and close to the parietal foramen, postorbital reaches moderately far ventrally on the postorbital bar, broad process of squamosal reaches slightly more anteriorly than the middle of the temporal opening; skull arches rather slender, suborbital arch narrow and straight, postorbital arch narrow dorsally and getting wider ventrally, zygomatic arch narrow but with a sligh ventral curvature; palate elongate, palatal fossa rather narrow, tuberosities rounded, separated from each other by a trench and with teeth, ectopterygoid large and elongated, transverse apophyses anteriorly situated, can have a few teeth, interpterygoid vacuity well developed, para-basisphenoid fossa small and narrow, basisphenoidal tubera small and slender, basioccipital short; occiput quadratic to rectangular, only slightly concave, parietal contributes only slightly to occipital face, interparietal slightly wider than high, supraoccipital wide and high, paroccipital process low; incisors comparatively strong, canine medium sized but rather slender, four to five rather medium to small postcanine teeth; lower jaw slender with ‘chin’, symphysis high but sloping, dentary long and slender, ridge on lamina reflecta well developed but delicate. For illustration see figure 41.

Systematic Palaeontology

Genus: ***Lycaenops*** Broom, 1925
Type species: *L. ornatus* Broom, 1925

Revised generic diagnosis: skull narrow, dorsal profile of snout only slightly convex, skull arches rather slender, ridge on maxilla moderately pronounced, postorbital arch widens somewhat ventrally, preparietal situated close to parietal foramen, palatine narrow, occiput moderately wide but interparietal considerably wider than high.

***Lycaenops ornatus* Broom, 1925**
Holotype: AMNH 2240
Referred material: BPI 260, BPI 334, RC 147 and 148
Specific diagnosis: snout convex, high, posterior part of skull slightly sloping, postorbital broad, occiput quadrate

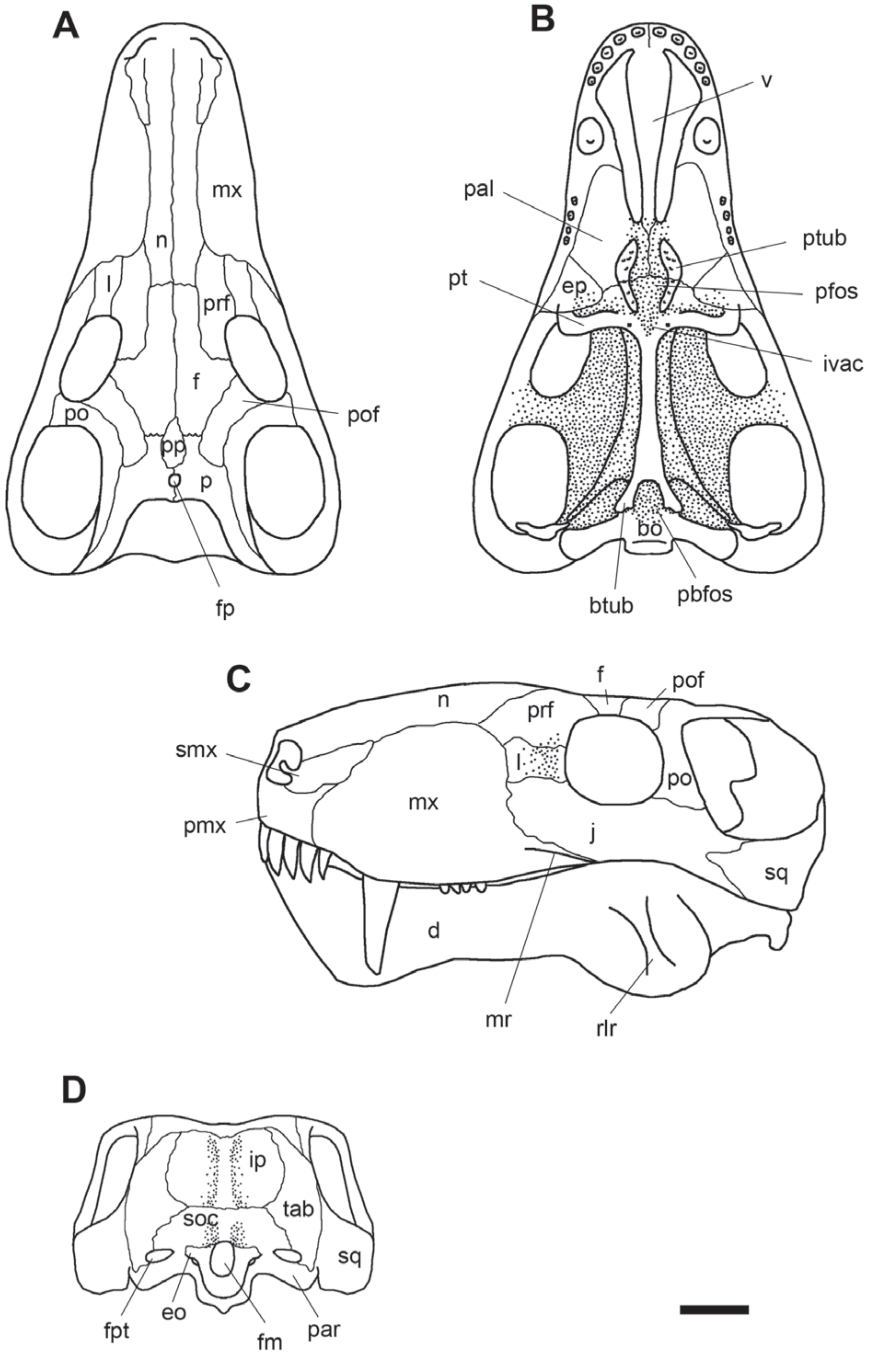


Figure 41. Illustration of the characters in the genus *Lycaenops* Broom, 1925 based on the holotype of the type species, *Lycaenops ornatus* (AMNH 2240). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

Bibliography: BROOM 1925, pp. 323-324
BROOM 1930, pp.349-351, fig. 1; pl 27, fig 2; pl. 29, fig.27
BROOM 1932, p. 126, fig. 39c, 43a, 44a, 45
COLBERT 1948, pp 359-402, fig 1-24, pl. 27-34
BRINK & KITCHING 1953, pp. 21-22
SIGOGNEAU 1970, pp. 188-195, fig. 106-110, pl. 44, 45a
SIGOGNEAU-RUSSELL 1989, pp. 93, fig. 228-229

Lycaenops angusticeps (BROOM, 1913) in SIGOGNEAU, 1970

(= *Scymnognathus minor* BROOM, 1913, = *Lycaenoides angusticeps* BROOM, 1925, = *Scymnognathus minor* BROOM, 1913)

Holotype: AMNH 5537

Referred material: AMNH 5535

Specific diagnosis: snout considerably long and slender, posterior part of skull sloping, skull arches extremely slender, preparietal small.

Bibliography: BROOM 1913, pp. 558-559, fig. 2
BROOM 1915, pp127, fig. 13-14
BROOM 1925, p. 314
BROOM 1930, pl. 29, fig.20
BROOM 1932, p. 132, fig. 41e, 44b
BOONSTRA 1935, pp. 12-13
COLBERT 1948, p. 370
BRINK & KITCHING 1953, pp. 20-21
SIGOGNEAU 1970, pp. 196-197, fig. 111b
SIGOGNEAU-RUSSELL 1989, p. 94

***Lycaenops quadrata* (HAUGHTON, 1927) nov. comb.**

(=*Dixeya quadrata* HAUGHTON, 1927, = *Aelurognathus quadrata* SIGOGNEAU, 1970)

Holotype: SAM 7856

Referred material: BPI 390, BPI 389, BPI (FN) 3303

Specific diagnosis: snout almost as high as wide, dorsal profile of skull rather straight, postorbital bar widens considerably in ventral direction, caninus small.

Bibliography: HAUGHTON 1927, p.74, fig. 6-7
BROILI & SCHROEDER 1936, p. 321
VON HUENE 1950, p. 91
BOONSTRA 1953b, pp 29-30, pl. X-XVI
PARRINGTON 1955, p. 9

SIGOGNEAU 1970, pp. 173-178, fig. 98-100, pl. 41, 42a+c
SIGOGNEAU-RUSSELL 1989, pp. 68-69, fig. 172

***Lycaenops sollasi* (BROILI & SCHRÖDER, 1935) nov. comb.**

(= *Aelurognathus sollasi* BROILI & SCHRÖDER, 1935, = *Scymnognathus holmesi* BROOM, 1948, =*Aelurognathus minor* BRINK & KITCHING, 1953, = *Lycaenops*? *minor* SIGOGNEAU, 1970)

Holotype: MS 1934 VIII 29

Referred material: RC 61, BPI 262, RC 119, BPI 264, BPI 281

Specific diagnosis: snout convex but external nares pointed dorsally, palatal fossa broad, teeth relatively strong, teeth on transverse apophyses.

Bibliography: BROILI & SCHRÖDER 1935, pp331-355, 7 figs
BROOM 1948, p.603, fig. 19a, 20a
BRINK & KITCHING 1953, pp. 23-25, fig. 25
SIGOGNEAU 1970, pp. 178-181 and 202-207, fig. 109 and 115-117, pl. 39, 48, 49, 50b
SIGOGNEAU-RUSSELL 1989, pp. 69 and 95, fig. 173, 213

***Lycaenops attenuatus* (BRINK & KITCHING, 1953) nov. sp.**

(= *Lycaeniodes angusticeps* BRINK & KITCHING, 1953, = *Aelurognathus* cf. *serratidens* SIGOGNEAU 1970)

Holotype: BPI 259

derivatio nominis: from the latin word ‘attenuatus’ which means unostentatious.

Specific diagnosis: orbit comparatively small, interparietal rather wide, the supraorbital portion of the frontal small, arches the thickest of the genus.

Bibliography: BRINK & KITCHING 1953, pp. 20-21, fig. 23
SIGOGNEAU 1970, pp. 170-172, fig. 96-97, pl. 38a
SIGOGNEAU-RUSSELL 1989, p. 68

***Lycaenops* sp.**

1. SAM 9344 (= *Aelurognathus microdon* BOONSTRA, 1934, = *Lycaenops*? *microdon* in SIGOGNEAU, 1970)

Bibliography: BOONSTRA 1934, p. 143, fig. 3
SIGOGNEAU 1970, pp. 207-208, pl. 45b
SIGOGNEAU-RUSSELL 1989, p. 95

2. RC 2 (= *Galerhinus rubidgei* Broom, 1936, = *Paragalerhinus rubidgei* Sigogneau, 1970)

Bibliography: Broom 1936, pp. 374-376, fig. 20-21
Sigogneau 1970, pp. 212-213, fig. 120, pl. 51
Sigogneau-Russell 1989, p. 96, fig. 233

3. BSP 1932 I 57 (= *Aelurognathus* cf. *serratidens* Broili & Schröder, 1934, = cf. *Aloposaurus tenuis* in Sigogneau 1970)

Bibliography: Broili & Schröder 1934, pp. 170-190, 1 fig., 2 pl.
Sigogneau 1970, pp. 111-112
Sigogneau-Russell 1989, p. 75

Discussion Aelurognathus and Prorubidgea

In the same way as the two genera *Lycaenops* and *Aelurognathus* also the species of the genus *Prorubidgea* are not clearly delimited against other taxa, especially concerning *Aelurognathus*. This is shown in the diagnoses Sigogneau (1970) and Sigogneau-Russell (1989) give for the genera *Aelurognathus* and *Prorubidgea*, which correspond in many characters: 'heavy skull, wide posteriorly, snout higher than wide, rounded, temporal opening high, orbit small, intertemporal space slightly wider than interorbital width, small supraorbital frontal, long postfrontal, transverse apophyses of pterygoid anteriorly situated, high dentary'.

As differences she pointed out that the interorbital and intertemporal spaces were narrow in *Prorubidgea* but wide in *Aelurognathus*. It is however not markedly smaller in *Prorubidgea* except for *P. brinki*. Further Sigogneau stated that *Aelurognathus* had a moderately thick postorbital and suborbital bar, whereas the zygomatic arch was more slender. The postorbital bar in *Prorubidgea* was described as broad with a convex posterior border, the suborbital and zygomatic arch broad with a moderate ventral expansion of the latter. In fact the broadness of the postorbital bar varies throughout the species of both taxa, the posterior margin is either straight or convex, the suborbital bar is broad and the zygomatic arch of medium thickness with a slight ventral expansion in both taxa.

As additional characters Sigogneau listed for *Aelurognathus* the parietal foramen which was near the occipital crest, the high occiput and the low paroccipital process. The first character also applies for *Prorubidgea*, whereas the occiput is high in *P. alticeps* and *brinki*, but lower in the other species. Concerning the paroccipital process, it seems that it is rather high and massive throughout the *Aelurognathus* species which is also the case in the *Prorubidgea* species. However the paroccipital process is indeed lower in *A.* cf *serratidens* and *A. quadrata*, but these specimens are considered here as congeneric with *Lycaenops*. As additional characters for *Prorubidgea*, Sigogneau listed the short and high lacrimal, the vertical and very concave occiput and the rather long basioccipital. The lacrimal is indeed slightly more elongate in *Aelurognathus* but shows the same shape in *P. maccabei*. The occiput is also concave in *A. tigriceps* and the basioccipital is long, too.

The hitherto five species of the taxon *Prorubidgea* are now reduced to three (see list above).

The species *maccabei* is retained because of its comparatively long snout, slender lower jaw but broad postorbital bar. In contrast to this taxon, the species *alticeps* and *brinki* share the heavy and high snout, the very small preparietal, the narrow interorbital and intertemporal spaces, the presence of teeth on the transverse apophyses, the massive lower jaw and the comparatively narrow postorbital bar. The species *robusta* and *broodiei* on the other hand have the same short lacrimal, medium broad postorbital bar and no preparietal.

Conclusion Aelurognathus and Prorubidgea

The above listed statements show that there is no generic difference between the taxa *Aelurognathus* and *Prorubidgea*, especially if the taxa *Aelurognathus* cf. *serratidens*, *A. quadrata* and *A. sollasi* are attributed to the genus *Lycaenops*. Thus I allocate the specimens of the former genus *Prorubidgea* to the genus *Aelurognathus*. With '*Lycaenops kingwilli'* and '*Arctops*? *ferox'* as additional species of *Aelurognathus*, this genus shows the following characters:

skull heavy, posterior part of skull well enlarged, outline in dorsal view forms a well proportioned triangle; snout heavy but higher than wide, somewhat rounded anteriorly with a strong constriction dorsolaterally, dorsal profile of snout convex, sometimes with a slight depression posterior to the external nares and anterior to the orbit, dorsal profile of posterior part of skull slightly declining, external nares situated dorsally, premaxilla high anteriorly and straight or bulging in anterior direction, ventral border of maxilla convex with a slight step in front of canine, orbit rather small, round, only visible as slit in dorsal view, interorbital space wide, intertemporal space as wide or slightly narrower, temporal opening quadratic or higher than wide, upper margin dorsally directed; septomaxilla rather large with constriction above septomaxilla foramen, maxilla with ridge above postcanine tooth row, nasal only slightly constricted in the middle, nasofrontal suture slightly pointed and serrated, posteriorly situated, prefrontal short and high, with a slight elevation in front of the orbit, lacrimal quadratic or slightly elongated, slight antorbital depression present, supraorbital portion of frontal small, postfrontal of normal size, possibly with a constriction in the middle, posterior margin rounded, preparietal medium sized or absent, well separated from the parietal foramen, postorbital reaches far ventrally on the postorbital bar, squamosal reaches up to the level of the posterior margin of the postorbital bar with a broad process; skull arches medium sized to thick, suborbital bar rather broad, postorbital bar medium-sized straight or with slight anterior curvature, zygomatic arch gets wider in posterior direction and curves ventrally to some extent; palate short and broad, palatal fossa rather narrow, tuberosities confluent, elongated, the palatine ones only slightly larger than the pterygoid ones, both can have teeth; ectopterygoid large, somewhat expanded medially, transverse apophyses anteriorly situated and without teeth, interpterygoid vacuity less developed, parabasisphenoid fossa broad, basisphenoidal tubera slender and elongated, basioccipital rather long; occiput rectangular to wide, concave, parietal contributes only slightly to occipital face, interparietal wider than high, supraoccipital wide and low, paroccipital process strong; incisors strong, canine strong, three to four rather small postcanine teeth; lower jaw heavy with 'chin', symphysis strong, high and straight, dentary high but elongated, ridge on lamina reflecta well developed and strong. For illustration see figure 42.

Systematic Palaeontology

Genus: ***Aelurognathus*** Haughton, 1924

Type species: *A. tigriceps* (Broom & Haughton, 1913) in Haughton,1924

Revised generic diagnosis: skull heavy and high, dorsal profile of snout strongly convex, lateral face of snout strongly constricted dorsally, orbit small, temporal opening high, septomaxilla rather large, ridge on maxilla well pronounced, palatal tuberosities well developed and broad, skull arches strong, zygomatic arch curves ventrally to some extent.

Aelurognathus tigriceps (Broom & Haughton, 1913) in Haughton, 1924

(= *Scymnognathus tigriceps* Broom & Haughton, 1913, = *Aelurognathus nyassaensis* Haughton, 1927, = *Aelurognathus* cf. *tigriceps* Sigogneau, 1970, = *Aelurognathus nyassaensis* Sigogneau-Russell, 1989, = *Aelurognathus serratidens* Haughton, 1915)

Holotype: SAM 2342

Referred material: SAM 4334, SAM 10071, SAM 7847, SAM 2792

Specific diagnosis: posterior part of skull sloping, preparietal comparatively large, suborbital arch thick, intertemporal space wide, lacrimal elongated, occiput sloping.

Bibliography: Broom & Haughton 1913, pp. 26-35
Broom 1913, pp. 230-232, fig.1
Broom 1913, pp. 227-229, pl. 37
Broom 1914, p. 46, pl. 6, fig. 66

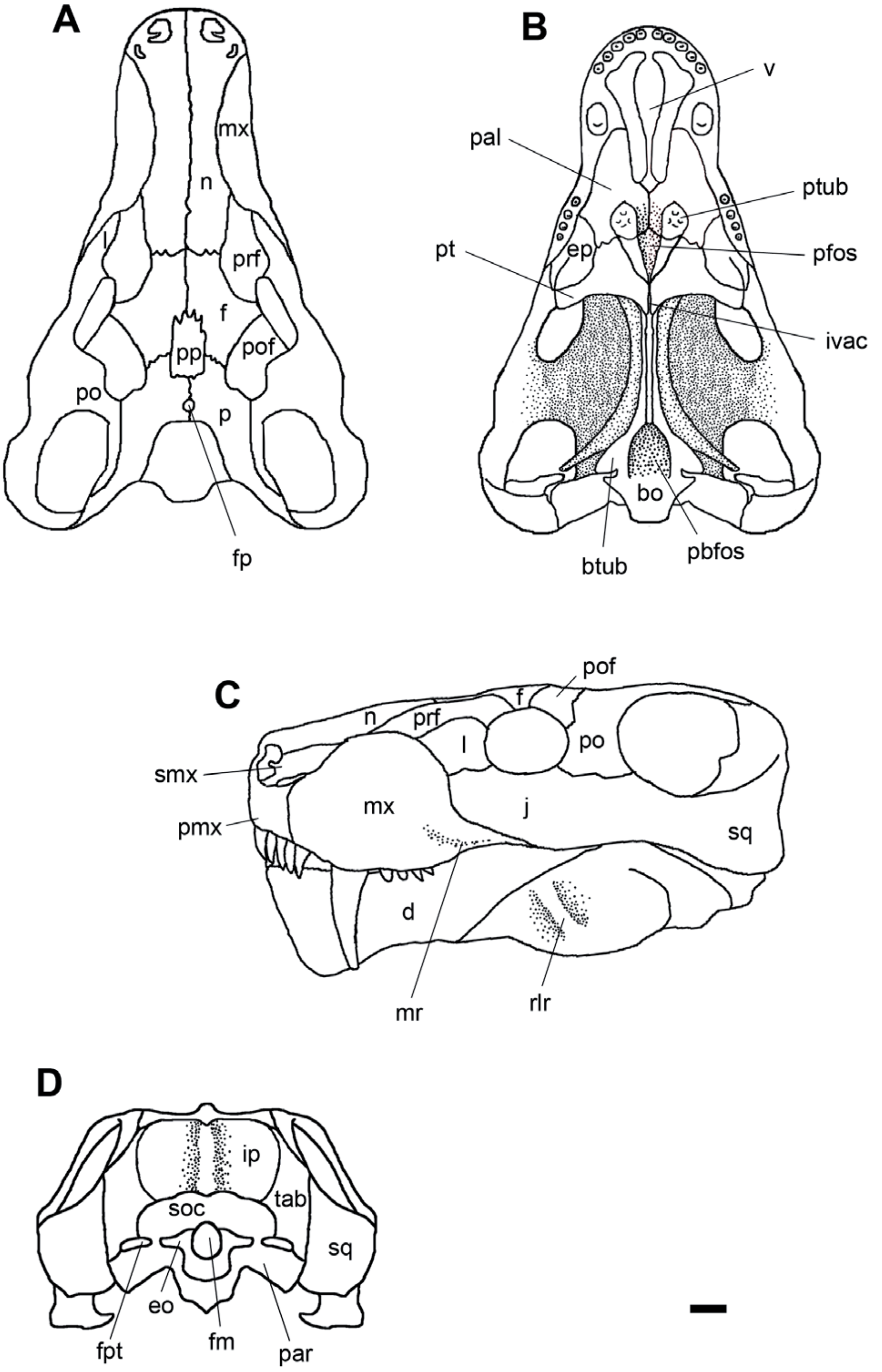


Figure 42. Illustration of the characters in the genus *Aelurognathus* Haughton, 1926 based on the holotype of the type species, *Aelurognathus tigriceps* (SAM 2342). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

HAUGHTON 1915, pp. 88-90, fig. 11, pl; 13, fig. 2-4
HAUGHTON 1918, p. 175
HAUGHTON 1924, pp. 503-505, fig. 3
HAUGHTON 1927, pp. 73-74, fig.5
BROOM 1930, pp. 52-53
BROOM 1932, pp 122-124, fig. 41a,c, 42a
BOONSTRA 1934, pp. 53-57, fig.1
BOONSTRA 1934, pp. 147-173, fig. 5, 6i, 9
SIGOGNEAU 1970, pp. 159-169, fig. 90-94, pl. 34-36, 37b, 38b
SIGOGNEAU-RUSSELL 1989, pp. 66-68, fig. 167-171

Aelurognathus kingwilli (BROOM 1948) nov. comb.

(= *Tigricephalus kingwilli* BROOM, 1948, = *Lycaenops kingwilli* SIGOGNEAU, 1970)

Holotype: RC 60

Specific diagnosis: no preparietal, posterior part of skull straight, lacrimal small, occiput wide, suborbital arch comparatively slender.

Bibliography: BROOM 1948, p. 599, fig. 17b, 18b
SIGOGNEAU 1970, pp.198-202, fig. 112-114, pl. 47
SIGOGNEAU-RUSSELL 1989, pp. 94-95, fig. 60

Aelurognathus ferox (BROOM, 1948) nov. comb.

(= *Smilesaurus ferox* BROOM, 1948, =*Smilesaurus maccabei* BROOM, 1948, = *Pardocephalus wallacei* BROOM, 1948, = *Arctops ? ferox* SIGOGNEAU, 1970)

Holotype: RC 62

Referred material: RC 81, RC 82, BPI 226, TMP 132

Specific diagnosis: snout comparatively broad, posterior part of skull least enlarged of genus, postorbital bar slender, no preparietal, interparietal quadrate, orbit small.

Bibliography: BROOM 1948, pp. 599-603, fig.19b, 20b, 21a-c
SIGOGNEAU 1970, pp. 148-155, fig. 84-86, pl. 30-33
SIGOGNEAU-RUSSELL 1989, pp. 79-80, fig. 195-197

Aelurognathus maccabei (BROOM, 1948) nov. comb.

(= *Prorubidgea maccabei* BROOM, 1948)

Holotype: RC 34

Speciefic diagnosis: snout longest of genus, preparietal and supraorbital frontal small, symphysis slightly sloping, lacrimal elongated, intertemporal space wide, postorbital bar broad.

Bibliography: BROOM 1940, pp. 169-170, fig. 11-12
BRINK & KITCHING 1953, p. 14

Manten 1958, pp. 73-75

Sigogneau 1970, pp. 264-268, fig. 154-156, pl. 67a-b

Sigogneau-Russell 1989, pp.105-106, fig. 257-258

Aelurognathus alticeps (Brink & Kitching, 1953) nov. comb.

(*Lycaenops alticeps* Brink & Kitching, 1953, = *Prorubidgea alticeps* Sigogneau, 1970, = *Prorubidgea brinki* Manten, 1958, =*Prorubidgea alticeps*? Sigogneau, 1970, = *Prorubidgea brinki* Sigogneau-Russell, 1989)

Holotype: BPI 261

Referred material: BPI 289

Specific diagnosis: snout strongly convex, postfrontal smallest of genus, intertemporal width smallest of genus, preparietal and supraorbital frontal very small, both palatal tuberosities with numerous teeth.

Bibliography: Brink & Kitching 1953, pp. 22-25, fig. 24

Manten 1958, pp. 67-74, fig. 23, 26-27, 29

Sigogneau 1970, pp. 269-257, fig. 157-160, pl. 67c, 68, 69a

Sigogneau-Russell 1989, p. 106, fig. 259-260

Aelurognathus broodiei (Broom, 1941) nov. comb.

(= *Sycosaurus broodiei* Broom, 1941, = *Prorubidgea broodiei* Sigogneau, 1970, = *Prorubidgea robusta* Brink & Kitching, 1953)

Holotype: TMP 149

Referred material: BPI 249

Specific diagnosis: dorsal profile of skull straighter than in the other species, no preparietal and supraorbital frontal, intertemporal space wide, lacrimal small, canine slender.

Bibliography: Broom 1941, pp. 198-200, fig. 4

Broom 1948, p. 598

Brink & Kitching 1953, pp. 14-15, fig. 15-18

Manten 1958, p. 74

Sigogneau 1970, pp. 257-279, fig. 161-162, pl. 69b, 70

Sigogneau-Russell 1989, p. 107, fig. 261

2.2.7 Sycosaurus Haughton, *1924, Leontocephalus* Broom, *1940 and Ruhuhucerberus* Maisch, *2002*

2.2.7.1 Introduction

The genera *Sycosaurus* and *Leontocephalus* do not seem to have a close relationship at first sight since they are according to Sigogneau (1970) and Sigogneau-Russell (1989) allocated to different subfamilies. *Leontocephalus* and *Ruhuhucerberus* are regarded by her as gorgonopsines whereas *Sycosaurus* belongs to the subfamily Rubidgeinae. In this reassessment of the Gorgonopsia a new and somewhat different phylogeny is presented which is, however, discussed in chapter 2.3. The reorganisation of the gorgonopsians reveals that the different species of the taxa *Sycosaurus*, *Leontocephalus* and *Ruhuhucerberus* show differences on such a small level, that a generic separation is unjustified. This applies especially for *Ruhuhucerberus* which in all parts, except for its conspiciuosly formed nasals, corresponds very well to the taxon *Sycosaurus*. The list below illustrates the modifications:

Sycosaurus laticeps	*Sycosaurus laticeps*
Sycosaurus vanderhorsti	*Sycosaurus laticeps*
Sycosaurus? *kingoriensis*	*Sycosaurus kingoriensis*
Leontocephalus cadlei	*Sycosaurus* sp.
Leontocephalus haughtoni	*Sycosaurus kingoriensis*
Leontocephalus? *intactus*	*Sycosaurus? intactus*
Leontocephalus? rubidgei	*Sycosaurus* sp.
Ruhuhucerberus terror	*Sycosaurus terror*

In the following text I will discuss the literature first and then explain my own observations and reasons why I think that the three genera should be grouped together. It is started with *Sycosaurus* Haughton, 1924 and its three species *L. laticeps*, *L. vanderhorsti* and *L.*? *kingoriensis*. The discussion is followed by the genus *Leontocephalus* Broom, 1940 and its four species *L. cadlei*, *L. haughtoni*, *L.*? *intactus* and *L.*? *rubidgei*. The last genus is the monospecific taxon *Ruhuhucerberus* Maisch, 2002 with its only species *R. terror*.

2.2.7.2 History of the genus *Sycosaurus* HAUGHTON, 1924

S. laticeps

The holotype (SAM 4022) of the type species *Sycosaurus laticeps* was first described by HAUGHTON (1924). The skull is somewhat weathered and measures 240 mm in length. HAUGHTON (1924, p. 510) mentioned the strong incisors, five small postcanine teeth, the long and narrow nasals and that 'the lacrymal region is slightly depressed and somewhat overhung by a preorbital ridge'. He also stated, that the parietal foramen was small and surrounded by a small ridge, the frontal was excluded from the orbit, there was no preparietal, the paroccipital process fairly broad but thin and the basioccipital thin. Although HAUGHTON made some references to other taxa such as *Scylacops capensis*, *Arctops willistoni* and *Scymnognathus whaitsi*, he did not discuss the reason why he established a new genus and species.

All subsequent authors only briefly mentioned the taxon whether in comparison with other taxa or to emphasise the absence of the preparietal and the exclusion of the frontal from the supraorbital rim, a feature that was unknown in gorgonopsians until 1938.

In her description of *Sycosaurus laticeps*, SIGOGNEAU (1970) mentioned the medium sized orbit, high temporal fossa and downturned zygomatic arch. However I observed that the orbit is comparatively large and the zygomatic arch is not more and not less downturned than in *Arctops*? *ferox* or some species of *Lycaenops* and *Aelurognathus*. Furthermore, SIGOGNEAU mentioned the triangular shaped postfrontal, the short parietal, the large and convace occiput, the long basioccipital, the posteriorly situated transverse apophyses of the pterygoid and the narrow and long ectopterygoid. Finally she stated that *Sycosaurus laticeps* did have a few similarities with *Scylacops* and in particular *S. bigendens* in the shape of the skull - broad posteriorly and narrower anteriorly - the interorbital width, the position of the transverse apophyses of the pterygoid and the tendency to reduce the supraorbital portion of the frontal in *Scylacops*, of which *Sycosaurus* could show a more evolved stage.

However I consider the skull in *Scylacops bigendens* as less broad posteriorly while the snout in *Sycosaurus* is broader and shorter. Moreover the skull arches of *S. bigendens* are thinner, the temporal opening is more elongate and the preparietal is larger. Thus I do not see a close relationship between these two taxa.

S. vanderhorsti

Broom & George (1950) described a rather well preserved and 350 mm long specimen (BPI 126) as the new genus and species *Leontosaurus vanderhorsti*. They assumed that the specimen was subadult since they considered both upper canines as too small. Broom & George compared BPI 126 with *Leontocephalus* both having a flattened and broad snout, no preparietal and no supraorbital portion of the frontal and the same general structure. Further they mentioned the broad and deep interparietal, the broad and short parietals, the long and narrow nasal, the absence of teeth on the palatal tuberosities and the three postcanine teeth.

Sigogneau (1970) allocated the specimen to the genus *Sycosaurus* but she also discussed its resemblance to *Leontocephalus* as already suggested by Broom & George. Although she saw some differences with *Sycosaurus* concerning the width of the snout, the size of the orbit and the broadness of the suborbital arch as well as the longer septomaxilla, the shorter parietals and the stronger incisors, she did not doubt that *Leontosaurus vanderhorsti* belongs to the genus *Sycosaurus*.

Indeed the differences she mentioned are considered as minor by me, too. Moreover in my opinion the taxa *S. laticeps* and *S. vanderhorsti* can be united in one species. Although *S. vanderhorsti* seems to be more flattened and at the same time narrower it is necessary to bear in mind that the specimen has undergone severe compression. After restoration the snout and the posterior part of the skull would therefore be broader. The specimen of *S. laticeps* on the other hand is somewhat damaged in the area of the orbit and postorbital arch which lets the orbit appear unusually large and the postorbital bar rather narrow. These differences are therefore attributable to preservation. Sigogneau distinguished both species by the intertemporal skull roof which was wider in *S. vanderhorsti* and its weaker incisors, but as already shown the first character is redundant and the incisors are of the same size in my opinion. Both taxa share the overall shape with a broad and well rounded snout, the broad and flat occiput and the large but in the middle restricted postfrontal.

S. kingoriensis (figs. 43 & 44)

Von Huene (1950) described a specimen (GPIT/RE/7116) from Tanzania that measures 340 mm in length and lacks the zygomatic arch. He allocated it to the genus *Lycaenops* as the new species *L. kingoriensis* and described it as having a broad snout, a thickened dorsal margin of the orbit, a large interparietal, teeth on the palatal tuberosities but not on the pterygoid transverse process and five postcanine teeth. As differences to *L. ornatus* he cited the broader postorbital and suborbital arch. Von Huene did not mention the already known

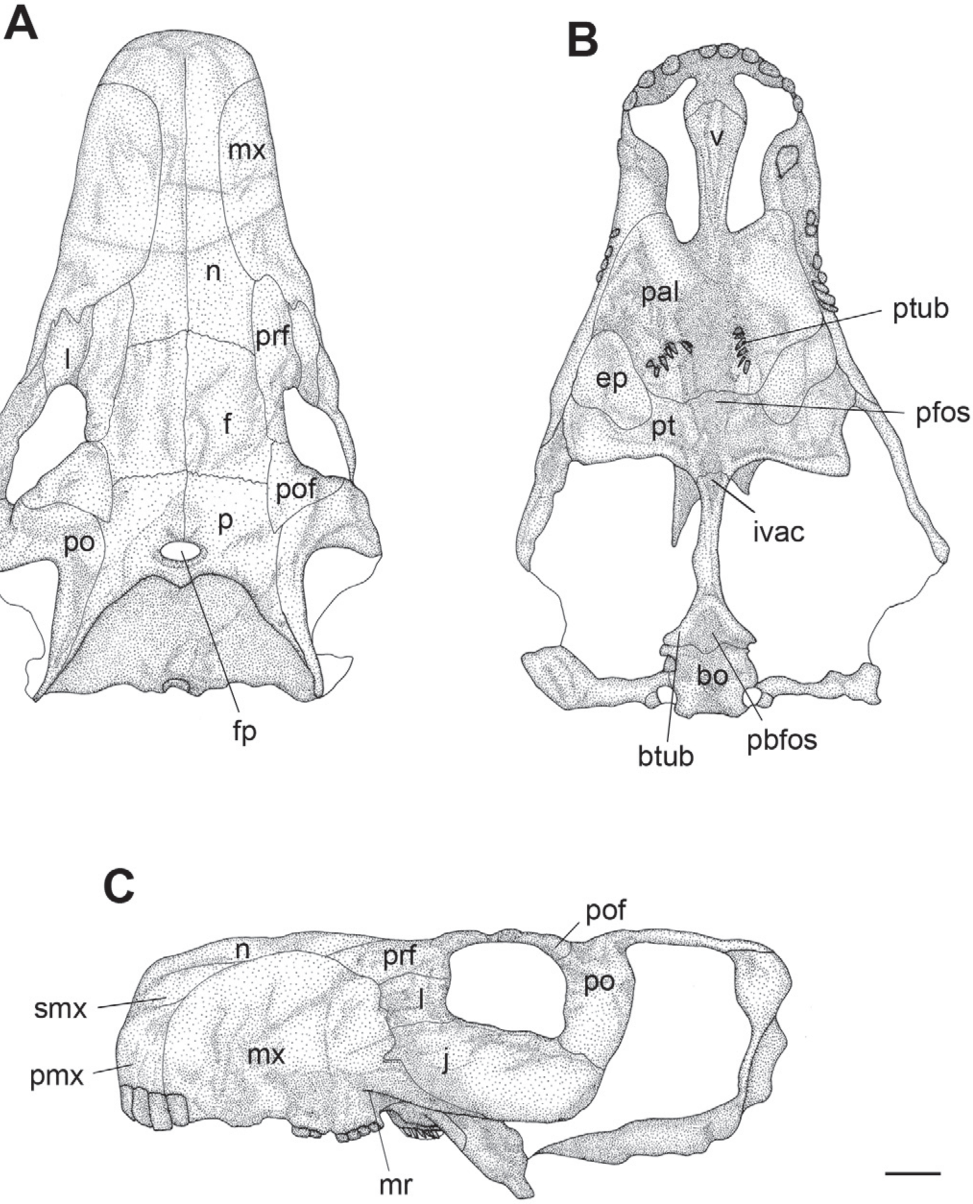


Figure 43. Drawings of GPIT/RE/7116 in **A**, dorsal; **B**, ventral; **C**, lateral view. Scale bar 30 mm.

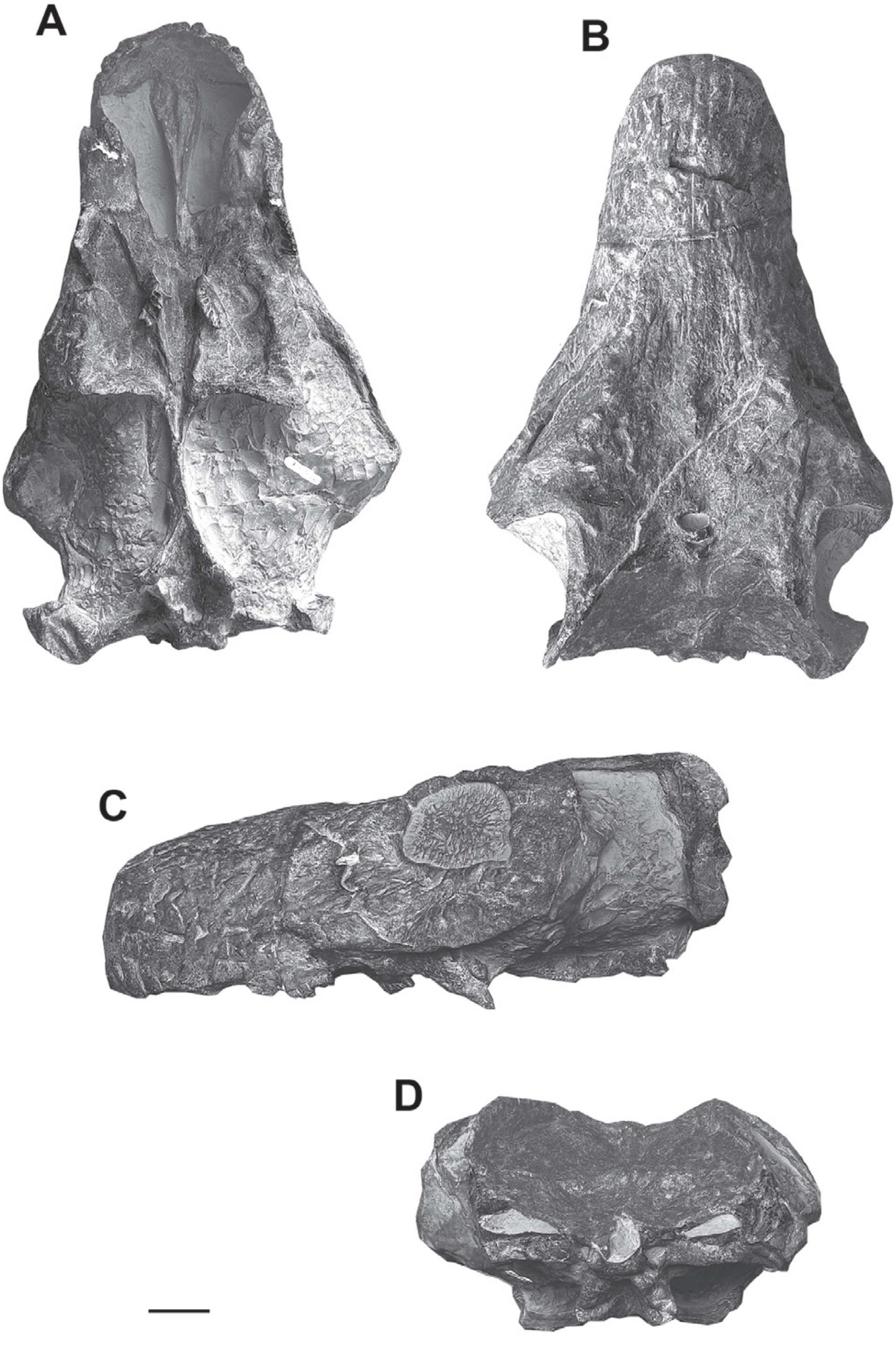


Figure 44. Photographs of GPIT/RE/7116 in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 30 mm.

genera *Sycosaurus* or *Leontocephalus*.

Sigogneau (1970) proposed that the specimen should rather be allocated to the genus *Sycosaurus*, although, according to her, the missing zygomatic arch did not allow a proper identification. However I agree with her suggestion that this specimen does not belong to the genus *Lycaenops* because of, as she wrote in 1970, 'its heavy and large skull, the wider interorbital and intertemporal space, the massive arches, the doubtful preparietal and the transverse apophyses situated more posteriorly'. She also mentioned the great number of postcanine teeth, which she stated as six to seven; but as von Huene already wrote there are only five. Sigogneau-Russell (1989) still maintained doubts about the rubidgeine nature of the specimen. Additionally she considered the suggestion made by Parrington (1955) to unite this skull with his genus *Cephalicustriodus* (now *Ruhuhucerberus* Maisch 2002) but rejected in doing so because of the 'major difficulties lying in the constitution of the cranial roof of the latter.' This problem will be discussed below as well as the combination of *S. kingoriensis* with *Leontocephalus haughtoni*.

2.2.7.3 History of the genus *Leontocephalus* Broom, 1940

L. cadlei

The holotype (RC 35) of the type species was first described by Broom (1940) and named *Leontocephalus cadlei.* The specimen is, however, rather incomplete since it contains only the anterior part of the skull. Broom (1940, p. 174) stated that 'In a number of characters the skull differs markedly from that of nearly all previously known gorgonopsians. Its nearest allied form is *Sycosaurus laticeps*.' He saw the close relationship of both genera in the absence of the preparietal and supraorbital portion of the frontal. As differences he cited the 'anchyclosed' frontals in *S. laticeps* which he had figured in 1930 and its five molars in contrast to the four in *L. cadlei*. However Haughton (1924) clearly figured the frontals with a median suture which I confirm from personal observation and which is even visible on photographs.

In the palate Broom (1940) described the strong canine, the broad palatines, the tuberosities of the palatine and pterygoid with teeth on them. At the end he stated that 'This new genus,…, may with *Sycosaurus* prove to belong to a distinct family of Gorgonopsians…' (p.176)

Sigogneau (1970) described the specimen as having a large skull with a heavy snout that has parallel borders and is rounded anteriorly. The interorbital skull roof was said to be thickened laterally, in the palate the palatal tuberosities were separated by a deep groove. In the subsequent text she also sees some resemblance with *Sycosaurus* but also with *Rubidgea*, *Gorgonops*, *Arctognathus*, *Arctops*, *Syclacognathus* or *Aelurognathus* but not enough to justify any close relationship. As for the association with the rubidgeines, she mentioned *Clelandina* and *Broomicephalus* but noted for *Leontocephalus* a longer and narrower skull; but it should be stressed that in comparison with these genera, almost any gorgonopsian skull has different dimensions. As differences from *Sycosaurus laticeps* she cited the length of the snout and the palate. In conclusion she left the taxon *Leontocephalus* within the Gorgonopsinae because of the incomplete state of the type specimen.

The incompleteness is also the reason why I think that this specimen should not be allocated to a certain species. Its relationship with the revised genus *Sycosaurus* is however not doubted and therefore it is allocated to this taxon as *Sycosaurus* sp.

L. haughtoni (figs. 45 & 46)

The holotype GPIT/RE/7117 from Tanzania, which measures 360 mm in length and lacks both zygomatic arches, was first described by von Huene (1950) as *Aelurognathus haughtoni*. Von Huene pointed out that this skull differed only slightly from *Aelurognathus serratidens* but gave no justification for his specific distinction. He mentioned the five postcanine teeth, the long orbits, the teeth on the tuberosities of the palatine, the relative large ectopterygoid and interparietal, the indistinct preparietal and the small supraorbital portion of the frontal.

Sigogneau (1970) described the specimen as large posteriorly and having a short and large snout. The arches were said to be broad, although it is not possible to make a statement about the condition of the zygomatic arch since it is missing. The foramen parietale was situated at the level of the posterior edge of the postorbital arch as in *Sycosaurus* and *Rubidgea*. She saw no preparietal. Sigogneau stated that the association of this specimen with *Aelurognathus* failed because of the same differences as for *Leontocephalus cadlei*: the breadth of the skull, the shortness of the snout, the size of the orbits, the larger postcanine teeth and the different form of the postorbital bar. Instead she saw some resemblance with *Sycosaurus* and especially with *Sycosaurus kingoriensis*: both had broad postorbital and suborbital arches, the parietal foramen was situated close to the occipital crest and the lacrimal had a depression. But she refrained from allocating this specimen to the genus *Sycosaurus* because of the wider intertemporal skull roof of the latter and the uncertainty of the curvation of the zygomatic arch in *L. haughtoni*.

Since both, *S. kingoriensis* and *L. haughtoni* have no complete zygomatic arch the character becomes irrelevant in this case. It is true that the intertemporal skull roof is somewhat

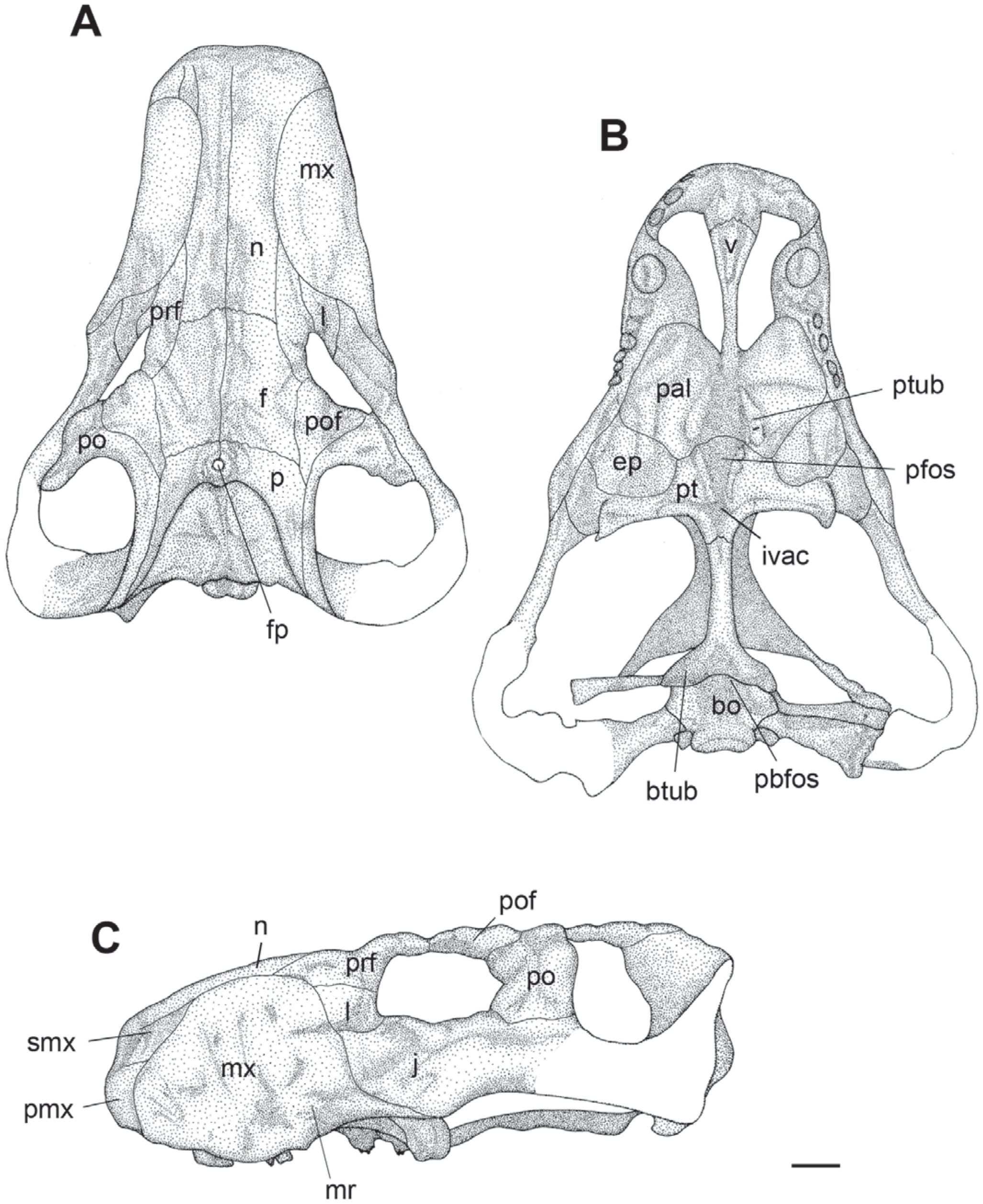


Figure 45. Drawings of GPIT/RE/7117 in **A**, dorsal; **B**, ventral; **C**, lateral view. Scale bar 30 mm.

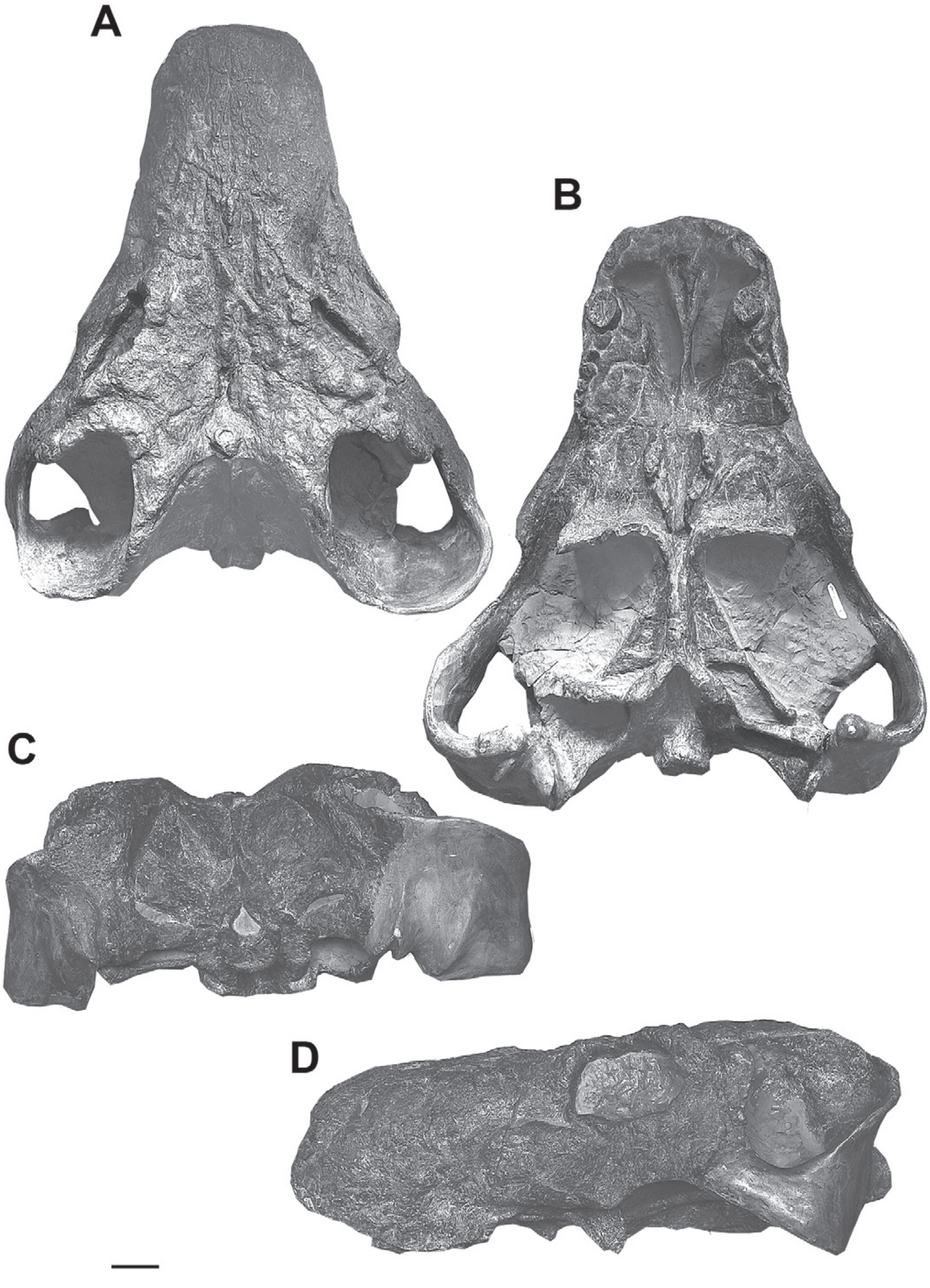


Figure 46. Photographs of GPIT/RE/7117 in **A**, dorsal; **B**, ventral; **C**, occipital; **D**, lateral view. Scale bar 30 mm.

narrower in *L. haughtoni* but this is only a matter of degree and besides the interorbital space is broad in both specimens. Both specimens share a number of characters: the blunt snout which is somewhat shorter than in the revised taxon *Sycosaurus laticeps*, the still broad but shorter postfrontal and the heavily sculptured dorsal skull roof. As far as the preparietal and supraorbital portion of the frontal are concerned I rather believe that they are absent in both specimens, but I, however, must admit, that the sutures are not easily traceable because of the above mentioned state of skull in this region.

L.?rubidgei

The holotype of this species (RC 19) measures 210 mm in length and lacks both zygomatic arches, parts of postorbital bar and suborbital arch as well as parts of the snout. It was first described by BROOM (1940) and named '*Broomisaurus' rubidgei* n. sp. BROOM pointed out that the skull resembled '*Broomisaurus'* more than '*Scymnognathus'* and that he provisionally placed it within the former genus. He mentioned the unusually thick facial bones and their corrugated surfaces, the irregularly rounded preparietal and the relatively large prefrontals. He limits his comparison to '*Scymnognathus'* although at the point of his writing quite a lot of different genera were known.

SIGOGNEAU (1970) saw the same heavy features in the specimen as in *Leontocephalus haughtoni*. In contrast to the type species, however, were the larger orbits. The temporal opening was elongated, the preparietal relatively large and the frontal participated in the supraorbital rim, the prefrontals were bulged, the septomaxilla short, the lacrimal quadrate shaped, there was no preorbital fossa, the large occiput was only slightly concave, the transverse apophyses of the pterygoid were situated extremely posteriorly. Further she rejected BROOM's suggestion of allocating the specimen to the genus *Broomisaurus* and discussed the idea of comparing it to '*Scymnognathus'* as BROOM has already done. I can confirm that this skull has not much in common with the genus '*Scymnognathus*', the species of which are now distributed mostly among the genera *Gorgonops* or *Aelurognathus*. Thus, the snout is broader and flatter, the skull arches are heavier, the lacrimal is shorter, the palate is more flattened and the occiput is wider, to list only some of the differences. Although the specimen shows some characters of the revised genus *Sycosaurus*, such as a blunt and rounded snout, anteriorly broad vomer and comparatively large orbits, the specimen is too incomplete to allow a specific distinction and thus it is allocated to the revised taxon *Sycosaurus* as *S.* sp.

L.? *intactus*

Another uncertain species is *Leontocephalus*? *intactus* (MZC 878) from Tanzaina which was established by KEMP (1969). KEMP allocated his 300 mm long specimen to the, at that time still valid family Arctognathoidae, but distinguished it from '*Arctognathoides' breviceps* and *Aelurognathus haughtoni* by the absence of a preparietal and the exclusion of the frontal from the supraorbital rim. He considered the other members of this family, *Leontocephalus cadlei* and '*Leontosaurus' vanderhorsti* (= *Sycosaurus vanderhorsti*) as at least congeneric if not conspecific and stated that MZC 878 was slightly narrower than *L. cadlei* and '*Leontosaurus*' *vanderhorsti*. However, according to him, the shape of many bones corresponded especially with the latter; furthermore he held the dorso-ventral crushing in *L. vanderhorsti* responsible for the differences in the width of the posterior part of the skull. The new species was diagnosed by KEMP as follows: 'skull moderately flattened, zygomatic arch shows light swelling in dorsal view, the squamosals extend behind the level of the occipital condyle, intertemporal width is slightly greater than interorbital width, the frontals are long and narrow and the prefrontals are large, much of the dorsal skull roof is is ornamented with pits and heavily rugose, especially the dorsal margin of the orbits'.

SIGOGNEAU-RUSSELL (1989) provisionally retained this species in the genus *Leontocephalus*.

The alphataxonomy of *L. intactus* could not be solved entirely since this specimen displays a number of characters, which separate it from the genus *Leontocephalus* such as the long snout, the rather slender skull arches and the elongated temporal opening. On the other hand it shows heavy rugosities at the dorsal margin of the orbits and the preparietal and the supraorbital portion of the frontal are absent which would fit well into the revised genus *Sycosaurus.* The species is therefore retained but with a dubious state.

2.2.7.4 History of the species *Ruhuhucerberus terror* MAISCH 2002

After dealing with the history of the genera *Sycosaurus* and *Leontocephalus* it is necessary to turn the attention to another specimen which resembles the previous taxa but was not allocated to any of the two genera because of its very particular snout and more precisely the nasals.

PARRINGTON (1974) described a well preserved and 300 mm long specimen (MZC 891) from Tanzania that reminded him strongly of the specimen of '*Lycaenops' kingoriensis* (= *Sycosaurus kingoriensis*) described by VON HUENE (1950). He, however, doubted VON HUENE's reference to the genus *Lycaenops* but continued to see his specimen conspecific with the specimen of *L. kingoriensis*. Thus he erected a new genus *Cephalicustriodus* with *L. kingoriensis* as type specimen.

PARRINGTON described MZC 891 as a moderately large form with a markedly triangular outline if seen from above. The snout was broad and the occiput wide. The preparietal was of moderate size, the frontal did reach the orbit but only slightly, it had four postcanines and teeth on the palatal tuberosities. But 'the outstanding feature lies in the nasals, coarsly sculptured bones which meet along the midline at an angle of about 90° for most of their length.' (PARRINGTON 1974, p. 50). I confirm this feature and I also can confirm that the specimen has not undergone any distortion. PARRINGTON further discussed the association with other taxa such as *Sycosaurus*, *Prorubidgea*, *Rubidgea*, *Gorgonops* and *Dinogorgon quinquemolaris* but eventually erected a new genus which he defined principally on the triangular shape of the skull. He also mentioned that 'it can probably best be placed in SIGOGNEAU's (1970) subfamily Rubidgeinae' (PARRINGTON 1974, p. 50).

SIGOGNEAU-RUSSELL (1989), however, stated that the skull evoked *Leontocephalus* but she refrained from allocating it to this genus because of the particular form of the nasals. She also mentioned, that the cranial roof and the zygomatic arch were not as specialised as those of the Rubidgeines. Thus she rejected a union of PARRINGTON's specimen with VON HUENE's '*Lycaenops kingoriensis*'. However, she did not realize that PARRINGTON determined VON HUENE's species as type species and she kept the name *Cephalicustriodus* for PARRINGTON's specimen. This nomenclatorial mistake was recognised by MAISCH (2002), who solved the problem by giving PARRINGTON's specimen the new name *Ruhuhucerberus terror*. MAISCH also saw the taxon as 'probably closest to *Leontocephalus* from which it is clearly distinguished by the presence of a preparietal, contribution of the frontal to the orbital margin and more anteriorly situated processus transversi of the pterygoids' (MAISCH 2002, p. 250). When comparing *Ruhuhucerberus terror* with *Sycosaurus*? *kingoriensis*, he saw the following differences: the latter had a longer, narrower and lower snout with flat nasals, a higher and narrower postorbital skull segment with a wider intertemporal space, no supraorbital portion of the frontal, no teeth on the tuberosity of the pterygoid but more on the palatine one, a well-developed interpterygoid vacuity, a somewhat larger lacrimal, more postcanine teeth. In my opinion these differences however partly result in the peculiar form of the nasals of MZC 891 and partly only are a matter of degree.

Discussion

In the following paragraphs it is shown that the three taxa *Sycosaurus*, *Leontocephalus* and *Ruhuhucerberus* are congeneric in my opinion. The doubtful position of the three genera within the two subfamilies Gorgonopsinae and Rubidgeinae becomes evident by their bibliographic history.

Sigogneau placed the genera *Leontocephalus* and *Ruhuhucerberus* in a different subfamily than *Sycosaurus*, whereas Kemp (1969) saw *Aelurognathus haughtoni* (= *Leontocephalus haughtoni*), *Leontocephalus cadlei* and *Leontosaurus vanderhorsti* (= *Sycosaurus vanderhorsti*) as very closely related. The only reason why Sigogneau grouped the genus *Sycosaurus* within the rubidgeines is the slightly downturned zygomatic arch and the probable absence of a preparietal and the exclusion of the frontal from the supraorbital rim. However, as it is illustrated in chapter 2.3. the subfamily Rubidgeinae is extended on some more taxa and the diagnosis is modified, which allows a non-problematical combination of the taxa *Sycosaurus*, *Leontocephalus* and *Ruhuhucerberus*.

The ventral expansion of the zygomatic arch is indeed more accentuated in *Sycosaurus* than in *Leontocephalus intactus* (in all other *Leontocephalus* species the zygomatic arch is missing) but by far not as marked as in *Clelandina*, *Broomicephalus*, *Rubidgea* and *Dinogorgon*. Further this slight ventral curvature is also indicated in *Ruhuhucerberus terror* and in other taxa of the subfamily Gorgonopsinae (sensu Sigogneau-Russell, 1989) such as *Aelurognathus*.

Sigogneau's diagnoses for the three genera correspond in many points. All genera are characterised by her as having a posteriorly wide skull with the intertemporal space slightly wider than the interorbital width, the skull arches were broad and the posterior margin of the postorbital bar was concave, the lacrimal was short and the interparietal wider than high. Additionally she listed some characters that were only shared by *Sycosaurus* and *Leontocephalus*. 'Snout wide and short, skull roof wide, no preparietal or supraorbital portion of the frontal, transverse process of the pterygoid posteriorly situated, occiput wide and concave, strong incisivi.' However the snout is also wide and especially short in *Ruhuhucerberus*, although also rather high but this is only due to the particularly formed nasals which meet almost perpendicular with their median suture and are thus considerably vaulted. This feature is regarded here as an individual variation or even pathological. The skull roof is indeed less wide especially the intertemporal space. But this is also the case in *L. rubidgei* and *L. intactus* whose membership to this genus was however questioned by Sigogneau. The same can be said for the preparietal and supraorbital frontal: it is present in *Ruhuhucerberus* but also in *L. rubidgei* and *L. intactus*. Concerning the transverse process of the pterygoid it lies only slightly more anteriorly in *Ruhucerberus* nearly matching the position in *L. intactus* and *L. haughtoni*. The occiput is also wide and concave in *Ruhuhucerberus* whereas the incisors are slightly less strong but not the canine.

Further SIGONGNEAU stated that *Leontocephalus* and *Ruhuhucerberus* had an elongated temporal fossa whereas it was higher than wide in *Sycosaurus*. However, it is nearly almost close to a quadrate shape in all the specimens except for *Sycosaurus laticeps* (in which it is higher than wide but this specimen is slightly deformed posteriorly) and *Leontocephalus intactus* where it is elongated. Additionally all specimens share the remarkable straight dorsal margin of the temporal fossa in dorsal view which is formed by the postorbital and the sharp rectangular angle at the anterodorsal corner where the dorsal postfrontal bends ventrally and shapes the postorbital bar.

For *Leontocephalus* SIGOGNEAU mentioned the heavy skull with an anteriorly rounded snout. This character also applies for the other two genera whereas the snout narrows only in the species *laticeps*. Further the orbits are said to be larger than in *Aelurognathus*. This is true but the orbits are larger than in *Aelurognathus* in all three taxa. The palate was flat and the palatine elongated: The first character matches all three taxa whereas the palatine is less elongated in *Ruhuhucerberus*.

For *Sycosaurus* SIGOGNEAU listed the slightly downturned zygomatic arch with the squamosal/jugal suture oriented in a ventral direction. This ventral expansion is indeed most conspicous in S. *laticeps*, but by far not as marked as in *Clelandina*, *Broomicephalus*, *Rubidgea* and *Dinogorgon* but comparable with *Lycaenops*, *Prorubidgea*, *Aelurognathus* and *Arctops ferox*. In the former taxa however not only the ventral margin of the zygomatic arch is bent ventrally but also the dorsal rim, whereas in *Sycosaurus*, *Leontocephalus* and *Ruhuhucerberus* the ventral expansion is only confined to the ventral margin. The curvature results from the strongly concave ventral margin of the postorbital bar which is present in all forms. No statement can be made about the shape of the zygomatic arch since it is missing in all specimens except for the species *intactus*. Here the zygomatic arch is rather narrow but also shows the concave ventral margin anteriorly. In *Ruhuhucerberus* it is however as strongly curved as in the *Sycosaurus* specimens and also shows the slight ventral expansion posteriorly. The postfrontal was triangular. This applies for *Ruhuhucerberus*, *Leontocephalus haughtoni* and probably *L. cadlei*, whereas it is rather elongated in the species *rubidgei* and *intactus*. The basioccipital was long: This is true for the species *L. laticeps* and *L. vanderhorsti* but not for *L. kingoriensis*.

From personal observation of all of the specimens I consider them as a well defined group which can be determined by a number of characters they have in common:

skull remarkably triangular in outline in dorsal view, posterior part broad, jugal slightly bulging in a lateral direction; snout broad with a stocky appearance, wider than high and well rounded anteriorly, dorsal surface rounded as well in tranversal view, no constriction behind the canine, choanae spacious and exceptionally wide anterior to the caninus, external nares dorsally situated, dorsal profile of the snout slightly concave, dorsal profile of the posterior part of skull straight, skull roof ornamented; orbita of medium size, visible in dorsal view, oval anteroposteriorly and slightly covered with tuberosities, temporal fossa quadrate shaped and dorsal margin at the same level as the dorsal margin of the orbita; septomaxilla short and low, ridge on maxilla present, nasal narrow, nasofrontal suture anteriorly situated and rectangular, prefrontal low, pointed anteriorly and situated on a slight elevation, lacrimal quadratic and with antorbital depression, frontal excluded from supraorbital rim, no preparietal, postfrontal triangular respectively restricted in the middle, broad at the orbita with rounded posterior margin, parietal short, foramen parietale posteriorly situated and surrounded by a ridge, postorbital reaches far ventrally on postorbital bar, squamosal reaches to the mid-length of the temporal opening with a broad squamosal process; skull arches broad, suborbital bar with a concave ventral margin posteriorly, postorbital bar with a convex margin posteriorly, ventral margin of zygomatic arch slightly expanded in ventral direction but dorsal margin straight; vomer broad anteriorly and narrows only far posteriorly, maxilla/vomerine suture situated posteriorly on vomeral bar, vomeral bar constricted anterolaterally, palatine broad, palatal fossa posteriorly situated with 'prefossa' anteriorly, very broad, round to oval and shallow, palatal tuberosities well developed, both are of the same size, can have teeth and are separated from each other by a distinct groove, ectopterygoid relatively large and tends to be elongated, transverse apophyses of the pterygoid posteriorly situated and without teeth, interpterygoid vacuity large, deep and oval shaped, parabasisphenoid fossa medium sized and shallow, basisphenoidal tubera rather slender; occiput wide and strongly concave, median ridge distinct, interparietal only slightly wider than high, supraoccipital large, parietal does not contribute to the occiput, paroccipital process low and wide; incisors well developed, canine strong, four to five postcanine teeth; symphysis strong but slightly sloping, dentary low, ridge on lamina reflecta well developed. See fig 47 for illustration.

The differences that occur are regarded as minor and considered as insufficient to justify a generic separation. The revised genus retains the name *Sycosaurus* HAUGHTON, 1924 and contains four species. The type species is *Sycosaurus laticeps* with SAM 4022 as holotype and BPI 126 ('*Sycosaurus vanderhorsti*') as referred specimen. The second species is *Sycosaurus kingoriensis* with GPIT/RE/116 as holotype and GPIT/RE/117 ('*Leontocephalus haughtoni*')

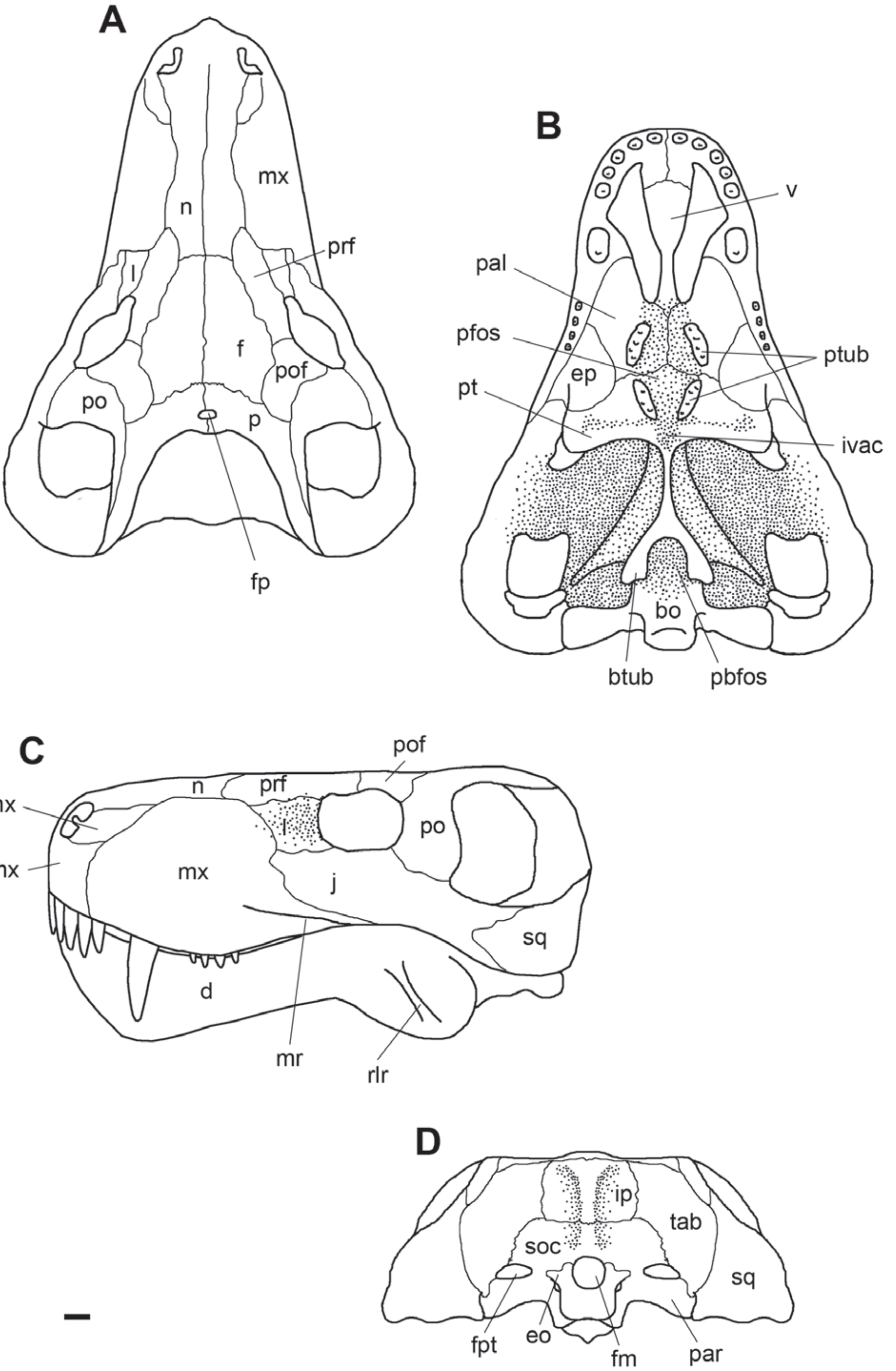


Figure 47. Illustration of the characters in the genus *Sycosaurus* HAUGHTON, 1924 based on the holotype of the type species, *Sycosaurus laticeps* (SAM 40222). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

as referred specimen. The third species is *Sycosaurus terror* (MZC 891, '*Ruhuhucerberus terror'*) which can not be allocated to any of the other species because of its peculiar nasals the narrower intertemporal width and the contribution of the frontal to the supraorbital rim. The fourth species is ?*Sycosaurus intactus* (MZC 878 '?*Leontocephalus intactus'*). It is allocated to the genus with a questionmark because of its long snout, the rather slender skull arches and the elongated temporal opening.

Systematic Palaeontology

Genus ***Sycosaurus*** HAUGHTON, 1924
Type species: *S. laticeps* HAUGHTON, 1924

Revised generic diagnosis: snout broad and rather flat, posterior part of skull considerably enlarged, preparietal and no contribution of frontal to supraorbital rim (except for the species *S. terror*), orbit comparatively large, nasal long and narrow, postfrontal broad, parietal short, interorbital width only slightly narrower than intertemporal width, both wide; skull arches massive, antero-dorsal corner of temporal opening angular, supraorbital thickening well developed, palatal fossa considerably broad, ectopterygoid elongate, basicranium broad, occiput wide and flat, symphysis somewhat sloping.

Sycosaurus laticeps HAUGHTON, 1924
(= *Leontosaurus vanderhorsti* BROOM & GEORGE, 1950, = *Sycosaurus vanderhorsti* SIGOGNEAU, 1970)

Holotype: SAM 4022
Referred material: BPI 126
Specific diagnosis: snout narrows slightly anteriorly, only very few teeth on palatal tuberosities, ectopterygoid elongated, palatine elongated.
Bibliography: HAUGHTON 1924, pp. 509-512, fig. 6
BROOM & GEORGE 1950, pp. 168-169, fig. 3-4
SIGOGNEAU 1970, pp. 255-261, fig. 149-152
SIGOGNEAU-RUSSELL 1989, pp. 109-110, fig. 266-267

Sycosaurus kingoriensis VON HUENE, 1950
(= *Lycaenops kingoriensis* VON HUENE, 1950, = *Aelurognathus haughtoni* VON HUENE, 1950, = *Leontocephalus haughtoni* (VON HUENE, 1950) in SIGOGNEAU, 1970)
Holotype: GPIT/RE/7116
Referred material: GPIT/RE/7117
Specific diagnosis: broad and anteriorly well rounded snout, no preparietal, dorsal skull surface

sculptured, lacrimal elongated, palatal tuberosities with numerous teeth.

Bibliography: von Huene 1950, pp. 87-91, fig 34-35
Sigogneau 1970, pp. 249-251 and 262-264, fig. 145-146 and 153
Sigogneau-Russell 1989, pp. 92 and 110-111, fig. 268

Sycosaurus terror (Maisch 2002)
(= *Cephalicustriodus kingoriensis* Parrington 1974, = *Ruhuhucerberus terror* Maisch 2002)
Holotype: MZC 891

Specific diagnosis: snout short, temporal width narrowest of genus, small preparietal, small supraorbital frontal, postfrontal short, teeth on palatal tuberosities.

Bibliography: Parrington 1974, pp. 47-52, fig 1-2
Sigogneau-Russell 1989, pp. 81-82, fig. 200-201
Maisch 2002, pp. 243-246, fig. 1

Sycosaurus*? *intactus Kemp, 1969
(= *Leontocephalus intactus* Kemp, 1969, = *Leontocephalus* ? *intactus* in Sigogneau-Russell, 1989)
Holotype: MZC 878

Specific diagnosis: orbit smallest of genus, no preparietal, frontal excluded from supraorbital rim, teeth on palatal tuberosities, skull arches more slender.

Bibliography: Kemp 1969, pp 11-27, fig. 4-10
Sigogneau-Russell 1989, pp. 92, fig. 226

***Sycosaurus* sp.**

1. RC 35 (= *Leontocephalus cadlei* Broom, 1940)

Bibliography: Broom 1940, pp. 174-176, fig.16
Sigogneau 1970, pp. 246-248, fig. 144, pl. 61b
Sigogneau-Russell 1989, pp.91- 92, fig. 225

2. RC 19 (= *Broomisaurus rubidgei* Broom, 1940, ?*Leontocephalus rubidgei* Sigogneau, 1970)

Bibliography: Broom 1940, pp. 75-77, fig 4-5
Sigogneau 1970, pp. 251-245, fig. 147-148
Sigogneau-Russell 1989, pp. 92-93, fig. 227

2.2.8 Clelandina Broom, 1948 and Broomicephalus Brink & Kitching, 1953

2.2.8.1 Introduction

The genera *Clelandina* and *Broomicephalus* both are represented by specimens, which display a remarkably widened posterior skull part with respect to the snout length. Such a shape is unique within the gorgonopsians and suggests a close relationship of the two taxa. In the following text I will explain the reasons why I consider a combination of both taxa as appropriate. It is started with the history of the taxon *Clelandina* Broom, 1948 and its two species *C. rubidgei* and *C. scheepersi*. The record is followed by the history of the taxon *Broomicephalus* Brink & Kitching, 1953 and its only species *laticeps*. In the subsequent discussion my own observations are illustrated and the combination of both taxa is considered.

2.2.8.2 History of the genus *Clelandina* Broom, 1948

C. rubidgei

The type species of the genus *Clelandina* is *C. rubidgei* (RC 57) which was first described by Broom (1948). It is based on a flattened and incomplete skull which measures 200 mm in length. Broom (1948, p. 578) stated that *Clelandina rubidgei* 'represents a type of gorgonopsian which differs in many characters from any previously known form'. He gave a rather detailed description of almost every bone that is visible, especially the palatal region and the basicranium. Most of the details he gives are however typical for any gorgonopsian, so I refer here only to the characters that are typical for this taxon. Thus Broom mentioned the broad skull and the massive symphysis with a chin as well as the absence of postcanine teeth in the upper and lower jaws. Furthermore *Clelandina rubidgei* had, according to him, a small oval preparietal, a large parietal foramen surrounded by a ridge, frontals excluded from the orbital rim, a broad postorbital arch, a marked thickening of the prefrontal in front of the orbit and few teeth on the palatal tuberosities.

Sigogneau (1970) added that the specimen was short and stocky, the snout wide, the intertemporal space wide, the orbit of middle size, the lacrimal short, the paroccipital relatively slender, the tuberosities on the palatine and pterygoid close to each other, the transverse apophyses were devoid of teeth and rather high, the ectopterygoid had a distinct ridge laterally, the basioccipital was long, the symphysis high and the dentary relatively slender.

C. scheepersi

Brink & Kitching (1953) described a somewhat distorted skull (RC 102), which measures 190 mm in length, and named it '*Dracocephalus*' *scheepersi*. They stated that it had a broad and well rounded snout 'not unlike that of *Broomicephalus*' (Brink & Kitching 1953, p. 5). They compared it mostly with this genus since they saw a close relationship between these two taxa, except for the absence of postcanine teeth in RC 102. Thus they stated that the skull 'can only be compared with *Clelandina* and '*Tigrisaurus'* (=*Dinogorgon pricei*), two forms which differ absolutely from the new form as well as from each other' (Brink & Kitching 1953, p. 6). Other typical characteristics in their description include: parietal foramen situated on a prominent ridge, symphysis broad and high, absence of postcanine teeth. Sigogneau (1970) allocated the specimen to the genus *Clelandina* as a second species because of the similar proportions between the two skulls. She admitted that she first believed this specimen was a juvenile form of *Broomicephalus laticeps* but refrained from this opinion because of the higher skull, the less broad occiput and the less wide intertemporal and interorbital space relative to the total length of the skull in RC 102. Finally Sigogneau-Russell (1989) considered the genus *Clelandina* 'as morphologically preceding *Broomicephalus* but it is at the same time more specialized by the loss of the postcanines.'

2.2.8.3 History of the genus *Broomicephalus* Brink & Kitching, 1953

B. laticeps

The holotype of the type species (RC 101) was first described by Brink & Kitching (1953). It concerns a nearly complete, undistorted, large and broad skull which measures 210 mm in length. On this specimen Brink & Kitching established the new genus and species *Broomicephalus laticeps* to distinguish it from '*Rubidgea laticeps'* (= *Broomicephalus laticeps*, RC 33, see below*)* because of the differences in shape, although they recognised the close resemblance between these two taxa. Brink & Kitching mentioned the very broad posterior part of the skull in RC 101 and proposed that *Broomicephalus laticeps* was an ancestor of *Rubidgea* rather than *Prorubidgea*. They noted that the specimen was extraordinarily short posteriorly and that the temporal openings were much higher than long. The snout was described as very broad, short and high and well rounded in all directions, the symphysis as broad as high and the number of the upper molars is given as four on each side. They mentioned the dorsal surface which was flat except for a low longitudinal ridge between the orbits and the parietal foramen which was situated on a slight elevation as well as the definite absence of a preparietal and supraorbital portion of the frontal.

Sigogneau (1970) pointed out that the skull was wider posteriorly than it was long, the postorbital bar constricted ventrally (this feature is however unique, especially within the Rubidgeinae and might therefore be considered as an individual feature or even of pathologic nature), the orbits were small and visible in dorsal view as a slit, the interorbital space being the widest of all Gorgonopsia relative to the total length of the skull, the rectangular nasofrontal suture was posteriorly situated, the postfrontal wide and short, the parietal foramen situated close to the occipital crest, the lacrimal was short, the occiput vertical, the high and vertical transverse apophyses anteriorly situated, the basioccipital very long, the dentary short, the lamina reflecta well developed and four postcanine teeth were present.

Referred specimen RC 33

Broom (1940) described a large skull (RC 33) and established the new species *Rubidgea laticeps* for it. He mentioned that the skull was ‘considerably weathered and somewhat crushed, and it is difficult to trace some sutures’ (Broom 1940, p. 173). Broom only figured and described the skull in dorsal view. He mentioned that the parietals were very broad, the parietal foramen was large and the postorbital formed most of the postorbital arch. He was not sure whether a preparietal was present or not but rather thought the latter might be true. He clearly recognised that the frontal was excluded from the orbital rim and hence the prefrontal meets the postfrontal. Broom briefly mentioned the small temporal openings, the upwards and outwards looking orbits and the broad and massive snout, as well as two postcanine teeth. Finally he realized that this skull might not have been very closely allied to any of the hitherto known species of *Rubidgea* and mentioned that it might even belong to another genus; but for the weathered condition of the skull he thought it might be reasonable not to erect a new genus. Sigogneau (1970) allocated this skull to the taxon *Broomicephalus laticeps*, although it was, with 320 mm in length, much larger than the type specimen and also posteriorly not as expanded in lateral direction. She however stated that most of the differences in both specimens could be due to a difference in age or a deformation to which I agree. Both specimens have the same heavy and massive form of the skull although some proportions are slightly different but certainly not as much as to justify a specific separation. Thus many of the characters already given by Sigogneau are the same as for RC 101: small orbit, parietal foramen situated close to the occipital crest, no preparietal, short prefrontal and lacrimal, vertical and wide occiput, the anteriorly shifted paroccipital process, long basioccipital, anteriorly situated transverse apophyses, flat palate but broad and deep palatal fossa, strong incisors, short and massive dentary and three or four postcanine teeth (Broom saw only two, and indeed the determination is difficult but there are most probably not more than three postcanines).

2.2.8.4 Discussion

The list above demonstrates the similarities between *Clelandina* and *Broomicephalus* evidently. Additionally, having examined the specimens personally, I do not see a generic barrier between the two taxa. Although the posterior widening of *Clelandina* and especially *C. rubidgei*, is not as considerable as in *Broomicephalus laticeps*, the resemblance of both genera is striking in my opinion. Thus both taxa have the following characters in common:

Skull remarkably wide and short posteriorly, with the squamosals flaring laterally to a great extent; orbits small and visible in dorsal view, however somewhat roofed by a supraorbital thickening; temporal opening short and higher than wide; dorsal profile of the skull straight or with a slight convexity in the area of the snout; snout relatively long, very broad and as broad as high or slightly wider than high, well rounded anteriorly and dorsally, external nares situated dorsally; septomaxilla relatively large, ridge on maxilla present, no antorbital depression, lacrimal short and high, prefrontal short anteriorly but wide and situated on an elevation, naso-frontal suture posteriorly situated and rectangular but slightly interdigitating, fontal excluded from supraorbital rim; no, or very small, preparietal, postfrontal broad throughout its entire length but short with an indented posterior margin, postorbital broad dorsally and reaching far ventrally on the postorbital bar, dorsal skull roof ornamented, parietal foramen large and surrounded by a ridge; suborbital arch broad with a slight constriction posteriorly, postorbital bar broad with a straight posterior border, dorsally covered with an anterior and posterior ridge, zygomatic arch very broad and expanded in a lateral and ventral direction with the squamosal reaching far anteriorly on it; palatine wide and short, ectopterygoid relatively large with ridge laterally, palatal fossa wide, deep and widely open anteriorly, palatal tuberosities short, massive and the ones on the palatine only slightly larger than the pterygoid ones, being only separated by the palatine/pterygoid suture, teeth only on palatine tuberosities, transverse apophyses situated anteriorly and without teeth, interpterygoid vacuity oval and deep, para-basisphenoid fossa extremely wide and deep, basisphenoidal tubera rather slender, basioccipital long; occiput vertical, only slightly concave but very wide; parietal contributes slightly to the occiput, interparietal wider than high, supraoccipital low and wide, paroccipital process shifted anteriorly; dentary short and massive, symphysis powerful but slightly sloping, lamina reflecta well developed; incisivi strong, caninus powerful, postcanine teeth lost. See fig. 48 for illustration

Considering SIGOGNEAU's diagnosis of the genus *Clelandina* most of the characters, such as skull wide posteriorly, snout wider than high, temporal fossa short and high, no supraorbital frontal, lacrimal short, interparietal wide, quadrate extending below the zygomatic part of the squamosal, basioccipital rather long and pterygoid transverse apophyses anteriorly situated,

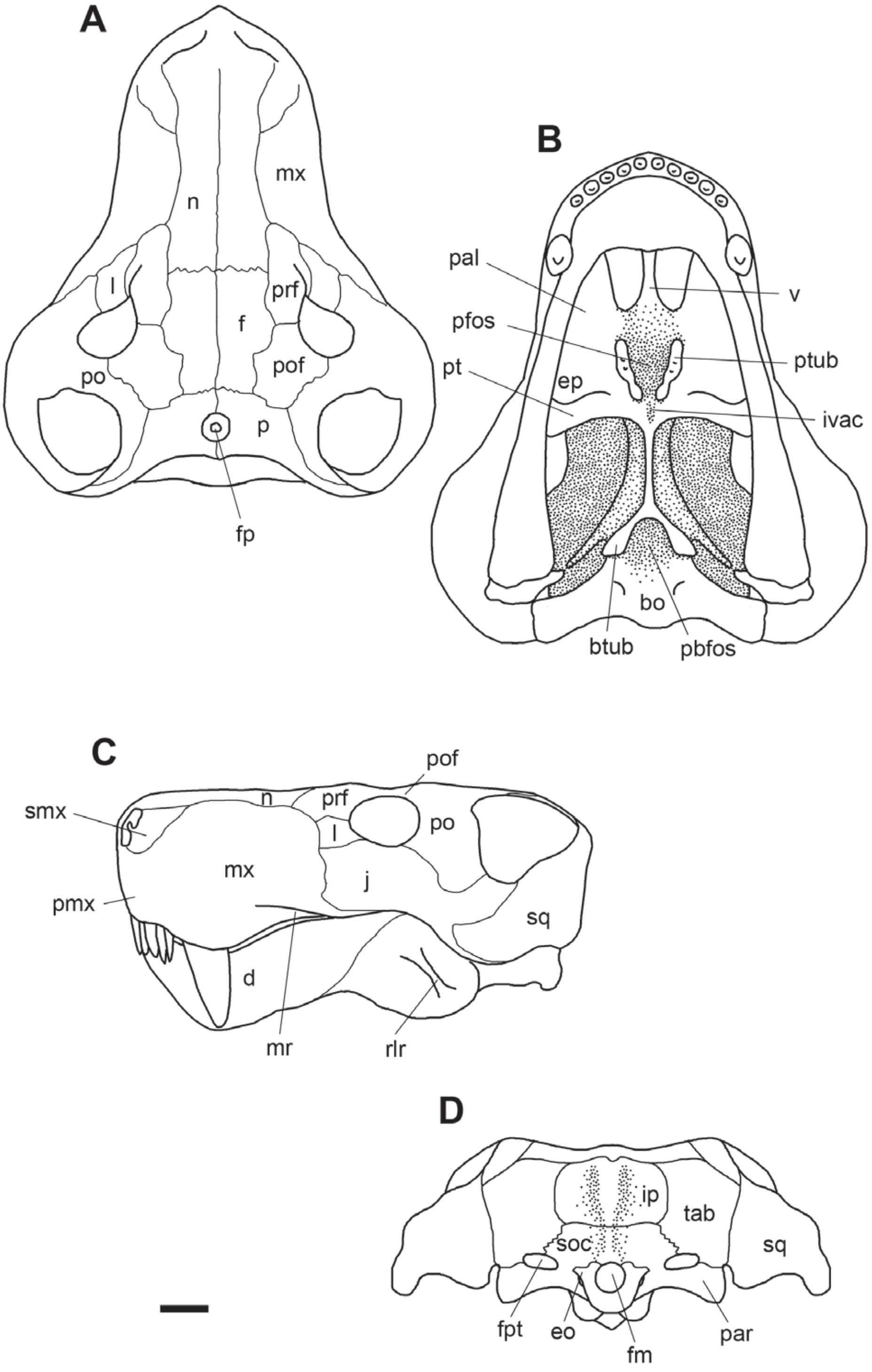


Figure 48. Illustration of the characters in the genus *Clelandina* BROOM, 1948 based on the holotype of the type species, *Clelandina rubidgei* (RC 57). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 20 mm.

are the same as the ones she gives for the genus *Broomicephalus*. Additional characters she listed for *Clelandina* are: 'postorbital bar wide with a convex border, occiput wide and low, palatal teeth under reduction, symphysis powerful', which also apply to *Broomicephalus*. Only the following characters are different: 'interorbital and intertemporal space slightly narrower than in *Broomicephalus.*' This, however, results only from the less broad posterior part of the skull of *Clelandina*; moreover compared to other gorgonopsians and even Rubidgeines, the space is still wide. 'Zygomatic arch with a ventral expansion less prominent than in *Broomicephalus*' only matches the species *C. rubidgei* but not *C. scheepersi*. 'lateral postorbital extends slightly more ventrally as in *Broomicephalus.*' The very slight difference can not be counted as generic barrier, because in the referred specimen (RC 33) of *Broomicephalus laticeps*, the lateral postorbital reaches as far ventrally as in *Clelandina*. 'Preparietal in process of disappearing. This character indeed separates *C. rubidgei* from *Broomicephalus* but also from *C. scheepersi* where the presence of a preparietal is doubtful. For *Broomicephalus* SIGOGNEAU listed the following additional points: 'Interparietal wide and not higher than the supraoccipital.' This is true for *C. rubidgei* but not for *B. laticeps*. 'Parietals participate in occiput.' This is also the case in *C. rubidgei* and *C. scheepersi*. 'Canine anteriorly sloping.' This character is considered as specific for *B. laticeps* as well as the last two characters ' basicranium and dentary short' which results mainly from the extremely shortened but laterally extended posterior part of the skull. However it is necessary to take into consideration that the comparatively short dentary is a diagnostic character of the Rubidgeinae, although of course exaggerated in *B. laticeps*.

Clelandina rubidgei differs in some ways from both *Broomicephalus laticeps* and *Clelandina scheepersi*. The poor condition of the specimen explains, however, some of the differences. Thus the dorsal skull roof is strongly weathered, as well as the lateral surface. Great parts are restored in plaster. This makes it impossible to recognise sculpturing, elevations in front or above the orbits and sutures. Two remarkable characters are, however, clearly visible, the very small and oval preparietal and few teeth on the palatine tuberosity. Both features do not occur in *Broomicephalus laticeps* (RC 101) and *Clelandina scheepersi*.

However, it is questionable to determine a gorgonopsian genus by the numbers of postcanine teeth, the presence or absence of a preparietal or the presence or absence of palatal teeth. Thus RC 101 of the species *Broomicephalus laticeps* has no teeth on the palate, whereas RC 33 does have some; *Clelandina rubidgei* has a preparietal and teeth on the palate, whereas *Clelandina scheepersi* lacks both.

Therefore I consider the differences to be minor and only interspecific and propose one genus *Clelandina*. The name *Clelandina* has priority over *Broomicephalus* since it was established by BROOM in 1948. The type species is *Clelandina rubidgei* (RC 57). The second species is *C. laticeps* with the holotype being RC 101 (=*Broomicephalus laticeps*) and RC 33 (= *Rubidgea laticeps*, = *Broomicephalus laticeps*) as referred specimen. The third species is *C. scheepersi* (= *Dracocephalus scheepersi*) with RC 102 as holotype. This species is retained because an allocation to the species *rubidgei* is hampered by the absence of a preparietal and to the species *laticeps* by the absence of postcanine teeth.

Systematic Palaeontology

Genus: ***Clelandina*** BROOM, 1948
Type species: *C. rubidgei* BROOM, 1948

Revised generic diagnosis: snout extremely broad, wider than high and well rounded anteriorly, posterior part of skull conspicuously broadened and thus at the same time shortened, occiput extremely wide and flat with a broad and distinct median ridge, interparietal wide, frontal excluded from the supraorbital rim, palatines short and broad, palatal tuberosities widely open anteriorly, basisphenoidal tubera elongate, symphysis high but very slightly sloping.

Clelandina rubidgei BROOM, 1948
Holotype: RC 57
Specific diagnosis: snout short, small preparietal, no postcanine teeth, few teeth on tuberosities of palatine.
Bibliography: BROOM, 1948, pp.587-590, fig 8-10
SIGOGNEAU, 1970, pp. 281-184, fig 164-165
SIGOGNEAU-RUSSELL, 1989, pp. 102, fig. 249

Clelandina laticeps (BROOM, 1940) nov. comb
(= *Rubidgea laticeps* BROOM, 1940; = *Dinogorgon laticeps* WATSON & ROMER, 1956; = *Broomicephalus laticeps* SIGOGNEAU-RUSSELL, 1989)
Holotype: RC 101
Referred material: RC 33
Specific diagnosis: extremely broad posterior part of the skull, three to four postcanine teeth, interparietal as high as supraoccipital, canine sloping anteriorly
Bibliography: BROOM 1940, pp. 173-174, fig. 15
BRINK & KITCHING 1953, pp. 3-5 and 12, fig. 1-2
SIGOGNEAU, 1970, pp. 308-313, fig 181-184

Sigogneau-Russell, 1989, pp. 101-102 fig. 246-247

Clelandina scheepersi (Brink & Kitching, 1953) in Sigogneau, 1970
(= *Dracocephalus scheepersi* Brink & Kitching, 1953)
Holotype: RC 102
Specific diagnosis: no preparietal, no teeth on palate, no postcanine teeth, interparietal less wide than in the other species.
Bibliography: Brink & Kitching 1953, pp. 5-6, fig. 3-4
Sigogneau, 1970, pp. 284-287, fig 166-167
Sigogneau-Russell, 1989, pp. 102

2.2.9 Dinogorgon Broom, 1936 and Rubidgea Broom, 1938

2.2.9.1 Introduction

The overview over the history of the genera *Dinogorgon* and *Rubidgea* reveals, that most of the authors already assumed a close relationship between these two taxa. Especially Sigogneau (1970) regarded them as congeneric, but a combination of both taxa would imply that this genus would be based on a largely incomplete specimen which she tried to avoid. Although the holotype of the type species *Dinogorgon rubidgei* (RC1) shows its existing sutures and proportions rather well, the palate and the posterior parts of the skull together with the posterior part of the lower jaw are unknown. This makes it nearly impossible to determine the specific allocation. Besides, it is questionable to establish a genus on such an incomplete specimen and thus RC 1 is regarded as *Dinogorgon* sp. respectively *Rubidgea* sp. However, before establishing the systematic palaeontology of the combined taxa I will discuss their history first. It is started with *Dinogorgon* Broom, 1936 and its three species *D. rubidgei*, *D. quinquemolaris* and *D. pricei* followed by *Rubidgea* Broom, 1938 and its three species *R. atrox*, *R. platyrhina* and *R. majora*.

2.2.9.2 *Dinogorgon* Broom, 1936

D. rubidgei

The type-species is *Dinogorgon rubidgei* (RC 1) which was first described by Broom (1936). However, it is based only on a snout which measures 260 mm (from the tip of the snout to the anterior border of the orbits).The preserved parts are rather well visible but the palate is inaccessible. Broom (1936) only gave a brief description which mostly concerns the dentition. Besides he mentioned that the nasal was narrow and 'a long ridge runs from near the middle of the anterior half to the upper part of the prefrontal' (Broom 1936, p. 374) and that this ridge was very coarsely rugose as well as that there was a median ridge at the posterior end of the nasals. This ridge might be more pronounced than in other forms but from personal observation I can state, that such ridges can occur in many large gorgonopsians such as '*Sycosaurus laticeps*' or '*Leontocephalus haughtoni*'. Broom also mentioned that this specimen was probably allied to *Aelurognathus tigriceps* because of its dental formula, but erected a new genus since it was the largest skull that was hitherto found and he simply lacked material for comparison. Today we know about forms like *Broomicephalus*, *Arctops ferox*, the other species of *Dinogorgon* and of course *Rubidgea*.

Sigogneau (1970) added that the snout was high and narrow, the suborbital bar was extremely broad, the nasal was wide but also strongly restricted in the middle, the naso-frontal suture was rectangular, the frontal did not contribute to the orbita, the prefrontal was short anteriorly, the lacrimal small, the dentary short and the incisors large. On the whole she confirms the description of Broom but also recognises the resemblance between *Dinogorgon* and *Rubidgea*:' …rien de fondamental ne sépare donc *Rubidgea* de *Dinogorgon*, et la distinction ne dépasse certainement pas la niveau spécifique' (Sigogneau 1970, p. 380). However, she refrained from grouping the two taxa together because of the priority of *Dinogorgon* over *Rubidgea* and the less representative type species of the resulting genus. In 1989 she continued to see *Rubidgea* 'as the last member of a satisfying morphological gradient: *Prorubidgea maccabei*, *Dinogorgon quinquemolaris*, *Rubidgea*' (Sigogneau-Russell 1989, p. 108). As already stated above, this specimen is regarded as *Rubidgea* sp. here. Especially the posterior part of the skull is diagnostic in the different species but the specimen does not show the characters sufficiently. However, an allocation to the revised genus *Rubidgea* is not doubted since characters such as the high and heavy snout, which is constricted laterally, the sculptured skull surface and the hardly visible orbits in dorsal view, demonstrate the relationship sufficiently.

D. qinquemolaris

The holotype of this species is *D. quinquemolaris* (GPIT/RE/3430) from Tanzania, which was first described by von Huene (1950). The only slightly deformed and almost completely preserved skull measures 410 mm in length. Von Huene compared GPIT/RE/3430 with *Dinogorgon rubidgei* and *Rubidgea atrox*, the hitherto only known large specimens of rubidgeines. According to him *D. quinquemolaris* had a high, dorsally flattened skull with a narrow snout and a high symphysis. The temporal region was wide, the orbit small, antero-ventrally facing and covered with tuberosities. He mentioned the narrow and long nasalia, which where covered with deep longitudinal grooves and the median elevation posteriorly. VON HUENE saw a preparietal, however the existence of such a bone is doubtful since neither SIGOGNEAU nor myself could observe any.

SIGOGNEAU (1970) remarked that the skull was, despite its heaviness, only slightly enlarged posteriorly, the bulges on the postorbital bar were very marked, the suborbital bar very broad, the wide interorbital space smaller than the intertemporal one, the prefrontal rather long anteriorly, the nasofrontal suture posteriorly situated, the septomaxilla elongated, the occiput slightly inclined, the supraoccipital low, the basioccipital long, the transverse apophyses anteriorly situated, the dentary short and massive, the ridge on the lamina reflecta well developed, the incisors and the canine strong and five postcanine teeth were present.

Referred material

The species *D. quinquemolaris* includes one referred specimen, which is RC 103 and was first described by BRINK & KITCHING (1953) as *D. oudebergensis*. It is an almost complete but somewhat deformed skull which measures 340 mm in length. BRINK & KITCHING only compared RC 103 with *D. rubidgei* and though admitting the close resemblance refrained from allocating their specmen to this taxon. They mentioned that the snout of '*D. oudebergensis*' was lower, shorter and narrower, the symphysis higher and it had five molars.

SIGOGNEAU (1970) recognised the close resemblance with *D. quinquemolaris* although, according to her, the intertemporal width was slightly narrower, the form of the postorbital bar different and the suborbital bar less high. However, she considers these differences as not as important to justify a specific distinction and allocated RC 103 to the taxon *D. quinquemolaris*. Further she stated that the parietal foramen was situated close to the occipital crest, the lacrimal short and high, the palate flat, the transverse apophyses anteriorly situated, the basioccipital long, the dentary short, the ridge on the lamina reflecta very pronounced and the dentition as strong as in the holotype. SIGOGNEAU-RUSSELL (1989) pointed out that 'this species may be conspecific with *D. rubidgei* but the type of the latter is too incomplete for adequate comparison.'

D. pricei

The last species to be discussed is *Dinogorgon pricei* with the holotype BPI 225, which was first described by BROOM & GEORGE (1950) and named '*Tigrisaurus pricei*' gen. et sp. nov.

The skull measures 320 mm in length and is rather incomplete posteriorly and ventrally. Broom & George mentioned the strongly developed and outwards facing postorbital bars, the absence of a preparietal, the exclusion of the frontal from the supraorbital rim, the long and narrow nasals, the square shaped lacrymal, the powerful incisors and the absence of postcanine teeth. According to them *D. pricei* shares the latter character only with *Clelandina*, but they did not consider those two genera as closely related because of the broad and flat snout of *Clelandina*. But they also stated that: 'In the structure of the temporal region this new form makes some approach to *Rubidgea*' (Broom & George 1950, p. 189).

Sigogneau (1970) remarked that Broom & George (1950) might have underestimated the proportions of the snout in their figure but overestimated the broadness of the posterior part of the skull. Indeed their drawing in dorsal view seems somewhat ill proportioned in my opinion, too. Thus I consider the snout slightly broader and the occiput slightly less wide, although the skull is compressed laterally and it is difficult to reconstruct the exact extension. Sigogneau further stated that the interorbital space relatively had the same width as in the preceding species, the orbits were also visible in dorsal view, the arches were broad, the nasal wide, the parietal foramen situated near the occipital crest, the parietal contributed to the occiput, the dentary was short and there were no postcanine teeth.

2.2.9.3 History of the genus *Rubidgea* Broom, 1938

R. atrox

The holotype of the type species is *Rubidgea atrox* (RC 13), which was first described by Broom (1938) as a new genus and species. It is based on a very large and well preserved skull that measures 470 mm in length. Broom mentioned the narrow and deep snout but also admitted that no sutures were delineable on the skull roof since the bones were thickened. But the nasals were relatively narrow, the lacrimal short and high, in dorsal view the orbits were hidden by the frontals and prefrontals, the broad and massive postorbital bar had a boss on its postero-dorsal edge, there was no preparietal, the interparietal was wide and the mandible powerful.

Sigogneau (1970) agreed with Broom's description and only added some more details. She remarked that the short prefrontals were flattened anteriorly as in *Dinogorgon quinquemolaris* (RC 101) and met the postfrontals posteriorly, thus excluding the frontal from the orbit; the small recess of the septomaxilla dorsal to the septomaxilla foramen and the very broad and concave occiput resembled that of *Dinogorgon quinquemolaris* RC 101, too. Further she observed that the parietal foramen was closely situated to the occipital crest, the parietal contributes to the occiput, the high paroccipital projected laterally, the jugal and squamosal were the bones which were situated ventralmost, as in *Dinogorgon*, the palatine was flat and even the vomer did not seem to subside anteriorly, the palatal fossa was large but shallow, the parabasisphenoid fossa deep, the basioccipital relatively short, the dentary short, thick and bulging, the ridge on the lamina reflecta remarkably strong and the teeth were also strong. In conclusion Sigogneau pointed out that the peculiar specimen combined supposed basic characters such as the relatively narrow interorbital space, the high vomer and the short dentary with highly specialized characters such as the large size, the curvature of the zygomatic arch, the thickenings and the strong anterior dentition. However, Sigogneau saw this development as secondarily acquired and the taxon as a highly specialized form which I confirm.

R. platyrhina

The holotype of this species is BPI 248 which was first described by Brink & Kitching (1953). The large and fairly well preserved skull measures 400 mm in length. Brink & Kitching stated that this specimen was peculiar because of its longitudinal grooves over the roof of the snout, the visibility of the orbits in dorsal view, the longer and more slender snout which tapers forward and the dorso-ventrally flattened external nares.

Sigogneau (1970) saw the same specialisation as in *R. atrox* although less accentuated and according to her the snout was shorter and narrowed somewhat anteriorly, the postfrontal had the same shape as in *Dinogorgon quinquemolaris*, the occiput was vertical, the paroccipital process protruded laterally and the posttemporal fenestra had the same orientation as in *R. atrox*, the basioccipital was short, the transverse apophyses were situated more posteriorly, the ectopterygoid was elongated in an antero-postero direction, the palatal fossa wide and shallow, the palate flat and the incisors strong. In the final discussion she stated that *R. platyrhina* could not be regarded as conspecific with *R. atrox* because of the stronger skull relief, smaller external nares, the smaller interorbital width and the more anteriorly placed transverse apophyses of the latter. Therefore she saw this species as the last member of a morphological line from *Prorubidgea robusta* over *Sycosaurus laticeps* similarly to the line *Prorubidgea maccabei – Dinogorgon quinquemolaris – Rubidgea atrox*.

R. majora

The holotype (BPI 246) measures 440 mm in length. The deformed and incomplete skull was first described by Brink & Kitching (1953). They stated that this specimen was, though of the same size as *Rubidgea atrox*, more massive, especially the posterior part of the skull. Further, according to them, the snout was broader and shorter, the postorbital arches heavier and the interorbital and intertemporal spaces greater.

Sigogneau (1970) remarked that the specimen differed not much from the preceding species in its structure, however, the thickened skull presented a short and wide snout with a heavy posterior part of the skull. She saw the intertemporal width between *R. atrox* and *R. platyrhina*, the orbits smaller, the tuberosities slightly more accentuated, the lacrimal depressed as in *Dinogorgon pricei*, the parietal contributing to the occiput, the paroccipital process high, the supraoccipital slightly higher than in the preceding species, the basioccipital short, the transverse apophyses anteriorly situated, the dentary thick, the incisors and canine strong and one postcanine tooth present. In the final discussion Sigogneau pointed out that this species was somewhat intermediate between *R. atrox* and *R. platyrhina*.

2.2.9.4 Discussion

The close examination of all specimens reveals that *Dinogorgon* and *Rubidgea* are congeneric because both taxa have a large number of characters in common:

very large and massive skull (between 320 and 480 mm in length), surface of skull sculptured dorsally, dorsal contour rather straight but slightly sloping in the posterior part of the skull; triangular in outline in dorsal view, restricted behind the canines and in front of the zygomatic arch which is well rounded and laterally flaring; snout long, high and relatively narrow with a constriction dorsally, external nares are situated dorsally; orbit small, facing outwards and covered with rugosities, only slightly or not visible in dorsal view; temporal fenestra clearly higher than long; septomaxilla long and relatively large, distinct ridge on maxilla present, nasal long and narrow, nasofrontal suture posteriorly situated, rectangular but interdigitating, prefrontal large and broad and situated on a bulging ridge at the level of the orbit, lacrimal square shaped and with antorbital depression, no preparietal nor supraorbital portion of the frontal, postfrontal large and broad with slightly rounded posterior margin, foramen parietale situated posteriorly and surrounded by a ridge, postorbital reaches far ventral on postorbital bar, squamosal reaches far anteriorly on zygomatic arch with broad process; zygomatic arch very broad and largely downturned with angular ventral margin, postorbital bar very broad with rugosities dorso-anteriorly and dorso-posteriorly which are separated by a shallow depression, posterior margin of the postorbital bar curved in an anterior direction, suborbital bar very broad with ventral margin convex; vomer dorsally situated, palatine short and broad, palatal fossa broad, oval shaped, slightly deeper anteriorly and rather shallow posteriorly, tuberosities well developed, only separated by the palatine/pterygoid suture, palatine tuberosities can have teeth and are only slightly larger than pterygoid ones, interpterygoid vacuity narrow, ectopterygoid large, parabasisphenoid fossa broad and deep, basisphenoidal tubera elongated, basioccipital rather short; occiput wide, slightly sloping and concave, interparietal slightly wider than high, not wider than supraoccipital which is relatively high, parietal contributes to the occiput, paroccipital process massive and short; strong dentition with massive caninus, zero to five postcanine teeth; strong symphysis in lower jaw, not sloping, dentary massive and rather short, ridge on lamina reflecta well developed. See fig 49 for character illustration

The combination of the two genera results on the one hand from their bibliographic history where the authors already suggested a very close relationship between *Dinogorgon* and *Rubidgea*. On the other hand a close examination of all the specimens by me allows a well-funded and sound phylogenetic re-classification.

SIGOGNEAU's (1970) and SIGOGNEAU-RUSSELL's (1989) diagnosis of the genus *Rubidgea* does in many points correspond with the diagnosis of the genus *Dinogorgon* given by her: 'temporal fossa higher than long, small orbits, wide interorbital and intertemporal space, extroversion of the jugal arch and dentary, wide and massive skull arches, zygomatic squamosal extends ventrally lower than the quadrate, no preparietal nor supraorbital frontal, very short lacrimal, anteriorly situated apophyses of the pterygoid, parietal contributes to the occiput, dentary massive, incisivi strong'. As differences she listed the posteriorly wider skull, the shorter basioccipital, the dorsally covered orbit, the reduced postcanine teeth and the moderate interparietal in *Rubidgea*. The only real differences are however the slightly wider skull and the shorter basioccipital, whereas the orbit is also covered dorsally in *Dinogorgon*. The interparietal is somewhat wider in RC 103 (referred specimen of *D. quinquemolaris*) but also rather moderately sized in GPIT/RE/7114 (holotype of *D. quinquemolaris*), whereas it is not determinable in *D. pricei* and *D. rubidgei*. The latter and *D. quinquemolaris* each have five postcanine teeth whereas *D. pricei* has none at all. Thus the number of the postcanines can not be used as a criterion to distinguish *Rubidgea* from *Dinogorgon*. Concerning the width of the posterior part of the skull all specimens are however compressed laterally and if reconstructed the difference remains only slight and might only justify a specific separation. The same is the case with the length of the basioccipital which is only known in *D. quinquemolaris* were it is indeed somewhat longer than in *Rubidgea*.

SIGOGNEAU further listed some additional characters for the genus *Rubidgea* such as the flat palate with the palatal teeth in the process of disappearing, and the pachyostosis. The palate of the *Rubidgea* species is indeed somewhat more flat than in *D. quinquemolaris* (again it is

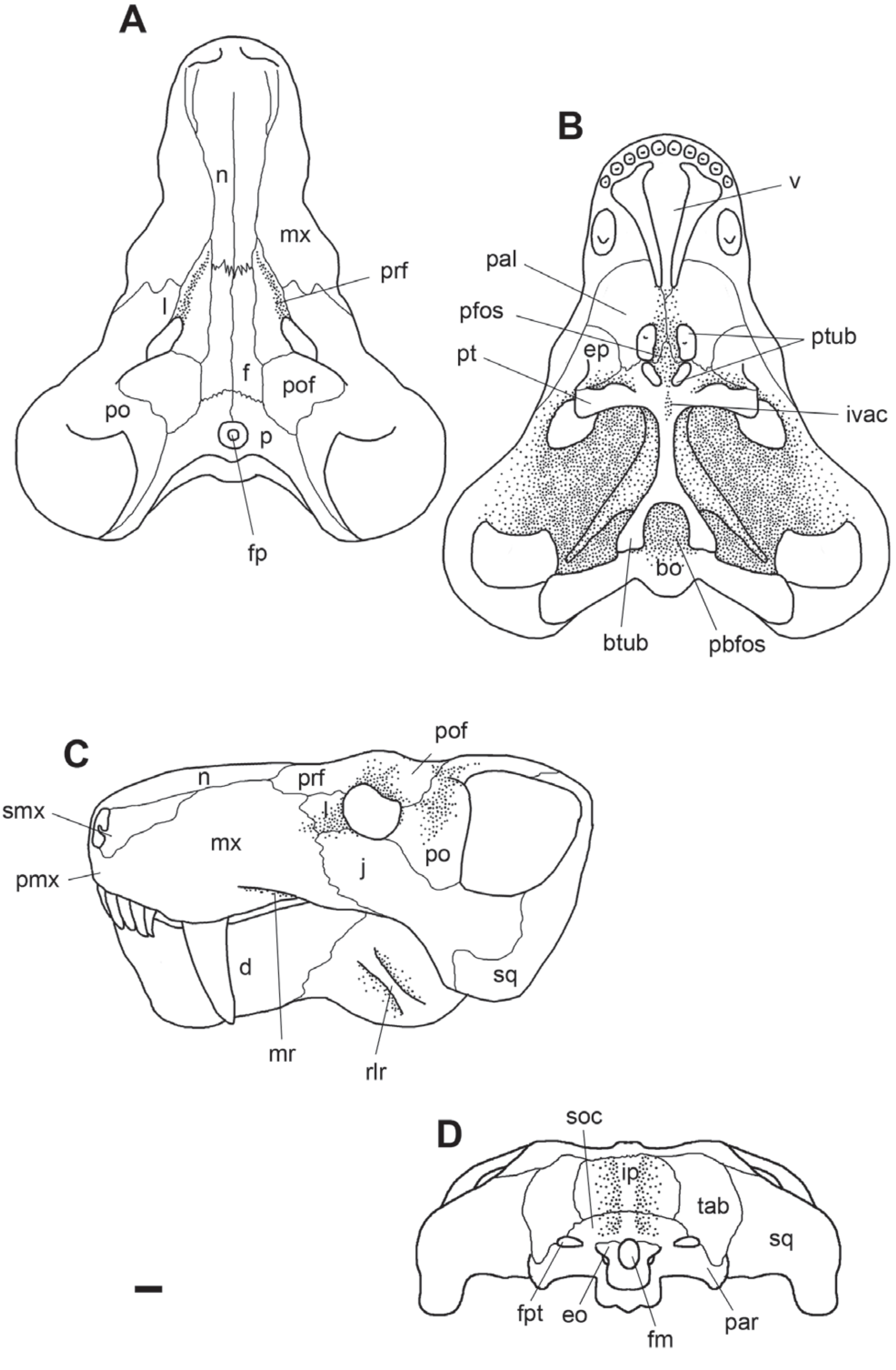


Figure 49. Illustration of the characters in the genus *Rubidgea* HAUGHTON, 1984 based on the holotype of the type species, *Rubidgea atrox* (RC 13). **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital view. Scale bar 40 mm.

hardly known in *D. rubidgei* and *D. pricei*). The pachyostosis is rather confined to *R. atrox* and *R. majora* which were the largest specimens of all the species in the two genera and thus such a feature is considered as typical for very large and probably rather old specimens.

The additional characters listed by Sigogneau for the genus *Dinogorgon* 'skull heavy and high and snout higher than wide' apply as well for the genus *Rubidgea*.

Having established the combination of both taxa in one genus, it is necessary to discuss the different species. Sigogneau considered the three species of the genus *Rubidgea* as not conspecific; however, her distinctions are in my opinion only a matter of degree. Thus she stated that the snout was long and narrow in *R. atrox*, shorter and wider in *R. platyrhina* but intermediate between the preceding two in *R. majora*. Since none of the specimens is considerably compressed this must be confirmed but occurs in my opinion only on an individual level. The interorbital and intertemporal widths were listed as narrowest in *R. atrox* and widest in *R. platyrhina* whereas the interorbital space in *R. majora* was the same as in *R. atrox*. The relations can be regarded as the same in *R. atrox* and *R. majora* and are indeed slightly larger in *R. platyrhina*. The orbits are described as small in *R. atrox*, very small in *R. platyrhina* and slightly larger in *R. majora.* Indeed the difference is minimal and the orbit is rather small in all specimens. Sigogneau somewhat overestimated the described high skull relief and tuberosities in *R. platyrhina* and also the drawings from Brink & Kitching (1953) are exaggerated in my opinion. Furthermore, a direct comparison is impossible because large parts of the nasals are restored in plaster in both *R. atrox* and *R. majora*. Finally Sigogneau described the transverse apophyses as slightly more anteriorly situated in the species *R. majora* with respect to the other two species. However this I can not confirm. Therefore I regard the three species *R. atrox*, *R. platyrhina* and *R. majora* as conspecific.

With *Dinogorgon rubidgei* regarded as undeterminable species, there are only the two species *D. quinquemolaris* and *D. pricei* of the old genus *Dinogorgon* left. However, they still will be regarded as two different species, mainly because of the number of postcanine teeth which is zero in *D. pricei* but five in *D. quinquemolaris*. The larger size in the latter excludes the assumption that larger (and probably older individuals) might have lost or reduced their postcanine teeth as it is the case in the three *Rubidgea atrox* specimens.

The name priority for the modified genus passes to *Rubidgea* which was established in 1938. The type species is therefore *R. atrox* with the holotype RC 13. Referred specimens are BPI 248 (= *R. platyrhina*) and BPI 246 (= *R. majora*). The second species is *R. quinqemolaris* with GPIT/RE/3430 as holotype and RC 103 as referred specimen. The third species is *R. pricei* (BPI 225).

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Genus: ***Rubidgea*** BROOM, 1948

Type species: *R. atrox* BROOM, 1948

Revised generic diagnosis:heavy and massive skull, snout narrow and high, markedly constricted dorso-laterally and ventrally behind the canine, dorsal surface of the skull with accentuated relief and tuberosities, orbits hardly visible in dorsal view, no preparietal, frontal excluded from supraorbital rim, palatal fossa oval, para-basisphenoidal fossa very broad, basioccipital short, occiput wide and strongly concave, tendency towards pachyostis.

Rubidgea atrox BROOM, 1948

(= *Rubidgea platyrhina* BRINK & KITCHING, 1953, = *Rubidgea majora* BRINK & KITCHING, 1953)

Holotype: RC 13

Referred Material: BPI 248 (‘*R. platyrhina’*); BPI 246 (‘R. *majora’*)

Specific diagnosis: orbits almost covered in dorsal view, basioccipital longer than in the following species, interparietal only slightly wider than high, one to two postcanine teeth.

Bibliography: BROOM 1938, pp. 527-529, fig.1-2
BROOM 1948, pp. 593-594, fig.13-14
VON HUENE 1950, p. 82
BRINK & KITCHING 1953, pp. 10-11
SIGOGNEAU 1970, pp. 298-308, fig. 174-179
SIGOGNEAU-RUSSELL 1989, pp. 108-109, fig. 262-264

Rubidgea quinquemolaris VON HUENE, 1950 nov. comb

(= *Dinogorgon quinquemolaris* VON HUENE, 1950, = *Dinogorgon oudebergensis* BRINK & KITCHING, 1953)

Holotype: IGP 16 (GPIT/RE/3430)

Referred material: RC 103 (‘*Dinogorgon oudebergensis*’)

Specific diagnosis: orbits visible in dorsal view as a small slit, teeth on both tuberosities of the palate, interparietal large, posterior part of skull less wide than in *atrox*, five postcanine teeth

Bibliography: VON HUENE 1950, pp. 81-86
BRINK & KITCHING 1953, pp. 6-7
SIGOGNEAU 1970, pp. 290-295, fig. 169-172
SIGOGNEAU-RUSSELL 1989, p. 103, fig. 253-254

Rubidgea pricei (Broom & George, 1950) in Sigogneau, 1970 nov. comb
(= *Tigrisaurus pricei* Broom & George, 1950)
Holotype: BPI 225
Specific diagnosis: orbits hardly visible in dorsal view, no postcanine teeth, postfrontal short.
Bibliography: Broom & George 1950, pp. 188-189, fig. 1-2
Sigogneau 1970, pp. 296-298, fig. 173
Sigogneau-Russell 1989, p. 104

Rubidgea sp.
RC 1 (= *Dinogorgon rubidgei* Broom 1936)
Bibliography: Broom 1936, pp. 373-374, fig. 19
Sigogneau 1970, pp. 289-290, pl. 74
Sigogneau-Russell 1989, p. 103, fig. 251

2.2.10 Conclusion on the East African specimens

This chapter summarises the modifications which were made during this study of the East African specimens in the various Museum collections. Obviously the main emphasis is on the specimens of the Tübingen Nowack-Collection since permanent access allowed for a thorough examination.

As shown in chapter 1.4. most specimens from the Nowack-Collection had a rather uncertain taxonomic position until the present study was carried out. This was partly due to the fact that scientists such as Sigogneau-Russell only had the opportunity to study the fossils in a limited period of time and then rely on drawings, notes and photographs for future work. On the other hand is their East African provenance another reason why the specimens sometimes did not fit easily into the taxonomic system of their South African relatives.

The list below illustrates the results of the alphataxonomic uncertainties of the East African specimen of the Nowack-Collection as carried out during this study. For better comparison with earlier literature the former names are listed with the old collection numbers.

Aelurognathus? *parringtoni* (IGP U 28)……………..….*Sauroctonus parringtoni* (GPIT/RE/7113)
Aloposaurus sp. (IGP K51)…………………………...*Cyonosaurus broomianus* (GPIT/RE/7123)
Dinogorgon quinquemolaris (IGP K 16)…………*Rubidgea quinquemolaris* (GPIT/RE/7113)
Arctognathus? *nasuta* (IGP K 52)……………………………….*Njalila nasuta* (GPIT/RE/7118)
Arctognathus? *nasuta* (IGP K 96)…………………………..…...*Njalila nasuta* (GPIT/RE/7119)

cf. *Arctognathus*? *nasuta* (IGP K 41)…………………………..*Njalila nasuta* (GPIT/RE/7120)
cf. *Arctognathus*? *nasuta* (IGP K 115)…………………………..*Njalila nasuta* (GPIT/RE/7121)
Leontocephalus haughtoni (IGP K 46B)……………….*Sycosaurus kingoriensis* (GPIT/RE/7117)
Sycosaurus? *kingoriensis* (IGP K 47)……………………*Sycosaurus kingoriensis* (GPIT/RE/7116)
Aelurosaurus? IGP 7412 (South Africa)……………….*Aelurosaurus wilmanae* (GPIT/RE/7124)

In this study it turned out that most of the specimens which were collected in the East African countries Malawi, Tanzania and Zambia constitute separate species if not even separate genera. Most of the authors who dealt with specimens from East Africa did not reflect on a possible geographic separation of South and East African animals. Only concerning the Russian specimens a clear cut was always made between the genera and species except for Hartmann-Weinberg (1938) who considered *Sauroctonus* progressus to be a new species of the genus *Arctognathus*.

Although many species of today's African animals like elephants, antelopes or crocodiles have a large distribution, there also exist many species which are restricted to a rather small area. This study has no intention to carry out a distribution map for gorgonopsians since the number of East African finds is still too small but it can provide an overview over the individual finds and specimens and demonstrate the alphataxonomic problems which did occur more frequently than with South African specimens. Below all East African specimens are listed. First the new name (if there was a modification) is given and afterwards the old name is shown for better faciliation.

Cyonosaurus broomianus (GPIT/RE/7123)………………………………………Aloposaurus sp.
Cyonosaurus tenuirostris (SAM 1174)…………………………………………Lycaenops tenuirostris
Gorgonops dixeyi (SAM 7846)…………………………………………………….Gorgonops? dixeyi
Njalila nasuta (GPIT/RE/7118, GPIT/RE/7119, GPIT/RE/7120, GPIT/RE/7121, MZC 886, MZC887, MZC876)………………Arctognathus? nasuta; cf. Arctognathus? nasuta
Njalila insigna (MZC 885)……………………………………………………Scylacops capensis
Lycaenops quadrata (SAM 7856, BPI 390, BPI 389, BPI (FN) 3303)………….Aelurognathus quadrata
Aelurognathus tigriceps (SAM 7847)………………………………….Aelurognathus nyassaensis
Sauroctonus parringtoni (GPIT/RE/7113)……………………………….Aelurognathus? parringtoni
Sycosaurus kingoriensis (GPIT/RE/7116, GPIT/RE/7117)…………………Sycosaurus? kingoriensis; Leontocephalus haughtoni
Sycosaurus terror (MZC 891)…………………………………………………Ruhuhucerberus terror
Sycosaurus? intactus (MZC 878)……………………………………………Leontocephalus? intactus

The genus *Cyonosaurus* has two species which were found in East Africa. *C. broomianus* illustrates its uncertain position in the history by varying allocations to almost all small sized genera whereas *C. tenuirostris* was seen as distinct genus by Boonstra (1953) but then allocated to the genus *Lycaenops* by Sigogneau (1970). Both species are considered here as clearly belonging to the genus *Cyonosaurus* but nevertheless sharply distinct from the other species by a number of unique characters.

Gorgonops dixeyi as well clearly belongs to the genus *Gorgonops* but as a species of its own.

The genus *Njalila* is the only one in this study which is new, although formed by specimens which already belonged to the separate genus '*Dixeya*'. As described in chapter 2.2.5.3 all specimens which were allocated to this genus are so highly unique that a separate genus is obligatory.

The specimens which belong to the species *Lycaenops quadrata* also show some unique characters but they still can be assigned to the genus *Lycaenops* and do form a separate species.

SAM 7847 which is now a referred specimen of *Aelurognathus tigriceps* is the only East African specimen which is assigned to a South African species in this study. Its somewhat ambiguous position is illustrated by the fact that Haughton (1927) erected the new species *A. nyassicus*, whereas Sigogneau (1970) assigned it to the species *A. tigriceps* as cf. but re-established the species *A. nyassicus* in 1989.

The genus *Sycosaurus* contains three species from East Africa and is thus the only gorgonopsian genus with mostly East African species. *S. kingoriensis* and *S. terror* correspond well with the diagnosis of the genus, although *S. terror* attracts attention by its peculiar formed nasals as described above. *S. intactus* might constitute a separate genus, however it is still allocated to *Sycosaurus* in this study because of a number of characters which are shared by both taxa.

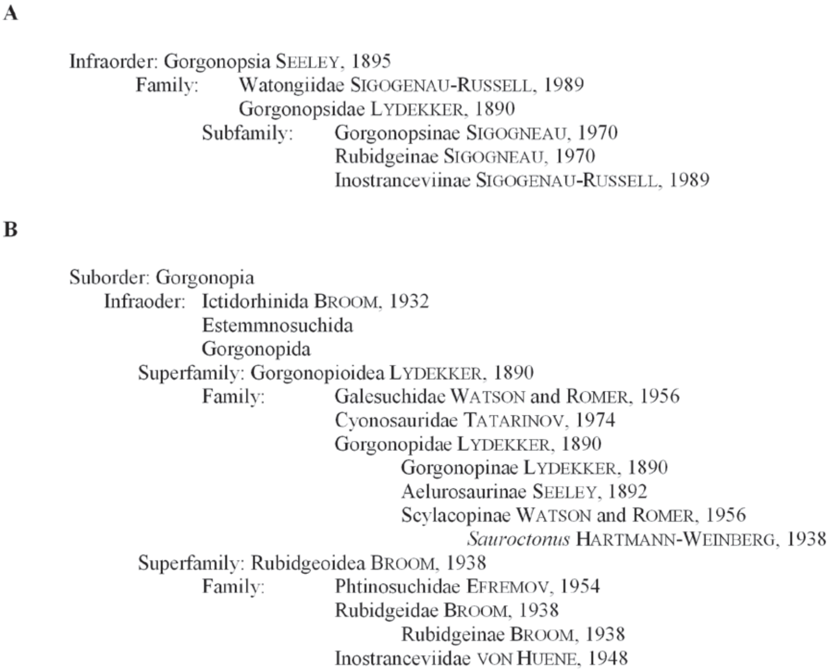
GPIT/RE/7113 is the only specimen of East African provenance which was allocated to a Russian genus as comprehensively described in chapter 2.1.

2.3 The In-group phylogeny of the Gorgonopsia

2.3.1 The classification of the Gorgonopsia sensu Sigogneau-Russell, 1989 and Ivakhnenko, 2002

At present, there exist two classifications of the Gorgonopsia, which are somewhat contradictory. The first was given by Sigogneau (1970) and slightly modified by Sigogneau-Russell (1989). Ivakhnenko (2002), on the other hand, provided a different view. However, it is necessary to bear in mind that Sigogneau's revision mainly discussed African material, whereas Ivakhnenko exclusively took Russian forms into consideration. Since this study considers mainly African forms as well, I will only briefly refer to Ivakhnenko's phylogeny. For a better overview of both classifications see table 1.

Sigogneau-Russell (1989) divided the infraorder Gorgonopsia in two families, the Watongiidae and the Gorgonopsidae. However, after a recent re-evaluation of *Watongia*, this animal is considered to be a varanopid synapsid (Reisz & Laurin, 2004)



A

Infraorder: Gorgonopsia Seeley, 1895
    Family: Watongiidae Sigogenau-Russell, 1989
        Gorgonopsidae Lydekker, 1890
            Subfamily: Gorgonopsinae Sigogneau, 1970
                Rubidgeinae Sigogneau, 1970
                Inostranceviinae Sigogenau-Russell, 1989

B

Suborder: Gorgonopia
    Infraoder: Ictidorhinida Broom, 1932
        Estemmnosuchida
        Gorgonopida
    Superfamily: Gorgonopioidea Lydekker, 1890
        Family: Galesuchidae Watson and Romer, 1956
            Cyonosauridae Tatarinov, 1974
            Gorgonopidae Lydekker, 1890
                Gorgonopinae Lydekker, 1890
                Aelurosaurinae Seeley, 1892
                Scylacopinae Watson and Romer, 1956
                    Sauroctonus Hartmann-Weinberg, 1938
    Superfamily: Rubidgeoidea Broom, 1938
        Family: Phtinosuchidae Efremov, 1954
            Rubidgeidae Broom, 1938
                Rubidgeinae Broom, 1938
            Inostranceviidae von Huene, 1948

Table 1. Classification of the Gorgonopsia. **A**, according to Sigogneau-Russell (1989), **B**, sensu Ivakhnenko (2002).

Sigogneau-Russell listed a number of characters in her diagnosis of the Gorgonopsia which I generally accept here. However, the form and size of the temporal opening needs to be emphasised, since it is the only autapomorphy of the Gorgonopsia within the character frame of this study. Thus the temporal opening is not only larger than the orbit but is additionally situated on the same level. This is in contrast to forms with the plesiomorphic character state, e.g., the Biarmosuchia and Phtinosuchia where the dorsal margin of the temporal fossa strongly slopes ventrally. The short premaxillary extension on the dorsal skull roof, the considerably shortened lacrimal and the ventrally directing canine can also be added to Sigogneau's diagnosis.

Ivakhnenko grouped the Gorgonopsia together with the Dinocephalia into the Order Gorgodontia, thus giving the Gorgonopsia the state of a sub-order. The diagnosis he gives for the Gorgonopsia mainly refers to characters that are related to the temporal opening:

'Temporal fenestra developed mainly posterosuperiorly; therefore upper region of occipital plate of squamosal curved posteriorly. Temporal fenestra almost lacking anterodorsal expansion; dorsoexternally, anterior part of temporal fenestra usually covered by postorbital.' (Ivakhnenko 2002, p. 392)

For the Gorgonopsida he listed: 'Temporal fenestra substantially enlarged posteriorly and dorsally, its dorsoposterior edge raised to level of parietal shield.' (Ivakhnenko 2002, p. 394). This corresponds with the results of this study.

Ivakhnenko, however, divided the Gorgonopsida in the two superfamilies Gorgonopioidea and Rubidgeoidea, a proposal, which is rejected here.

Sigogneau, on the other hand, combined the gorgonopsines and rubidgeines in one family, the Gorgonopsidae. In her diagnosis for the Gorgonopsidae she only mentioned two skull characters: '2 upper canines functioning alternately' and 'Less than 10 postcanines' (Sigogneau-Russell 1989, p. 66)

2.3.2 Character discussion and data matrix

For the phylogenetic analyses all 13 genera remaining after the re-evaluation in chapter 2.2. were taken as in-group. Additionally the Russian genera *Sauroctonus* and *Inostrancevia* (Figure 50) were considered, the first taxon including the species *S. parringtoni* with GPIT/RE/7113 as holotype. As outgroups *Biarmosuchus* Chudinov, 1960 and *Rubidgina* Broom, 1942 were chosen.

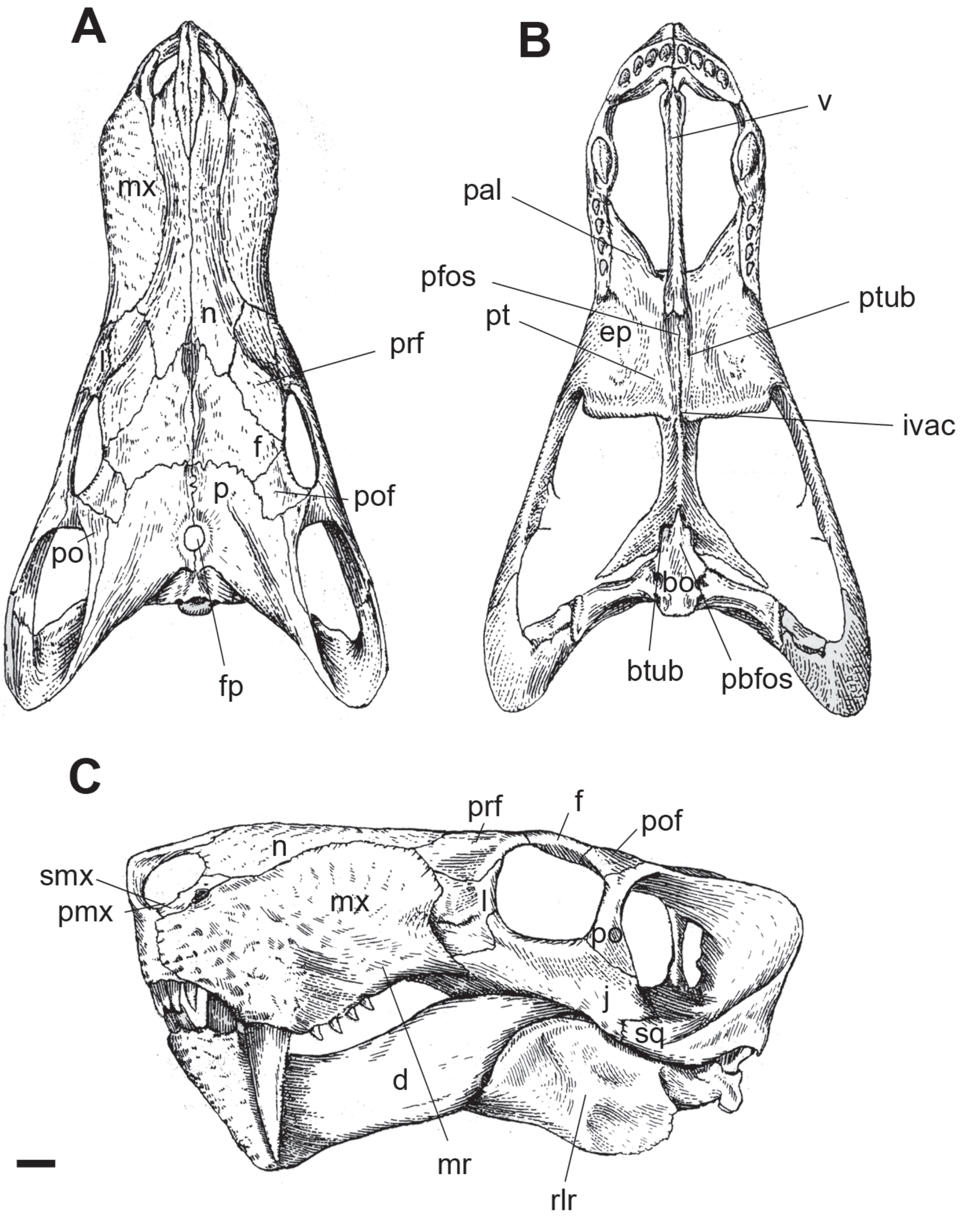


Figure 50. Illustration of the characters in the genus *Inostrancevia* AMALITZKY, 1922 based on the lectotype of the type species *Inostrancevia alexandri* (PIN 2005/1587). **A**, dorsal; **B**, ventral; **C**, lateral view. Scale bar 25 mm (modified from IVAKHNENKO 2001).

Below a list with the 43 cranial characters, which were used in the analysis, is provided for better overview. Figure. 51 illustrates certain of the less obvious character states.

1) average skull length in adult less than 150mm (0) up to 300mm (1) larger than 300mm (2)
2) skull widens continually in posterior direction (0) skull is considerably constricted at the area of the suborbital arch (1)
3) posterior part of skull moderately enlarged (0) somewhat enlarged (1) considerably broadened (2)
4) orbit comparatively large (0) small in relation to the size of the skull (1)
5) orbit well visible in dorsal view (0) only visible as a slit in dorsal view (1)
6) supraorbital thickening absent (0) present (1)
7) temporal opening quadratic but sloping (0) elongate (1) quadrangular and non-sloping (2)
8) interorbital and intertemporal spaces of approximately the same width (0) intertemporal space wider than interorbital space (1)
9) lateral face of snout constantly sloping (0) laterally constricted dorsally (1)
10) external nares ventrally situated (0) dorsally situated (1)
11) ventral border of maxilla straight or only slightly convex (0) strongly convex (1)
12) ridge on maxilla postero-dorsal to postcanines absent (0) present (1)
13) septomaxilla long and narrow latero-posteriorly (0) short and rather high latero-posteriorly (1)
14) lacrimal oblong (0) quadrangular or higher than long (1)
15) antorbital depression absent (0) present (1)
16) naso-frontal suture pointed and anteriorly situated (0) straight and posteriorly situated (1)
17) prefrontal long anteriorly (0) short anteriorly (1)
18) contribution of frontal to dorsal orbital margin large (0) small (1) absent (2)
19) postfrontal narrow at the orbit and continually narrowing posteriorly (0) considerably broad at the orbit, constricted in the middle and terminating in a broad process (1)
20) preparietal large (0) small (1) absent (2)
21) lateral process of squamosal on zygomatic arch reaches up to the level of the postorbital bar (0) reaches only up to the mid-level of the temporal opening (1)
22) suborbital arch slender (0) moderately enlarged (1) massive and thick (2)
23) postorbital bar slender (0) moderately enlarged (1) massive and thick (2)
24) posterior margin of postorbital bar posteriorly directed or straight (0) anteriorly directed (1)
25) zygomatic arch slender and straight (0) moderately broad and straight (1) broad and downturned (2)
26) vomer about the same width throughout its length (0) considerably broadened anteriorly (1)
27) palatine narrow and longish (0) broad and short (1)
28) palatal tuberosities narrow (0) well developed and broad (1)
29) palatal tuberosities confluent (0) well separated by a trench (1)

30) teeth on both palatal tuberosities and additionally on transverse apophyses (0) teeth present only on palatal tuberosities (1) teeth only present on tuberosities of palatine (2)
31) palatal fossa narrow and long (0) broad and considerably shorter (1)
32) transverse apophyses posteriorly situated (0) anteriorly situated (1)
33) interpterygoid fossa large and deep (0) small and shallow (1)
34) para-basisphenoid fossa narrow (0) broad (1)
35) basisphenoid tubera slender (0) massive (1)
36) base of braincase long (0) short (1)
37) occiput almost straight (0) somewhat concave (1) strongly concave (2)
38) interparietal about as high as wide (0) considerably wider than high (1)
39) supraoccipital high (0) low (1)
40) symphysis sloping (0) almost straight (1)
41) dentary slender (0) dentary massive and high (1)
42) incisors and canine slender (0) moderately strong (1) considerably strong (2)
43) numerous postcanine teeth (five and more) in upper jaw (0) less than five postcanine teeth (1)

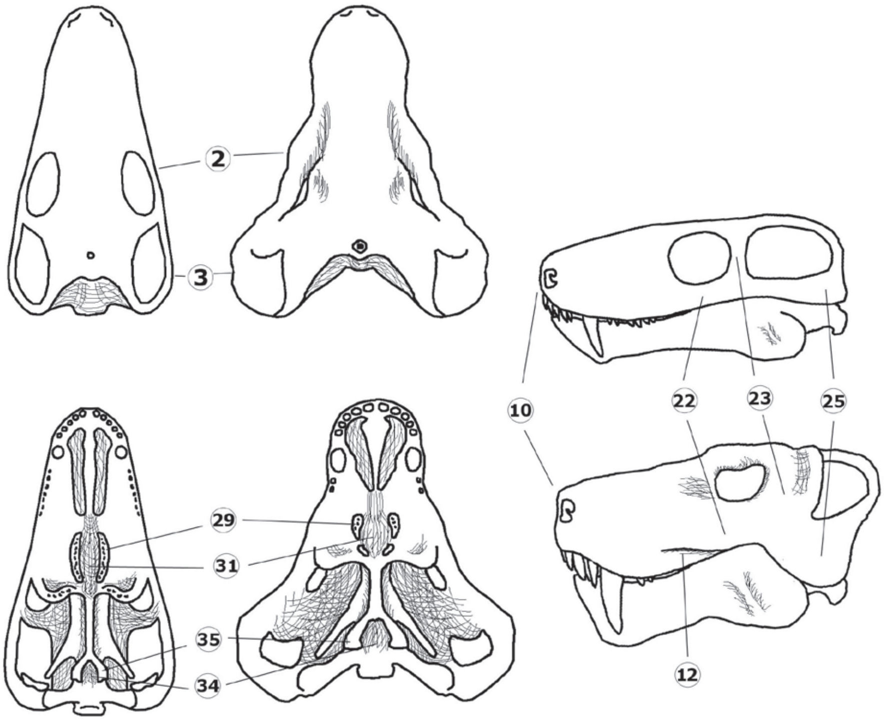


Figure 51. Graphic illustration of the less obvious character states used in the analysis and listed above.

A data matrix with the 43 characters (see table 2) of the cranial skeleton was analysed with Paup* 4.0b10. The analysis with branch-and-bound search yields two most parsimonious trees with a length of 93 steps, a consistency index of 0.58, a retention index of 0.83 and a rescaled consistency index of 0.48. Bremer-support and Bootstrap records are depicted in fig. 52. where the strict consensus tree of the phylogenetic relationships of the Gorgonopsia is shown. Below, the characters are discussed:

(1) Average skull length in adult less than 150 mm (0) up to 300 mm (1) skull length larger than 300 mm (2)

A small skull size is regarded as the plesiomorphic state as it is shown by *Biarmosuchus* and *Rubidgina*. It might be difficult sometimes to determine whether it concerns only a young individual or a real taxon but this question was already discussed in chapter 2.2.3 The plesiomorphic condition is found in *Aloposaurus*, *Cyonosaurus*, *Aelurosaurus* (= the three plesiomorphic small sized genera) and homoplastic in *Eoarctops*. *Scylacognathus*, *Sauroctonus*, *Gorgonops*, *Njalila*, *Lycaenops* and *Arctognathus* have an intermediate skull length and are coded as (1) whereas *Inostrancevia* and the rubidgeines, which have considerably larger skulls, are coded as (2). This is seen as a support for the sister-group relationship of the latter taxa.

(2) Skull widens continually in posterior direction (0) skull is considerably constricted at the area of the suborbital arch (1)

In *Biarmosuchus* and *Rubidgina* the skull widens more or less continually from the snout to the zygomatic arches if seen in dorsal view. This plesiomorphic state is found in the three plesiomorph small sized genera as well as in *Sauroctonus*, *Scylacognathus*, *Eoarctops*, *Njalila* and *Lycaenops*. In the derived state the area of the suborbital arch projects laterally and thus the skull is somewhat constricted anteriorly and posteriorly to the orbit. This condition is found homoplastically in *Gorgonops*, *Arctognathus, Inostrancevia* and the *Rubidgeinae*.

(3) Posterior part of skull less enlarged (0) somewhat enlarged (1) considerably broadened (2)

Biarmosuchus and *Rubidgina* display a narrow posterior skull part. The plesiomorphic state is only found in the three plesiomorph small sized genera. Moderately laterally flaring squamosals are shown by *Sauroctonus*, *Scylacognathus*, *Eoarctops*, *Gorgonops*, *Njalila,* *Lycaenops*, *Arctognathus* and *Inostrancevia*, a character state coded as (1). A considerably wide posterior skull part (2) is an autapomorphy of the Rubidgeinae.

(4) Orbit comparatively large (0) small in relation to the size of the skull (1)

The plesiomorphic state is found in all taxa except for *Inostrancevia* and the rubidgeines. This character therefore supports the sister-group relationship of *Inostrancevia* and the rubidgeines.

(5) Orbit well visible in dorsal view (0) only visible as a slit in dorsal view (1)

In *Biarmosuchus* and *Rubidgina* the large orbits are well visible in dorsal view. The slit-like appearance of the orbit is due to a steeper oriented postorbital bar and a less laterally flaring suborbital arch. It is correlated with a comparatively high skull. The derived state is found as a homoplasy in *Scylacognathus*, *Gorgonops*, *Lycaenops*, *Arctognathus*, *Inostrancevia* and the Rubidgeinae.

(6) Supraorbital thickening absent (0) present (1)

The dorsal margin of the orbit in *Biarmosuchus* and *Rubidgina* is of constant height. The presence of a supraorbital thickening is an autapomorphy of the Rubidgeinae.

(7) Temporal opening quadratic but sloping (0) elongate (1) quadrangular and non-sloping (2)

The form and position of the temporal opening is an unequivocal autapomorphy of the Gorgonopsia. In the outgroup it is quadratic and comparatively small and it is sloping ventrally. Thus its dorsal margin is not situated at the same level as the dorsal margin of the orbit as it is in all Gorgonopsia. In the derived condition (1) the temporal fenestra is rather long, whereas it is again quadratic (but larger than in the outgroup) in the derived state (2). This condition is shown by all taxa from *Lycaenops* onwards.

(8) Interorbital and intertemporal spaces of approximately the same width (0) intertemporal space wider than interorbital space (1)

This character again is somewhat subject to preservation but it is nevertheless retained after thorough investigation of the specimens. It turned out that the derived character state is an autapomorphy of the Rubidgeinae.

(9) Lateral face of snout constantly sloping (0) laterally constricted dorsally (1)

In *Biarmosuchus* and *Rubidgina* the lateral face of the snout is smoothly rounded. This plesiomorphic state is found as a homoplasy in the three plesiomorph small sized genera as well as in *Sauroctonus*, *Scylacognathus*, *Eoarctops*, *Gorgonops*, *Sycosaurus* and *Clelandina*. In the derived condition, shown by *Njalila*, *Lycaenops*, *Arctognathus*, *Inostrancevia*, *Aelurognathus* and *Rubidgea*, a more or less pronounced depression is established laterally in the area of the maxillary/nasal contact.

(10) External nares ventrally situated (0) dorsally situated (1)

Ventrally situated external nares are correlated with a comparatively low anterior premaxillary and a sloping snout. This condition is displayed by *Biarmosuchus* and *Rubidgina* and is therefore regarded as plesiomorphic here. The plesiomorphic state is only shown by *Aloposaurus*, *Sauroctonus* and *Scylacognathus*.

(11) Ventral border of maxillary straight or only slightly convex (1) strongly convex (1)

In *Biarmosuchus* and *Rubidgina* the curvature of the ventral margin of the maxillary is only slight and hence the arrangement of the tooth row is almost straight. This plesiomorphic condition is found as a symplesiomorpy in *Aloposaurus*, *Cyonosaurus* and *Aelurosaurus*.

(12) Ridge on maxilla postero-dorsal to postcanines absent (0) present (1)

In the outgroup no ridges are found at the lateral wall of the maxilla. A more or less pronounced ridge postero-dorsal to the postcanines, which continues on the ventral margin of the suborbital arch in posterior direction, is considered as the derived condition. It is shown homoplastically by *Njalila*, *Arctognathus* and as potential synapomorphy by *Inostrancevia* and the rubidgeines.

(13) Septomaxilla long and narrow latero-posteriorly (0) short and rather high latero-posteriorly

The size of the lateral septomaxillary exposure is connected to the shape of the maxilla and hence subject to the size of the canine and the position of the canine root. The plesiomorphic state is found in the three plesiomorph small sized genera and in *Sauroctonus*, *Scylacognathus*, *Eoarctops* and *Gorgonops*, whereas the derived condition is shown by *Njalila*, *Lycaenops*, *Arctognathus*, *Inostrancevia* and the rubidgeines.

(14) Lacrimal oblong (0) quadratic or higher than long (1)

The shape of the lacrimal is supposed to be connected to the size of the canine on the one hand but it is also the length of the snout that seems to be important. Thus the plesiomorphic state is not only found in *Aloposaurus*, *Cyonosaurus*, *Aelurosaurus*, *Sauroctonus*, *Scylacognathus*, *Gorgonops*, *Njalila* and *Lycaenops* but also in *Inostrancevia*, which has a strong canine but a considerably elongated snout. On the other hand the derived state is not only shown by *Arctognathus* and the rubidgeines but also by *Eoartops*, which has a rather weak canine but a short snout.

(15) Antorbital depression absent (0) present (1)

An antorbital depression is expressed by a concavity in the lacrimal area in front of the orbit and is not found in the outgroup. The derived character state is present as a synapomorphy in all taxa from *Lycaenops* onwards.

(16) Naso-frontal suture pointed and anteriorly situated (0) straight and posteriorly situated (1)

Biarmosuchus and *Rubidgina* have a pointed naso-frontal suture which is anteriorly situated. The derived state is found as a homoplasy in *Aelurosaurus*, *Cyonosaurus*, *Sauroctonus*, *Eoarctops*, *Gorgonops* and *Lycaenops*.

(17) Prefrontal long anteriorly (0) short anteriorly (1)

The size of the prefrontal is again connected to the size of the maxilla and the canine. The derived state is found as a synapomorphy in all taxa from *Njalila* onwards.

(18) Contribution of frontal to dorsal orbital margin large (0) medium sized to small (1) absent (2)

In *Biarmosuchus* and *Rubidgina* the supraorbital portion of frontal is large. The plesiomorphic condition is found in the three plesiomorph small sized genera and *Sauroctonus* and *Eoarctops*. The derived state (1) is distributed homoplastically in *Scylacognathus*, *Gorgonops*, *Njalila*, *Lycaenops*, *Arctognathus*, *Inostrancevia* and *Aelurognathus*. *Sycosaurus*, *Clelandina* and *Rubidgea* have lost the supraorbital portion of the frontal and thus the state (2) is a synapomorphy of these taxa.

(19) Postfrontal narrow at the orbit and continually narrowing posteriorly (0) considerably broad at the orbit, constricted in the middle and terminating in a broad process (1)

The derived state is found as a homoplasy in *Gorgonops* and as a synapomorphy in *Arctognathus*, *Inostrancevia* and the rubidgeines. In *Biarmosuchus* and *Rubidgina* the postfrontal is always narrow.

(20) Preparietal large (0) small (1) absent (2)

The size of the preparietal is distributed rather homoplastically. Thus it is large in *Aloposaurus*, *Eoarctops* and *Gorgonops* and small in all other taxa except for *Sycosaurus*, *Clelandina* and *Rubidgea*, where the derived state (2) is found as a synapomorphy.

(21) Lateral process of squamosal on zygomatic arch reaches up to the level of the postorbital bar (0) reaches only up to the mid-level of the temporal opening (1)

In the outgroup the lateral process of the squamosal reaches far anteriorly. However, the anterior extension of the squamosal on the zygomatic arch is not correlated with the thickness of this skull arch. The derived condition is shown as a homoplasy by *Aelurosaurus*, *Sauroctonus*, *Scylacognathus*, and as a potential synapomorphy by *Inostrancevia* and the rubidgeines. The condition is unknown in *Aloposaurus* and *Eoarctops*.

(22) Suborbital arch slender (0) moderately enlarged (1) massive and thick (2)

Biarmosuchus and *Rubidgina* display very slender skull arches. A slender suborbital arch is shown by the three plesiomorph small sized genera and by *Eoarctops*, *Gorgonops*, *Njalila* and *Lycaenops*. *Sauroctonus*, *Scylacognathus*, *Arctognathus* and *Inostrancevia* have an intermediately thickened suborbital arch, a condition which is coded with (1) here. The massive and thick suborbital arch (2) is a synapomorphy of the rubidgeines.

(23) Postorbital bar slender (0) moderately enlarged (1) massive and thick (2)

This character is a symplesiomorphy of the three plesiomorph small sized genera. The derived condition is again divided in (1) and (2). The latter state is another synapomorphy of the rubidgeines.

(24) Posterior margin of postorbital bar posteriorly directed or straight (0) anteriorly directed (1)

Biarmosuchus has a posteriorly directed posterior margin of the postorbital bar whereas in *Rubidgina* it is straight. The derived state constitutes a synapomorphy of the rubidgeines.

(25) Zygomatic arch slender and straight (0) moderately broad and straight (1) broad and down-turned (2)

The plesiomorphic state is another symplesiomorphy of the three plesiomorphic small sized genera, whereas the ventral curvature of the zygomatic arch clearly is a synapomorphy of the rubidgeines.

(26) Vomer about the same width throughout its length (0) considerably broadened anteriorly (1)

In the outgroup the vomer is rather narrow throughout its length. The derived state is found as a synapomorphy in all genera from *Scylacognathus* onwards except for *Inostrancevia* which is therefore coded for the plesiomorphic condition although this character state certainly is a matter of reversion.

(27) Palatine narrow and oblong (0) broad and short (1)

Biarmosuchus and *Rubidgina* have narrow and elongate palatines. The derived state is found homoplastically in *Eoarctops*, *Njalila*, *Arctognathus*, *Inostrancevia* and the rubidgeines.

(28) Palatal tuberosities narrow (0) well developed and broad (1)

The palatal tuberosities are bulbous swellings on the palatine and pterygoid which border the palatal fossa laterally. They are narrow and elongate in *Biarmosuchus* and *Rubidgina*. The derived condition is found as a homoplasy in most taxa except for *Aloposaurus*, *Cyonosaurus*, *Njalila* and *Arctognathus*.

(29) Palatal tuberosities confluent (0) well separated by a trench (1)

In *Biarmosuchus* and *Rubidgina* the palatal tuberosities of the palatine and pterygoid are virtually fused. This plesiomorphic condition is shown by *Aloposaurus*, *Eoarctops*, *Gorgonops*, *Njalila* and *Lycaenops*. In the derived condition, shown by *Cyonosaurus*, *Aelurosaurus*, *Sauroctonus*, *Scylacognathus*, *Arctognathus*, *Inostrancevia* and the rubidgeines, both tuberosities are well separated and the palatine/pterygoid suture runs in a trench.

(30) Teeth on both palatal tuberosities and additionally on transverse apophyses (0) teeth present only on palatal tuberosities (1) teeth only present on tuberosities of palatine (2)

Biarmosuchus and *Rubidgina* both have numerous teeth on the palatal tuberosities as well as on the transverse apophyses of the pterygoid. The derived state (1) is shown as a homoplasy in the three plesiomorphic small sized genera and *Eoarctops*, *Arctognathus*, *Aelurognathus* and *Sycosaurus* whereas (2) is also found homoplastically in *Inostrancevia*, *Clelandina* and *Rubidgea*.

(31) Palatal fossa narrow and long (0) broad and considerably shorter (1)

This character is distributed in such a way that the three small sized genera and *Sauroctonus*, *Scylacognathus*, *Eoarctops* and *Gorgonops* show the plesiomorphic and *Njalila*, *Lycaenops*, *Arctognathus*, *Inostrancevia* and the rubidgeines the derived condition.

(32) Transverse apophyses posteriorly situated (0) anteriorly situated (1)

The position of the transverse apophyses is connected with the pterygoideus jaw musculature. An anteriorly situated attachment area provides a better leverage for a presumed more massive lower jaw. The plesiomorphic state is found in the three plesiomorph small sized genera and in *Sauroctonus*, *Scylacognathus*, *Eoarctops* and *Njalila*, whereas the derived state is shown homoplastic by *Gorgonops*, *Arctognathus*, *Inostrancevia* and the rubidgeines.

(33) Interpterygoid fossa large and deep (0) small and shallow (1)

Biarmosuchus and *Rubidgina* display a large interpterygoid fossa which is considered here as a plesiomorphic state. However the character is somewhat problematical since it might be subject to preservation. Nevertheless it is used in this analysis after thorough observation of the specimens. The derived state is distributed as a homoplasy among *Eoarctops*, *Inostrancevia*, *Aelurognathus* and *Rubidgea*.

(34) Para-basisphenoid fossa narrow (0) broad (1)

Biarmosuchus and *Rubidgina* display a rather narrow and elongate para-basisphenoid fossa. The derived character is a homoplasy of *Eoarctops*, *Arctognathus* and the rubidgeines. *Inostrancevia* has a comparatively narrow fossa in relation to its large skull and is therefore coded for the plesiomorphic condition.

(35) Basisphenoid tubera slender (0) massive (1)

The outgroup shows slender basisphenoid tubera. This plesiomorphic state is shown by the three stem group representatives and the Gorgonopsidae. The derived character state is a synapomorphy of the rubidgeines.

(36) Base of braincase long (0) short (1)

As base of the braincase are seen here the ventral parts of the para-basisphenoid complex together with the basioccipital which are elongate and narrow in the outgroup. The derived state is found as a synapomorphy in all taxa from *Eoarctops* onwards.

(37) Occiput almost straight (0) somewhat concave (1) strongly concave (2)

Biarmosuchus and *Rubidgina* display an almost straight occiput. The grade of occipital concavity might be correlated with the neck musculature to some extent. The plesiomorphic state is a symplesiomorphy of the three plesiomorph small sized genera. The derived state (1) is found from the taxa *Sauroctonus* to *Arctognathus*, whereas the derived condition (2) is shown as a synapomorphy in *Inostrancevia* and the rubidgeines. This supports the sister-group relationship of the latter two taxa.

(38) Interparietal about as high as wide (0) considerably wider than high (1)

The width of the interparietal usually depends on the enlargement of the posterior skull part. Thus the derived state is obviously found in the rubidgeines but it is also found as a homoplasy in *Lycaenops* which shows only a moderately wide posterior skull part. The condition is not known in *Inostrancevia*.

(39) Supraoccipital high (0) low (1)

The derived state is shown homoplastically in *Scylacognathus*, *Eoarctops*, *Gorgonops*, *Arctognathus* and the rubidgeines. The condition is unknown in *Inostrancevia*.

(40) Symphysis sloping (0) almost straight (1)

Biarmosuchus and *Rubidgina* display a strongly sloping symphysis of the lower jaw. The derived condition is found as a homoplasy in *Arctognathus* and the rubidgeines. *Inostrancvia* has, despite its strong canines and heavy lower jaw, a sloping symphysis and is therefore coded for the plesiomorphic condition. However, this might be subject to the extremely elongate anterior skull part which would become too heavy with a straight symphysis.

(41) Dentary slender (0) dentary massive and high (1)

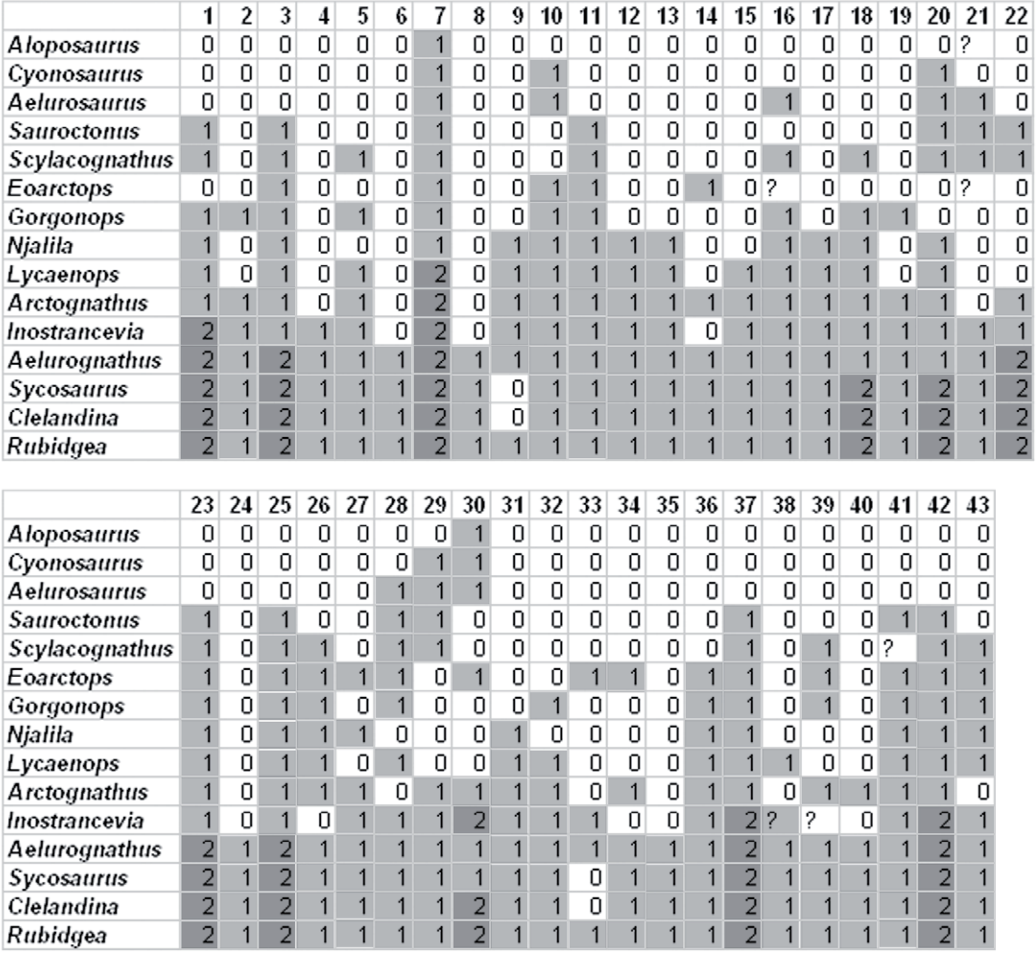
This character is a symplesiomorphy of the three plesiomorphic small sized genera. The condition is not known in *Scylacognathus*.

(42) Incisors and canine slender (0) moderately strong (1) considerably strong (2)

The plesiomorphic condition is found in the three plesiomorph small sized genera and therefore constitutes a symplesiomorphy. The derived state (1) is found in *Sauroctonus*, *Scylacognathus*, *Eoarctops*, *Gorgonops*, *Njalila*, *Lycaenops* and *Arctognathus*. The derived state (2) is found as a synapomorphy in *Inostrancevia* and the rubidgeines and supports the sister-group relationship of these taxa.

(43) Numerous postcanine teeth (five and more) in upper jaw (0) less than five postcanine teeth (1)

Biarmosuchus can have up to ten postcanine teeth and *Rubidgina* six to seven. The derived state is found as a homoplasy in all genera from *Scylacognathus* onwards except for *Arctognathus* which has five to seven postcanine teeth which are, however, rather large. Nevertheless it is coded here for the plesiomorphic condition.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Aloposaurus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
Cyonosaurus	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Aelurosaurus	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0
Sauroctonus	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
Scylacognathus	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	1
Eoarctops	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	?	0	0	0	0	?	0
Gorgonops	1	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0
Njalila	1	0	1	0	0	0	1	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0
Lycaenops	1	0	1	0	1	0	2	0	1	1	1	1	1	0	1	1	1	1	0	1	0	0
Arctognathus	1	1	1	0	1	0	2	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Inostrancevia	2	1	1	1	1	0	2	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Aelurognathus	2	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Sycosaurus	2	1	2	1	1	1	2	1	0	1	1	1	1	1	1	1	1	2	1	2	1	2
Clelandina	2	1	2	1	1	1	2	1	0	1	1	1	1	1	1	1	1	2	1	2	1	2
Rubidgea	2	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2	1	2	1	2

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Aloposaurus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyonosaurus	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Aelurosaurus	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sauroctonus	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0
Scylacognathus	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	?	1	1
Eoarctops	1	0	1	1	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	1	1
Gorgonops	1	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1
Njalila	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1
Lycaenops	1	0	1	1	0	1	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1
Arctognathus	1	0	1	1	1	0	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0
Inostrancevia	1	0	1	0	1	1	1	2	1	1	1	0	0	1	2	?	?	0	1	2	1
Aelurognathus	2	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1
Sycosaurus	2	1	2	1	1	1	1	1	1	1	0	1	1	1	2	1	1	1	1	2	1
Clelandina	2	1	2	1	1	1	1	2	1	1	0	1	1	1	2	1	1	1	1	2	1
Rubidgea	2	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	2	1

Table. 2. Data matrix for the in-group phylogeny of the Gorgonopsia.

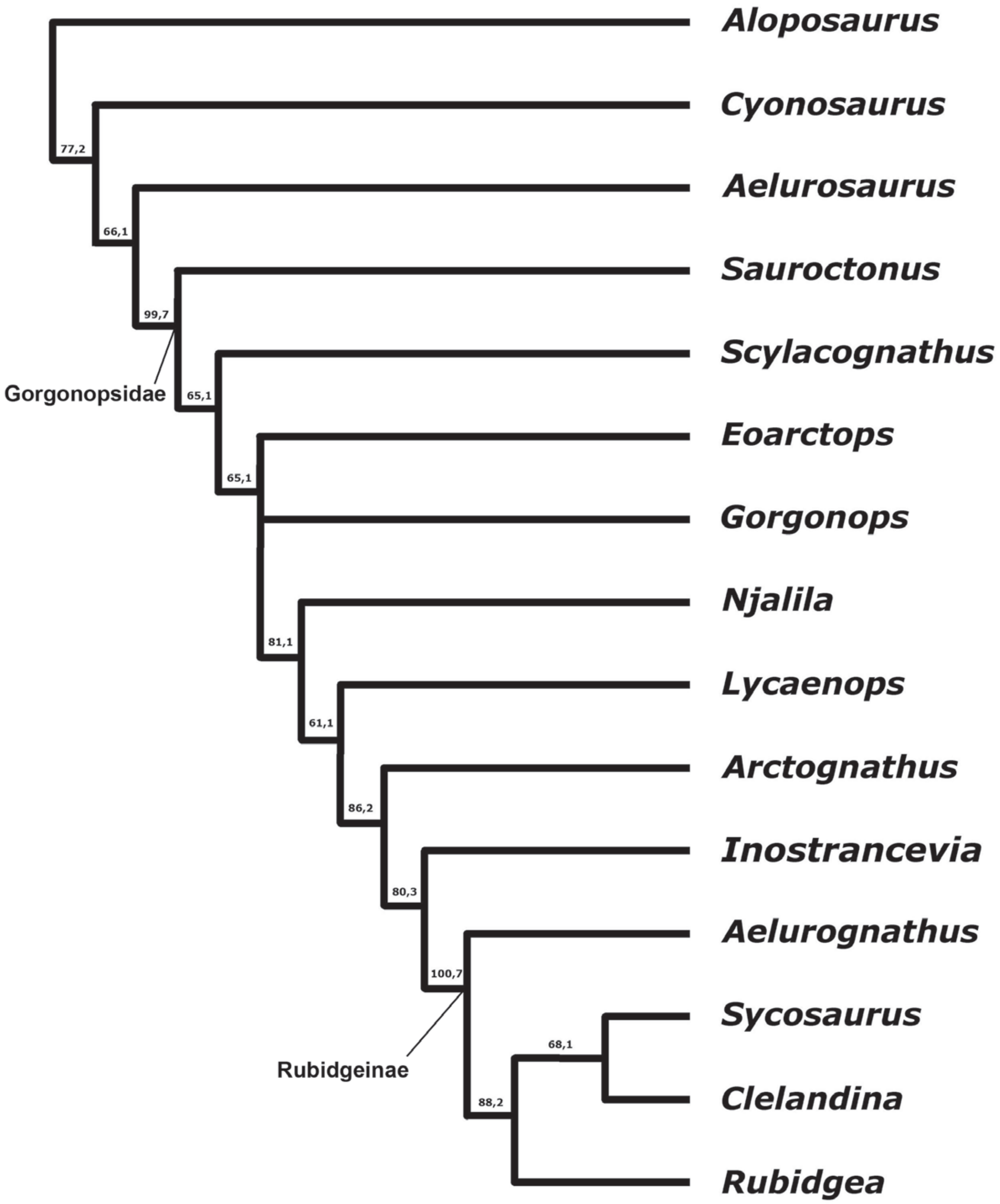


Figure 52. Strict consensus tree of the phylogenetic relationships of the Gorgonopsia.

2.3.3 Discussion and conclusion

According to Sigogneau's classification, the taxa *Aloposaurus*, *Cyonosaurus* and *Aelurosaurus* would be included into the family Gorgonopsidae, whereas all three are excluded in the present phylogeny. This is because they show no autapomorphies but only a number of symplesiomorphies. As plesiomorphic character states do not provide any evolutionary historic information and are useless for discovering monophyletic groups, the three taxa are regarded here as stem-group representatives of the family Gorgonopsidae.

Consequently the family Gorgonopsidae exclusively includes the last common ancestor of *Sauroctonus parringtoni* and *Rubidgea atrox* and all of its descendants. With relation to the stem-group, the Gorgonopsidae is characterised by the following autapomorphies: posterior skull part enlarged, external nares situated dorsally, suborbital and zygomatic arches comparatively broad, occiput concave, incisors and canines strong.

Within the Gorgonopsidae only one monophyletic group is recognisable, the subfamily Rubidgeinae. In contrast to Sigogneau's phylogeny the group additionally includes the taxa *Aelurognathus* and '*Leontocephalus'*, the latter being congeneric with *Sycosaurus* now. The Rubidgeinae as defined here includes the last common ancestor of *Aelurognathus tigriceps* and *Rubidgea atrox* and all of its descendants. The group is diagnosed by the following autapomorphies: posterior skull part considerably broadened, presence of a supraorbital thickening, intertemporal wider than interorbital space, all three skull arches considerably broadened, posterior margin of postorbital bar anteriorly directed, zygomatic arch ventrally curved.

Inostrancevia is the sister taxon to this subfamily since both share a remarkably concave occiput and considerably strong incisors and canines. Although *Inostrancevia* is therefore well established as sister-group to the Rubidgeinae it shows a number of homoplastic plesiomorph character states at the same time. However, most of them can be assigned to its peculiar skull morphology and are only a reversal to the plesiomorph condition. Thus the lacrimal is elongate although the canine is large and the maxillary high but in this case the long lacrimal is due to the considerably long snout region in *Inostrancevia*. Another plesiomorph character state is the sloping symphysis, which might as well be connected with the long snout region. The snout is additionally already rather heavy and thus, a straight and therefore all the more massive symphysis would bear too much weight. The somewhat sloping dorsal profile of the posterior skull roof, which is more accentuated than in any other taxon, is also considered as a counterpart to the snout region. In contrast the zygomatic arch is not considerably curved ventrally as in the rubidgeines. As shown above *Inostrancevia* displays a number of peculiar character states that allow retaining a separate subfamily Inostranceviinae for this taxon.

The remaining taxa can not be grouped further since they either share plesiomorph character states (relative to the level of the rubidgeines) on the one hand or the characters are distributed in an extreme mosaic pattern, which basically obstructs the formation of monophyletic groups. This homoplastic distribution is either subject to convergence of characters or reversals to the plesiomorph character state, or both. The non-rubidgeinid Gorgonopsidae seem to undergo an evolution that merges gradually from the respective plesiomorphic into the derived state since each higher taxon is always as closely related to its last common ancestor as to its next descendant. This is also shown by the Bremer-Support index which is 7 for the non-rubidgeinid Gorgonopsidae altogether but only 1 or 2 for the respective taxa. Additionally *Eoarctops* and *Gorgonops* form a polytomy. However, *Eoarctops* is somewhat peculiar since it shows the most homplastic mosaic distribution of the characters of all taxa. Since *Eoarctops* is from the *Tapinocephalus* Zone, this might be subject to an early specialisation where some derived characters states already had been invented and others not. Thus it shows a compact and rather massive overall appearance with a short snout, short lacrimal, broad para-basisphenoid fossa and straight symphysis on the one hand, but the overall size is small, the skull arches are slender and the supraorbital portion of the frontal as well as the preparietal are large on the other hand.

- Infraorder: Gorgonopsia Seeley, 1895
  - *Aloposaurus* Broom, 1910
  - *Cyonosaurus* Olson, 1937
  - *Aelurosaurus* Owen, 1881
  - Family: Gorgonopsidae Lydekker, 1890
    - *Sauroctonus* Bystrow, 1955
    - *Scylacognathus* Broom, 1913
    - *Eoarctops* Haughton, 1927
    - *Gorgonops* Owen, 1876
    - *Njalila* nov. gen.
    - *Lycaenops* Broom, 1925
    - *Arctognathus* Broom, 1911
    - Subfamily: Inostranceviinae Sigogenau-Russell, 1989
      - *Inostrancevia* Amalitzky, 1922
    - Rubidgeinae Sigogneau, 1970
      - *Aelurognathus* Haughton, 1924
      - *Sycosaurus* Haughton, 1924
      - *Clelandina* Broom, 1948
      - *Rubidgea* Broom, 1938

Table 3. Revised classification of the Gorgonopsia.

In conclusion it can be stated that the Gorgonopsia form a homogenous group which comprises only one family Gorgonopsidae with the three taxa *Aloposaurus*, *Cyonosaurus* and *Aelurosaurus* as its stem-group representatives. Within the Gorgonopsidae only one monphyletic group, the subfamily Rubidgeinae, is present whereas the non-rubidgeine gorgonopsians constitute a gradual evolutionary pattern with *Inostrancevia* as sister-taxon to the rubidgeines. Table 3. presents the revised classification which is the result of the discussion of gorgonopsian phylogeny.

3 PART II: FUNCTIONAL ANALYSES

3.1 Introduction

In this part, the different functional aspects of the skeleton of GPIT/RE/7113 are investigated. However, as this examination primarily refers to osteological evidence, I do not claim to present a comprehensive biomechanical report. The jaw mechanics and the limb movements are emphasised, as these studies are considered as a base for the final comparison with the saber toothed cat *Smilodon*. Obviously, this comparison is confined to a functional level, since any closer phylogenetic relationship between the two taxa can be ruled out.

Research on fossil material always depends exclusively on osteological evidence. This implies that all reconstructed features are more or less hypothetical and, additionally, biased by the subjectivity of the author. Even so, it is possible to provide a realistic approach by careful examination and comparison.

The first chapter deals with the jaw musculature and jaw articulation in the gorgonopsian *Sauroctonus parringtoni*. Although KEMP (1969) has already presented a detailed study of gorgonopsian jaw mechanics, I consider it important to provide another account on this topic, based on a different, very well preserved skull. Furthermore, some differences to KEMP's model will be demonstrated.

The second chapter deals with gorgonopsian limb movement, and provides an interpretation of the position of the forelimb in relation to the shoulder joint which contrasts with that proposed by KEMP (2005).

Both studies conclude in chapter three. The comparison between *Sauroctonus parringtoni* and *Smilodon fatalis* reveals some common features in the skull and skeleton which are presumably shared because of the enlarged canines in both taxa.

3.2 Jaw mechanics in GPIT/RE/7113

3.2.1 Musculature

3.2.1.1 Introduction

ADAMS (1919) was one of the first authors to work on therapsid jaw musculature. He carried out an extensive comparative study of the anatomy of the mandibular musculature of vertebrates. In this study, ADAMS (1919) considered a large number of taxa, from fishes to mammals, and included a reconstruction of the jaw musculature of the cynodont *Cynognathus*. Lakjer (1926) presented another comparative account in which he examined the pattern of differentiation of the jaw musculature in reptiles.

Romer & Price (1940) and Watson (1948) discussed the relevance of the lamina reflecta of *Dimetrodon* with particular respect to the jaw musculature. Watson proposed an insertion of the anterior pterygoideus muscle on the external surface of the lower jaw in *Dimetrodon* in a manner such that the muscle must have wrapped around the ventral mandibular surface, as in many extant reptiles.

Parrington (1955) was the first to reconstruct the gorgonopsian jaw musculature. He proposed a special jaw articulation, which included a medial shift of the quadrate during the opening of the jaws to allow for a larger gape. This theory was accepted by all subsequent authors, such as Crompton (1963), Barghusen (1968) and Kemp (1969, 1982, 2005). However, his suggestion that gorgonopsians had a mammal-like masseter that originated from the lateral face of the jugal and ran posteroventrally to insert at the transverse ridge of the lamina reflecta was rejected by both Barghusen and Kemp. Instead, both authors proposed a musculus zygomatico-mandibularis, which originated from the medial face of the zygomatic arch and inserted in the depression posterior to the ridge of the lamina reflecta. This indeed seems to be the most reasonable course of such a muscle, and explains the differences in the width of the zygomatic arch and the position and development of the ridge on the lamina reflecta in the diverse gorgonopsian genera.

Figure 53 provides a reconstruction of the most relevant muscles described below.

3.2.1.2 Musculus adductor mandibularis externus

In extant reptiles this muscle is composed of a profundus, a medial and lateral part. In this study only the latter two will be taken into consideration.

In contrast to therocephalians, gorgonopsians have a well developed coronoid process, though this is not as broad as in cynodonts. Naturally, the gorgonopsian coronoid process served as an attachment area for a muscle that originated from the posterior part of the temporal fossa. Since the main bulk of the muscle mass attached dorsally on the undersurface of the temporal fossa and inserted on the adductor fossa on the medial side of the lower jaw I will not use the term temporalis, but rather medial external adductor 1 and 2.

Kemp (1969) divided the medial (temporalis) branch of the adductor mandibularis into three muscle slips: the temporalis 1, temporalis 2 and one that he termed zygomatico-mandibularis. The existence of the latter was first suggested by Barghusen (1968), who rejected a correspondence of this muscle in gorgonopsians with the mammalian masseter, as mentioned above. According to both authors, the zygomatico-mandibularis is a specialisation of gorgonopsians, and is convergent with the condition found in therocephalians and cynodonts. Concerning the question of the masseter in gorgonopsians, I will continue to use the term musculus adductor mandibularis externus lateralis (Kemp's zygomatico-mandibularis) because of the current lack of a comprehensive and comparative investigation into this topic. As this study does not claim to determine muscle homologies or probable phylogenetic relationships between the different therapsid groups, these aspects are only considered as minor here. Instead, this examination has been undertaken exclusively from a functional point of view.

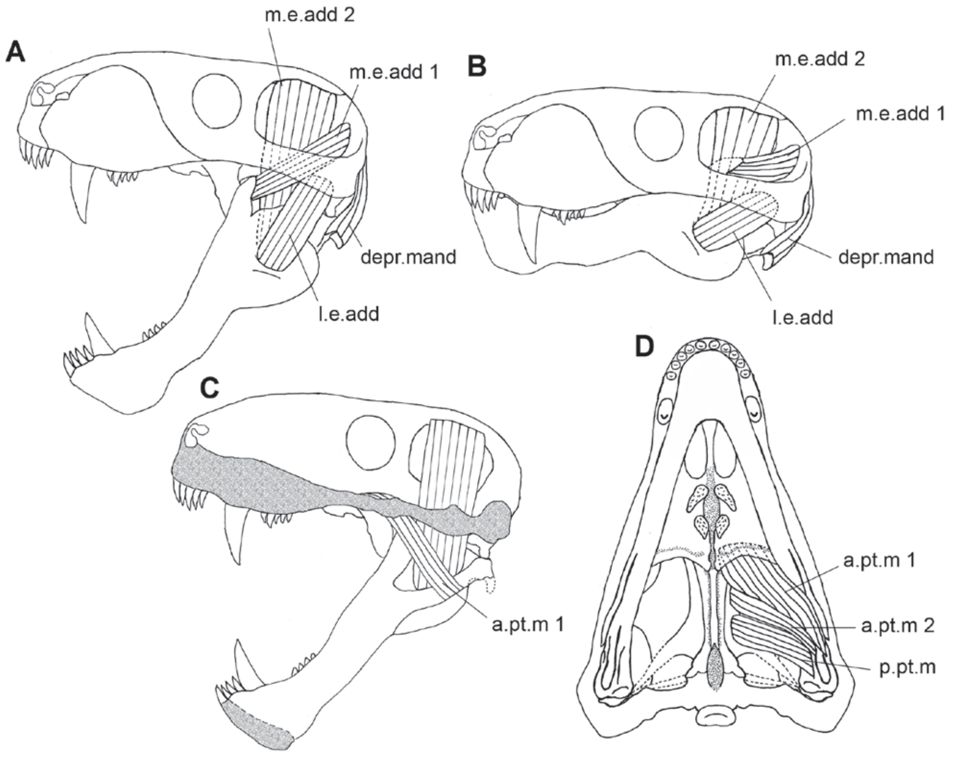


Figure 53. Reconstruction of the insertions and attachments of the main jaw musculature in GPIT/RE/7113. **A**, lateral view with jaws opened; **B**, lateral view with jaws closed; **C**, mesial view with jaws opened; **D**, ventral view.

3.2.1.2.1 Musculus adductor mandibularis externus medialis

Medial external adductor 1. This muscle originates from the squamosal in the posterior corner of the temporal fossa. Here a concave recess is formed above the dorsal parts of the occipital wall. It provides a rough area for muscle insertion of a tendinous nature. This area is slightly expanded in lateral and even more in medial direction.

As the muscle was anteriorly directed, it inserts on the processus coronoideus of the dentary. The dorsal tip and dorsal and ventral edges of the process are rough and covered with corrugations, whereas the internal surface of the process is rather smooth. PARRINGTON (1955) proposed a partial insertion of the medial external adductor 1 on the external side of the coronoid process, an interpretation confirmed by KEMP (1969). A similar condition can be assumed for *Sauroctonus parringtoni* since it shows the same features, i.e. the coarsely ridged ventro-lateral face of the process for tendinous muscle attachment, and the smooth and slightly concave medial surface for a fleshy insertion.

The function of the temporalis 1 was mainly to pull the lower jaw, with its heavy and massive symphyseal part, upwards and backwards. The backwards component was more dominant towards the end of the jaw closing movement.

Medial external adductor 2. This muscle originates from the dorsal margin of the fenestra temporalis. Here the postorbital forms a roof-like structure with a slightly rounded lateral margin. Ventrolaterally and laterally this margin is rather sharp to provide a site for firm muscle attachment about 45 mm long. It is not expanded onto the dorsal surface of the postorbital, but onto its lateral margin instead. Here the bone surface shows thin and long parallel corrugations, whereas the area medial to the ridge is rather smooth.

The insertion area is the adductor fossa where the prearticular forms a rod-like element, which covers the angular and the surangular medially. On the dorsal margin a sharp ridge is established. This ridge also constitutes the ventral border of the meckelian fossa. This fossa is a narrow and shallow trough between the prearticular and angular dorsally, and measures 45mm in length. This matches exactly the length of muscle attachment on the postorbital.

The medial external adductor 2 acted as an adductor mainly in a dorsal direction. The muscle slip was relatively broad concerning the antero-postero expansion, but short ventrodorsally. However, this broadness was required to pull the lower jaw upwards since the temporalis 1 mainly acted as a posteriorly directed force (as described above).

3.2.1.2.2 Musculus adductor mandibularis externus lateralis

This muscle originates from the medial surface of the posterior part of the zygomatic arch. In this area the zygomatic arch is slightly thickened since the squamosal and jugal form a scarf joint here. The surface is covered with smooth parallel corrugations, which would indicate a fleshy attachment. However, there is evidence for an aponeurotic attachment, too, since the postero-ventral margin of the zygomatic arch exhibits a sponginous surface, which is also expanded on the ventral-most parts of the external surface of the arch. This might indicate an additional area of muscle attachment on the external surface of the zygomatic arch.

It is clear that the insertion was on the lamina reflecta of the lower jaw. Here a diagonal dorsally rounded ridge, 3 mm high and 3 mm broad, is established and runs in an anterodorsal-posteroventral direction. Anterior and posterior to the ridge, the surface of the lamina is concave. As already suggested by Kemp (1969), this ridge served for a muscle that ran postero-dorsally, rather than antero-dorsally as proposed by Parrington (1955). The muscle must have been relatively short in *Sauroctonus* since the ridge is not markedly anteriorly situated, and the zygomatic arch does not flare to such an extent as, for example, in the rubidgeines. It therefore performed a rather quick movement with a dorsal and backwards but also lateral component.

3.2.1.3 Musculus adductor mandibularis internus

This muscle is devided into an anterior and posterior pterygoideus part, and the pseudotemporalis muscle. Kemp (1969) additionally proposed two slips of the anterior pterygoideus muscle in gorgonopsians, which he termed pterygoideus anterior 1 and 2.

This differentiation is, however, rejected here since no clear distinction between a probable anterior pterygoideus 1 and 2 or an anterior pterygoideus 2 and the posterior pterygoideus could be detected in *Sauroctonus*. Instead, Kemp's anterior pterygoideus 2 seems to be the posterior pterygoideus muscle, whereas Kemp's posterior pterygoideus muscle is reminiscent of the posterior adductor, at least in its origin as described by this author. The insertion of Kemp's posterior pterygoideus, on the other hand, is a matter of debate.

3.2.1.3.1 Musculus pterygoideus anterior

As proposed by Parrington (1955) and Kemp (1969), this muscle originates from the dorsal surface of the pterygoids, and on the posterior and ventrally sloping face of the transverse process of the pterygoid. These authors also mentioned the dorsal surfaces of the ectopterygoids as probable areas for attachment. However, large parts of the ectopterygoids are missing in GPIT/RE/7113, and therefore no information can be given about the anterior extension of the anterior pterygoideus muscle.

As well as the posterior face of the transverse process, the dorsal surface of the pterygoid is very smooth and indicates a fleshy attachment. Here, the surface is somewhat concave from side to side. This has the effect that the muscle was channelled ventral-wards. However, the postero-lateral margin of the transverse process is too sharp for any expansion onto its lateral face to be assumed.

The insertion of this muscle onto the lower jaw is subject to discussion. KEMP (1969) proposed an area of insertion on the medial face of the ventral keel of the angular for the anterior pterygoideus 1, and on the medial face of the angular and the prearticular for the anterior pterygoideus 2. The pterygoideus 1 musculature was required to pull the lower jaw forwards and upwards to act as the antagonist of the temporalis 1. However, the force must have been too small to perform this function, due to the position of the insertion far anterior on the medial keel of the angular. But if the insertion was expanded more posteriorly and up to the prearticular it would have come into conflict with the insertion of the posterior pterygoideus muscle, which has been proposed to have wrapped around on the external surface of the lower jaw. It therefore seems more reasonable to assume that the anterior pterygoideus muscle inserted on the external side of the lower jaw. This was already reconstructed by WATSON (1948) for *Dimetrodon*, and also applies to dicynodonts (KING et al. 1989, MAISCH 2003).

In *Sauroctonus*, the ventral face of the prearticular medial to the lamina reflecta is smoothly rounded and provides a good area for the muscle to bend from the internal to the external side of the lower jaw. Further posteriorly, the now distinct and sharp ventral keel on the prearticular prohibits a medial shifting of the muscle, and the laterally following parallel trough serves as area for attachment on the external side. This trough terminates in a deep elongated fossa, which is situated lateral to the processus retroarticularis. This fossa probably served for the insertion of the anterior pterygoideus too, but it is also likely that the depressor muscle inserted here. This possibility will be discussed below.

The anterior pterygoideus muscle acted as the antagonist to the medial external adductor 1 by pulling the lower jaw forwards. The attachment posteriorly and on the external face of the lower jaw additionally provided a better leverage for lifting the heavy symphysis.

3.2.1.3.2 Musculus pterygoideus posterior

This muscle inserted mainly on the ventral face of the ramus quadratus and on the lateral face of the para-basisphenoid complex. It was probably expanded over the entire length of the braincase. On the parasphenoid a faint ridge is established dorsally before the quadrate ramus covers the basisphenoid. This ridge terminates 5 mm anterior to a knoblike structure on the quadrate ramus at the level of the suture with the parasphenoid. Ventral to the ridge, a shallow depression is visible. These features are evident on both sides of the specimen.

The insertion of this muscle was at the posterior part of the medial face of the prearticular-articular complex. Here a 25mm long depression is established which is bordered by the prearticular ridge ventrolaterally, and postero-medially by the articular condyles. Anteriorly the prearticular becomes more convex, but the prearticular ridge continues as a faint line before it bends dorsally at the level of the anterior margin of the adductor fossa. It is conceivable that the posterior pterygoideus muscle attached on the entire length of the prearticular ridge, which would therefore correspond with the area of origin on the skull.

The main function of the posterior pterygoideus muscle was a stabilising one, but it also acted as the antagonist of the lateral external adductor by pulling the lower jaw medially.

3.2.1.3.3 Musculus pseudotemporalis

In Crocodilia and Testudina, this muscle originates from the lateral surface of the epipterygoid and inserts around the anterior area of the adductor fossa. BARGHUSEN (1973) described this muscle in *Dimetrodo*n, but in dicynodonts the origin and insertion of this muscle can not be defined with any certainty (KING et al. 1989, MAISCH 2003).

This also applies to *Sauroctonus parringtoni*. The epipterygoid, which is missing in GPIT/RE/7113 and many other specimens, was rather thin and fragile, and it seems unlikely that an adductor muscle was attached to it. Also, the presumed insertion area on the lower jaw was already occupied by the ample medial external adductor 2, and therefore the pseudotemporalis must have been quite insignificant in *Sauroctonus*, if it was present at all.

3.2.1.4 Musculus adductor mandibulae posterior

In *Sphenodon* this muscle originates from the anterior face of the quadrate and in turtles also from the prootic. The insertion of this muscle is into the adductor fossa or along its margins. Although BARGHUSEN (1973) could not observe any direct evidence for attachment of adductor posterior musculature in *Dimetrodon*, he postulated an origin and insertion comparable with *Sphenodon*. Although this muscle was present in dicynodonts, it was rather weakly developed and played only a minor role (MAISCH 2003).

The evidence for an adductor posterior is, again, rather uncertain in *Sauroctonus*. KEMP (1969) reconstructed an additional attachment area for the posterior pterygoideus muscle on a dorsal depression on the anterior face of the quadrate. However, this interpretation is rejected here since the posterior pterygoideus muscle already occupies the braincase area as described above. It might have been possible that an adductor posterior originated from the quadrate, but the insertion area was again already occupied by the medial external adductor 2. Therefore, it seems that this muscle either was rather insignificant or already absent in *Sauroctonus*, indicating that the animal was sufficiently equipped with adductor musculature.

3.2.1.5 Depressor mandibulae

In contrast to the massive adductor musculature, the depressor is rather small. However, the heavy symphysis of the lower jaw additionally acts as a depressing force and thus compensates for the small size of the muscle.

This muscle originates from the posterior surface of the squamosal. Here a shallow and broad depression is established that runs transversely in a dorsolateral-ventromedial direction. It terminates in a round fossa, which is situated dorsal to the paroccipital process and lateral to the ventrally directed flange of the tabular.

The insertion point was on the processus retroarticularis of the articular, though only the first 10 mm is preserved on both sides in *Sauroctonus parringtoni*. Since this part seems to be rather weakly developed, and therefore the process could not have been much enlarged, the laterally situated deep and elongated fossa mentioned above is of interest. This depression is clearly visible on both sides of the specimen, and is nearly 5 mm deep and 7 mm broad. Medially it is bordered by the prearticular ridge, posteromedially and posteriorly by the processus retroarticularis and laterally by a ridge formed by the articular. Anteriorly it merges into the shallow trough, which served as the insertion for the anterior pterygoideus muscle as described above. Since the area of origin on the squamosal is of greater size than the presumed insertion area, the processus retroarticularis, this fossa might have served as additional insertion area for the depressor muscle.

3.2.2 Jaw articulation

The jaw articulation in gorgonopsians shows a rather basal pre-mammalian articular-quadrate contact. The dentary is only moderately enlarged, and the postdentary bones are well developed. However, the quadrate is reduced in size compared to pelycosaurs, dinocephalians and dicynodonts.

As already described by PARRINGTON (1955) and KEMP (1969), gorgonopsians have a very peculiar jaw joint. The quadrate has a loose contact with the squamosal, and was therefore able to move forwards and backwards to a certain degree in the recess of the squamosal. LAURIN (1998) and IVAKHNENKO (2003) doubted that such a movement was possible. LAURIN proposed a non streptostylic quadrate in gorgonopsians, since the articulation of the quadrate with the epipterygoid and the stapes would only allow slight bending. IVAKHNENKO suggested a streptostylic quadrate that was firmly fixed in the articular condyle of the lower jaw, so that only a ‘wobbling’ motion from the vertical position forwards would have been possible.

As already stated above, only the right quadrate is complete in *Sauroctonus parringtoni* but together with the preserved parts of the left side an almost complete account can be given.

The two condyles of the articular smoothly merge into one another, the lateral one being situated more posteriorly than the medial one. The medial condyle is more rounded and saddle shaped whereas the lateral condyle is elongated and cylindrical. Both form a deeply concave recess that slopes dorso-ventrally so that the anterior margin is situated on a higher level than the posterior one. The dorso-laterally expanded process described and figured by PARRINGTON (1955) and KEMP (1969) has broken off, but did exist in the specimen judging from the broken margin in this area.

The corresponding condyles on the quadrate fit exactly into their counterparts on the articular. Both are convex, the lateral one being elongated and the medial one round. They are clearly separated by a shallow, antero-posteriorly running depression, which fits into the constricted margins of the articular. When the jaws were closed, the quadrate was firmly abutted against the articular, and only a small amount of movement of the lower jaw relative to the upper jaw was possible.

In *Sauroctonus parringtoni*, the articular-quadrate contact changed significantly with the relative movement of the lower jaw. This can only be explained by a streptosylic quadrate. Furthermore, another component of movement was apparent. As mentioned above, the medial condyle of the articular is situated anterior to the lateral one. This is true for all gorgonopsians, but usually to a lesser extent. In *Sauroctonus*, a line drawn from the antero-medial corner of the medial condyle to the postero-dorsal edge of the lateral condyle runs almost diagonal to the long axis of the lower jaw. Attaching the quadrate and simulating the position with closed jaws, the quadrate must also have been oriented diagonally with an angle of almost 45° to the long axis of skull. Therefore, the contact with the recess of the squamosal was only with the narrow lateral margin of the quadrate and the quadratojugal, and it is clear that the quadrate was able to rotate around its long axis to a certain degree as well (fig. 54).

If the jaws were open, the nature of the articular-quadrate contact must have been different as the posterodorsal process of the lateral condyle prohibited a larger gape. Therefore the quadrate moved medially following the spiral of the articular condyles, and thrusting the articular, with its hampering posterodorsal process, laterally. This mechanism was first described by PARRINGTON (1955), and is fully accepted in all following discussions. *Sauroctonus parringtoni* also shows this typical feature (fig. 55). Furthermore, it demonstrates a rotation of the quadrate relative to the recess of the squamosal. With the jaws open, the quadrate moved not only medially, but also with its posterior face parallel to the posterior face of the recess, thus fitting firmly into the squamosal recess and abutting against the paroccipital process.

As mentioned above, the position of the quadrate was different if the jaws were closed. At first sight this arrangement seems very unstable, having in mind a probably struggling prey when

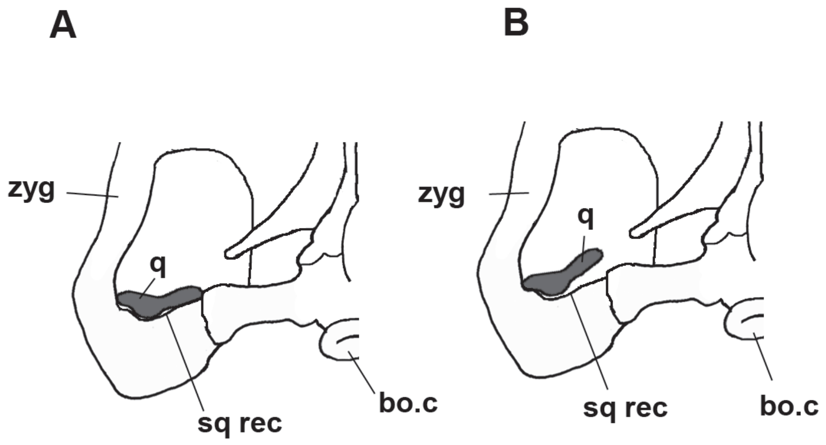


Figure 54. Position of the quadrate in GPIT/RE/7113 relative to the rest of the upper jaw. **A**, ventral view, jaws opened; **B**, ventral view, jaws closed.

the animal was hunting. However, the cavity of the squamosal recess must have been filled with cartilage and additional muscles to move the quadrate so that these components might have clasped the quadrate sufficiently. Furthermore, the quadrate ramus of the pterygoid and the epipterygoid, (provided that these bones articulated with the quadrate) as well as the stapes, would have served as stabilisation. Such a position might at least have served as support for the lower jaw when it shifted laterally during the interdigitating type of bite. With such a bite, the serrated edges of the teeth of the lower jaw met the corresponding ones of the upper jaw during the jaw-closing movement, providing a cutting action as described by Kemp (1969).

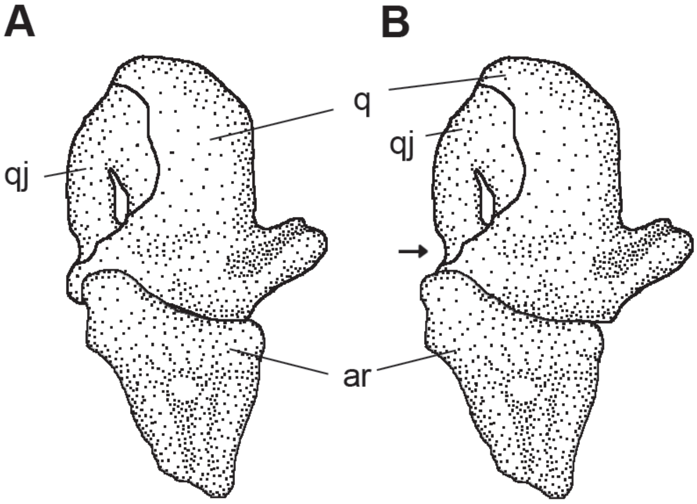


Figure 55. Position of the quadrate in GPIT/RE/7113 relative to the articular. **A**, jaws closed; **B**, jaws opened; both in posterior view.

3.2.4 Conclusions

Although gorgonopsians are a basal therapsid group, their jaw musculature was rather specialised. It is certain that this was due to their enlarged canines, and the hunting and killing behaviour associated with such teeth. For the first time a coronoid process was developed that provided a longer lever for the medial external adductor 1. This muscle pulled the lower jaw backwards, and made an accelerated mouth closing movement possible. Although the medial external adductor 2 had not yet invaded the external side of the temporal fossa, it was a broad and thick muscle strip. Its insertion area on the lower jaw was almost directly beneath the area of origin on the skull, and therefore this muscle pulled the lower jaw exclusively dorsalwards. The lateral external adductor finally moved the lower jaw not only dorsally but also laterally, depending on the degree of lateral flaring of the zygomatic arch.

The internal adductor musculature is arranged in more or less the same way as in other therapsids. By moving the jaw anteriorly, the anterior pterygoideus muscle acted as the antagonist to the medial external adductor 1, whereas the posterior pterygoideus pulled the lower jaw medially, thus compensated for the lateral force of the lateral external adductor. Additionally, those two muscles could shift the jaw during the interdigitating type of bite. Although the origin and course of the internal adductor musculature is clear, its insertion on the lower jaw is a matter of debate. In *Sauroctonus*, the attachment on the lateral face of the prearticular and on the angular recess as proposed by KEMP seems unlikely because the sharp prearticular ridge on the ventral face of the prearticular would inhibit such a course. Instead, it is more reasonable to presume an attachment on the internal side of the prearticular with the prearticular ridge as its ventral limit. This would also correspond with the exclusively medially directed force of this muscle, and its stabilising function. The anterior pterygoideus, on the other hand, could well have inserted into the angular recess, which provided a well established area for attachment.

As for the musculature, the jaw articulation of gorgonopsians is unique, again due to their enlarged canines. In *Sauroctonus* it is clear that the quadrate was not only able to move medially and somewhat ventrally, but also transversely to the long axis of the skull. With the jaws closed, stability was achieved by the firm articular-quadrate articulation, and the quadrate is placed in the squamosal recess but transversely to the long axis of the skull. If a larger gape was required, the quadrate shifted medially following the spiral of the articular condyle. At the same time it moved perpendicular to the long axis of the skull and thus was firmly arranged in the squamosal recess.

LAURIN (1998) doubted this streptostylic condition of the quadrate. He supported his rejection of this idea with the tight link between the stapes and the quadrate.

If the stapes had a tight connection with the quadrate, and the latter was streptostylic, the stapes must have been able to assimilate this movement. Indeed, the quadrate shows a recess on the medio-ventral edge of its dorsal face which PARRINGTON (1955) named the stapedial groove. This elongated fossa is also clearly visible in *Sauroctonus parringtoni*. As mentioned above, the stapes is not preserved in specimen GPIT/RE/7113, but, assuming a similar shape as in other gorgonopsians, it developed a plug of rough bone mesially which connected the fenestra ovalis and was terminated laterally in a boss that was framed by the stapedial groove. It is certain that the connection with the fenstra ovalis was of such a nature that the bone could be moved in all directions to a certain degree. On the other hand, the stapedial groove of the quadrate allowed a sliding motion of the lateral end of the stapes and thus might have compensated for the movement of the quadrate.

In conclusion it can be stated that the specialised musculature and jaw articulation in *Sauroctonus* (which is basically comparable to all other gorgonopsian forms) required a streptostylic quadrate as otherwise an adequate gape was impossible. If this could not be achieved, the modified musculature would have been redundant.

3.3 Limb movement in GPIT/RE/7113

3.3.1 Introduction

As indicated by many features in the skull and skeleton, therapsids display various convergences and transitions to the mammalian condition. Two important areas are the pectoral and the pelvic girdle. The latter generally shows advanced characters earlier in evolution than does the pectoral girdle. This is due to the fact that the power of the hind limbs provided propulsion and speed, whereas the forelimbs mainly had a supporting function. Therefore, various groups display a rather plesiomorphic shoulder girdle with the humerus positioned horizontally from the glenoid. Such animals are supposed to move only in a sprawling manner, like extant reptiles or pelycosaurs. According to Kemp (1980, 2005), only more advanced cynodonts had the anatomic capacity to develop a more erect forelimb stance and gait. In contrast, the pelvic girdle and the femur were modified earlier during therapsid evolution, so the more erect gait was already achieved in such groups as gorgonopsians and dicynodonts. However, according to some authors, the animals used this semi-erect gait only for short periods when faster speeds were needed and otherwise moved in a reptilian sprawling manner. Kemp (1978) referred to the Crocodilians, which are known to use a dual gait system. However, according to Kemp (1978), crocodiles only lift their belly off the ground when moving very fast with the limbs nearly vertically positioned under the body. For travels over greater distances, they would again move with horizontally spread limbs. He did not mention whether the fore and hindlimbs were taken under the body during the erect gait. Reilly & Elias (1998), on the other hand, reported that a crocodile uses the primitive sprawling gait only for short distances, e.g. to crawl from the shore into the water, but moves in a semi-erect gait when travelling longer distances. Since I was unable to carry out a thorough observation of living crocodilians, these contradictory statements cannot be verified or falsified and must therefore be left as equally likely for the moment.

My new model sees gorgonopsians as relatively agile and active hunters, which were able to move with the fore and hindlimbs in a semi-erect gait. Although gorgonopsians are often considered as capable predators, Kemp's proposal was never questioned or thoroughly re-examined. It is true that many lizards can run very fast in a sprawling manner. However, in those animals the humerus and femur are both horizontally positioned, and the animal moves with the body evenly raised at the front and the back. Another point which must be taken into consideration is the presumed lifestyle of the animal. A large and heavy herbivorous dicynodont that does not need to move fast might not have been able to develop the ability to move in a faster gait like the near-gallop of a rhinoceros or the trot of an elephant. A carnivorous animal, on the other hand, relies on its ability to make quick movements to catch its prey since no potential victim would calmly await its fate. Even if the hunter hides in ambush and is not detected, the predator still needs to rush at its prey in a sudden and fast movement. Therefore, it should be necessary for the position of both the fore and hindlimb to be well-balanced, making the animal more agile.

3.3.2 Shoulder joint

The gorgonopsian shoulder joint is very peculiar, as already mentioned by Kemp (1982, 2005). He proposed a rolling of the surface of the humeral head over the glenoid with only limited points of contact during the step cycle (fig.56). This does seem to be the only possible way of motion. However, Kemp (1982, 2005) saw the humerus as exclusively horizontally oriented, and thus the forelimb of the animal could only be moved in a typical sprawling manner.

To understand the shoulder articulation it is necessary to have a closer look at the areas involved (fig.57). The glenoid is composed of two slightly convex articulation facets, which enclose an angle of about 95° between them. Medially they do not meet in a smoothly rounded surface, but instead are arranged at a sharp angle to one another. The dorsal component, which is formed by the scapula, is somewhat higher than wide, and faces ventrally and postero-laterally. The ventral surface, which is formed by the coracoid, is slightly wider than high, and faces dorsally and postero-laterally. At first sight, the corresponding articulation of the humerus does not appear to match this form at all. It is cylindrically shaped and rather flattened dorso-ventrally. Anteriorly, the facet commences posterior to the deltopectoral crest and extends backwards up to the attachment area for the m. subscapularis. However, the articulation area moved onto the dorsal surface of the humerus for the posteriormost

10 mm, and is therefore somewhat divided into an anterior terminal and a posterior dorsal area. This can be judged from the appearance of the bone, namely the articulating area is smooth whereas the surrounding parts are rather rugose. Consequently, the humeral articulation is composed of two areas that merge into each other in the middle, but have their anterior and posterior margins twisted. The entire facet is therefore longer than the glenoid, though this is advantageous for extensive rotational movement of the humerus. This in turn adds considerably to the stride length, which is important because the humerus cannot be positioned far anteriorly due to the strongly posterior facing glenoid. However, the incongruity of the glenoid and the humerus is such that the humerus does not fit well into the cavity in either position and it must be presumed that a relatively large layer of cartilage was present. With this assumption in mind, theoretically the humerus can be placed in a number of positions from 80° to 145° to the sagittal plane (fig.58). The first position would have meant that the humerus would have pointed dorsally, and was perhaps only needed if the animal was about to push its body off the ground. But only in this position would both articulation facets fit tightly into the glenoid. Thus, the postero-dorsal one would meet the scapular facet whereas the lower one abutted the coraciodal facet. If the humerus was placed horizontally in the glenoid, the

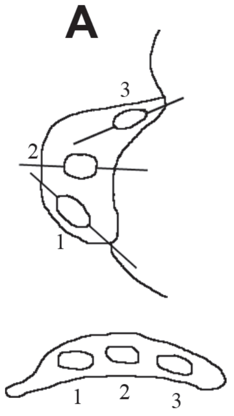


Figure 56. Movement of the humeral head (**B**) in the glenoid (**A**). Successive areas of contact of these two bones are indicated by 1-1, 2-2, 3-3. The lines indicate the orientation of the antero-posterior line of the head in the glenoid at each phase (from KEMP 1982).

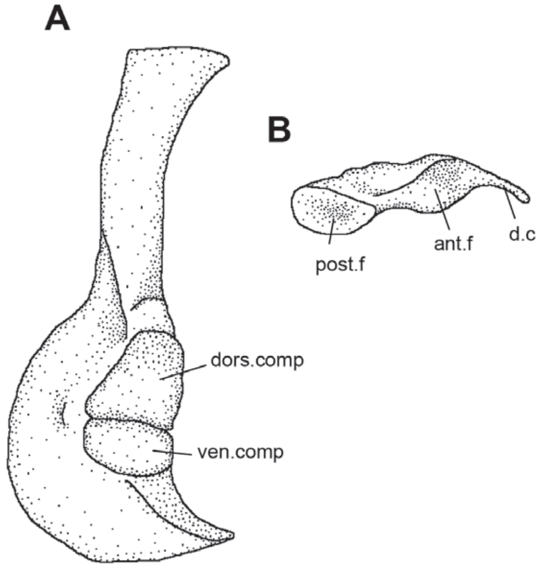


Figure 57. Articulation areas of the left pectoral girdle and forelimb in GPIT/RE/7113. **A**, pectoral girdle with glenoid in posterolateral view; **B**, humeral head in terminal view.

contact of the glenoid with the dorsal facet was somewhat lessened and the terminal facet instead faced the interconnecting space between the two articulation facets of the glenoid. This means that the joint must have been covered with a relatively extensive layer of cartilage during life. The articulation certainly was somewhat less tight, and rotation about the long axis of the humerus severely hindered because the anterior and posterior margins of the humeral articulation facet would hit the glenoid quickly. Therefore, the stride length must have been rather small since an extensive forwards thrust of the humerus was also permitted by the nature of the glenoid cavity as mentioned above. Additionally, extensive lateral bending of the vertebral column, which adds considerably to the stride length of lizards, was restricted because of the less horizontal position of the zygapophyses. This implies that the animal could not move in an extensive undulating manner. However, it is conceivable that the animal used this relatively stable stance when moving at a more leisurely pace. What's more, such a firm joint would enable a carnivore to better get hold of a struggling prey or to press the cadaver down when tearing chunks of meat from the body. Of course, *Sauroctonus* did not have retractable claws and paws to seize and tightly clasp its victim, but its claws

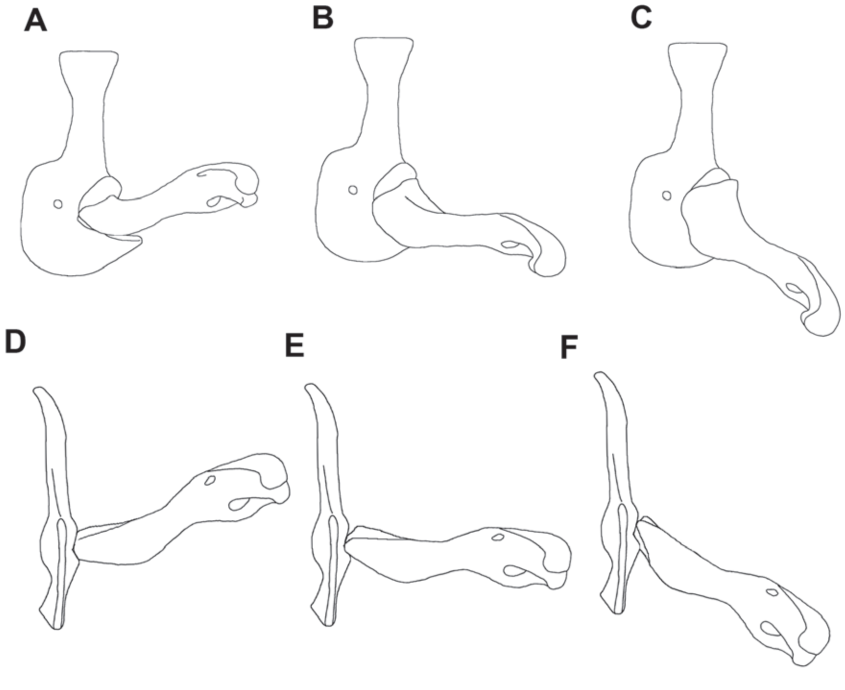


Figure 58. Positions of the humerus relative to the glenoid in GPIT/RE/7113. **A**, humerus dorsally placed; **B**, humerus horizontal; **C**, humerus sloping; all lateral view; **D**, humerus dorsally placed; **E**, humerus horizontal; **F**, humerus sloping; all anterior view.

were long, sharp and pointed. This could mean that they were possibly used to get a better grip of prey already lying on the ground.

As mentioned above it is also possible that the humerus was placed in a more sloping posture. However, then the articulation joint would be even more restricted, in such a way that only the terminal facet of the humerus would abut on the scapular part of the glenoid. Alternatively, long axis rotation could be more extensive and thus the stride length would be considerably enlarged. It is possible that the animal used this posture for fast movement as required for an attack or short chase. Moreover, this stance would better match the one of the hindlimb which certainly could be positioned in the acetabulum in a more sloping manner (Kemp 1982, 2005). In summary, it can be stated that *Sauroctonus* was capable of walking in a more erect gait with the forelimb if it was required. The discrepancy between the posture of the fore-and hindlimb was reduced, although the humerus was still somewhat more spread from the body than the femur. Therefore, I propose that *Sauroctonus* was a relatively agile animal, which could move in a somewhat semi-erect gait with both its fore-and-hindlimbs. This stands in contrast to Kemp' s (1982, 2005) theory where the dual gait arrangement only applies to the hindlimb.

3.3.3 Forelimb (figs. 59 & 60)

The humerus is mainly protracted by the m. supracoracoideus and in parts the m. scapulo-humeralis anterior. The former almost completely occupies the lateral face of the precoracoid and the ventral face of the scapula where it originates from a shallow depression. A smooth ridge that merges into another concave area borders this depression dorsally. This second concavity is sharply delimited from the rest of the scapular blade and faces almost anteriorly. Here the scapulo-humeralis originates with a rather large dorsal extension. If the humerus is placed horizontally this muscle can act exclusively as elevator and thus adds strength to the already strong deltoideus muscle. However, if the humerus slopes somewhat from the body this muscle can produce a considerable forward force. Posterior to this the scapular blade protrudes laterally providing a large attachment area for the deltoideus muscle.

The insertion areas for all three muscles on the humerus are well developed. The rugose attachment areas for the supracoracoideus and the deltoideus cover the whole anterodorsal face of the humerus, with the supracoracoideus situated somewhat dorsally and anteriorly to the deltoideus. The scapulo-humeralis inserts on a triangular depression posterior to the deltoideus, from which it is separated by a ridge. This depression is remarkably well developed and elongated, which suggests that this muscle played an important role.

Retraction was generated by the m. subscapularis. This muscle originates from the internal surface of the scapular blade and inserts on the postero-dorsal corner of the humerus. Here the humeral head is somewhat offset from the anterior parts of the proximal extremity. It is also slightly expanded in its posterior direction.

The main elevator muscle is the m. deltoideus together with the m. latissimus dorsi and in parts, the m. scapulo-humeralis anterior as mentioned above. The m. latissimus dorsi originates as a great fan from the dorsal fascia and inserts on a short but marked ridge on the postero-dorsal margin of the humerus. This area merges into the attachment area for the m. subscapularis. However, the posterior fibres of the m. latissimus dorsi might also have pulled the humerus backwards.

The main adductor muscle is the m. pectoralis which originated from the interclavicle and clavicle. It inserts at the well developed delto-pectoral crest on the anterior margin of the humerus. However the attachment area is markedly distinguished from the m. deltoideus and m. supracoracoideus origin by forming a tuberous bulge that is somewhat directed medially. A second adductor muscle is the m. coracobrachialis that originates from the ventral face of the coracoid and precoracoid. It also extends on the posterior process of the coracoid and thus acts additionally as rotational force. The insertion is on the large adductor fossa on the medial face of the humerus.

All muscles mentioned above also have some rotational function. This is particularly important for the rolling movement of the humeral head over the glenoid, which increases the stride length considerably. Here the anterior margin of the humerus is raised by the m. deltoideus and the posterior margin lowered by the m. coracobrachialis during protraction. During retraction the opposite happens and the posterior margin is raised by the m. subscapularis and the anterior margin lowered by the m. pectoralis.

3.3.4 Hindlimb

The pelvis and femur in *Sauroctonus* show a typical ball and socket articulation and are thus distinguished from the pectoral girdle with its particular articulation as described above. All three pelvic bones compose the acetabulum, although the greatest part is formed by the ilium. The femoral head, which is somewhat flattened but still rounded, can be placed into the acetabulum in a variety of positions, and for this reason KEMP (1982) proposed the dual gait model for gorgonopsians, therocephalians and early cynodonts. According to him, the animal was able to place the hindlimb horizontally as found in the sprawling gate, but the limb could also be positioned in a more vertical arrangement. KEMP argued that the femoral

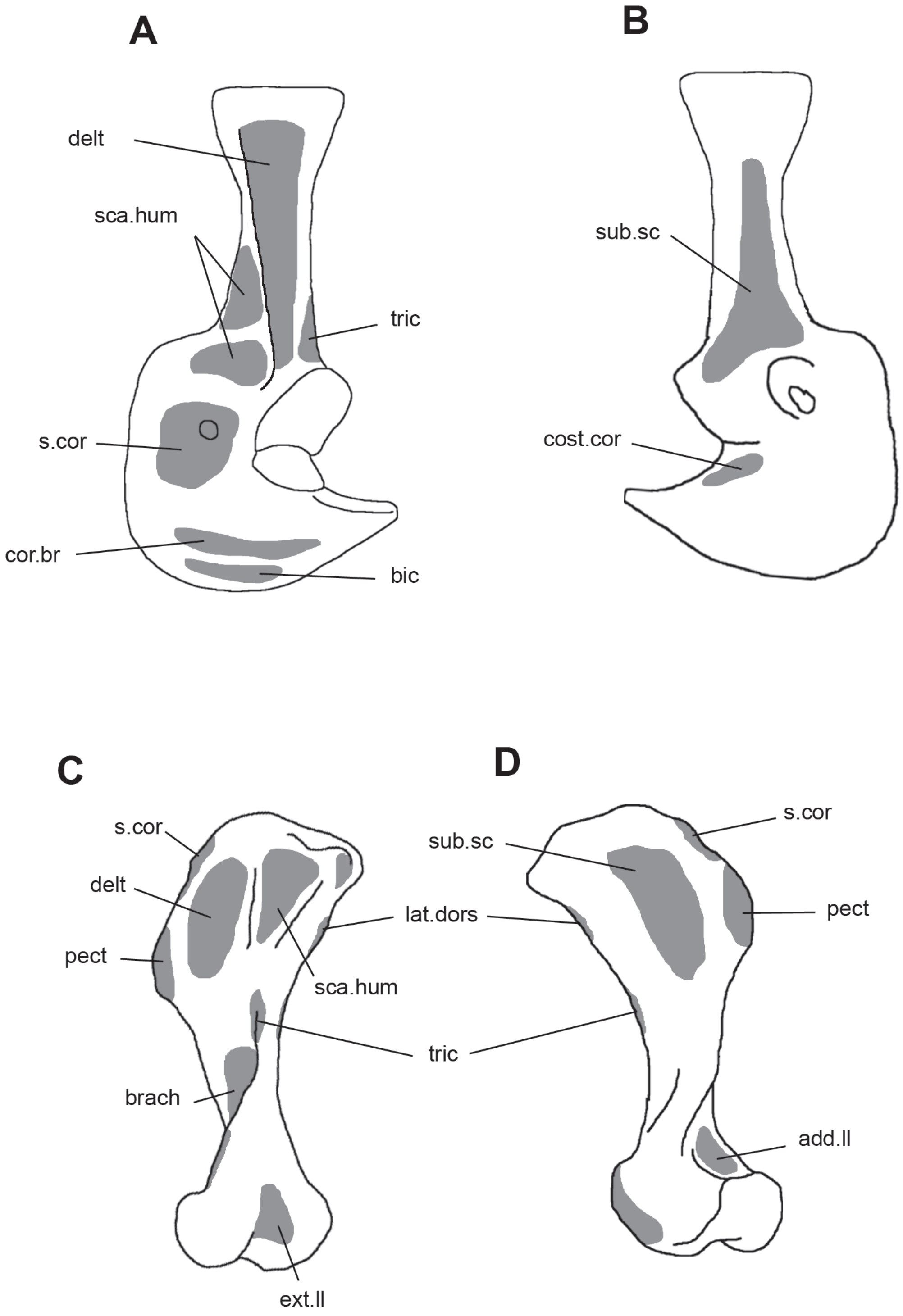


Figure 59. Muscle attachment areas on the left pectoral girdle and humerus in GPIT/RE/7113. **A**, pectoral girdle in lateral; **B**, mesial view; **C**, humerus in dorsal; **D**, ventral view.

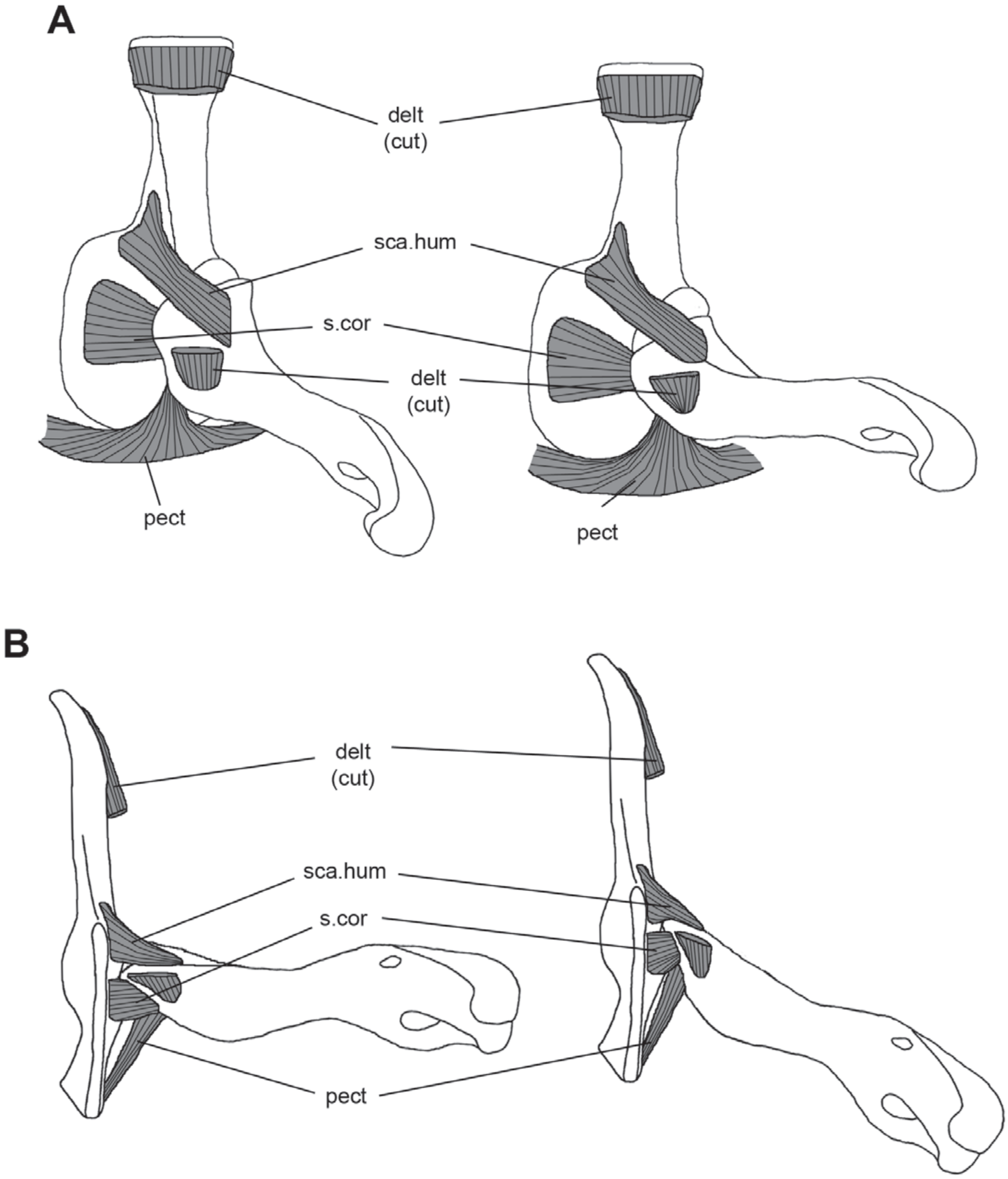


Figure 60. Reconstruction of the main pectoral muscles in GPIT/RE/7113. **A**, lateral view with humerus horizontal and sloping; **B**, anterior view with humerus horizontal and sloping.

head was set off from the shaft and thus could be moved at almost any plane between the horizontal and nearly vertical planes.

Before I discuss this theory in more detail, with special reference to *Sauroctonus* and my own results, it is necessary to elucidate a few points that concern the therapsid-mammalian transition.

The modifications in the pelvic girdle result in a change of the musculature. This can be explained graphically by the main three pelvic muscles, the ilio-femoralis, the pubo-ischio-femoralis internus and the pubo-ischio-femoralis externus (fig.61).

The ilio-femoralis had a rotational and elevational function in early synapsids. The iliac plate was expanded in both the anterior and posterior directions and in particular the posteriorly situated parts of the muscle rotated the femur about its long axis. Advanced cynodonts and mammals have this part reduced and thus the former rotational function of this muscle was abandoned. In these groups the ilio-femoralis would now exclusively act as retractor, and therefore the anterior part of the ilium was expanded in this direction.

The pubo-ischio-femoralis internus is confined to the dorsal and internal face of the pubis and acts as the main protractor in primitive synapsids. In later synapsids, however, the pubis is somewhat reduced and thus parts of the muscle had to migrate dorsally and insert on the body fascia, ribs and inner surface of the ilium. In later cynodonts and mammals this muscle, the homologue iliacus, inserts exclusively on the underside of the anteriorly protruding iliac blade.

The pubis reduction also affects the pubo-ischio-femoralis externus, which covers the lateral and ventral face of the pubis and ischium in early synapsids but is confined to the ischium in advanced cynodonts. In the early synapsids, it acted as adductor and was particularly important in animals which moved with a sprawling gate. Advanced cynodonts and mammals with a more erect gait did not require such strong adductor musculature anymore. Thus, the pubo-ischio-femoralis externus could be restricted to the ischium and had an exclusively retracting role. Additionally this muscle replaced the caudo-femoralis which was the main retractor in the non-mammalian synapsids.

In its character composition and muscle attachment areas, *Sauroctonus* shows an intermediate stage between basal synapsids such as *Dimetrodon* and more advanced cynodonts represented by *Luangwa* (figs.62 & 63). The ilium is considerably less expanded in a posterior and more expanded in an anterior direction than in *Dimetrodon*. The iliofemoralis muscle no longer acts exclusively as an elevational and rotational force, but also pulls the femur backwards as required in a more erect gait. The pubis is still well developed but also somewhat reduced

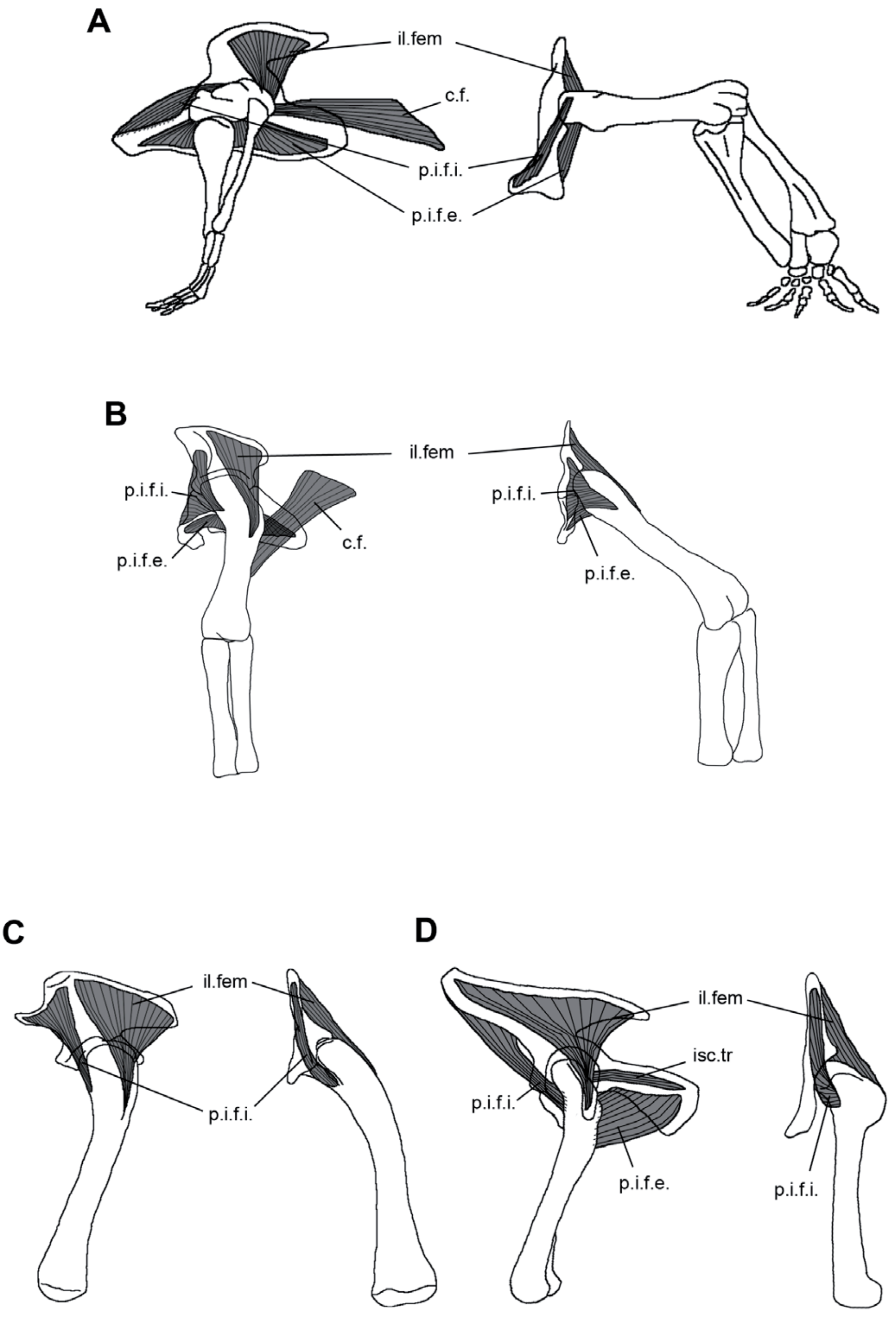


Figure 61. Therapsid - mammalian transition of pelvic musculature and illustration from sprawling to semi-erect gait shown in lateral and anterior view. **A**, *Dimetrodon*; **B**, GPIT/RE/7113, **C**, *Regisaurus*; **D**, *Luangwa*. (**A**, modified from Jenkins 1971; **C** and **D** modified from Kemp 1978, 1980).

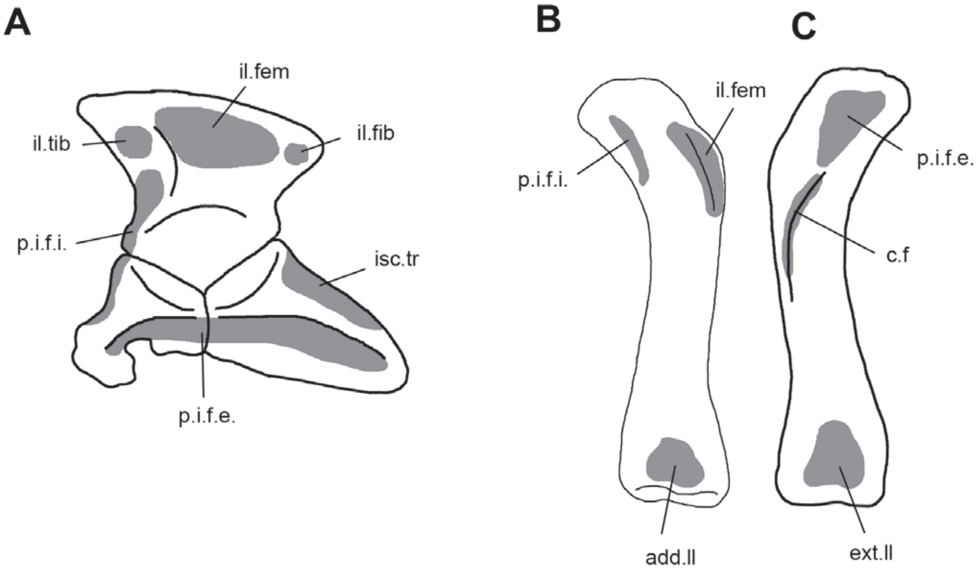


Figure 62. Muscle attachment areas on the left pelvic girdle and femur in GPIT/RE/7113. **A**, pelvic girdle in lateral view; femur in **B**, lateral and **C**, mesial view.

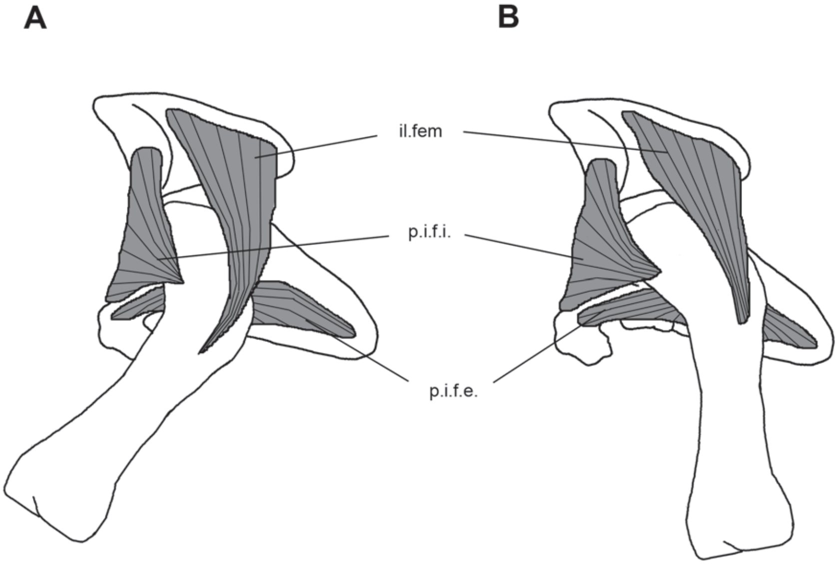


Figure 63. Reconstruction of the main pelvic muscles in GPIT/RE/7113. **A**, hindlimb protracted; **B**, hindlimb retracted.

in comparison to *Dimetrodon*. However, the pubo-ischio-femoralis externus still extensively attaches to the ventral face of the pubis and ischium, and is considered to produce a strong and necessary adductor force when the animal moves in the sprawling gate. With regard to the proposed hunting action, however, it is likely that a strong pubo-ischio-femoralis externus stabilized the animal, when wrestling with its prey. The pubo-ischio-femoralis internus has already migrated dorsally in *Sauroctonus,* and thus indicates a trend towards a more erect gait, in this genus.

The pubo-ischio-femoralis internus acted as the main protracting muscle. It inserted on the anterior and medial surface of the pubis but also on the antero-ventral face of the ilium. Here a concave attachment area is developed which is separated from the attachment area of the ilio-femoralis by a distinct ridge. The anterior part of the pubo-ischio-femoralis externus on the ventral face of the pubis probably had a slight additional protracting function but mainly acted as adductor muscle. In addition, the posterior parts of the pubo-ischio-femoralis externus also had a small retracting role but the main retraction muscle was the caudofemoralis from the vertebrae of the tail. It inserted on the medial surface of the femur ventral to the adductor fossa. The ilio-femoralis was the main abductor muscle but it also had some retracting function, although the degree of its retracting force depended on the stance of the animal.

3.4 Comparison with *Smilodon fatalis*

3.4.1 Introduction

The gorgonopsian *Sauroctonus* (GPIT/RE/7113) and the saber-tooth cat *Smilodon* (GPIT/MA/1340) both attract attention because of their hypertrophied canine teeth. Gorgonopsians were the first tetrapod group to develop such a feature, though not to such an extreme extent as some of the saber tooth cats, particularly the Smilodontidae. Early reptiles such as the captorhinomorph *Paleothyris* or the synapsid *Archaeothyris* from the Carboniferous had a row of several small, pointed teeth that were not much differentiated and the ‘canines’ were only slightly larger at best. The pelycosaurs and especially *Dimetrodon* were the first group with clearly elongated canines and this was retained in all the following carnivorous therapsid groups. However, gorgonopsians were the only group that developed such extreme sabers, which were particularly emphasized in the subfamilies Rubidgeinae and Inostranceviinae. Although some dinocephalian, therocephalian or cynodont forms had also developed markedly elongated canines, the enlargement was almost never to such a degree as in gorgonopsians. Furthermore, these groups were rather heterogeneous, including herbivorous, insectivorous and fish-eating forms.

During the Jurassic and Cretaceous, dinosaurs were the main carnivorous predators, and their teeth were less differentiated, but no less sharp and pointed.

Only 30 million years ago in the Oligocene, the first nimravids with the saber-tooth forms *Hoplophoneus* and *Dinictis* occurred, and in the Pleistocene, the subfamily machairodontinae of the neofelids produced such beasts as *Machairodus*, *Homotherium*, *Meganthereon* and finally *Smilodon*.

As stated earlier these particularly elongated canines evolved several times independently which implies that these weapons must have been very useful for the animal. The fact that these animals were clearly carnivorous, suggests obviously that the sabers must have been quite functional when taking prey.

Various authors dealt with this topic and different theories concerning the mode of hunting and the function of the canini were developed (e.g. MATTHEW 1910). AKERSTEN (1985) formulated the canine shear bite model, which is, with some modifications, still valid today.

Although gorgonopsians were examined with regard to different functional aspects such as the stance and gait, or the jaw function, there exists no overall examination that considers all aspects together (teeth, cranial morphology, jaw function, postcranial morphology with muscle function).

Theories based on fossil material are always hypothetical even if a more or less direct comparison with an extant group is possible (such as the comparison of the saber tooth cats with the extant pantherine cats). However, gorgonopsians do not have any close extant relatives, as both living reptiles and mammals are too distantly related. Therefore this comparison is not based on phylogenetic relationships but on similar morphological features. It is investigated whether a feature such as the distinctively elongated caninus of two unrelated taxa might imply other similar characters of the skull and skeleton and point to a comparatively similar mode of life.

For this purpose it is necessary to analyse each taxon in comparison with its relatives. On this basis it is possible to establish the differences that set the taxon apart from its closest relatives with a most similar character-set, habitus and life-style. At best, both analysed taxa will differ from their relatives in more or less the same characters, especially in those, which are connected with the elongated caninus. However, the fact that *Sauroctonus* is a basal synapsid and *Smilodon* a mammal makes comparison difficult.

Another difficulty is the selection of the relatives to act as a comparison. In the case of *Sauroctonus*, the closest relative would be another gorgonopsian genus. However, the different genera do not differ greatly from each other morphologically. Furthermore, postcranial material is too rare to provide sound information for an overall comparison concerning phylogenetic assignments. For that reason, other carnivorous therapsid taxa such as therocephalians (KEMP 1972, 1978, 1982; MENDREZ 1975) and cynodonts (KEMP 1979, 1980, 1982) are used for comparison (figs. 64 & 65).

Smilodon shares the markedly elongated canines only with other members of the subfamily Machairodontinae within the Felidae (the nomenclature of TURNER & ANTÓN, 1997 is followed here, where the Nimravidae are considered to constitute a separate family). In contrast, the second subfamily Felinae consists only of taxa with 'normally' developed canines. Another advantage is the fact that this subfamily is mostly constituted of extant cats which in certain aspects contribute well to a comparison. The investigation is based on the literature (GONYEA 1976a&b, 1978, EMERSON & RADINSKI 1980, TURNER & ANTÓN 1997, ANTÓN & GALOBART 1999) and on personal observations of *Panthera leo* (SZ 328), see figure 66.

Both taxa, *Sauroctonus* and *Smilodon* are always considered in comparison with therocephalians and cynodonts and the extant pantherine cats, respectively, if no other reference taxon is given. First the skull is considered and then the postcranial skeleton. In both sections there is concurrent reference to the musculature when it is appropriate.

The different shape of the bones implies a different pattern of muscles in mammals and reptiles. However, it is possible to compare the size and form of attachment areas with regard to the lifestyle these animals presumably led. For example, a more cursorial animal will develop different sizes of different muscles and different areas of attachment (i.e. variation in size and position) than an animal that is built for strength. In this context, the assertion was again investigated as to whether the presumed similar lifestyle of a gorgonopsian and a saber-tooth cat is also expressed in an analogy of muscle shape.

3.4.2 Skull

Upon first observation both skulls seem incomparable because the skull of *Sauroctonus* is more or less typical theriodont: rather elongated with a slightly convex dorsal profile and a parabolic incisor arc. In contrast, the skull of *Smilodon* is relatively shortened which is a typical character of the felines (figs 67 & 68). However, compared with their respective relatives, the skulls differ in some ways from them, and show some similarities to each other.

The form of the skull in gorgonopsians varies from relatively flat and broad to extremely

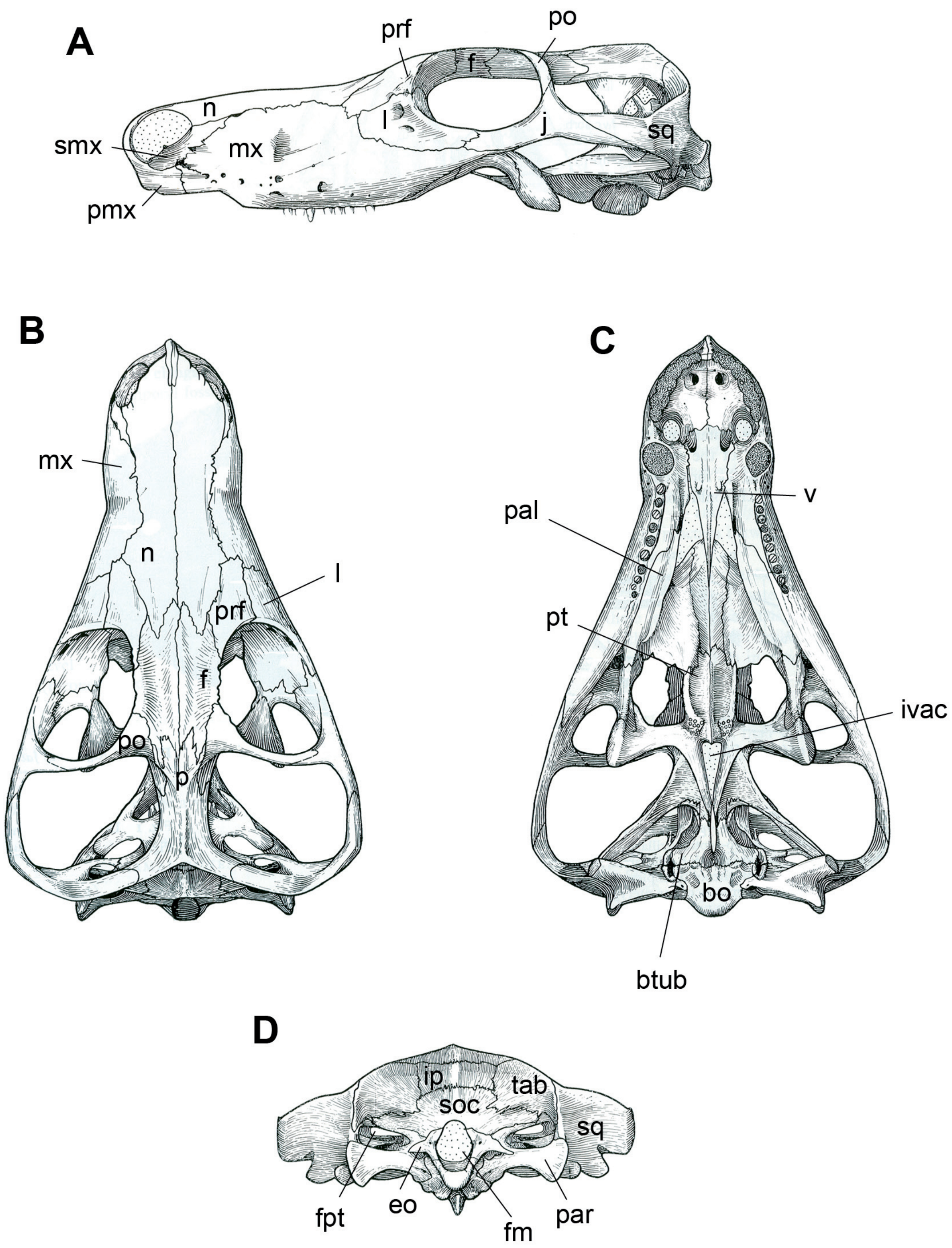


Figure 64. Skull of the therocephalian *Regisaurus* in **A**, lateral; **B**, dorsal, **C**, ventral and **D**, occipital view (modified from MENDREZ 1972).

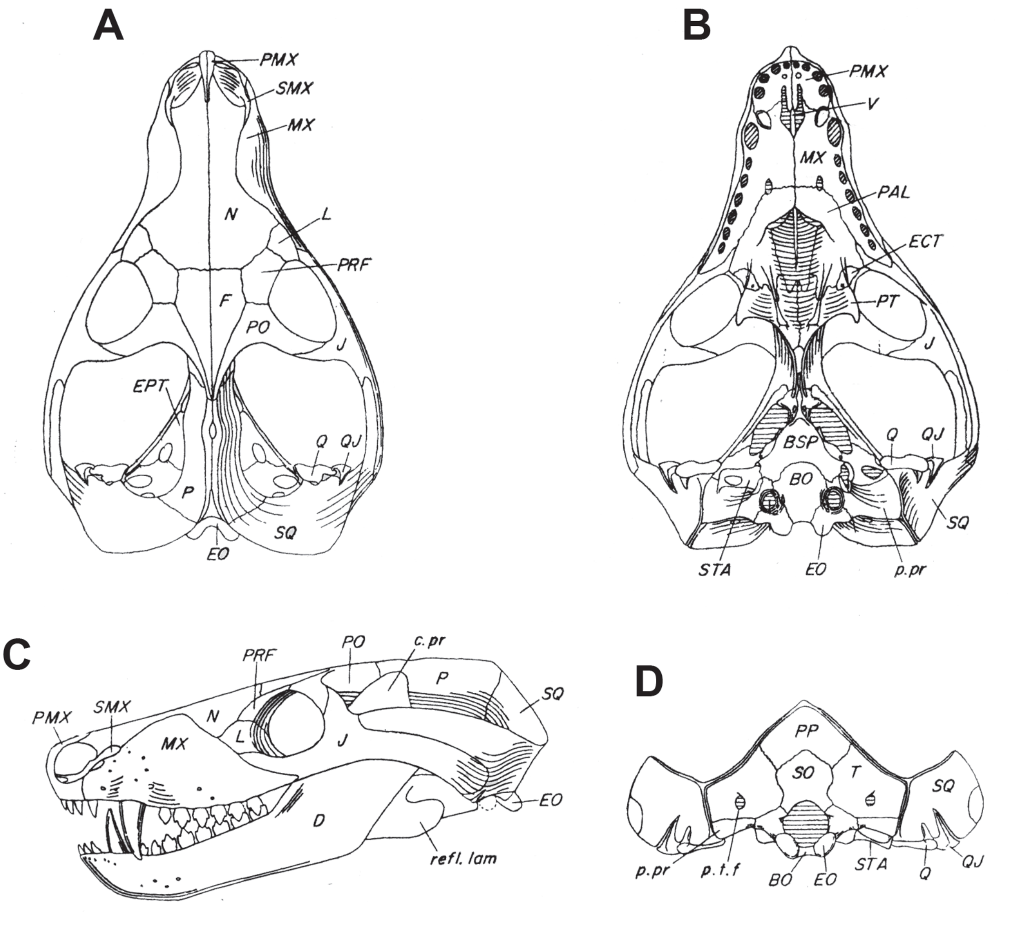


Figure 65. Skull of the cynodont *Thrinaxodon* in **A**, dorsal; **B**, ventral, **C**, lateral and **D**, occipital view (modified from PARRINGTON 1946).

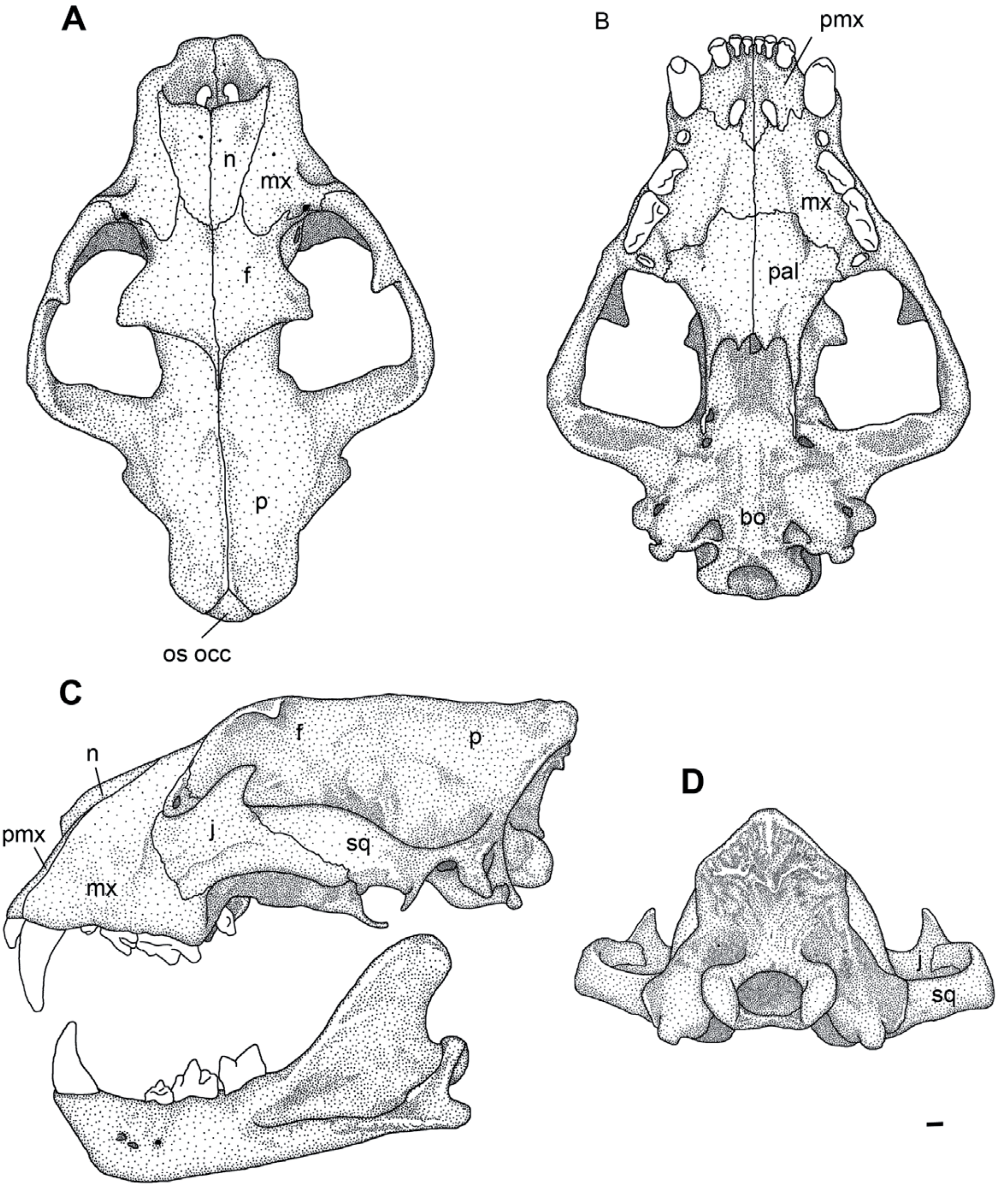


Figure 66. Skull of *Panthera leo* (SZ 328) in **A**, dorsal; **B**, ventral, **C**, lateral and **D**, occipital view. Scale bar 10 mm.

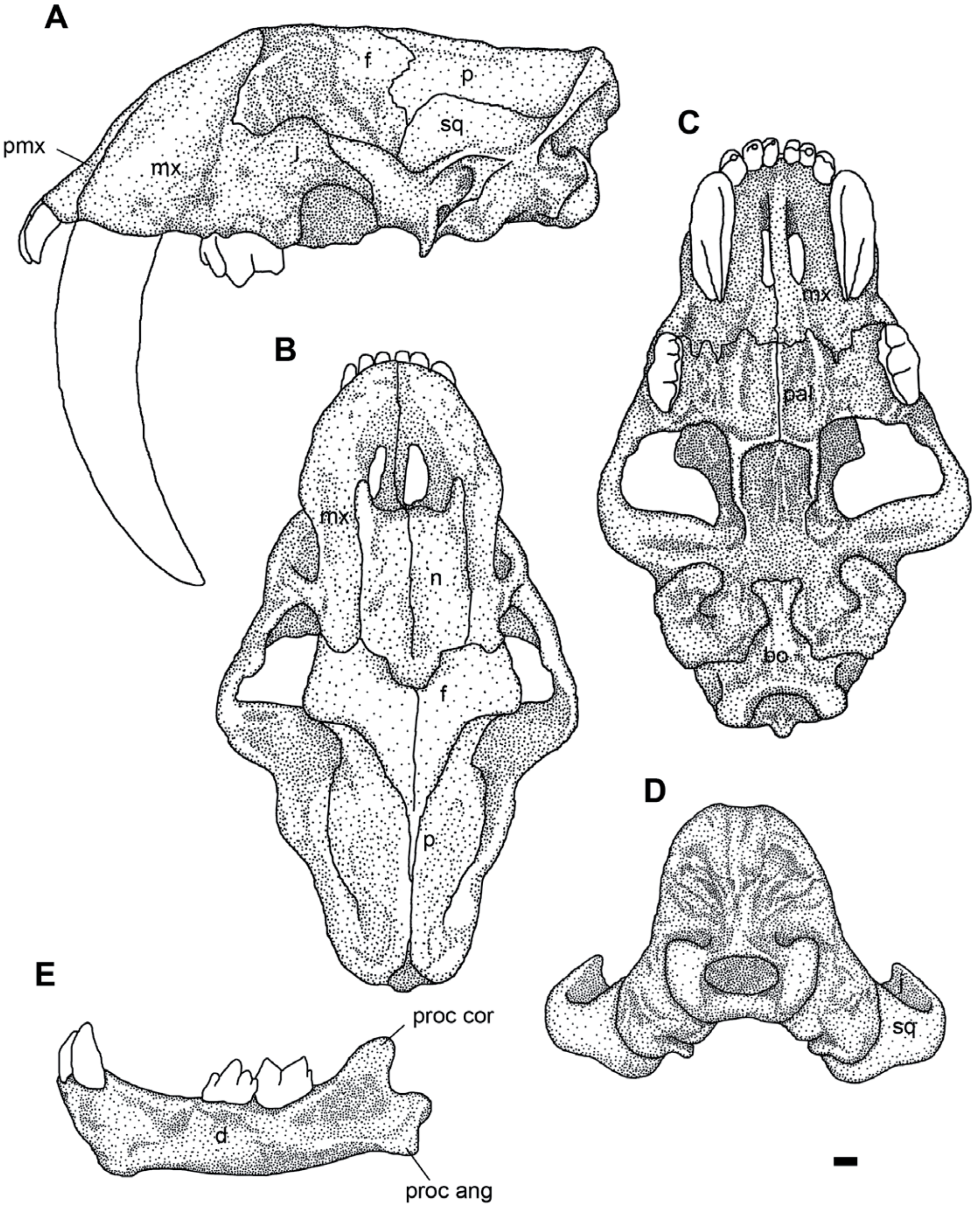


Figure 67. Skull of *Smilodon fatalis* (GPIT/MA/1340) in **A**, lateral; **B**, dorsal, **C**, ventral; **D**, occipital view; **E**, lower jaw in lateral view. Scale bar 10 mm.

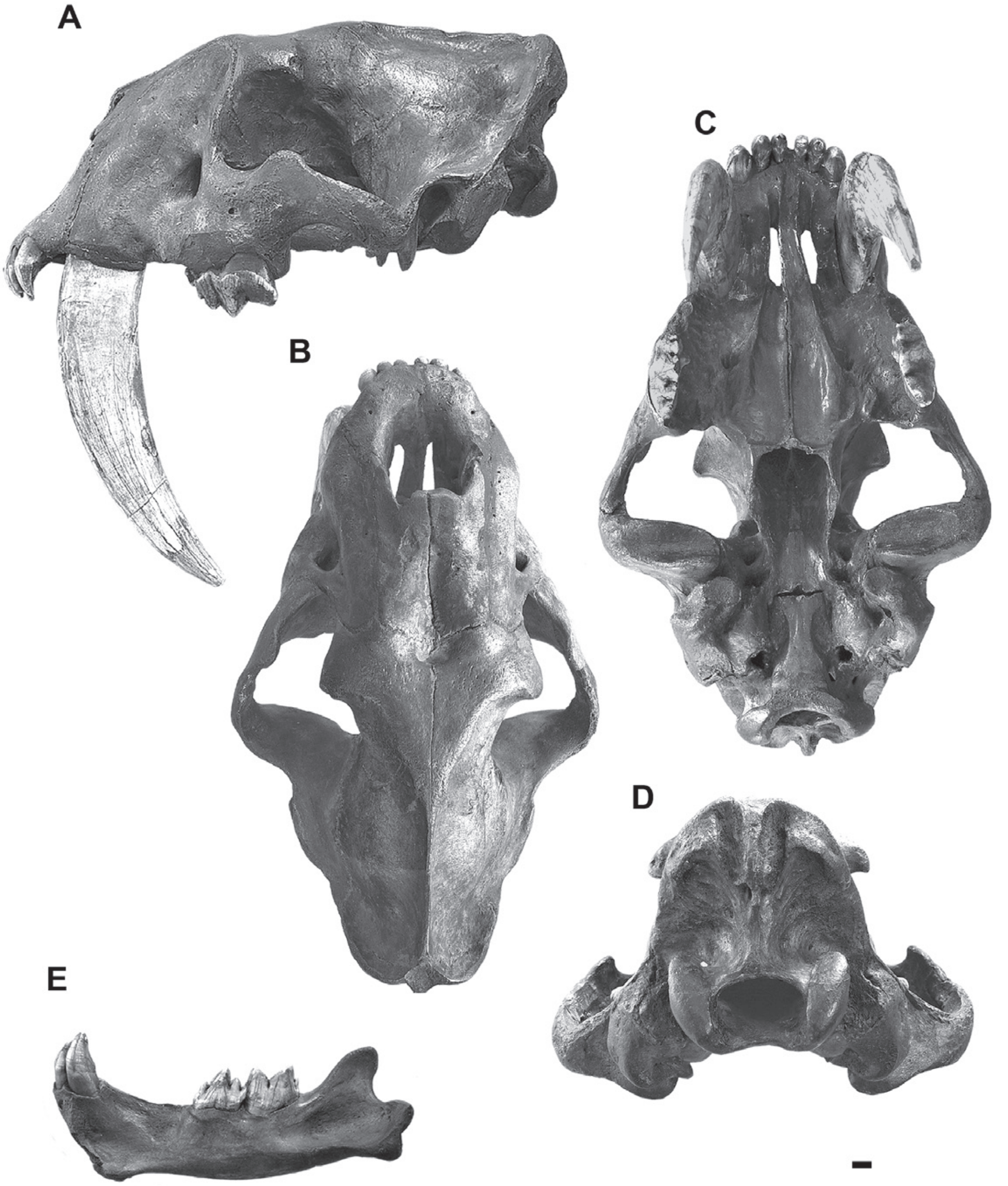


Figure 68. Photographs of the skull of *Smilodon fatalis* (GPIT/MA/1340) in **A**, lateral; **B**, dorsal, **C**, ventral; **D**, occipital view; **E**, lower jaw in lateral view. Scale bar 10 mm.

high and narrow. Consequently the forms with the most elongated and strongest canines have the highest skulls and snouts. The latter became shorter and more massive in its overall appearance. *Sauroctonus* is intermediate between the more generalised and the more advanced forms in this respect. *Smilodon* on the other side has a more elongated, narrower and higher skull compared to the extant cats. In particular, the snout is higher to accommodate the long root of the caninus. The face is rotated upwards relative to the braincase (EMERSON & RADINSKI 1980) so that the anterior part of the skull is extended downwards less than in extant cats (fig. 69). The dorsal skull roof is not as extremely concave, its posterior part is rather straight and the temporalis fossa is shortened. This feature is related to the temporalis muscle that is directed more vertically than in extant cats to allow for a larger gape, which in turn provides the same clearance between the upper and lower canini as in a pantherine cats with 'normal' canines.

Gorgonopsians have an external adductor jaw musculature which is not yet differentiated into a temporalis and a masseter muscle as found in mammals. However, it is modified from the plesiomorphic condition found in pelycosaurs since three parts of external adductor musculature are developed: a medial part (from the underside of the skull roof to the internal face of the postdentary bones), a lateral part (from the anterior face of the squamosal to the coronoid process) and a zygomatic part (from the internal face of the zygomatic arch to the ridge on the lamina reflecta). The medial part is oriented vertically as in *Smilodon* whereas the lateral part has a strongly posterior component particularly during the later phase of the mouth closing process. The zygomatic part mainly stabilises the mandible and pulls it dorsally and laterally.

Within gorgonopsian evolution, the zygomatic arch gets stronger as the caninus becomes larger. This feature culminates in the down-turned zygomatic flange of the rubidgeines with their heavy and massive mandible and long canine. In comparison with therocephalians and early cynodonts where the zygomatic arch is continuously convex, it widens more gradually in a posterior direction and the posterior corner is rather angular if seen in ventral view in *Sauroctonus*. The same applies for *Smilodon* in comparison with the pantherine cats. The zygomatic arch is more angular posteriorly, more massive in its overall appearance, less convex in lateral direction and in addition, shortened. The latter implies a less lateral but more vertical component of the masseter musculature (MATTHEW 1910). However, the posterior convexity could well point to a lateral force that would act later during the closure of the mouth. The fact that the zygomatic arch in *Sauroctonus* is more expanded in its posterior corner is related to the origin of the zygomatic part of the external adductor musculature which was responsible for the lateral component of the lower jaw as mentioned above.

Turner & Antón (1997) noted that the incisors in *Homotherium* were larger than in *Smilodon* whereas the lateral ridges on the palate were less pronounced. Additionally, the forelimb was stronger in *Smilodon* and so they suggested that *Homotherium* had a more cursorial lifestyle and was probably less adapted for capturing its prey with the forelimbs. However, the incisivi might have compensated for this since they were larger and thus provided a better grip of the prey.

The occiput in *Sauroctonus* differs significantly from that of *Smilodon*. This is partly caused by the modified zygomatic arch and braincase of the mammal and partly by the different neck musculature which resulted in different areas for muscle attachment. The gorgonopsian occiput has a rectangular outline and is wider than high, concave, and sloping in posterior direction. Therocephalians and cynodonts show a change from this condition to a more triangular and less concave form which is due to the skull modifications mentioned above. *Smilodon* also has the typical mammalian triangular occiput but the dorsal margin is rather flat and angular which is due to the strong bulbous ridges for muscle attachment. The median ridge is well developed in both taxa.

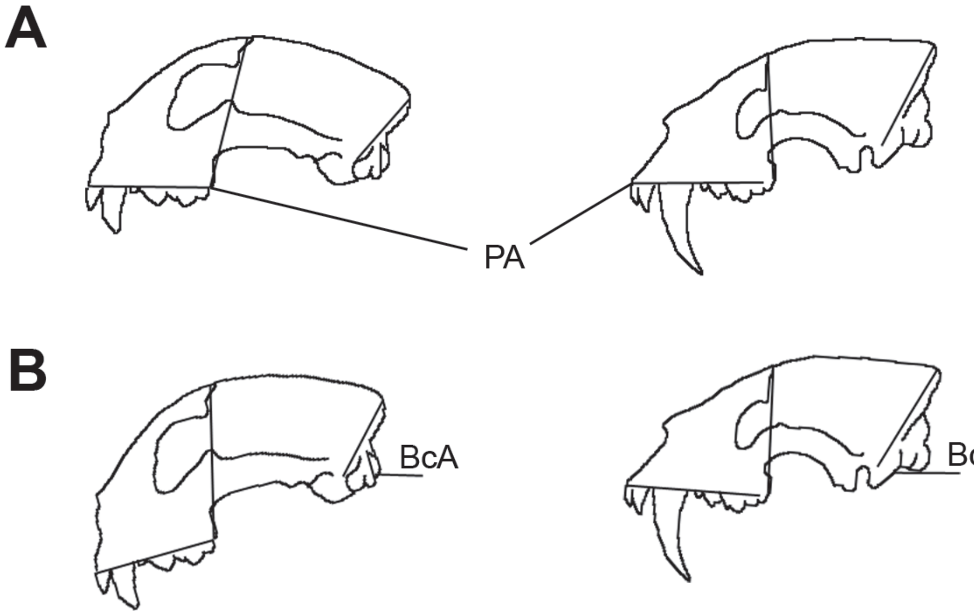


Figure 69. Facial rotation in *Felis* and *Hoplophoneus*. **A**, skulls in usual orientation, with palate horizontal; **B**, skulls oriented with basicranial axis horizontal to illustrate upward rotation of facial skull relative to braincase in saber-tooth cats (from Emerson & Radinski 1980).

The gorgonopsian palate is rather difficult to compare since it shows all typical reptilian features such as a missing secondary palate, the transverse flanges of the pterygoid and the plesiomorphic small and poorly ossified braincase. The articulation with the lower jaw is situated posteriorly, whereas the position of the transverse process of the pterygoid was situated relatively anteriorly. This distance allowed enough length for the muscle fibres to prevent gape limitation since the pterygoideus musculature originated from the back of the transverse process. Furthermore, a forward pull and the closing of the mouth was provided at the same time (KEMP 1982). Although the skull of *Smilodon* is longer in comparison with extant cats, the jaw articulation is situated more anteriorly. This is caused by a reduced distance between the jaw articulation and the carnassials and allowed for more strength of bite at the carnassials since the resistance moment arm is shorter (EMERSON & RADINSKI 1980). *Sauroctonus* did not need the strength of bite in the area of the postcanine teeth since they are reduced. Instead gorgonopsians were more adapted to a fast and rapid bite (KEMP 1982). Furthermore, the secondary palate was not yet developed in this group and thus the animals could not chew the chunks of meat but rather swallowed them whole.

In both taxa it was necessary to allow a large gape and thus to provide enough clearance between the upper and lower canines. *Sauroctonus*, as well as all other gorgonopsians, was able to move the quadrate relative to the skull. This was also the case in therocephalians and early cynodonts before this bone became incorporated into the middle ear. In gorgonopsians the gape would be very limited if the quadrate simply shifted anteriorly and ventrally since the dorsal process of the articular facet would hinder any further movement. Therefore the quadrate was additionally capable to screw on the correspondingly shaped articular facet and thus to move medially relative to the lower jaw (PARRINGTON 1955). With this shift, the limiting dorsal articular process was avoided and the maximum gape was possible.

In *Smilodon* the maximum gape was achieved by a more ventrally situated jaw articulation, as well as the above mentioned dorsal rotation of the facial skull which provided a greater option for the mandible to move relative to the braincase.

Gorgonopsians have strongly developed palatal ridges or tuberosities. They border a palatal fossa and are often equipped with more or less distinct teeth. This additional gripping device might have helped to better hold a struggling large prey and to prevent too much lateral force which would be dangerous for the canine.

ANTÓN & GALOBART (1999) described palatal ridges of various forms in the machairodont *Homotherium*. These also would point to an additional gripping device and would correspond well with the palatal teeth on the palatal tuberosities of most of the gorgonopsian taxa. Extant cats on the other hand have only slightly developed lines in this part of the palate.

As mentioned above, the paroccipital process in *Smilodon* is rather small, whereas it is well developed in *Sauroctonus*. However in comparison with therocephalians it is somewhat shorter, though the paroccipital process can become rather massive and stout in larger gorgonopsians.

The ventral face of the basisphenoid and basioccipital provides a large and somewhat tuberous area for attachment of the longus capitis muscle which depresses the head. In therocephalians and cynodonts this area is less developed and in particular the basisphenoid fossa is rather shallow and the margins less prominent.

The lower jaw in *Sauroctonus* is longer in comparison to *Smilodon* and the two rami diverge at a greater angle. This is, however, due to the relatively narrow skull of *Smilodon* with the anteriorly situated jaw articulation. The coronoid process in *Sauroctonus* is well developed, whereas it is reduced in *Smilodon*. This character is also different from that of the extant cats where the coronoid process is rather high. According to various authors (MATTHEW 1910, EMERSON & RADINSKI 1980) this feature allows a longer temporalis muscle and makes it possible that the difference between the normal and stretched condition (large gape) is reduced. EMERSON & RADINSKI (1980) used the Herring & Herring model which predicts a greater amount of stretch with increasing origin/insertion ratio and angle φ and found that indeed the ratio and the angle φ is greater in all saber-tooth cats and thus a larger gape was again possible.

On the other hand, it provides less leverage and therefore a reduced bite force at the carnassials. This was however compensated for by the shortened tooth row and the more vertical orientation of the masseter musculature, which in turn increases the bite strength.

Sauroctonus needed the coronoid process as an attachment area for the lateral part of the external adductor musculature. This portion pulled dorsally but mainly in a posterior direction, especially during the later phase of the jaw closing movement; whereas the medial portion of the external adductor musculature serves as the main adductor in dorsal direction. If one applies the Herring & Herring model to this muscle part for comparison, the origin/insertion ratio and the angle φ is greater in gorgonopsians than in therocephalians. The situation in cynodonts is found to be different since this group is too heterogeneous.

The symphysis of the lower jaw is well developed, massive and almost straight in both taxa. In the smaller gorgonopsians with smaller canines, however, it is comparatively weak and sloping as is seen in extant cats. Therocephalians and cynodonts also have a rather weak, short and low symphysis. It is obvious that the size of the canine is in relation to the massiveness of the symphysis. This feature is even more developed in Nimravidae and *Thylacosmilus* where a distinct ventral flange is developed, that supports the canine medially. Such an extension is, however, not found in any member of the Felidae whether fossil or extant. On the other hand, it was never developed amongst the Gorgonopsia, not even in forms with exceptionally large canines such as *Rubidgea* or *Inostrancevia*.

The retroarticular process of gorgonopsians curves ventrally and is rather elongated in comparison with therocephalians and some cynodonts, where it is directed more posteriorly. Again this allows a greater gape since an almost anteriorly directed retroarticular process contacts the occiput later when the jaw is largely opened as a straight posteriorly facing process. Further, a ventrally expanded process provides more leverage for the depressor mandibulae to allow a larger gape. In *Smilodon* the jaw opening muscle is, however, modified to the mammalian digastricus-complex with a different origin and attachment area. Here the wider gape (related to the lower jaw) is ensured by the angular process which is directed more laterally so that it would not hinder the lower jaw to be opened to a great extent.

3.4.2.1 Dentition

Different carnivores use different modes of killing prey, which requires a different cranio-dental morphology, amongst others things. Felids mostly kill by a deep and precise bite into the neck region or suffocate their victim, whereas canids for example weaken their prey by repeated ripping bites. Thus, the canine teeth of a felid are pointed and conical, the ones of a canid however more blade like. In saber tooth cats the upper canini are not conical and sharply pointed as in pantherine cats but saber-like, extended, laterally compressed and rather blade-like as in canids whereas the carnassials also become longer, narrower and scissor-like. Thus, the ability for bone crushing is even more reduced (TURNER & ANTÓN 1997).

The dentitions in *Sauroctonus* and *Smilodon* differ considerably at first sight apart from the elongated canine. The mammalian *Smilodon* has a typical carnivorous dentition, especially concerning the molars, premolars and the carnassials which are formed by P4 and M1. However, the parabolic arrangement of the incisors in *Smilodon* somewhat resembles the gorgonopsian condition and differs from the straight tooth row in extant cats. All cats have a reduced postcanine dentition in comparison with other carnivores due to the specialisation that a cat does not crack bones but instead slices the meat. With the help of the incisors, the soft parts will be torn from the bones, which are left intact.

Although the presence of elongated canine in *Sauroctonus* and *Smilodon* is an obvious similarity, the teeth are nevertheless different. *Sauroctonus* has a more oval tooth in cross-section with only slightly flattened anterior and posterior margins.

If compared to the incisors, the caninus in *Sauroctonus* is shorter in comparison to *Smilodon*. It is also not that much flattened laterally and less curved. However, it is markedly flattened and remarkably elongated in comparison and relation to the incisors. There are serrations on both the anterior and posterior margins and wear facets on the anterior margin of the left tooth.

Smilodon of course exhibits the largest canines of all neofelid saber-tooth cats. However, in forms such as *Homotherium* which have somewhat smaller canines they still are flattened and blade like (Turner & Antón 1997). The serration is strong on the posterior margin, whereas it seems that on the anterior margin it is only restricted to the ventral half.

The canines of the lower jaw differ considerably in both forms since the canine in *Smilodon* is not enlarged at all and thus the tooth has the shape of a large incisor. It is curved, somewhat flattened and cusped only medially with a serration on the posterior margin. The lower canine of *Sauroctonus* is elongated with respect to the incisors, although it is not as large as the upper one. It has serrations on both margins but wear facets only on the anterior margin. The five incisors of the upper jaw in *Sauroctonus* are arranged in a well rounded parabolic arc and the canini follow postero-laterally to them.

The incisor tooth row in *Smilodon* is arranged in a distinct parabolic arcade, which resembles that of hyaenids, and is therefore in contrast to the rather straight tooth row of extant cats. This arc allows an animal with enlarged saber-like canines to tear flesh from a carcass because the incisors are set off well from the enlarged canini. Additionally, area and volume of a bite made by incisors and canines together would be greater in animals with curved rather than straight arcades (Biknevicius et al. 1996).

Incisors in a parabolic tooth row must resist some mediolateral loads independently because they were not protected by the lateral most teeth as would be the case in a straight tooth row. Consequently, the teeth are more robust and larger. However, this is explained by the different hunting methods of felids and e.g. canids. Extant felids use their claws to immobilize their victim whereas canids that hunt in packs and fell it by repeated tearing bites would need the incisors as an additional gripping device for the canines (Biknevicius et al. 1996).

The incisivi of *Sauroctonus* are serrated in such a way that each tooth faces the serration of the following, so the serration is situated on the posterior and anterior margin in the fifth incisivus but rather on the lateral and medial margin at the first tooth (fig. 70). They were capable to interdigitate and thus could tear flesh more precisely. This is not observed in therocephalians and is only indicated in early cynodonts (Kemp 1982).

The incisors in *Sauroctonus* are rather conical, only somewhat curved and of medium size; whereas they are stronger in forms with extremely large canines. The fourth incisor is usually the largest but the difference to the other teeth is minimal.

The strongly curved incisors in *Smilodon* are more conical at the base but somewhat flattened at the tips. They are cusped, and also serrated in the same manner as in *Sauroctonus*. The third incisivus here is considerably larger than the other two. In both taxa, the strong incisors serve as a stabilisation during the bite and as support for the elongated caninus by preventing too much lateral bending of the latter.

The lower jaw of *Sauroctonus* contains four incisors. They are more curved and conical at the base but become more triangular towards the tips with the serrations somewhat expanded. The first tooth is the largest.

Smilodon has two incisors in the lower jaw, which are arranged in a well defined arc. They are cusped however, only on the lateral side, and the tips are curved. The second tooth is considerably larger and the serrations on both are relatively weakly developed.

It is difficult to compare the postcanine dentition because the mammalian *Smilodon* has P4 and M1 modified to the carnassials, which are typical for carnivorous animals and allow the animal to slice meat. According to TURNER & ANTÓN (1997) the carnassials in the saber tooth cats are even more specialized in this direction than the ones of the pantherine cats that were already less adapted for crushing bones compared with canids or hyaenids.

Sauroctonus has four or five small postcanine teeth, which certainly were not used for slicing meat but as an additional gripping device. Furthermore, most other gorgonopsians had no large or strong postcanine teeth except for *Inostrancevia*. However, other large species such as *Rubidgea pricei* had no postcanine teeth at all. In these forms, the incisors and canines are well developed and it is probable that the animal did not require the postcanine teeth as additional gripping devices.

Figure 70. Tooth function in gorgonopsians. Movement of a lower incisor relative to an opposing upper incisor (from KEMP 1982).

3.4.3 Postcranial skeleton (figs. 71-73)

3.4.3.1 Shoulder girdle

As described above, the shoulder girdle in *Sauroctonus* points to a rather reptilian stance and gait. The nature of the articulation facet and the humeral head requires a peculiar mode of movements. The scapular blade is of moderate width, straight and slightly expanded on its dorsal extremity. The precoracoid has a convex anterior margin, the coracoid forms the distinct therapsid posterior process and the glenoid facet is composed as described above. In contrast, the scapular blade is rather narrow and curved in therocephalians whereas it is comparatively short and stout in cynodonts. The coracoid and precoracoid are comparable in therocephalians whereas the scapular component of the glenoid is circular in outline. In most cynodonts, the coracoid and precoracoids are already somewhat reduced and the glenoid shows a more rounded and open facet. Since the scapular blade is narrow in therocephalians, the deltoideus might not be much developed in this group. Although the scapular blade is rather wide in cynodonts the deltoideus is confined to the anterior part, whereas the posterior part is occupied by the teres major (Kemp 1979). The attachment areas for the supracoracoideus and coracobrachialis are similar to the corresponding ones in *Sauroctonus*, at least in therocephalians and early cynodonts. However, neither of these two groups developed the following particular feature. The area of origin of the scapulo-humeralis anterior is situated antero-medially to the deltoideus attachment area on the scapular blade of *Sauroctonus*. This is in contrast to the other groups where it has its origin above the supracoracoideus but not as dorsally on the scapular blade as in *Sauroctonus*.

Concerning the muscle function, it can be stated that the deltoideus is larger in *Sauroctonus* than in therocephalians and cynodonts. This muscle was, however, required to be strong if the animal moved in the sprawling gate but also during the more erect stance when the scapulo-humeralis anterior had a more protracting than elevational function.

The scapulo-humeralis anterior is situated more dorsally on the scapular blade and can act as a powerful protraction and rotational force during the semi-erect gait.

The shoulder in *Smilodon* is clearly modified in the typical mammalian style. It consists only of the scapula with the scapular spine dividing the blade into two fossae for attachment of the supraspinatus and infraspinatus muscle. The glenoid fossa is directed ventrally and provides a round, concave articulation facet for the head of the humerus. This ball and socket articulation enables the animal to move the forelimb freely in an anterior and posterior direction. In contrast to the extant cats the posterior margin of the scapular blade is more rounded and the posterior extension which provides the attachment area for the teres major is situated more ventrally. The teres major rotates the limb medially together with the latissimus dorsi and the subscapularis, respectively acts as an adductor. The less posteriorly expanded scapula indicates a shorter lever arm for the teres major. Together with an insertion on the humerus further away from the shoulder joint evidence is given that *Smilodon* achieved high velocity slowly but was also more powerful. Furthermore, the acromion process is directed laterally rather than postero-laterally. This means that the acromiodeltoid muscle, which is responsible for the humerus abduction together with the spinodeltoid has a more laterally directed force.

3.4.3.2 Forelimb

Humerus. As already mentioned the humeral head in *Sauroctonus* is flattened dorsoventrally but expanded anteriorly (where the pectoral crest is developed) and posteriorly (where the articulation with the glenoid fossa is developed). The diaphysis is comparatively short and somewhat flattened dorsoventrally which reduces the potential bending in an antero-posterior plane. All muscle attachment areas are well defined which allows the conclusion that the animal could perform a variety of strong muscle movements. The two extremities are twisted against each other with an angle of about 40 degrees. Anteriorly the deltopectoral crest is expanded and postero-dorsally the insertion area for the subscapularis is broad. On the dorsal surface a deeply concave area for the scapulo-humeralis anterior is present. The distal extremity shows a round ectepicondyle and a somewhat flattened entepiconyle.

The therocephalian humerus in comparison, is, like the shoulder girdle, rather slender and muscle attachment areas are less developed. The extremities are somewhat less twisted, the epicondyles less distinct from each other and the deltopectoral crest is weaker. Early cynodonts however, have a rather stout and twisted humerus too. The deltopectoral crest is well developed but the insertion areas for the subscapularis and the scapulo-humeralis anterior are less marked.

Smilodon has a relatively short and particularly stout and strong humerus in comparison to the extant cats. This might indicate that the forelimb was used more as a hunting weapon than in lions or leopards and that saber-tooth cats were well adapted for predation on large, struggling prey. The diaphysis is distinctly compressed medio-laterally. The attachment area for the pectoralis is well visible as a distinct and long ridge on the anterior and medial face of the humerus. Opposite to this the latissimus dorsi and the teres major insert, with the latter situated comparatively far away from the shoulder joint. This position imposes a restriction of quick movements but also provides more power.

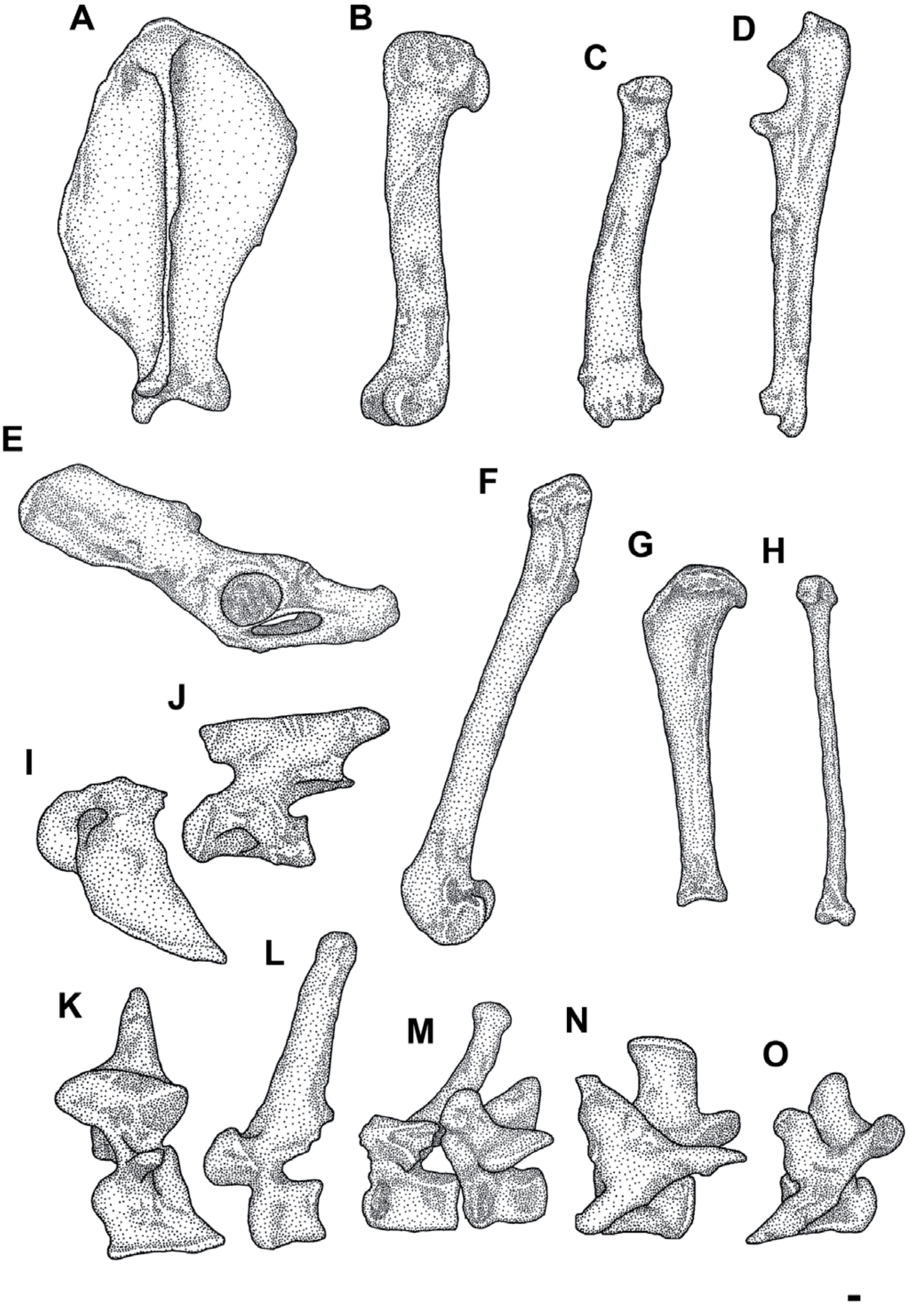


Figure 71. Postcranial skeleton of *Smilodon fatalis* (GPIT/MA/1340) in leftlateral view. **A**, scapula; **B**, humerus; **C**, radius; **D**, ulna; **E**, pelvis; **F**, femur; **G**, tibia; **H**, fibula; **I**, atlas; **J**, axis; **K**, fifth cervical; **L**, sixth dorsal; **M**, tenth and eleventh dorsal; **N**, fifteenth dorsal; **O**, lumbar vertebra. Scale bar 10 mm.

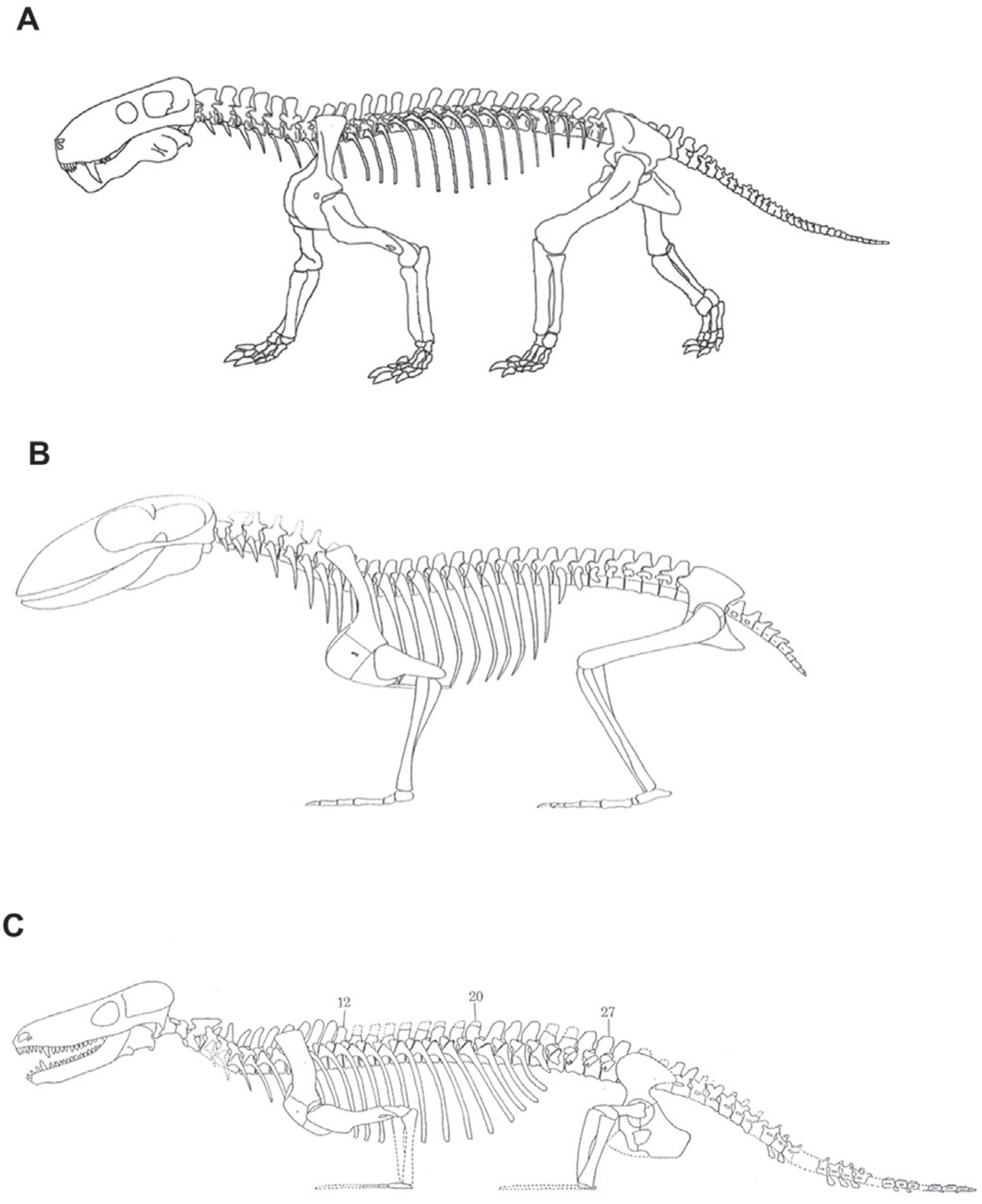


Figure 72. Therapsid skeletons. **A**, the gorgonopsian *Sauroctonus parringtoni* (GPIT/RE/7113); **B**, the therocephalian *Regisaurus* (from KEMP 1986); **C**, the cynodont *Procynosuchus* (from KEMP 1980).

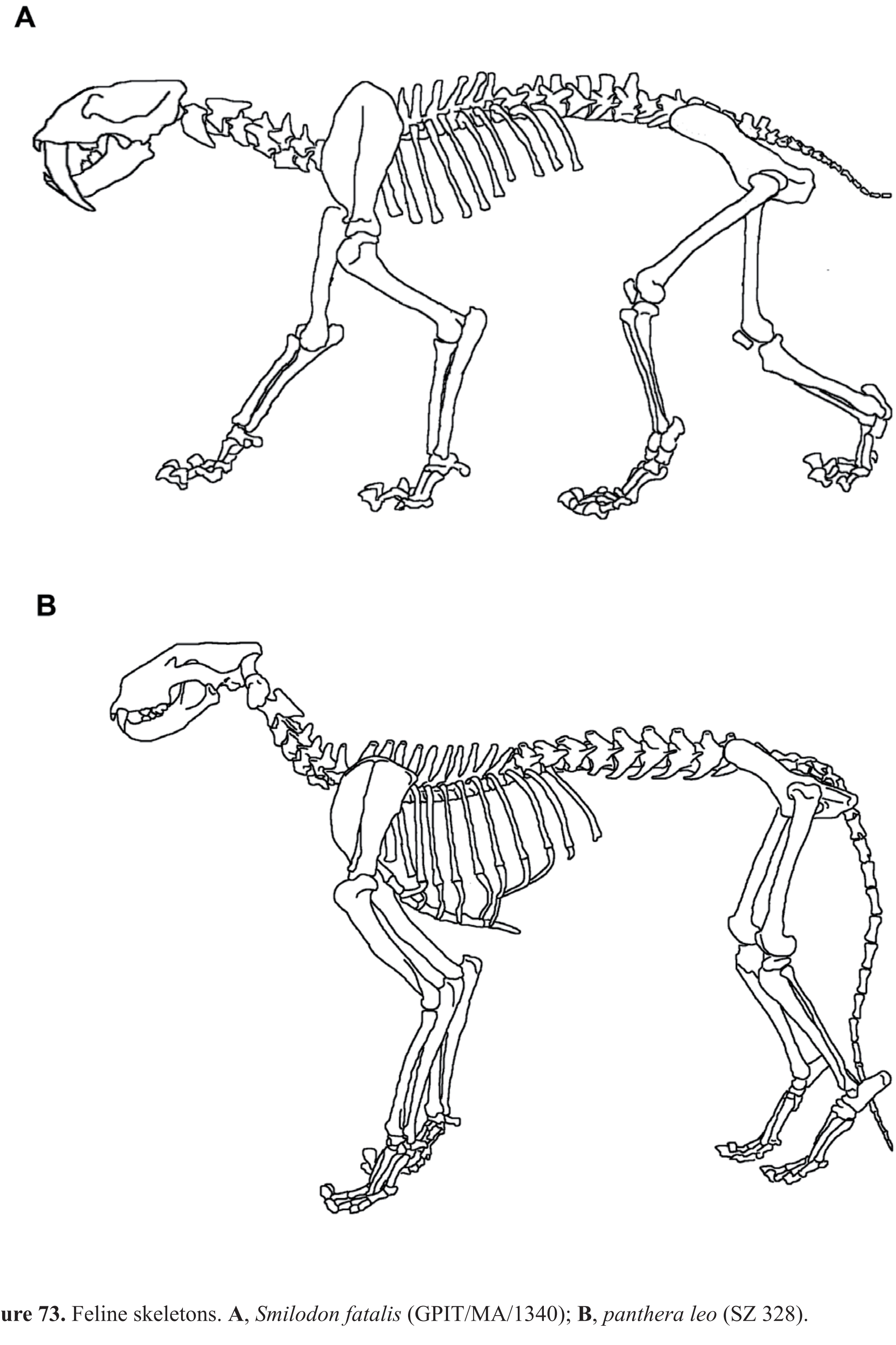


Figure 73. Feline skeletons. **A**, *Smilodon fatalis* (GPIT/MA/1340); **B**, *panthera leo* (SZ 328).

Both humeri are comparable despite their rather different appearance. They are both heavily built and the muscle attachment areas for adductor and abductor muscles are distinctly shaped.

The distal extremities also resemble each other to a high degree. Both are twisted against the proximal extremity, however, in *Sauroctonus* this feature is somewhat stronger than in *Smilodon*. The epicondyles are rather massive, well differentiated and well separated from each other indicating a well developed extensor and flexor musculature of the lower foot. The trochlea is more pronounced in *Smilodon*, which is due to the greater freedom of movement of the ulna and the more prominent olecranon process.

Radius/Ulna. The antero-posteriorly flattened ulna in *Sauroctonus* is a short, stout and straight bone. The proximal extremity is only slightly widened with respect to the distal one. The insertion area for the extensor muscles is more pronounced as is the one for the flexors. An olecranon process is developed which shows a distinct ridge for the triceps muscle. In comparison to this the ulna in therocephalians and cynodonts is longer, more slender and in addition more curved. In therocephalians the olecranon process is absent and the flexor fossa more distinct than the one for the extensors. This can be seen as compensation for the absent olecranon process and the need for the triceps to attach here. Cynodonts have an olecranon process which is, however, not as markedly developed as in gorgonopsians.

The radius in *Sauroctonus* is shorter than the ulna and slightly curved medially. It is more slender and exhibits an oval cross-section. With respect to the narrow diaphysis the distal and proximal extremities are moderately expanded. The radius in cynodonts is rather comparable whereas in therocephalians it has the same length and is approximately the same size as the ulna. Longer distal limb bones in therocephalians would have been able to compensate for a more horizontally placed humerus since the stride length could again be increased in this way. The contrasting shorter distal limb bones in *Sauroctonus* support the theory of a more erect gait in this animal.

In comparison to extant cats, the radius and ulna of *Smilodon* are relatively short. This contrasts to a cursorial specialization since an elongation of the distal limb segments provides a better leverage and thus makes a higher speed possible. A short distal limb on the other hand enables the animal to grasp and hold its prey with more strength. The olecranon process which is more significant than in *Sauroctonus* is, however, not markedly higher than in extant cats. This is somewhat unexpected because one would assume that the sturdy limb bones with their well developed areas for muscle attachment would require an equally strong triceps muscle. This muscle, which inserts at the olecranon process arises from the scapula and humerus and is responsible for any pushing action away from the body.

However, Gonyea (1976a) pointed out that there was a difference in size of the lateral and medial tuberosities on the olecranon process between highly cursorial cats as the cheetah and the pantherine cats. Thus, the lateral tuberosities were larger than the medial ones in the second group (in the cheetah it is just the opposite). This indicated that the lateral head of the triceps was also stronger than the medial slip. Although *Smilodon* has an olecranon process of similar length as the pantherine cats, the lateral tuberosities are somewhat stronger.

The straight radius in *Smilodon* is more massive and the area of muscle attachment is greatly emphasized which is in contrast to extant cats. Schmieder (2000) has shown that *Smilodon* had a greater flexibility in the movements of the elbow than extant cats since its radial notch was situated more laterally and thus the angle of inclination of the olecranon fossa was comparatively high.

Summarised it can be stated that the distal limb bones in both taxa are relatively massive with well developed areas for extensor and flexor musculature. The articulation facet of the ulna in *Smilodon* is, however, much more recessed and concave than in *Sauroctonus* embracing the trochlea of the humerus like a wrench. Furthermore, the contact with the radius is modified in such a way that this bone can rotate to a certain degree within its articulation areas to perform the prone and supine movements. In *Sauroctonus* the articulation areas are only restricted to relatively small spots. Of course the distal articulation with the respective bones of the manus is completely changed since mammals developed a different hinge joint.

3.4.3.3 Vertebrae

Atlas axis complex. *Sauroctonus* displays a typical reptilian or synapsid articulation. The single, kidney-shaped occipital condyle articulates with a concavity on the centrum of the atlas. The latter is composed of an intercentrum and centrum and the neural arches, which are loosely articulated. Anteriorly on the neural arch, the proatlas is attached that also articulates with the occiput presumably near the exoccipitals. Thus, a dorso-ventral flexion of the head is somewhat restricted, however, lateral bending was well possible. The centrum of the atlas is short and higher than long, the neural arch, which articulates dorsally, forms a short and narrow posteroventrally directed transverse process and a postzygapophysis that acts as a splint for the prezygapophysis of the axis.

Smilodon, on the other hand, shows the typically mammalian condition. The intercentrum and neural arches have fused and form a bony ring that embraces the double condyle of the occiput. Extensive dorso-ventral movement is now possible since the proatlas is lost. The transverse process of the atlas has an unusual shape because of its broad wing-like flanges that are directed posteroventrally. Here the strong head turning muscles obliquus capiti cranialis and caudalis attach. This flange is shorter and less laterally and ventrally flaring in extant cats but differs also within the saber tooth forms. Thus, it is more posteriorly directed in *Machairodus* and even more laterally and posteriorly in *Thylacosmilus*. This modification of the atlas wings as well as the ventral extension of the mastoid process is related to the canine shear bite and was developed for rotating the neck rather than stabilizing it during the bite (ANTÓN & GALOBART 1999).

The comparatively massive and large atlas centrum is elongated and displays a slight keel on its ventral surface whereas the dorsal surface is evenly convex.

The axis is formed almost as the other cervicals in both taxa but more so in *Sauroctonus* than in *Smilodon*. In the first taxon, the articulation with the respective parts of the atlas is via the reptilian disc-like joint. The centrum slopes posteroventrally and has a smooth ridge on its ventral face. The transverse process is rather long, blunt and slopes in a ventrolateral direction with its tip somewhat curved dorsally. In comparison the transverse process in therocephalians is very short (KEMP 1986). The prezygapophysis is short and the postzygapophysis oval and almost horizontally oriented. The dorsal spine is fan-like expanded but more in anterior direction and displays a sharp dorsal margin that slopes convexly in an anterior direction.

The atlas-axis articulation in *Smilodon* on the other hand is of course provided by the odontoid process of the axis, which protrudes into the vertebral canal of the atlas. Thus a rotational movement is made possible here. The centrum is still elongated and the ventral face displays a distinct keel for the neck flexor muscle longus colli. The transverse process is long and narrow and points in posteroventral direction. Since articulation with the atlas is sufficiently provided by the odontoid, there is no prezygapophysis developed, the postzygapophysis, however, is round to oval and is oriented at an angle of 45° to the horizontal plane. The neural spine is slightly expanded in anterior direction forming a pointed tip with a sharp keel dorsally. Posteriorly it is more expanded and broadened forming two rounded knob-like processes. In pantherine cats the neural spine is truncated which indicates that the obliquus capitis caudalis was less developed than in *Smilodon*. Ventro-laterally and dorsally to the postzygapophysis a small pointed hyperapophysis is developed.

Cervicals. The remaining cervicals do not differ much from each other in *Sauroctonus*. The centra are as high as long, only the seventh cervical it is slightly shorter. The keel on the ventral face is only weakly pronounced at the third cervical but gets stronger posteriorly and is especially well developed on the seventh cervical. This indicates a strong longus colli and an extensive neck flexion especially in the posterior part of the neck. The posteroventrally directed transverse process is broad, massive and short at the third cervical but gets slightly pointed and longer posteriorly. Up to the fifth the zygapophyses are oval and almost horizontal, at the sixth and seventh they are, however, more steeply oriented. This would also correspond to a good flexion-extension ability of the posterior neck and a more lateral bending action of the anterior part as indicated by the horizontally oriented zygapophyses in this area. At the third cervical the dorsal spine is as blunt and high as the one of the axis but it gets narrower and slightly higher posteriorly. The spines are exclusively dorsally directed, except for the seventh one which points slightly in an anterior direction. In comparison with therocephalians and *Procynosuchus* the spines in *Sauroctonus* are comparatively broader and more sheet-like. This also indicates a stronger attachment area for the neck muscles.

The centra of the cervicals in *Smilodon* are slightly longer than the one of the axis. The keel on the ventral face is weakly developed but rather strong at the seventh cervical. The transverse processes display a rather unique feature since they develop a sheet-like plate, which has a postero-dorsally pointed process. This feature is mostly developed at the fifth cervical. At the seventh the transverse process is still expanded ventrally, but narrower and the lateral tips point almost vertically in dorsal direction. This lateral projection with a more marked upward turn of the tips acts as a greater leverage for muscles that rotate the neck, respectively allows a better movement in all directions (ANTÓN & GALOBART 1999). The zygapophyses are round-oval and are oriented at an angle of 45° to the vertical plane at the third cervical. They get larger posteriorly and the postzygapophyses of the seventh cervical are oriented more vertically. Because of the posteriorly expanded dorsal spine of the axis the one of the third cervical is less developed. The dorsal spines of the following cervicals are triangular if seen in lateral view, more or less pointed and directed dorsally. As in *Sauroctonus*, the dorsal spine of the seventh cervical faces slightly in an anterior direction.

Concerning the neck, both taxa display comparable features. The whole neck is long with well developed attachment areas for muscles that turn or flex and extend the neck. On the other hand, it was sufficiently stabilized during those actions by the intertransversalis musculature and the articulation between the centra. ANTÓN & GALOBART (1999) stated that such a neck would serve the animal well when it sunk its teeth into the flesh of the throat of their prey.

Dorsals. The first dorsal in *Sauroctonus* still has a short centrum which gets, however, longer in the following ones. The ventral keel is less pronounced at the first dorsal, stronger from the second to the fourth, absent in the following four dorsals but broad at least up to the twelfth. The centra of the thirteenth and fourteenth are restored and the remaining centra have a flattened ventral face. The zygapophyses are oval and almost vertical in the first four dorsals, get more elongated and are oriented at a 45° angle in the next seven dorsals, are again more vertical and even slightly longer in the fifteenth to sixteenth dorsal and are finally again shorter and less steep in the last two dorsals. The transverse process extends laterally and posteriorly in the anterior dorsals, gets broader and more horizontally oriented in the middle ones and then again shorter and more posteriorly facing in the last dorsals. The dorsal spine is broken off at the first dorsal but is relatively long and narrow in the second. The fifth is the longest and narrowest. From the tenth dorsal onwards, the spine gets shorter and is more inclined in a posterior direction.

The dorsal centra in *Smilodon* are broad but short in the anterior dorsals. From the third onwards, they are slightly longer than high and from the tenth onwards they are rather large. The ventral keel is well developed at the first two dorsals, rather weak in the next four dorsals and slightly more pronounced again from the sixth to the tenth. At the eleventh dorsal, the ventral keel is markedly broadened but gets again somewhat narrower in the last posterior dorsals. The zygapophyses are large, round-oval and oriented at a 45° angle in the first two dorsals. Further posteriorly they get smaller and more horizontally oriented with a somewhat ‘scaly’ articulation. From the tenth they are round and vertical and from the seventeenth a hyperapophysis is developed. Again only at the first two dorsals the transverse process is directed ventrolaterally with a large articulation facet but gets more horizontally up to the tenth. From the eleventh dorsal onwards, an accessory articulation facet is developed posteriorly, which protrudes into the adjacent centrum and acts almost like a strut. At the first five dorsals, the dorsal spine is long, pointed and vertically oriented, the dorsal extremity however gets more thickened and the spine more inclined posteriorly up to the tenth which again stands vertically. In the tenth and eleventh it is very short but then gets triangular if seen in lateral view. From the fifteenth the dorsal margin is flattened and from the eighteenth it is triangular and pointed again.

The back and especially the lumbar region are shorter in *Smilodon* than in extant cats. The articulation between the vertebrae is relatively strong to provide an adequate stabilization when the animal holds its prey down (TURNER & ANTÓN 1996). Additionally a shorter back would provide a more effective contraction of the latissimus dorsi, which originates from the lumbar fascia and inserts on the medial side of the humerus acting as a forearm flexor (SCHMIEDER 2000). The neural spines of the dorsals eleven to sixteen are straight in *Smilodon* whereas they are pointing more or less anteriorly in extant cats. This indicates less sprinting capability in *Smilodon*.

Sauroctonus has no division in a thoracic and lumbar region as in therocephalians and cynodonts and therefore displays a rather plesiomorphic condition. However, in contrast to therocephalians and some cynodonts the zygapophyses are oriented more steeply in the posterior part of the column. This indicates a good stabilization and can be somewhat compared with the tightly articulated lumbar vertebrae of *Smilodon*.

Sacrals. *Sauroctonus* has three sacral vertebrae. The first sacral has the longest centrum as well as the most massive and expanded sacral ribs, which are fused to the transverse process. The ventral face shows a strong ridge that provides a strong muscle attachment area. The second sacral is considerably smaller. Its rib is reduced, since the first sacral rib already articulates extensively with the ilium. The third sacral again is somewhat larger but the rib is narrow and dorso-ventrally flattened. The zygapophyses are relatively steeply oriented and the neural spine is massive, long and tapers slightly in dorsal direction.

The therocephalian sacrum contains three vertebrae, too. In Regisauridea indet. the difference between the first sacral and the two following is less marked and especially the ribs are more equal in size. The zygapophyses are wide, have a round-oval shape and are relatively horizontally oriented. This suggests, that some degree of lateral movement was well possible in the posterior part of the trunk. The neural spines of the sacrals are long antero-posteriorly but rather short.

Cynodonts mostly have four sacral vertebrae. In general, the first exhibits the largest and laterally most expanded rib. However, the following sacral vertebrae are also extended laterally which provides a firm attachment to the ilium. Furthermore, the zygapophyses are relatively steeply oriented and the dorsal spine is broad but short. The rigid articulation of the sacrals with each other and the pelvis suggest an advantage in stability but the smooth ventral face of the centrum and the short dorsal spines indicate a comparatively weak muscle force.

Smilodon fatalis again has three sacral vertebrae, which are however completely fused with one another. The first two have expanded ribs that attach firmly and extensively to the sacrum. The second sacral rib is reduced and only a dorso-ventrally flattened sheet-like transverse process is formed. The oval zygapophyses are placed extremely far apart and are oriented relatively steeply. The dorsal spine is massive and broad, the spine of the first sacral tapers somewhat dorsally but the dorsal margin of all three sacrals is considerably thickened.

Together with the short back and rigid lumbar region the sacral region in *Smilodon* also contributes to the stabilization of the posterior part of the body. This would be particularly needed if the animal had to struggle with large prey respectively stood on its hindlimbs when seizing its victim with the forepaws. It can not be stated if *Sauroctonus* did catch its prey with the forelimbs as cats do, but the shape of the sacrals with the muscle attachment areas and the steeply oriented zygapophyses indicates a firmly stabilized posterior part of the back, too.

Caudals. The caudal vertebrae are rather incomparable, since the tail is markedly different in both taxa. *Sauroctonus parringtoni* displays a rather long tail, which is in contrast to most therocephalians and cynodonts. In synapsids the transverse processes of the caudal vertebrae serve as attachment area for the m. caudo-femoralis which draws the femur backwards. Since this movement generates propulsion in the step cycle, the tail is supposed to be comparatively long in animals with a presumed sprawling gate. *Sauroctonus* however was capable to move with a semi erect stance, respectively was able to perform a variety of movements of the femur as mentioned above. Thus, the long tail must have had certain other advantages. It is well reasonable to assume that the strong caudo-femoralis supported the femur when the animal was wrestling with prey and additionally stabilized the posterior part of the body.

Smilodon, on the other hand, has a greatly reduced tail with presumably no advantageous functions. In mammals, the tail musculature is reduced anyhow because the gluteus muscles have taken over the retracting function of the femur. Most living cats have comparatively long tails, which serve them however, for climbing in trees or as a counterbalance when running like it is seen in the Cheetah. The short tail in *Smilodon* indicates that the animal was no frequent tree climber or chasing runner.

3.4.3.4 Pelvic girdle

The pelvis in *Sauroctonus* is still reptile-like with a separated ilium, ischium and pubis. The ilium is expanded slightly more in posterior than in anterior direction forming a sheet-like iliac plate. There is a medium sized supraacetabular crest developed and the articulation surface of the acetabulum is mostly formed by the ilium. A somewhat concave area on the antero-ventral corner, which is separated from the rest of the iliac blade, indicates the dorsal migration of the pubo-ischio-femoralis internus. The ischium forms a thin plate, which is only slightly thickened anteriorly at the acetabulum. On its ventral half, it provides the attachment area for the posterior part of the m. pubo-ischio-femoralis externus. The pubis is, as far as it is preserved, short and stout. On its dorsal part the ventral portion of the pubo-ischio-femoralis internus inserts and ventrally the anterior part of the pubo-ischio-femoralis externus is attached. Medially on the ilium, the articulation area for the sacral ribs is well developed and shows that the articulation with the sacrals was mostly established by the first sacral rib as mentioned above. The acetabulum faces almost exclusively laterally and not ventrally but it allows a variety of movements of the femoral head. The pelvic girdle was not much different in therocephalians and early cynodonts as they were all capable of the so called dual gate (Blob 2002, Kemp 2005)

Smilodon has a modified mammalian pelvic girdle with an anteriorly expanded ilium, a shortened pubis and ischium and a large obturator foramen. However, the iliac blade is somewhat broader and especially the posterior margin of the ischium is more expanded than in extant cats. Here the m. obturator internus inserts as well as the adductor musculature of the femur. This feature might also indicate a better stabilization of the hindlimb when *Smilodon* leaves the ground with its forelimbs to catch prey.

3.4.3.5 Hindlimb

Femur. The femur in *Sauroctonus* is slightly flattened dorsoventrally and somewhat s-shaped. The femoral head is even more flattened dorsoventrally and slightly turned in medially. On the posterior margin, and rather ventrally situated to the femoral head, a trochanter major is developed. It forms a rugose thickening followed by a depression in anterior direction. This concave area also separates the trochanter major from the rather weakly developed trochanter minor on the anterior margin. On the ventral surface, a rather long internal trochanter is developed for attachment of the pubo-ischio-femoralis externus and caudofemoralis. The distal articulation condyles face either more ventrally or more posteriorly depending on the position of the femoral head in the acetabulum. Both condyles are nearly equal in size. Between the epicondyles a medium sized interpopliteal fossa is developed.

The therocephalian femur is more slender, longer and less sigmoid, the epicondyles are only slightly expanded and the flexor fossa is little developed. The femur in early cynodonts is as massive as in gorgonopsians, but the femoral head is more rounded and the trochanter major situated more dorsally. The epicondyles are expanded in different stages according to the genus but the flexor fossa is well developed. In summary it can be said that gorgonopsians have a comparatively short femur with a distinctly developed trochanter major and internus. This indicates a strong adductor and abductor musculature but also provided a good stabilisation of the leg when possibly wrestling with prey.

In the same way as the humerus, the femur of *Smilodon* is completely different, because of the mammalian gait. The bone is straight and proximally the femoral head is distinctly set off from the shaft and strongly turned in medially where it fits into the acetabulum in a ball-and-socket articulation. The trochanter major is distinctly developed and slightly exceeds the dorsal height of the femoral head. In extant cats, the trochanter major reaches only the same height as the femoral head at best. The trochanter minor in *Smilodon* is situated relatively ventral on the medio-posterior face of the femur. The posterior face of the diaphysis is flattened and widens distally to form the articulation condyles with the lower leg. They are separated from each other by a deep intercondylar fossa. The medial epicondyle is somewhat larger than the lateral one, which indicates a strong adductor magnus muscle that moves the limb inward and backward (Schmieder 2000). Anteriorly a concave and smooth area for the patella is developed which is comparatively broad but less high than in extant cats.

The femur in both taxa shows little differences with the respective relatives and thus provides scarce evidences for a sound comparison. However, it is rather short and equipped with well developed muscle attachment areas both in *Sauroctonus* and in *Smilodon*.

Tibia/fibula. The tibia in *Sauroctonus* is somewhat flattened antero-posteriorly and measures approximately three fourths of the length of the femur. It is a stout bone that is somewhat bow-shaped towards the fibula. The articulation facet with the femur is expanded lateromedially. Thus the articulation covers almost both condyles of the femur, however the joint between the femur and the shank must have been widely filled with cartilage since the articulation does not fit well together. The anterior face is somewhat concave dorsally whereas the posterior face has developed an attachment area for the m. cnemius dorsally. The distal articulation with the astragalus is oval in shape and only very slightly concave.

The fibula in *Sauroctonus* is incompletely preserved and thus rather indistinctive. It is slightly longer than the tibia, less curved and shows a lateromedially expanded proximal extremity. The diaphysis has a round diameter.

The tibia in Regisauridae indet is comparatively less flattened and longer with respect to the femur. Consequently, the fibula is also longer with respect to the femur, however shorter than the tibia. Both bones are less concave towards each other than in gorgonopsians. The cynodont tibia and fibula vary considerably according to the genus (Jenkins 1971) but are usually again shorter with respect to the femur.

The tibia in *Smilodon* is extremely shortened relative to the femur (Schmieder 2000). Furthermore, it is an exceptionally robust bone with a markedly expanded and massive dorsal extremity that receives all the weight of the upper leg. The fibula is rather slender compared to the tibia, shorter and serves mostly for muscle attachment and as articulation with the calcaneus in the ankle joint.

Summarised both lower leg bones in *Sauroctonus* and *Smilodon* are shortened in relation to the femur, the tibia is very robust whereas the fibula is rather slender. Thus, the hindlimb displays bones that are robust with well developed areas for muscle attachments. The shank is comparatively short with respect to the femur and this indicates that the animals were less adapted for a cursorial lifestyle but rather performed powerful movements.

3.4.4 Conclusions

Concerning the skull, most similarities between *Sauroctonus* and *Smilodon* occur because of the enlarged canines. In general, such a feature is inevitably involved with a rearrangement of certain bones. In the present case there are mainly three adaptations that result from the altered caninus. First the elongated root of the caninus had to be accommodated and therefore the snout became higher. Additionally the caninus needed protection against breakage during a bite and this was achieved by the parabolic arch of the incisor row. Finally to ensure that the mouth could be opened wide enough at all to get prey between the teeth, the jaw mechanism must have been modified in a certain way. This gape problem involved some further changes for the respective taxa.

Both animals however had to follow different constructional pathways since the jaw bauplan has changed from the therapsid to the mammalian condition. Thus, the musculature in *Sauroctonus* is still reptile-like and the temporalis was not yet differentiated into a masseter and temporalis muscle. The high coronoid process was a useful achievement for gorgonopsians to increase the attachment area for the temporalis muscle. Whereas the lateral portion of the temporalis, which inserted on the coronoid process but originated from the posterior part of the braincase, mainly pulled the lower jaw upwards, the medial slip, from the underside on the temporal fenestra to the internal face of the lower jaw, only had a dorsal-wards component. With this arrangement the mouth could be opened widely and be shut acceleratory. Other related features as the medial shifting of the quadrate and the bow-shaped and anteriorly facing articular process also helped to increase the gape.

Saber-toothed cats, and especially *Smilodon* with its extremely enlarged canines, had to overcome even more problems to ensure a wide enough gape. By reducing the height of the coronoid process and the lowering of the glenoid fossa, the potential for longer temporalis fibres was given, which in turns provides much greater amount of stretch of this muscle. In the same way as *Sauroctonus* the saber-toothed cat modified the lower jaw by shifting the angular process laterally and by reducing the postglenoid process. A new invention was the facial inclination on the braincase which does not occur in gorgonopsians.

Similarities between both taxa in the postcranial skeleton are not as easy discernable. *Smilodon*, as all other cats, immobilized prey with its claws and then conducted a lethal bite. In contrast to extant cats, the neck was longer with stronger head depressing as well as head turning muscles. This guaranteed a good stabilisation of the posterior neck during the accomplishment of a powerful throat bite whilst the victim was secured to the ground with the claws. The back in *Smilodon* is shorter and more adapted to stabilise the body than to flex and extend during a chase. In this connection and in the context of a less cursorial lifestyle also belong the more robust upper leg bones and the shortened lower limbs as well as the larger pelvis. *Sauroctonus* on the other hand is considered less cursorial in any case since it is supposed to move in the typical reptilian sprawling gate. However, as shown in the previous chapter the animal was additionally able to move in a somewhat semi-erect gait not only with the hindlimbs as pointed out by KEMP (1982, 2005) but also with the forelimbs. The neck musculature is well developed and the back somewhat shortened with respect to certain therocephalians and early cynodonts. The girdles are not much different but the limb bones are without exception more massive and additionally the lower limbs are shorter. The limb musculature with strong adductor muscles on the one hand was needed for sprawling locomotion but furthermore stabilised the animal when capturing prey and wrestling with it. The gorgonopsian claw is well developed and curved with a sharp and pointed tip. Therefore, it is plausible that those animals could hold and bring down their victims to conduct a precise throat bite as it is proposed for saber-toothed cats. However, with the probably rather sluggish and slow dicynodonts in mind, which are the presumed diet, a predator probably did not need all too much grasping force. On the other hand, if prey also covered more agile animals such as other gorgonopsians or therocephalians, it is well conceivable that the claws additionally were used to seize the victim.

From the facts listed above it can be well imagined that *Sauroctonus* in all probability occupied the same ecological niche than its mammalian relative 230 million years later.

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ABBREVIATIONS USED IN FIGURES

add ll	adductor muscles of lower leg
ang	angular
an (lr)	lamina reflecta of angular
ant.f	anterior facet of humeral head
a.pt.m. 1	m. pterygoideus anterior 1
a.pt.m. 2	m. pterygoideus anterior 2
ar	articular
BcA	basicranial axis
bic	m. biceps
bo	basioccipital
bo.c	basioccipital condyle
brach	m. brachialis
btub	basisphenoidal tubera
c.f	m. caudo-femoralis
cor	coracoid
cor.br	m. coracobrachialis
cost.cor	m. costocoracoideus
d	dentary
d.c	deltopectoral crista
delt	m. deltoideus
depr mand	m. depressor mandibulae
dors.comp	dorsal component of glenoid
eo	exoccipital
ep	ectopterygoid
ext ll	extensor muscles of lower leg
f	frontal
fm	foramen magnum
fp	foramen parietale
fpt	fenestra posttemporalis
il.fem	m. ilio-femoralis
il.fib	m. ilio-fibularis
il.tib	m. ilio-tibialis
ip	interparietal
isc.tr	m. ischio-trochantericus

ivac	interpterygoid vacuity
j	jugal
l	lacrimal
lat.dors	m. latissimus dorsi
l.e.add	m. adductor mandibulae externus lateralis
m.e.add 1	m. adductor mandibulae externus medialis 1
m.e.add 2	m. adductor mandibulae externus medialis 2
mr	maxillary ridge
mx	maxilla
n	nasal
os occ	os occipitalis
p	parietal
PA	palatal axis
pal	palatine
par	paroccipital process
pbfos	parabasisphenoid fossa
pect	m. pectoralis
pfos	palatal fossa
p.i.f.e.	m. pubo-ischio-femoralis-externus
p.i.f.i.	m. pubo-ischio-femoralis-internus
pmx	premaxilla
po	postorbital
pof	postfrontal
post.f	posterior facet of humeral head
pp	preparietal
p.pt.m	m. pterygoideus posterior
pra	prearticular
prf	prefrontal
proc ang	processus angularis
proc cor	processus coracoideus
pt	pterygoid
ptub	palatal tuberosities
q	quadrate
qj	quadratojugal
rlr	ridge on lamina reflecta
rq	ramus quadratus pterygoidei
s	stapes

sa	surangular
sca.hum	m. scapulo-humeralis
s.cor	m. supra-coracoideus
smx	septomaxilla
soc	supraoccipital
sp	splenial
sq	squamosal
squ rec	squamosal recess
sub.sc.	m. subscapularis
tab	tabular
tric.	m. triceps
v	vomer
ven.comp	ventral component of humeral head
zyg	zygomatic arch

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