

1 INTRODUCTION

This project contributes to a larger project of the Evolutionary Studies Institute at the University of the Witwatersrand to understand and document biodiversity change during the middle Permian leading to the end Guadalupian extinction event (Boonstra, 1971; Pearson et al., 2013; Day et al., 2015). Inferences relative to this extinction are dependant on reliable taxonomic assessment of coeval tetrapods. These included a range of temnospondyl amphibians, parareptiles, basal synapsids (“pelycosaurs”), and especially a wide diversity of therapsids. The latter included dinocephalians, anomodonts, biarmosuchians, gorgonopsians and therocephalians (Boonstra, 1969; Smith et al., 2012; Day, 2013) of which the most abundant in terms of numbers of individuals and taxonomic diversity were the herbivorous anomodonts and dinocephalians. In particular the tapinocephalid dinocephalians, because of their large size, formed an important component of terrestrial tetrapod biomass during the middle Permian. Dinocephalians are most abundantly known from South Africa (Boonstra, 1969; Kitching, 1977), the former USSR (Tchudinov, 1983) and more recently from Brazil (Langer, 2000; Cisneros, 2012), China (Cheng and Ji, 1997; Liu, 2013), Zimbabwe (Lepper et al., 2000), Zambia and Tanzania (Sidor et al. 2014; Simon et al. 2010) (Figure 1.1). Apart from those from South Africa and Russia, most dinocephalian occurrences are known from relatively incomplete skeletal or cranial remains.

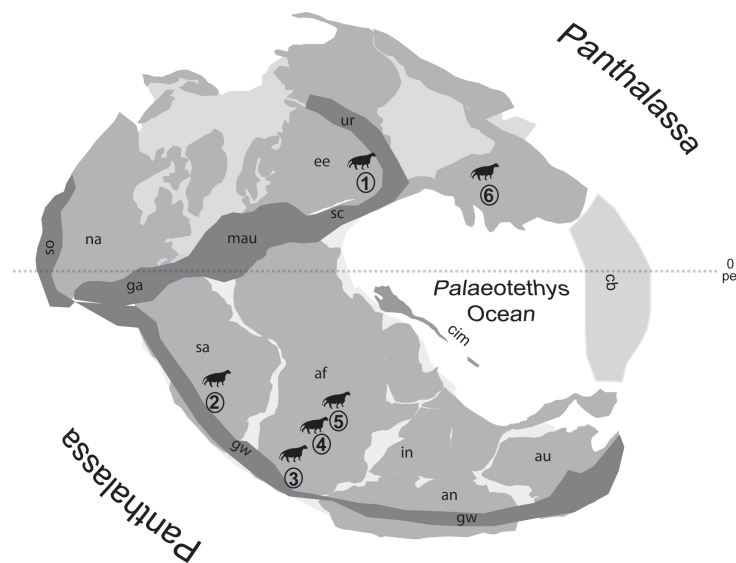


Figure 1.1. Geographic distribution of Dinocephalia during the middle Permian. Localities indicated with numbers: 1, Russian platform, 2, Paraná Basin, Brazil, 3, Karoo Basin, South Africa, 4, Karoo Basin, Zimbabwe, 5, Karoo Basin, Zambia and Tanzania, 6. Ordos Basin, China. The base map is modified from the proposed Late Permian palaeogeographic configuration developed by Şengör & Atayman (2009, fig.15) which was modified for the middle Permian with partial contact between the Palaeo-Tethys and Panthalassian ocean in Cisneros et al. (2012, fig. 3). Key to lettering: af, Africa; an, Antarctica; au, Australia; cb, Cathaysian Bridge (*incl.* north China, Korea, south China, and Indochina); cim, Cimmerides; ee, Eastern Europe; ga, Great Appalachides; gw, Gondwanides; in, India; mau, Mauritenides; na, North America; pe, palaeoequator; sc, Scythides; sa, South America; so, Sonoma; ur, Uralides.

Dinocephalians were traditionally divided into two subclades mainly according to their diet: the herbivorous Tapinocephalia or Tapinocephalidae and carnivorous Titanosuchia or Titanosuchidae (Haughton, 1919; Broom 1923ab; Haughton 1924; Boonstra, 1936ab, Boonstra 1953; Haughton and Brink 1954). After the exclusion of the true carnivorous forms from the latter, the following taxonomic revision by Boonstra (1969) for the South African dinocephalians was proposed: the herbivorous Tapinocephalidae, Titanosuchidae and Styracocephalidae; and the carnivorous Anteosauridae. King (1988) considered Dinocephalia in two

superfamilies: Estemmenosuchoidea and Anteosauridea. The Anteosauroidea which included the families Brithopidae and Titanosuchidae. While the former included the carnivorous forms in the subfamilies Brithopodinae and Anteosaurinae; the latter included the herbivorous forms in the subfamilies Titanosuchinae and Tapinocephalinae. Currently the Dinocephalia are considered in two monophyletic groups, viz the carnivorous Anteosauria and herbivorous Tapinocephalia which comprise respectively Anteosauridae, and the tapinocephalians Estemmenosuchidae, Styracocephalidae, Titanosuchidae and Tapinocephalidae (Hopson and Barghusen, 1986; Rubidge and van den Heever, 1997; Sidor, 2000; Kammerer, 2009, 2011). Kemp (2005) however excluded Estemmenosuchidae from Dinocephalia, and considered Anteosauria within the Brithopia.

Until recently the Dinocephalia received relatively little research attention, but an upsurge in interest in middle Permian biodiversity has resulted in proliferation of research on this important therapsid taxon. Kammerer (2011) in his revision of Anteosauria divided the group in two monophyletic subfamilies, Syodontinae and Anteosaurinae, and reduced the number of valid species from 21 to nine (six from Russia, two from South Africa and one from China). Cisneros et al. (2012) increased the number to ten with the description of a new species, *Pampaphoneus biccai*, from Brazil.

The Tapinocephalia, which are most abundantly known from the Lower Beaufort Group of South Africa, have received little attention, largely because of the poor

and fragmentary state of preservation of specimens, coupled with their large size which makes preparation challenging. Hopson and Barghusen (1986) regarded the presence of the transverse flanges of the pterygoid with a posterior shelf in the tapinocephalians to be the main differentiating character from the anteosaurians. *Estemmenosuchus* and *Styracocephalus* have in the past been considered the most basal tapinocephalians. (Rubidge and van den Heever 1997; Sidor 2000; Rubidge and Sidor 2001).

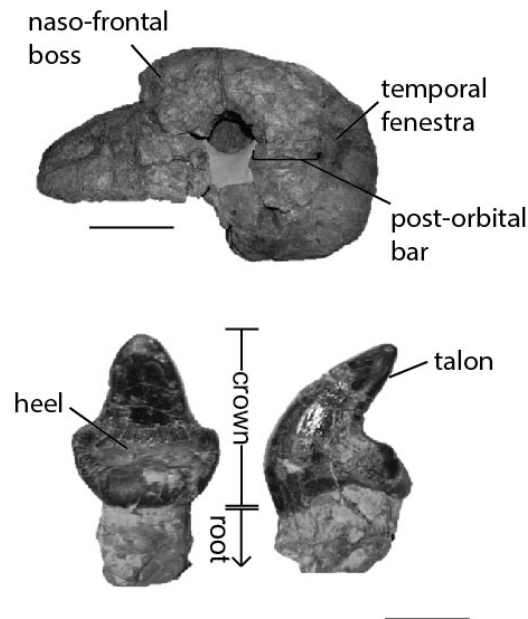


Figure 1.2. Photograph showing the general cranial outline of an adult short-snouted tapinocephalid (top) and the lingual (bottom left) and mesial (bottom right) views of a large tapinocephalid incisor showing the characteristic talon and heel morphology. Scale bar for top figure is 10 cm and for the incisor is 1 cm.

The other group of tapinocephalians, the titanosuchids are known only from South Africa. Boonstra (1963a, 1969, King, 1988) considered that titanosuchids differ

from anteosaurians because of their greatly enlarged incisors, large canines, and the postcanines are leaf shaped with serrated crown (Boonstra, 1936a, 1969; King, 1988). Leaf shaped postcanines also occur in Estemmenosuchids and Tapinocephalids. In tapinocephalids leaf-shaped teeth are present posteriorly in the jaws of short snouted forms, and in the long snouted forms they appear to occur more anteriorly. Boonstra (1969), recognised two titanosuchid genera: '*Jonkeria* (comprising eight species) and *Titanosuchus* (comprises one species) which are distinguished on the basis of limb length. Kammerer (2009) considered *Jonkeria truculenta* and *Titanosuchus ferox* to be the only valid species.

The most abundantly represented tapinocephalian family in terms of numbers of specimens is the Tapinocephalidae, which is also the most derived dinocephalian clade (Boonstra, 1969; King, 1988; Kemp, 2005). Synapomorphies defining the family include pronounced incisor heels (Fig. 1.2), intermeshing jaw batteries (excluding the posteriormost postcanines), canine no higher than incisors (except in the basalmost members) (Boonstra, 1936b; 1963a; 1969; 1972; Kemp, 1982; Rubidge, 1991; Ivakhnenko, 2003). Increased cranial pachyostosis in some tapinocephalid genera results in reduction of the temporal opening into a small and narrow slit-like opening, a unique feature for the family (Fig. 1.2; Boonstra, 1963a,b; Boonstra 1969; King, 1988; Hopson and Barghusen 1986).

A total of 31 tapinocephalid species have been described from three countries, Russia, South Africa and Zimbabwe (Boonstra, 1969; Riabinin, 1938; Efremov, 1954; Boonstra, 1968; Tchudinov, 1983; Ivakhnenko, 1997). This excludes the

Chinese tapinocephalid species *Taihangshania imperfecta* which was latter considered to be a pareiasaur (Liu et al., 2014). The last critical revision of the group was undertaken by Boonstra (1969) who recognized 17 South African species in 13 genera. This number was increased to 18 species and 14 genera with the description of *Tapinocaninus pamela* by Rubidge (1991). Recently, Kammerer (2009) recognized the tapinocephalid representation in the *Tapinocephalus* Assemblage Zone with six species. With the exception of the two Russian species (Riabini, 1938; Efremov, 1954), one Zimbabwean species (Boonstra, 1946, 1968), and fragments from Tanzania (Simon et al., 2010), Zambia (Sidor et al., 2014), and Brazil (Booss et al., 2015), all tapinocephalids are known from the *Eodicynodon* (Rubidge 1991, 1995) and *Tapinocephalus* (Smith and Keyser, 1995) assemblage zones of the lower Beaufort Group of South Africa. These South African biozones have been correlated with the Russian Zone I (Ocher) and Zone II (Ishevo) deposits (Ivakhnenko, 1997, 2008; Rubidge, 2005).

2 HISTORICAL REVIEW OF TAPINOCEPHALIDAE

2.1 Introduction

This section presents the first detailed review of the description and recognition of the Tapinocephalid Dinocephalia. The taxonomy of these animals developed in three stages: The first was the recognition of Dinocephalia parallel to the recognition of “reptiles” with mammalian affinities (aka mammal-like reptiles) and naming the orders Synapsida and Therapsida, which includes the Dinocephalia (Kutorga, 1838; Owen, 1876; Osborn, 1903; Broom, 1905a). The second episode included the description of a large number of dinocephalian species and the recognition of subgroups (*e.g.* Broom, 1911, 1915; Haughton, 1915ab; Watson, 1914). The third phase, which continues to the present, includes synonymy of taxa, taxonomic refinement and understanding the phylogenetic relationships of the different species (*e.g.* Gregory, 1926; Boonstra 1936ab, 1969).

2.2 Recognition of Dinocephalia as mammal-like reptiles

The first tapinocephalid species to be described, *Tapinocephalus atherstonei* (Owen, 1876) is also the first described dinocephalian from South Africa (Fig. 2.1). Thirty eight years earlier *Brithopus*, *Orthopus*, and *Syodon* were described from Russia (Kutorga, 1838) but were considered Carboniferous mammals at that stage. *Tapinocephalus atherstonei* itself has had a complex taxonomic history and was first considered under Dinosauria, one of the three orders of the extinct Reptilia of Owen (1841). The original fossil of this species was part of a

consignment of fossil material from the Beaufort Group of South Africa which was sent to the British Museum by Dr. W.G. Atherstone and Mr. A.G. Bain who were early pioneers of South African geology.

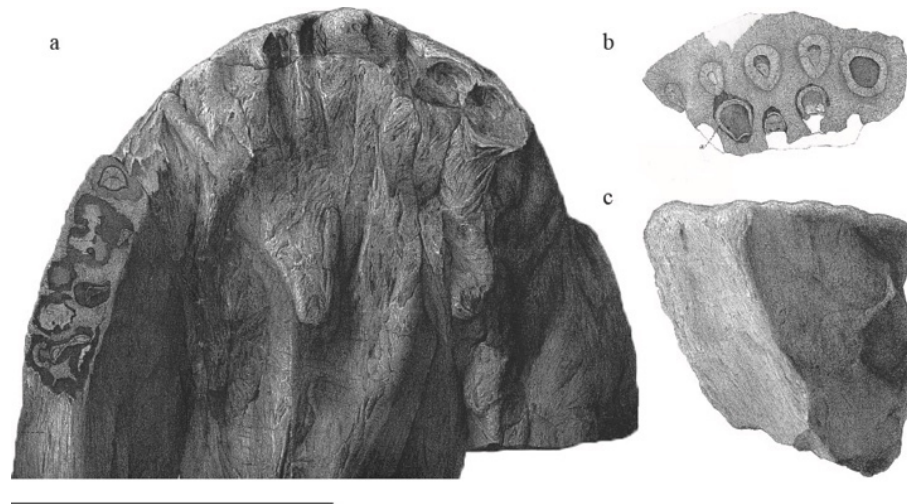


Figure 2. 1. The cranial fragments of the holotype of *Tapinocephalus atherstonei* (NHMUK PV R1707), the genotype of the Family Tapinocephalidae, as illustrated in Owen (1876, fig. 1-3): showing the ventral surface of the snout portion (a), the dorsal (b) and lateral (c) surfaces of the lower jaw fragment. Scale bar: 10 cm.

Owen (1876, pl.22, figs. 1-3) described *Tapinocephalus atherstonei* (originally spelled as *atherstoneii*) on the basis of the anterior portion of a large snout, a lower jaw fragment and various vertebral fragments. He described it as a reptile with a “great flat head” and “a low, broad and obtuse snout” (Owen 1876, p.1). The type locality of the species was recorded as being close to the farm Abrahamskraal in the Prince Albert district and it was considered Triassic in age (Owen, 1876). Owen’s placement of *Tapinocephalus* in the Dinosauria was based

on his observations on a rib fragment. By 1859, Owen considered Reptilia as comprising 13 orders including Dinosauria and Anomodontia. Anomodontia included the extinct reptiles from the Triassic and was characterized by dental features including “tusk-shaped premaxillaries” of the family “Dicynodontia” (Owen, 1859, p. 161).

Cope (1878, 1880) recognized the correlation between the South African, Russian and North American Palaeozoic-Triassic reptile faunas and coined the term Theromorpha to include Pelycosauria and Anomodontia.

Seeley (1888b, pl. 21, figs. 1-3) described *Phocosaurus megischion* from a pelvic bone (BMNH PV OR 43525) as an Anomodont which had been previously referred to *Pareiasaurus* by Owen (1876b, pl. 17, fig. 8.). Seeley (1889) classified the fossil Reptilia under Anomodontia which comprised eight subgroups (including Pelycosauria) and every subgroup he designed to represent an organizational level based on their affinities to mammals (Seeley, 1889, p. 292-293).

Following Cope’s (1880) proposal of Theromorpha, Lydekker (1889, p.1051, 1053) used the term “Theromorous Branch” to include only the order Anomodontia (as an equivalent to Cope’s Theromorpha). He established the family Tapinocephalidae under Anomodontia for *Tapinocephalus* and *Titanosuchus* (Lydekker, 1889). He considered *Phocosaurus nomen nudum* and referred the specimen described by Seeley (1888b) to *Tapinocephalus*. Lydekker

(1890) discarded the lower jaw fragment presented as part of the holotype of *Tapinocephalus atherstonei* by Owen (1876) as it was delivered to the Natural History Museum before the consignment from Dr. G. Atherstone and was therefore not part of the same specimen. Lydekker (1890 p.82) also enhanced the diagnosis of the type genus *Tapinocephalus*, mentioning that judging from the depressed anterior portion of the snout the frontal region of the skull probably rose abruptly above the facial part of the skull.

Seeley (1888a, p. 135) noted the morphological similarity between the morphology of a loose tooth found in the South African Karoo and a tooth that Twelvetrees (1882, fig.2) figured as *Deuterosaurus* incisor: in both specimens the crown had a lingually enlarged extension that he described as ‘cusp’ with elevated lateral borders. Lydekker (1889, 1890, p. 95) considered *Deuterosaurus* and *Rhopalodon* within a separate family that he referred as “Family Uncertain” noting the resemblance of the humerus of *Deuterosaurus* to that of *Tapinocephalus*. Both subfamilies were placed under the suborder Theriodontia.

Seeley (1892a) suggested that the Karoo rocks of South Africa to be divided into five zones of which the second zone (*Pareiasaurus* Zone) hosted and included *Pareiasaurus* and *Tapinocephalus*. He stated that the fossils found in the Permian rocks of Russia are similar to the Theriodonts of the *Pareiasaurus* beds. Seeley (1892a), in his revision of the Anomodontia, recognized four suborders, Gennetotheria, Cotylosauria, Theriodontia (including Pelycosauria) and Procolophonina (including Pareiasauria). He described *Delphinognathus*

conocephalus from Beaufort West, South Africa on the basis of a small and distorted skull and placed it in the suborder Gennetotheria (Seeley, 1892b, figs. 1-2). Seeley (1892b) considered *Delphinognathus* to be phylogenetically between Theriodontia and Dicynodontia.

Seeley (1894a), after the analysis of the skeleton of the animals with Theriodont type teeth, compared the Russian *Deuterosaurus* and *Rhopalodon* to the South African theriodonts. Although they demonstrated similarities in certain postcranial elements to theriodonts like *Dicynodon*, *Pareiasaurus* and *Phocosaurus*, he concluded that these Russian forms belonged to a distinct group that he named Deuterosauria. Soon afterwards Seeley (1894b) coined the term Dinocephalia for *Delphinognathus conocephalus* and *Tapinocephalus atherstonei*. This taxon corresponded to the term Tapinocephalidae of Lydekker (1889) but did not include *Titanosuchus ferox*. Seeley (1894b) revised the classification of the Permo-Triassic Reptilia, the Theriodontia. The Theriodontia (including Lycosauria, Cynodontia and Gomphodontia) became a suborder under Therosuchia together with Dinocephalia, Deuterosauria, Gorgonopsia and others. He characterized Dinocephalia by the presence of thickened cranial bones, small temporal fenestra, broad cerebral region between the temporal fenestrae (*i.e.* broad intertemporal region), narial openings far anteriorly placed, single and convex occipital condyle. Dentition included the presence or absence of a canine, pointed and serrated postcanines which were labially convex and lingually concave with a transverse inwardly developed ledge (Seeley, 1894b, p. 1014). In the same paper, Seeley (1894b) reduced the orders of Anomodontia to only

Therosuchia and Therochelonina. Therosuchia was similar to the usage of Lydekker (1890) but excluded dicynodonts and comprised Pareiasauria, Gorgonopsia, Theriodontia (including Cynodontia), Theromora (including Pelycosauria), Deuterosauria (including *Rhopalodon* and *Deuterosaurus*) and Dinocephalia.

Osborn (1903) used the terms Diapsida and Synapsida, based on the number of temporal openings, as the two main phyla of Reptilia. He considered Pelycosauria as primitive diapsids and Anomodontia as synapsids. The latter group included all extinct reptiles with mammal affinities but excluded dinocephalians. Broom (1905a) was the first to use the term Therapsida to include Dinocephalia, Therocephalia, Anomodontia (for *Dicynodon* and its allies), and Cynodontia (=Theriodontia). Broom (1905) considered Dinocephalia at that stage to be represented by the holotypes of *Delphinognathus* and *Titanosuchus* and but not *Tapinocephalus*. Broom (1910) considered the dinocephalians to be primitive therapsids and argued that the South African and North American Permian faunas had a common ancestor which most probably inhabited the northern part of South America (Broom 1910, p. 233).

2.3. Description of dinocephalian taxa and recognition of subgroups

Over a relatively short period Broom described several new dinocephalian forms from the Permian of South Africa: *Scapanodon duplessisi* (1904), *Archaeosuchus cairncrossi* (1905b), *Pelosuchus priscus* (1905b) and *Eccasaurus priscus* (1909a). He considered *Scapanodon* as an ally to *Titanosuchus*; *Archaeosuchus* as a

therocephalian with noted similarities to *Titanosuchus*; *Pelosuchus* and *Eccasaurus* as diapsids. He (Broom, 1909b) referred the posterior two thirds of a cranium and a second slightly distorted cranium to *Tapinocephalus*. These were specimens which had been collected in the Beaufort Group by Seeley. Broom did not provide any characters for his identifications but remarked that the latter specimen had a shallow and short snout as in *Tapinocephalus*. Broom (1911) reported finding of several dinocephalian skulls with postcranial remains from a single site. As the skulls differ from each other only in size and cranial thickening he considered them to be individuals of a single species. He described and figured one of these skulls as the holotype of *Moschops capensis*. This skull was previously included by Broom (1910a, fig.4) in the revised description of *Delphinognathus*. Broom (1912, pl. xc, fig. 1) described *Taurops macrodon* which he considered *Tapinocephalus*-like but with a narrower and deeper snout. Broom (1913) placed *Scapanodon*, *Archaeosuchus* and *Titanosuchus* in the Therocephalia; while the rest of the taxa comprised Dinocephalia, *i.e.* *Tapinocephalus*, *Delphinognathus*, *Pelosuchus*, *Eccasaurus*, *Moschops*, *Taurops* and *Tamboeria* in Dinocephalia. *Tamboeria* was described by Seeley (1904) on the basis of weathered vertebral fragments which and the taxon was later considered *nomen dubium* by van den Heever (1987).

Haughton (1913, figs. 4-5) described a large, well-preserved cranium from Uitkyk, Beaufort West, and referred it to *Tapinocephalus atherstonei*. Although he did not provide a diagnosis in his description he mentioned the abrupt

transition from the facial to the cranial surface which Lydekker (1890) had mentioned for the holotype of *Tapinocephalus atherstonei*.

Broom (1914a, fig.2) described *Moschognathus whaitsi* on the basis of a well-preserved lower jaw from Beaufort West, which he allied to *Moschops*. In his comparison of North American and South African Permian synapsid faunas, Broom concluded that dinocephalians were more closely related to the North American Pelycosauria than they are to any other synapsid group (Broom, 1914a). He paid particular attention to the resemblance between dinocephalian and pelycosaurian lower jaws on the basis of *Dimetrodon*, *Moschops* and *Moschognathus whaitsi*.

Watson (1914, pl.iv, figs. 1-9, 16a) described *Mormosaurus seeleyi*, *Pnigalion oweni* and *Lamiasaurus newtoni* from respectively: a distorted but fairly complete cranium; the posterior two-thirds of a cranium with associated lower jaw and postcranial elements; and cranial fragments including a weathered posterior skull roof, partial occiput, posterior portion of the zygoma and anterior portion of the palate. The first two skulls were previously referred to *Tapinocephalus* by Broom (1909b).

Watson (1914) presented the first comprehensive review of dinocephalian taxonomy and morphology and considered them in two branches: tapinocephaloid and titanosuchoid. He considered *Titanosuchus* and *Rhopalodon* as Titanosuchoid and *Phocosaurus*, *Delphinognathus*, *Eccasaurus*, *Moschops*, *Taurops*,

Moschognathus, *Mormosaurus*, *Pinigalion*, *Lamiasaurus* and *Deuterosaurus* as Tapinocephaloid.

Broom (1915) presented a complete account of the type material of *Moschops* and *Moschognathus* which were not mentioned in Broom (1911 and 1914b): The holotype of *Moschognathus* includes also a partial upper jaw, lower jaw, partial zygoma and some postcranial elements (*i.e.* vertebrae, portions of ribs, pelvis and both femora). The type series of *Moschops capensis* comprises a series of specimens which include the holotypic cranium with lower jaw and remains of eight skeletons regarded as topotypes by Broom (1915). He presented observations on sexual dimorphism and ontogenetic development in *Moschops* (Broom, 1915, p. 112), pointing out that postcranial differences between separate individuals pertain mainly to the size of the limb and girdles and the thickening of the cranial bones around the temporal fenestra. He considered the larger individuals with greater cranial pachyostosis to have been males.

Haughton (1915a, pl X. figs. 1-3, 1915b, figs. 8-9) described *Struthiocephalus whaitsi* and *Moschosaurus longiceps* on the basis of skulls with relatively long snouts and lower jaws. He considered that *S. whaitsi* differs from other tapinocephaloids in having less thickened frontal and temporal regions, and a reduced contribution of the squamosal in the occiput.

Watson (1917, p. 175) considered dinocephalians as anomodonts because of their unreduced quadrates, no supra-temporal element, a dorsally positioned,

postorbital-squamosal contact in the temporal fenestra, and a basicranium with a deep wall below the occipital condyle. Following this systematic scheme the two main dinocephalian branches proposed by Watson (1917) were maintained as “super-family Tapinocephalidae” and “super-family Titanosuchidae” which were differentiated on the basis of snout length, with tapinocephalids having a short snout. Despite its long snout, *Struthiocephalus* was classified in the Tapinocephalidae.

Watson (1917, fig.2) suggested a captorhinomorph origin for the Therapsida and that Dinocephalia and Dicynodontia arose from a “common stock” and evolved on separate but parallel lines throughout the middle Permian, with the Dinocephalia becoming extinct by the end of the middle Permian.

Haughton (1919), following Broom (1914a), pointed out the great similarity between Dinocephalia and Pelycosauria and considered Karoo dinocephalians in two families: Tapinocephalidae for short snouted skulls which included all the described taxa (even *Struthiocephalus*) and Titanosuchidae with elongated skulls and carnivorous dentition that included *Titanosuchus*. Haughton (1919) emphasized that the difference between the two dinocephalian branches was not only the snout length, but also their diet.

Watson (1921, p. 93) recognised that his previous attribution (Watson 1914) of the snout and occiput to the same individual as the holotype of *Lamiasaurus newtoni* may have been a mistake.

Broom (1923) provided a review of the titanosaurs and, following the dual scheme of Watson (1914), divided them into the herbivorous suborder Tapinocephalia and carnivorous suborder Titanosauria. He also suggested that the holotype of *Moschosaurus longiceps* was an immature titanosaurid. Broom further proposed that the holotype of *Lamiasaurus newtoni* comprises only the snout portion and placed it in Titanosauria. He considered the occiput of the original holotype to be a tapinocephalian (Broom, 1923, p. 662). Williston (1925) divided the Dinocephalia into four families which included Deuterosauridae, Rhopalodontidae, Tapinocephalidae and Titanosauridae (included only *Titanosuchus*). Contra Broom (1923) he considered the holotype of *L. newtoni* to be only the occipital fragment.

Gregory (1926) presented a detailed skeletal description of *Moschops capensis*, the first comprehensive work on the dinocephalian skeleton (Fig. 2.2A). He interpreted differences in cranial characters between individuals, such as the width of the postorbital bars and zygomatic arches and the thickening of frontals, as a manifestation of evolutionary changes within the group. For example *Moschosaurus*, with its relatively narrow postorbital bar and slender skull, was considered to be the most primitive, and *Mormosaurus*, with its broad postorbital and wide skull, to be the most derived. He argued that similar changes occurred in the ontogenetic development of *Moschops*. Accordingly he interpreted the difference between *Delphinognathus conocephalus* and *Moschops capensis* to be “more of degree rather than of kind” (Gregory, 1926, p. 229).

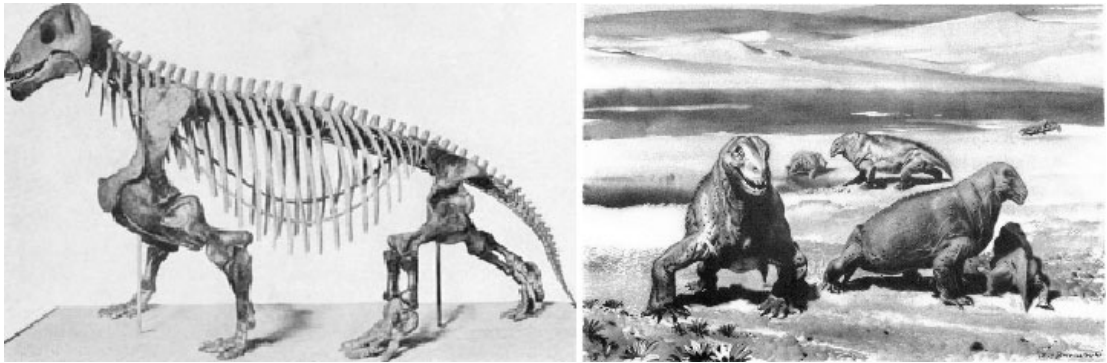


Figure 2. 2. A. Mounted skeleton of *Moschops capensis* in the AMNH (Gregory 1926, pl.1, scale x1/12). B. An early reconstruction of a dinocephalian: a herd of *Moschops* as depicted by Zdeněk Burian in *Prehistoric Animals* (Augusta & Burian, 1960).

2.4 Variation within Tapinocephalidae.

Gregory (1926) proposed a provisional subfamily division of Tapinocephalidae into: Moschosaurinae for *Moschosaurus* characterized by a long snout; Moschopinae for *Delphinognathus*, *Moschops*, *Taurops*, *Pnigalion* and *Lamiasaurus*, characterized by a short skull and deep snout; Tapinocephalinae characterized by a short skull and shallow snout for *Tapinocephalus*, *Mormosaurus* and *Struthiocephalus*. He regarded these subfamilies to be grades of organization rather than representing an evolutionary succession. Gregory (1926) also drew attention to the poorly preserved state of the *Tapinocephalus atherstonei* holotype, suggesting the skull which Haughton (1915) referred to the taxon should be designated a neotype.

Nopcsa (1928a, fig. 3, 1928b, fig.3) erected the Russian species *Mnemeiosaurus jubilai* on the basis of a skull which Seeley (1894a) had previously referred to

Deuterosaurus. He defined *M. jubilaei* as a non pachyostotic tapinocephalid which had a relatively large lacrimal and a foramen between the quadratojugal and jugal which was similar to that of *Delphinognathus*. Nopsca concluded that the newly defined *Deuterosaurus* differed from the South African dinocephalian types in many ways, particularly the morphology of the lower corner of the zygoma and occiput. He placed Deuterosauridae under Titanosuchia because he argued “the squamosal is not yet in contact with the postorbital, the quadrate, and quadratojugal are elongated and foramen quadrati is present” (Nopsca, 1928b, p. 19).

Nopsca (1928b, p. 170-171) considered Dinocephalia in two suborders: Titanosuchoidea and Tapinocephaloidea. The former included dinocephalians which had an elongated snout, frontal contribution to the orbits, and undifferentiated teeth; the Tapinocephaloidea had a relatively shortened snout, no frontal contribution to orbit, upward oriented temporal fenestra, and short quadrate without foramen. The Titanosuchoidea comprised four families: 1) Moschosauridae (for *Moschosaurus*) with no cranial thickening, postparietal-squamosal contact, “conical teeth” and moderate size canine. 2) Deuterosauridae (for *Deuterosaurus*) with no contact between postorbital-squamosal, lateral position of the temporal opening, short skull and quadrate with foramen. 3) Titanosuchidae (for *Titanosuchus* and *Burnetia*) with elongated snout and “projections above orbits”. 4) Lamiasauridae (for *Lamiasaurus*). In contrast the Tapinocephaloidea comprised only one family, Tapinocephalidae, which included

the South African *Delphinognathus*, *Eccasaurus*, *Mnemiosaurus*, *Moschognathus*, *Moschops*, *Pelosuchus*, *Pnigalion*, *Struthiocephalus*, *Tapinocephalus*, *Taurops*.

Broom (1928) described a large cranium which he referred to *Tapinocephalus*. He could not go down to species level due to the inadequacy of the *T. atherstonei* holotype, casting doubt on the reliability of any identification of specimens as *T. atherstonei*. In the same publication he erected *Taurocephalus lerouxi* and *Criocephalus vanderbyli* (Broom, 1928, fig. 6a,b, 7). Both were found on the farm Abrahamskraal in the Prince Albert district. He considered *Taurocephalus lerouxi* to be close to *Struthiocephalus whaitsi* differing with its “much narrower frontal region and its powerful beak” (Broom, 1928, p. 436). The cranial description of *Criocephalus vanderbyli* is very short and highlighted the very narrow interorbital width and large rounded skull roof.

Haughton (1929) described *Styracocephalus platyrhynchus* based on a dorso-ventrally flattened skull with a lower jaw. He suggested it had affinities to both Gorgonopsia and Dinocephalia and should thus constitute a new suborder. Broom (1929) published a review of the carnivorous dinocephalians, which comprised nine species (including *Lamiasaurus*), and more clearly established the separation between the herbivorous and carnivorous Dinocephalia.

In 1931 von Huene described *Keratocephalus moloch* on the basis of a cranial roof with a distinct horn-like boss and a snout tip found on the farm Abrahamskraal, Prince Albert district, in association with vertebrae, pelvis, femur

and tibia. He, similar to Nopsca (1928b), considered the Tapinocephalidae to include 14 species (including *Mnemeiosaurus*,) and Titanosuchidae to comprise 19 species (including *Moschosaurus*, *Deuterosaurus*).

Broom (1932, p.34, 41) reviewed the herbivorous Dinocephalia. He retained the same taxa but excluded *Phocosaurus megischion* in agreement with Lydekker (1890). He also considered the possibility that *Mormosaurus seeleyi* is a subadult *Tapinocephalus atherstonei*, and *Knigalion oweni* a juvenile of *M. seeleyi*.

Boonstra (1936a,b) presented a review of the cranial morphology of tapinocephalians and titanosuchians. He proposed that they diverged at a morphological stage represented by *Moschosaurus* and *Rhopalodon*. Boonstra (1936a) considered the Tapinocephalia in four groups: Moschosauridae (*Moschosaurus*); Moschopidae (*Delphinognathus*, *Moschops*, *Moschognathus*, *Knigalion* and possibly *Lamiasaurus*); Mormosauridae (*Mormosaurus*, *Taurocephalus* and *Struthiocephalus*); Tapinocephalidae (*Taurops*, *Keratocephalus*, *Tapinocephalus*). This classification was largely based on the extent of cranial pachyostosis, skull size and snout length, width of postorbital bar, size and shape of temporal fenestra. He (1936a, p. 93) mentioned the possibility that *Delphinognathus*, *Moschops* and *Moschognathus* are cogenetic. Following Gregory (1926), Broom (1936b) discussed evolutionary trends within the group emphasizing the possibility that these families represented evolutionary stages with *Moschosaurus* being the most primitive tapinocephalid.

In 1937 three more tapinocephalid species from Beaufort West were described: *Struthiocephalus rheederi* by Broom (1937, fig. 3), *Struthiocephalus milleri* by Olson and Broom (1937, fig.4), and *Moschoides romeri* by Byrne (1937, Pl. 1-3, figs. 1-31). Both *S. rheederi* and *S. milleri* are based on well-preserved skulls, which were briefly described without providing any diagnosis. Olson & Broom (1937) considered *S. milleri* closely allied to *S. rheederi* differing only in its large pineal opening. *Moschoides romeri* was described on the basis of a lower jaw fragment and associated postcranial fragments. It was considered to differ from *Moschops* in having a relatively larger and more massive skeleton (Byrne, 1937).

Riabinin (1938, figs. 1-22, 25) described *Ulemosaurus svijagensis* from two fairly well preserved skulls and skeletons found near the Isheevo village of Tatarstan in Russia during the 1930-1931 Isheevo excavations. *U. svijagensis* was considered to be similar to *Moschops* (Riabinin, 1938). Latter excavations at Isheevo from 1934-1939 by I. Efremov resulted in the discovery of more dinocephalian fossils (Efremov, 1940a; Ochev & Surkov, 2000).

Efremov (1940b, figs. 1-11, 16) provided a detailed redescription of the cranium and dentition of *Ulemosaurus svijagensis*. He concurred with Riabinin (1938) that it is similar to *Moschops capensis* but noted that it was less derived in that it still had an enlarged canine. He (1940b) commented on *Delphinognathus*, *Moschops*, *Tapinocephalus* and *Mormosaurus* suggesting that they may represent an ontogenetic series of the same animal, especially since the main differences between the genera concerned the degree of cranial thickening.

Watson (1948) reviewed the distinguishing characters of *Dicynodon* relative to a tapinocephaloid and a pelycosaur. He concluded that dinocephalians occupied a phylogenetic position between “pelycosaurs” and dicynodonts, and were thus the most primitive therapsid group, with the Russian *Rhopalodon* and *Deuterosaurus* being among its earliest representatives. Watson (1948, p. 839, 841) differentiated titanosuchids from the tapinocephalids on the basis of the large canine and long, straight lower jaw of the former group.

Boonstra (1951, fig. 1,2) referred the weathered cranial roof (SAMPK10557) to *Keratocephalus* and pointed out the differences between *Keratocephalus* and *Struthiocephalus*. He considered SAM-PK-10557 to be a female individual and that the *Keratocephalus* holotype is a male.

Boonstra (1952a, b, c, d, e, f, g), at the time the most prolific dinocephalian researcher, described seven tapinocephalid species from the Karroo: five with a long snout (*Struthiocephalus akraalensis*, *S. duplessisi*, *Struthiocephaloides cavifrons*, *Riebeeckosaurus longirostris*, *Struthionops intermedius*) and two short-snouted forms (*Agnosaurus pienaari*, *Avenantia kruisvleiensis*). The holotype of *S. akraalensis*, found in the Prince Albert district, comprises a skull and was considered similar to *S. rheederi* (Boonstra, 1952a, figs. 1,2). The holotype skull of *Struthiocephalus duplessisi* is from the Laingsburg district (Boonstra, 1952b); although this specimen is similar to *Struthiocephalus whaitsi* it lacked a nasofrontal boss and was shorter and broader than the *S. whaitsi* holotype.

Struthiocephaloides cavifrons was described from a skull found in the Prince Albert district (Boonstra, 1952c). Boonstra (1952g, figs. 1,2) described *Struthionops intermedius* from a smaller and distorted cranium with a beak-like snout and considered it morphologically intermediate between mormosaurids and moschopids but classified it with the mormosaurids because of its relatively long preorbital region.

Haughton and Brink (1954) published a list of recognised dinocephalian species in their bibliographical list of the Karoo reptiles. They, following Boonstra (1936), considered the herbivorous dinocephalia (Tapinocephalia) in the same four families, leaving the imperfectly known taxa *i.e Pelosuchus*, *Eccasaurus* and *Criocephalus* of Broom (1905b, 1909a, 1928) unclassified and excluding *Lamiasaurus* completely from the group. They placed *Styracocephalus* under a separate infraorder, Styracocephalia.

Efremov (1954) published a monograph on the Permian tetrapods from the Copper Sandstone of the Cis-Urals. He described the dinocephalians and introduced the new species *Deuterosaurus gigas* based on loose teeth.

In 1955a Boonstra named *Struthiocephalellus parvus* based on a small distorted skull with a long snout which had associated postcrania. This species differs from *Struthiocephalus whaitsi* in that it is a smaller skull with less pachyostotic thickening, has a thin postorbital bar, no naso-frontal boss, and more upright occiput. Although Boonstra had previously considered these characters to be

juvenile for *Struthiocephalus* he reasoned that the holotype of *Struthiocephalus whaitsi* was an adult because it had already erupted teeth.

Boonstra (1956, 1957) provided a composite cranial description of the South African genera which he in 1936 had included in the Tapinocephalidae and Moschopidae and included a revised diagnosis for each genus. The diagnosis of *Tapinocephalus* was, to a large extent, based on the skull SAM-PK-2344 described by Haughton (1913). *Phocosaurus megischion* was given a cranial diagnosis even though the holotype does not have a skull. This diagnosis was done from specimen SAMPK11997 because of the similarities between the postcrania of SAMPK11997 and the holotype of *Phocosaurus*.

Watson and Romer (1956) published a revised classification for Therapsida which differed from previous revisions by applying Theriodontia for carnivorous therapsids and Anomodontia for herbivorous therapsids. Accordingly they split the Dinocephalia and grouped the carnivorous dinocephalians as infraorder Titanosuchia under Theriodontia and the herbivorous dinocephalians as infraorder Dinocephalia under Anomodontia. Titanosuchia comprised the families Brithopididae, Anteosauridae and Jonkeriidae. Jonkeriids were differentiated from anteosaurids in having a smaller temporal fenestra and more anteriorly positioned quadratojugal. Watson and Romer (1956, p.77), as opposed to Seeley (1894b), limited the term Dinocephalia to the herbivorous forms and defined them as primitive anomodonts, with Dinocephalia comprising Deuterosauridae (*Deuterosaurus*), Moschopidae (*Delphinognathus*, *Moschognathus*, *Psigalion*),

and Tapinocephalidae (*Tapinocephalus*, *Phocosaurus*, *Mormosaurus*, *Agnosaurus*, *Avenantia*, *Criocephalus*, *Eccasaurus*, *Keratocephalus*, *Moschosaurus*, *Pelosuchus*, *Struthiocephalus*, *Struthiocephaloidea*, *Struthiocephalellus*, *Taurocephalus*, *Taurops* and *Ulemosaurus*). Watson and Romer (1956) considered Deuterosauridae to be primitive dinocephalians which differed from others in having a slightly pachyostosed skull and a large canine. They pointed out that the tapinocephalid *Ulemosaurus* also has a canine but this is less distinct than that of *Deuterosaurus*. Moschopidae was differentiated from Tapinocephalidae in that the former has less cranial pachyostosis and a smooth transition from the facial to the cranial surface.

Olson (1962), in his monograph on late Permian terrestrial vertebrates from USA and Russia (former USSR), presented a classification of dinocephalians which differs from that of Watson and Romer (1956, p. 70, 84) in that: Brithopididae was placed under the infraorder Eotheriodonta; the term Dinocephalia (designated as “Deinocephalia”) referred to a suborder which included two infraorders: Eodeinocephalia (*incl.* Deuterosauridae) and Eudeinocephalia and they were excluded from Anomodontia. Olson (1962) referred to the Eudeinocephalia as the real Dinocephalia or “progressive dinocephalians”. It comprised two superfamilies: tapinocephaloidea (Moschopidae and Tapinocephalidae) and titanosuchoids (Titanosuchidae). Olson (1962, p.186) concluded that the tapinocephalids originated from deuterosaurids and the association with the latter and the carnivorous brithopodid dinocephalians was superficial. He acknowledged Watson and Romer (1956) in their conclusion

regarding Deuterosauridae that the similarities between the two families (the brithopopids and deuterosaurids) are the result of convergence.

Boonstra (1962) published on the Titanosuchian dentition, tooth replacement, and jaw articulation. He pointed out the importance of the intermeshing incisors for Dinocephalia as a novelty that separated it from the rest of the therapsid groups and how the variation of this character amongst Dinocephalia marks the stages of separation from the common ancestor (i.e. from only intermeshing incisors of anteosaurians to intermeshed incisors and canines of titanosuchians, and finally to the fully intermeshed jaw batteries of tapinocephalians).

Boonstra (1965) personally examined *Deuterosaurus biarmicus* (Eichwald, 1848) and *Mnemeiosaurus jubilai* (Nopcsa, 1928b) type materials and concluded that *Deuterosaurus* manifested both titanosuchian and anteosaurian characters. It had anteosaurian-like long incisors, bulbously spatulate postcanines, medial shift of the quadratojugal, slight upward sweep of the alveolar border of the premaxillaries, higher than broad snout, weak infratemporal bar and deep temporal fossa; it possessed titanosuchian-like intermeshing canines with the lower canine passing outside the upper jaw, absence of angular boss and little general pachyostosis. Boonstra (1965) concluded that *Deuterosaurus* be placed in a separate family within Anteosauria and that *Mnemeiosaurus jubilai* was a tapinocephalian, probably a moschopid.

Tatarinov (1965) published a reinterpretation of the basicranium and palate of

Ulemosaurus svijagensis and proposed the synonymy of *Ulemosaurus svijagensis* as *Moschops svijagensis*.

After Watson & Romer (1956) had split the carnivorous and herbivorous dinocephalian groups, Romer (1966) presented a reunited Dinocephalia. He considered the herbivorous dinocephalians under superfamily Tapinocephaloidea that also included Deuterosauridae and Tapinocephalidae. Boonstra (1969) considered South African Dinocephalia in four families. Anteosauridae are primitive carnivores with long pointed intermeshing incisors and are more derived than the Russian brithopids. Titanosuchidae are primitive herbivorous Dinocephalia with a slightly pachyostosed skull bearing a canine, intermeshing incisors with a talon and heel morphology, and spatulate postcanines with serrated edges. Tapinocephalidae included derived herbivorous Dinocephalia with moderate to heavy cranial pachyostosis, no canine, teeth with talon and heel morphology and the upper and lower jaws fully intermeshed. Styracocephalidae are advanced herbivores with a canine and tabular bosses.

Boonstra (1969) reduced the number of valid South African dinocephalian species from 65 to 29. They comprised one out of twelve in Anteosauridae, nine out of 24 in Titanosuchidae and 18 out of 28 in Tapinocephalidae. He considered the Tapinocephalidae in four subfamilies on the basis of snout length and variation in the degree of cranial pachyostosis. Subfamilies Struthiocephalinae and Riebeeckosaurinae both had long snouts and moderate pachyostosis but the intertemporal area of the latter is narrow and forms a sagittal crest. Both

Moschopinae and Tapinocephalinae had short snouts and moderate to great cranial pachyostosis. Struthiocephalinae included *Struthiocephalus whaitsi*, *Struthiocephaloides cavifrons* and *S. duplessisi*, *Struthionops intermedius* and *Taurocephalus lerouxi*. He considered that the holotypes of *Struthiocephalus parvus*, *S. longiceps*, *S. milleri*, *S. rheederi*, *S. akraalensis*, *S. kitchingi* and *Moschosaurus longiceps* demonstrated a growth series of *Struthiocephalus whaitsi* and synonymized all these species. Moschopinae included *Delphinognathus conocephalus*, *Avenantia kruisvleiensis*, *Moschops capensis*, *M. koupensis*, *M. oweni*, *M. whaitsi* and synonymized *Moschognathus whaitsi*, *Pnigalion oweni*, *Moschoides romeri* and *Agnosaurus pienaari* with *Moschops*. Tapinocephalinae included *Tapinocephalus atherstonei*, *Keratocephalus moloch*, *Mormosaurus seeleyi* and *Phocosaurus megischion*. He synonymized *Pelosuchus priscus* with *Keratocephalus* and *Taurops macrodon* with *Tapinocephalus*. Although Boonstra (1969) referred *Taurops* to *Tapinocephalus* he did not indicate whether it was a new species of *Tapinocephalus*. Riebeeckosaurinae included *Riebeeckosaurus longirostris*.

Boonstra (1971, p. 40, fig. 3) considered that the early- middle Permian synapsids formed a morphological series starting from a pelycosaur ancestor. He suggested an eastern European origin for Therapsids, emerging from the Cisuralian and spreading to the Karoo so that the earliest *Tapinocephalus* Zone strata of the Beaufort Group already had a diverse fauna. Dinocephalians were the dominant element of this fauna and thrived until the end of the middle Permian when they became extinct (Boonstra, 1971, figs. 1, 2).

In 1972, Boonstra provided a revised taxonomy for Therapsida. He discarded the names Anomodontia and Theriodontia, and introduced the clades Alphatherapsida, Betatherapsida and Gammatherapsida. Alphatherapsida included the most primitive therapsid Eotitanosuchia, Dinocephalia and Gorgonopia. Dinocephalia comprised two suborders Brithopia (Brithopidae & Anteosauridae) and Titanosuchia (Titanosuchidae, Tapinocephalidae, Styracocephalidae & Estemmenosuchidae).

Tchudinov (1983) classified Dinocephalia in two main branches: the carnivorous dinocephalia as Titanosuchia and herbivorous Dinocephalia as Tapinocephalia. He synonymized *Deuterosaurus gigas* with *Moschops gigas* and renamed the subfamily Moschopinae as Delphinognathinae.

King (1988) grouped the derived herbivorous forms in the subfamily Tapinocephalinae which included the tribes Struthiocephalini, Tapinocephalini and Riebeeckosaurini. The family Styracocephalidae was considered *incertae sedis*.

Rubidge (1991) described *Tapinocaninus pamela* on the basis of three well preserved skulls and two incomplete specimens as the most primitive tapinocephalid dinocephalian. This conclusion was later confirmed by Rubidge et al. (2019) who described the postcranium of *Tapinocaninus pamela*. Ivakhnenko (1994) later named the family Ulemosauridae for *Ulemosaurus svijagensis* and *T.*

pamelae.

Grine (1997, figs. 2,3) presented detailed illustrations of the holotype of *Moschognathus whaitsi* and pointed out the presence of a coronoid bone in *Moschognathus*, thus questioning the inclusion of Dinocephalia in the Anomodontia.

Rubidge and Sidor (2001) followed Hopson and Barghusen (1986) in considering the dinocephalians in two main groups, the carnivorous anteosaurs, and herbivorous tapinocephalians. Morphological variation related to adaptations to herbivory, body size, and cranial pachyostosis has formed the basis for most tapinocephalian classifications as manifested above. The most derived tapinocephalians are the family Tapinocephalidae which were highly specialized herbivores and comprise most of the middle Permian terrestrial tetrapod biodiversity.

Ivakhnenko (2003) considered Dinocephalia as a suborder with three infraorders: Eotitanosuchida, Titanosuchida and Tapinocephalida. Titanosuchida included two superfamilies: Titanosuchidae (*e.g. Titanosuchus, Archaeosyodon*) and Deuterosauridae (*Deuterosaurus*). Tapinocephalida included superfamilies Tapinocephaloidea and Struthiocephaloidea. *Ulemosaurus* and *Tapinocaninus* were placed in Ulemosauridae. The same author later proposed a different taxonomic scheme for Dinocephalia where the Superfamily Deuterosauroidae comprised of Anteosauridae and Deuterosauridae. The latter included

Deuterosaurus and *Tapinocaninus* which represented an early less specialized stage. The superfamily Tapinocephaloidea was comprised of Ulemosauridae (*Ulemosaurus*) and Tapinocephalidae which he considered to progress from the subfamily Riebeeckosaurinae into Tapinocephalinae and Struthiocephalinae (Ivakhnenko, 2008).

Kammerer (2009) provided, as part of his PhD thesis, an evaluation of the fauna of the *Tapinocephalus* Assemblage Zone of South Africa. He recognized six valid species of tapinocephalid dinocephalians from this zone (*Mormosaurus seeleyi*, *Moschognathus whaitsi*, *Moschops capensis*, *Riebeeckosaurus longirostris*, *Struthiocephalus whaitsi*, *Tapinocephalus atherstonei*) but did not provide morphological descriptions.

With the recent upsurge in interest on the end Capitanian extinction, which has been recognized in both the marine and terrestrial realms (e.g. Jin et al., 1994, Retallac et al., 2006, Şengör & Atayman, 2009, Bond et al., 2010; Day et al. 2015) where dinocephalians were one of the victims in the terrestrial realm, it is essential to sort out the taxonomy of the tapinocephalid dinocephalians, the most diverse dinocephalian taxon, to fully understand the nature of this extinction event.

3 MATERIALS AND METHODS

Tapinocephalid dinocephalians comprise numerous genera of which all, except for the Russian *Ulemosaurus*, are from the *Tapinocephalus* Assemblage Zone of the South African Karoo. This biozone is notorious for the very hard rock in which these animals are preserved, and preparation of the material presents a huge challenge to a project of this nature.

As a result of more than a century of fossil collecting from the lower Beaufort Group of the Karoo Supergroup, collections of tapinocephalid dinocephalians have been accumulated in various museums in South Africa, the United States of America, England and Germany (Table 1).

This thesis is presented as eight chapters. Chapters 4, 5, 6 and 7 are presented as papers which have been formatted to be submitted to journals for publication. Chapter 5 and some results from the Chapter 6 have already been published (Güven et al., 2013, Day et al., 2015) (Appendix 1). Because this thesis is set out in the format of publications there is unavoidable repetition in some chapters. All references are presented as a single reference list at the end.

Institution	Country
American Museum of Natural History.	New York, United States of America
Field Museum of Natural History*	Chicago, United States of America
Palaeontological Institute	Moscow, Russia
Evolutionary Studies Institutes (formerly Bernard Price Institute for Palaeontology)	Johannesburg, Republic of South Africa
McGregor Museum	Kimberley, Republic of South Africa
The Ditsong National Museum of Natural History	Pretoria, Republic of South Africa
Iziko South African Museum	Cape Town, Republic of South Africa
Karoo National Park, SANPARKS	Beaufort West, South Africa
Universität Tübingen Museum und Institut für Geologie und Paläontologie	Tübingen, Germany
The Natural History Museum	London, United Kingdom
Natural History Museum of Bulawayo	Bulawayo, Zimbabwe
National Heritage Conservation Commission of Zambia*	Lusaka, Zambia
Universidade Federal do Rio Grande do Sul*	Porto Alegre, Brazil.

Table 3.1. Museum Collections which curate fossils of tapinocephalid dinocephalians. * indicates institutions which are not visited.

3.1 Specimens

To undertake a reliable taxonomic assessment of the tapinocephalid dinocephalians this project required visits to all of the collections around the world, with few exceptions (indicated with ‘*’ in Table 3.1), which curate fossils of tapinocephalid dinocephalians to study and assess all the holotype material and also to describe the best comparative material in the collections. Most of the holotypes were described on skulls, but there are a few taxa described on

postcranial material. For the purposes of this study all holotype material was studied, but only cranial material was analyzed. Postcranial studies will be undertaken in future projects. Tapinocephalids examined for this study are listed in the Appendix 2.

3.2 Preparation

Much of the cranial material (both holotypes and referred specimens) is fragmentary and still relatively unprepared. To ensure the most reliable assessment of the material required much of it to be further prepared. Most of the holotypes have not been prepared for decades, with the result that the preparation which had previously been undertaken on the specimens is poor quality and was done using hammers and chisels which was the standard method employed in earlier years.

The largest collections of tapinocephalid fossils are curated within South Africa. Through the kind co-operation of numerous museum curators in South Africa, relevant material was taken on loan to the Evolutionary Studies Institute at the University of the Witwatersrand in Johannesburg (ESI) and prepared at the fossil preparation laboratory of this Institute. All preparation was undertaken using compressed air driven air scribes fitted with tips of tungsten carbide, and even although the specimens are very large, all preparation was done under binocular microscopes to ensure that surface bone details were not damaged. The temporary bringing-together of all the best specimens of tapinocephalid dinocephalians at the ESI facilitated, for the first time, direct comparison of all the specimens and the

opportunity to check the validity of previously described taxa, often from very fragmentary material. This also enabled detailed description and illustration of the specimens to provide a good database of the best tapinocephalid cranial material.

3.3 Figures

Computer illustrations are prepared on the photographs by using Adobe Illustrator CS3-CS6 for Mac.

The x-ray images of some crania (KNPI, KNPII, KNPIV and SAM-PK-11582) were produced by a Siemens PET/CT scanner at the Charlotte Maxeke Johannesburg Academic Hospital (South Africa) using “RT Head 0.6” protocol.

Relevant parameters included: 140 kVp, a tube current of 360 mAs, a slice thickness of 0.6 mm, and a reconstruction increment of 0.3 mm. The image data for each specimen were reconstructed as 16-bit DICOM images using a bone reconstruction algorithm (i.e., a “H60” kernel). Image data were opened and relevant images were saved for comparison using Avizo 6.3.1 software (Visualization Sciences Group, Mérignac cedex, France). These images were used to produce the figure 6.60 in Chapter 6.

3.4 Phylogenetic analysis

Relationships among tapinocephalids were investigated using TNT (Tree Analysis Using New Technology) Version 1.5 (Goloboff et al., 2008; Goloboff & Catalano, 2016).

4 COMPARISON OF THE BASAL *TAPINOCANINUS* FROM SOUTHERN AFRICA AND *ULEMOSAURUS* FROM EASTERN EUROPE

4.1 Introduction

Dinocephalians, the dominant therapsids of the middle Permian, had a seemingly cosmopolitan distribution, but despite their early success they were victims of the end Capitanian mass extinction. The Tapinocephalidae, which were exclusively herbivorous, were the most abundant and taxonomically diverse dinocephalian group. They are known from Tanzania, Zambia, Zimbabwe, Brazil and Russia, but by far the richest record is from the Karoo of South Africa where they are known from the *Eodicynodon* and *Tapinocephalus* assemblage zones. The only tapinocephalid from the *Eodicynodon* Assemblage Zone is *Tapinocaninus* (the most recently described genus from South Africa), and the only member of this family from Russia is *Ulemosaurus* from the Isheevo Complex (Fig. 4.6).

All published descriptions of *Ulemosaurus* and *Tapinocaninus* were done by researchers working independently in Russia and South Africa. This synthesis is the first work providing a detailed descriptive comparison of the cranial anatomy of both genera, which are generally considered the most basal tapinocephalid dinocephalians (*e.g.* Rubidge 1991; Rubidge et al. 2019; Romano and Rubidge 2019). Co-incidentally both genera are among the best preserved and most complete tapinocephalid cranial material. Because detailed cranial descriptions of

each of the genera have previously been published the following account is presented as a cranial single description but highlighting the differences between the two genera.

4.2 Historical Review

Ulemosaurus svijagensis from Isheevo in Russia was described by Riabinin (1938) based on a portion of a cranial roof (PIN 123/3805) and two skulls of which one complete (PIN 2207/ 2: previously, PIN 2/3805) with associated complete skeleton and the other (PIN 2207/1: previously, PIN 1/3805) is missing the cranial roof. The first discovery of remains of *Ulemosaurus* (PIN 123/3805) goes back to a geological trip undertaken in 1929 to the area around the Ulemo River of Tatarstan. Excavations at the Isheevo locality were carried out in 1930-1931 resulting in the discovery of PIN2207/1 and 2. Riabinin (1938) considered *U. svijagensis* to be closely related to the South African herbivorous dinocephalians, particularly to *Moschops capensis* but pointed out that *Moschops* differed in the absence of a canine tooth. Later excavations at Isheevo (1934-1935) were lead by Efremov who found a skeleton of a large skull of another herbivorous dinocephalian (PIN 157/4) which he referred to *Moschops* (Efremov, 1940a).

Efremov (1940b) provided a comprehensive redescription of the skull of *Ulemosaurus*, comparing it to the South African tapinocephalids and to the Russian *Deuterosaurus*. In agreement with Riabinin (1938), he considered *Ulemosaurus* more primitive than *Moschops* because it had less “pachyostotic

thickening of the skull roof, a higher skull with a large temporal opening, jaw articulation positioned further posteriorly, and the presence of a smaller parietal” (Efremov 1940b, p.193). He further differentiated *Ulemosaurus* from *Moschops* by pointing out the anteriorly positioned naris, strongly developed septomaxilla and lacrimal, less inclined occiput, weakly developed pterygoid flanges of *Ulemosaurus*. He considered the slit-like temporal fossa and resultant smaller jaw adductor muscles and shortened lower jaw of *Moschops* to be derived characters.

Efremov (1954) described loose tapinocephalid teeth as *Deuterosaurus gigas* and Vjuschkov (1955) described *Ulemosaurus minutus*, from the Orenburg region, on the basis of an incomplete humerus and a postcanine tooth. Tatarinov (1965, p.96, fig.2) reinterpreted the braincase and the occiput of *Ulemosaurus* and recognized it as a separate species of *Moschops*, *Moschops svijagensis*. *M. svijagensis* differed from *M. capensis* in having a more elongated snout and also on the morphology of its parietal.

Boonstra (1965) restudied *Deuterosaurus biarmicus*, intrigued by its apparent combination of anteosaurian and tapinocephalian characters. He considered it more anteosaurian than tapinocephalian and included it in the Anteosauria. However, he considered the holotype of *Mnemeiosaurus jubilai*, a taxon originally based on referred material of *Deuterosaurus*, to represent a type of moschopid tapinocephalid with a distinct canine.

Kalandaze et al. (1968) synonymised *Ulemosaurus minutus* as *Moschops minutus* and Tchudinov (1983) synonymised *Deuterosaurus gigas* as *Moschops gigas* and suggested that *Moschops svijagensis* and *Moschops gigas*, based on cranial morphology, are older and more primitive than the South African *Moschops*. King (1988), by contrast, maintained *Deuterosaurus gigas* as a valid species and retained *Ulemosaurus* as a genus distinct from *Moschops*.

Rubidge (1991) described *Tapinocaninus pamela* based on four skulls (NMQR 2985, 2986, 2987; ROZ-K95) from the farm Modderdrift, Prince Albert. Specimens NMQR 2985, 2986 and 2987 were all from the same sandstone in close proximity to each other and ROZ-K95 was found 100m stratigraphically lower.

Ivakhnenko (1994) proposed the family Ulemosauridae for *Ulemosaurus* and possibly the South African tapinocephalid *Riebeeckosaurus longirostris*; while he considered *Tapinocaninus* together with *Deuterosaurus* in Deuterosauridae which he allied with the carnivorous anteosaurs. Ivakhnenko et al. (1997) synonymised *Deuterosaurus gigas* with *Ulemosaurus* but retained it as a distinct species *Ulemosaurus gigas* which differs from *Ulemosaurus svijagensis* in that the latter has a strongly serrated canine cingulum and many longitudinal undulating ridges running from the heel base up to the crown apex. Ivakhnenko (1997) additionally tentatively referred a large incomplete skull (PIN2972/1) to the new species *Ulemosaurus gigas*.

Recently the well-preserved skeleton of *Tapinocaninus* was described by Rubidge et al.(2019), and Romano and Rubidge (2019), using a volumetric body mass estimate, determining a weight of 892.63Kg for the holotype of *Tapinocaninus*, NMQR 2987.

4.3 Stratigraphic Context

All specimens of *Tapinocaninus pamela* are from the *Eodicynodon* AZ (Rubidge, 1987) which is the oldest vertebrate biozone of the Beaufort Group (Rubidge, 1995) and has been correlated to the Ocher Subassemblage of Russia (Battail 2000; Modesto and Rybczynski 2000; Rubidge, 2005; Golubev, 2005) (Fig.4.7). *Ulemosaurus* is from the Isheevo Subassemblage of the Mezen River Basin (Ivakhnenko 1990), which has been correlated with the overlying *Tapinocephalus* AZ of South Africa (Modesto and Rybczynski, 2000; Rubidge, 2005; Golubev 2005). In the absence of radiometric dates, Golubev (2015) considers the Ocher Subassemblage to be Urzhumian and the Isheevo Subassemblage as upper Urzhumian and lower Sverodvinian stages. Compared to the global stratigraphic scale, these ages correspond approximately to Wordian for the Ocher assemblage and upper Wordian and Capitanian for Isheevo (Golubev 2015; Menning et al. 2006). A Wordian age is generally agreed for the *Eodicynodon* AZ (Catuneanu et al. 2005; Rubidge 2005; Abdala 2008), implying a correlation with the Ocher Subassemblage (Golubev, 2015) and the overlying *Tapinocephalus* Assemblage Zone is Capitanian (Day et al. 2015). Assuming the accuracy of these correlations would make *Tapinocaninus* slightly older than *Ulemosaurus*.

Epoch		International stages	Russian stages					
260	Lopingian	Changhsingian	Tatarian					
		Wuchiapingian						
	Guadalupian	Capitanian		Biarmanian	Eastern Europe		South Africa	
		Wordian			Tetrapod assemblage zone		Tetrapod faunal complexes	
<i>Ulemosaurus svijagensis</i>			Zone III		Isheevo	<i>Tapinocephalus</i>		
<i>Estemmenosuchus uralensis</i>			Zone II					
265	Radian		<i>Parabradysaurus silanfevi</i>	Zone I	Ocher	<i>Eodicynodon</i>		
270	Cisuralian	Kungurian	Cisuralian					

Figure 4.1. Stratigraphic correlation of the Eastern European and South African dinocephalian-bearing beds (Rubidge, 1995, Efremov, 1952, Golubev, 2005, 2015, Menning, 2006).

4.4 Material

4.4.1 *Tapinocaninus pamela*

NMQR 2987: Holotype, of *Tapinocaninus pamela*, a large well-preserved almost complete skull with lower jaw, lacking only the right postorbital portion of the skull and the posterior portion of the skull roof, as well as an almost complete skeleton.

NMQR 2986: Paratype of *T. pamela*, a large skull with attached lower jaw. The snout is missing and the occipital crest is damaged.

NMQR 2985: Paratype of *T. pamelae* comprising a large skull with lower jaw, lacking the tip of the snout. Left postorbital portion of the skull and the posterior portion of the skull roof are damaged.

ROZ-K 95: Paratype of *T. pamelae*. A large skull with the right lower jaw preserved.

NMQR 2987, 2986 and 2985 are all from the same sandstone outcrop on the farm Modderdrift, Prince Albert. ROZ-K 95 was collected on the same farm, but from a lower stratigraphic horizon. An additional isolated skull roof, NMQR 3097, from the lowermost Beaufort Group on the farm Swartgrond in the Rietbron district is catalogued as *Tapinocaninus* but is not included in this description because it is so fragmentary. Additional preparation was undertaken on specimens NMQR 2987, NMQR 2986 and NMQR 2985 at both the Evolutionary Studies Institute (ESI) at the University of the Witwatersrand in Johannesburg and the National Museum in Bloemfontein.

4.4.2 *Ulemosaurus svijagensis*

PIN 2207/2 (PIN 2/3805): Complete cranium and lower jaw. The lectotype of *Ulemosaurus svijagensis*. Isheevo locality, Russian Federation, Tatarstan, Apastovskii District. See. Riabinin, 1938, fig. 2, 3, 5,6, 8; pl. IV, VI, VIII (1-1a), X, XII(1-2); Efremov, 1940, figs. 1-5, 8; Tchudinov, 1983, p. 154, fig. 50ab.

PIN 2207/1(PIN 1/3805): Cranium (lacking skull roof) and a lower jaw. The paralectotype of *Ulemosaurus svijagensis*. Isheevo locality, Russian Federation, Tatarstan, Apastovskii District. See. Riabinin, 1938, fig.1,7, pl. III, V, VII(1 &1a) and XI (1,1a, 2).

PIN 2972/1: Large incomplete cranium (This specimen is exhibited at the museum with the collection number 2977/1 but recorded with this collection number as *Ulemosaurus gigas* in Ivakhnenko, 1997, p.70; Ivakhnenko, 2003, p. 392).

PIN 157/4: Large incomplete cranium and partial lower jaw. (Efremov, 1940, Tchudinov, 1983, p. 153).

PIN 4337/4: large incisor (*Ulemosaurus gigas* in Ivakhnenko, 1997, p.64; Ivakhnenko, 2003, p. 392).

PIN 2207/3, 4 & 5: Comprises respectively a 1st upper and additional two incisors, probably between i2 and i5, from the upper jaw of *U. svijagensis* from Isheevo, Tatarstan Republic. (Ivakhnenko et al., 1997, p. 63; Ivakhnenko, 2008).

PIN 1955/3, 1955/4 and 1955/5: *Ulemosaurus* canine and incisor from Klyuchevskii Mine-2 locality, Russian Federation. (Efremov, 1954, fig. 19-21; Ivakhnenko et al., 1997, p. 32, pl. 76, fig. 2; Ivakhnenko, 2008, p.87.)

4.5 Systematic Palaeontology

Tapinocaninus, Rubidge 1991

Type species: *T. pamela*

Holotype: NMQR2987

Paratypes: NMQR 2986, NMQR 2985 and ROZ K-95. *Note.* NMQR 3130, a fragmentary fragment of skull roof of a tapinocephalid dinocephalian is catalogued as *Tapinocaninus*; however I could not find any justification to confirm this identification.

Previous diagnosis for *Tapinocaninus pamela*: Large tapinocephalid with moderate pachyostosis and broad postorbital bar; relatively large temporal opening and relatively narrow intertemporal region; premaxilla forms anterior and anterolateral border of the internal nares; maxilla has only short contact on lateral side of internal nares resulting in palatine almost meeting premaxilla; very narrow vomer; medium sized canine without clear heel development; lower canine passes in front of upper canine rather than on lingual side; premaxilla with five incisors with heel development; quadrate condyle situated below posterior border of orbit; small palatal teeth on palatine boss (Rubidge, 1991).

Revised diagnosis for *Tapinocaninus pamela*: Autapomorphy: Pronounced wide horizontal ridge extending forward from contact between parietal and squamosal in temporal opening. Defining combination of characters:

Homogenous heavy cranial pachyostosis forming interorbitally wide and rather flat cranial roof with narrow (but not crest-like as in *Riebeeckosaurus*) intertemporal region. Short, narrow and high snout which broadens posteriorly onto a thickened but flat cranial surface; large temporal fenestra; while it is shallower on its dorsoventral axis; jaw joint close to the posterior border of postorbital bar; dorsal extension of premaxilla extends half of the snout length; moderate sized canine with mesodistally elongated narrow lingual heel which is more like a ridge and narrower than it is in *Ulemosaurus*.

Ulemosaurus Riabinin, 1938

Type species: *Ulemosaurus svijagensis*, Riabinin 1938

(= *Moschops svijagensis* Tatarinov, 1965; Tchudinov, 1983, *Deuterosaurus gigas* Efremov, 1954, *Ulemosaurus gigas* Ivakhnenko, 1997)

Lectotype: PIN 2207/2

Referred material: PIN 2207/1 (syntype), PIN 157/4, PIN 2972/1, PIN nos.

1955/3, 4 and 5. Riabinin (1938, p. 40) mentions another cranial specimen of *Ulemosaurus svijagensis* from the same locality as with the types which has not been mentioned elsewhere.

Remarks. Currently the genus *Ulemosaurus* comprises two species; the type species *U. svijagensis* of Riabinin (1938) and *U. gigas* (*Deuterosaurus gigas* [Efremov, 1954]) of Ivakhnenko et al. (1997). Efremov (1954, Figs.19-21) based *D. gigas* on three isolated teeth PIN 1955/3, PIN 1955/4 and PIN 1955/5 of which Ivakhnenko (2008) considered PIN 1955/5 as lectotype and identified it as a canine. Ivakhnenko (2008) considered the canine of *U. gigas* (PIN1955/5) to

differ from that of *U. svijagensis* in that it has a transversely expanded and lingually elongated crown, strongly serrated cingulum margin, and undulating horizontal ridges. From personal observation I concur that the holotype specimen of *U. gigas* does exhibit typical tapinocephalid incisor characteristics and most probably belonged to *Ulemosaurus svijagensis*: PIN 1955/4 is a 1st upper incisor with a mesiodistally compressed crown and elongated heel; PIN 1955/3 is most probably either the 4th lower incisor or the 5th upper and has a small obliquely positioned heel. Based on the information gathered from the dental morphology of the *Ulemosaurus svijagensis* holotype PIN 1955/5, with its obliquely positioned heel, this also resembles the canine of *Tapinocaninus*. The fact that the heel margins exhibit ridges and are serrated suggests that the heel margin is of an unworn tooth as suggested by Tchudinov (1983) and does not differ from that of *Ulemosaurus svijagensis*. Ivakhnenko (1997) tentatively referred PIN 2972/1 to *U. gigas* and considered different to *U. svijagensis* in having a more extended skull. In my opinion the skull (Figure 13B) is a large damaged incomplete skull of *Ulemosaurus svijagensis* and, apart from its large size, does not present any features (including the canine) to differentiate it from *U. svijagensis*.

Previous diagnosis for Ulemosaurus svijagensis: Dental formula $I_3^3C_1^1PC_{11-12}^{11}$.

“Postorbitally wide and deep skull; narrow tapering snout with great nasofrontal tumescence; large pineal foramen; slightly developed parietal; antero-posteriorly elongated temporal fenestra; quadrangular orbit; irregularly oval narial opening with a notch in the upper part; no septomaxillary foramen; prevomer widened posteriorly; interpterygoid vacuity narrow and long and positioned toward the

middle of the palatal surface; basisphenoid with a crest and tubera ; tripartite occipital condyle; quadrangular foramen magnum; distal end of stapes widened and without a foramen” Riabinin, 1938, p. 47.

Ulemosaurus “differ from *Moschops* in skull being narrower, higher, with snout more elongated; postorbital arches wide, high, curved over backward; incisors and anterior maxillary teeth very powerful; interorbital region wider; intertemporal region narrower; lesser pachyostosis; occiput higher, narrower; temporal fossae wider anteroposteriorly; pterygoids more constricted across interpterygoid fossa; jaw articulation farther back” Brink, 1988.

“Very large; narrow and tapering snout; wide and very high skull in postorbital portion; thick cranial roof; strongly pachyostosed supraorbital border; broad postorbital bar; relatively large temporal opening; relatively narrow intertemporal region; large incisors and medium sized canines and postcanines anteriorly larger than the posterior ones.” Battail and Surkov, 2000, p. 102.

Revised diagnosis for Ulemosaurus svijagensis: Autapomorphy: Dome shaped cranial roof caused by the inhomogeneous cranial pachyostosis restricted to the supraorbital region. Defining combination of characters: Short, narrow and high snout which tapers posteriorly onto a domed cranial roof; large temporal fenestra which is dorsoventrally deep while anteroposteriorly narrow; jaw joint in line with the posterior border of postorbital bar; dorsal extension of premaxilla extends half

the snout length; posteriorly narrow nasal; moderate sized canine with mesodistally elongated narrow heel.

4.6 Comparative Cranial Description

4.6.1 Skull Roof

The skulls of *Ulemosaurus* and *Tapinocaninus* are roughly the same size and both demonstrate pronounced pachyostosis of the bones of the skull roof which in turn has influenced the shape of the skulls. *Tapinocaninus* (particularly in the interorbital area and posterior portion of the cranium) has a relatively wide skull whereas that of *Ulemosaurus* is high and narrow. In *Ulemosaurus* cranial pachyostosis tends to be localized to the frontal and postfrontal. By contrast the skull roof of *Tapinocaninus*, is more homogenously pachyostosed to include thickening of the bones forming the zygoma and occipital crest. Accordingly, in *Tapinocaninus* the dorsal profile of the skull roof forms in a broad obtuse angle ($\sim 140^\circ$) relative to the palate; whereas in *Ulemosaurus* the angle is lower ($\sim 120^\circ$). The highest part of the *Tapinocaninus* skull is the anterior portion of the postorbital bar, whereas in *Ulemosaurus* the highest point is at the level of the posterior part of the postorbital bar. Accordingly in *Tapinocaninus* the skull roof slopes posteriorly from the level of the fronto-parietal suture, and in *Ulemosaurus* the posterior slope begins further posteriorly on the parietal.

The temporal fenestra in both genera is relatively large for a tapinocephalid dinocephalian but is antero-posteriorly narrower in *Ulemosaurus*. However in

Tapinocaninus this opening is antero-posteriorly narrower in NMQR 2986 than in NMQR 2987.

Premaxilla: The premaxillae (Fig. 4.2-4.5, 4.8-4.22) are paired, form the narrow anterior tip of the snout, and extend far posteriorly as a narrow elongated internarial process which contacts the nasal on the skull roof half-way along the pre-orbital region of the skull (Efremov 1940b, Rubidge, 1991). The contact of the premaxilla with the nasal is bifurcated such that the paired nasals extend anteriorly along the midline between the two premaxillae (PIN 2207/2-1, PIN 2207/1, NMQR 2897 and NMQR 2895). The premaxilla forms the anterior and dorsal border of the narial opening, and laterally contacts the maxilla. In *Ulemosaurus* (PIN 2207/2-1) and *Tapinocaninus* (NMQR 2897) the narial process of the premaxilla slopes posterodorsally giving a slight angle to the anterior tip of the snout. The premaxilla-maxilla suture on the lateral surface below the external naris (NMQR 2897, PIN 2207/2-1 and 2207/1) extends from the lower ventral border of the septomaxilla to the half way point along the alveolar margin of the fourth incisor as was interpreted previously for *Ulemosaurus* (Efremov 1940b, Ivakhnenko 1997). On the ventral surface in both species, it continues on the dental margin of the palate between the alveolus of fifth incisor and the canine as was previously interpreted for *Tapinocaninus* (Rubidge 1991). Ventral continuation of this suture was shown as occurring between the third and fourth incisors in Efremov (1940b) and Ivakhnenko (1997).

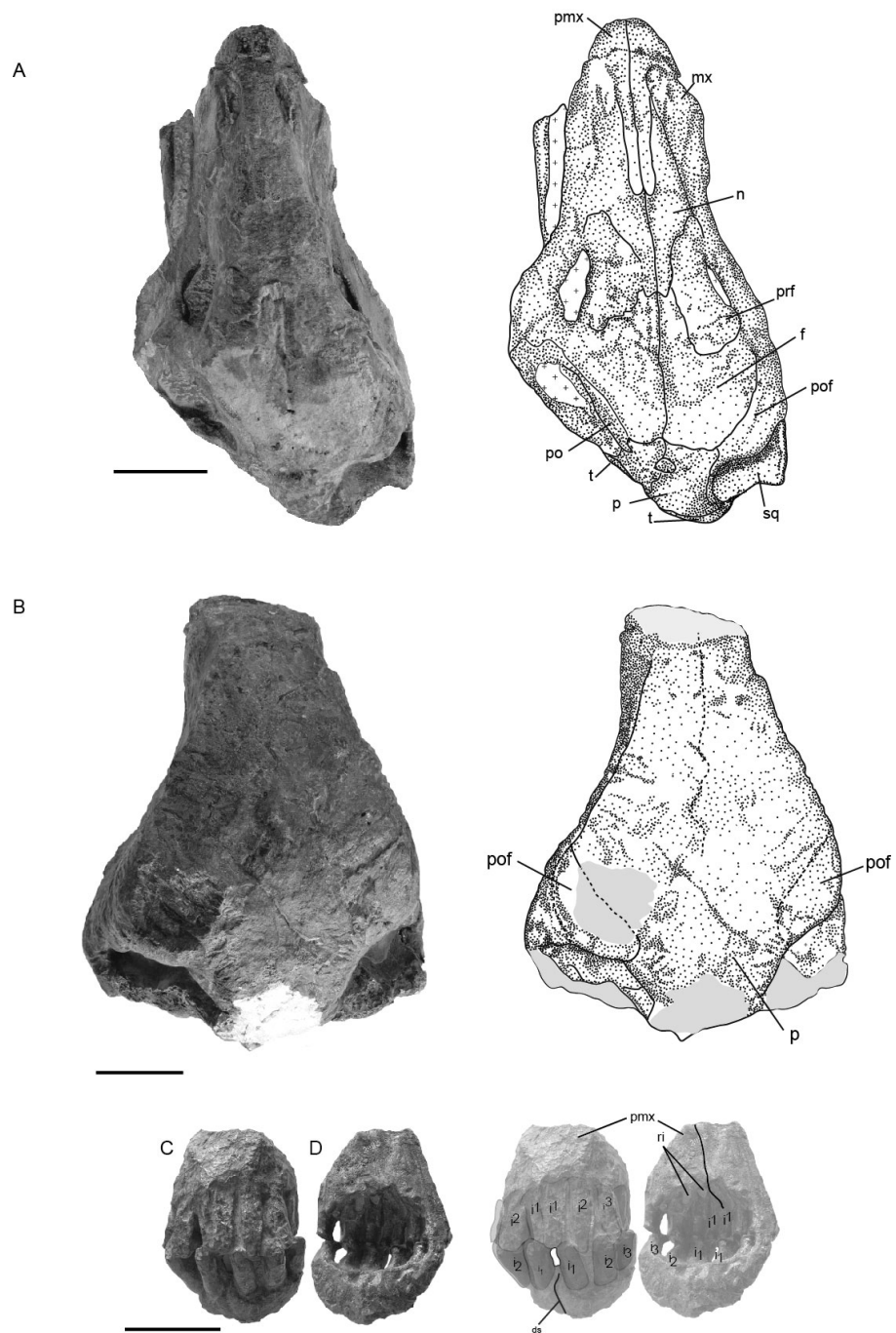


Figure 4.2. *Tapinocaninus*: skull roof photograph (left) & illustration (right) of NMQR 2985 (A), NMQR 2986 (B) and the anterior (C) and the medial view of the anterior portion of the snout. Scale:10cm.

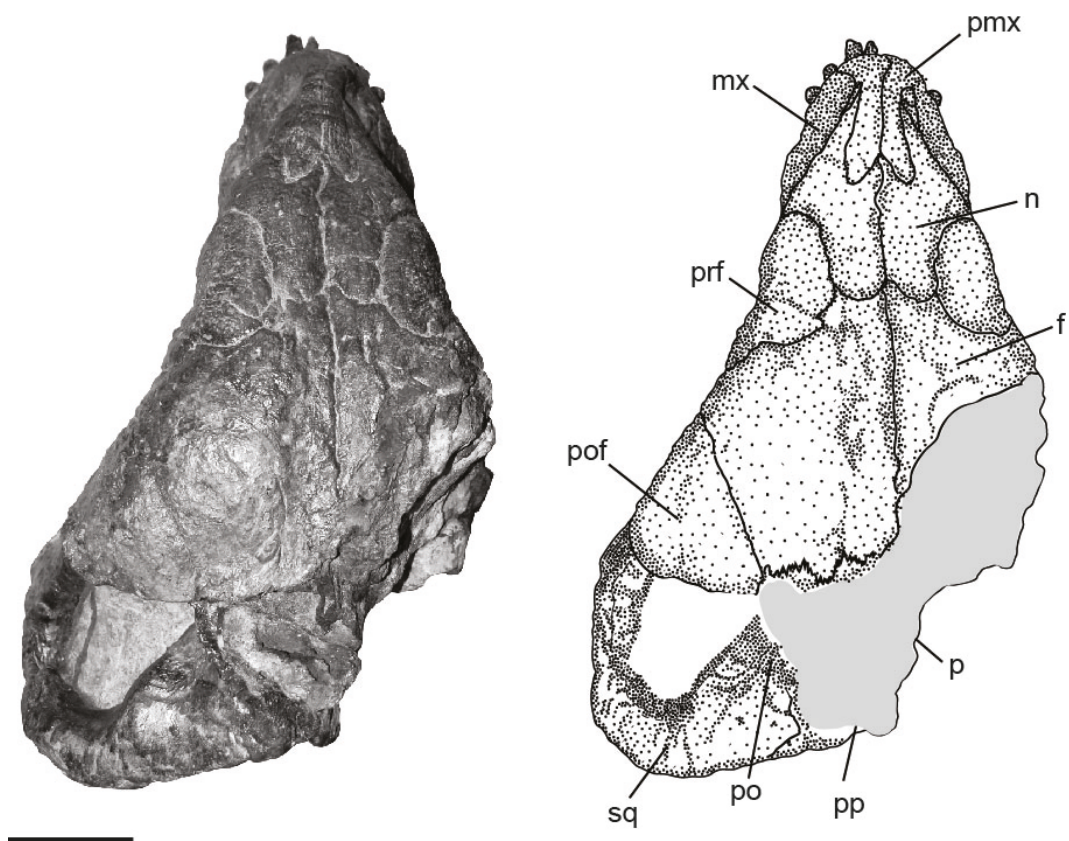


Figure 4. 3. *Tapinocanius*: skull roof photograph (left) & illustration (right) of NMQR 2987.
Scale: 10cm.

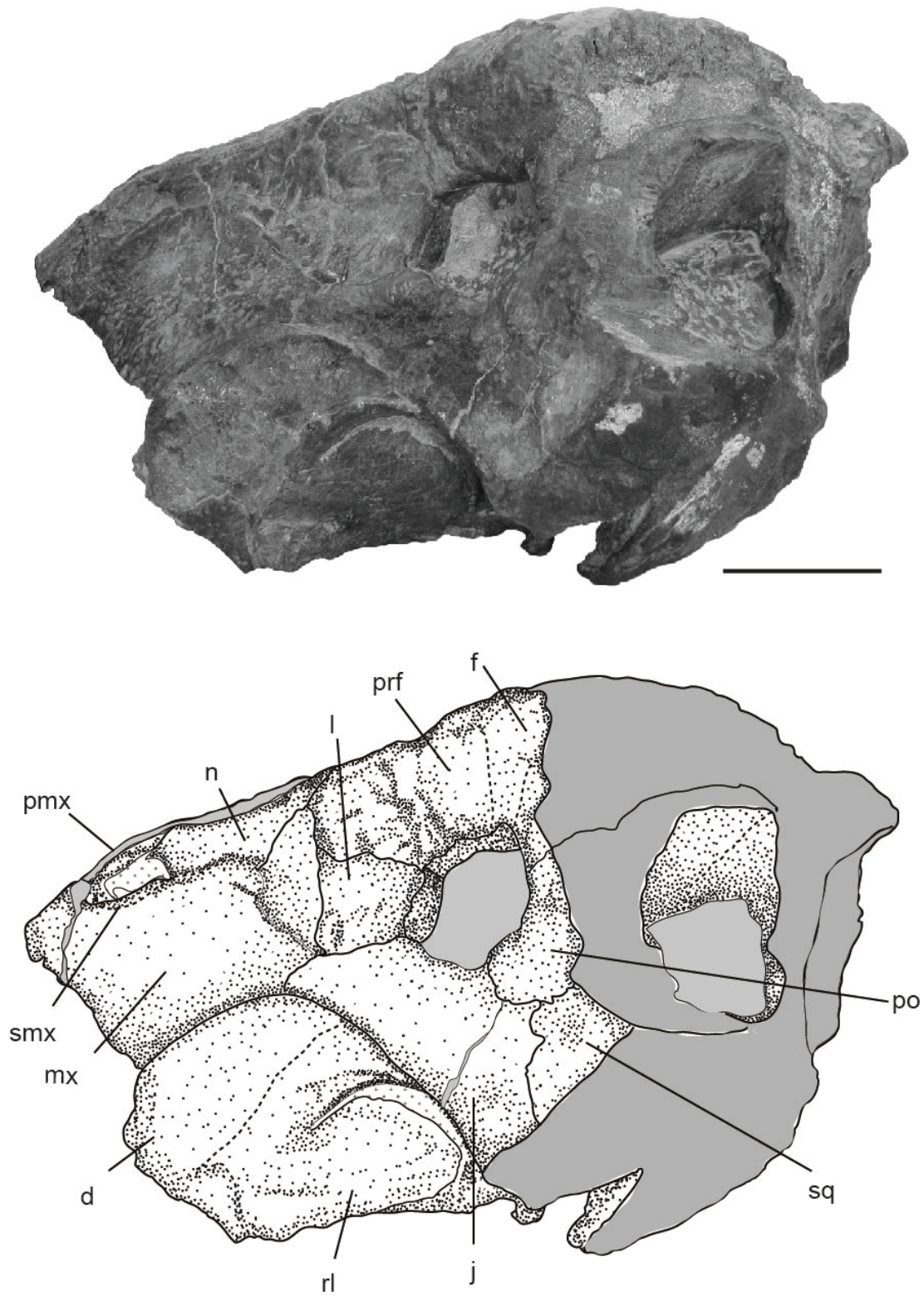


Figure 4.4. *Tapinocaninus*: left lateral view photograph (top) and illustration (bottom) of NMQR 2985. Scale: 10 cm.

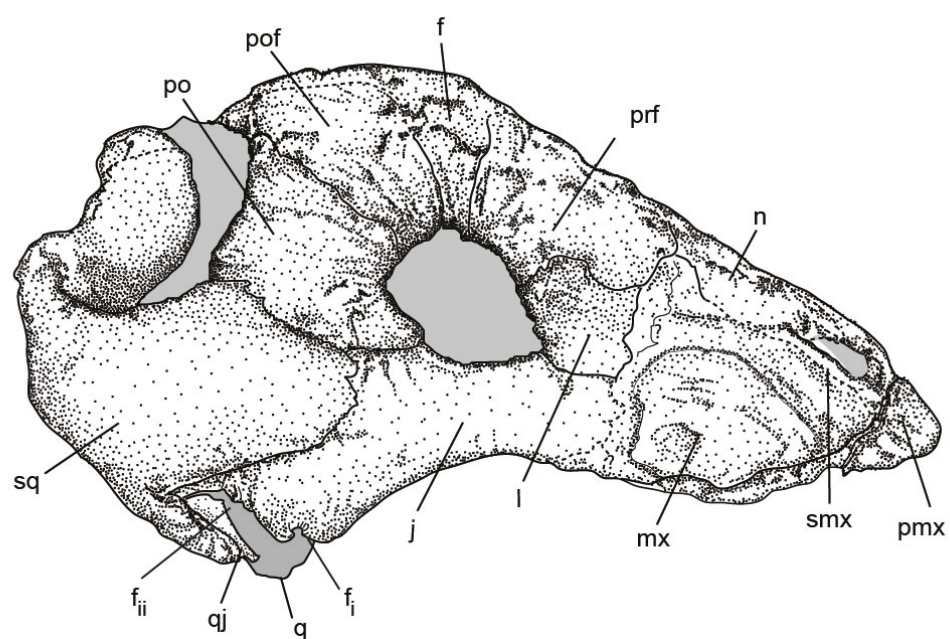


Figure 4.5. *Tapinocaninus*: right lateral view of NMQR 2985, photograph (top) and illustration (bottom). Scale: 10 cm.

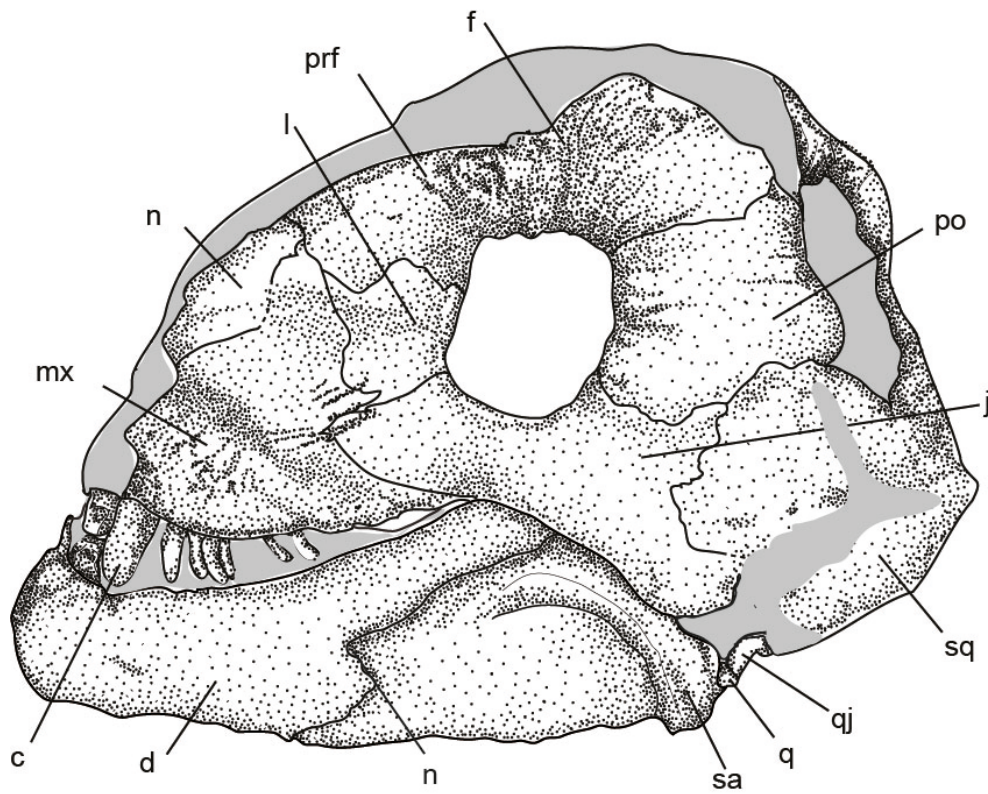


Figure 4.6. *Tapinocaninus*: left lateral view of NMQR 2986, photograph (top) and illustration (bottom). Scale: 10 cm.

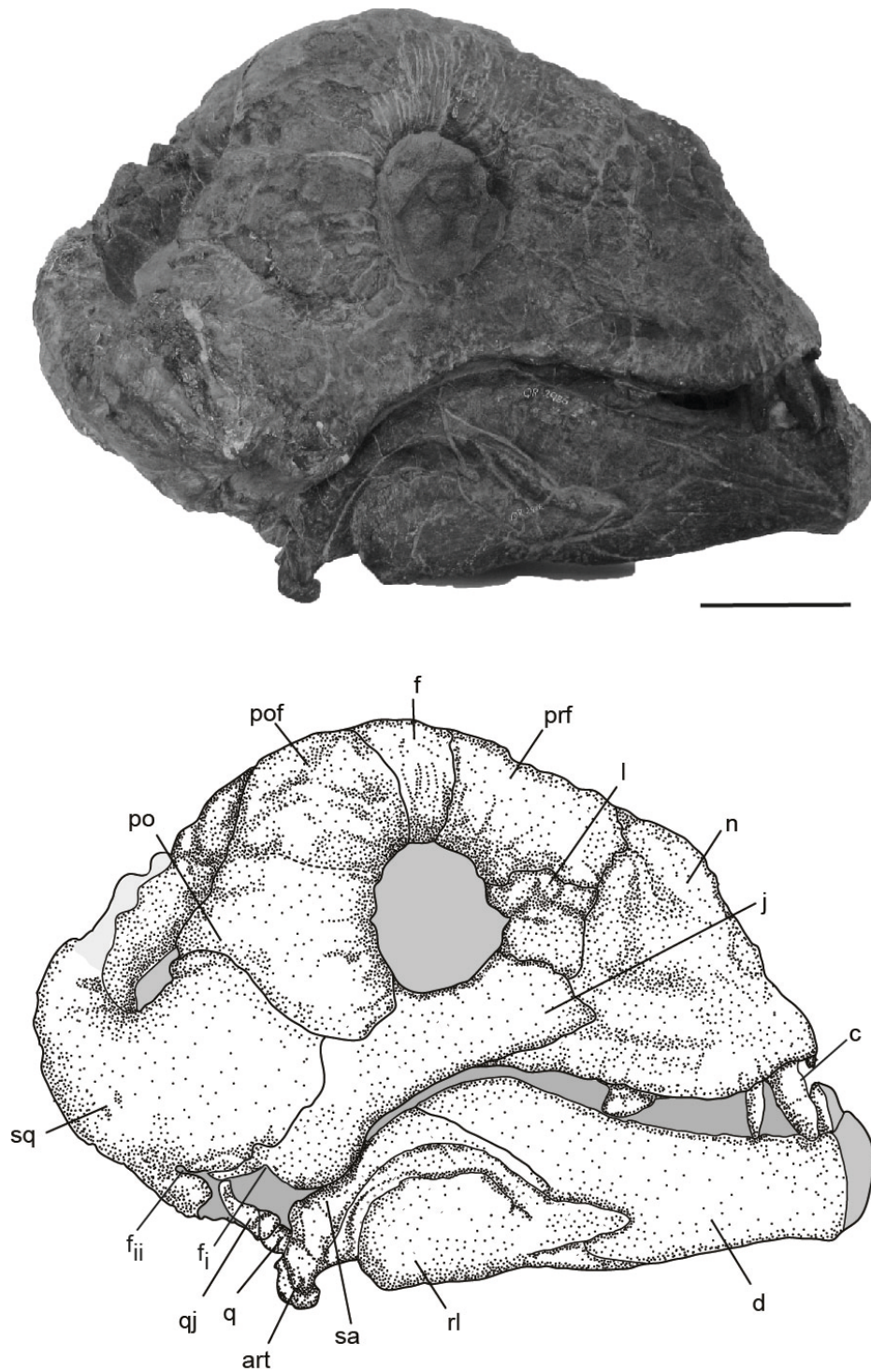


Figure 4.7. *Tapinocaninus*: right lateral view of NMQR 2986, photograph (top) and illustration (bottom). Scale: 10 cm.

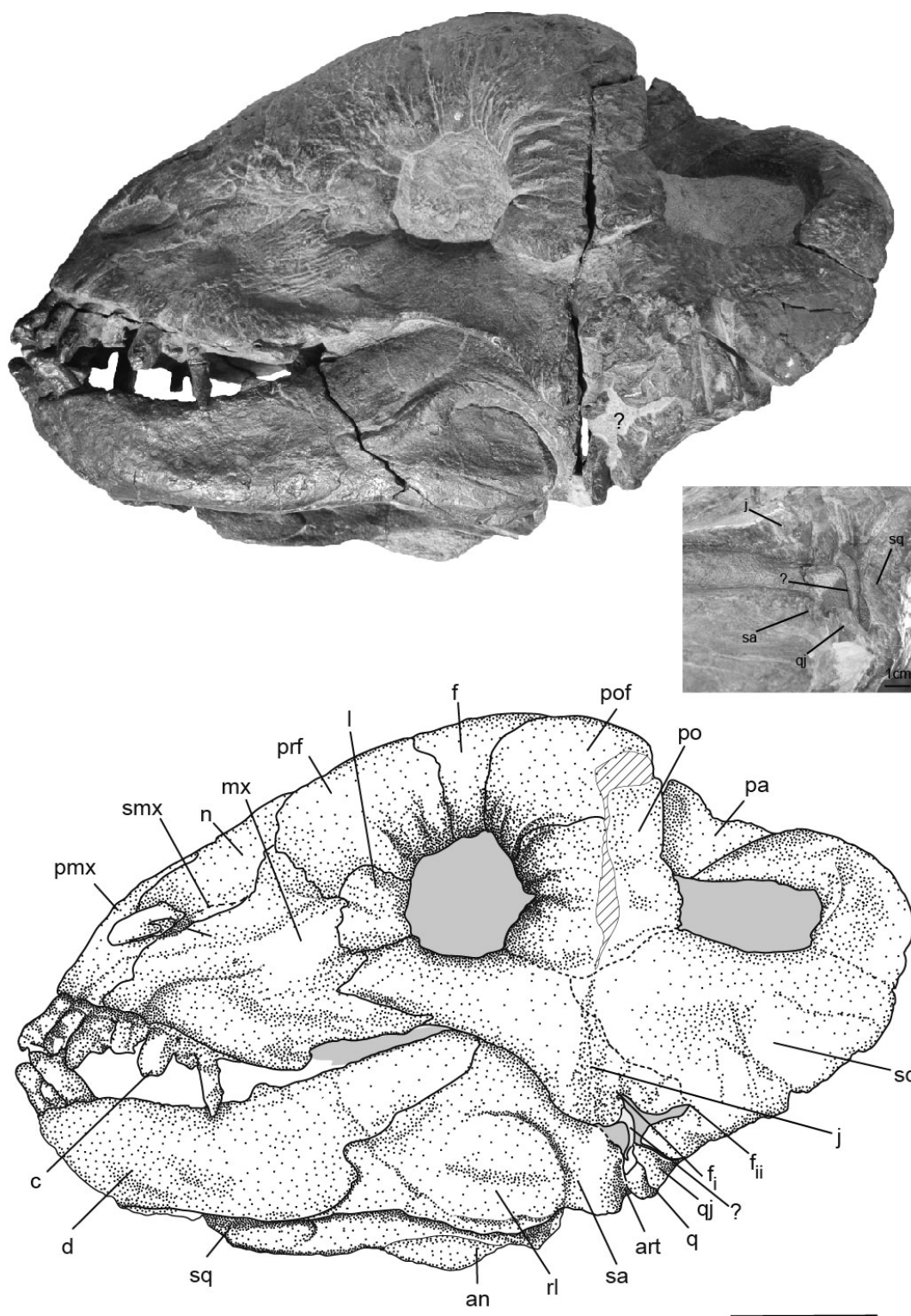


Figure 4.8. *Tapinocaninus*: left lateral view of NMQR 2987, photograph (top) & illustration (bottom). A close-up photo showing the area marked with question mark in the top photograph after preparation indicating the unidentified strip-like bone with question mark. Scale: 10 cm.

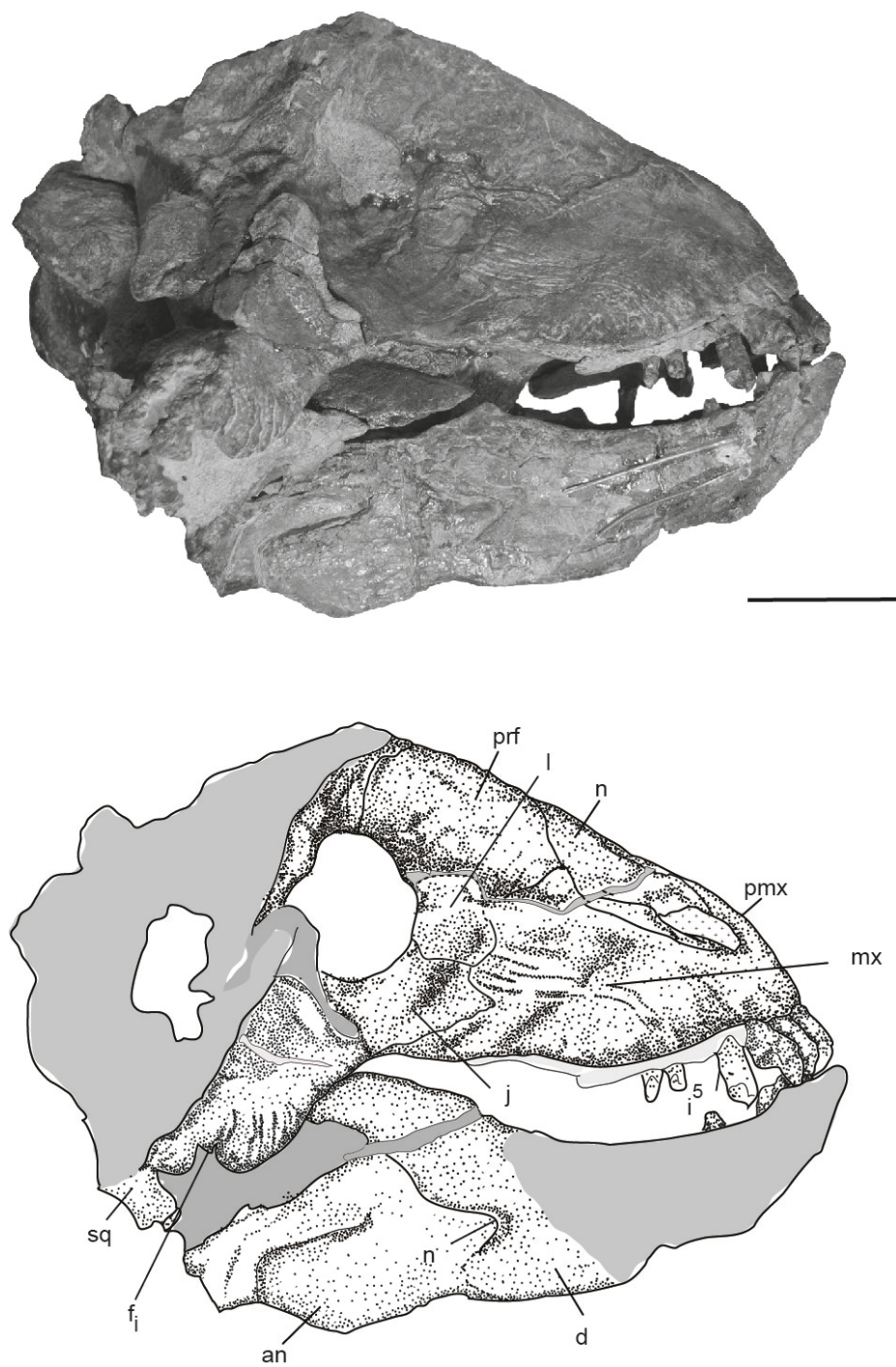


Figure 4.9. *Tapinocaninus*: right lateral view of NMQR 2987, photograph (top) & illustration (bottom). Scale: 10 cm.

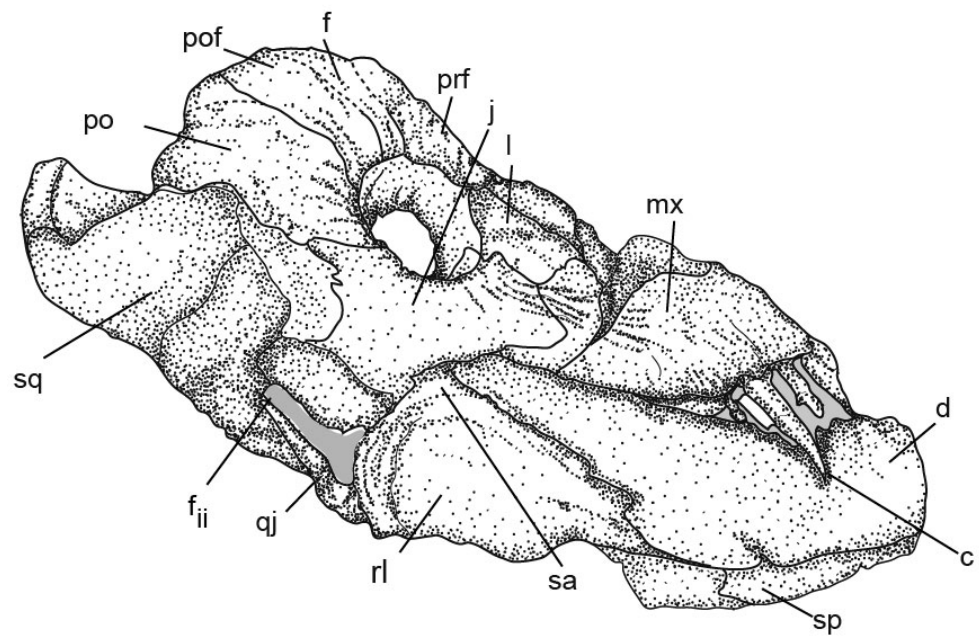
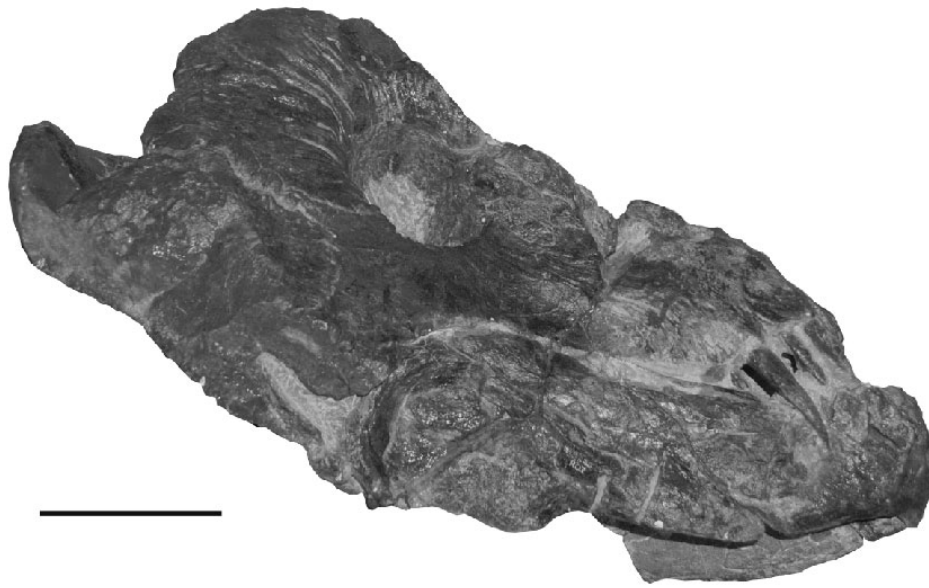


Figure 4.10. *Tapinocaninus*: right lateral view of ROZ K 95, photograph (top) & illustration (bottom). Scale: 10 cm.

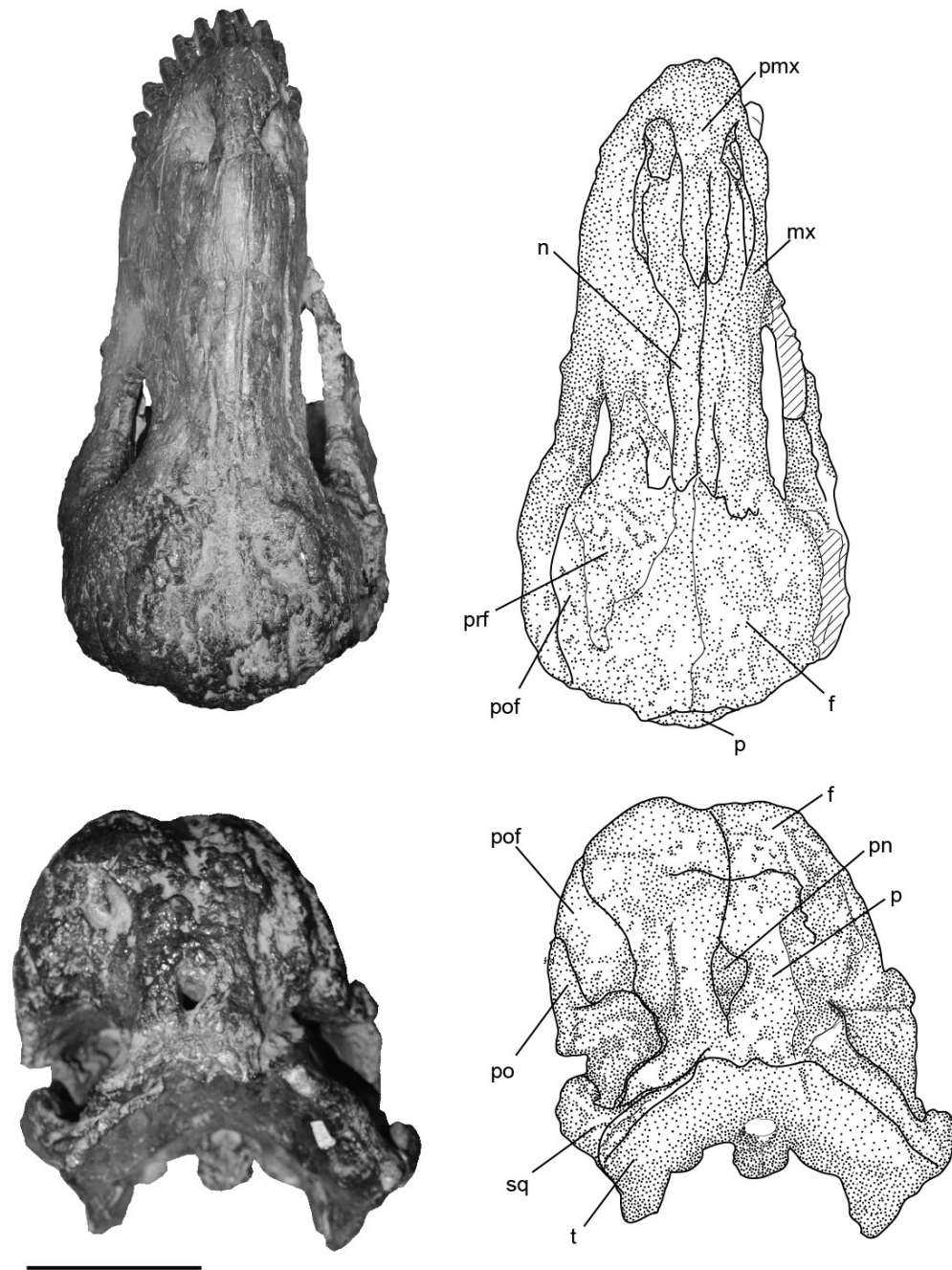


Figure 4.11. *Ulemosaurus*: skull roof of PIN2207/2 showing antero-dorsal (top) and postero-dorsal (bottom) views, photograph (left) and illustration (right). Scale: 10 cm.

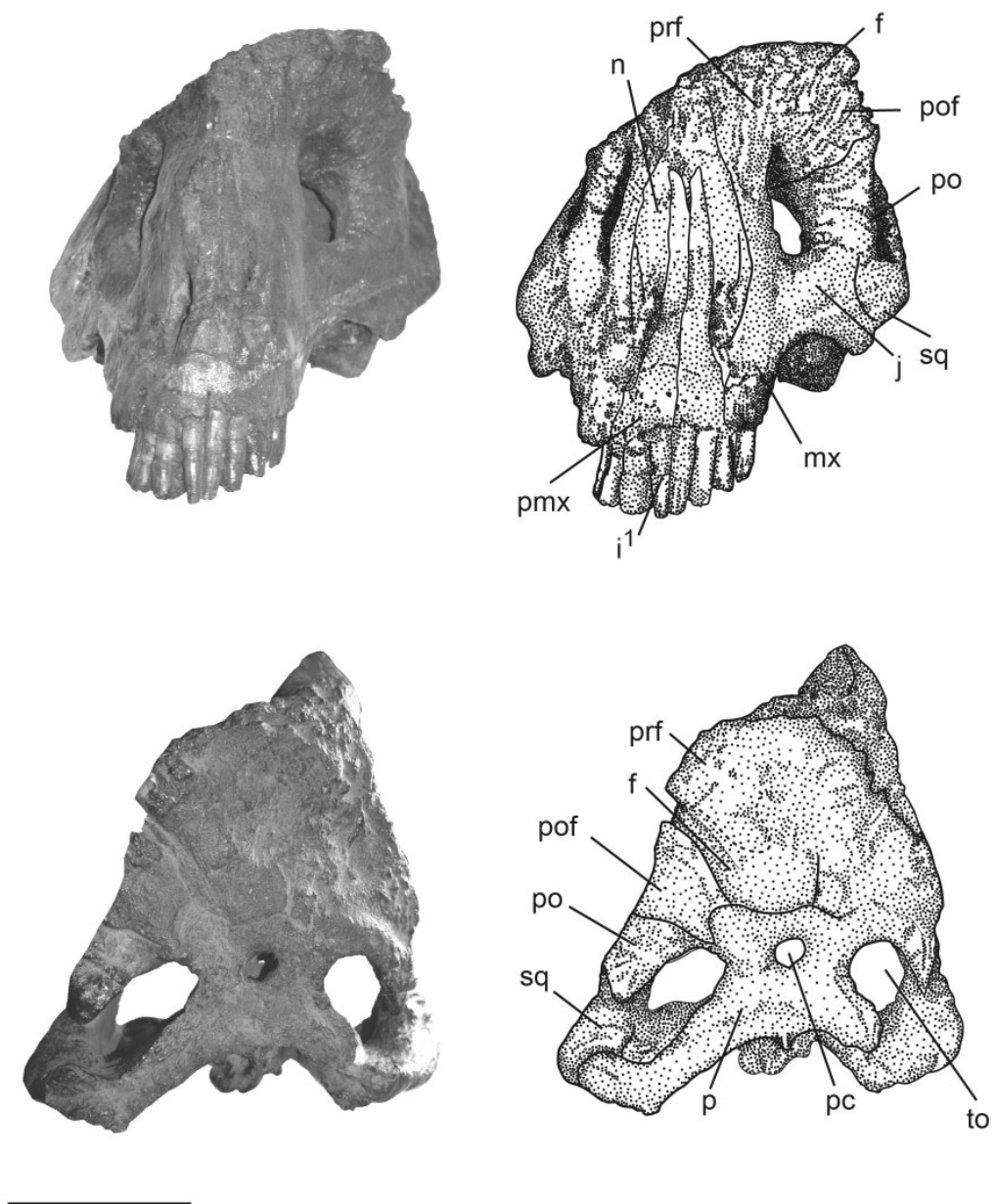


Figure 4.12. *Ulemosaurus*: skull roof of PIN2207/1 showing anterior (top) and dorsal (bottom) views, photograph (left) and illustration (right). Scale: 10 cm.

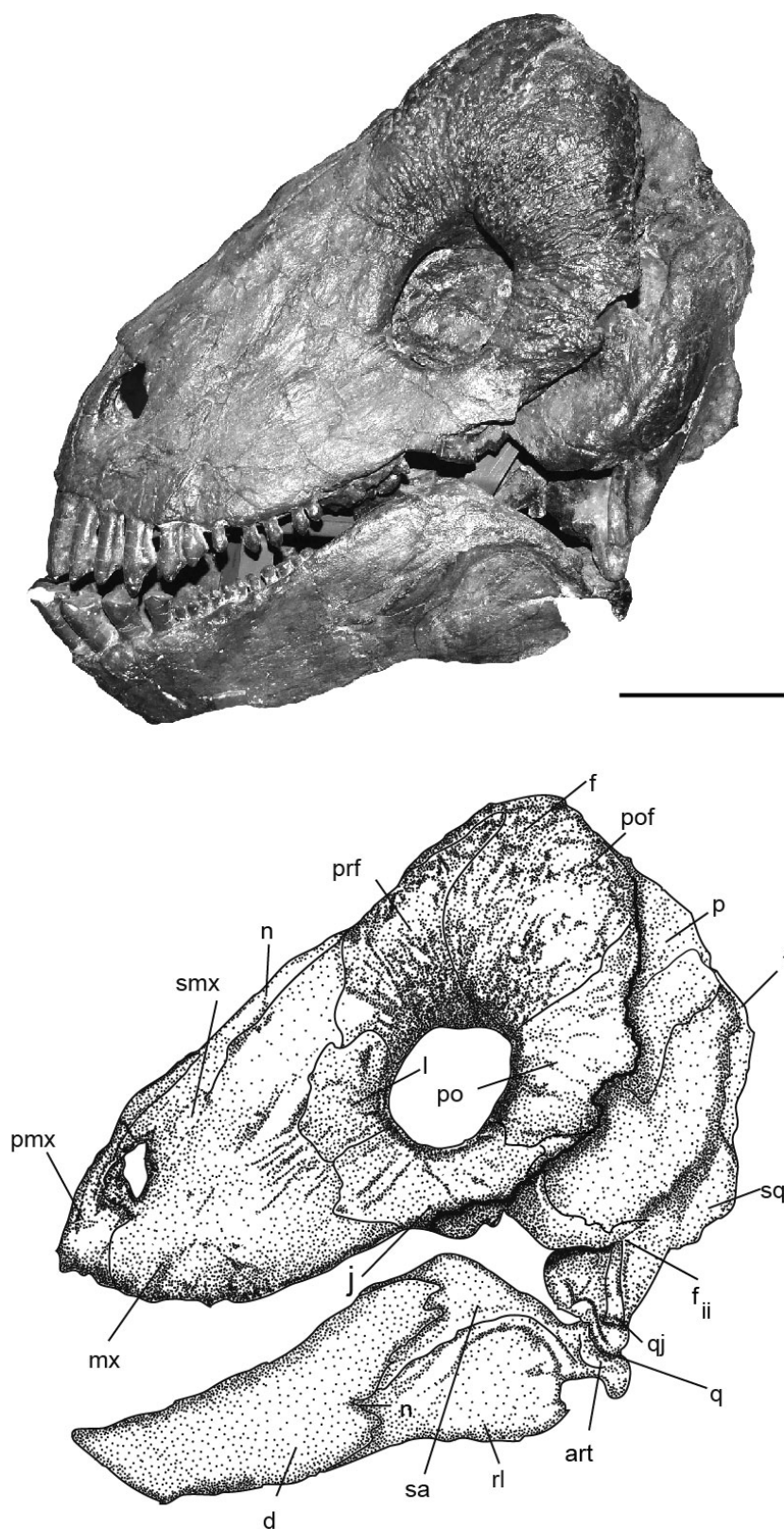


Figure 4.13. *Ulemosaurus*: left lateral view of PIN2207/2, photograph (top) and illustration (bottom). Scale: 10cm.

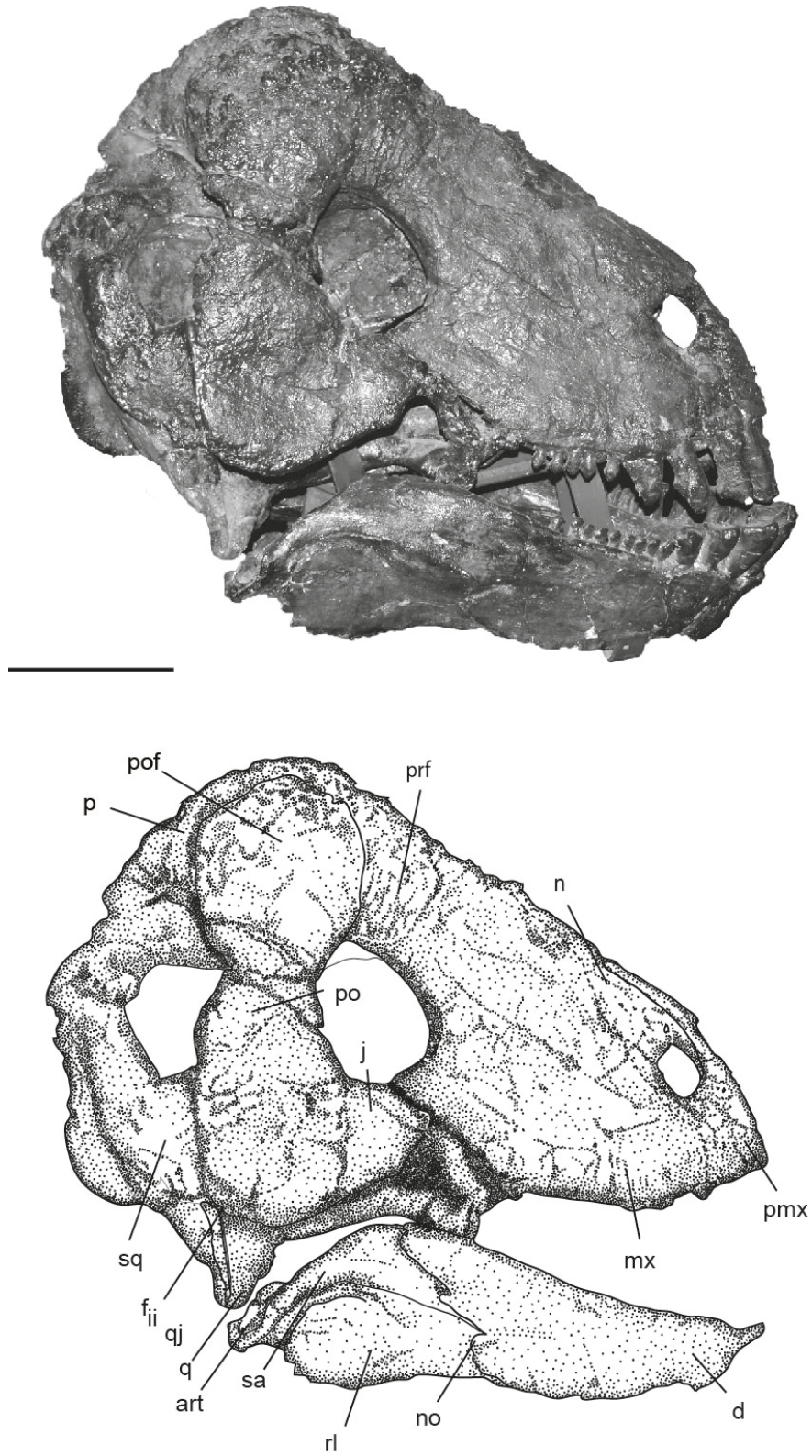


Figure 4.14. *Ulemosaurus*: right lateral view of PIN2207/2, photograph (top) and illustration (bottom). Scale: 10cm.

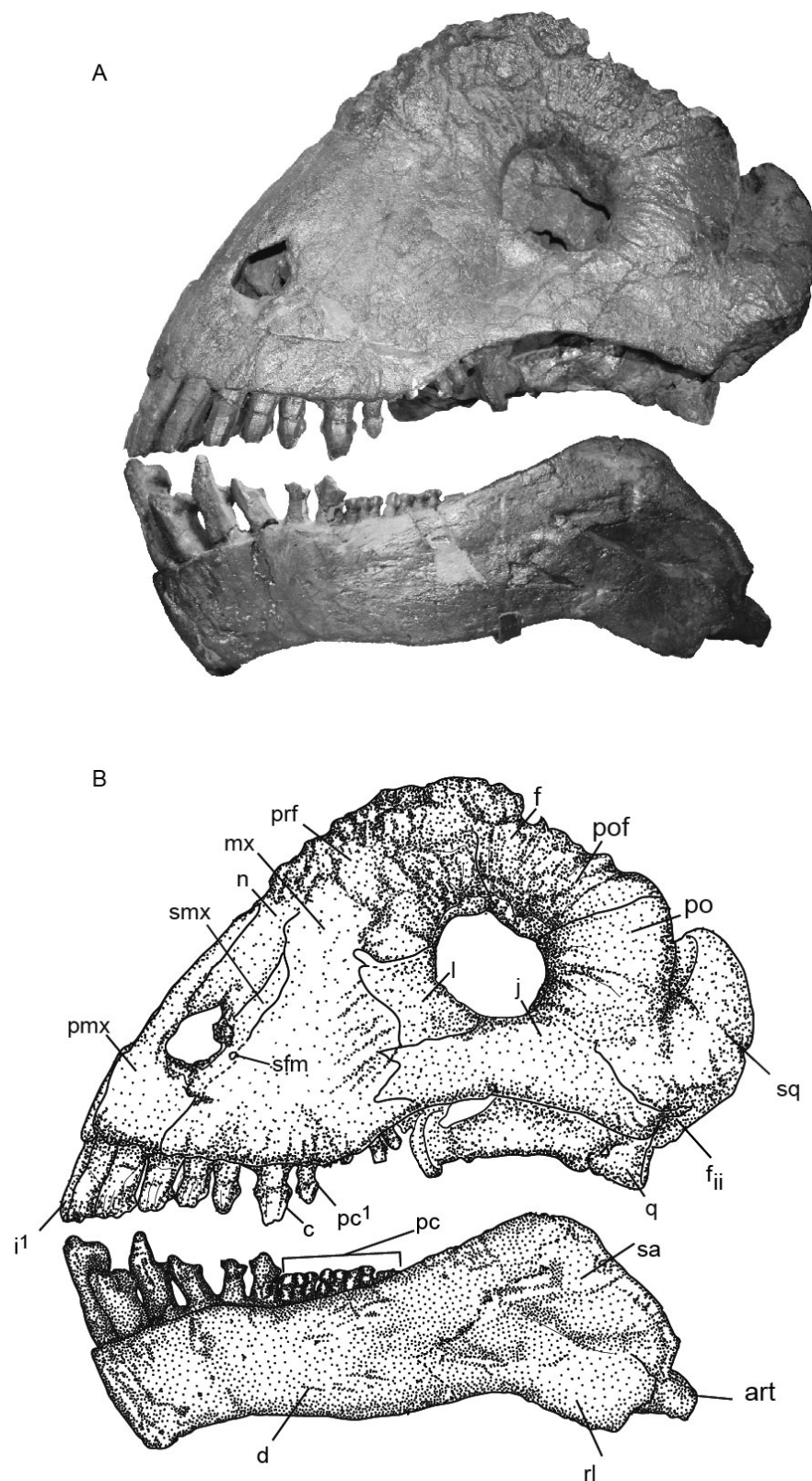


Figure 4.15. *Ulemosaurus*: left lateral view of PIN2207/1, photograph (top) and illustration (bottom). Scale: 10cm.

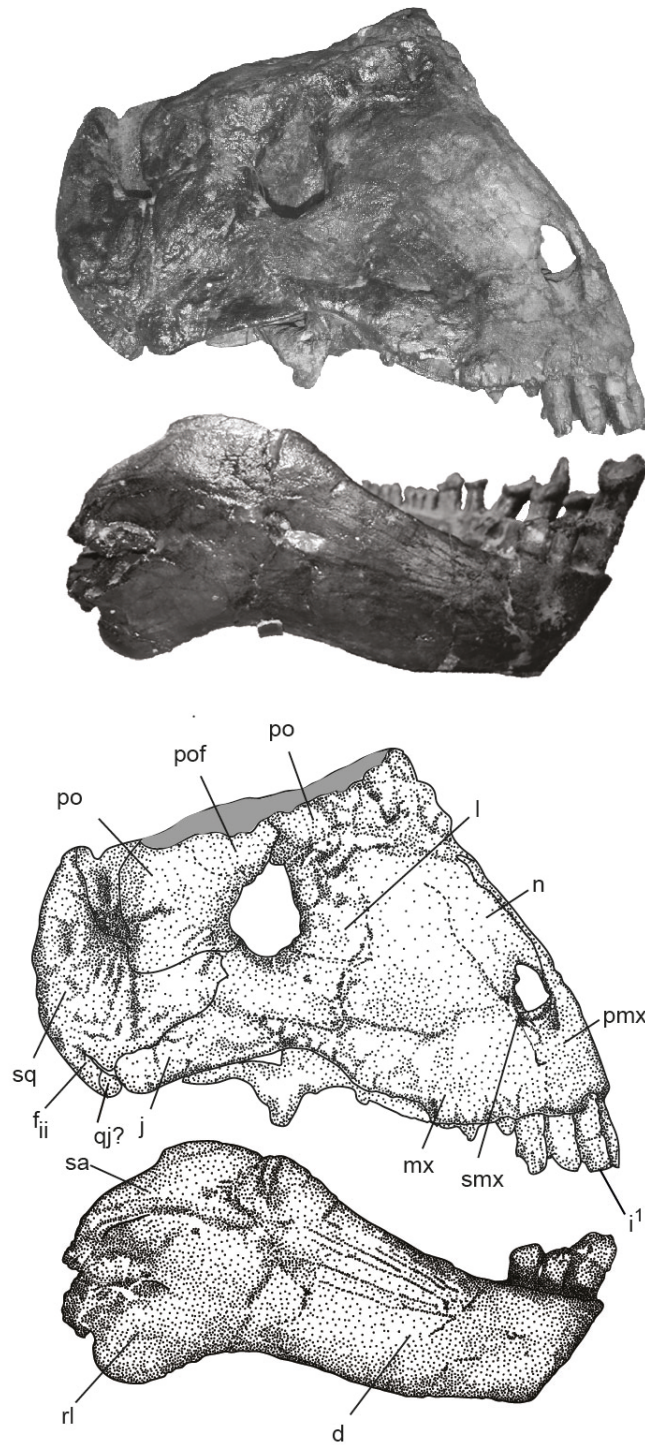


Figure 4.16. *Ulemosaurus*: right lateral view of PIN2207/1, photograph (top) and illustration (bottom). Scale: 10cm.

Septomaxilla: The septomaxilla (Figs. 4.5, 4.6, 4.8, 4.9, 4.13-16) covers the base of the external naris. Within the naris a posterodorsal portion of the septomaxilla extends along the lateral edge of the naris and ends with a hook shaped posterior portion, which curves medially before it gives rise to the facial extension of the septomaxilla (Fig. 4.17 A & B). The hook-like internarial process of the septomaxilla has greater medial extension in more derived tapinocephalids such as *Tapinocephalus* and *Struthiocephalus* (Fig. 4.17 C,D) and covers two thirds of the posterodorsal border of the narial opening in these forms. A septomaxillary foramen is present, in both *Ulemosaurus* (PIN 2207/1) and *Tapinocaninus* (NMQR 2987), as a small depression on the right side of the skull. In both genera, a posterior septomaxillary extension on the facial surface covers almost half of the antorbital snout length. Contra Efremov (1940) and in agreement with Ivakhnenko et al. (1997), the posterior margin of the facial exposure of the septomaxilla does not extend backwards further than the posterodorsal margin of the premaxillary process.

Nasal: On the skull roof the nasal dorsally is an elongated strip-like bone in *Ulemosaurus* (Figs. 4.11-15) and is broader in *Tapinocaninus* (Figs. 4.2-4.10). In *Ulemosaurus*, the posterior portion of the nasal has a dorsal swelling, which contributes to the height of the cranium and is not present in *Tapinocaninus*. In both genera the nasal contacts the lateral border of the premaxillary inter-narial process, the posterior margin of the external naris, the septomaxilla and further posteriorly the dorsolateral border of the maxilla and prefrontal, and anterior border of the frontal (Rubidge, 1991; Tchudinov, 1983). In the earlier descriptions

(Riabinin, 1938 and Efremov, 1940) the nasal of *Ulemosaurus* was described as being in contact with the lacrimal. Riabinin (1938) suggested extensive contact between these bones, whereas Efremov (1940b), interpreted this contact as reduced to a short suture with the apex of the dorsally elongated and anteroposteriorly short lacrimal process in front of the orbit. This suture was later correctly illustrated as having no contact with the lacrimal by Tchudinov (1983), Ivakhnenko et al. (1997) and Ivakhnenko (2003). In *Ulemosaurus* (PIN /2-1 and PIN 2207/1) the posterodorsal border of the external naris is deeply notched, but this notch is only incipiently present in *Tapinocaninus* (NMQR 2987).

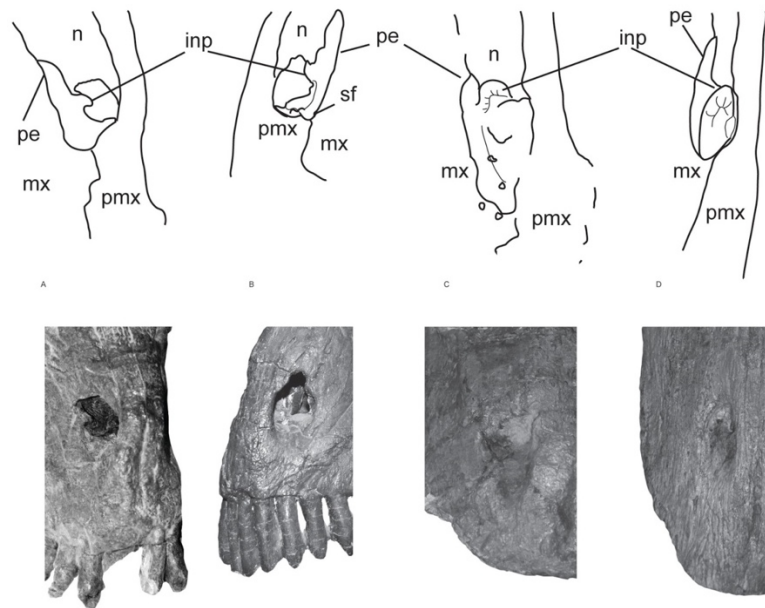


Figure 4.17. Photos (bottom) and illustrations (top) of lateral facial portions showing the morphology of the septomaxilla in (from left to right) the holotypes of *Tapinocaninus pamela* (NMQR 2987) (A) and *Ulemosaurus svijagensis* (PIN2207/2) (B) and the referred specimens of *Tapinocephalus atherstonei* (SAM-PK-2344) (C) and *Struthiocephalus whaitsi* (SAM-PK-K272) (D). C and D represent more derived short and long snouted tapinocephalids.

In *Tapinocaninus*, because of the degree of pachyostosis the posterior-end of the nasal transversely overhangs the maxilla. This contact is high in NMQR 2987 and NMQR 2986, is less pronounced in NMQR 2985 and does not occur in *Ulemosaurus*.

The external naris in both genera is positioned non-terminally, relatively high from the ventral margin of the premaxilla. In *Tapinocaninus*, the dorsoventral axis of the external naris is more or less parallel to the horizontal axis of the skull and it is dorsoventrally more expanded; whereas in *Ulemosaurus* there is a more acute angle in between long axis of the external naris and the horizontal plane of the skull and it is dorsoventrally less expanded than in *Ulemosaurus*.

Frontal: An anterolateral projection of the frontal (Figs. 4.2- 4.16, 4.18) contributes to the posterodorsal margin of the orbit in both genera. Posteriorly it is excluded from the dorsal border of the temporal fenestra in *Tapinocaninus* (Rubidge, 1991), whereas in *Ulemosaurus* it produces a narrow v-shaped projection on the dorsal border of the temporal fenestra between the postfrontal and parietal. In both genera the frontal is thickened dorsally. In *Tapinocaninus* pachyostosis extends forwards to the nasal, resulting in an increase the width of the interorbital region. This does not apply in *Ulemosaurus* where pachyostosis of the frontal is less developed and does not include the posterior portion of the nasal (Efremov, 1940).

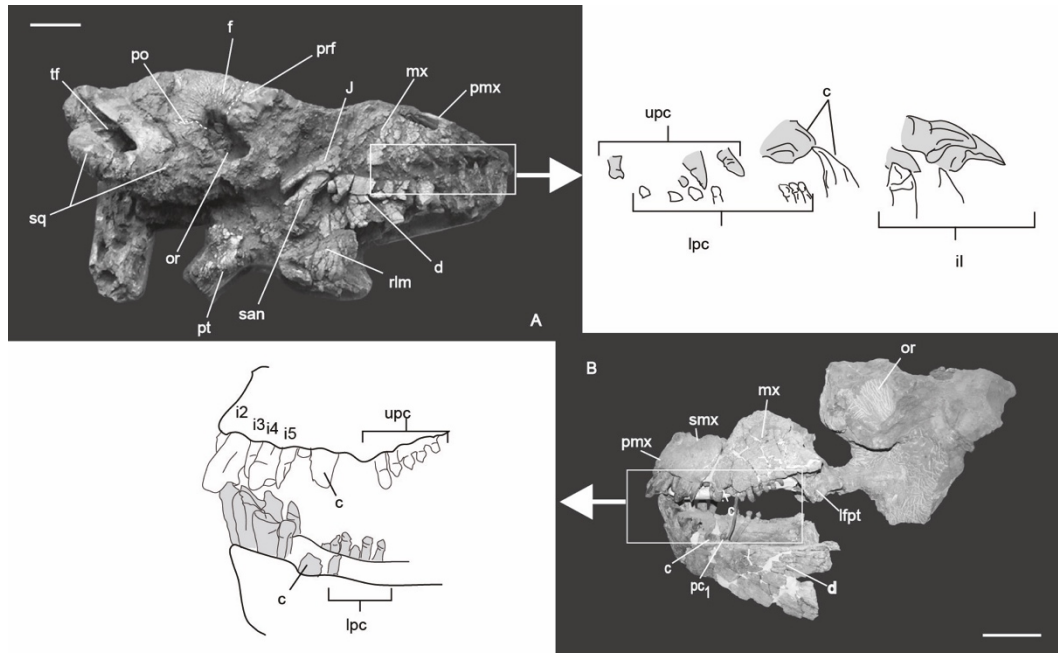


Figure 4.18. *Ulemosaurus*: lateral view and dentition of PIN 157/4 (A) and PIN 2972/1 (B). Scale: 10cm.

Parietal: The dorsal bone surface of the parietal (Figs. 4.2- 4.16, 4.18) is not well preserved in specimens of *Tapinocaninus* with the result that it is difficult to define the boundaries of this bone. An anterior zigzag suture is evident between the parietal and frontal in NMQR 2897 and NMQR 2895. In dorsal view the parietal has broad exposure and is larger than the frontal. The anterior process of the parietal is restricted laterally by the postorbital in *Ulemosaurus* (specimen PIN 2207/2-1) and does not contact the postfrontal on the medial border of the temporal fenestra (Efremov 1940b).

In both genera (PIN 2207/2-1 and NMQR 2897) the parietal forms a sutural contact with the postparietal on the posterior edge of the skull roof, and forms a short section of the posterior part of the temporal fenestra. There is a great deal of individual variation in the position of the pineal opening in different *Ulemosaurus* specimens which might be result of taphonomic distortion. In PIN 2207/1 the pineal foramen is present on the anterior half of the parietal, whereas it occurs on the posterior half in PIN 2207/2-1. The posterolateral process of the parietal in both genera forms a posterior suture with the postparietal (Efremov 1940b), and anteriorly with the postorbital and squamosal. The area surrounding the pineal foramen is flat and slopes laterally in both genera.

In the temporal opening posterodorsally along the contact with the parietal and squamosal a pronounced ridge is formed in *Tapinocaninus* which is best preserved in NMQR 2987.

Prefrontal: In each genus the prefrontal (Figs. 4.2- 4.16, 4.18) has different degrees of exposure in lateral view. In *Tapinocaninus* more than half of the prefrontal contributes to the dorsal portion of the skull roof and overhangs the posterior portion of the snout anterior to the orbit, whereas in *Ulemosaurus* it contributes to the skull roof with a deep and rather narrow projection which wedges into the frontal and thickens posteriorly (Efremov 1940b). Because of the greater exposure of the prefrontal on the lateral surface of the snout in *Tapinocaninus*, there is a long sutural contact between the anterior portion of the

prefrontal and the nasal. In *Ulemosaurus*, there is only a short suture between prefrontal and nasal, restricted to the posterior portion of the latter.

Postfrontal: In both genera the postfrontal (Figs. 4.2- 4.16, 4.18) is thickened and, as in the prefrontal and postorbital, it also has a sculptured surface texture in the area surrounding the orbit. Contrary to Efremov (1940b) the postfrontal forms the dorsal third of the postorbital bar in *Ulemosaurus* (PIN 2207/2-1_[w1]) and the posterodorsal margin of the orbit. From specimens NMQR 2987 and PIN 2207/2-1 the contribution of postfrontal to the medial portion of the anterior region of the temporal fenestra is blocked by the posterior extension of the frontal and the ascending extension of the postorbital.

Postorbital: In both genera the postorbital (Figs. 4.4-4.10, 4.13-4.16, 4.18) makes up most of the postorbital bar, contributes to the medial border of temporal fenestra and the posterior border of the orbit.

Maxilla: The maxilla (Figs. 4.4-4.8, 4.10, 4.13-4.16, 4.18) is a triangular bone in both taxa with its apex wedging between the nasal and the prefrontal. The apex is positioned dorsally in *Tapinocaninus* and posterodorsally in *Ulemosaurus* where the apex wedges more deeply and extends posteriorly on the dorsal snout margin, reaching approximately the level of the anterior margin of the orbit. In lateral view in both species the maxilla contacts the premaxilla anteriorly and the nasal anterodorsally, the lacrimal posteriorly and jugal posteroventrally, and ventrally it forms the alveolar margin. The alveolar margin of the maxilla is slightly upturned

anteriorly in both genera, and starts rising from the level of first postcanine as is evident in specimens ROZ-K 95, PIN 2207/2-1, PN 2207/1 and PIN 2972/1. Posterior to the canine, the ventral margin of the maxilla is gently convex. Posteriorly the ventral margin of the maxilla rises sharply below the jugal in *Ulemosaurus* but is more horizontal in *Tapinocaninus*. The maxillary protrusion over the alveolar region of the canine which is strongly manifested in *Tapinocaninus* (Rubidge 1991), is only weakly represented in *Ulemosaurus*. The stronger manifestation of this protrusion is the result of having a larger canine with deeper root in *Tapinocaninus*.

Posteroventrally the maxilla extends beyond the anterior end of the jugal. Riabinin (1938) and Efremov (1940b) illustrated this suture in PIN 2207/2-1 as continuing posteriorly as far as the anterior border of the orbit, whereas for PIN 2207/1 Riabinin (1938) shows this posterior projection of the maxilla as reaching the level of the posterior border of the orbit. Re-examination of this material manifests that the structure which (1938) interpreted as a suture in PIN 2207/1 is in fact a fracture on the bone surface and for both taxa the extension is more or less the same, and has been noted to extend posteriorly to the level of the anterior border of the orbit (see Rubidge 1991: figure 1).

The facial surface of the maxilla has a laterally convex outline in *Tapinocaninus* (NMQR 2897 and NMQR 2896). Posterior to the swollen area over the canine, the maxilla forms a ventral longitudinal ridge which is most prominent in NMQR 2897 and NMQR 2895. By contrast in *Ulemosaurus*, the maxillary surface of the

snout is smooth and flat without any depression and any ridge on the ventral margin.

In ventral view the maxilla projects between the premaxilla and palatine along the lateral margin of the choana. This projection is narrow in *Tapinocaninus* (NMQR2985) and more developed in *Ulemosaurus*. In *Tapinocaninus* specimen NMQR 2987 the maxilla is totally excluded from the choana margin and the palatine contacts the premaxilla.

Lacrima: The lacrimal (Figs. 4.4-4.18, 4.10, 4.13-4.16, 4.18) is a rectangular bone in both genera. It forms a sutural contact with the prefrontal anterodorsally, the maxilla anteriorly (partly anterodorsally in *Ulemosaurus* PIN2207/1-1; and anteroventrally in *Tapinocaninus* NMQR 2987), and the jugal ventrally. It is a relatively taller bone in *Tapinocaninus* (height is between 26-28 % of the skull height), whereas it is 23 % of the skull height in *Ulemosaurus*. The ratio of the length of the lacrimal to the preorbital skull length is similar in both genera. In *Ulemosaurus* the prefrontal contacts the lacrimal for two-thirds of its dorsal margin, the remaining third being in contact the maxilla. In *Tapinocaninus*, the lacrimal contacts the maxilla only along its anterior margin.

Jugal: The jugal (Figs. 4.4-4.8, 4.10, 4.13-4.16, 4.18), in both genera, is a long dorsoventrally narrow bone (relative to most other therapsids it is relatively short and extremely tall) with a pointed anterodorsal suture with the maxilla. It forms

the ventral border of the lacrimal, the orbit and meets the postorbital posterodorsally. Posteriorly the jugal has a convex suture with the squamosal.

In *Tapinocaninus* the posterior portion of the jugal is thickened and forms a fissure (f_i) before it continues below the squamosal to contact the quadratojugal. This could be a breakage or a crease around the pachyostosed bones. A second fissure (f_{ii}) occurs on the squamosal-end and is closed by the lateral appendage of the quadrate -jugal. Only the latter fissure is represented in *Ulemosaurus*. In NMQR2987, there is a small strip-like unidentified bone between the articular and the posterior extension of the jugal which has not been recognised in any other specimens.

Squamosal: The squamosal (Fig. 4.2-4.5, 4.8-4.16, 4.18) is a large bone in both genera and is more robust and pachyostosed in *Tapinocaninus* compared to that of *Ulemosaurus*. In lateral view it contacts the jugal anteriorly, the postorbital dorsally, and posteriorly it forms the ventral and the posterior ascending branch of the temporal fenestra. In dorsal view the squamosal expands and meets the posterior extension of the postorbital and the parietal dorsomedially. The zygomatic portion of the squamosal is considerably wider and thicker in *Tapinocaninus* than in *Ulemosaurus*. Because of the different shape of the temporal fenestra in the two genera, the rising branch of the squamosal appears almost at right angle to the horizontal plane of the skull in *Ulemosaurus*, whereas in *Tapinocaninus* it broadens horizontally. In both genera the dorsal portion of the

squamosal contacts the parietal and postorbital on the posterodorsal border of the temporal opening.

On the occiput the squamosal forms a large part of the occipital crest and contacts the tabular dorsomedially, the paraoccipital process of the opisthotic medially, and the dorsal process of the quadrate and the quadratojugal ventrally. Along its medial contact with the tabular, the squamosal forms a vertical ridge. In *Ulemosaurus* this ridge is relatively thin and diminishes ventrally close to the quadrate contact. In *Tapinocaninus* the ridge is thick and forms a scroll-like medial border over the distal end of the paraoccipital process of the opisthotic. The exposed squamosal surface adjacent to the paraoccipital process is here called the squamosal facet and is wider in *Tapinocaninus*. A dorsoventrally elongated sulcus (defined as the auditory meatus in Rubidge, 1991 and a depression in Efremov, 1940b) is present between the thickened lateral margin of the squamosal and its medial ridge and the distal end of the paraoccipital in both genera.

Quadratojugal: The quadratojugal (Figs. 4.5-8, 4.10, 4.13-16) is a small plate-like bone that is positioned ventro-laterally on the skull in both genera (Riabinin, 1938, Efremov, 1940b, Rubidge, 1991). Dorsomedially it is overlapped by the squamosal and ventrally it covers the lateral condyle of the quadrate. Dorsally the exposed portion of the quadratojugal has two extensions, one directed anterolaterally and the other posteriorly.

4.6.2 Palate

The palates of both genera are much better preserved and prepared in *Tapinocaninus* and *Ulemosaurus* than in any other tapinocephalid genus, which facilitates more detailed description. The pre-maxillary portion of the palate is anteriorly very narrow in both genera, contra the broadly expanded premaxilla illustrated for *Ulemosaurus* in Ivakhnenko (1997 and 2003). Different from the condition in *Ulemosaurus*, in *Tapinocaninus* the premaxilla (lateral to the vomer) forms a platform with wide palatal exposure. In *Ulemosaurus* this palatal exposure of the premaxilla is narrow.

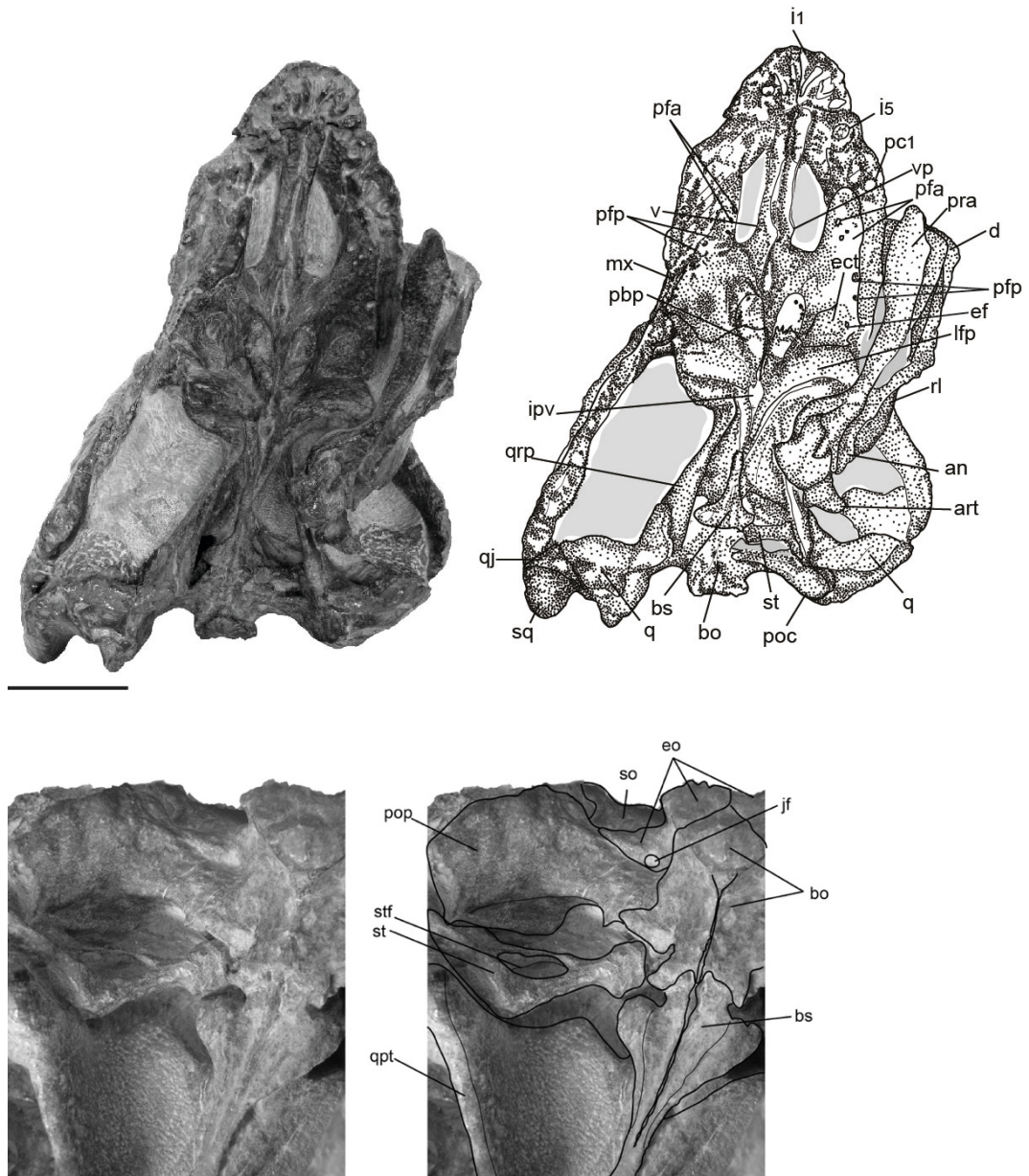


Figure 4.19. *Tapinocaninus* palate: photograph (left) and illustration (right) of NMQR 2985 (top) and basicranium of NMQR 2985 (bottom) with line drawings on photo showing details of stapes and its relationship to the basioccipital, basisphenoid and quadrate bones. Scale bar: 10cm.palate. Scale bar: 10cm.

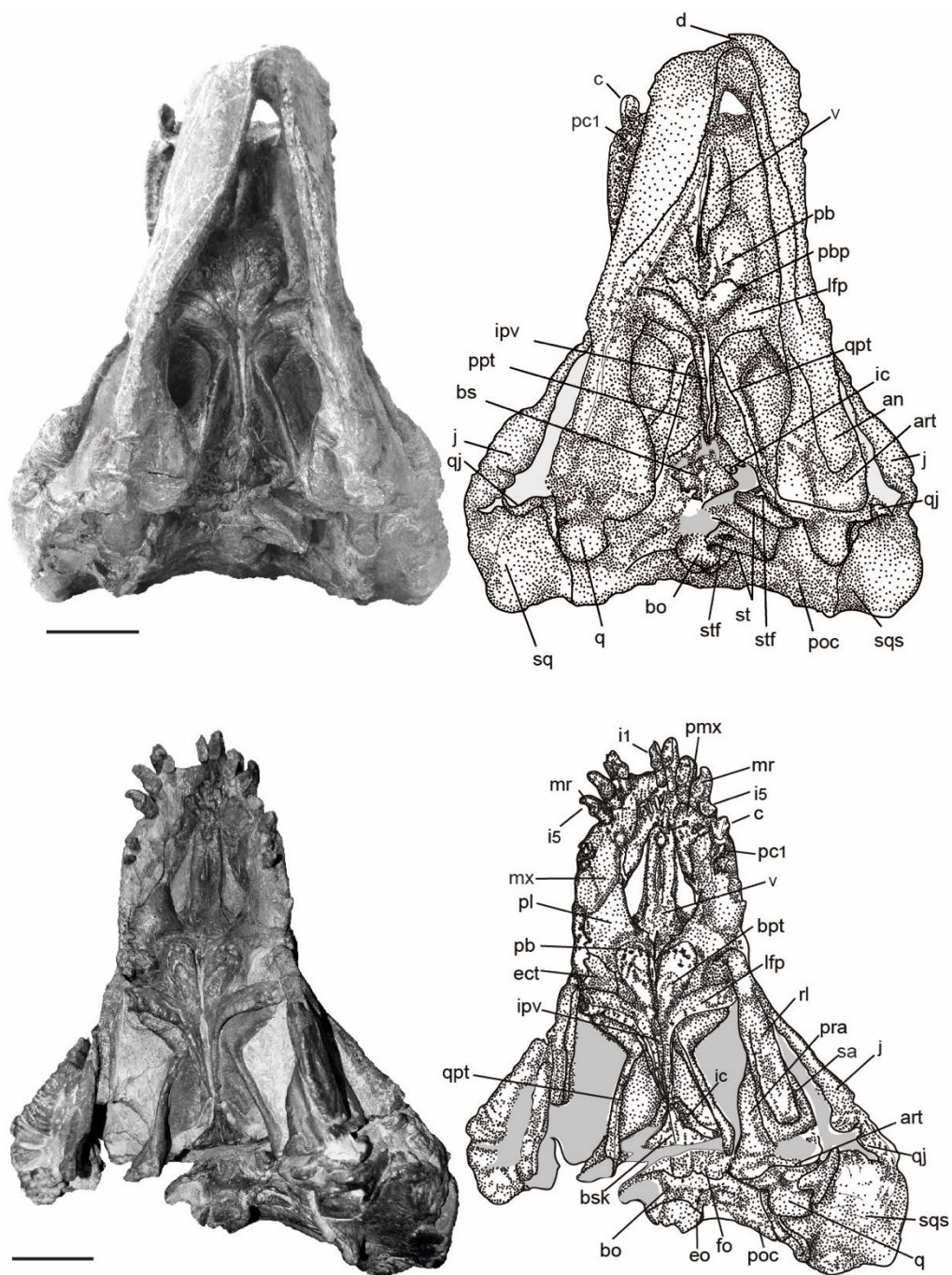


Figure 4.20. *Tapinocaninus* palate: photograph (left) and illustration (right) of NMQR 2986 (top) and NMQR 2987 (bottom) palate. Scale bar: 10cm.

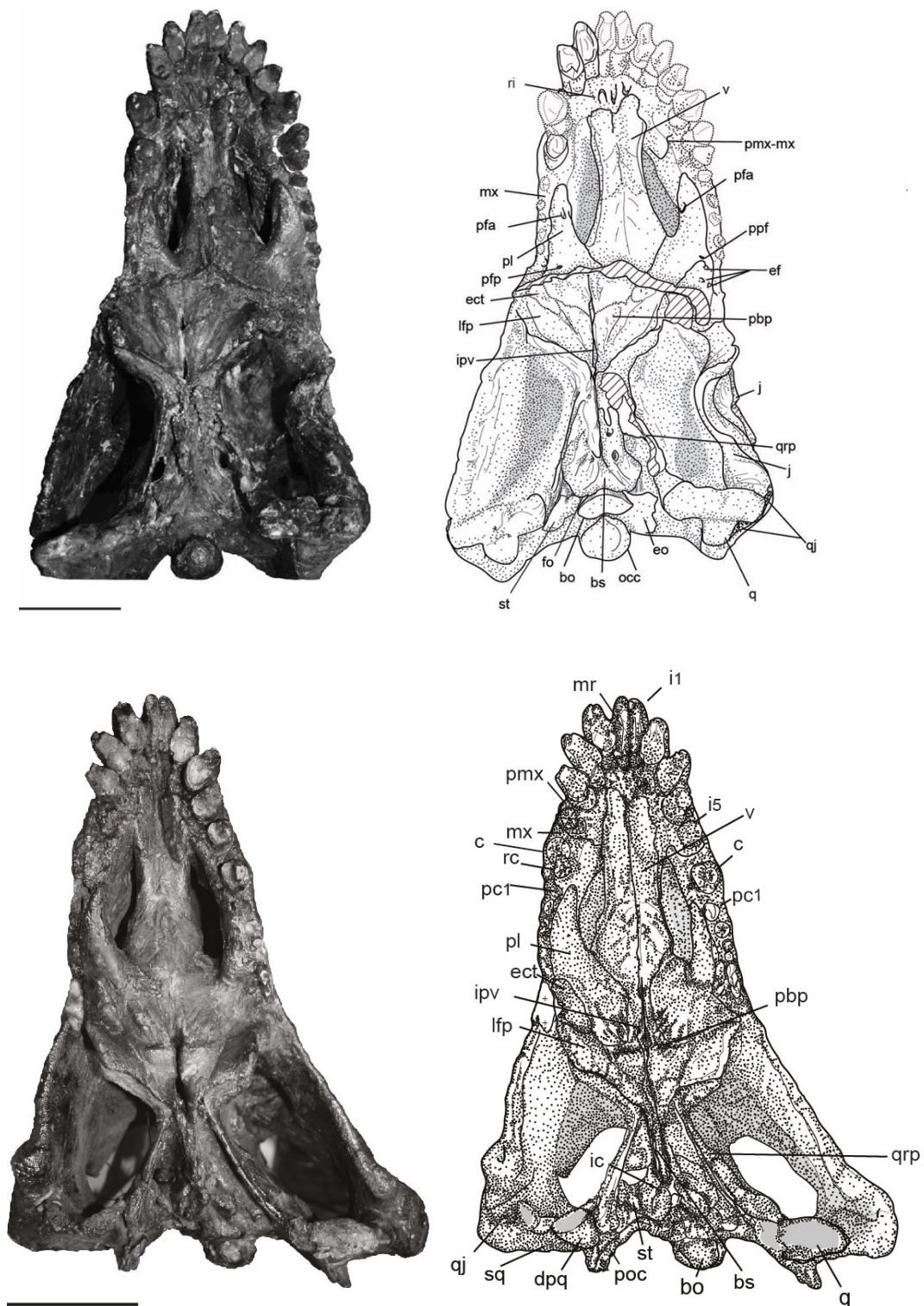


Figure 4.21. *Ulemosaurus* palatal view: photograph (left) and illustration (right) of PIN 2207/1 (top) and PIN 2207/2 (bottom). Scale: 10cm.

Vomer: The vomer of the two genera differs greatly in morphology. In both *Tapinocaninus* (Figs. 4.19, 4.20) and *Ulemosaurus* (Figs. 4.21), the vomer is present as a paired elongated bone, which abuts anteriorly on the posteroventral side of the premaxilla and broadens posteriorly to form the posterior margin of the choana. Posteriorly it meets the palatine with a long oblique sutural contact extending posteromedially toward the midline (Efremov 1940b, Tatarinov 1965, Rubidge 1991). Contra the situation in *Ulemosaurus*, the posterior portion of the vomer in *Tapinocaninus* has a broad lateral expansion and, at its most posterior extent, thins dramatically to meet the pterygoid.

Along the ventral midline the paired vomers form a groove along the entire bone in *Tapinocaninus* (Rubidge 1991), while it is grooved only anteriorly in *Ulemosaurus*. In *Tapinocaninus*, on the sides of the midline groove, the vomer forms lateral ridges (NMQR 2987 and NMQR 2985) which project ventrally on the posterior half of the vomer. In specimen NMQR 2985 a low median ridge is present along the midline at the posterior end of the vomer and extends onto the anterior part of the pterygoid. The lateral ridges are well developed in *Tapinocaninus* specimen NMQR 2987, more posteriorly the ridges are more pronounced in NMQR 2985.

Lateral to the vomers both genera have short elliptical choanae (in *Tapinocaninus* the choana narrows anteriorly) extending backwards from the level of the fourth and fifth incisor to the level of the fourth postcanine in *Ulemosaurus* (PIN 2207/1,

PIN 2207/2-1) and even further posteriorly in *Tapinocaninus* (NMQR 2985, 2987). The choanal borders are formed anterolaterally by the premaxilla, laterally by the maxilla, posterolaterally by the palatine for at least half of the border and medially by the vomer. In *Tapinocaninus* the maxillary contribution is very short and is much longer in *Ulemosaurus*. In *Tapinocaninus* (specimen NMQR 2987) the choanal area narrows anteriorly, possibly be as a result of distortion, which has resulted in enlarged exposure of the lateral margin of the premaxilla in the ventral view.

Palatine: The palatine (Figs. Figs. 4.19, 4.20, 4.21) is a broad bone in both genera. Anteromedially it contacts the vomer and anterolaterally it overlies the maxillary medial surface. Foramina are present on the anterior projection of the palatine in both genera. *Ulemosaurus* has two foramina, a large one which is anteromedially positioned and another smaller one which is positioned on the border of the maxilla posterior to the large one. *Tapinocaninus* (NMQR 2985) by contrast has three foramina, one large positioned anteromedially on the palatine and the other two are smaller and are positioned ventral to the anteromedial foramen. On the posterior portion of the palatine in *Tapinocaninus* are two additional foramina positioned closer to the border with the maxilla and have been called posterior palatine foramina (van den Heever, 1994). Only one posterior palatine foramen is present in *Ulemosaurus* (Efremov, 1940).

The palatine bosses of *Ulemosaurus* form a low ridge compared to the well-developed boss structure of *Tapinocaninus*. A suture separates the palatine and

pterygoid bosses with the palatine portion of the boss being notably broader than the pterygoid portion although these bosses are confluent in both genera. In *Tapinocaninus* the palatine bosses are high, large, and anteroposteriorly elongated, whereas in *Ulemosaurus* the palatine does not form prominent bosses. Along the ventral midline the left and right palatine and pterygoid bosses are separated by the vomer. Here the bosses are separated by a deep canal which is closed posteriorly by the pterygoid boss. In *Tapinocaninus* the roots of several palatine teeth are present on the anterior regions of the palatine boss in specimen NMQR2985, and alveoli are present in specimens NMQR2987, NMQR 2987, NMQR 2986, ROZ-K 95 (Rubidge 1991). In *Ulemosaurus* specimen (PIN 2207/2-1), the ventral surface of palatine boss is sculptured but bears no teeth.

Ectopterygoid: The ectopterygoid (Figs. 4.19-4.21) is a triangular bone that connects the lateral flange of the pterygoid and posterolateral margin of the palatine with the maxilla on the ventrolateral side of the skull. It has a concave ventral surface which is broad in *Tapinocaninus* (NMQR 2987, NMQR2985), whereas in *Ulemosaurus* (PIN 2207/1) it is a narrower antero-posteriorly elongated bone. This interpretation of the bone in *Ulemosaurus* is contra Efremov (1940, fig. 5) and Tatarinov (1965, fig. 5) who show a posterolateral extension of the bone suggesting a longer contact with the maxilla. Three foramina are present close to the suture with the maxilla on the anterolateral margin of the ectopterygoid of *Ulemosaurus* (Efremov, 1940b). In *Tapinocaninus* (NMQR 2987) two foramina, separated by a ridge, are present to the side of the bone.

Pterygoid: The pterygoid (Figs. 4.19- 4.21) in both genera covers more than a half of the length of the palate. The relatively prominent lateral flanges of *Tapinocaninus* are more anteroventrally inclined in *Ulemosaurus* (Rubidge 1991, Efremov 1940b). The dorsal margin of the lateral flanges forms a ridge, which extends posteriorly along the lateral margin of the interpterygoidal vacuity. This ridge is smooth and thin in *Ulemosaurus*, and it is thicker and manifests sculpturing in *Tapinocaninus*. The palatine process of the pterygoid is located anterior to the lateral flanges. It is transversely wide in *Ulemosaurus* specimen PIN 2207/1 and is considerably narrower and more elongated in PIN 2207/2 and all the *Tapinocaninus* specimens. Distally the palatine process has a small medial notch on either side close to the interpterygoidal vacuity and is best preserved in NMQR 2987, PIN2207/1. Posterior to the lateral flanges, the pterygoid bends posterodorsally to form an extended platform which continues posteriorly as the quadrate ramus of the pterygoid. In *Tapinocaninus* this platform is extensive and forms a vertical lamina whereas in *Ulemosaurus* it is narrower and horizontal. In *Ulemosaurus* the interpterygoid vacuity is positioned relatively far anteriorly and extends backwards only as far as the posterior edge of the pterygoid flanges. Efremov (1940b) described the short interpterygoidal vacuity of *Ulemosaurus* as a partial closure of the vacuity. Tatarinov (1965) considered this to be related to the thickened adjacent connection of the sphenoid bone, whereas Tchudinov (1983) ascribed this to secondary deformation (as in PIN 2207/2) as a result of lateral displacement of the pterygoid complex resulting in closure of the vacuity. The different *Tapinocaninus* specimens demonstrate different degrees of closure of the interpterygoidal vacuity. In NMQR 2987 and NMQR 2986 the vacuity is

elongated and extends along the entire basicranial girder, whereas in NMQR 2985 the vacuity is heart shaped, broad anteriorly and remarkably short anteroposteriorly.

The pterygoid forms a platform in the cranial girder, which is wide in *Tapinocaninus* and relatively narrower and shorter in *Ulemosaurus*. This platform is separated from the quadrate rami of the pterygoid by the anterior-end of the basisphenoid, and typically the distal end of the quadrate ramus contacts the medial condyle of the quadrate (Rubidge 1991, Efremov 1940b).

Quadrate and quadratojugal: In both species the dorsal ramus of the quadrate (Figs. 4.19- 4.21) is a plate like bone in front of the squamosal and lateral to the occiput. Ventrally it has the typical double condyles which articulate with the articular of the lower jaw. In *Tapinocaninus* this bone is more robust than in *Ulemosaurus*. The dorsal process is in contact with the quadratojugal, which is a small plate-like bone that is ventrolaterally positioned in both genera, with a quadrate foramen between them (Riabinin, 1938, Efremov, 1940, Rubidge, 1991). Between the dorsal process and the dorsal portion of the medial condyle, the quadrate has a medial stapelial groove to receive the distal end of the stapes. The lateral margin of the medial condyle is in contact with the distal end of the quadrate ramus of the pterygoid.

Stapes: In both genera the stapes (Figs. 4.19- 4.21) is a robust rod-like bone with a rounded proximal end in contact with the fenestra ovalis and has a widened distal platform which articulates in the stapedial groove of the medial quadrate. It appears that the stapedial platform of *Ulemosaurus* (PIN 2207/1) is positioned relatively more anteriorly on the quadrate than is the situation in *Tapinocaninus*. The waisted body is perforated by a relatively large and elongated stapedial foramen in both genera.

4.6.3 Occiput

The occiput in both genera slopes anteroventrally as in all tapinocephalids and results in a forward shift of the jaw articulation relative to the back of the skull such that the craniomandibular joint is positioned in line with the posterior margin of the postorbital bar (Efremov, 1940, Rubidge, 1991). The occiput is large, almost rectangular, and its surface is relatively flat in *Tapinocaninus*, while it is roughly square and concave in *Ulemosaurus* (Efremov, 1940; Rubidge, 1991).

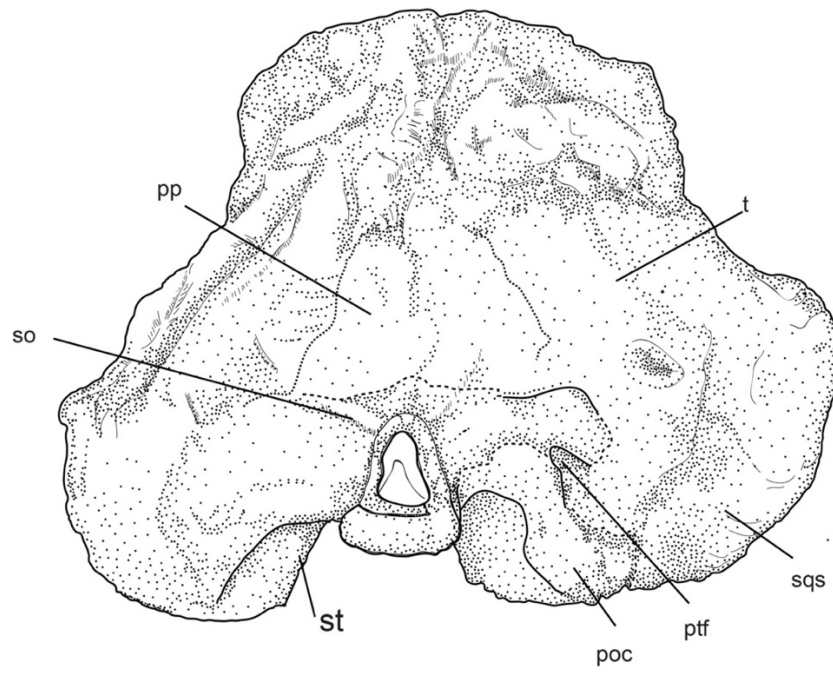
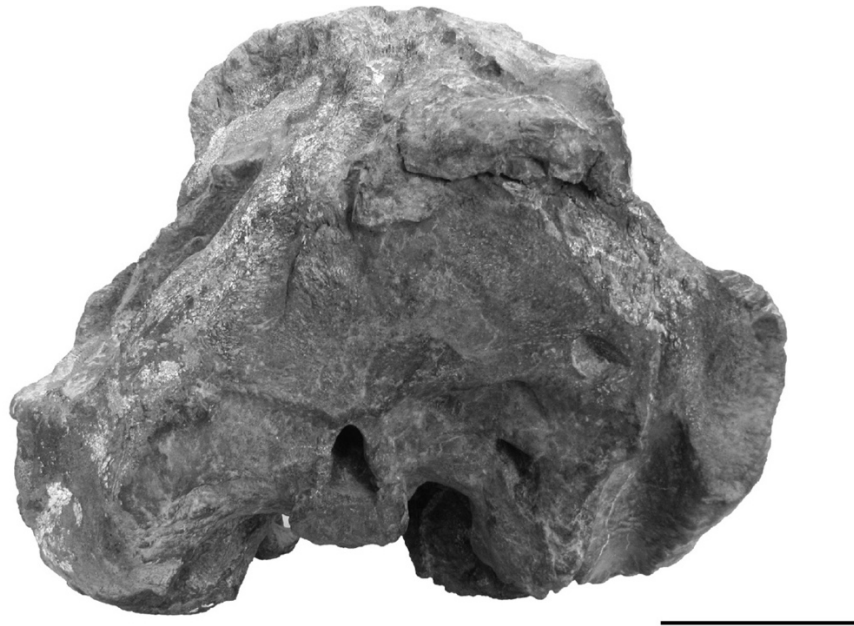


Figure 4. 22. *Tapinocaninus* occipital view: photograph (top) and illustration (bottom) of NMQR 2986. Scale: 10 cm.

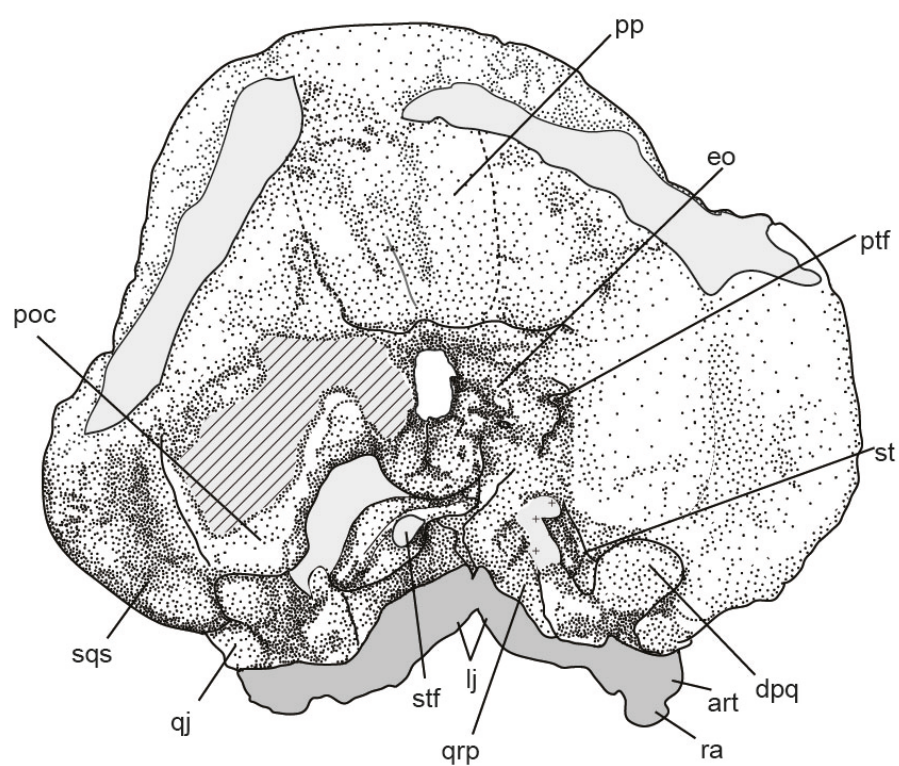
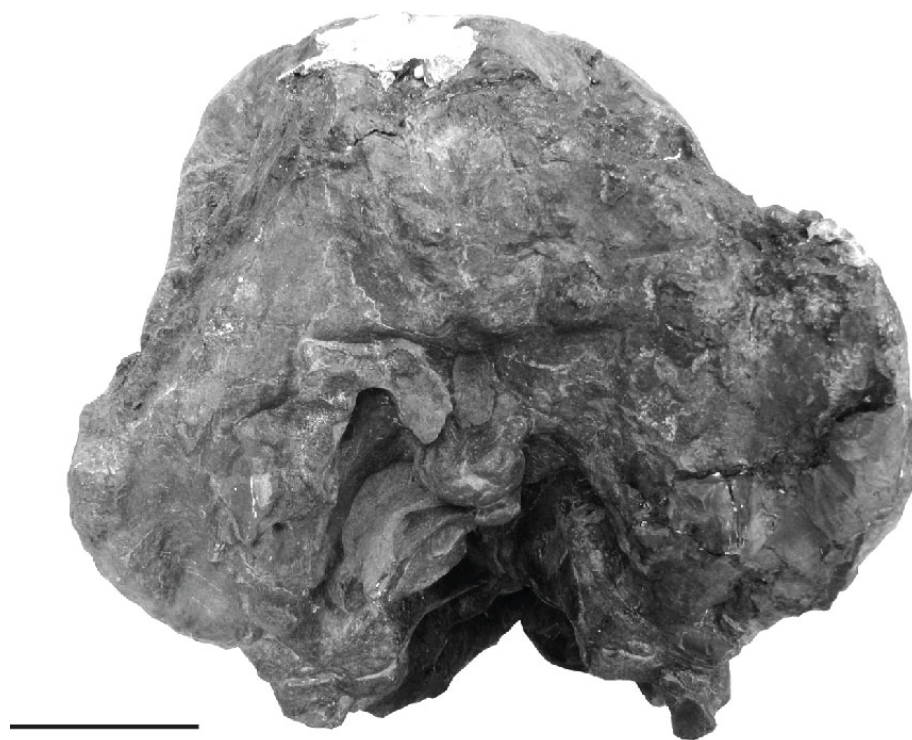


Figure 4.23. *Tapinocaninus* occipital view: photograph (top) and illustration (bottom) of NMQR 2986. Scale: 10 cm.

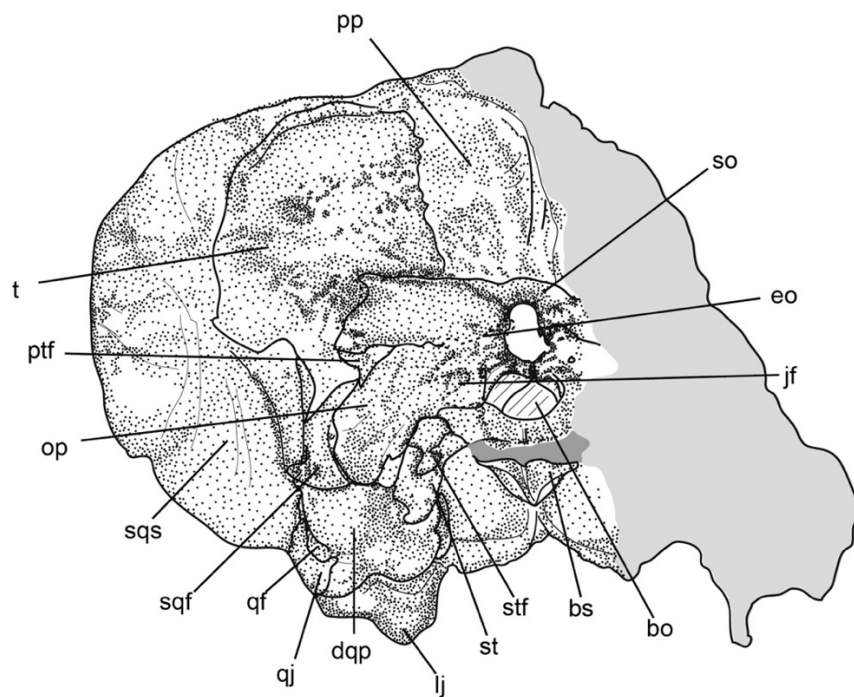
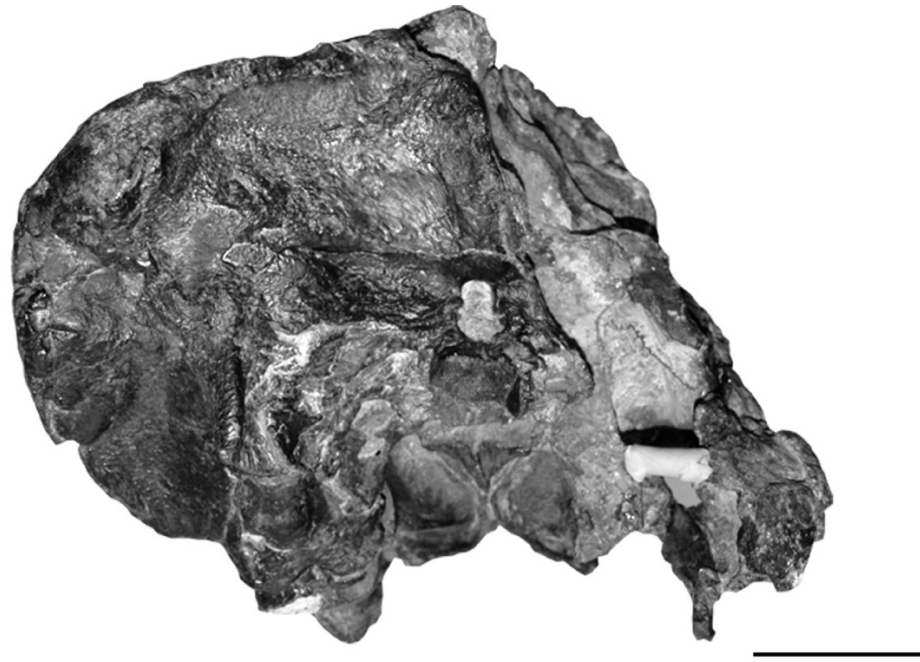


Figure 4.24. *Tapinocaninus* occipital view: photograph (top) and illustration (bottom) of NMQR 2987,. Scale: 10cm.

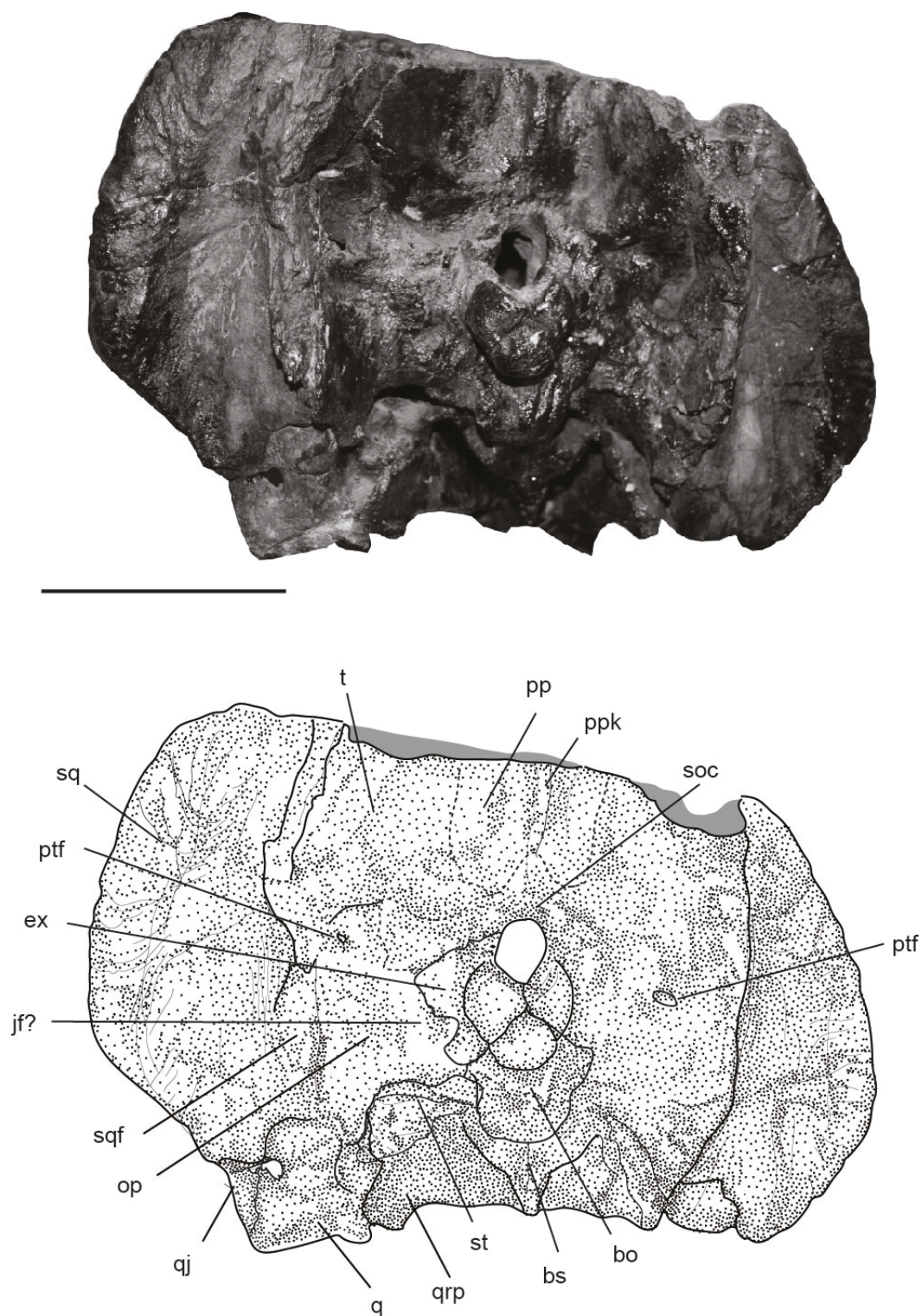


Figure 4. 25. *Ulemosaurus* occipital view: photograph (top) and illustration (bottom) of PIN 2207/1. Scale: 10cm.

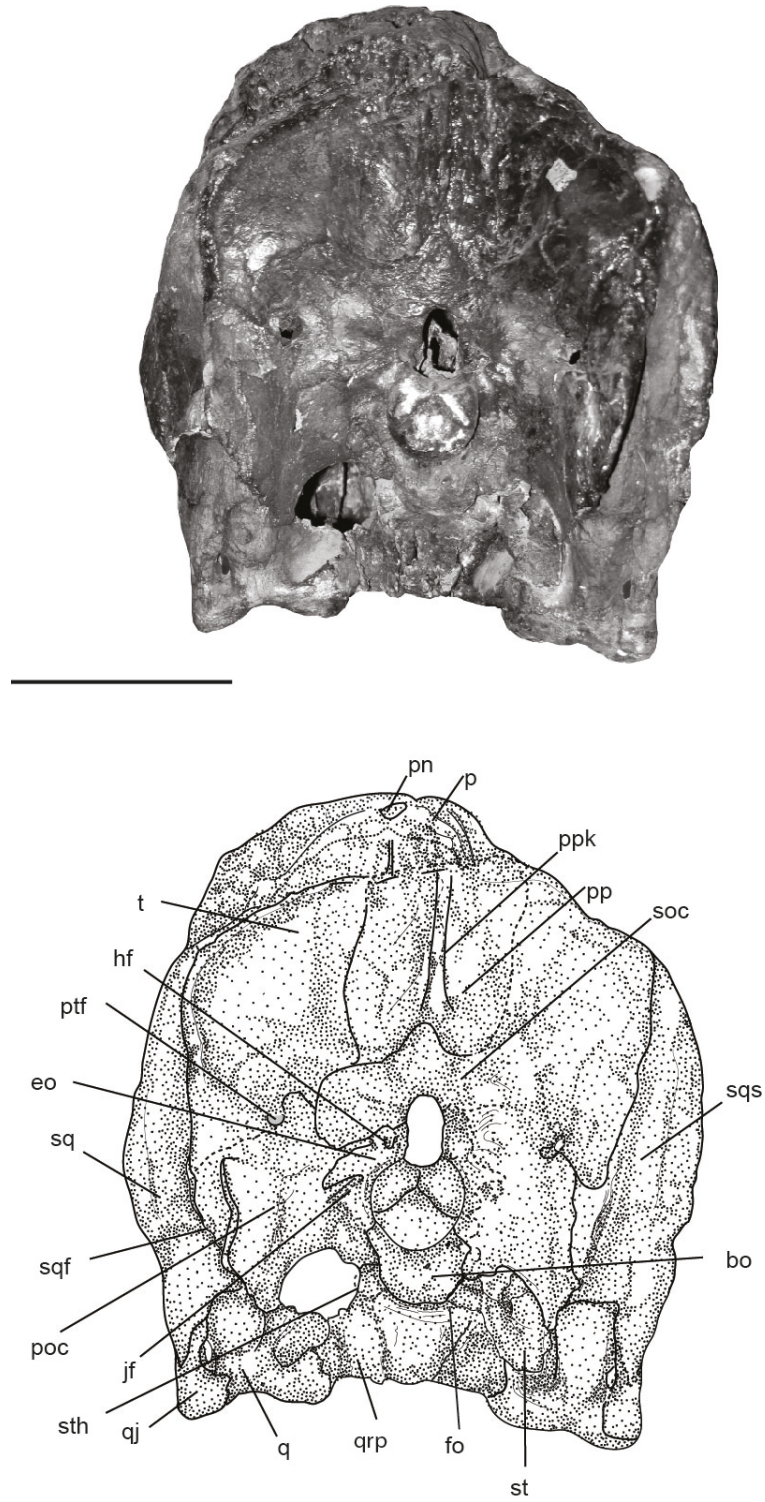


Figure 4. 26. *Ulemosaurus* occipital view: photograph (top) and illustration (bottom) of PIN 2207/2. Scale: 10cm.

Tabular: In both genera the tabular (Figs. 4.22-4.26) is a large flat and broadly quadrangular bone with a ventral extension which curves medially to form the lateral and dorsal borders of the posttemporal foramen (Tatarinov 1965, Rubidge 1991). The tabular meets the postparietal medially, the supraoccipital ventromedially, and has a short contact with the opisthotic on the ventrolateral side. Dorsally it is in contact with the parietal, and laterally it contacts the squamosal. On the dorsal side the tabular contributes to the occipital crest, which is much thinner in *Ulemosaurus* than it is in *Tapinocaninus*.

Postparietal: The postparietal (Figs. 4.22-4.26) is a dorsomedially elongated quadrangular bone in both taxa. It has a midline keel in both taxa and its surface is slightly depressed in *Ulemosaurus*. In both forms the postparietal is in contact dorsally with the parietal along the occipital crest, it contacts the tabular laterally and ventrally has contact with the supraoccipital.

Supraoccipital: The supraoccipital (Figs. 4.22-4.26) in both genera is a large quadrangular bone, which is dorsoventrally narrower and laterally longer in *Tapinocaninus*. Dorsally it has a horizontal sutural contact with the postparietal and sends a short midline spur dorsally onto the postparietal. This spur is more strongly developed in *Ulemosaurus* (Figs. 4.25-26). Laterally the supraoccipital is in contact with the ventral extension of the tabular. Ventromedially the supraoccipital forms the border of the foramen magnum while it sutures dorso-laterally with the tabular on either side of the occiput.

In both genera the supraoccipital forms the dorsal margin of the foramen magnum and does not border on the posttemporal foramen as was noted earlier for *Ulemosaurus* by Efremov (1940). This is contra Tatarinov (1965, p.100, fig.4) who considered that the supraoccipital in *Ulemosaurus* forms the dorsal, medial and ventral borders of the posttemporal fossa (Efremov 1940, Tatarinov 1965).

Exoccipital: In both genera the exoccipital (Figs. 4.22-4.26) is a laterally elongated wing-like bone, which forms the lateral border and covers the base of the foramen magnum (Efremov, 1940). It contacts the supraoccipital dorsally and laterally it meets the opisthotic. Ventro-medially it has an inverted v-shaped contact with the basioccipital.

Opisthotic: The opisthotic (Figs. 4.22-4.26) is a large bone extending between the squamosal sulcus laterally and the exoccipital and basioccipital medially, and also has a short dorsolateral contact with the tabular. Dorsally and dorsolaterally it meets the supraoccipital and forms the medial border of the post-temporal fenestra. In both *Ulemosaurus* and *Tapinocaninus* the paraoccipital process of the opisthotic forms the entire ventral margin of the occiput.

Basioccipital: The basioccipital (Figs. 4.22-4.26) is well preserved in *Ulemosaurus* and *Tapinocaninus* NMQR 2986 but has been weathered in NMQR 2985 and NMQR 2987. In occipital view, the basioccipital forms the medial portion of the tripartite occipital condyle and covers the entire ventral area below the condyle in both genera. Dorsally, to the side of the condyle, the basioccipital

has sutural contact with the exoccipital. The contact of basioccipital with the opisthotic is indistinct in NMQR 2987 and NMQR 2986.

In palatal view, the basioccipital of *Ulemosaurus* (PIN 2207/1) is triangular with anteriorly oriented apex abutting the basisphenoid (Efremov, 1938) (Figs. 4.19-4.21). In *Tapinocaninus*, the bone is quadrangular and forms a horizontal suture with the basisphenoid (Rubidge, 1991), and in ventral view a midline ridge continues anteriorly onto the basisphenoid. In both genera the basioccipital and basisphenoid together form the posterior border of the foramen ovalis.

Parabasisphenoid: In both genera the parabasisphenoid (Figs. 4.22-4.23) is a relatively small triangular bone which has a pointed anterior contact with the posterior end of the interpterygoidal keel and posteriorly meets the basioccipital (Efremov 1940, Rubidge 1991). The parabasisphenoid in *Ulemosaurus* is more ventrally positioned than the level of the basioccipital, whereas in *Tapinocaninus* these bones are present at the same level. A midline ridge extends down the ventral surface of the parabasisphenoid in both genera, but is less pronounced in *Ulemosaurus*. The ventral surface of the basisphenoid in *Tapinocaninus* is flatter and broader than that of *Ulemosaurus* and in the latter the anteroventral surface is concave. This concave region is limited anteriorly by the rostrum of the parabasisphenoid in *Ulemosaurus*. In both genera the posterior- end of the interpterygoidal keel forms a wedged contact with the basisphenoid (Rubidge 1991, Efremov 1940), but in *Ulemosaurus*, the medial ridge of the pterygoid

overlies the basisphenoid posteriorly and is not continuous with the basisphenoidal ridge (Tatarinov 1965).

4.6.4 Lower Jaw

The lower jaw (Figs.4.27, 4.28, 4.29) of *Tapinocaninus* is known from specimens NMQR 2987, NMQR 2986, NMQR 2985, ROZ K 95, and for *Ulemosaurus* from PIN 2207/2, PIN 2207/1, PIN 2977-1. The symphysial portion is preserved for both genera in the specimens NMQR 2987, ROZ K 95, PIN 2207/2, PIN 2972/1.

Dentary: The dentary is the largest element of the lower jaw, comprising two-thirds of the length of the jaw in both genera. Anteriorly it forms a strong symphysis with its counterpart along the midline of the lower jaw which is evident in NMQR2987 and in PIN 2207/2. In both *Tapinocaninus* and *Ulemosaurus* the posterior margin of the dentary slopes posterodorsally to form the coronoid eminence and meets the surangular at the posterodorsal margin of the jaw. The dentary, approximately half-way up its height, is notched before it slopes posteriorly and this notch is anteriorly orientated in both genera.

In the medial view (Figs. 4.28 , 4.29) the dentary is exposed over a shorter distance than in lateral view and makes up a little more than half of the length of the jaw. Posterodorsally it thins and in this region it contacts the anterior portion of the surangular. Dorsomedially the dentary was overlain by the coronoid as indicated by an indentation on the dentary, but this bone is not preserved in *Tapinocaninus*. Anteromedially the dentary widens on either side of the

symphysis to form a dorsal shelf and a ventral depression which accommodates the symphyseal portion of the splenial.

Surangular: The surangular of both genera is morphologically similar and forms most of the coronoid eminence and the posterodorsal margin of the lower jaw. In lateral view (Figs. 4.6-10, 4.13-16, 4.18) in both genera, a laterally projecting ridge of the surangular separates the surangular from the angular between the posterior-most extension of the dentary anterodorsally and the articular posteroventrally. On the lateral aspect of the lower jaw in both genera, a laterally projecting ridge of the surangular separates the surangular from the angular and a clear sutural contact is present between these two bones (Efremov, 1940, Rubidge, 1991). In ventral view the surangular is widely exposed and forms most of the posterior end of the lower jaw in both genera. Here it is in contact with the posterior portion of the prearticular anteroventrally and meets the articular posteroventrally.

Angular: The angular forms the posterior two-thirds of the lower jaw in lateral view (Figs. 4.6-10, 4.13-16, 4.18, 4.28, 4.29). The anterior-most portion of the angular is exposed below the dentary and makes up almost the half of the length of the lower jaw. Anteriorly it wedges between the splenial ventrally and the dentary on the dorsal side.

Splenial: In both *Ulemosaurus* and *Tapinocaninus* the splenial extends for approximately half of the anterior length of the medial side of the lower jaw

(Efremov 1940, Rubidge 1991) and its posterior margin extends slightly beyond the lower postcanine series. The splenial (Figs. 4.28, 4.29) forms the anteroventral margin of the lower jaw and posteriorly is underlain by the angular. Posterodorsally it contacts the anterior projection of the prearticular. The splenial posteriorly forms two (dorsal and ventral) spurs in *Tapinocaninus*. In both *Ulemosaurus* and *Tapinocaninus*, an elongated meckelian foramen (Efremov, 1940) is positioned at the posterior end of the splenial. On the lateral side of the jaw this foramen corresponds to a depression positioned between the angular and dentary. In medial view the meckelian foramen is bordered by the prearticular dorsally and angular the ventrally.

Prearticular and Articular: The articular makes up the posteromedial end of the lower jaw where it is in contact with the surangular, angular and the posterior end of the prearticular. In both *Ulemosaurus* and *Tapinocaninus* the prearticular is an elongated bone extending over two-thirds of the posteromedial side of the lower jaw. Anterodorsally it forms a wedged contact between the dentary and the splenial. In both genera, the prearticular makes up the medial wall of a deep slit (adductor fossa) between the posterior half of the prearticular (which is longer in *Tapinocaninus*) and the surangular (Efremov, 1940). Along the length of the adductor fossa the prearticular forms a lateral ridge, which broadens anteriorly to a descending shelf. In *Tapinocaninus* (NMQR 2987) the prearticular has a short contact with the angular posteriorly before it embraces the articular. Posteriorly a widened part of the surangular covers the articular ventrolaterally in

Tapinocaninus (NMQR 2987) whereas in *Ulemosaurus* (PIN 2207/2-2) the articular is embraced ventrally by the prearticular.

4.6.5 Dentition.

The following is a comparison of in-situ dentition of *Tapinocaninus* specimens NMQR 2987, NMQR 2986, ROZ-K 95 and *Ulemosaurus* specimens PIN 2207/1, PIN 2972/1 and PIN 157/4. The teeth of PIN 2207/2 which appear to be well preserved, are in fact all reconstructed in plaster, with the exception of the third and fourth upper incisors, the upper right canine, and a few right lower postcanines on the right side of the lower jaw (see pls. IV, VI, X, XII in Riabinin, 1938). Dental preservation in NMQR 2987 and PIN 2207/1 is quite good and most of the comparison below has been gleaned from these two specimens.

Both genera have five upper and four lower intermeshing incisors and a canine but the preserved number of postcanines differs: for *Tapinocaninus* between two and nine upper, and three to 15 lower postcanines have been noted; and in *Ulemosaurus* one to eight upper and four to ten lower postcanines were counted.

The dental formula of all the specimens of both genera are: NMQR 2897 - $I_4^5 C_1^1 PC_{10}^{2+}$; NMQR 2896 - $I_4^5 C_1^1 PC_{9-12}^{9?}$; NMQR 2895 - $I_4^5 C_1^1 PC_{15}^8$; ROZ K 95- $I_4^5 C_1^1 PC_{3+}^{2+}$. Dental formula of the *Ulemosaurus* specimens: PIN 2207/2 - $I_4^5 C_1^1 PC_{9-10}^{7-8}$; PIN 2207/1 - $I_4^5 C_1^1 PC_9^8$; PIN 2972/1 - $I_4^5 C_1^1 PC_4^6$; PIN 157/4 $I_4^5 C_1^1 PC_8^3$.

Incisors: Both *Tapinocaninus* and *Ulemosaurus* have five upper and four lower intermeshing incisors (Rubidge, 1994) in contrast to Riabinin (1938), Efremov (1940) and Tatarinov (1965) who interpreted three incisors on the premaxilla for *Ulemosaurus*. Riabinin (1938) does mention the possibility of a fourth lower incisor.

In both genera the crowns of the incisors are labio-lingually expanded to form a lingual heel and a labial talon. The crown heels and talons of the incisors are mesiodistally enlarged with the exception of the first upper incisors which are laterally compressed. The heels of the second and third upper incisors are large and inclined anteriorly in both genera, but are largest in the third incisor. The heels of the fourth and the fifth incisors are rather elongated mesiodistally (Efremov, 1940).

In both genera the crown width (across the base labiolingually) is much more than its length (across the base anteroposteriorly) for the first upper incisors but decrease towards the fourth. In both genera the crown length of the fifth incisor is equal to its width. The fifth incisor of *Ulemosaurus* is smaller than the rest of the incisors (Efremov, 1940) and in *Tapinocaninus* is much smaller than incisors 2,3 and 4. In occlusal view a mediodorsal ridge, starting from the apex and diminishing inside the heel, is present in both taxa and is preserved in the right fifth incisor in *Tapinocaninus* and in the first incisors in *Ulemosaurus*.

Canine: The canine is preserved on the upper jaw of specimens NMQR 2987, NMQR2986, ROZ K 95 and the lower jaw of NMQR2985 of *Tapinocaninus*. In

Ulemosaurus the upper canine is preserved in-situ in PIN 2207/1 and damaged lower and upper canines are preserved in specimens PIN 2972/1 and PIN 157/4 and a loose canine PIN 1955/5. Riabinin (1938) considered the fourth upper tooth of *Ulemosaurus* to be the canine which is corrected by Efremov (1940) and Rubidge (1991) who recognized the sixth tooth, the first tooth on the maxilla, as the canine in both taxa.

In both taxa the neck of the canine is rounded in cross section (PIN 2207/1, 1955/5 and NMQR 2987) and has a small heel which has differing morphology in *Tapinocaninus* and *Ulemosaurus*. In *Tapinocaninus* the heel is reduced to an upward sloping mesodistal ridge, whereas in *Ulemosaurus* the heel is more developed (still much reduced compared to the heels of the incisors) and positioned parallel to the crown-root line (Figs. 4.27D, 4.30C&D1). In PIN1955/5 the heel margin is not weathered and the denticled heel morphology curves inward, forming horizontal ridges which ascend towards the apex of the crown (Fig. 4. 30C&D2) (Ivakhenko, 2003). A different canine crown morphology is present in *Ulemosaurus* (specimen PIN 157/4) and *Tapinocaninus* (specimen ROZ K 95) where the tooth is laterally flattened and has a pointed apex. This difference in feature was explained as a possible result of a this canine being more mature in Rubidge (1991) who quoted Boonstra (1953a) on this as a support. Boonstra (1953a) reported a similar canine morphology on an *Anteosaurus* specimen and interpreted it as the canine became flattened closer to its replacement. I agree with Rubidge (1991) and consider this as a feature related to ontogeny.

In occlusion of the jaws, in both *Ulemosaurus* and *Tapinocaninus*, the lower canine passes anterior to the upper and thus intermeshing occurs between the last upper incisor and the canine (Rubidge 1991, Efremov 1940).

Postcanine: In-situ postcanine teeth are preserved articulated in *Tapinocaninus* specimens NMQR 2986, NMQR 2985, ROZ K 95 and *Ulemosaurus* specimens PIN 2207/1 (upper and lower jaw), PIN 157/4 and PIN 2972/1. Rubidge (1991) and Efremov (1940) demonstrated that the post-canines in both taxa have tripartite, triangular crowns with weakly developed small heels. The upper post-canines are larger than the lower and were positioned labially during occlusion, without intermeshing with the lowers (*eg.* PIN 2207/1, PIN157/4, in Figs. 4.18A, 4.22). In *Ulemosaurus* the crown margins are anteroposteriorly denticled as well as of the heel margin (Efremov 1940). Because of poor preservation these features cannot be confirmed for *Tapinocaninus* but the heels on the upper post-canines are larger in the anterior postcanines, relative to those of the posterior postcanines. The lower post-canines have lesser-developed heels than the uppers ones in *Ulemosaurus*.

Ulemosaurus postcanines show superimposition by being positioned obliquely on the tooth margin, thus the posterior flank of the first postcanine is partially overlain by the anterior flank of the second postcanine crown and so on (Fig. 4.29) (Efremov, 1940). The upper postcanines anteriorly are less superimposed and larger (PIN 2207/1, PIN 157-4, PIN 2977-1) than the lower ones (PIN

2207/1) and superimposition diminishes posteriorly on the maxillary tooth row (PIN 2207/1, PIN 157-4, PIN 2977-1) in contrast to the lower lower posterior postcanines which show slight superimposition. There is no evidence of placement and pattern of lower postcanines in *Tapinocaninus*.

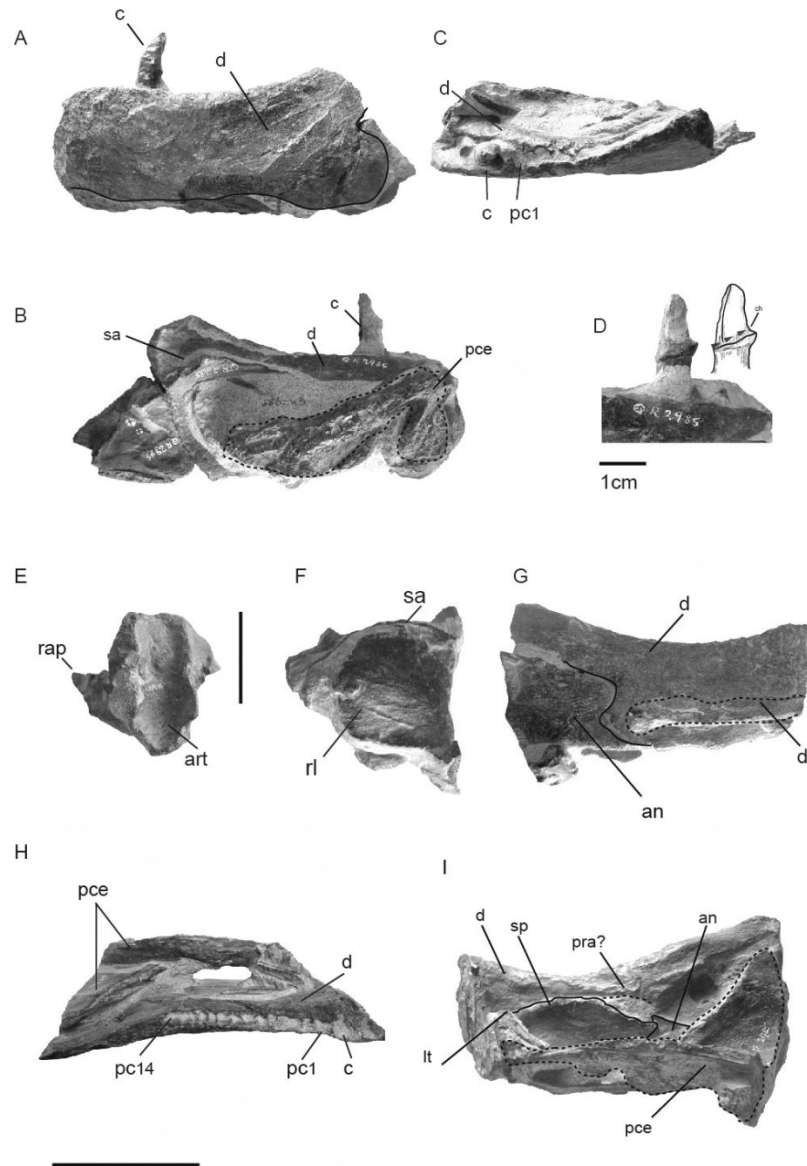


Figure 4.27. *Tapinocaninus*: photographs of the lower jaw of NMQR 2985: A, B, C and D show respectively the lateral, dental border, and medial views of two-thirds of the left mandible and close-up view of from the left lower canine (Arrowheads indicate the direction of upward inclination of the heel margin). E, F, G, H and I show respectively the dorsal view of articular, posterior one-thirds of the left mandible and the lateral, dental border and medial views of the left mandible. Scale: 10 cm.

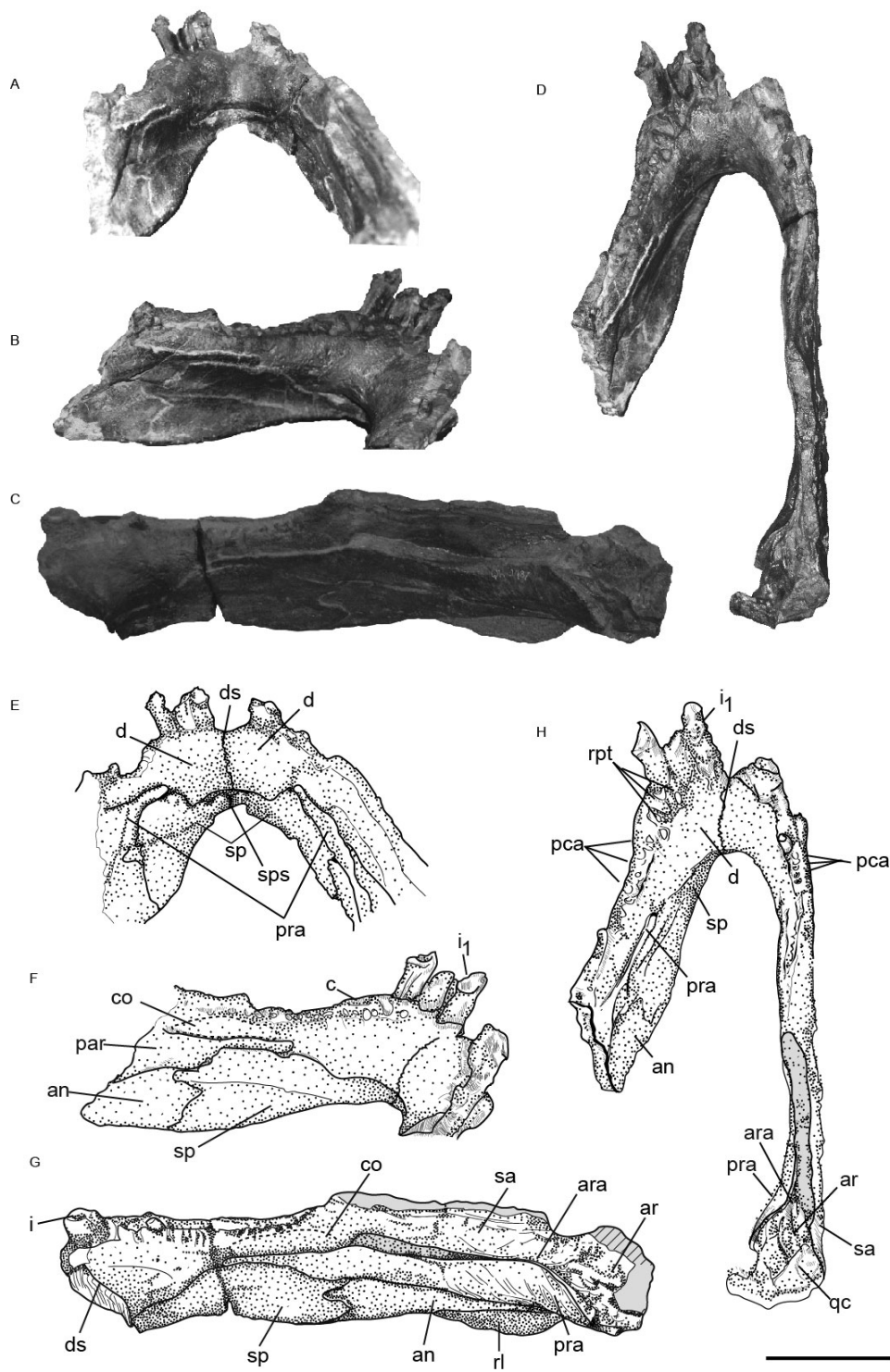


Figure 4.28. *Tapinocaninus*: photographs (A-D) and illustrations (E-H) of the lower jaw of NMQR 2987: A and E show the dentary and splenial symphysis medially. B and F show the left medial view. C and G show right medial view. D and H show lower jaw dorsally. Scale. 10 cm.

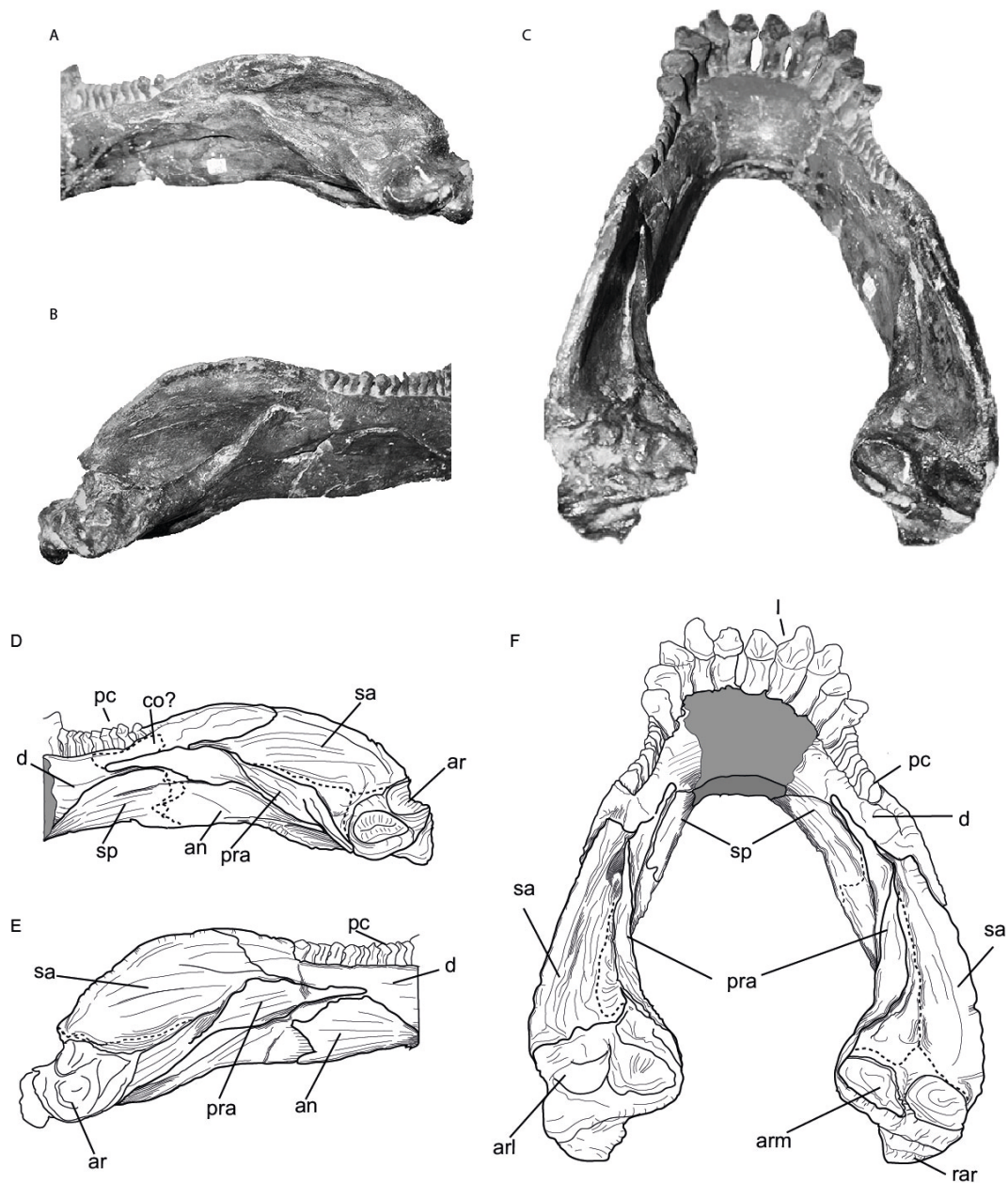


Figure 4.29. *Ulemosaurus*: photographs (A-C) and illustrations (D-F) of the lower jaw of PIN 2207/2, showing medial view of right (A and D) and left (B and E) mandibles and dorsal view (C&F). Scale: 10 cm.

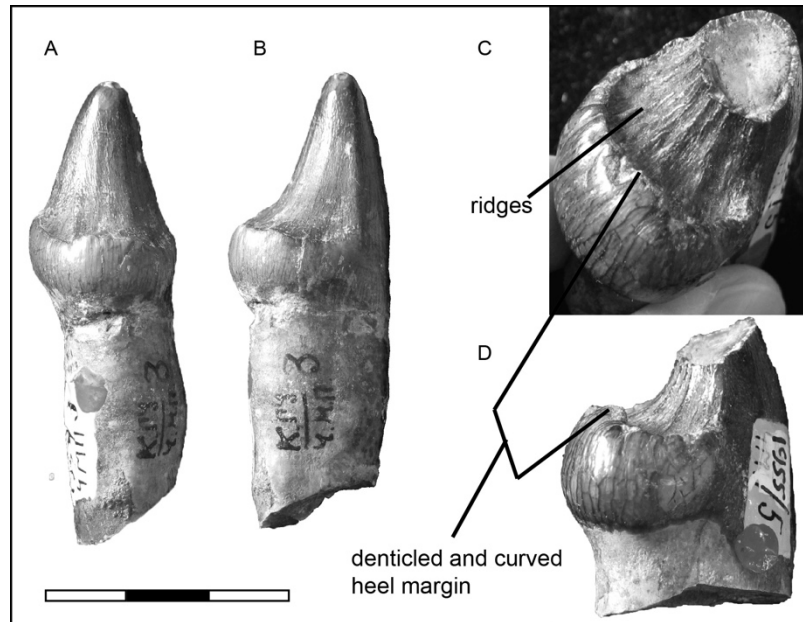


Figure 4.30. *Ulemosaurus gigas* (holotype): Photographs of the incisor PIN 1955-3 (A and B) and the canine PIN 1955-5 (C and D) showing views from lingual (A and C) and proximal surfaces (B & D). Scale: 3 cm.

4.7 Discussion

As both *Tapinocaninus* and *Ulemosaurus* are known from well preserved and prepared specimens, a more complete understanding of their cranial morphology provides a good baseline for the comparison of all tapinocephalid dinocephalians.

It is currently considered that derived tapinocephalian genera manifest increasing cranial pachyostosis resulting in a broad bony skull roof in the intertemporal region, a narrow temporal opening, the occiput slopes further anteroventrally resulting in a further anteriorly positioned jaw joint (as far as the level of orbit); and the canines are reduced to have incisiform morphology. In comparison both *Ulemosaurus* and *Tapinocaninus* exhibit features that are considered plesiomorphic for tapinocephalid dinocephalians (Efremov 1940; Rubidge, 1991;

Ivakhnenko, 1994): *i.e.* a narrow intertemporal region with a large temporal opening, and posteriorly positioned jaw joint (Boonstra 1972, Barghusen 1975, Rubidge 1991). In addition to these characters the enlarged canines, although they do have a lingual ridge like heel structure, differ from the incisiform canines of the derived tapinocephalid taxa.

Ulemosaurus and *Tapinocaninus* present different degrees and styles of pachyostosis. In *Tapinocaninus* there is uniform cranial roof pachyostosis similar to that of other more derived South African tapinocephalids. In contrast *Ulemosaurus* has inhomogeneous thickening of the skull roof bones formed by dorsoventral thickening of the nasal, frontal and anterior portion of the parietal which results in a domed skull roof.

In the dentition both taxa show an intermediate position between the basal members of Tapinocephalia and the derived tapinocephalid taxa by having a canine which is neither as large and curved as in the more basal forms, nor has large lingual heels and the upper and lower canines intermesh as in the derived forms. The postcanine teeth however, in contrast to the pattern of derived tapinocephalids, do not demonstrate a pattern of intermeshing.

The size of individual *Ulemosaurus* and *Tapinocaninus* skulls varies, and there are concomitant changes in the morphology of the temporal fenestra and also degree of cranial thickening. For example the skulls of *Ulemosaurus* specimens PIN 157/4 and PIN 2972/1 are much larger than PIN 2207/1 and PIN 2207/2. It

appears that PIN 2207/1 and PIN 2207/2 are thus most probably younger individuals. Thus it seems that differences between these two skull groups relating to increased thickening of the skull roof and concomittent reduction in the size of the temporal fenestra could be attributed to age. The lower portion of the temporal fenestra of PIN 2207/1 is narrower than it is in PIN 2207/2, and the angle between the quadratojugal and jugal is more acute due to the thicker zygoma in the first specimen.

In *Tapinocaninus* there is also a difference in the size and degree of cranial pachyostosis between different individuals. Specimen NMQR 2986 is the largest specimen and exhibits greatest thickening of the postorbital bar. NMQR 2986 and NMQR 2987 are most similar to each other. They both have a similar outline in lateral view and also share the following characters: the ventral part of the temporal fenestra is wider and both skulls have a protrusion on the orbital border where postorbital meets the jugal.

In both *Ulemosaurus* and *Tapinocaninus* the parietal on the dorsal surface of the temporal fenestra provides a large surface for attachment of jaw adductor musculature, which differs from the situation in the pachyostosed skulls of more derived tapinocephalids where excessive pachyostosis results in a slitlike temporal fenestra (Boonstra 1963b).

Although the temporal fenestra is relatively large in both *Ulemosaurus* and *Tapinocaninus*, the overall volume is greater in the latter genus. In *Ulemosaurus*

the size of the temporal fenestra in lateral view is larger and the dorsoventral diameter is much smaller, as is the situation in more derived tapinocephalids and the bones of zygomatic arch ventrally are not tickened as in *Tapinocaninus*.

On the posterodorsal border of the temporal fenestra the posttemporal arch forms a ridge which projects into the fenestra in both genera. This ridge connects to a dorsally exposed shelf which is wider in *Tapinocaninus*, and is also prominent in *Riebeeckosaurus*. This shelf increases surface area for jaw adductor muscle attachment on the parietal and squamosal in *Tapinocaninus*. Although this structure is not similarly represented in *Ulemosaurus*, the space for the muscle attachment is enlarged through the dorsoventrally enlarged surface of the parietal on the dorsal border of the temporal fenestra.

4.8 Conclusion

The type materials of *Tapinocaninus* and *Ulemosaurus* present by far the best cranial preservation for tapinocephalids and provide a good opportunity to understand the cranial morphology of a taxonomic group which is based on largely incomplete materials.

Both *Ulemosaurus* and *Tapinocaninus* have a combination of basal and derived tapinocephalian characters. Both genera display strong cranial pachyostosis, as in the derived tapinocephalid taxa, but also have a narrow intertemporal region, roomy temporal fenestra and a more posteriorly positioned jaw joint, as in the

basal tapinocephalian taxa. Their large canine with only an incipient ridge-like heel adds credence to their basal position within Tapinocephalidae.

Members of the both taxa manifest indications of ontogenic and individual variation with differentiation degree of cranial thickening, the size of the temporal fenestra, and the angle formed in the contact area of quadratojugal and jugal.

These manifestations of both ontogenetic and phylogenetic variation have implications for understanding the taxonomy of more derived forms.

5 REVISION OF THE SUBFAMILY RIEBEECKOSAURINAE: THE SYNONYMY OF *RIEBEECKOSAURUS* AND *AVENANTIA*

(The content of this chapter was published in Palaeontologia africana vol.48, December 2013)

5.1 Introduction

Dinocephalians formed the major component of the Middle Permian terrestrial tetrapod diversity as is evidenced by the large number of taxa of herbivorous tapinocephalids from the rocks of the Abrahamskraal Formation, Karoo Supergroup of South Africa (Rubidge, 1995; Smith et al., 2012). Several of these taxa are based on fragmentary holotypes in which diagnostic characters are hardly evident, suggesting that the number of tapinocephalid genera from the Karoo may be inflated. In the most recent taxonomic revisions of dinocephalians, Boonstra (1969) recognized four and King (1988) two groups of tapinocephalids, in which the snout length was considered one of the main diagnostic characters.

Avenantia and *Riebeeckosaurus* are monospecific tapinocephalid genera from the Lower Beaufort Group of the Karoo Basin. Boonstra (1952e) described

Riebeeckosaurus longirostris, represented by the holotype (a distorted and fragmented cranium with lower jaw) and a referred specimen (the dorsal portion of cranium), as a long-snouted species. Boonstra (1952f) described *Avenantia kruisvleiensis* as a *Moschops*-like tapinocephalian with a short-snout. Both species are described as having a large and roomy temporal opening [there is inconsistency regarding this character because in the same contribution, Boonstra (1952f, p.254) refers to the temporal opening of *A. kruisvleiensis* as small]. Despite the fact that the specimens of both genera lack a snout, Boonstra (1952e) interpreted the holotype of *R. longirostris* as being long snouted, based on the length of the lower jaw. The author considered the species as morphologically intermediate between the short snouted Moschopidae and long-snouted Mormosauridae as described in Boonstra (1936b) but did not allocate *R. longirostris* in any particular subgroup. Later, *A. kruisvleiensis* was considered a member of the Moschopidae by both Haughton and Brink (1954) and Boonstra (1957), and *R. longirostris* a member of the long-snouted Tapinocephalidae. In 1963 Boonstra founded the subfamily Riebeeckosaurinae for *R. longirostris* while Orlov (1964, p. 258) assigned *R. longirostris* to the family Mormosauridae, which was defined as having forms with a relatively longer snout and lesser pachyostosis than the members of the Tapinocephalidae. Barghusen (1975) interpreted the dentary of the holotype of *R. longirostris* as having been displaced forward in relation to the post-dentary bones, casting doubt on Boonstra's interpretation of a long snout for the taxon, and suggested the re-placement of *R. longirostris* in the subfamily Moschopinae of Boonstra (1969). Van den Heever and Grine (1981) and King (1988)

maintained *Riebeeckosaurus longirostris* in the tribe Riebeeckosaurini, whereas *Avenantia kruisvleiensis* was included by King (1988) in the tribe Tapinocephalini (a combination of the previous subfamilies Moschopinae and Tapinocephalinae, e.g., Boonstra 1969). Kammerer (2009) proposed the synonymy of *Riebeeckosaurus longirostris* and *Avenantia kruisvleiensis*.

Re-evaluation of the taxonomic disparity between *A. kruisvleiensis* and *R. longirostris* is necessary as the materials comprising these two genera has not been studied in detail since Boonstra's (1952e, 1952f) original descriptions. Additional preparation of the specimens has revealed important new information and enabled a detailed redescription of the material attributed to these species.

5.2 Material And Methods

The holotype specimens, SAM-PK-3400 (*Riebeeckosaurus longirostris*, Figs 5.1-5.4), SAM-PK-9166 (*Avenantia kruisvleiensis*, Figs. 5.5- 5.6) and referred specimen SAM-PK-11955 (*R. longirostris*, Fig.5.1A) were mechanically prepared with the aid of aircsribes. Comparative materials utilised include specimens of the short-snouted tapinocephalids *Moschops*, *Criocephalosaurus* and *Tapinocaninus*: SAM-PK-11582 (holotype of *M. koupensis*), SAM-PK-K0319 (identified here as *Moschops* but it is registered as *Criocephalosaurus* in the SAM database), NMQR 2987 (*Tapinocaninus pamela* holotype), NMQR 2985 and NMQR 2986 (*T. pamela* referred). Descriptive terminology for the margins of the teeth follows Heckert (2004).

5.3 Revised Descriptions

5.3.1 *Riebeeckosaurus longirostris*

In the holotype (SAM-PK-3400) both the cranium and the lower jaw were previously reconstructed from several weathered, poorly fitting fragments. It is evident that the skull has suffered postmortem distortion, which affected the width of the skull roof and caused the occiput to be pushed relatively forward. The left side of the skull is less distorted than the right. Re-examination indicates that the width between the squamosals is greater than reconstructed by Boonstra (1952c). The skull of the referred specimen (SAM-PK-11955), which comprises the posterior portion of the skull roof (Fig. 5.1A), is larger than that of the holotype. Both specimens display a moderate degree of pachyostosis of the skull roof, a feature which is clearly demonstrated by the thick, robust nature of the postorbital bar (width of 100mm in the holotype). The temporal opening in the holotype is large and roomy, with the anteroposterior diameter being larger than the dorsoventral diameter. The palate is not preserved in either of the specimens.

5.3.1.1 Skull roof

In both specimens of *Riebeeckosaurus* the inter-temporal area is a narrow crest produced by thin posterior projections of the parietal (Figs 5.1). These form the dorsomedial border of the temporal opening and curve backwards, but not at a sharp angle as described by Boonstra (1952e). The squamosal forms the posterior and lateral borders of the relatively large temporal opening. The contribution of this bone to the posterior border of the temporal opening is not

fully preserved in the available specimens (in contrast to Boonstra 1952e, fig.2, illustration of the squamosal on the posterior branch of the temporal opening in the holotype). This bone, as evidenced by the medial portion of the right temporal opening of SAM-PK-11955, makes up a short section of the posterior dorsomedial border. Posteroventrally, the squamosal extends to the base of the skull. Because of the weathered nature of the zygomatic arch, the contact of the squamosal with the jugal is not evident on the left side and only the posterior portion of the zygoma is preserved on the right (Fig 5.1B).

The parietal has narrow exposure in the form of a crest in the intertemporal region, broadens to its greatest width in line with the pineal foramen, and tapers anteriorly to a point on the midline between the frontals. In both specimens the pineal opening is situated on a slightly raised boss in the centre of the parietals (Fig. 5.1A-B).

The frontal (Figs 5.1) forms the greatest portion of the skull roof in the interorbital region, contributing to the orbital border in both specimens and extending posteriorly between the parietal and postfrontal to make a small contribution to the temporal opening. An elongated midline depression on the skull roof extends along the frontals but is absent from the nasals anteriorly, and the parietals posteriorly. The partially preserved prefrontal is a large bone which contributes to the anterodorsal margin of the orbit, and contacts the frontal posteriorly, and the narrow posterior projection of the nasal medially. In SAM PK 11955, the posterior ends of the two thin elongated nasals have a short

posterior contact with the frontal. An anteroposteriorly elongated postfrontal contributes to the anterior border of the temporal opening and the posterodorsal margin of the orbit, and is in contact with the frontal medially and the postorbital on the lateral side. The postorbital meets the squamosal at the base of the postorbital bar as it is evident in the holotype. The cranio-mandibular joint, as preserved, is located below the mid-point of the orbit. This rather anterior placement of the jaw joint seems to be the result of dorsoventral deformation of the skull.

5.3.1.2 Occiput

The occiput in the holotype is mostly complete, but poorly preserved and reconstructed from weathered fragments (Fig. 5.2) and, as a result, sutural pathways are not clear. There is a striking transverse thickening which extends across the occiput at a level corresponding to the lower limit of the tabular, parallel to the dorsal border of the supraoccipital. Dorsally the parietals have a small exposure on the occiput above the postparietal. The postparietal is a prominent long rectangular unpaired bone on the occiput, which has a long sinuous contact with the parietal dorsally and the supraoccipital ventrally, and a short contact with the tabular laterally. The latter is a large ovoid paired element with a well-developed ventral projection forming the dorsolateral border of the occiput. Dorsomedially the tabular has a short contact with the parietal, ventromedially with the postparietal, and laterally with the squamosal. There is a long sutural contact with the supraoccipital in which a thin ventrolateral tongue of the tabular extends between the supraoccipital and squamosal.

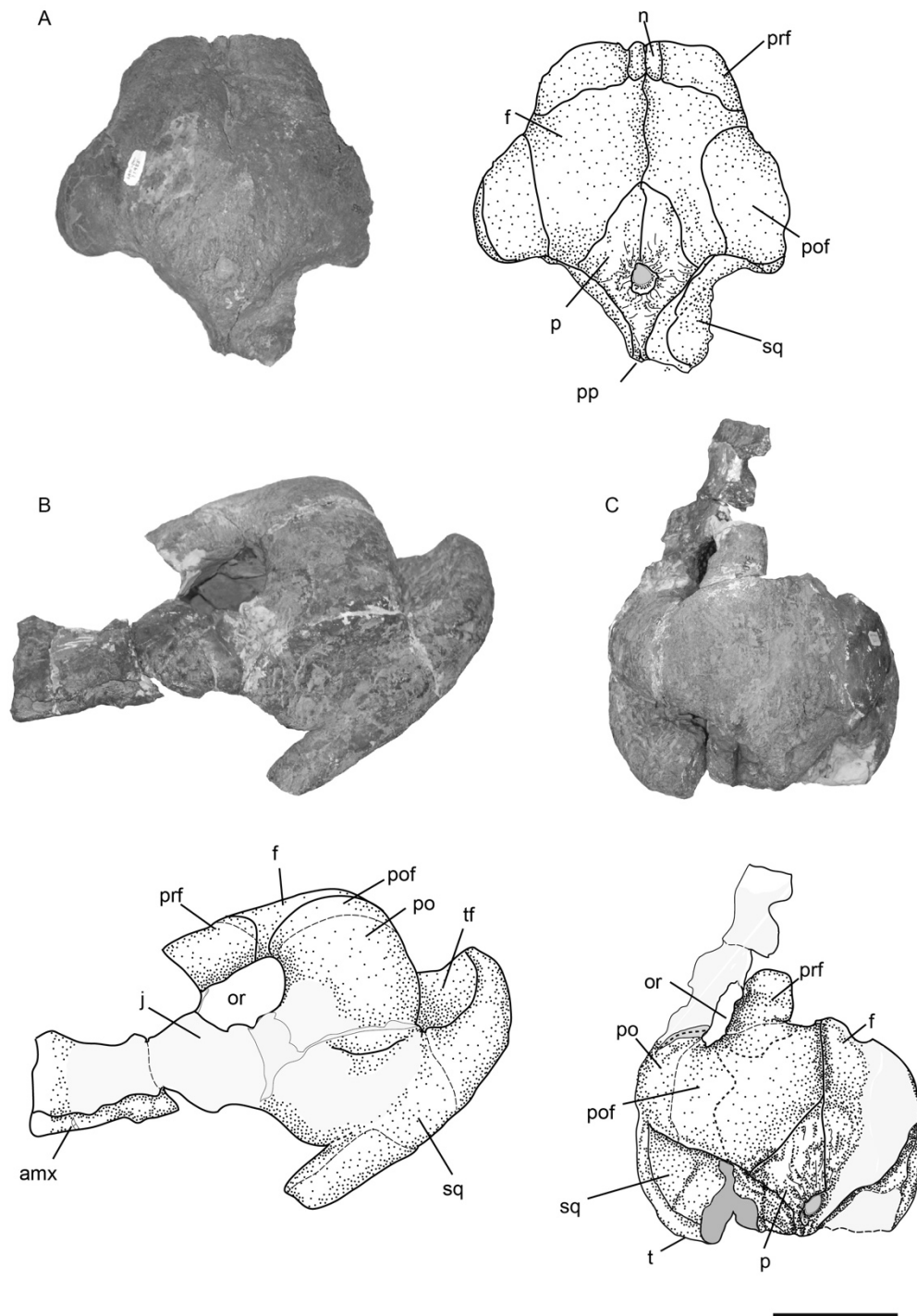


Figure 5.1. Photograph and drawings of the dorsal view of (A) of SAM-PK-11955 (*R. longirostris* referred specimen) and (B) SAM PK 3400 (holotype of *R. longirostris*) and left view (C), left of SAM PK 3400. Solid lines are visible and dashed lines are interpreted sutures; narrow dashed lines are borders of bone fragments; light grey are reconstructed areas and matrix infilling. Scale 10 cm.

The squamosal is a massive bone, which forms a large part of the lateral side of the occiput, and has a prominent dorsoventrally orientated squamosal sulcus. It contacts the tabular dorsomedially, the paraoccipital process of the opisthotic medially, and the dorsal process of the quadrate anteriorly.

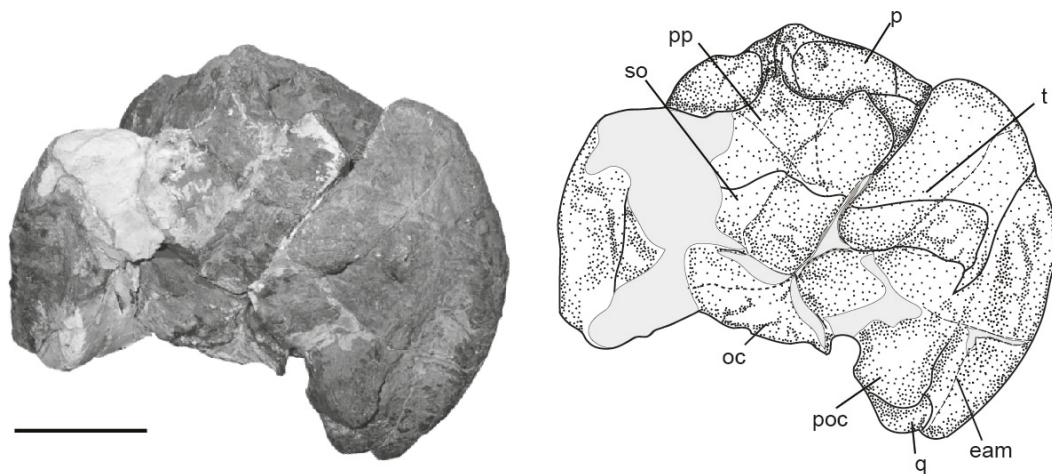


Figure 5.2. The holotype of *Riebeeckosaurus*: photograph (left) and illustration (right) of SAM-PK-3400 occiput. Scale: 10 cm.

5.3.1.3 Lower jaw

The lower jaw has the complete left ramus, which is composed of five fragments, and the anterior symphyseal portion of the right ramus (Figs. 5.3-4). The fact that the right symphyseal region is much shorter, but higher, than the left indicates significant deformation of the material (Fig. 5.4C). The left anterior portion of the dentary bears the roots of four functional and, two replacement incisors, a canine, three postcanines and alveoli for three more postcanines, while the right portion bears two functional incisor roots (Fig. 5.3). Incisor roots are

labiolingually elongated with the exception of the last incisor which is rounded in cross section and is similar in size to the canine root. Postcanine roots are significantly smaller than the canine root and the second postcanine root is relatively larger than the first one.

In lateral view (Fig. 5.4A), the dentary is a large bone comprising the entire anterolateral side of the lower jaw. Almost half way along the ventral length of the ramus the dentary meets the angular with an oblique suture, which slopes posterodorsally onto the surangular. The angular and the surangular are well exposed due to anterior displacement of the dentary. The posterodorsal portion of the dentary, which would have overlain the surangular is not preserved, and as a result the angular makes up most of the posterolateral side of the jaw. There is a prominent and rounded reflected lamina. The angular is dorsally in contact with the surangular, the posterior margin of which is rather vertically oriented.

In medial view (Fig.5.4B), the dentary also forms the anterior half of the lower jaw. The splenial is not preserved anteriorly, but the posterior end is a thin bone which tapers posteriorly and overlies the angular. A prominent articular, only visible from the medial side, is present on the posteroventral margin of the jaw and forms a well developed articular fossa bounded anteriorly by the prearticular. The prearticular sutures are not clearly represented and its anterior extension is inferred. This is a large and robust bone on the posterior half of the medial side of the jaw. This portion of the prearticular appears to be shorter and

more vertically oriented than in lower jaws of other similar sized tapinocephalids. The prearticular swings anteriorly and appears to taper to a point half way along the jaw.

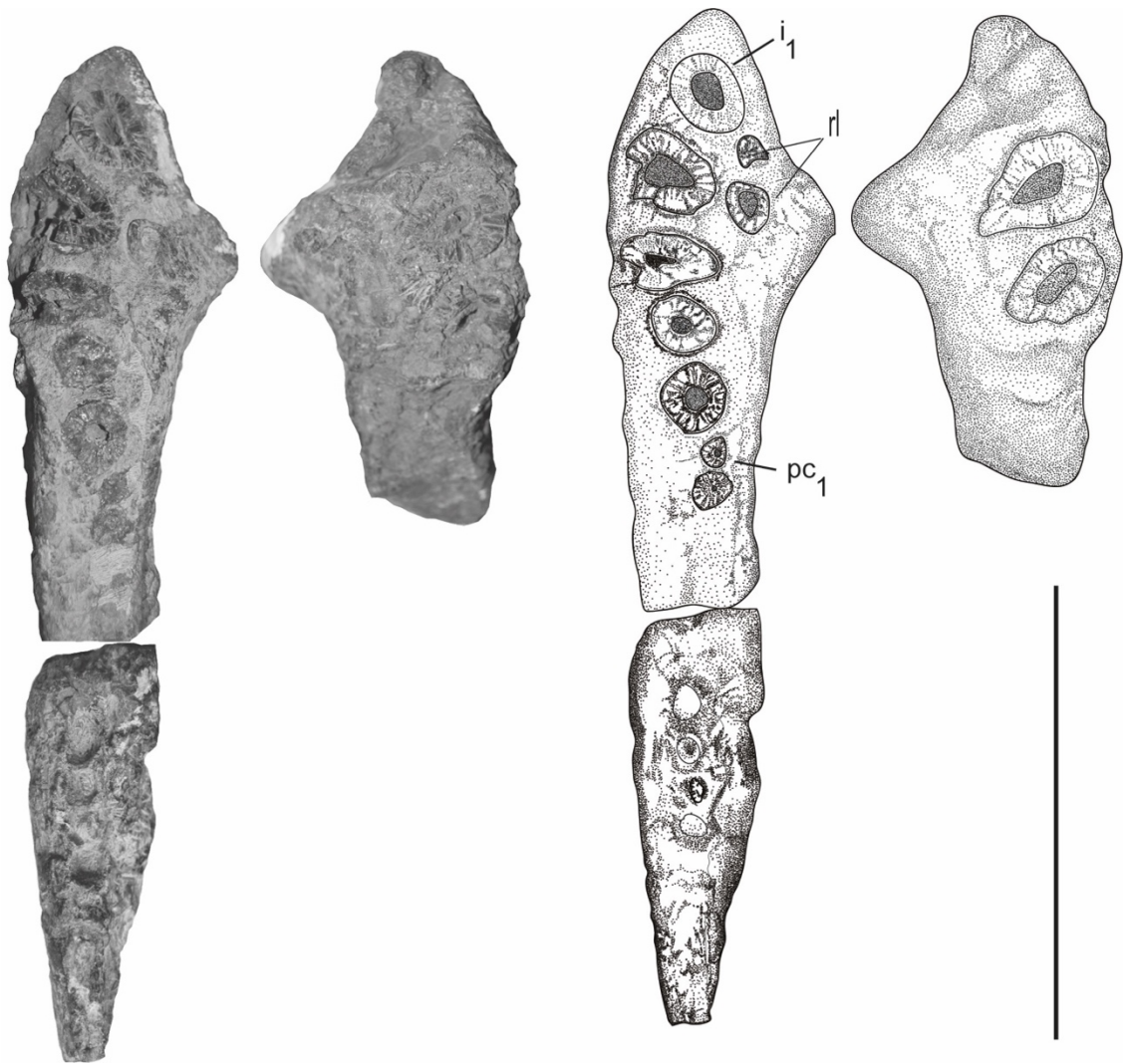


Figure 5.3. Photograph and drawing of the dorsal view of the left mandible and the anterior portion of the right mandible of *Riebeeckosaurus longirostris* (SAM-PK-3400). Scale 10 cm.

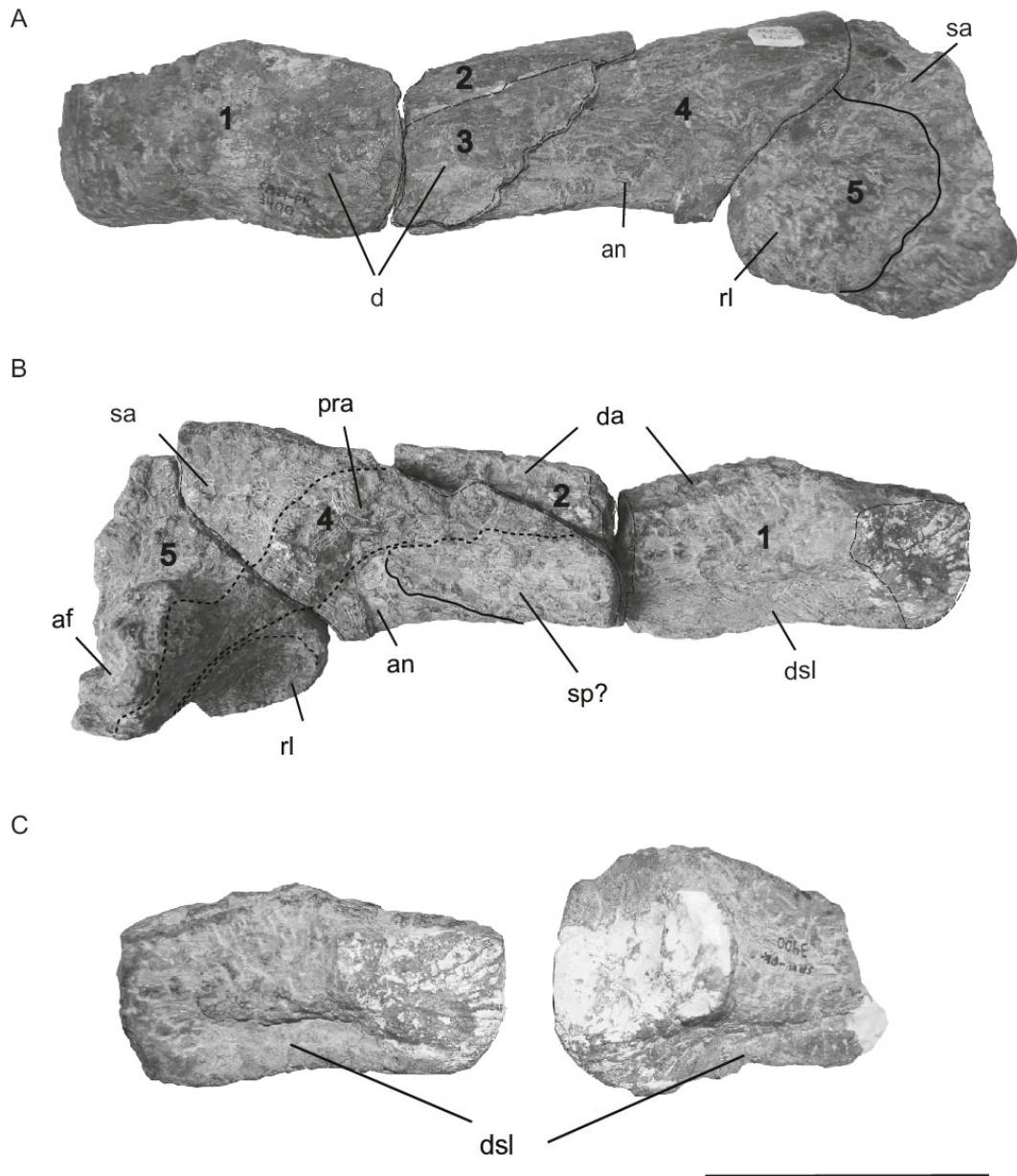


Figure 5.4. Photograph and drawings of the lateral (A), medial view (B) of left mandible of *Riebeeckosaurus longirostris* (SAM-PK-3400) and medial view (C) of the symphyseal portions of both sides of the mandible; note the deformation that resulted in both sides being strongly asymmetric. Arabic numbers are fragments of the lower jaw. Dashed lines are interpreted sutures. Scale 10 cm.

5.3.2 *Avenantia kruisvleiensis*

The holotype (SAM-PK-9166, Figs. 5.5-5.6) consists of the posterior portion of the skull extending anteriorly as far as the level of the canine on the left side, and lacks a lower jaw. It has undergone significant distortion, which resulted in the skull being compressed dorsoventrally and the basicranium and the occiput being pushed upwards. Consequently, the occiput has been rendered almost continuous with the palate and the right temporal region has been displaced laterally. The intertemporal, interorbital and postorbital regions are represented by weathered cranial fragments, some of which were imperfectly glued together when the skull was reconstructed by Boonstra (1952f). Cranial roof thickening is weak to moderate when compared to that of other tapinocephalids, contra Boonstra (1952f, 1957), who considered it to be extensive. Post-burial deformation has caused lateral displacement of the left postfrontal and portions of the zygoma. This deformation resulted in exposure of the dorsomedial surface of the postorbital on the dorsal view, which would normally be situated medially in the temporal opening (see Boonstra 1952f, fig. 2, Boonstra 1957, fig.11; Brink 1982). This opening is large and roomy, with anteroposterior diameter being larger than its dorsoventral diameter.

5.3.2.1 Skull roof

The parietal is a relatively large bone forming the sagittal crest in the temporal region and broadening to its greatest width at the level of the pineal foramen. The parietal tapers anteriorly between the paired frontals (Fig. 5.5A), thus being

different from the straight and transverse condition of the parietal-frontal suture described by Boonstra (1952df 1957). The dorsal midline surface of the parietal is slightly concave in the area between the frontals and the prominent pineal foramen, which is situated on a slightly raised boss. As illustrated by Boonstra (1952f, 1957), the parietal makes up the dorsomedial surface of the temporal opening and is in contact anterolaterally with the postorbital, and posterolaterally with the squamosal. Posteriorly it wedges out between the tabular and the squamosal on the posterior branch of the temporal opening. The squamosal and parietal form a wide horizontal platform dorsally, which is exposed in the posterior portion of the temporal opening.

The frontal forms the greatest portion of the skull roof in the interorbital region. It is difficult to assess whether the frontal participates in the orbital margin, as the bones in the supraorbital region are fragmented and weathered but it appears that a limited contribution of the frontal on the right orbit is present. Likewise it is difficult to make a reliable assessment about the frontal contribution to the anterior margin of the temporal opening because this region of the cranium on both sides of the skull, is assembled by weathered and poorly fitting cranial fragments. Anteriorly it has a long anterior sutural contact with the prefrontal and also has a short medial contact with the posterior end of the nasal (Fig.5.5A). The prefrontal is a relatively large and slightly thickened bone, which forms the largest part of the supraorbital margin. The left prefrontal is represented by an isolated bone fragment which has the same morphology as that of the right but has been weathered along sutural boundaries. The

prefrontal slightly overhangs the posterior portion of the snout presenting a thickening that is continuous with the posterior end of the nasal (Boonstra 1952d, 1957).

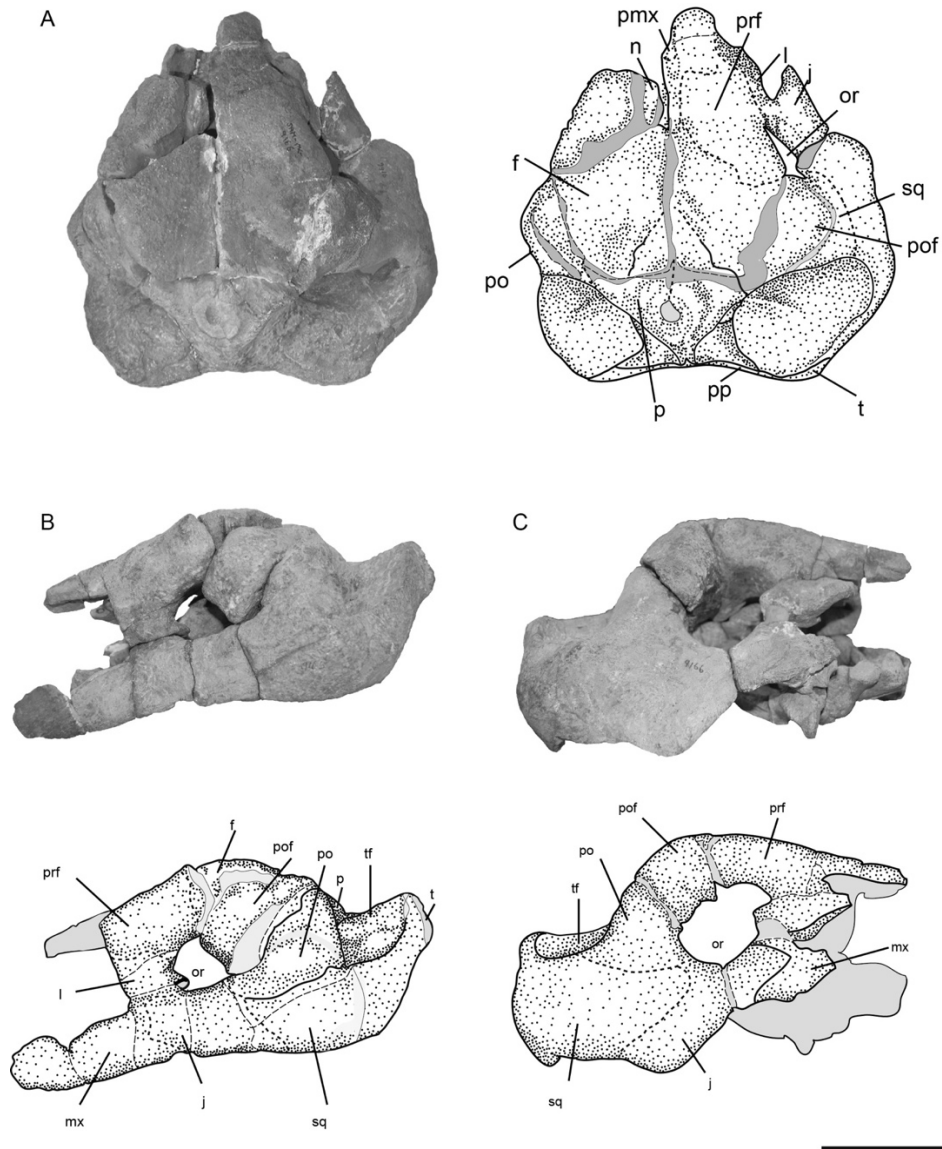


Figure 5.5. Photograph and drawing of dorsal (A), right (B) and left (C) view of SAM PK 9166 (holotype of *Avenantia kruisvleiensis*). Solid lines are visible and dashed lines are interpreted sutures. Narrow dashed lines are boundaries of bone fragments that correspond to cranial sutures except the one which extends across the parietal.

The nasal, preserved only posteriorly and on the left, is displaced posteriorly together with a portion of the left prefrontal. Its posteriormost portion forms a narrow tongue between prefrontals and it meets the frontal at the level of the anterior margin of the orbit. The anterior contact of the nasal with the premaxilla is evidenced by a grooved impression on the right side of the nasal, corresponding to a posteromedial protrusion of the premaxilla which extends up to the end of the prefrontal.

The maxilla is preserved posteroventrally on both sides of the skull, and is more complete on the left side. On the ventral side of the left maxilla, three anterior teeth and succeeding alveoli for seven postcanines are preserved. The first tooth, adjacent to the maxillopremaxillary suture, is considerably larger than the next two and it is interpreted as a canine. Further preparation of the alveolus revealed a partially erupted canine with a worn but distinctively denticulated mesiodistally but the heel is not visible and might be lacking it (Figs 5.6E). Only the first postcanine is well preserved, showing a triangular crown in lateral view and bearing denticles along the edge (Figs 5.6C-D). The second postcanine is substantially smaller (Fig. 5.6B). The alveoli of the remaining postcanines are visible toward the posterior end of the maxilla.

Contrary to Boonstra's (1952f, 1957) description, the jugal forms the entire ventral margin of the orbit and presents an anterior spur-like contact with the maxilla, which continues anteriorly further than the anterior border of the orbit. The squamosal is a large bone forming the entire posterior and lateral margins

of the temporal opening and having a long anterodorsal sutural contact with the postorbital.

5.3.2.2 Palatoquadrate complex

Only the posterior portion of the palate is preserved, extending anteriorly up to the posterior end of the vomer. The vomer is paired, bearing a ventromedial trough that incorporates the midline suture with a weakly developed lateral ridge which does not extend as far as the posterior end of the vomer between the palatine bosses (Fig. 5.6B). The palatine is represented by a partial fragment and its sutural contacts are not clear. There is an anteroposteriorly elongated and bulbous palatine boss, lacking teeth. The posterior margin of the left choana is narrow and elongated, formed equally by the vomer medially and the palatine laterally. A deeply positioned ectopterygoid is partially visible on the left side, anterior to the lateral process of the pterygoid. This is in contrast to Boonstra (1952f, 1957) and Brink (1982) who described this bone as being posterolateral to the process of the pterygoid, between the jugal and palatine.

The pterygoid is a tripartite bone comprising a central corpus, lateral process and the quadrate ramus. The central corpus has a midline suture and a narrow interpterygoidal vacuity that extends posteriorly along the midline from behind the lateral process up to the contact with the parasphenoidal rostrum. The pterygoid bosses are short and elongated in the same direction as the palatine bosses. A prominent lateral process, best preserved on the left, has a thin ventral ridge on its anterior margin which grades posteriorly into a horizontal shelf and

posteromedially continues as a longitudinal ridge bordering the interpterygoidal vacuity. A posterolaterally directed, rather short, quadrate ramus meets the paraoccipital process of the opisthotic posterolaterally. It forms a strong ventral ridge, which merges anteriorly with the pterygoid corpus posterior to the lateral process.

The parasphenoid rostrum is preserved between the pterygoid bones on the posterodorsal portion of the basicranial girder and forms a pointed V-shaped midline contact with the pterygoid on the anterior side. The basisphenoid swells posterolaterally as far as the fenestra ovalis where it forms a transverse sutural contact with the basioccipital. A basisphenoid keel is present on the ventral midline, followed posteriorly by a basioccipital midline trough flanked by ridges, which diminishes as it extends posteriorly onto the basioccipital. Lateral to these structures, the basisphenoid and basioccipital form the tubera which attenuates posteriorly on both bones. The stapes (more completely preserved on the left side) are both located in situ. It is a short and stout rectangular bone with the proximal end located on the fenestra ovalis. Postmortem deformation of the stapes prevents further analysis of its morphology.

5.3.2.3 Occiput

The entire occiput is preserved, but has been slightly dorsoventrally compressed, particularly on the right side, thus becoming laterally weakly concave (Fig. 5.6A). The occipital crest is slightly thickened on its posterior portion but it does not bend posteriorly towards the occiput, as described by Boonstra (1952f). The

squamosal and part of the parietal form a rather horizontal platform which is exposed dorsally medial to the posttemporal arch. There is almost no convexity in the occiput and the occipital crest does not overhang the plate.

The postparietal is present as a relatively small, medially positioned and unpaired bone. Dorsally, it meets the posteroventral ends of the parietals and intrudes slightly between them, and contacts ventrally the supraoccipital. The postparietal has a crested midline ridge, which extends dorsoventrally across the entire bone surface, but becomes less prominent onto the dorsomedial side of the supraoccipital. A large and flat tabular bone forms the dorsolateral portion of the occipital plate. Dorsally it has a long sutural contact with the parietal, which is visible in dorsal view. Ventrolaterally a long spur of the tabular extends between the external auditory meatus and the supraoccipital as a long ribbon-shaped element, which is in contact with the postparietal dorsomedially. The ventral portion of the supraoccipital forms the dorsal margins of the posttemporal fenestra and the foramen magnum. Towards the ventrolateral end of the supraoccipital, Boonstra (1952f; 1957) illustrated a long horizontal sutural contact between the supraoccipital and the paraoccipital process of the opisthotic. However, we interpret this contact as being very short.

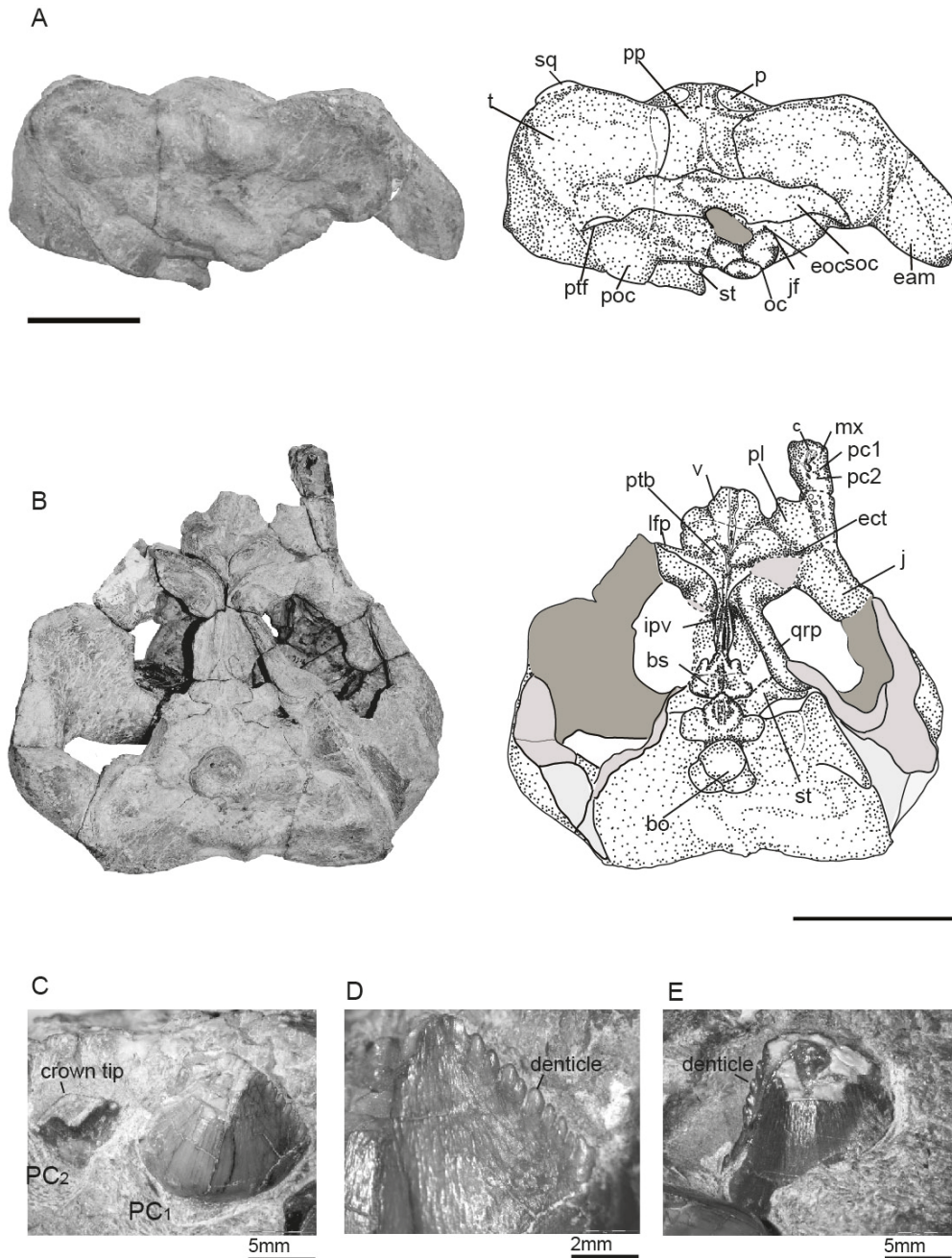


Figure 5.6. Photographs and drawings of palatal (A) and occipital (B) views of SAM-PK-9166 (holotype of *Avenantia kruisvleiensis*) and details from its dentition: photographs of lateral views of postcanines 1 and 2 (C); detail of denticles on the crown of the first postcanine in lateral view (D) and lingual view of the canine (E). Scale 10 cm. In A and B the solid lines are for visible and dashed lines are interpreted sutures. Narrow dashed lines are boundaries of bone fragments that correspond to cranial sutures except the one which extends across the parietal. Light grey is plaster-reconstructed areas and matrix infilling.

The exoccipital has a short wing-like morphology lateral to the foramen magnum of which it forms the lateral and ventral borders. This bone is in line with the supraoccipital, having a rather short contact between them. A clear tripartite occipital condyle is present, with a contribution from the basioccipital. Due to distortion, the paraoccipital process appears to almost contact the medial surface of the dorsal process of the quadrate, whereas the distal margin of the left paraoccipital process, broken in two pieces, ends near the distal margin of the stapes. The left paraoccipital process overhangs distally the occipital portion of the squamosal and forms part of the medial margin of the external auditory meatus. The left quadrate is partially preserved, its dorsal process being in contact dorsolaterally with the squamosal and medially with the quadrate process of the pterygoid. The quadratojugal is not preserved.

5.4 Discussion

Re-examination of the holotypes of *Avenantia kruisvleiensis* and *Riebeeckosaurus longirostris* shows that some of the features which were considered diagnostic for these taxa are in fact not unique to them, whereas others are indeed a by-product of the poor preservation of the specimens. Thus, the heavily weathered nature of the skull roof of the holotype of *A. kruisvleiensis* significantly influenced previous interpretation of its morphology. For example, the described features such as the distinct ‘ring wall’ surrounding the pineal opening, and the ‘low intertemporal crest’ included in the diagnosis by Boonstra (1952f, p. 250, 254, 255 and 1957, p. 19, 35) appear to be the remnant of a raised

pineal opening rim and a once prominent intertemporal crest (like the one which is observed in *Riebeeckosaurus*) which was weathered away. Other alleged diagnostic characters of *A. kruisvleiensis*, such as the contribution of the exoccipital to the occipital condyle and the contact between the squamosal and postorbital along the temporal opening, are also features which are observed in other tapinocephalids such as *Tapinocaninus* (SG, personal observation) and *Moschops* (e.g. Boonstra, 1957).

Of great taxonomic consequence is the inferred condition of a long snout for *Riebeeckosaurus longirostris*, which besides being considered diagnostic for this species, led to its being considered in a separate taxonomic group to *Avenantia kruisvleiensis* (Boonstra 1952f; 1963b; 1969; King 1988). There is no preservation of the snout in any specimen of *R. longirostris*, and the assumption of a long snout was based on the length of the lower jaw of the holotype of *R. longirostris*. Barghusen (1975, p. 298) however, considered that the dentary has been “displaced forward relative to the postdentary bones as a result of a distortion,” thus increasing the apparent length of the lower jaw. The comparison of the lower jaw of *R. longirostris* with that of a similar sized specimen of the well-known short snouted *Moschops* reveals that there is little difference in length between these elements.

From our detailed analysis of the specimens attributed to *A. kruisvleiensis* and *R. longirostris*, it is evident that these taxa are very similar in morphology and share the following characters: a relatively large and mediolaterally and

anteroposteriorly expanded temporal opening which is similar to *Tapinocaninus*; the presence of an intertemporal crest; a weak concavity of the occiput in posterior view; anterior position of the quadrate condyles extended anteriorly below the orbit (the position of this bone is inferred for *A. kruivleiensis* after the orientation of the squamosal); weak thickening on the dorsal portion of the occipital crest; wide exposure of the parietal lateral to the sagittal crest on the medial portion of the temporal fossa. Some of the above mentioned features in *R. longirostris* and *A. kruivleiensis*, such as the narrow intertemporal region and relatively large temporal openings, are similar to the condition observed in the basal tapinocephalid *Tapinocaninus* but the former taxa show a more developed sagittal crest and a less prominent but wider ridge of the squamosal on the dorsomedial portion of the temporal opening.

Despite some similarity to the basal tapinocephalid *Tapinocaninus*, the latter is known from the *Eodicynodon* Assemblage Zone (AZ). In contrast the specimens of *R. longirostris* and *A. kruivleiensis* come from localities which are stratigraphically high in the Abrahamskraal Formation, corresponding to the top of the *Tapinocephalus* AZ (Dr M. Day, pers. comm.).

The characters differentiating *A. kruivleiensis* from *R. longirostris* can be explained by distortion or weathering. Main differences of *A. kruivleiensis* in comparison with *R. longirostris* are: an anteroposteriorly longer temporal opening; absence of thickening of the parietal surface in front of the pineal

opening; a reduced postorbital bar and a rounded lower corner of the posterior margin of the zygoma in lateral view. Some of these character variations have also been observed between similar sized, subadult to adult specimens of *Moschops* and *Tapinocaninus* which suggest that such differences could be linked with sexual dimorphism (in particular, differences in the pachyostotic development of the postorbital bar), or individual variation.

The morphological similarity between the skulls of *Riebeeckosaurus longirostris* and *Avenantia kruisvleiensis* lead us to conclude that they belong to the same species. This is strengthened by the close geographic and stratigraphic proximity of their localities which are both situated at the top of the *Tapinocephalus* AZ. As the name *Riebeeckosaurus longirostris* has priority under Article 23 of the Code of Zoological Nomenclature, this is the name that will be retained, with *Avenantia kruisvleiensis* becoming the junior synonym.

5.5 Systematic Palaeontology

Riebeeckosaurus Boonstra, 1952e

Synonym. *Avenantia* Boonstra, 1952f

Type species *Riebeeckosaurus longirostris* Boonstra, 1952e

Synonym. *Avenantia kruisvleiensis* Boonstra, 1952f

Holotype: SAM-PK-003400, posterior half of the cranium and a lower jaw fragments (Figs 1-3).

Type locality: Boonstra (1952e) gives the locality as close to Viviershalte, Beaufort West. The farm name is recorded as Leeuwkraal (with Viviers as an alternative name in the Karoo vertebrate database at the Evolutionary Studies Institute of the Witwatersrand University.)

Revised diagnosis for genus and species. *Riebeeckosaurus longirostris* differs from the other tapinocephalids with the following autapomorphies. Short-snouted tapinocephalid that can be distinguished from other members of the family by the presence of a crest like intertemporal region; parietals bend moderately backward in the intertemporal area posterior to the pineal opening; and lacking the squamosal facet between the squamosal and the lateral end of the paroccipital process of the opithotic.

Referred specimens. SAM-PK-11955, posterior portion of a skull roof (Fig. 1A). Boonstra (1952e) gives the location as the Koup, which is a flat area between Beaufort West and a southward projection of high ground about 30 km east of Laingsburg, bounded on the north by the Great escarpment and the south by the Swartberg mountains. SAM-PK-9166 (holotype of *A. kruisvleiensis*), skull (lacking snout and lower jaw, Figs 3, 4) and some postcranial fragments including a femoral head. From the farm Kruisvlei, near Merweville, Beaufort West (Boonstra 1952f). SAM-PK-9167, postcranial bones (scapula, ilium and femur). From the farm Kruisvlei near Merweville Beaufort West (Boonstra 1955b). There is no cranial material associated to this specimen, thus the taxonomic identification of this material is only tentative, and final confirmation

will require additional discoveries of *R. longirostris*. It is interesting that Boonstra (1955f) quoted SAM-PK-9167 as the holotype of *A. kruivleiensis* instead of SAM-PK-9166, which was considered a mistake by van den Heever and Grine (1981). In the same contribution, Boonstra (1955b) mentions an associated cranium under SAM-PK-9167.

Stratigraphic information. All specimens occur stratigraphically high in the *Tapinocephalus* AZ, towards the top of the Abrahamskraal Formation of the Beaufort Group (Dr M. Day, pers. comm.) and have been found in close proximity to specimens of *Moschops*. The locality of SAM-PK-11955 is listed only as the Koup which is an extensive area covering various stratigraphic levels of the *Tapinocephalus* AZ.

Comment. *R. longirostris* and *A. kruisvleiensis* were described in the same volume (12, no 2) of the *Tydskrif vir Wetenskap en Kuns* (Journal for Science and Art - South African Academy for Science and Art). *Avenantia* was mentioned in the description of *R. longirostris*, but the fact that the mention of the name lacked a prior description and reference (Article 13 of the Code of Zoological Nomenclature) makes the name a *nomen nudum* (see also van den Heever and Grine, 1981). As the description of *A. kruisvleiensis* was published after the description of *R. longirostris*, the latter species has priority under the Code of Zoological Nomenclature-Article 23.

5.6 Conclusions

From the detailed morphological comparison it is clear that the holotype and only representative of *Avenantia kruisvleiensis* (SAM-PK-9166) shares several cranial and dental features with the holotype and referred specimens of *Riebeeckosaurus longirostris* (SAM-PK-3400 and SAM-PK-11955).

Accordingly in agreement with Kammerer (2009) *A. kruisvleiensis* is considered to be a junior synonym of *R. longirostris* and contrary to most previous proposals, the species should be included in the short-snouted tapinocephalid taxa. The morphological differences between the two genera (e.g. surface thickening of parietal, postorbital bar and general cranial thickening) are best interpreted as being the result of sexual or ontogenetic variation. The fact that the specimens are of similar size suggests that the former is more likely.

6 REVISION OF THE SHORT SNOUTED TAPINOCEPHALID: SUBFAMILIES TAPINOCEPHALINAE AND MOSCHOPINAE, BOONSTRA (1969)

6.1 Introduction

The majority of the described tapinocephalid dinocephalians from the *Tapinocephalus* Assemblage Zone are short-snouted species. Boonstra (1969), in his review of the dinocephalian fauna of the *Tapinocephalus* AZ, recognized 12 species of short-snouted tapinocephalid out of 28 described species. These twelve species comprised the short-snouted subfamilies Tapinocephalinae and Moschopinae. The Tapinocephalinae included *Tapinocephalus atherstonei*, *Phocosaurus megischion*, *Keratocephalus moloch* and *Mormosaurus seeleyi* which Boonstra considered to have large and greatly pachyostosed skulls with short and weak snouts, and a prominent nasofrontal boss or greatly swollen frons. The Moschopinae (*Moschops capensis*, *M. koupensis*, *M. whaitsi*, *M. oweni*, *Delphinognathus conocephalus*, *Criocephalus vanderbyli*, *C. gunyankaensis* and *Avenantia kruisvleiensis*) are smaller, have less pachyostosed skulls with a short snout and no nasofrontal boss (swollen frons).

Boonstra (1969) considered the rest of tapinocephalid species as longirostrin or long snouted and placed all of them in the Struthiocephalinae, except for *Riebeeckosaurus longirostris* which was the only member of the longirostrin

subfamily Riebeeckosaurinae. The holotype of *Riebeeckosaurus* does not have a snout preserved and differs from other longirostrin dinocephalians in having a sagittal crest. *Riebeeckosaurus* was later recognised as a short snouted tapinocephalid (Barghusen, 1975; Kammerer, 2009, Chapter, 3; Güven et al. 2013; see chapter 5). Boonstra (1969) recognised *Struthiocephalus whaitsi*, *Struthiocephaloides cavifrons*, *S. duplessisi*, *Taurocephalus lerouxi*, and *Struthionops intermedius* as members of the Struthiocephalinae. Because of perceived affinities between *Mormosaurus* and *Keratocephalus* of the Tapinocephalinae with members of the Struthiocephalinae, Boonstra (1969,p.42) considered these genera to be a phylogenetic link between the two families. In earlier taxonomic publications Boonstra (1936b, 1953b) considered *Mormosaurus* the type genus of the logirostrin tapinocephalids. *Keratocephalus* on the other hand was considered short-snouted despite the fact that neither the holotype nor the referred specimens had a snout or lower jaw preserved, and thus there was no supporting evidence to determine the length of the snout (Boonstra, 1956, 1969).

Without providing reasons (Boonstra, 1969) proposed the following synonymies for the short-snouted taxa: *Moschognathus whaitsi*, *Pnigalion oweni*, *Agnosaurus pienzaari* and *Moschoides romeri* were synonymised with *Moschops*. *Pelosuchus* and *Taurops* were synonymised with *Keratocephalus* and *Tapinocephalus* respectively. King (1988) accepted all the synonymies suggested by Boonstra (1969) but recognised the Tapinocephalinae as the only short-snouted subfamily and included the Russian *Ulemosaurus* in this subfamily as well. Rubidge (1994) introduced *Tapinocaninus pamela* as a tapinocephalin tapinocephalid. In his PhD

thesis Kammerer (2009) provided a brief review of the group and without providing anatomical descriptions reduced the number of valid tapinocephalid species from the *Tapinocephalus* AZ. to six. He suggested the following synonymies: *Criocephalosaurus vanderbyli* with *Moschops capensis*, *Avenantia kruisvleiensis* with *Riebeeckosaurus longirostris*, *Taurocephalus lerouxi* and *Struthiocephalus rheederi* with *Mormosaurus seeleyi*; *Struthiocephaloides duplessisi* and *S. cavifrons* with *Struthiocephalus whaitsi*. Kammerer further considered *Delphinognathus* and *Phocosaurus nomen dubia* and retained *Moschognathus whaitsi* which was later synonymized with the longirostrin *Struthionops intermedius* (Kammerer, 2009; Boos et al., 2010). Güven et al. (2013) provided a description of *Avenantia kruisvleiensis* and *Riebeeckosaurus longirostris* and supported their synonymy. The synonymy of *Criocephalosaurus vanderbyli* with *Moschops capensis* proposed by Kammerer (2009) was later questioned and *C. vanderbyli* reinstated on the basis of new discoveries (Güven et al., 2012, Day et al., 2015).

This chapter contributes to understanding of the cranial morphology of the short snouted tapinocephalids of the subfamilies Moschopinae and Tapinocephalinae of Boonstra (1969) (=Tapinocephalinae of King, 1988) providing for the first time, comprehensive cranial descriptions with figures of all valid species.

Accordingly the following five species are considered valid in this contribution:

Tapinocephalus atherstonei, *Moschops capensis*, *Moschognathus whaitsi*, *Agnosaurus pienaari*, and *Criocephalosaurus vanderbyli*. These taxonomic conclusions support the findings of Kammerer (2009) in: the validity of

Moschognathus whaitsi (although not as synonym of *Struthionops intermedius*), the synonymy of *Avenantia kruisvleiensis* with *Riebeeckosaurus longirostris* (Chapter 5), and synonymies of *Keratocephalus moloch* with *Struthiocephalus whaitsi* and *Struthiocephalus rheederi* and *Taurocephalus lerouxi* with *Mormosaurus seeleyi*. The following taxa are considered *nomen dubia*: *Phocosaurus megischion*, *Pelosuchus priscus*, *Moschoides romeri*, *Criocephalosaurus gunyankaensis* and *Taurops macrodon*. This result agrees with the suggestions made by Kammerer (2009), excluding *Taurops macrodon*, *Moschoides romeri* and *Pinigalion oweni* which he in accordance with Boonstra (1969) regarded as synonyms with, respectively, *Tapinocephalus atherstonei* and the latter two *Moschops capensis*.

6.2 Material and methods

The skulls of 40 short-snouted tapinocephalid specimens were examined personally, except for the specimens indicated by an asterisk in Appendix 2. In addition skulls of some longirostrin tapinocephalids were examined for comparative purposes. Many of the specimens required further preparation which was done mechanically with aircutters at the fossil preparation laboratory of the Evolutionary Studies Institute of the University of the Witwatersrand University in Johannesburg. Basic linear measurements of specimens, when required were taken with the use of a measuring tape.

6.3 *Tapinocephalus atherstonei* OWEN 1876

Holotype: NHMUK PV R 1705, anterior end of upper jaw from Jan Willem's Fontein, Beaufort West (Owen, 1876, p. 1-6) (Fig. 6.1). A cast of the upper jaw is housed in the South African Museum catalogued under the number SAM-PK-733.

6.3.1 Previous diagnosis for genus and species. Diagnoses previously set up by different authors:

Below is an abbreviation of the description of Owen 1876. Instead of a diagnosis he provided a brief description, highlighting affinities with the Reptilia: "... low, depressed form of the broad, obtuse fore part of the skull" Owen, 1876, p.1.

Boonstra (1956, p. 152-153) instead of a diagnosis for the genus provided a list of "skull characters for genus." This description was later used as a diagnosis by King (1988). "1. The preorbital length is 51-52 % of the total median length; the snout is short (preorbital length 273 mm.) and it is broad (330 mm.) and low (144 mm), with the height being 44% of the width; the dorsal facial surface of the snout is short and does not extend to the plane of the anterior orbital border; transition from facial to cranial surface is very abrupt. 2. The dorsal cranial bones are very strongly pachyostosed, with centres of thickening coalesced and the transition on to the face is by an abrupt step along a U-shaped line; the thickening extends very far forward- well anterior to the plane of anterior orbital border; along the median line the pachyostotic cranial roof is 339 mm in length and this is 58-63% of the total median length of the skull; this great anterior extension is

due to the greatly thickened naso-frontal boss, which does not, however, stand out dorsally above the general cranial surface. On the sharply up-bent face of the posterior end of each nasal there is a fairly deep hollow. The prefrontal is greatly thickened and this is confluent with the pachyostosis of the nasal and frontal and it overhangs the orbit forming the greatly thickened antero-dorsal part of the orbital border and limits anterior vision. The area around the pineal foramen is raised, but its general surface is lower than of the surrounding bones. 3. The postorbital bar is very wide and very massive. 4. The posttemporal arch is very thick and the temporal fossa is small with its antero-posterior diameter greatly reduced. 5. The dorsal parietal surface is very broad (210-240 mm.) with in one specimen a narrow constricted bay to the temporal fossa; and interorbital width is 88-100% of the intertemporal width. 6. Anteroposterior length of the parietal is fairly long (105-114 mm.), frontal fairly large. 7. The intersquamosal width is very great (495-540 mm.), and is 99-100% of the median length and the skull is thus nearly or quite as broad as long. 8. The quadrate is situated well forward; mandibular length is 57% of the median length of skull; the quadrate ramus of the pterygoid, although it extends to well posterior of the condyles of the quadrate and underlies the distal end of the stapes, is short; lateral pterygoid rami form a weak transverse bar of small width. Dentition is poorly preserved but probably feeble.”.

6.3.2 Historical background and remarks on the holotype. *Tapinocephalus atherstonii* was described by Owen (1876, pp. 1-6, Fig. 6.1) on the basis of an anterior end of an upper jaw (Owen’s No. S.A. 1 [NHMUK PV R 1705]), which

had been received by the British Museum in London (NHMUK) in 1872 from the collector William G. Atherstone (a South African medical practitioner and amateur geologist). *Tapinocephalus atherstonii* was the original spelling used by Owen (1876) but in the following publications up until now the specific name was spelled as *atherstonei*. As it is spelled in this way consistently in the literature according to the Article 33.2.3.1 of the ICZN Code, the species name of *Tapinocephalus* is automatically replaced with *atherstonei* as previously suggested by Kammerer (2009).

The collector Atherstone had found a number of large fossil bones during a journey through the ‘Gouph’ region of Cape Colony (now Western Cape Province, South Africa) in early 1870, and from these Owen (1876) assigned a further 11 specimens to *Tapinocephalus*. These were: part of a lower jaw positioned closer to the symphysis (No. S.A. 2-3 [NHMUK PV R 1708]), a number of fragmentary vertebrae (Nos. S.A. 4–11) and a partial rib (No. S.A. 12). Owen (1876) did not provide a proper diagnosis for *Tapinocephalus atherstonei*.

Lydekker (1890, p. 93, Fig. 6.2) considered the dentary element mentioned by Owen to represent a specimen received at an earlier date from another fossil collector and geologist, A. G. Bain, which he considered to resemble *Titanosuchus* in its dentition. He also considered some of the postcranial elements referred by Owen to *Tapinocephalus atherstoneii* to be indeterminate or more likely to be pareiasaurian. He referred appendicular and pelvic material from the Atherstone collection, that had been previously described by Owen (1876) as

Pareiasaurus, to *Tapinocephalus*. Broom (1909b) referred an almost complete cranium (NHMUK PV R 3594) to *Tapinocephalus*, but he changed his mind after Haughton (1913) described another skull in the South African Museum (SAM-PK-2344) as *Tapinocephalus atherstonei*. Shortly thereafter, Watson (1914a) redescribed NHMUK PV R 3594 and made it the holotype of a new genus, *Mormosaurus seeleyi*. In this paper, Watson listed two additional cranial pieces as part of the holotype of *Tapinocephalus atherstonei* (the right occiput and the left supraorbital region). Apparently he associated these pieces with the anterior snout fragment of the holotype of *Tapinocephalus atherstonei* because of the colour and textural similarity of the matrix (Watson 1914, p. 762). Despite this, Broom (1928) still mentioned the dentary and omitted to mention the skull roof fragments in his reference to the type specimen, as have other subsequent authors (e.g. King, 1988).

The referral of SAM-PK-2344 to *Tapinocephalus atherstonei* by Haughton (1913) was supported by both Watson (1914) and later by Gregory (1926), who suggested this skull should be considered as a *neotype* for *Tapinocephalus atherstonei* because of the poor state of preservation of the holotype. Broom (1928) referred AMNH FARB 5626 (the posterior two thirds of a cranium from Ganskraal, Prince Albert) to *Tapinocephalus*, and probably *T. atherstonei*, because of its similarity to SAM-PK-2344. Boonstra (1936b), in his revised description of AMNH FARB 5626, confirmed this identification. However, in none of the above referrals to *Tapinocephalus*, were characters of the referred specimens compared with those of the holotype. Broom (1928) was the only to

question the unsatisfactorily defined taxonomic identity of *T. atherstonei*. A thorough diagnosis for *T. atherstonei* was only later provided by Boonstra (1956) who later wrote that *T. atherstonei* was a tapinocephalid in which ‘the skull is large with relatively short and a weak snout [and] the skull roof is greatly pachyostotic’ (Boonstra 1969, p. 42). Most recently, autapomorphies for the genus were given by Kammerer (2009, p. 238) as ‘entire frontal region massively pachyostosed confluent with postorbital bar, snout extremely short and broad’.

6.3.3. Systematic Palaeontology

Tapinocephalus atherstonei Owen 1876

Holotype: NHMUK PV R 1705

Neotype suggestion: SAM-PK-2344

Referred specimen: AMNH FARB 5626, NHMB 1556, CGP/1/2266

Revised diagnosis for genus and species: *Tapinocephalus atherstonei* can be diagnosed on a combination of the following characters: Tapinocephalid with a broad and extremely short snout, the entire frontal region in the adult forms is massively pachyostosed confluent with the thickening of the nasofrontal boss and postorbital bar, rounded and swollen zygoma corner. Oval outline of the nasofrontal boss in dorsal view with the longer axis positioned transversely between the orbits (modified after Boonstra 1956; Kammerer, 2009).

6.3.4 Description

6.3.4.1 Material

The description below is based on the following specimens: NHMUK PV R 1705 (holotype), anterior extremity of the snout. SAM-PK-2344 is a well-preserved

skull without a lower jaw, from the farm Uitkyk, Beaufort West, Western Cape. It was previously referred to *Tapinocephalus* by Haughton (1913). AMNH FARB 5626, posterior two-thirds of a cranium from the farm Gans Kraal, Prince Albert, Western Cape. This specimen was described and figured in Broom (1928) who referred it to *Tapinocephalus* and this description was revised by Boonstra (1936). CGP/1/2266 is a large posterior two-thirds of a cranium which was identified during this study. NHMB 1556 is a cranium lacking the tip of its snout, from the Madumabisa Mudstone Formation in northwest Zimbabwe. This specimen was described and illustrated by Munyikwa (2001) and was identified during this study as a juvenile specimen of *Tapinocephalus*. None of the specimens identified as *Tapinocephalus* have the lower jaw preserved.

6.3.4.2 Cranial pachyostosis and general preservation

NHMUK PV R1705 is the extreme anterior tip of a snout which includes the portion between the premaxillary tip of the snout anteriorly and the anterior margin of the external naris posteriorly. Comparison of this specimen with the snout of SAM-PK-2344, where the snout is well preserved, indicates that the skull of NHMUK PV R 1705 was of similar size. SAM-PK-2344 is a fairly well preserved and complete skull that lacks a lower jaw. It is a large skull with a heavily pachyostosed cranial roof which is emphasized by the bones of the supraorbital margin, the nasofrontal boss and posterior part of the zygoma. The basal length of the skull is almost equal to its basal width (between the posterior ends of the squamosals).

AMNH FARB 5626 is a heavily thickened weathered posterior two-thirds of a skull without a lower jaw. Although it is distorted and weathered, the specimen exhibits some diagnostic features on the posterior end of the snout, the basicranium and the occiput. Skull size is estimated to be intermediate between those of SAM-PK-2344 and CGP/1/2266 .

The skull of NHMB 1556, which is the smallest *Tapinocephalus* skull known, is well preserved on the posterior portion of the cranial roof and the almost complete left zygoma. The bones of both the circumorbital and temporal regions are fairly well preserved except for the ventral portion of the right temporal opening. The specimen display some palatal and occipital characters, but the bone surface is quite weathered. Being the smallest *Tapinocephalus* skull, NHMB 1556 has less cranial pachyostosis than the other skulls, the largest temporal fenestra, and narrowest postorbital width. Because of its relatively smaller size, less cranial thickening, relatively large orbits and large temporal fenestra, NHMB 1556 is considered to be an immature *Tapinocephalus* individual.

6.3.4.2 Skull roof

Premaxilla: The premaxilla (Figs. 6.1, 6.3-6.6) makes up the anteriormost extremity of the snout and contributes to the dorsal, anterior and anteroventral borders of the external naris. It is completely preserved only in SAM-PK-2344; while its anterior extremity is partially preserved in NHMUK PV R 1705 and its posterior end in the rest of the skulls. The premaxilla is in contact with the septomaxilla posteriorly where it borders the anterior and anteroventral margins of

the external naris. On the dorsal surface of the cranium, the premaxilla extends posterodorsally as a narrow projection as far as the mid orbital level. Along its posteromedial extension, the premaxilla has a long posterolateral suture with the nasal and ventrolaterally shares a short contact with the maxilla. In SAM-PK-2344 the premaxilla-maxilla suture is visible in lateral view and extends posterodorsally from behind the alveolus of the fifth incisor to the anteroventral border of the external naris. The nature of the posterior contact of the premaxilla with the nasal varies in different skulls but in all specimens it forms part of the frons and the posterior end of the premaxilla extends dorsally. The premaxilla has a bifurcated contact with the nasal in CGP/1/2266 but not in the rest.

Septomaxilla: The septomaxilla (Figs. 6.3C, 6.5A) is preserved in SAM-PK-2344 as a relatively thin elongate bone contacting the premaxilla on the anterior border of the external naris. It expands posteriorly to cover the base of the external naris, and continues posteriorly as a narrow elongate bone along the ventral border of the external naris where it forms a hook-like projection on the posterior border of the external naris (contra Boonstra 1956, fig. 1). Posteriorly, on the lateral surface of the skull roof behind the external naris, the septomaxilla forms a wedge-shaped contact between the nasal dorsally and maxilla on the ventral side.

Nasal: The nasal (Figs. 6.3-6.6) is a paired elongated bone. It is completely preserved in SAM-PK-2344; and the posterior part is preserved in NHMB1556, AMNH FARB 5626 and CGP/1/2266. Anteriorly it contributes to the

posterodorsal border of the external naris, and has a short contact with the septomaxilla as is evident in SAM-PK-2344. Posterior to the external naris the nasal has a long contact with the premaxilla which extends backwards as far as the anterior margin of the orbit. Here it meets its mate along the dorsal midline of the skull. Anterolaterally it has a long horizontal sutural contact with the maxilla, a short sutural contact with the prefrontal, and a long transverse contact with the frontal half way along the orbit as evident in SAM-PK-2344, NHMB 1556, AMNH FARB 5626 and CGP/1/2266. In NHMB 1556 the paired nasals together form a pointed contact between the frontals.

Anterior to the orbit the nasal and premaxilla together slope dorsally to form the naso-frontal boss which is best preserved in SAM-PK-2344, AMNH FARB 5626 and CGP/1/2266. This pronounced naso-frontal boss is well developed in SAM-PK-2344 and AMNH FARB 5626, but is more gentle in CGP/1/2266 and NHMB 1556 where there is less cranial pachyostosis. In SAM-PK-2344 the dorsal surface of the nasal is depressed before it contributes to the nasofrontal boss on either side.

Maxilla: The maxilla (Figs. 6. 1, 6.3, 6.5-6.6) is an anteroposteriorly elongated triangular bone that covers most of the snout in the lateral view. It is completely preserved in SAM-PK-2344; but lacks the anterior portion in CGP/1/2266, AMNH FARB 5626 and NHMB 1556. In SAM-PK-2344 it is evident that the maxilla anteriorly forms a short vertical contact with the premaxilla below the external naris, and has a vertical posterior sutural contact with the prefrontal

lacrimal and jugal as is evident in most specimens studied. Because of distortion caused by the formation of nasofrontal boss, the posterior sutural contacts of the maxilla are not clearly visible.

Lacrimal: The lacrimal (Figs. 6.5-6.6) is a relatively small quadrangular bone (Boonstra, 1956) forming the anteroventral margin of the orbit and is best preserved in SAM-PK-2344, CGP/1/2266, AMNH FARB 5626 and NHMB 1556. On its dorsal side it has a horizontal sutural contact with the prefrontal and ventrally with the jugal. Anteriorly it meets the maxilla.

Prefrontal: The prefrontal (Figs. 6.3-6.6) preserved in all the specimens studied, is a relatively large bone forming the antero-dorsal border of the orbit. It is in contact with the nasal anterodorsally, the maxilla anteroventrally and the frontal posteriorly and posterodorsally. Ventrally it has a horizontal sutural contact with lacrimal half way down the orbit. The prefrontal portion of the supraorbital border is thin in the relatively small NHMB 1556, and greatly thickened in the large specimens SAM-PK-2344, AMNH FARB 5626 and CGP/1/2266, and meets up with the nasofrontal boss.

Frontal: The frontal (Figs. 6.3 - 6.6) is a paired bone forming the largest element of the skull roof. It is preserved in all crania studied and contributes to the nasofrontal boss. It is excluded from the dorsal border of the orbit (except in NHMB 1556, the smallest skull) and has a short contact with the temporal fenestra. Anterolaterally the frontal forms a long sutural contact with the

prefrontal and meets also with a long contact with the nasal anteriorly. Posteriorly the frontal has contact with the parietal by means of a long interdigitating suture which extends anteromedially from the dorsal border of the temporal fenestra. The dorsal surface of the bone in this area is swollen and forms a depression behind the nasofrontal boss in all specimens except NHMB 1556 in which the frontal surface is smooth and only slightly pachyostosed.

Postfrontal: It is well preserved in SAM-PK-2344. In lateral view the postfrontal (Figs. 6.3- 6.6) is roughly triangular and forms the dorsal third of the postorbital bar and the posterodorsal border of the orbit. The postfrontal is in sutural contact with the frontal dorsally and has a ventral anteriorly inclined contact with the postorbital. The postfrontal extends dorsomedially into the temporal fenestra and has a postero-dorsal depression to receive the jaw adductor muscles. This depression is evident on both sides of SAM-PK-2344 and on the left side of CGP/1/2266.

Postorbital: The postorbital (Figs. 6.3 -6.6) forms the posterior border of the orbit and the anterior border of the temporal fenestra. On its medial surface, the postorbital contacts the postfrontal with an oblique suture slanting posterodorsally; whereas ventrally it forms a short anterior contact with the jugal (evident in SAM-PK-2344 and NHMB 1556) and meets the squamosal posteroventrally.

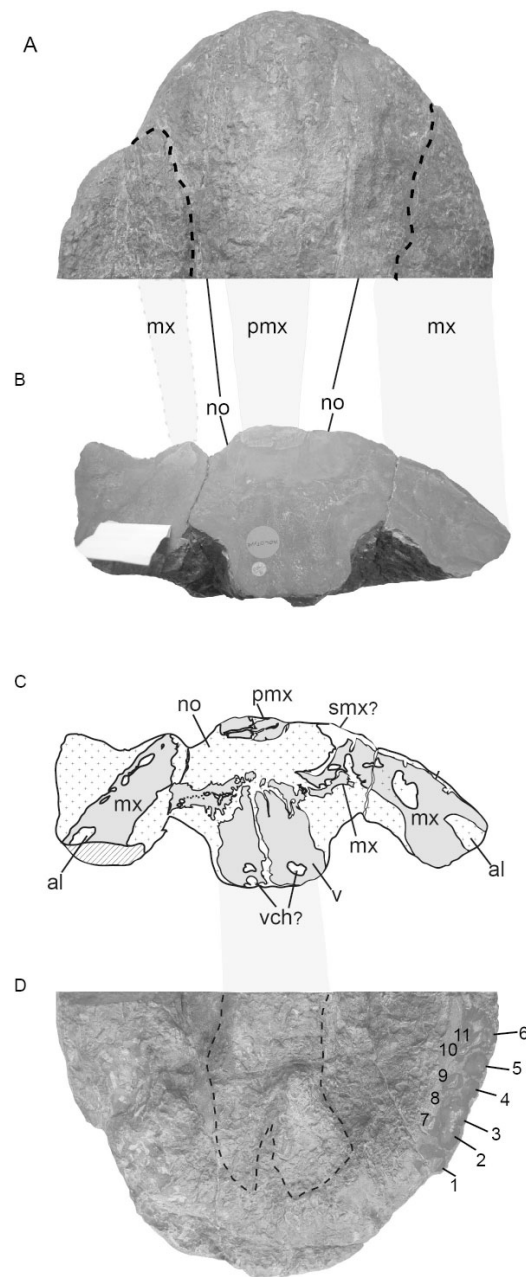


Figure 6. 1. *Tapinocephalus*: photograph and interpretative drawing of NHMUK PV R 1705, holotype of *Tapinocephalus atherstonei*, represented by the anterior portion of the snout, in dorsal view (B), sagittal section (B&C) and ventral view (D). Scale. 10cm.

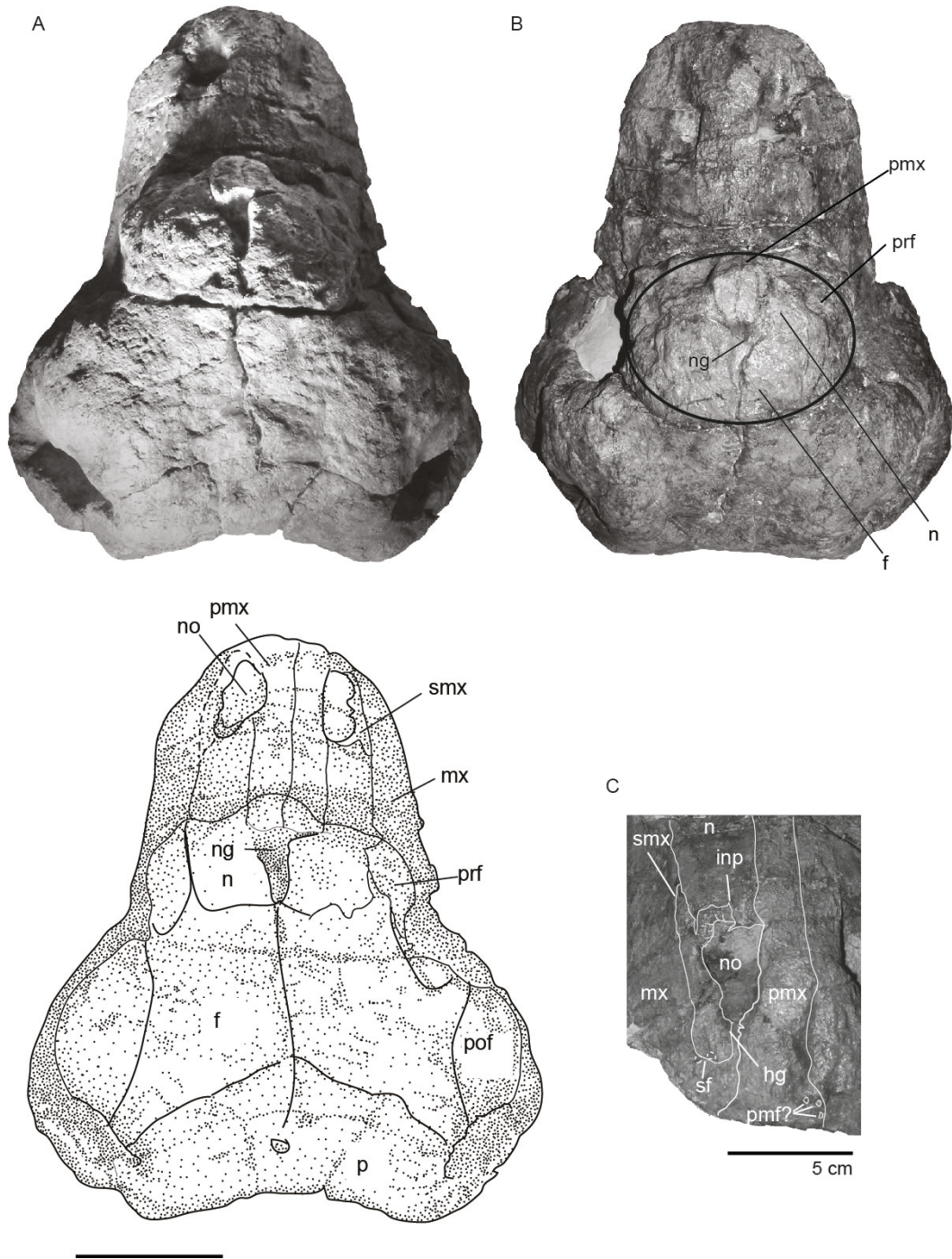


Figure 6. 2. *Tapinocephalus*: Photographs (A and B) and illustration (C) of the dorsal view, detail of the right side of the antero-dorsal surface (D) of *Tapinocephalus atherstonei* specimen SAM-PK-2344 . B shows the contribution of the prefrontal to the area of the nasofrontal boss. Scale:10cm.

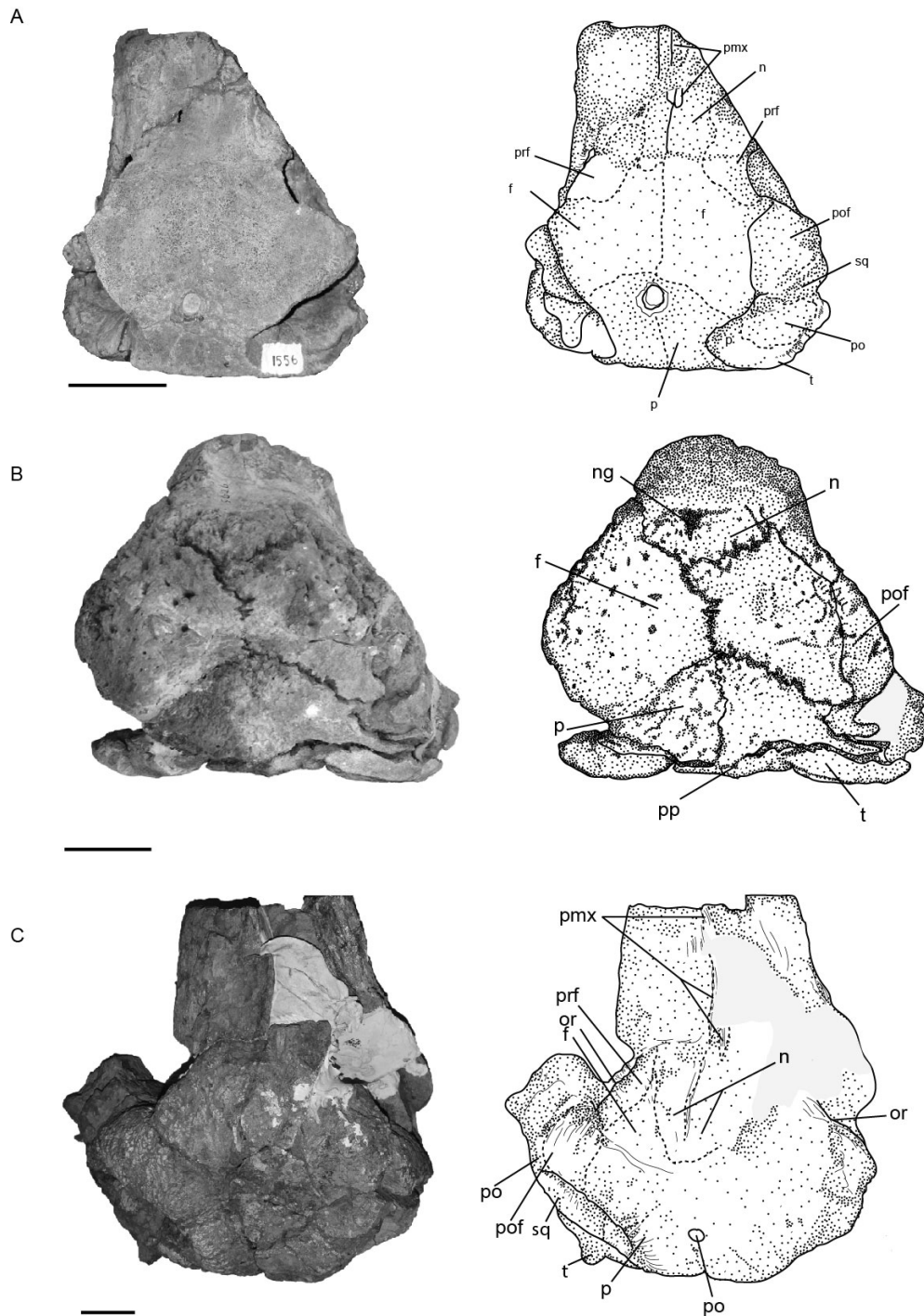


Figure 6. 3. *Tapinocephalus*: photograph (left) and illustration (right) of the skull roof of NHMB 1556 (A), AMNH FARB 5626 (B) and CGP/1/2266 (C). Scale: 10cm.

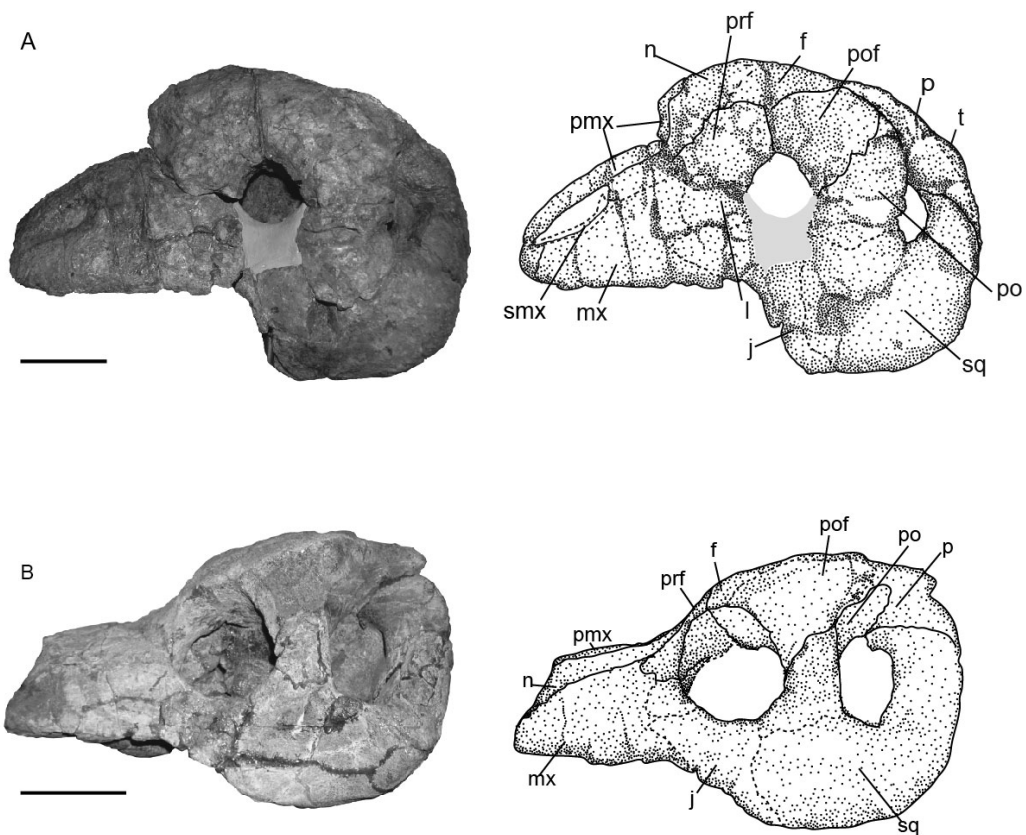


Figure 6. 4. *Tapinocephalus*: photograph (left) and illustrations (right) of the left lateral view of SAM-PK-2344 (A) and NHMB 1556 (B). Scale: 10 cm.

Jugal: The jugal (Figs. 6.4 - 6.6) is an anteroposteriorly elongated bone forming the ventral border of the orbit and contributes to the anterior part of the zygomatic arch. Anteriorly it is in contact with the maxilla, antero-dorsally with the lacrimal, posterodorsally with the postorbital and posteriorly with the squamosal. Posteroventrally the jugal thins to a point on the ventral surface of the lower arch of the temporal fenestra and has a long sutural contact with the squamosal dorsally.

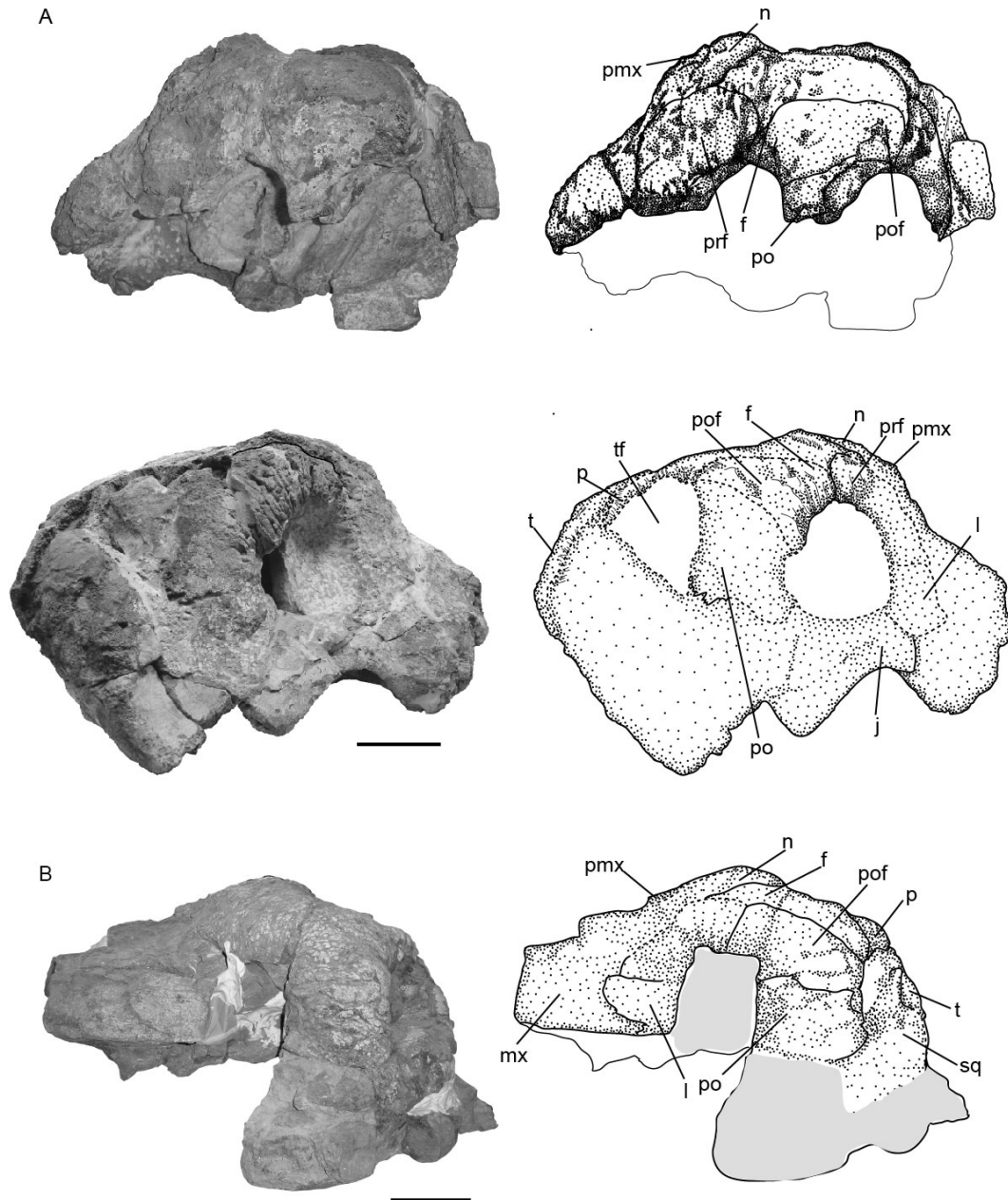


Figure 6. 5. *Tapinocephalus*: Photographs (left) and illustrations (right) of the lateral view of AMNH FARB 5655(A) and the left lateral view of CGP/1/2266 (B). Scale:10 cm.

Squamosal: The squamosal (Figs. 6.4- 6.6) is a large robust bone presenting two distinct surfaces: posterolateral and posteroventral. The posterolateral surface

forms the ventral and posterior borders of the temporal fenestra, while the latter makes up the posteroventral margin of the skull. The squamosal is best preserved in SAM-PK-2344 and on the left side of NHMB 1556. On the lateral surface of the skull, the squamosal contacts the jugal anteriorly and anteroventrally, the postorbital dorsally and contributes to the ventral and posterior borders of the temporal fenestra. On its posterior ascending portion the squamosal meets the parietal on the posterodorsal rim of the temporal fenestra. The posterior end of the squamosal is greatly thickened on its lateral portion and the surface is rounded in SAM-PK-2344 and AMNH FARB 5655. It is less thickened in the smaller NHMB 1556. On the posteroventral margin of the skull the squamosal contacts the quadratojugal and quadrate ventrally, and the paraoccipital process and tabular medially. Posteroventrally the squamosal forms the external auditory meatus. The posteroventral portion of the squamosal is orientated more anteroventrally than it is in the basal forms *Tapinocaninus* and *Ulemosaurus* due to more pronounced posterodorsal sloping of the occiput as the jaw joint is more anteriorly positioned.

Parietal: The parietal (Figs. 6.3- 6.6) is a paired thickened strip like bone that forms the posterior portion of the skull roof extending between the temporal openings. It demonstrates a wide anteriorly pointing “V” shaped sutural contact with the frontal, while posteriorly it forms a horizontal sutural contact with the postparietal. It contributes to the posterodorsal border of the temporal fenestra where it is in contact to the postorbital’s medial extension anteriorly and the squamosal’s posterodorsal extension and tabular posteriorly. Posterolaterally the parietal has a wedged contact between the squamosal laterally and the tabular

medially as pointed out by Boonstra (1956, fig. 1-2). The parietal surface is smooth and slightly depressed with the exception of the area surrounding the pineal opening. The parietal surface on the border of the temporal opening is thickened and rugose in all specimens except NHMB 1556.

6.3.4.3 Occiput

The surface of the occiput and the occipital crest are well preserved in SAM-PK-2344 (Fig. 6.6A) but are weathered in NHMB 1556 (Fig. 6.6C) and AMNH FARB 5626 (Fig. 6.6B) and the sutures between the bones are not clearly visible. In posterior view the occiput is trapezoidal with the lateral edge and occipital crest greatly thickened, particularly in SAM-PK-2344, but is less developed in the smaller NHMB 1556. The occipital surface is flat, with the exception of thickening of the postparietal median keel and the dorsolateral margins in SAM-PK-2344.

Postparietal: The postparietal (Fig. 6.6) is a robust unpaired bone forming the dorsomedial portion of the occiput and is relatively well preserved in SAM-PK-2344, but the surface is weathered in AMNH FARB 5626 and NHMB 1556. Dorsally it contributes to the occipital crest where it contacts the parietal, laterally it contacts the tabular and it has a long horizontal ventral contact with the supraoccipital. Along its ventral contact with the supraoccipital in SAM-PK-2344, and less markedly in NHMB 1556 and AMNH FARB 5626 because of poor preservation, the supraoccipital exhibits a prominent dorsal midline spur extending over the postparietal. The surface of the postparietal has a midline ridge

(prominent in SAM-PK-2344 and only slightly developed in NHMB 1556), and has a depression on either side of the ridge.

Tabular: The tabular (Fig. 6.6) is a relatively large, plate-like somewhat triangular bone forming the lateral margins of the occiput with a short dorsal contact on the occipital crest (most evident in SAM-PK-2344). It is best preserved and most complete in SAM-PK-2344; while its surface is heavily weathered in NHMB 1556 and AMNH FARB5626. Medially the tabular is in contact with the postparietal, medioventrally with the supraoccipital, ventrally with the paraoccipital process of the opisthotic, and laterally it is in contact with the squamosal. Along its ventromedial contact with the opisthotic the tabular contributes to the dorsal border of the posttemporal fenestra as evident in SAM-PK-2344.

The tabular surface is moderately thickened and flat except the portion which contributes to the lateral and dorsolateral border of the skull as is evident in SAM-PK-2344.

Supraoccipital: The supraoccipital (Fig. 6.6) is a transversely wide quadrangular unpaired bone. It is well preserved in SAM-PK-2344, but its contacts are not discernable in AMNH FARB 5626 and NHMB 1556. Dorsally the supraoccipital contacts the postparietal, dorsolaterally and laterally the tabular, while ventrally it meets the exoccipital and forms the dorsal border of the foramen magnum. As is evident from specimens SAM-PK-2344 and AMNH FARB 5626, on its

posterolateral-end the supraoccipital contributes to the dorsal border of the posttemporal foramen together with the tabular.

Exoccipital: The exoccipital (Fig. 6.6) is a wing-like and relatively small element forming the lateral and ventrolateral borders of the foramen magnum. It is better preserved and more complete in SAM-PK-2344 than it is in NHMB 1556 and AMNH FARB 55626 where, due to surface weathering, the contacts of the bone with the surrounding bones are not discernable. The exoccipital is in contact with the supraoccipital dorsally, the basioccipital ventrally and opisthotic ventrolaterally. The foramen for the jugular vein is positioned on the border of the opisthotic and exoccipital, which is visible in SAM-PK-2344.

Opisthotic: The opisthotics (Fig. 6.6) form the large and robust paraoccipital process linking the back of the skull with the basioccipital and is better preserved in SAM-PK-2344 than it is in NHMB 1556 and AMNH FARB 5626. Dorsally the opisthotic is in contact with the supraoccipital and the tabular, laterally with the ventral extension of the squamosal, and ventrally with the dorsal process of the quadrate. Ventromedially the opisthotic meets the basioccipital where it forms the posterior border of the fenestra ovalis.

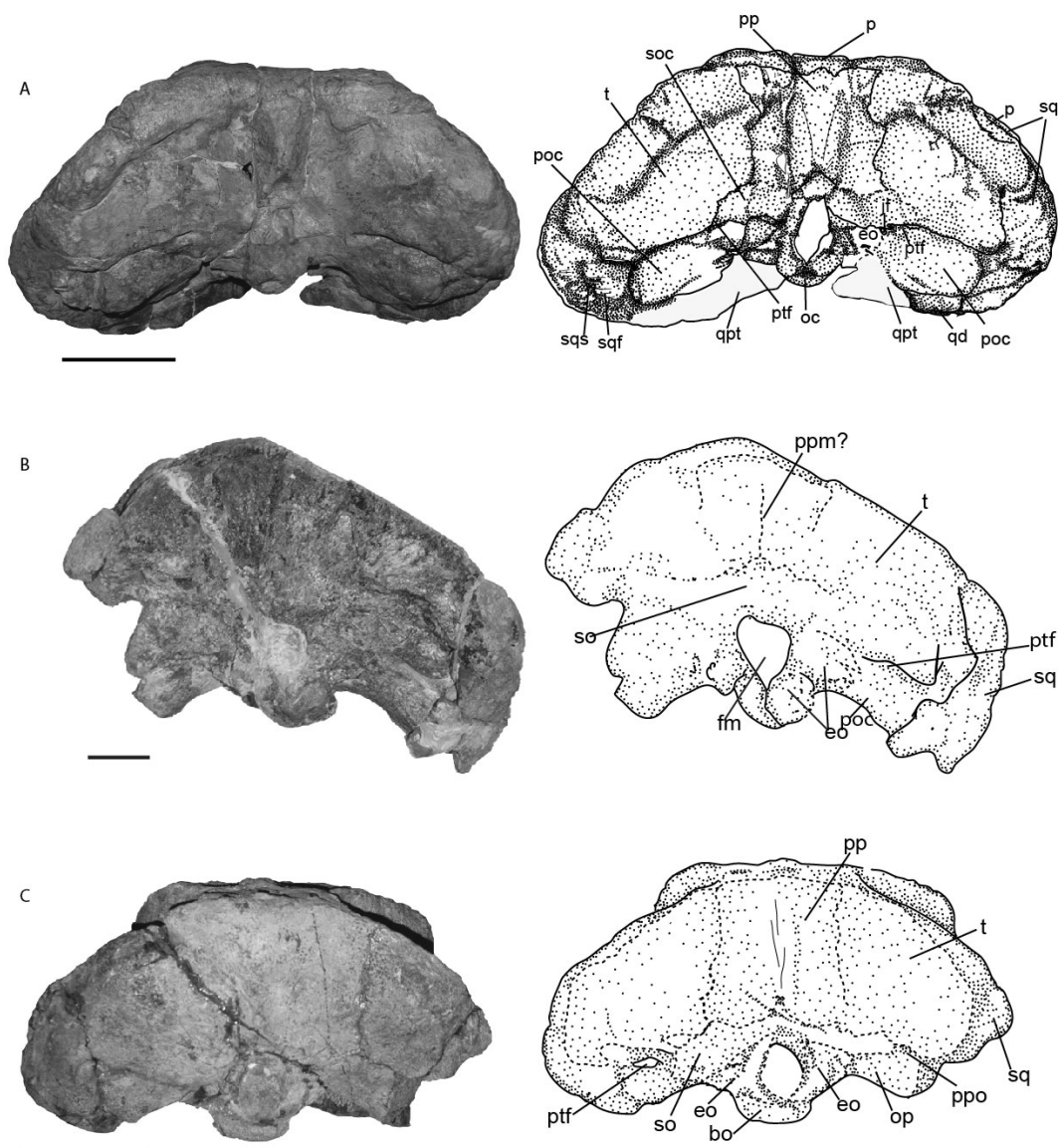


Figure 6.6. *Tapinocephalus*: photographs (left) and illustration (right) of the occiput of SAM-PK-2344 (A), AMNH FARB 5626 (B) and NHMB 1556 (C). Scale: 10cm.

Exoccipital: The exoccipital (Fig. 6.6) is a wing-like and relatively small element forming the lateral and ventrolateral borders of the foramen magnum. It is better preserved and more complete in SAM-PK-2344 than it is in NHMB 1556 and AMNH FARB 5626 where, due to surface weathering, the contacts of the bone

with the surrounding bones are not discernable. The exoccipital is in contact with the supraoccipital dorsally, the basioccipital ventrally and opisthotic ventrolaterally. The foramen for the jugular vein is positioned on the border of the opisthotic and exoccipital, which is visible in SAM-PK-2344.

Opisthotic: The opisthotics (Fig. 6.6) form the large and robust paraoccipital process linking the back of the skull with the basioccipital and is better preserved in SAM-PK-2344 than it is in NHMB 1556 and AMNH FARB 5626. Dorsally the opisthotic is in contact with the supraoccipital and the tabular, laterally with the ventral extension of the squamosal, and ventrally with the dorsal process of the quadrate. Ventromedially the opisthotic meets the basioccipital where it forms the posterior border of the fenestra ovalis.

Basioccipital: The basioccipital (Fig. 6.6) is a relatively small bone that forms the posteriormost portion of the ventral surface of the skull. It extends onto the occipital surface by contributing to the ventral part of the occipital condyle. It is best preserved in SAM-PK-2344 and in AMNH FARB 5626 and NHMB 1556 its contribution to the occipital condyle is barely visible. In SAM-PK-2344 the basioccipital, on the ventral surface of the skull, has elongate lateral tubera which slopes anteromedially onto the basisphenoid. On the palatal surface the basioccipital forms the posterior wall of the fenestra ovalis and along the midline is a prominent ridge at its anterior-end.

6.3.4.4 Palate

Specimen SAM-PK-2344 (Fig. 6.7B) preserves the entire palate, and only the anterior portion of the vomer is present in NHMUK PV R 1705 (Fig. 6. 2D).

Premaxilla: The premaxilla (Fig. 6.7) forms the anterior extremity of the palatal surface. It forms the anterolateral margin of the choana, and contacts the maxilla by means of poorly exposed suture behind the fifth incisor. Posteromedially it is ventrally overlain by the anterior end of the vomer.

Maxilla: The maxilla (Fig. 6.7, 6.2D) forms portion of the lateral border of the internal nares between the premaxilla and palatine. Medial to the palatine it forms a thin alveolar margin which extends posteriorly towards the distal end of the lateral process of the pterygoid. Apart from the five incisors all the marginal teeth of the skull are borne in the maxilla and are poorly preserved in all specimens. SAM-PK-2344 has a single tooth crown which is assumed to be the first postcanine on the right. This tooth is mesiodistally wide and it is lingually heeled. Part of the right maxilla of NHMUK PV R1705 was polished by Owen (1876) to reveal cross-sections of 11 maxillary teeth. The posterior five teeth appear to be the tips of emerging replacement teeth.

Vomer: The paired vomer (Fig. 6.7) is a robust, broad and vertically expanded bone that makes up the medial and posteromedial walls of the internal nares. The vomer ventral surface has a shallow midline trough between the vomer pair, and this bone is in contact with the premaxilla anteriorly and the pterygoid posteriorly.

Posteriorly it broadens as it contacts the palatine laterally and then narrows to a point to form a short posterior contact with the pterygoid.

Palatine: The palatine (Fig. 6.7B) is a large and complex paired bone preserved completely in SAM-PK-2344. It contacts the maxilla anterolaterally by means of the anterior process, the ectopterygoid posterolaterally, and the pterygoid posteriorly. The broad anterior process contributes to the lateral and lateroventral margins of the choana and ventrally overlies the posterior part of the maxilla. Posteromedially the palatine forms a small edentulous reniform palatine boss. Medially it has an oblique sutural contact with the posterolateral end of the vomer.

Ectopterygoid: From SAMPK2344 (Fig. 6.7A) it is evident that the ectopterygoid is small triangular bone positioned between the palatine anteriorly, the jugal posterolaterally and the lateral process of the pterygoid on the posterior side.

Pterygoid: Paired pterygoids (preserved in SAM-PK-2344) form the entire posterior part of the palate and stretch between the palatine anteriorly, the quadrate posterolaterally, and the basisphenoid posteromedially (Fig. 6.7B). Anteromedially the pterygoid forms a boss but the sutural transition from the palatine to the pterygoid boss is not discernable. The pterygoid meets the posterior end of the vomer anteromedially and a short interpterygoid vacuity is present between the prominent lateral flanges of the pterygoid. These flanges are thick and are weathered in the available skulls. The proximal ends of the

transverse flanges curve posteromedially to meet on the midline and form a constriction anterior to the quadrate ramus.

The quadrate ramus of the pterygoid emerges from the posteromedial end of the lateral flanges and extends posteriorly to meet the medial condyle of the quadrate. The wide and flat posterior pterygoid platform is positioned on the cranial girdle between the quadrate rami and extends posteriorly to form a sutural contact with the parabasisphenoid.

Quadrate: The quadrate (Fig. 6.7B) is preserved in SAM-PK-2344 and is a robust bone on the posteroventral surface of the skull. It comprises a large sheet-like dorsal process, and small ventrally protruding condyles which make up a screw-like ventral articulatory surface. A foramen quadratum (preserved on the left quadrate) is present between the quadratojugal and the dorsal process of the quadrate. A stapedial groove is present between the medial condyle and the dorsal process of the quadrate to receive the stapes.

Quadratojugal: The quadratojugal (Fig. 6.7B) is a small bone situated on the posteroventral corner of the zygoma, having a laterally exposed portion positioned under the posteroventral portion of the squamosal while medially it contacts the lateral condyle of the quadrate. It is preserved on the both sides of SAM-PK-2344 being exposed partly on the lateral surface of the skull but its sutural contacts with the quadrate could not be discerned. It is not clear whether the quadratojugal touches the jugal as they come very close to each-other. Boonstra (1956, fig. I)

illustrated a horizontal contact between jugal and quadratojugal exposed on the lateral surface of the skull.

Stapes: The stapes is preserved in SAM-PK-2344 (Fig. 6.7B) as a short, stout, spindle-shaped bone. It has a rounded proximal-end in contact with the fenestra ovalis; while the broad distal end is positioned in the stapedial groove between the medial and the dorsal condyles of the quadrate. The right stapes is displaced which resulted in its proximal end being shifted slightly towards the posterior edge of the fenestra ovalis and its distal end to be positioned more anteriorly on the medial surface of the quadrate and to have contact with the lower-end of the paraoccipital process. The left stapes is completely displaced and is positioned more anteriorly in the ventral view of the skull. A stapedial foramen is not visible.

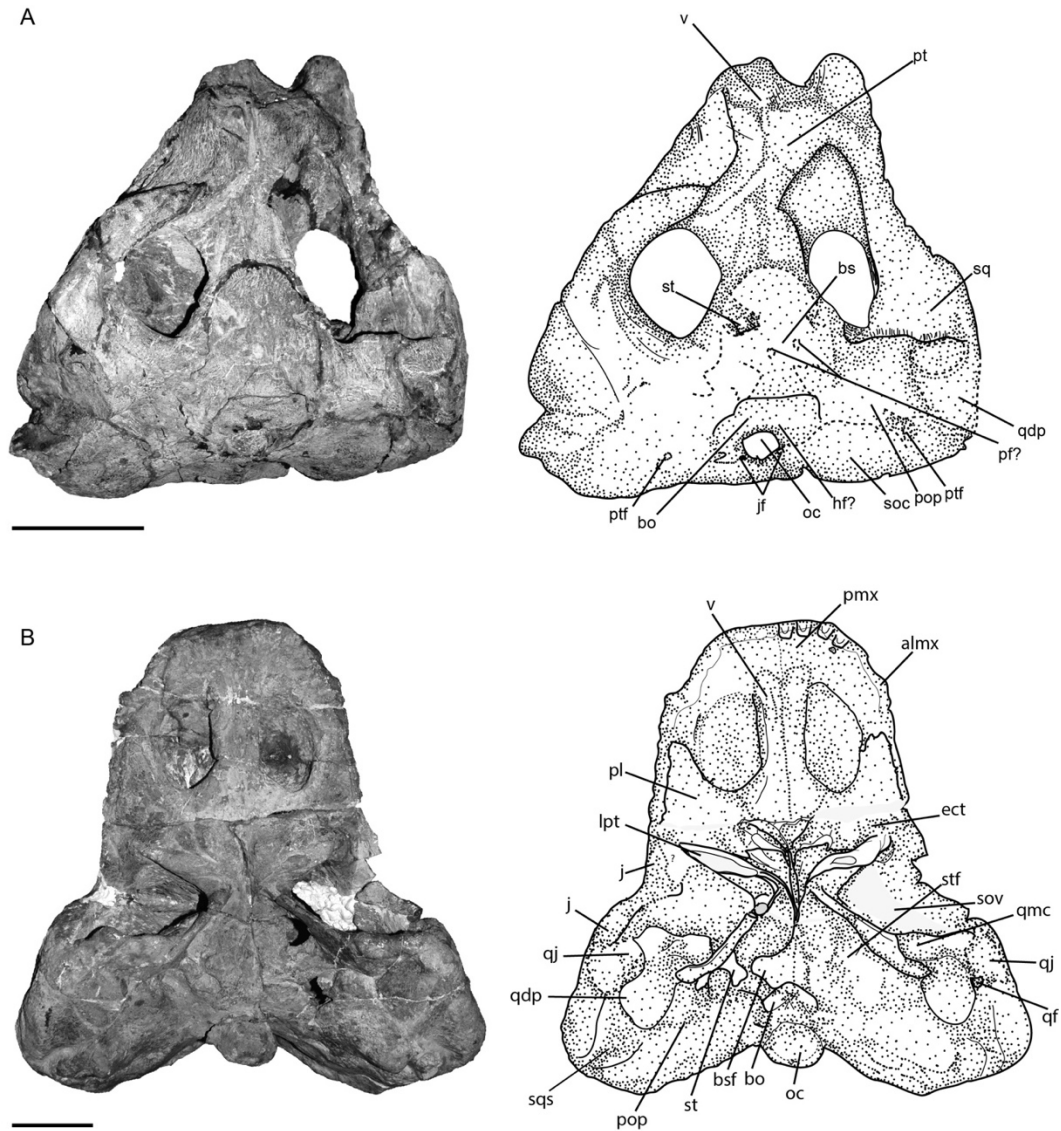


Figure 6. 7. *Tapinocephalus*: Photographs (left) and illustrations (right) of the ventral view of NHMB 1556 (A) and SAM-PK-2344 (B). Scale: 10cm.

6.3.5 Results and discussion. Taxonomic considerations of *Tapinocephalus atherstonei* have suffered as a result of uncertainty surrounding the association of the bones in the Natural History Museum presented by W G Atherstone in 1872. Owen (1876) described several specimens from this collection that he assigned to *Tapinocephalus atherstonei*; these included the holotype snout and a vertebra

from ‘Four miles from Jan Willem’s Fontein’ – as well as the errant jaw fragment collected earlier by A. G. Bain, and a string of vertebrae from ‘Gats Plaatz’. Owen (1876) referred most of the bones from the Atherstone collection to *Pareiasaurus*. Seeley (1888) observed that much of this material, particularly the pelvis, was not in fact pareiasaurian, and referred the skeletal elements from ‘Vers Fontein’ to a new taxon, *Phocosaurus megischion*; he did not consider the possibility that it represented the postcranium of *Tapinocephalus*, presumably because it came from a different locality than the holotype. Haughton (1913) and Boonstra (1936) both expressed doubt over the accuracy of the localities provided by Owen. Apparently ignoring Seeley’s work, Haughton (1913, p. 41) was the first to suggest some error and stated ‘From the Brit. Mus. Catalogue there would appear to be nearly a whole skeleton of *Tapinocephalus*—all bones sent by Atherstone in 1872. Some of the bones are said to come from Gats-Plaatz, others from Vers Fontein, but as there is admittedly some doubt about some of the localities, and as no bone occurs in duplicate, one suspects that all the bones are from one locality and of one individual.’

This conclusion was disputed by Broom (1928), who expressed fair certainty in the existence of multiple individuals, and Boonstra (1936b, p. 3) stated that ‘... Atherstone did not keep his various finds separate but lumped bones derived from an area together to constitute a single specimen and this initial mistake was apparently aggravated by faulty labelling in the British Museum.’

To pursue this matter further the original list of material collected by Atherstone on his Gouph trip in 1870 was reinvestigated. Atherstone, although he did not keep his notes in an orderly fashion, did provide sketches and notes of the *in situ* findings which are presented below as they provide clues to the provenance of the holotype material. According to Owen (1876) the tip of the snout and the lower jaw fragment of the type material come from a locality “four miles from Jan Willem’s Fontein” and the vertebral column is from Gats’ Plaat (from now on referred as JWF and GP respectively). As the snout portion at the Natural History Museum is not registered with locality information (Day, M., *pers. comm.*, June 2018) the locality of the snout- tip of the holotype is questionable and indeed whether it is associated with the postcrania as claimed by Owen (1876).

Atherstone’s field notes indicate that the postcranial elements in association with cranial elements came only from Gats’ Plaat: ‘...from the ‘Gats Plaats’ where the gold nugget was found as also are the vertebrae and bones of the *Oudenodon*- part of the skull of which was also sent, and of which I took the following sketch before removing the bones from the soil as they lay in situ.’ The field sketch (Fig. 6.8A) shows only postcranial elements (6 portions of vertebrae, denoted by the letter “A”), 5 portions of a “hind leg” (denoted by the letter “B”), but not the cranial element which he refers to as *Oudenodon*. In the text he noted ‘The extraordinary bone A [referring to his sketch, see Fig. 6.8A] was sent- at least I brought it away with me as also the vertebra I packed the afterwards- a wagon load altogether was exhumed- How much of these bones were sent by the Boer I cannot say-’.

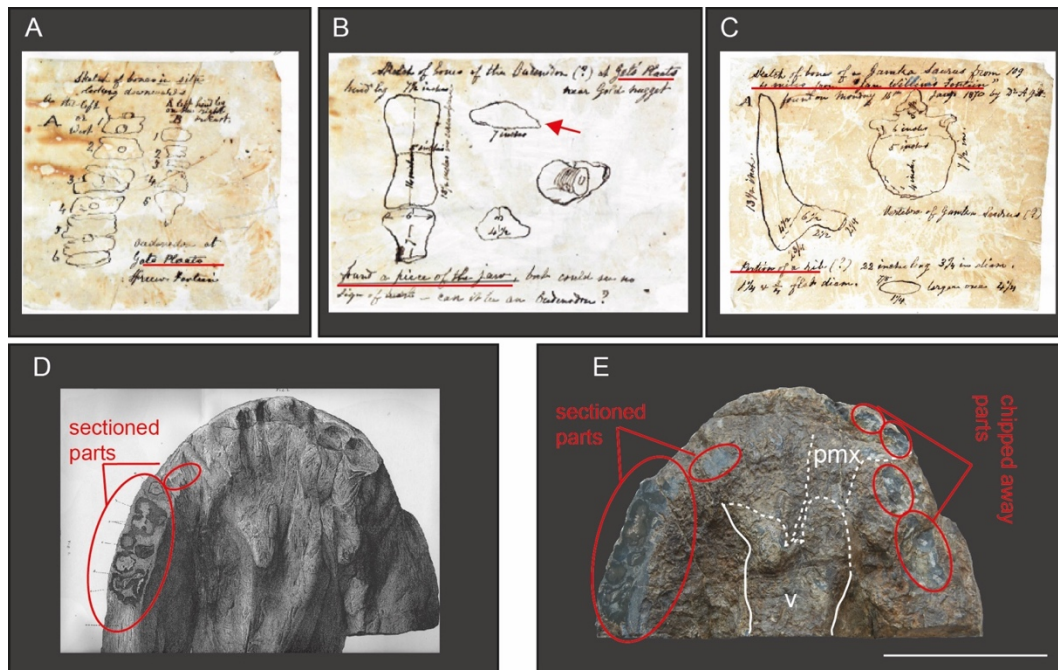


Figure 6. 8. Field sketches of W.G. Atherstone relating to his Gough trip in 1870 (A, B and C). Sketches A and B, are from his in-situ findings on the farm Gats Plaats while sketch C is from a locality he noted as ‘four miles from Willem’s Fontein’. Locality information is underlined in red. Sketch A, as noted by Atherstone in his related text, shows an incomplete vertebral column and a B is the left hind leg. A and B were apparently found together. The arrow in (B) points to a piece which is similar in outline to the snout of the holotype. Below the sketch, underlined in red, Atherstone wrote: “found a piece of the jaw, but could see no sign of teeth.” Figure D shows the illustration of the snout by Owen (1876, pl.I, fig. 1) and E, a recent photograph of the same view of the holotype showing the anterior extremity of the palate with vomer (v) and premaxilla (pmx). Figures D and E both show that Owen polished a portion of the right maxillary alveolar surface to expose the dentition. On the left side there are indications that it was worked lightly with a chissel.

In the second figure he sketched a complete long bone and four other skeletal fragments, including what appears to be the extreme tip of a snout (Fig. 6.8B). Although Atherstone does not indicate this piece with an arrow, the outline of the bone on the upper right corner of the sketch is strongly suggestive of the snout piece. At the bottom of the sketch Atherstone wrote “ found a piece of the jaw, but

could see no sign of teeth”. The sketch notes this snout portion as being 17 inches long along the horizontal axis which coincides with the size of the holotype fossil. Atherstone mentions that there is no sign of teeth. Indeed the unprepared holotype does not have any teeth preserved except the roots later revealed by Owen (1876) by sectioning on the right side and light chisseling on the left side (Fig. 6.8DE).

In his last sketch (Fig. 6.8C) Atherstone figures a single vertebra and a rib portion which he notes as coming from “four miles away from JWF”. From his notes the only specimen which appears to come from JWF is the well-preserved skull and almost complete skeleton of *Pareiasaurus bombidens*.

In summary it appears highly likely that the the extreme tip of the snout, described by Owen (1876), comes from GP and not from the locality “four miles from JWF” as recorded by Owen (1876). From JWF Atherstone reported his findings as including “a piece of lower jaw with teeth, vertebrae of great size, ribs and other bones”, which excludes the *T. atherstonei* type. The only candidate for the cranial portion mentioned by Atherstone was the lower jaw fragment figured by Owen (S.A. 2 & 3), but Lydekker (1890) correctly identified this as a specimen collected earlier by A. G. Bain. It is worth noting that, contra Leydekker (1890), this lower jaw fragment does not have titanosuchian features (Fig. 6.9).

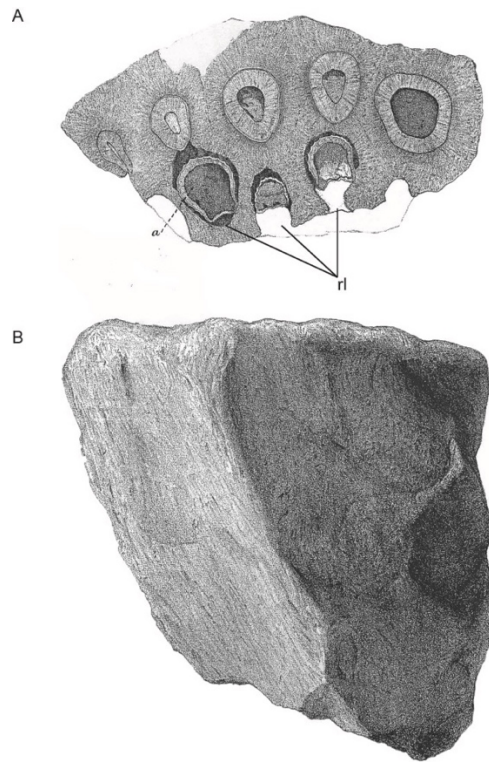


Figure 6. 9. The dentary fragment that Owen (1876) referred to the holotype of *Tapinocephalus atherstonei* (as it is illustrated by Owen, 1876, pl.II, figs.1-2) showing (A) the dorsal surface of the piece showing five dentary teeth and crown tips of three replacement teeth; (B) the lateral surface of the piece. Scale: 10 cm.

As for the cranial pieces that Watson (1914) referred to the holotype: these two pieces do belong to a large-sized tapinocephalid but the only feature that can be deduced from the zygoma portion show similarities to *Mormosaurus seeleyi* with its rather angled and relatively slender zygoma. Neither the notes of Atherstone (1870), nor the description of Owen (1876), nor the first comprehensive catalogue of the museum presented by Lydekker (1890), confirm the association of this cranial material with the holotype. Therefore, until there is conclusive evidence of

their association with the holotype, they cannot be considered part of that specimen.

In summary, it is here proposed that the only cranial material which can be verified as belonging with the postcranial elements is the snout tip NHMUK PV R 1705 which Owen (1876) mistakenly considered to come from JWF, whereas it was more probably found on GP. As there is uncertainty as to which of the postcranium described by Owen (1876) actually belongs to the holotype, it appears that the holotype of *Tapinocephalus atherstonei* is possibly a compilation of different individuals. The ICZN Code Article 73.1.5 enables subsequent authors to exclude components of the holotype if found to not be derived from an individual animal. Thus, in this case where the snout tip comes from GP, all the holotype material must have been collected from the same locality. Accordingly only the snout tip and the postcranial elements that the notes of Atherstone (1870) indicate were found together are here considered as comprising the holotype of *Tapinocephalus atherstonei*.

The next difficulty to overcome was raised by Watson (1914) and Gregory (1926): whether the holotype of *Tapinocephalus atherstonei* is sufficiently preserved to provide a diagnosis for the taxon. The only feature, one which most probably helped Haughton to identify SAM-PK-2344 as *T. atherstonei*, is based on the assumption made by Lydekker (1890) about the transitional angle from the facial to cranial surface. Lydekker (1980, p. 93) suggested that “*Tapinocephalus*

atherstonei evidently formed a flat and projecting muzzle, above which the region of the brain was probably much elevated”.

Because of its completeness, specimen SAM-PK-2344 has been treated as the de facto neotype of *T. atherstonei*, but has not been officially designated as such (e.g. Watson, 1914, Broom 1928, Boonstra 1936b, 1956, 1969, King, 1988). Specimen SAM-PK-2344, where the snout is separated from the facial surface with the rise of the nasofrontal boss towards the cranial roof, supports Leydekker’s assumption and provides the link between the snout tip of Owen (1876) and SAM-PK-2344. However, the snout tip of specimen NHMUK PV R 1705 is not preserved in connection with a nasofrontal boss, thus this character is not preserved in the holotype. Boonstra (1956) and Kammerer (2009) agreed on the ‘great breadth of premaxilla’ to be used as a basis in the synonymy of *Taurops macrodon* (of which the holotype is based on only a snout) as *Tapinocephalus atherstonei*. However, this feature on its own is not enough to define the taxon. While this feature allows us to differentiate between complete skulls of *Tapinocephalus* and *Mormosaurus*, and *Struthiocephalus* (the premaxilla tip of the latter two taxa are narrower and anteroposteriorly more elongated than it is in *Tapinocephalus*); it will be difficult to make the same judgment from the snout tip in the case of *Taurops*.

Kammerer (2009, p. 238) used the following autapomorphies for *Tapinocephalus atherstonei*: “entire frontal region massively pachyostosed confluent with postorbital bar, snout extremely short and broad”. As Kammerer (2009) does not mention the additional cranial material of Watson (1914) as being part of the

holotype, it appears that these features described by Kammerer were deduced from both NHMUK PV R 1705 and SAM-PK-2344.

As is apparent from this discussion, *Tapinocephalus atherstonei* is not a well-defined species, and the holotype (the snout tip) does not provide satisfactory diagnostic cranial characters. However as this is the first fossil to have been described as a tapinocephalian and the type genus of the Tapinocephalidae, its name is entrenched in literature, and as it is also a biozone defining fossil of the Middle Permian, the name should be retained. In view of the above, as SAM-PK-2344 is a well-preserved skull and is also topotypic (comes from the type locality and geological horizon as the holotype) it is here suggested that SAM-PK-2344 replaces the holotype specimen as a *neotype*.

The ICZN code (Art. 85) states that a neotype can only be designated in the absence of the name-bearing type specimen (*e.g.* holotype, lectotype, syntypes). However, in the case of an exceptional need, as in the case of an unidentifiable name-bearing type, Art. 75.5 and 81 of the ICZN code states that when “the taxonomic identity of a nominal species-group taxon cannot be determined from its existing name-bearing type (i.e. its name is a *nomen dubium*), and stability or universality are threatened thereby, the author may request the Commission to set aside, under its plenary power, the existing name-bearing type and designate a neotype.” This precedent has previously been set where the holotype of the ammonite species *Cycloceras laevigatum* McCoy, 1844 lacked important diagnostic features. Upon request the Commission under its plenary power set

aside the type status of this specimen and designated a neotype (Opinion 1720 (1993)).”

6.4 *Moschops capensis* BROOM 1911

Holotype: AMNH FARB 5550

Previous generic diagnosis: “The preorbital length is 45-49 percent of the total median length and the orbit does not, thus, lie wholly in the posterior half of the skull; the snout is thus short (preorbital length 160-190 mm.) and fairly broad to broad (156-227 mm.) and fairly low to fairly high (108-162 mm.) with the height 74-95? percent of the width. The dorsal cranial bones are strongly pachyostosed. The prefrontal is greatly thickened and this is confluent with the pachyostosis of the nasal and frontal, but this does not greatly overhang the orbit although the orbital border is thick. The area around the pineal foramen is greatly thickened but does not stand out above the general skull surface. The postorbital bar is fairly to very wide and moderately to very massive. The posttemporal arch is moderately to very thick and massive and the temporal fossa is moderate to small with its antero-posterior diameter fairly to very greatly reduced. The dorsal parietal surface is broad to very broad (142-172 mm) and the interorbital width is 70-100 per cent of the intertemporal width. The intersquamosal width is moderate to great (210-395 mm.) and the median length is 103-159 per cent of the width. The *Moschops* skull is thus fairly short and broad.” Boonstra, 1957, p. 29, 32.

“No discrete autopomorphies for *Moschops* can be determined at present, but this taxon is readily distinguishable from other tapinocephalids by the combination of

a short, tall, laterally narrow snout, gently sloping frontonasal transition, and a relatively weakly anteroventrally angled occiput.” Kammerer (2009, p. 229). As Kammerer (2009) recognised only one species of *Moschops* this is also a species diagnosis.

Previous species Diagnoses: “The skull of *Moschops capensis* differs from the Tapinocephalid already described in having a short bent down conical snout. The bones of the top of the head are thickened but relatively much less so than in *Tapinocephalus* and its allies.” Broom, 1932, p. 43.

“Medium to wide across parietals, with the interorbital width 73-100 per cent of the intertemporal width. Snout relatively wide. Occipital surface unreduced and transverse pterygoidal rami weak.” Boonstra, 1957, p. 32.

6.4.1 Historical background

Moschops capensis was described by Broom (1911) on the basis of several skulls and skeletal remains which were found scattered around an area about a quarter of an acre on the farm Spitzkop, Liansburg district in the Moordenaars Karoo. As the remains differ from each other in size and degree of cranial thickening, Broom (1911) suggested that they were individuals of one species at different ontogenetic stages and sexes. He briefly described and illustrated one skull from these remains and stated that he will provide a full account of the rest of the material later (Broom, 1914b, pl.1, figs.1-11, pl. 2, figs.12-23, 25,26, 27A). He sent the material to the American Museum of Natural History where the remains were re-organized

as including three complete skulls (AMNH FARB 5550, AMNH FARB 5552 and AMNH FARB 5553), two partial occiputs (AMNH FARB 5555a&b) and several postcranial elements. Broom (1911) considered *Moschops capensis* as dinocephalian (mentioning dental similarities with *Deuterosaurus* and *Eccasaurus*) and to be very similar to *Delphinognathus conocephalus* which was the second described tapinocephalid from South Africa, and is based on a small incomplete skull (Seeley 1892b, figs. 1-2, p.471, 472). Of the holotypes of both *Eccasaurus* and *Deuterosaurus* only the latter had good preservation of the dentition with talon and heel morphology (Broom, 1909a, Eichwald, 1848) and *Eccasaurus priscus* has been considered an anteosaurid; the latter referred to as both anteosaurian and tapinocephalid by different authors (e.g. Watson, 1914; Boonstra, 1965). Broom (1911, p. 2) defended the description of a new genus despite the close similarity with the previously described *Delphinognathus* because of “the marked difference in the temporal region” and a foramen between the quadratojugal and jugal bones in *Delphinognathus* (Fig. 5.11).

Gregory (1926) described the postcranium of *Moschops capensis* and compared it to the postcranium of other dinocephalian taxa known at the time. Gregory later (1926) pointed out the similarities between *Moschops* and *Delphinognathus* but maintained the validity of *Moschops* as a separate genus because of the “concavity” between the quadratojugal and jugal (which Broom [1911] had interpreted as a foramen), the thinner postorbital bar, much more prominent pineal boss, and larger posterior postcanines in the latter despite the fact that none of the *Moschops* type skulls had in-situ postcanine teeth preserved.

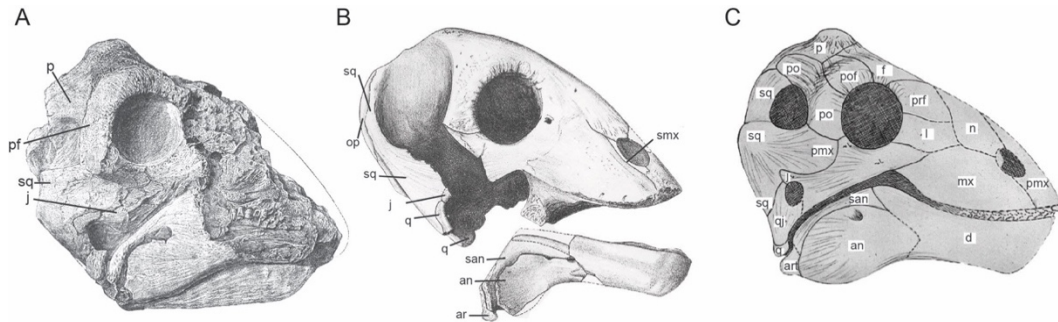


Figure 6. 10. (A) SAM-PK-0713, the holotype of *Delphinognathus conocephalus* as illustrated in Seeley (1892b, fig.1); (B) AMNH FARB 5550, figure 2 the holotype skull of *Moschops capensis* from figure 2 of Broom (1911); (C) Broom’s reconstruction of the holotype of *Delphinognathus* with the help of AMNH FARB 5550, latter to be described as the holotype skull *Moschops capensis* (Broom, 1910, fig.4) . The figures are relabelled. Scale: 10 cm.

Broom (1932) considered that the holotype skulls of *Delphinognathus* and *Moschops* belong individuals of the same size but *Delphinognathus* differs from *Moschops* in having a large pineal foramen in the middle of a prominent boss, a concave prefrontal region, a small temporal opening and “a small opening between the quadratojugal and the jugal”.

Boonstra (1957) described a second species, *Moschops koupensis*, on the basis of a complete large and heavily pachyostotic skull, SAM-PK-11582. He (Boonstra 1957, p.32) characterised the new species as being very wide across the parietals, and having a relatively narrow snout, greatly reduced occipital surface caused by both dorsal and lateral bone overgrowth, and strong transverse process of the pterygoid. Boonstra (1957) provided a composite description of the moschopid

skulls in the South African Museum (Iziko Museum) but did not include a description of the holotype of this new species. Boonstra (1957, 1969) synonymized four already described small-sized tapinocephalid genera (*Agnosaurus*, *Moschognathus*, *Moschoides* and *Pnigalion*) with *Moschops* and considered them to be separate species of *Moschops*. This increased the number of *Moschops* species to four with the inclusion of *M. oweni* (= *Pnigalion oweni* of Watson, 1914) and *M. whaitsi* (*Moschognathus whaitsi* of Broom 1914a). He considered the holotypes of *Agnosaurus pienaari* (Boonstra 1952d) and *Moschoides romeri* (Byrne, 1937) to be *Moschops* sp.. Kammerer (2009) accepted all these synonymies, except *Moschognathus whaitsi* which he reinstated as a valid species. He further added the synonymy of *Moschops koupensis* and *Criocephalosaurus vanderbyli* as *Moschops capensis*. Kammerer (2009) considered that *Criocephalosaurus* represented the final stage of cranial pachyostosis in *Moschops*. He also argued that *Delphinognathus* should not be synonymised with *Moschops*, as the preserved portion of the mandible in *Delphinognathus* was taller than that of *Moschops*. He considered *Delphinognathus conocephalus* (Seeley, 1892b) *nomen dubium* because of the lack of diagnostic characters in the holotype, suggesting that the holotype skull was based on a juvenile and that the features displayed by the specimen would be obliterated with age as a result of ontogenetic cranial thickening.

6.4.3 Systematic Palaeontology

Moschops capensis Broom 1911

Holotype: AMNH FARB 5550 is a small cranium with mandibles from Spitzkop farm, Laingsburg, Moordenaar's Karoo, South Africa (Broom, 1911, fig.1).

Topotypes: AMNH FARB 5552, skull with associated postcrania; AMNH FARB 5553, skull with with associated postcrania and AMNH FARB 5555 comprising two partial occiputs. AMNH FARB 5551, a partial skeleton, AMNH FARB 5554, a vertebral series with ribs, AMNH FARB 5556, a humerus, AMNH FARB 5557, partial humeri.

Comment. Broom (1911) chose AMNH FARB 5550 as holotype and meant this publication as a preliminary report which would be expanded to include the description of all the rest of the material. As all the specimens were collected from the same locality they are called topotypes in the museum records, as well as in the literature (*e.g.* Gregory, 1926, Boonstra, 1936b, Kammerer, 2009). The term “type series” is in the literature to refer to all associated material of the same species (*e.g.* Boos et al., 2010). According to the ICZN Article 72.4, for the specimens to be part of the “type series”, they should have been described together with the holotype or mentioned with a reference. In the case of *Moschops capensis* as well as Broom (1911) clearly states that he found the skeletons together, they all belong to the same species and that he will provide a detailed account of the material later which was done in Broom (1914b). Thus the *Moschops capensis* material in the AMNH clearly fulfils the requirements to be called type series.

Revised genus and species diagnosis. No discrete autapomorphy but the defining combination of characters is: Closely related to *Criocephalosaurus* and *Tapinocephalus*, differing from *Criocephalosaurus* in the larger angle between the cranial roof and occipital plane and from *Tapinocephalus* in the lack of a the nasofrontal boss, more gentle slope from the cranial surface to the facial surface and having a laterally narrower snout.

6.4.3 Description

6.4.3.1 Material

AMNH FARB 5550, a skull with mandibles; AMNH FARB 5552, a skull; AMNH FARB 5553, a skull with mandibles; AMNH FARB 5555a&b, two occiputs. These series are the type material of *Moschops capensis* found in Spitzkop farm, Moordenaar's Karoo, South Africa. Also included in the *Moschops* sample are SAM-PK-11582, a skull with partial lower jaw, the holotype of *Moschops koupensis* found on Die Krans Farm, Prince Albert, South Africa. SAM-PK-12067, a skull from Skoenmaker (Bovenste) Farm, Beaufort West, South Africa. KNPI, KNPII, KNPIII, KNPIV, are all skulls with lower jaws found on Boeteke farm, Beaufort West, South Africa. SAM-PK-K319, is a skull with a mandible from Boontjes Akker farm, Beaufort West, South Africa. This skull is registered in the Iziko Museum catalogue as *Criocephalosaurus sp.* and was subsequently correctly referred to *Moschops capensis* by Kammerer (2009). However Kammerer used this specimen to base his proposed synonymy of *Criocephalosaurus* with *Moschops* (Kammerer, 2009, p. 231). As in the case of

the genotype skulls (AMNH FARB 5550-5555), the recently discovered sample of four specimens (KNPI-IV; comprising relatively small skulls of differing size and degree of pachyostosis) were also found in close association at the same locality. With the exception of the holotypes (SAM-PK-0713, AMNH FARB 5550, 5552, 5555, SAM-PK-11582) (Seeley, 1892b, Broom, 1911; Gregory, 1926; Boonstra, 1936, 1957) none of these specimens have been described or figured elsewhere in the literature.

6.4.4.2 General proportion, size, cranial thickening and preservation

Basal cranial length varies from 210 to 300 mm in the smaller specimens (SAM-PK-0713, AMNH FARB 5550, 5552, 5553, KNP1-4) to 380 mm in the large individuals (SAM-PK-11582, SAM-PK-K319, SAM-PK-12067). With an increase in cranial size the degree and nature of cranial thickening differs from small to large skulls and concerns mainly the frontal bone, postorbital bar (varies from 29 to 80 mm in thickness) and the zygomatic arch. Interorbital and intertemporal breadth is relatively narrow in small individuals (50 to 110 mm) and is much broader in the larger skulls (120 to 170 mm).

6.4.4.3 Skull Roof

Premaxilla: The premaxilla (Figs. 6.11-6.18, 6.19-6.21) is a paired bone forming the anteriormost portion of the snout. It is well preserved in AMNH FARB 5553 and SAM-PK-11582 and preserved to varying degrees in AMNH FARB 5550, AMNH FARB 5552, SAM-PK-K319, SAM-PK-12067 and the KNP skulls. On the skull roof the premaxilla borders the dorsal, anterior and anterodorsal margins

of the external naris, laterally it contacts the maxilla below the naris and the suture between the premaxilla and maxilla extends to the alveolar margin of the maxilla between the fifth incisor and the “canine” as is evident in specimens AMNH FARB 5550, SAM-PK-12067, SAM-PK-011582 and KNPIV. Posteromedially it meets the nasal mid-way between the orbit and external naris as is evident in specimens AMNH FARB 5553, KNPIV, KNPI, SAM-PK-11582, SAM-PK-12067 and SAM-PK-K319.

Maxilla: The maxilla (Figs. 6. 11- 6.14, 6.16-6. 21) is a large, broadly triangular bone that forms most of the lateral surface of the snout. It has a short vertical anterior contact with the premaxilla ventral to the external naris, a long dorsal contact with the nasal and and a short posterodorsal contact with the prefrontal. Posteriorly it has a vertical sutural contact with the lacrimal and meets the jugal posteroventrally. The maxilla forms the alveolar margin of the snout and extends posteriorly as a narrow spur half way along the orbit beneath the ventral border of the jugal as seen in specimens AMNH FARB 5550, SAM-PK-11582, SAM-PK-12067. On the maxillary surface anterior to the lacrimal is a long horizontal depression. This depression is more prominent in larger skulls as a result of thickening of the nasal posteriorly and prefrontal anteriorly.

Lacrimal: The lacrimal (Fgs. 6.16, 6.17C,D, 6.19, 6.20) is a small quadrangular bone that is preserved in AMNH FARB 5550, AMNH FARB 5553, SAM-PK-11582, KNPIV and partially in SAM-PK-0713. It forms the anteromedial border of the orbit, is in sutural contact with the prefrontal dorsally, the jugal ventrally, and has a vertical suture with the maxilla anteriorly. In KNPII, which is a small

skull, the bone surface has been completely eroded away exposing the mold of the ductus naso-lacrimalis which opens into the anteroventral border of the orbit (Fig. 5.65B).

Prefrontal: The prefrontal (Figs. 6.11- 6.21) is crescentric bone that forms the anterodorsal margin of the orbit. It contacts the nasal anterodorsally, the frontal dorsally and posteriorly, and the lacrimal ventrally. In the larger specimens the prefrontal manifests considerable pachyostotic thickening in confluence with thickening of the surrounding bones of the skull roof.

Frontal: The paired frontal is the largest bone of the cranial roof (Figs. 6.11- 6.21) and is greatly thickened in larger specimens. It has a short contact with the nasal anteromedially, prefrontal anterolaterally, the postfrontal posterolaterally and the parietal posteriorly. Important is the fact that the frontal has a short exposure on the dorsal orbital border in both large and small specimens. There is a light depression along the midline suture of the frontal pair on the skull roof of AMNH FARB 5553 and SAM-PK-11582.

Posterolaterally the frontal has a narrow extension between the postfrontal and parietal which contributes to the dorsal border of the temporal opening in specimens AMNH FARB 5553, KNPIV and SAM-PK-11582, SAM-PK-K319, SAM-PK-12067 and is excluded from the border in AMNH FARB 5552 as was described by Boonstra (1957). This possibly is related to the fact that AMNH FARB 5552 is the smallest of all the skulls.

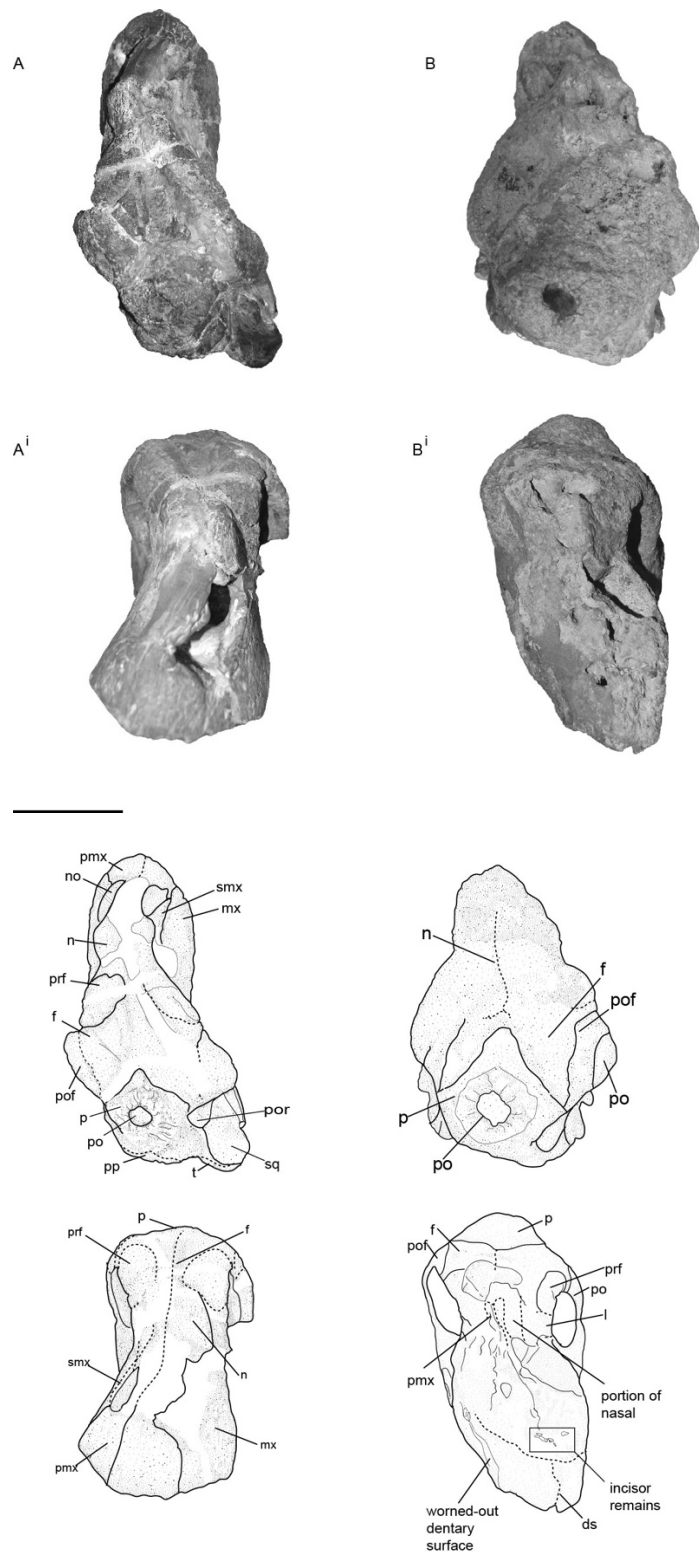


Figure 6.11. *Moschops*: photographs and illustrations showing the skull roof of AMNH FARB 5550 (holotype of *M. capensis*) (A & Aⁱ) and SAM-PK-0713 (holotype of *Delphinognathus conocephalus*) (B & Bⁱ) in dorsal view (A & B) and anterior view (Aⁱ and Bⁱ). Scale: 10 cm.

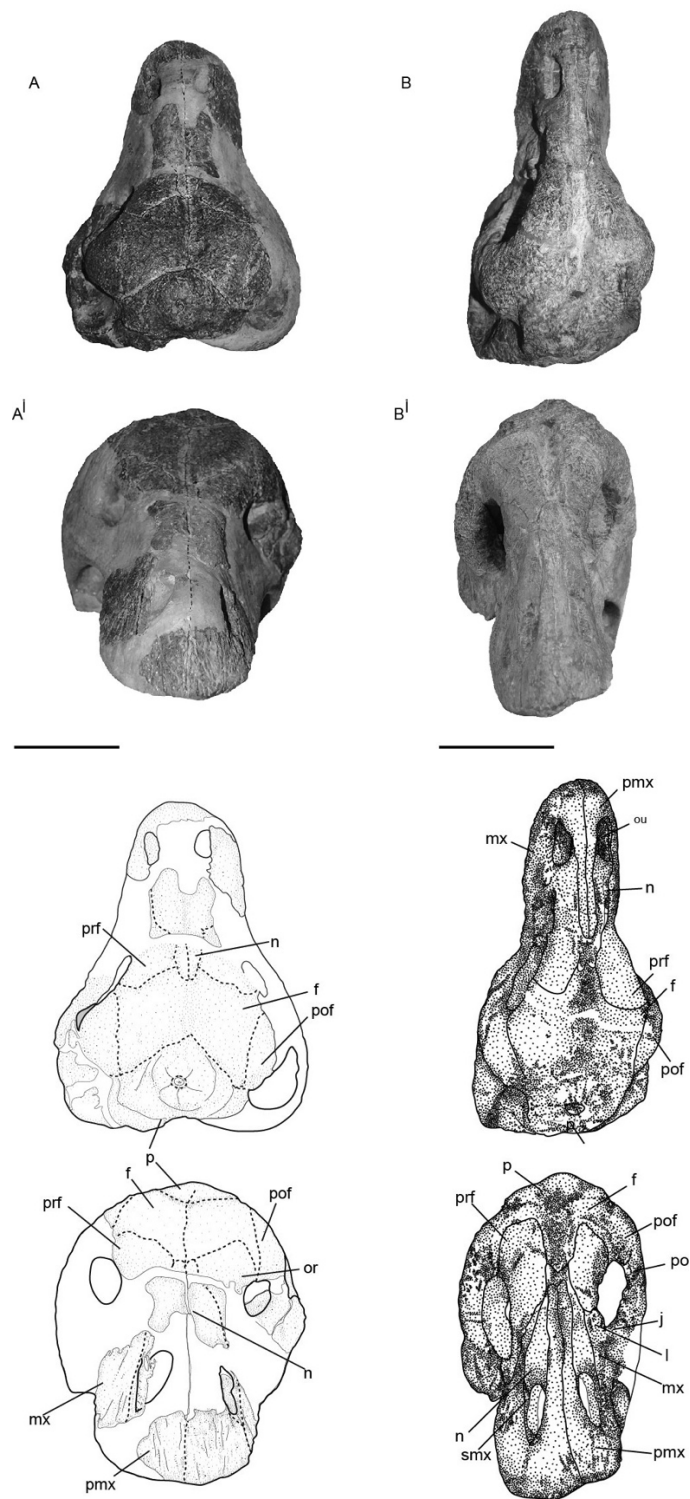


Figure 6. 12. *Moschops*: photographs and illustrations showing the skull roof of AMNH FARB 5552 (A & A¹) and AMNH FARB 5553 (B & B¹) in dorsal view (A & B) and anterior view (A¹ and B¹). Note that the outline of AMNH FARB 5552 is similar to that of SAM-PK-11582 which differs from the rest of the specimens in its larger size and broader intertemporal width. Scale: 10 cm.

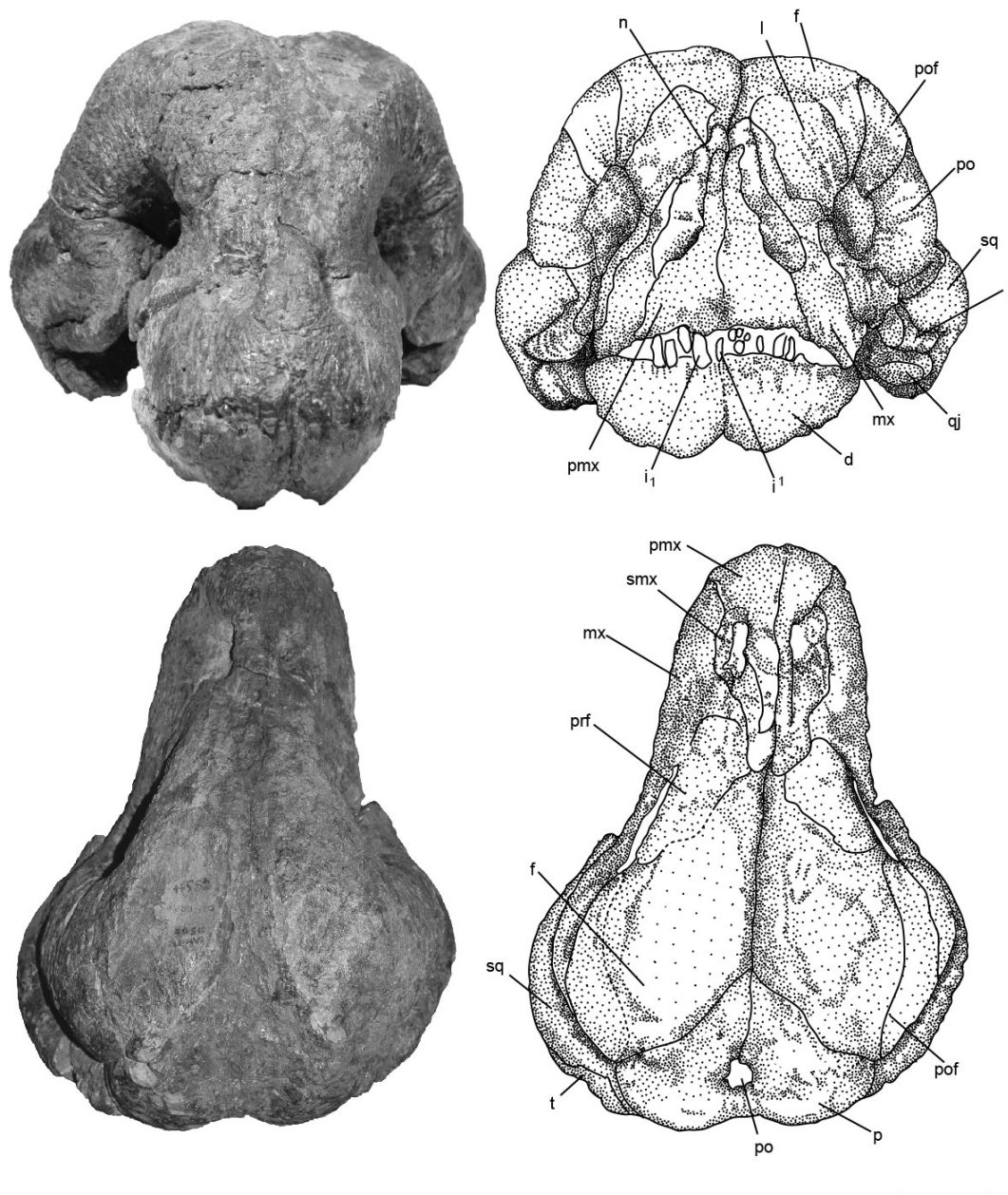


Figure 6. 13. *Moschops*: photograph and illustration showing the skull roof of SAM-PK-11582 (holotype of *M. koupensis*). Scale: 10 cm.

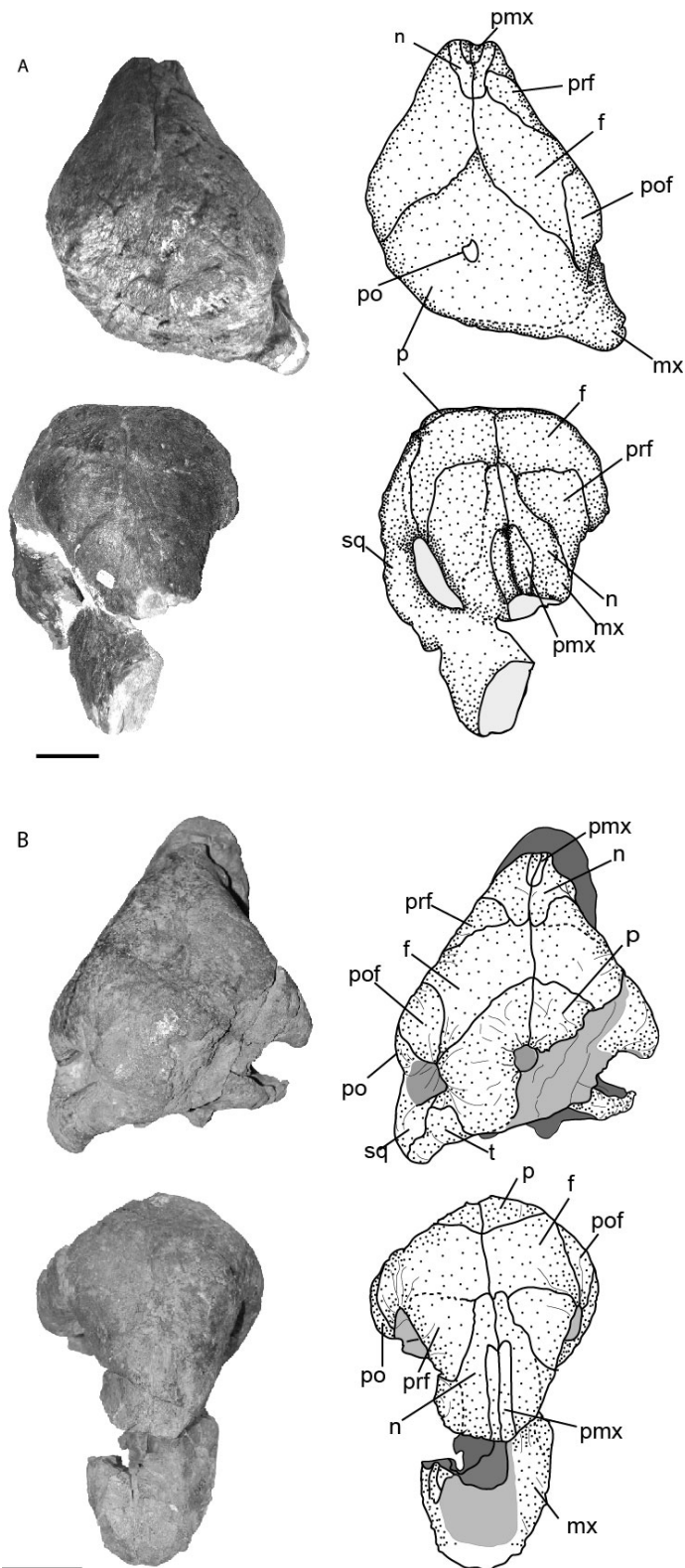


Figure 6.14 . *Moschops*: photograph and illustration showing the skull roof of SAM-PK-12067 (A), SAM-PK-K319 (B). Scale: 10 cm.

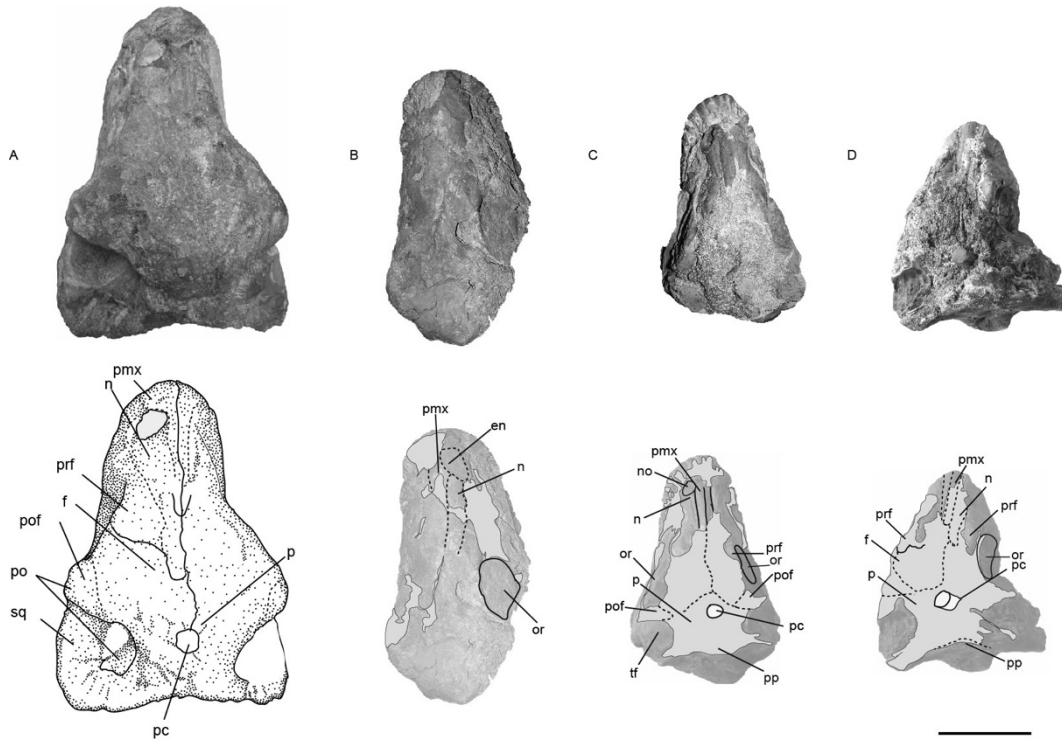


Figure 6. 15. *Moschops*: photograph (top) and illustration (bottom) showing the skull roof of the subadult skulls KNPIV (A), KNPIII (B),KNPII (C) and KNPI (D). Gray shaded areas show portions with bone preservation. Scale :10 cm.

Postfrontal: The postfrontal (Figs. 6.11- 6.21) is a somewhat triangular bone extending between posterodorsal margin of the orbit and the anterodorsal margin of the temporal fenestra but does not contribute to its border. It demonstrates varying degrees of preservation in the different specimens, and in KNPI, II, and III the bone surface has been completely weathered away leaving the triangular outline of the postfrontal (Figs. 6.21).

Dorsally the postfrontal has a long contact with the frontal, and a third of the way down the postorbital bar it has a slanting sutural contact with the postorbital. In the small skulls the postfrontal is a small thin bone and in the larger skulls it is larger and thickened.

Worthy of note is the fact that, although this portion of the cranial roof is similar in *Tapinocephalus* and large *Moschops* skulls, there is a depression on the posterior end of the postfrontal in *Tapinocephalus* which is not present in *Moschops*. This depression was possibly for attachment of jaw adductor musculature. This may be an important distinguishing feature between the two genera.

Postorbital: The postorbital (Figs. 6.11- 6.21) makes up the lower two-thirds of the postorbital bar and forms part of the anterior border of temporal fenestra. Dorsally the postorbital is in contact with the postfrontal on the postorbital bar and ventrally, at the base of the postorbital bar, it meets the jugal anteriorly and the squamosal on the posterior side. The contact of the postorbital with the squamosal and the postorbital on the postorbital bar continues medially in the temporal fenestra until the two bones meet the parietal on the posterodorsal border of the temporal fenestra. This is preserved in SAM-PK-12067, SAM-PK-11582, SAM-PK-K319, and all the small skulls except SAM-PK-0713, KNPI-III, AMNH FARB 555, AMNH FARB 5550. In the smaller skulls the postorbital bar is relatively thin (*e.g.* 29 mm in KNPI and SAM-PK-0713, 34 mm in KNPIV, 30 mm in AMNH FARB 5550 and AMNH FARB 5553) and in the larger, more

pachyostosed skulls it is thicker (85 mm in SAM-PK-11582, 75mm in SAM-PK-319 and SAM-PK-12067).

Jugal: The jugal (Figs. 6.11- 6.21) forms the entire ventral margin of the orbit and the anterior part of the postorbital bar. Anteriorly it contacts the maxilla, anterodorsally the lacrimal (as manifested in KNPI,III,IV, SAM-PK-12067, SAM-PK-K319, SAM-PK-11582), and has a long zig-zag ventral contact with the squamosal. This posteroventral exposure of the jugal is not wide but robust in the larger specimens as is evident in SAM-PK-11582, SAM-PK-12067 and K319. The jugal's posterior extension is preserved only in KNPIV and SAM-PK-0713, and in contrast to the large skulls, forms a short spur abutting the squamosal posterodorsally at its contact with the quadratojugal. Unfortunately the posterior end of the jugal is not preserved in any of the *Moschops capensis* type skulls. In KNPIV (Fig. 6.21D) which is a small individual, the jugal is not thickened and it has relatively broad exposure on the side of the skull below the squamosal as noted by Broom (1911, pl. lxii, fig.1) for AMNH FARB 5550.

Squamosal: The squamosal (Figs. 6.11- 6.21) is a large robust bone contributing to the posterolateral, lateral and occipital views of the skull and makes up the lateral and posterior borders of the temporal fenestra. The bone is well preserved in SAM-PK-11582, on the left of specimens KNPIV and SAM-PK-K319, and the right side of SAM-PK-12067. Anterodorsally the squamosal has a long horizontal sutural contact with the postorbital extending across most of the base of the postorbital bar. Anteriorly the squamosal has a forward oriented and pointed

contact with the jugal. This point is dorsally positioned on the zygoma of KNPIV, SAM-PK-12067, SAM-PK- K319 and is more ventral in SAM-PK-11582 and SAM-PK-0713.

The squamosal curves medially into the temporal fenestra on the dorsal side. It is overlain by the the tabular on the occiput and meets the parietal and postorbital dorsally. Posteroventrally it supports the quadrate, and posteromedially it is overlapped by the paraoccipital process of the opisthotic. In occipital view the squamosal has three distinct surface features: (1) A sulcus (external auditory meatus) which runs parallel to the contact with the paraoccipital process, (2) a keel which separates this sulcus from the contact, (3) a squamosal surface, *i.e.* facet, exposed between the keel and the contact which are evident in KNPIV, SAM-PK-11582, SAM-PK-K319, SAM-PK-12067. Here specimen KNPIV differs from the larger specimens in having the sulcus oriented less anteroventrally and the squamosal facet almost being exposed between the keel and the paraoccipital.

The squamosal is preserved in all small skulls except KNPI-III, AMNH FARB 5552-5553 and is not thickened, while it is thicker and its surface swollen in the larger specimens. Thus the corner of the zygoma, as in *Tapinocephalus*, is rounded in the large specimens as evidenced in SAM-PK-11582, SAM-PK-12067 and SAM-PK-K319.

Parietal: The parietal (Figs. 6.11- 6.21) of *Moschops* is a large paired bone positioned across the skull roof between the temporal openings and forms the dorsal border of this fenestra where it is in contact with the postorbital on the anterior side and the squamosal posteriorly. Together with its counterpart it has an anteriorly pointing “V” shaped sutural contact with the frontal; while posteriorly has a long horizontal contact with the postparietal which forms the contact between the skull roof and occiput. Similar to *Criocephalosaurus* the parietal of *Moschops* slopes posteriorly behind the pineal foramen which is positioned on a raised chimney on the midline of the skull roof.

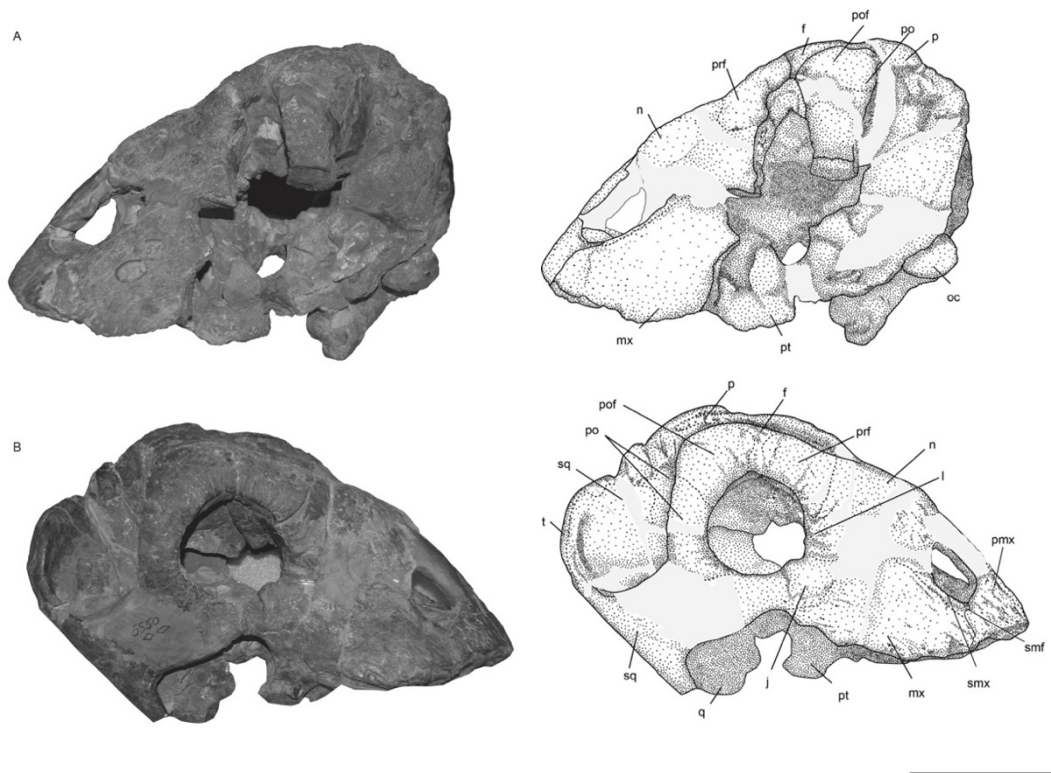


Figure 6. 16. *Moschops*: photographs (left) and illustrations (right) of the left (A) and right (B) lateral views of AMNH FARB 5550 (holotype of *M. capensis*). Scale: 10 cm.

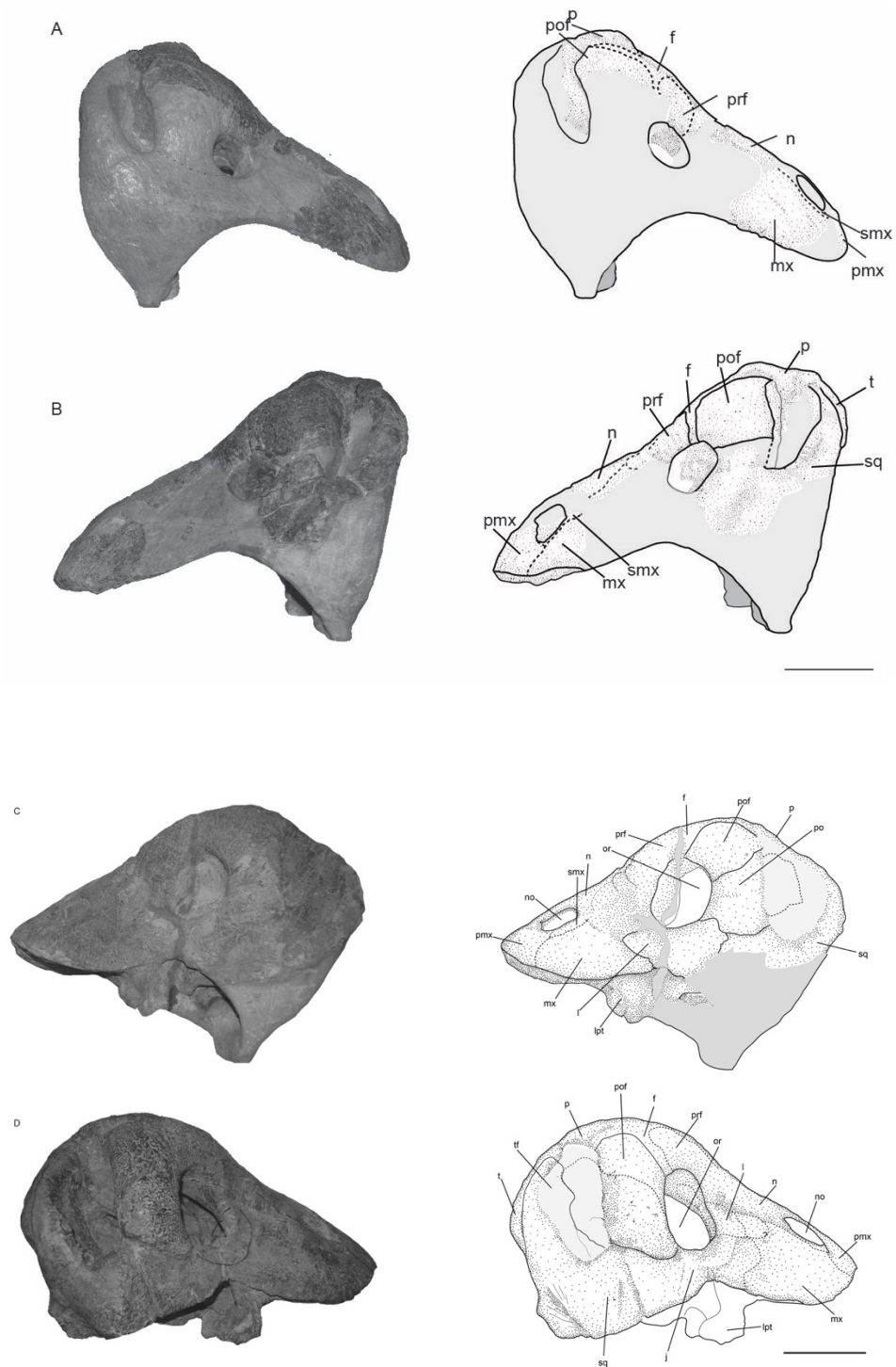


Figure 6. 17. *Moschops*: photograph (left) and illustration (right) of the left (B, C) and right (A, D) lateral views of AMNH FARB 5552(A,B) and AMNH FARB 5553 (C,D). Scale 10 cm.

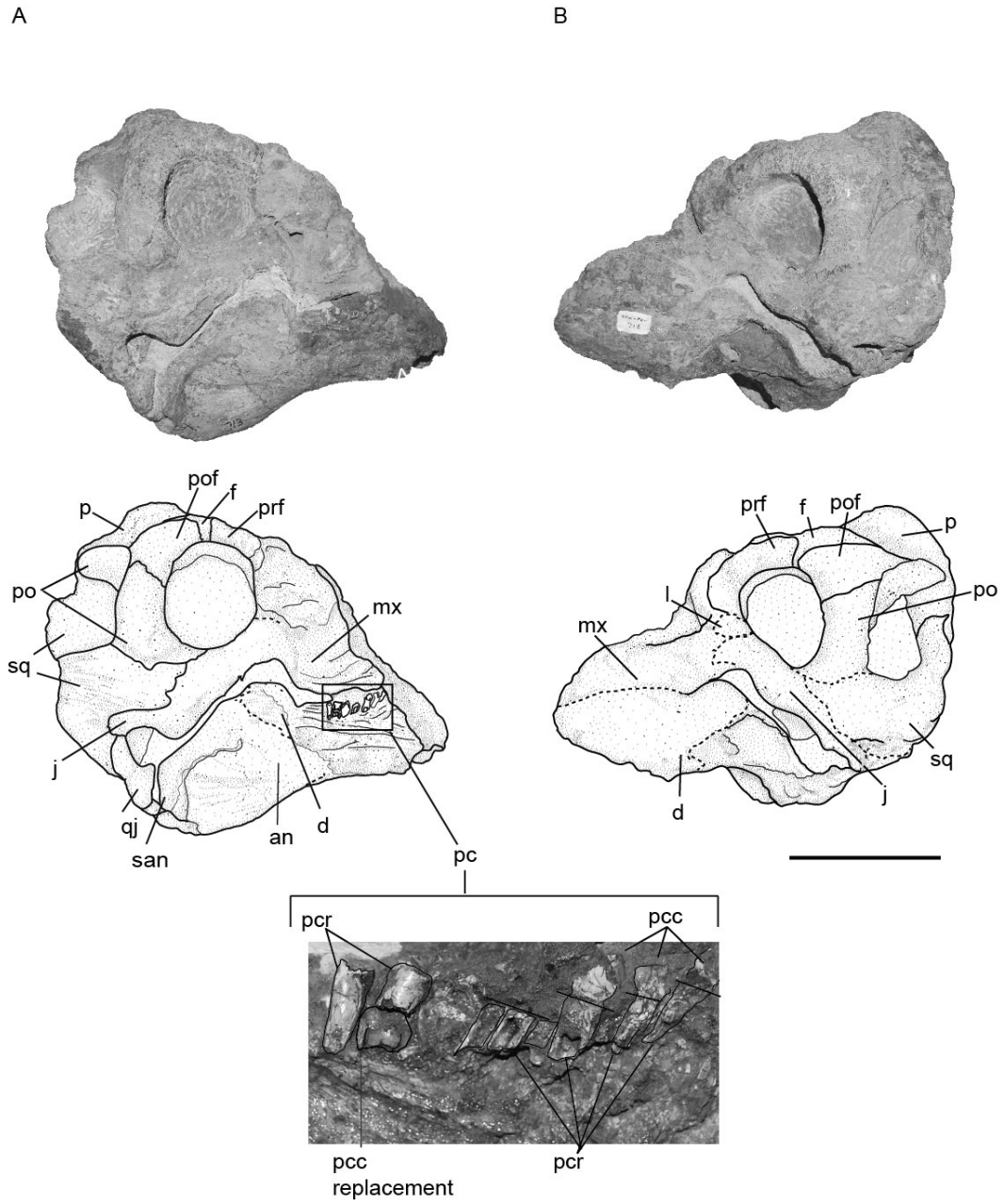


Figure 6. 18. *Moschops*: photographs (top) and illustrations (bottom) showing the lateral view of SAM-PK-0713 (holotype of *Delphinognathus conocephalus*) with a detail photograph of the postcanines on the right side. Scale 10 cm.

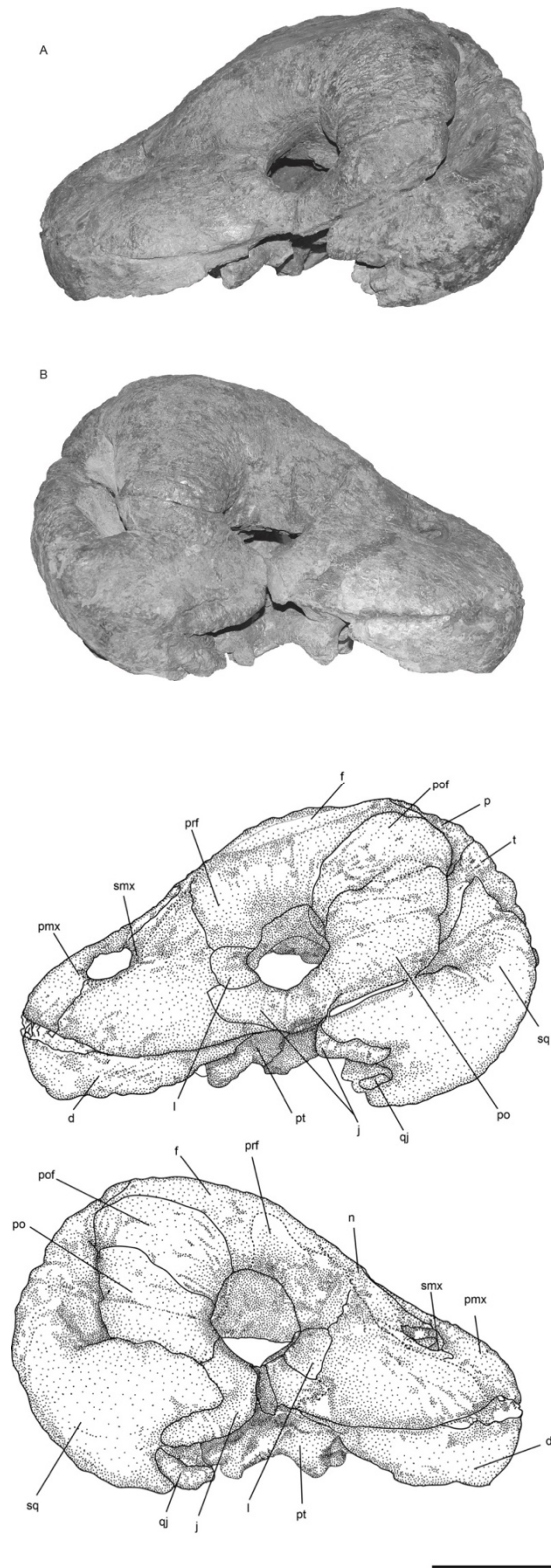


Figure 6. 19. *Moschops*: photograph (top) and illustration (bottom) of the lateral view of SAM-PK-11582 (holotype of *M. koupensis*). Scale 10 cm.

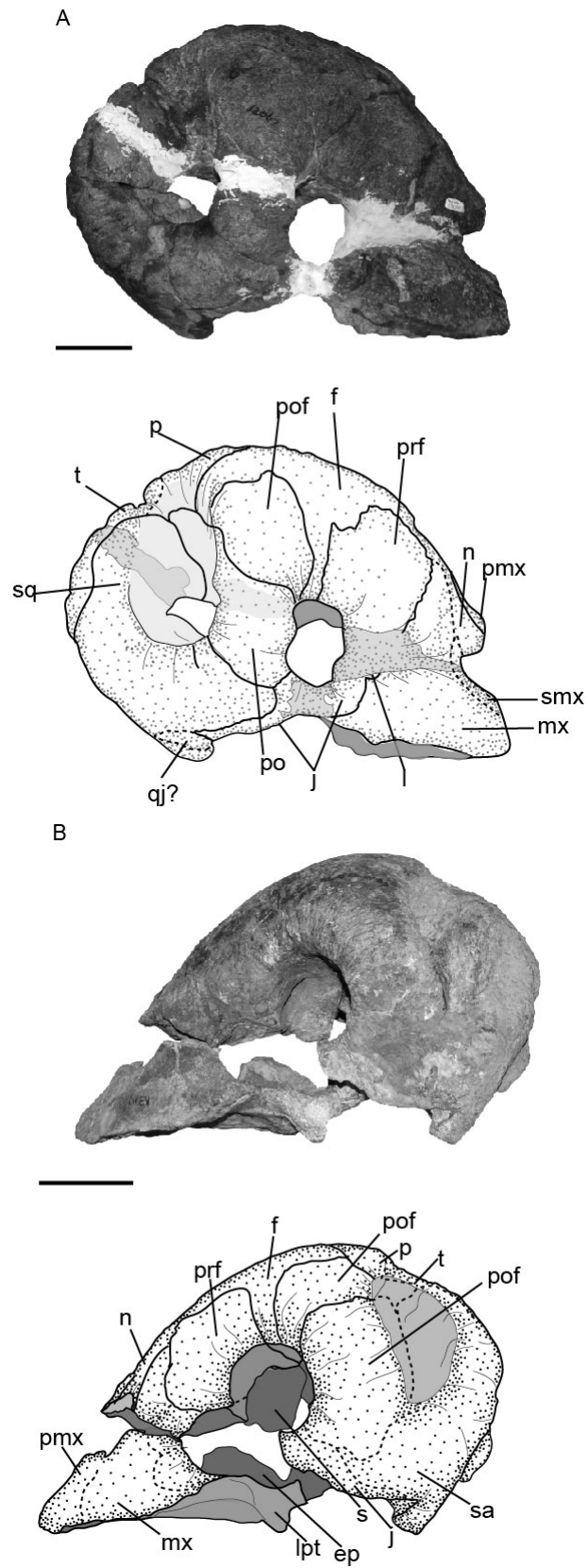


Figure 6. 20. *Moschops*: photographs (top) and illustrations (bottom) of SAM-PK-12067 (A) and SAM-PK-K319 (B). Scale 10 cm.

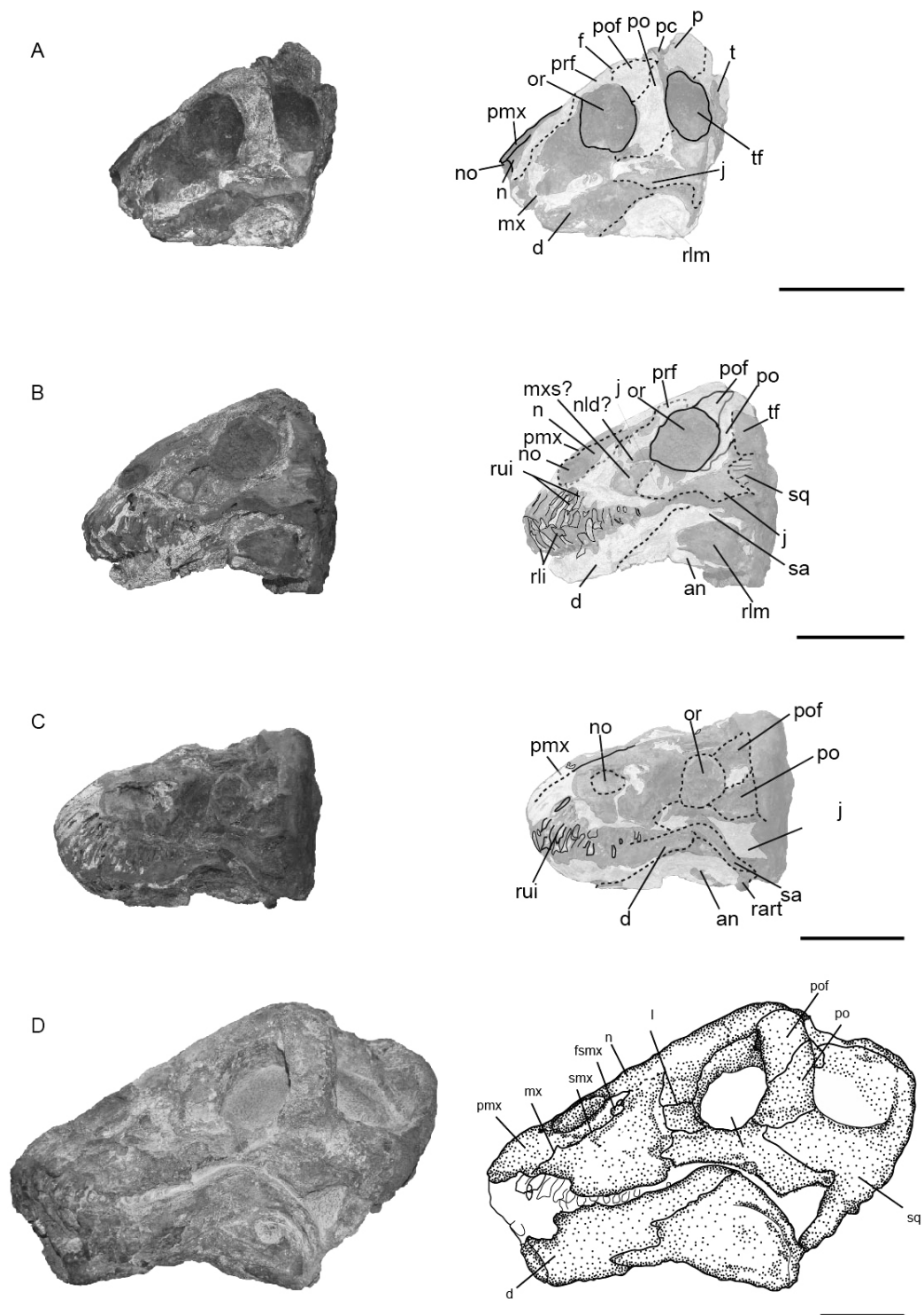


Figure 6. 21. *Moschops*: photographs (left) and illustrations (right) of KNPI (A), KNPII (B), KNPIII (C) and KNPIV (D). Gray shaded areas show portions with bone preservation. Scale :10 cm.

6.4.3.4 Occiput and braincase

The occiput (Figs. 6.22-6.24, 6.25Aⁱ, Bⁱ, 6.26) of *Moschops capensis* is similar in general shape to that of *Tapinocephalus* and *Ulemosaurus* but is not as broad as that of *Tapinocephalus*. In large skulls (SAM-PK-K11582 and SAM-PK-K319) the greatly thickened occipital crest is positioned further posteriorly than its ventral edge causing the occiput to slope forwards toward the ventral side, however in the smaller skulls the slope of the occiput is less pronounced. The degree of the anteroventral tilt of the occipital plate also affects the plane of the occipital condyle: as the small skulls show less anteroventral tilt of the occipital surface, the plane of the occipital condyle is less anteroventrally orientated than it is in the larger skulls.

The occiput of *Moschops* is best preserved in SAM-PK-11582. Other skulls have suffered varying degrees of weathering, making them difficult to interpret:

AMNH FARB 5550 is damaged on the left side, AMNH FARB 5552 preserves only the left dorsal portion including the tabular, postparietal and dorsomedial part of the supraoccipital. In SAM-PK-0713, the dorsal and lateral borders of the occiput are lost and the main occipital surface suffered heavy surface weathering.

This specimen shows the postparietal with a prominent midline keel and the posterolateral end of the right tabular. In KNPI and IV the right part of the occiput is missing. SAM-PK-K319 has the left portion of the occiput preserved and SAM-PK-12067 preserves only the right postparietal, tabular and paroccipital process.

The surface of the occiput is deeply indented in the larger specimens as a result of thickening of the dorsal and lateral borders.

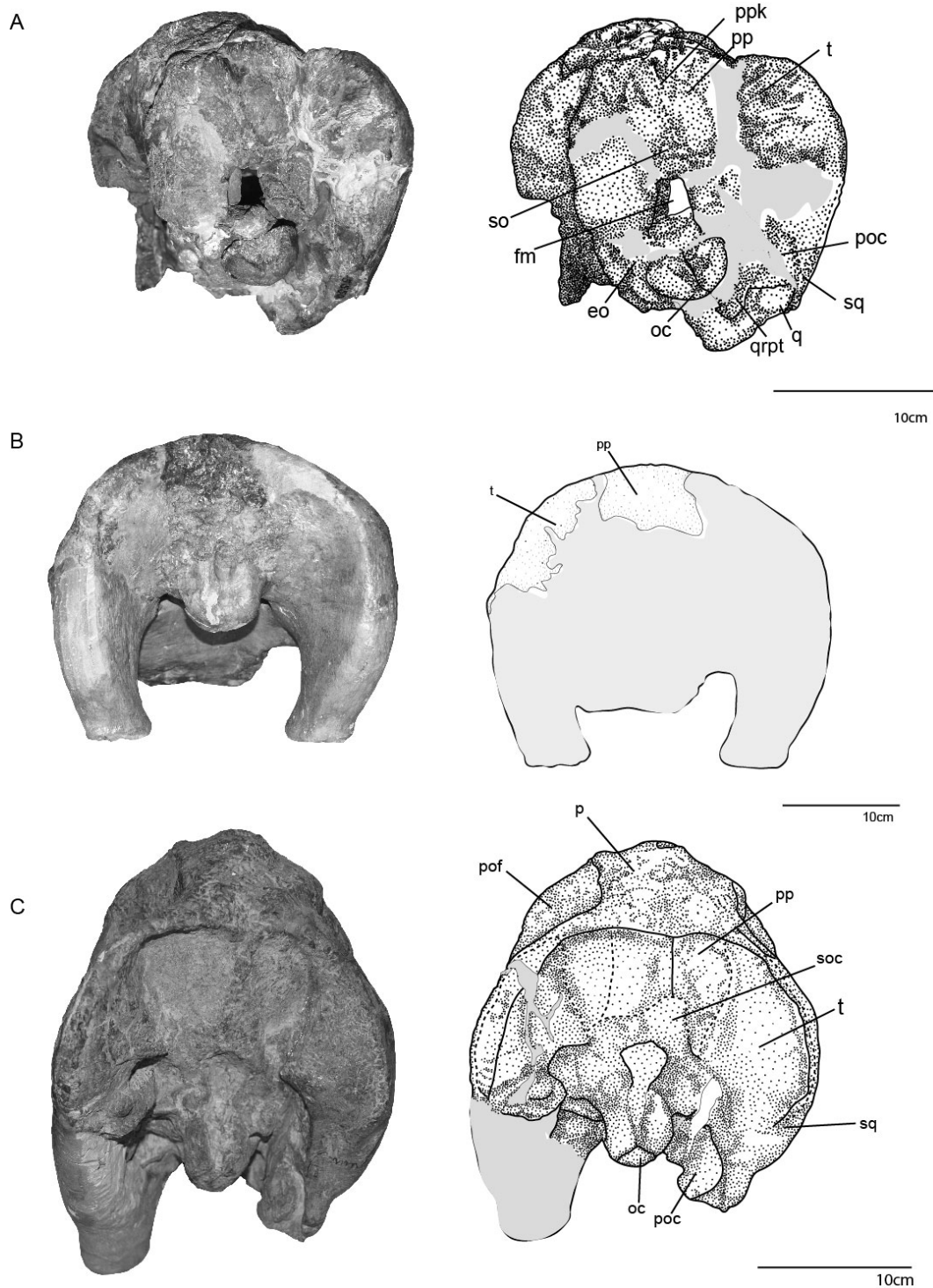


Figure 6.22. *Moschops*: photograph (left) and illustration (right) of the occipital views of AMNH FARB 5550 (holotype of *M. capensis*) (A.), AMNH FARB 5552 (B) and AMNH FARB 5553 (C). Scale: 10 cm.

Postparietal: The rectangular postparietal (Figs. 6.22-6.25Bⁱ, 6.26) forms a third of the dorsomedial occipital surface. Its posterior surface is slightly depressed and has a midline keel. Dorsally, as in all tapinocephalids, the postparietal contacts the parietal along the occipital crest and in SAM-PK-11582, AMNH FARB 5550 and AMNH FARB 5553 it has a short medial sur which overlies the dorsal part of the parietal. Laterally the postparietal contacts the tabular and has a long horizontal ventral sutural contact with the supraoccipital.

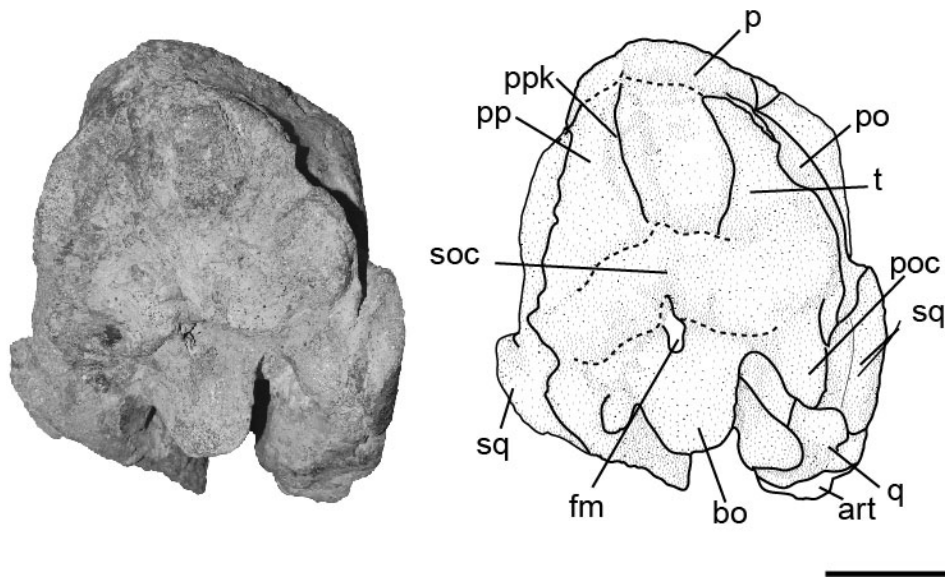


Figure 6. 23. *Moschops*: photograph (left) and illustration (right) of SAM-PK-0713 (holotype of *Delphinognathus conocephalus* Scale: 10 cm.

Tabular: The tabular (Figs.6.22-5.24, 6.26) is a large, flat and semilunate bone that forms the largest portion of the occiput. It is in contact with the parietal dorsally, the squamosal laterally, the postparietal medially and the supraoccipital ventrally. The medial contact of the tabular with the postparietal is curved in

AMNH FARB 5553 and SAM-PK-0713 and forms a straight line in SAM-PK-11582. An elongated spur extends ventrally to form part of the dorsal border of posttemporal foramen as is evident in SAM-PK-11582 and SAM-PK-K319. The posterior surface of the tabular is smooth and flat with tickened lateral margins which curve over the bone in the largest specimens such as SAM-PK11582.

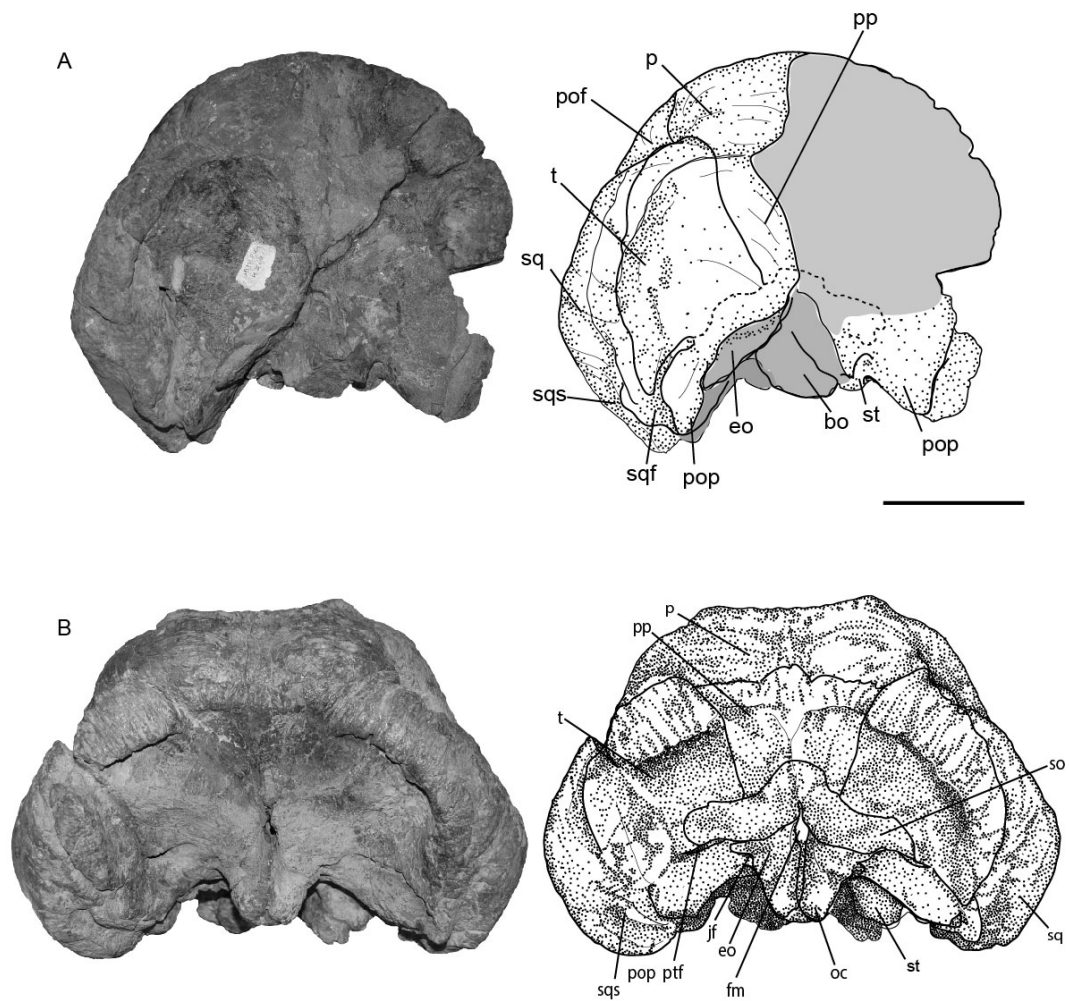


Figure 6. 24. *Moschops*: photograph (left) and illustration (right) of SAM-PK-K319 (A) and SAM-PK-11582 (holotype of *M. koupensis*) (B). Scale: 10 cm.

Supraoccipital: The supraoccipital (Figs.6.22-5.24, 6.26) is a relatively large rectangular bone with lateral wing-like extensions, and forms the dorsal margin of the foramen magnum. It is best preserved in AMNH FARB 5553, SAM-PK-11582 and KNPI. In the dorsal midline the supraoccipital sends a spur which overlies the postparietal. Laterally the supraoccipital contacts the tabular, and ventrally it meets the exoccipital and the paroccipital process as is evident in SAM-PK-11582.

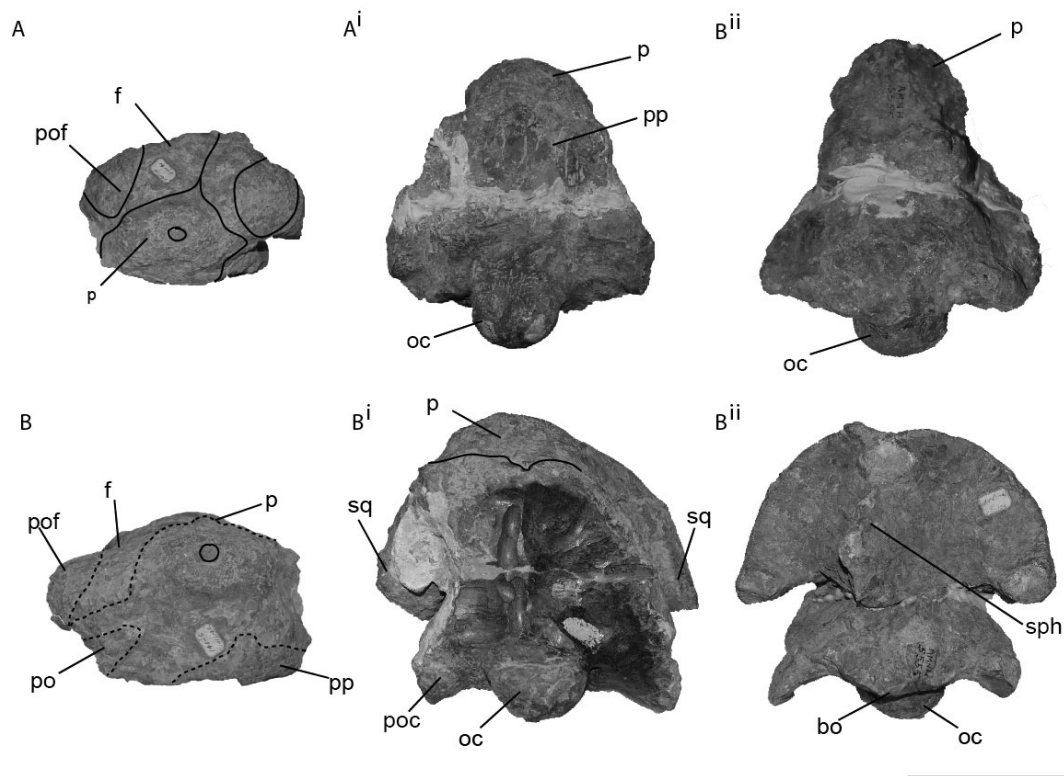


Figure 6. 25. *Moschops*: photograph of AMNH FARB 5555a (top row) and AMNH FARB 5555b (bottom row) showing the cranial roof (A, B), occipital view (Aⁱ, Bⁱ) and the dorsal view of the occipital surface (Aⁱⁱ, Bⁱⁱ). Scale bar: 10 cm.

Exoccipital: The exoccipital (Figs.6.22-5.24, 6.26) is relatively small bone forming the lateral and ventrolateral borders of the foramen magnum and the dorsal lobes of the tripartite occipital condyle. It has ventral contact with the basioccipital. It is best preserved in SAM-PK-11582 and KNPI, with partial and distorted preservation of the bone in AMNH FARB 5550 and KNPIV. Each exoccipital has a wing-like lateral extension that contacts the opisthotic but does not extend as far as the posttemporal foramen. The exoccipital forms the lateral margin of the jugular foramen which is situated at the lower border of the exoccipital and opisthotic as evidenced in SAM-PK-11582 and KNPIV.

Opisthotic: The opisthotics (Figs.6.22-5.24, 6.26) make up a large part of the occiput with the robust paraoccipital process which is preserved in AMNH FARB 5553, KNPII and KNPIII. In occipital view the paraoccipital process is medially narrow where it borders on the ventral side of the jugular foramen and expands laterally towards its contact with the squamosal and the dorsal process of the quadrate. Dorsally it has a long contact with supraoccipital, a short contact with the tabular dorsolaterally, and makes up the the ventral border of the posttemporal foramen. Ventromedially, in ventral view, it has a short sutural contact with the basioccipital where it contributes to the posterior border of the fenestra ovalis.

Basioccipital: The basioccipital (Figs.6.22-5.24, 6.26) forms the posteriormost element of the ventral surface of the skull and the ventral lobe of the the tripartite occipital condyle and thus contributes to both the occipital and ventral surfaces of

the skull. On the occipital surface the basioccipital forms a dorsolateral contact with the exoccipital and the opisthotic laterally. In the ventral view it contacts the basisphenoid anteriorly and contributes to the anterolateral margin of the fenestra ovalis. As is evident in SAM-PK-11582 (Fig. 6.24), in ventral view it is oblong with a low median keel which extends anteriorly onto the basisphenoid. This morphology is similar to that of the holotype of *Avenantia kruisvleiensis*, SAM-PK-9166 (= *Riebeeckosaurus longirostris*).

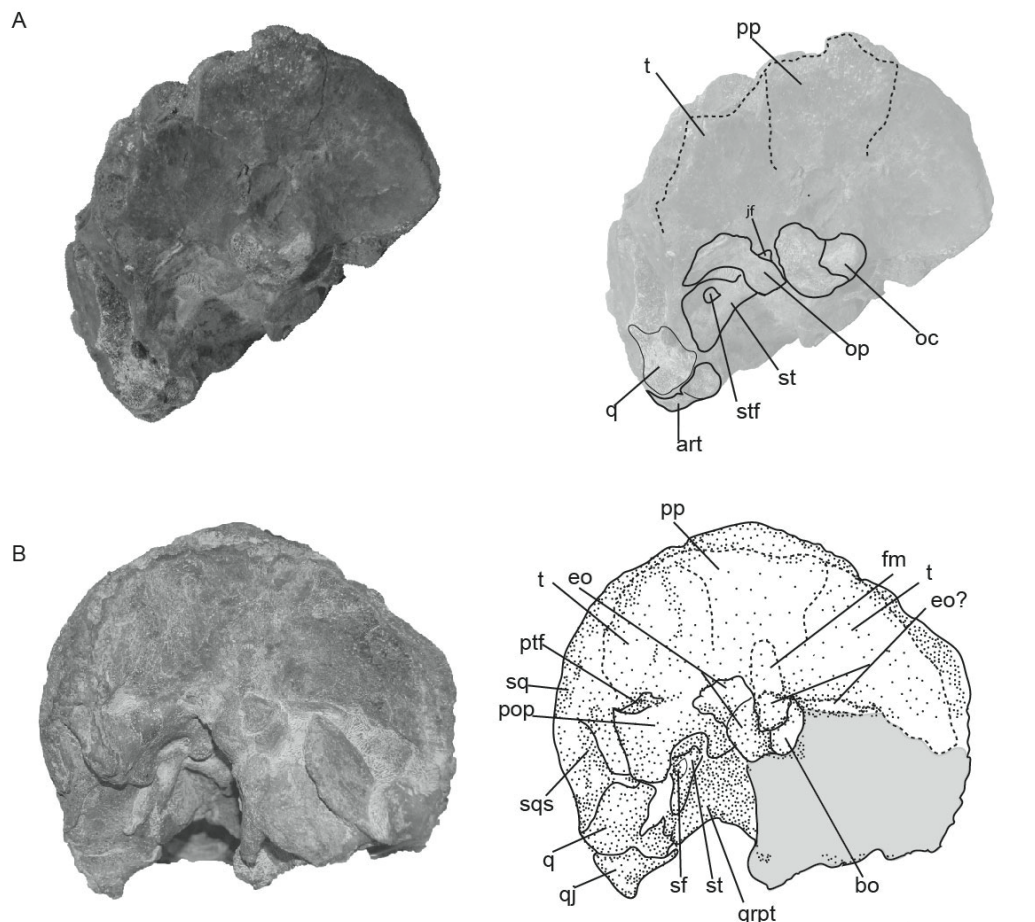


Figure 6. 26. *Moschops*: photographs (left) and illustrations (right) of the occipital view of KNPI (A) and KNPIV (B). Scale equals 10 cm.

6.4.3.5 Palate

As pointed out by Boonstra (1957p. 24), because of the extreme posteroventral orientation of the occiput, the basicranium and the palate of *Moschops* are visible on the same plane.

Premaxilla. The premaxilla (Figs. 6.27- 6.29, 6.34- 6.35C) forms the anterior extremity of the palatal view with a wide and roughly triangular shelf which bears five incisors (as evidenced by the number of alveoli in AMNH FARB 5550) and forms the anterior and anterolateral borders of the internal naris. The continuation of the premaxilla-maxilla suture is tentatively identified only on AMNH FARB 5550, while it is not clearly visible in AMNH FARB 5553 and SAM-PK-K319. While AMNH FARB 5553 is preserved with several alveoli on the premaxilla; SAM-PK-K319 is preserved with an emerging small crown, the tips of five on the left, and a relatively large crown with obliquely orientated heel on the right side.

Maxilla: The maxilla (Figs. 6.27, 6.29, 6.37) is best preserved in AMNH FARB 5550, AMNH FARB 5553 and SAM-PK-K319 and it forms a thin alveolar margin lying medial to the choana and the palatine.

Vomer: The vomer (Figs. 6.28, 6.30-6.31, 6.33-6.35, 6.36) is a paired elongated bone that forms the floor of the narial cavity and the medial margin of the choana. It is best preserved in specimens SAM-PK-K319, AMNH FARB 5553 and SAM-PK-11582 with incomplete preservation in AMNH FARB 5550, AMNH FARB 5552, SAM-PK-0713, KNPI, KNPII and KNPIV.

Anteriorly the vomer contacts the premaxilla and as it broadens posteriorly it contacts the palatine laterally and has a short posterior contact with the pterygoid. The posteroventral surface of the vomer has a longitudinal lateral ridge which extends posteriorly as far as the palatine boss as is evident in AMNH FARB 5553, KNPII, SAM-PK-K319, SAM-PK-11582.

In SAM-PK-K319 (Fig. 6.35) it is evident that the vomerine pair forms the part of the dorsal wall of the choana where the anterior two-thirds of the vomer is long and narrow with ventrally curved lateral margins and posteriorly it has a median keel with a dorsally projecting sail-like surface. In lateral view this median keel is triangular with the apex oriented dorsally.

Palatine: The palatine (Figs. 6.28, 6.20- 6.35) is preserved in SAM-PK-11532, KNPIII, SAM-PK-K319 (left side), AMNH FARB 5553, AMNH FARB 5550 (right side), KNPI (left side), KNPII, KNPIV. It is a complex bone with a broad posterior portion and a large anterolateral projection which ventrally overlies the maxilla and forms the posterior half of the choanal border. The posterior portion comprises a relatively insignificant edentulous palatine boss which appears as a small and low ridge positioned obliquely relative to the midline. The suture between the palatine and pterygoid bosses is discernable only in AMNH FARB 5553 and KNPII.

Pterygoid: The pterygoid (Figs. 6.28, 6.29- 6.34) is a large paired bone making up slightly less than half of the length of the ventral view of the skull and comprises

three rami; anterior, transverse and posterior. The anterior ramus is a very short anteromedial projection of the pterygoid which is in contact with the palatine boss anteriorly by means of a transverse interdigitating suture which is manifest in AMNH FARB 5553, KNPIV and SAM-PK-11582. The transverse ramus comprises the lateral flange of the pterygoid which is highest laterally and decreases in height toward the midline. Its ventral surface appears as a broad edentulous rugous ridge which narrows as it curves posteromedially toward the interpterygoidal vacuity. The posterior side of the lateral flange forms a slightly concave platform which is broad laterally and narrows towards the ventral midline to connect with the posterior ramus of the pterygoid. This contact is evident in SAM-PK-11582, AMNH FARB 5553, KNPII and KNPIV. The posterior ramus extends posteromedially to meet the parabasisphenoid and posterolaterally to the medial condyle of the quadrate as the quadrate ramus of the pterygoid. The quadrate ramus is relatively short and thick in SAM-PK-11582 as noted by Boonstra (1957) and is slender in the smaller skulls SAM-PK-0713, AMNH FARB 5553, KNPII, KNPIV. The oval interpterygoidal vacuity extends posteriorly from behind the level of palatine-ptyerygoid contact up to the posterior side of the lateral flange.

Ectopterygoid: The ectopterygoid (Figs. 6.29, 6.32- 6.33) is a relatively small plate-like bone between the medial side of the jugal and the lateral flange of the pterygoid and has been recognised in AMNH FARB 5553, KNPIV, and SAM-PK-11582. It lies anterolateral to the lateral flanges and contacts the palatine anteriorly and medially.

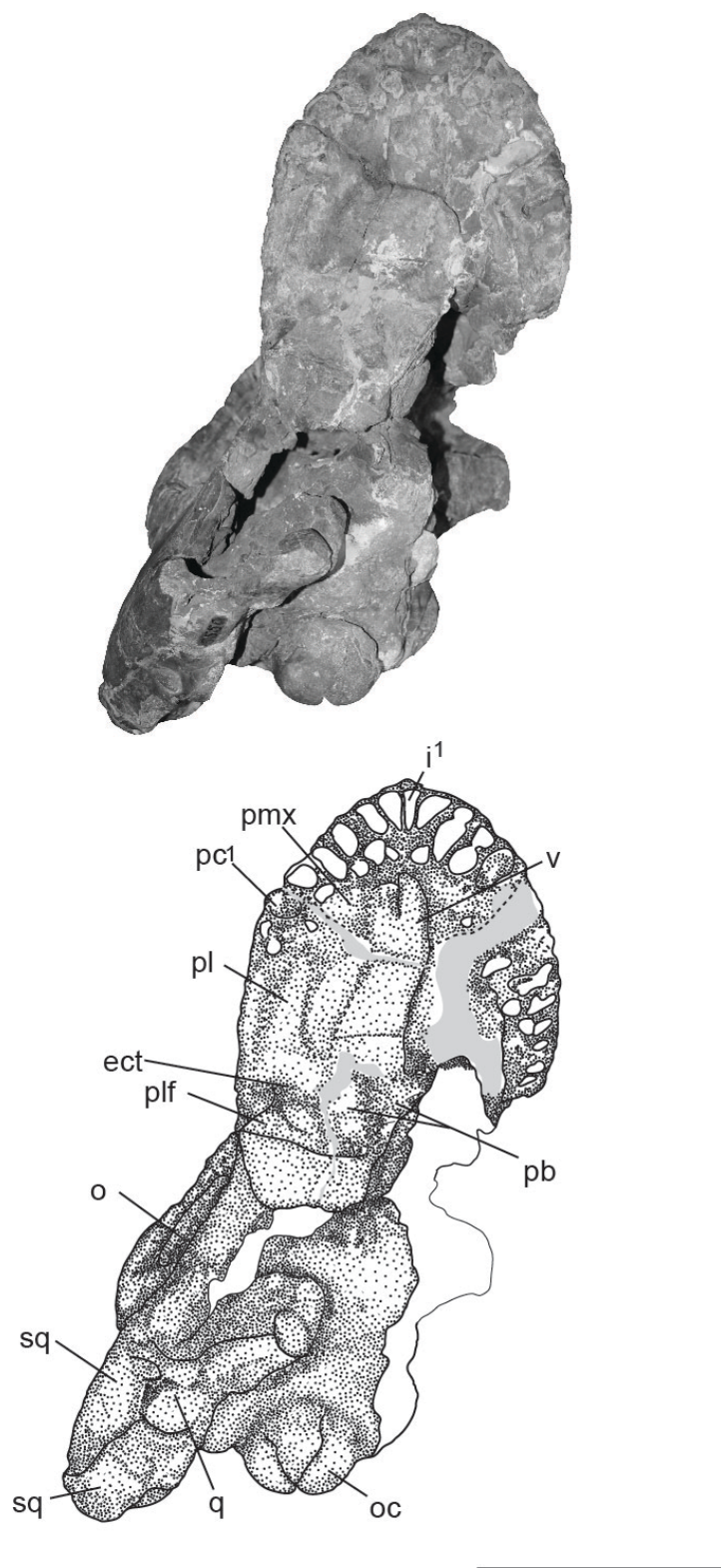


Figure 6. 27. *Moschops*: photograph (top) and illustration (bottom) of the palatal view of AMNH FARB 5550 (holotype of *M. capensis*). Scale: 10 cm.

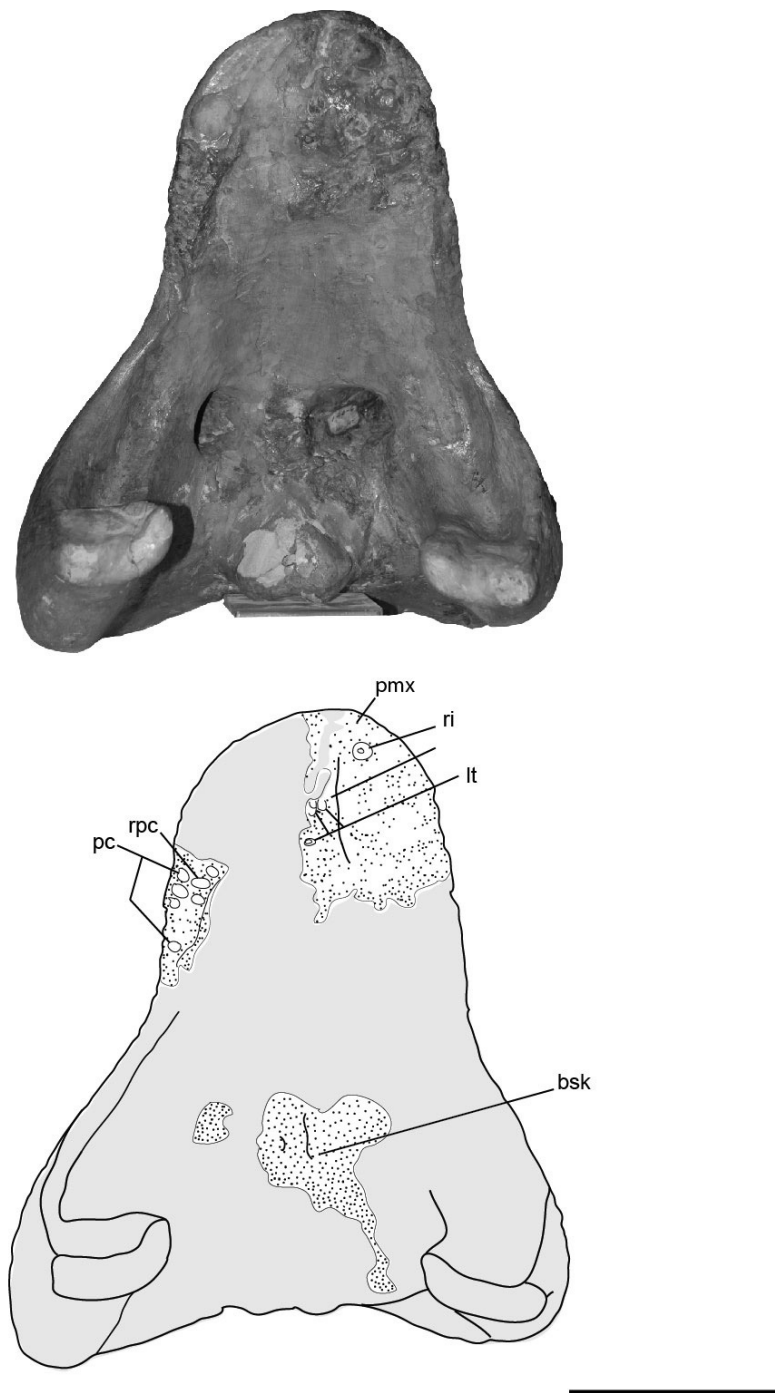


Figure 6. 28. *Moschops*: photograph (top) and illustration (bottom) of the palatal view of AMNH FARB 5552. Scale: 10 cm.

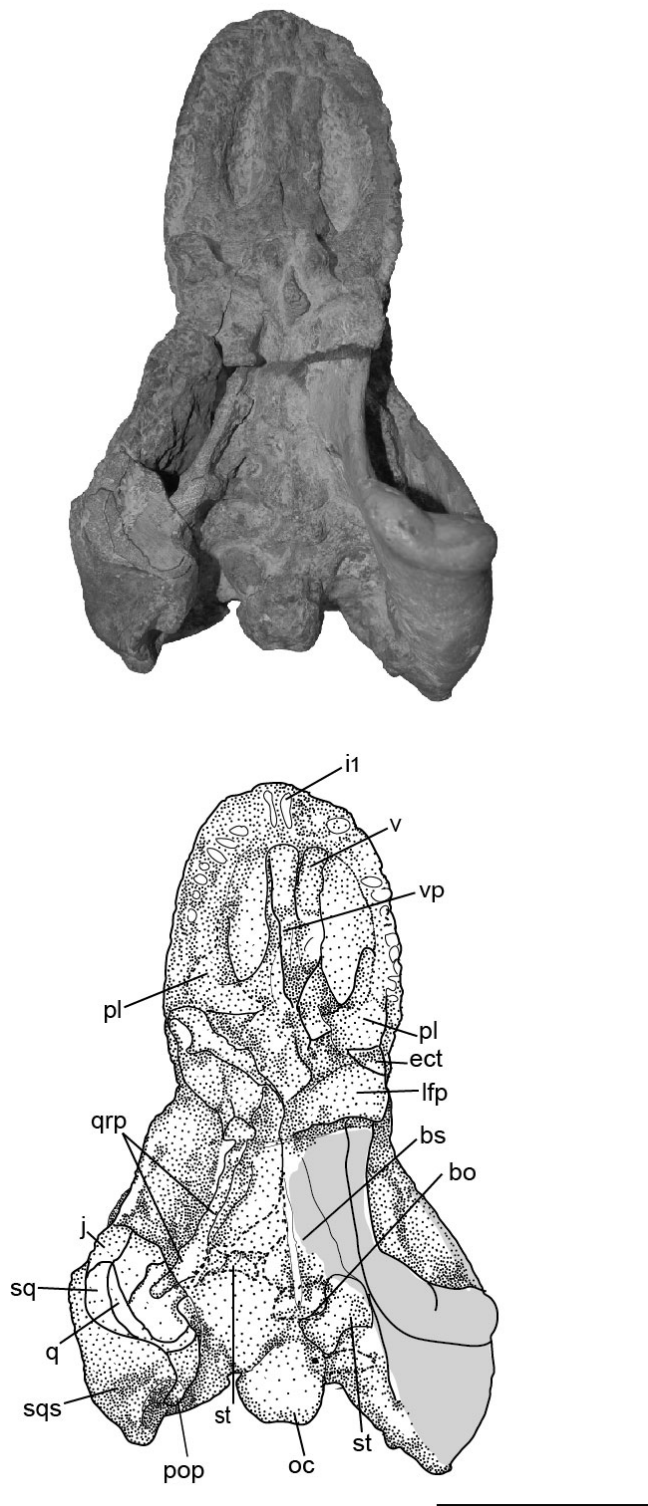


Figure 6. 29. *Moschops*: photograph (top) and illustration (bottom) of the palatal view of AMNH FARB 5553. Scale: 10 cm.

Parabasisphenoid: The parabasisphenoid (Figs. 6.29, 6.32-6.33) is a triangular bone which anteriorly is in contact to the pterygoid, while posteriorly it contacts the basioccipital. It is best preserved in SAM-PK-11582. Posteriorly it forms a pair of lateral tuberae which unite medially along a keel like midline ridge as preserved in AMNH FARB 5553 and SAM-PK-11582, and is less prominent in KNPIV. Although the bone is not well preserved, the midline ridge is also visible in SAM-PK-0713. The posterior end of the parabasisphenoid is broad and has a transverse sutural contact with the basioccipital toward the posterior end of the fenestra ovalis such that the parabasisphenoid forms the largest portion of the fenestra ovalis as is evident in KNPIV and SAM-PK-11582. The opening for the internal carotid artery is situated anterior to the basisphenoidal tubera, and for the external carotid it is lateral to the tubera.

Stapes: A poorly preserved stapes is present in specimens AMNH FARB 5553, KNPIV and SAM-PK-11582 (Figs. 6.29, 6.32- 6.33). It has an anteriorly rounded proximal end which is positioned in the fenestra ovalis, a slender posterodorsally projecting portion which does not manifest a stapedia foramen in any of the specimens, and a distal footplate which articulates with the medial condyle of the quadrate.

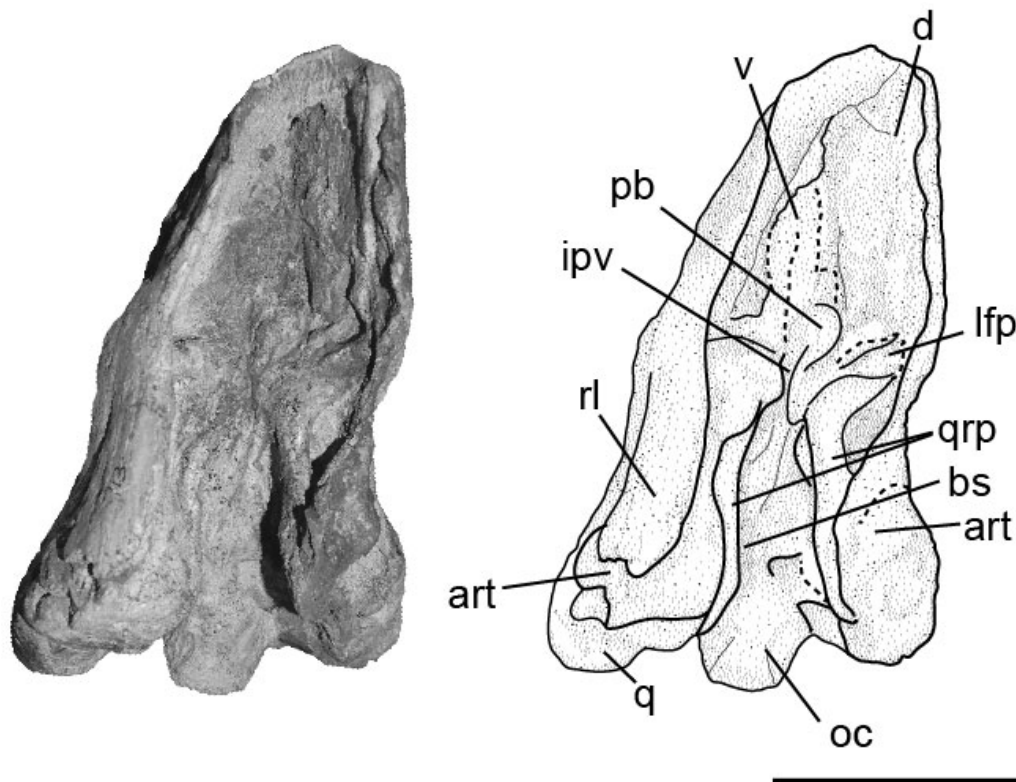


Figure 6.30. *Moschops*: photograph and illustration of the palatal view of SAM-PK-0713 (holotype of *Delphinognathus conocephalus*). Scale: 10 cm.

Quadrate: As is typical for tapinocephalid dinocephalians, the flat dorsal process of the quadrate is positioned anterior to the ventral process of the squamosal, and the quadrate has a lateral and medial condyle for articulation with the lower jaw. A stapedial groove is present between the dorsal process and the medial condyle of the quadrate to receive the distal end of the stapes which is preserved on the right side of SAM- PK-11582 and left of KNP IV (Figs. 6.31- 6.32). The quadrate ramus of the pterygoid articulates with the medial surface of the medial articular condyle.

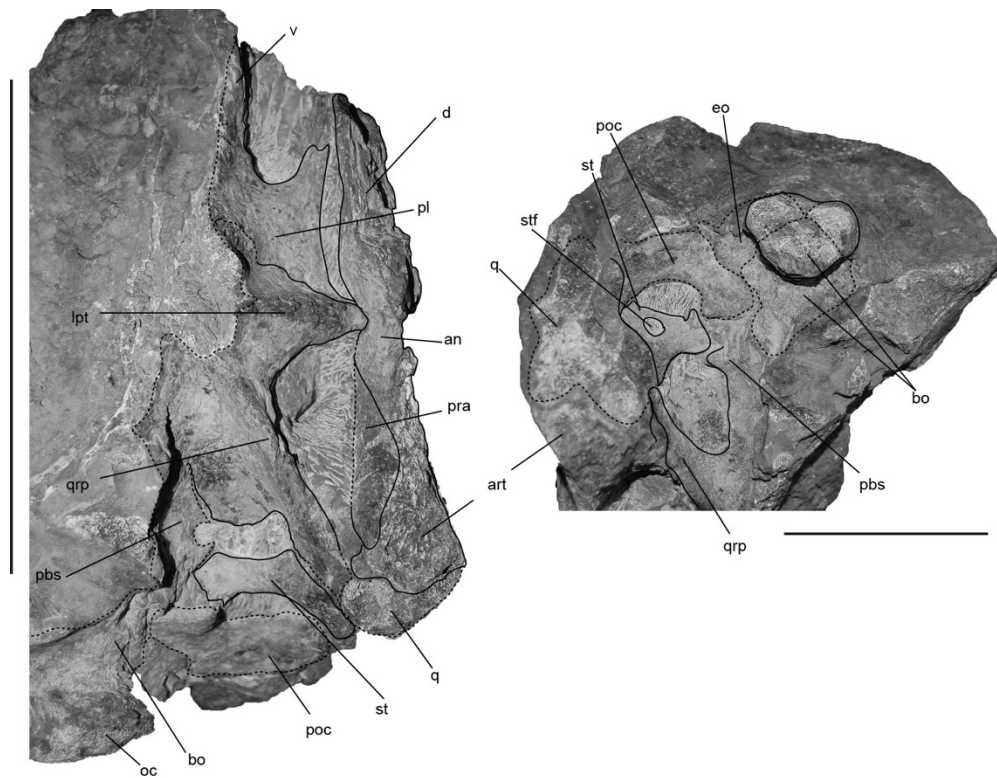


Figure 6. 31. *Moschops*: photograph and interpretative drawing of the palatal and basicranial view of KNPI.

Quadratojugal: The quadratojugal is a small triangular plate-like bone, is overlapped by the squamosal, and medially is in contact to the quadrate as can be seen in SAM-PK-11582 and SAM-PK-0713. While the plane of the quadratojugal is almost parallel to the posterior end of the jugal a large notch is present in the jugal. A quadrate foramen is typically present between the quadratojugal and the dorsal process of the quadrate.

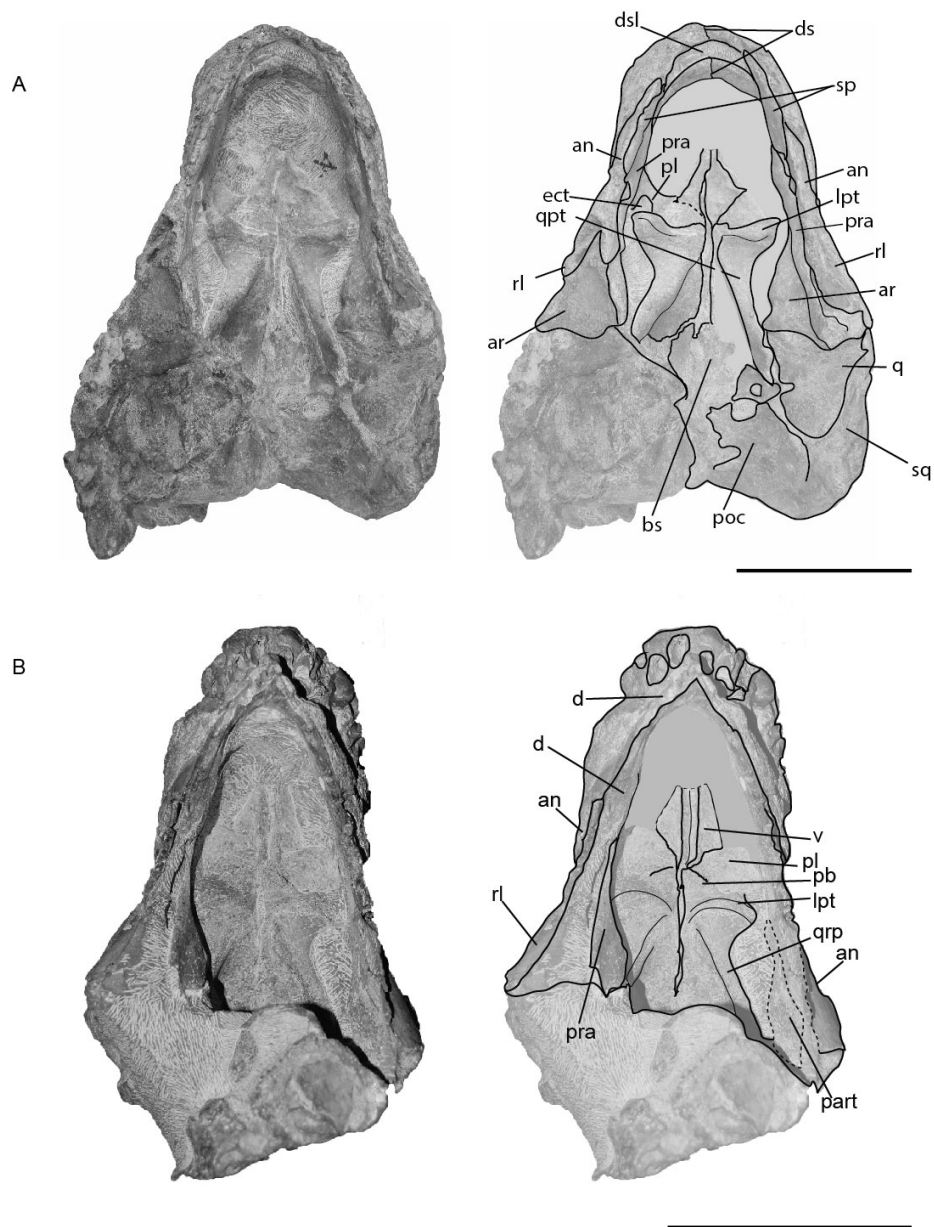


Figure 6.32. *Moschops*: photograph and interpretative drawing of the palatal and basicranial view of KNPIV (top). And KNPII (below). Scale: 10 cm.

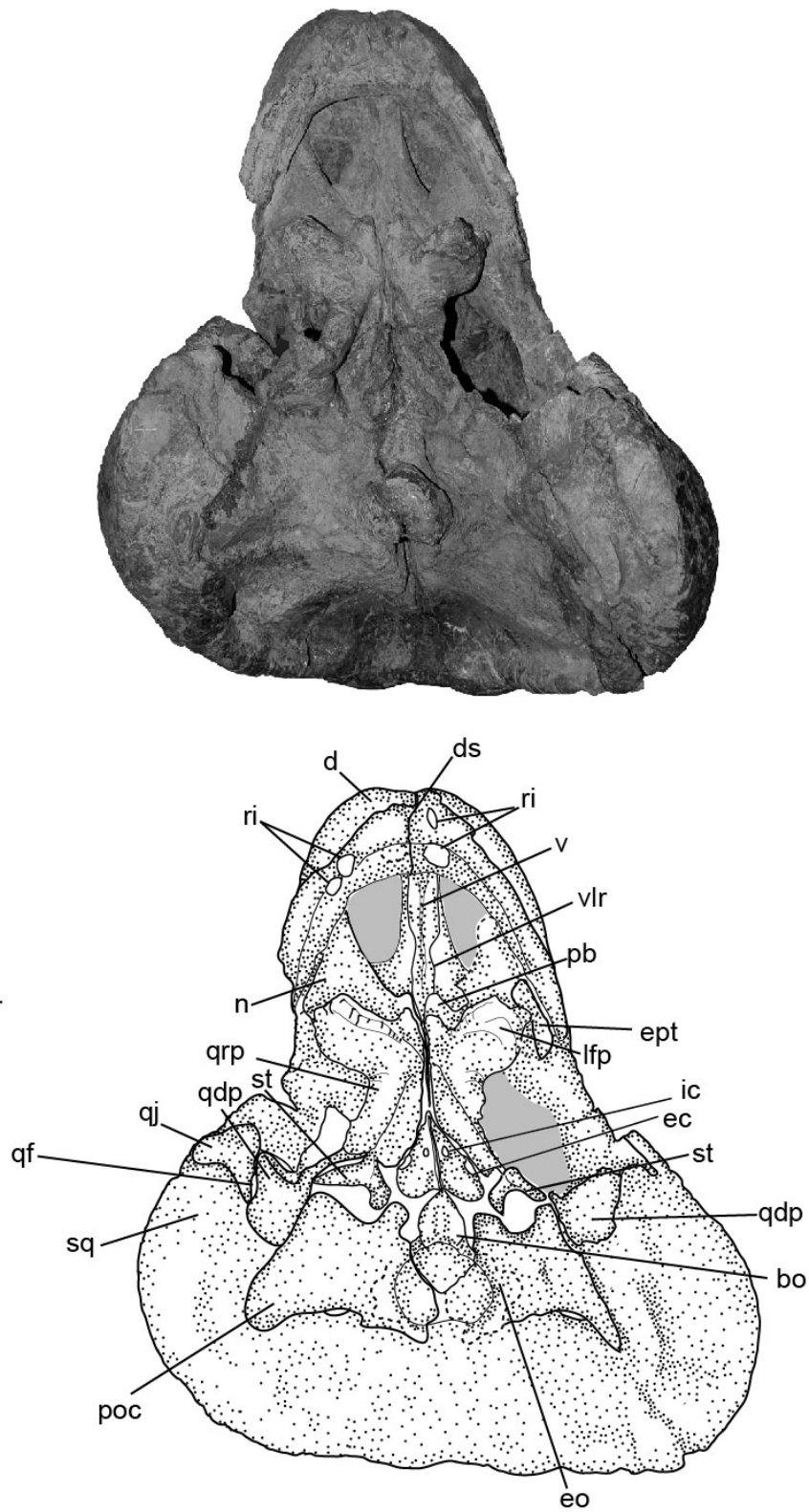


Figure 6. 33. *Moschops*: photo and illustration of the palatal view of SAM-PK-11582 (holotype of *M. koupensis*). Scale: 10 cm.

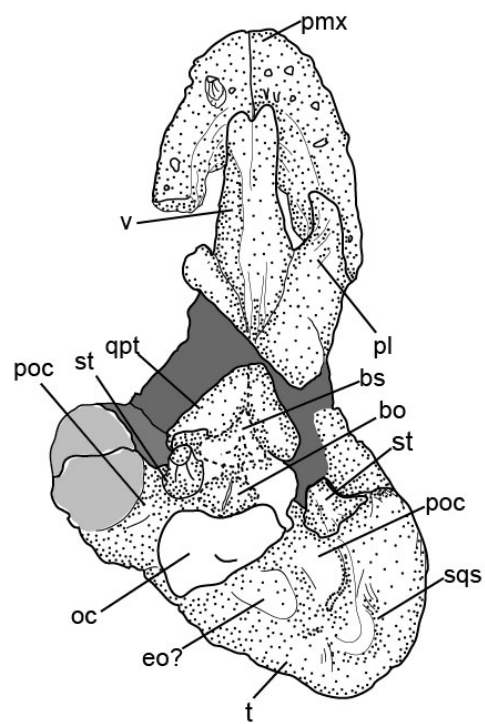


Figure 6. 34. *Moschops*: photograph and illustration of the palatal view of SAM-PK-K319. Scale: 10 cm.

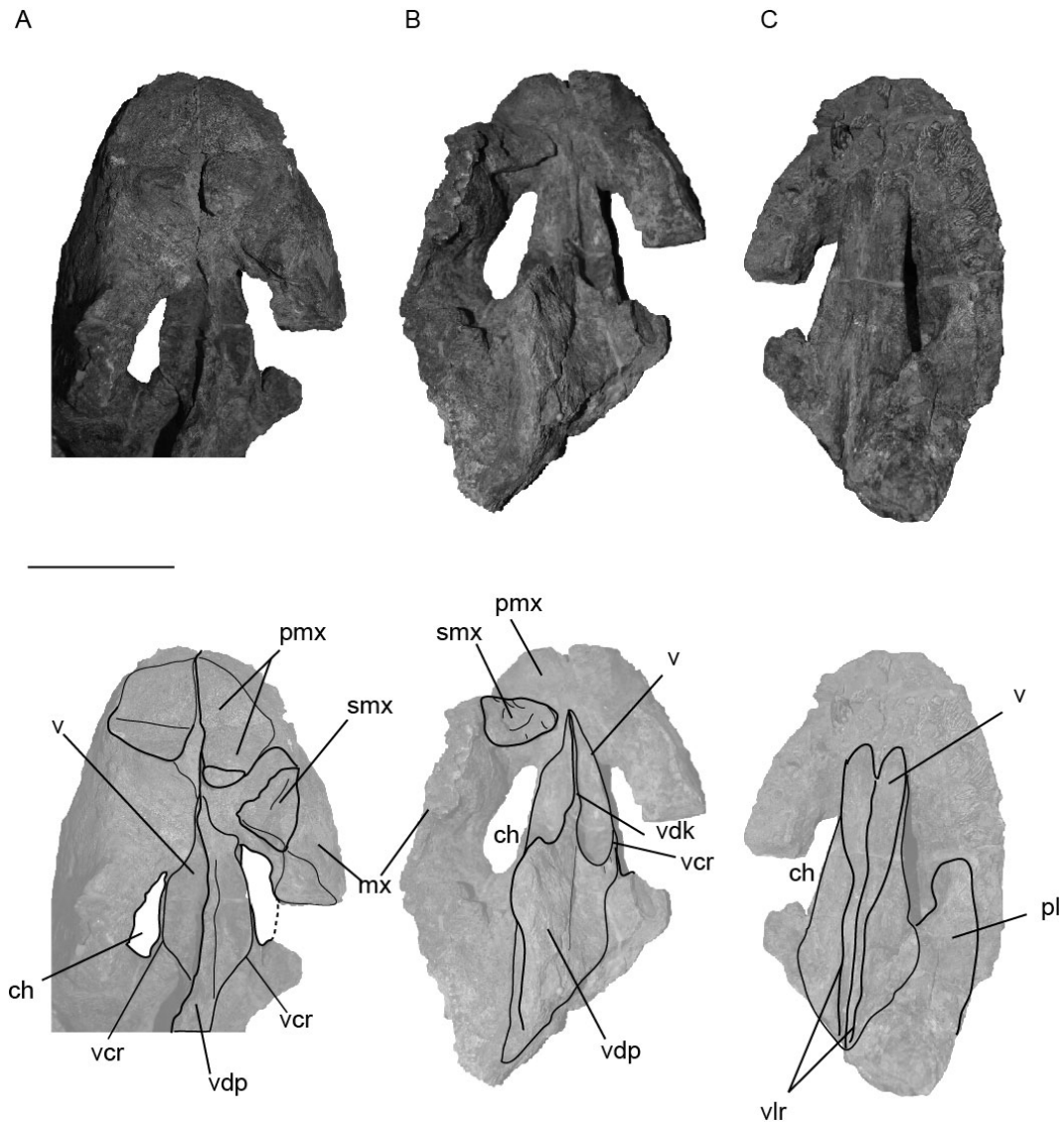


Figure 6.35. The vomer and portion of the footplate of the septomaxilla of SAM-PK-K319: A and B show dorsal views of the vomerine area and C shows the ventral view. Scale: 5 cm.

6.4.3.6 Lower jaw

The following skulls of *Moschops capensis* are preserved with a lower jaw: AMNH FARB 5550, AMNH FARB 5553, SAM-PK-K319, KNPI, KNPII, KNPIII, KNPIV, SAM-PK-0713, SAM-PK-11582 (Figs. 6.36- 6.39). The mandibles of the first three specimens are relatively complete.

Mandibles of AMNH FARB 5550 and AMNH FARB 5553 are preserved articulated to the skull and large parts of the mandible have been reconstructed in plaster. AMNH FARB 5555 (a and b) comprises mandible fragments from two individuals. The left mandible of SAM-PK-K319 is well preserved and complete and includes a small anterior portion of the right dentary. Typically for dinocephalians the lower jaw comprises the dentary, splenial, angular, surangular, prearticular and articular bones, but a coronoid is not present in any of the specimens.

Dentary: The dentary forms almost half of the lateral surface of the mandible (Figs. 6.36B,D, 6.37A,D, 6.38A,C,E, 6.39B) which is smaller in proportion than that of *Tapinocaninus*, *Ulemosaurus* and *Moschognathus*. In these forms the lower jaw is relatively longer and the dentary covers almost two-thirds of the lateral surface of the mandible.

On the lateral surface, the dentary forms the anterior part of the lower jaw and is in contact with the angular ventrally and posteriorly, and with the surangular posterodorsally by means of an inclined suture extending anteroventrally from the coronoid eminence. On the medial side it has a long horizontal ventral sutural contact with the splenial and is overlain by the prearticular posteromedially. Posteroventrally it has sutural contact with the angular and posterodorsally with the surangular. Half way along the lower jaw the angular forms a wedged contact between the dentary laterally and the splenial on the lateral side as is evident in SAM-PK-K319.

The alveolar surface of the dentary is preserved in AMNH FARB 5550, AMNH FARB5553, AMNH FARB5555 and SAM-PK-K319. In these specimens there are few fully erupted incisiform teeth. In AMNH FARB 5550, there are small rounded tips of two emerging crowns anteriorly on the left mandible and one large not completely emerged crown which has a long enlarged talon on the right mandible. In AMNH FARB 5553, one large crown base (talon and heel are lost) is visible on the right mandible. In the right mandible of AMNH FARB 5550 there are nine alveoli and one large rounded empty socket is preserved anteriorly on the left mandible of AMNH FARB 5553. In this specimen there are replacement teeth at different stages of eruption: the pair of teeth which have a labiolingually elongated crown and are located close to the dentary symphysis are interpreted as the first dentary teeth. In the upper jaw of SAM-PK-K319, there is one replacement incisor and this is for the third incisor. This tooth is not completely erupted and reveals the heel and partial talon. The tooth lingually forms two prominent ridges that extend from the apex of the talon and diminish ventrally closer to the heel edge. The edges of the heel are mostly weathered away but the lateral edges show partial preservation and they are serrated. In the lower jaw of the same specimen there two emerging dentary crowns anteriorly on the left and two on the right which are preserved with the tips of their talons broken.

In medial view the dentary has a wide shelf-like anterodorsal extension which slopes posteroventrally and houses the splenial symphysis which is preserved only in SAM-PK-K319.

Angular: The angular (Figs. 6.36B-E, 6.37D-E, 6.39) is exposed on both the lateral and the medial surfaces of the lower jaw as is evident in SAM-PK-K319, AMNH FARB 5550, AMNH FARB 5553, KNPIV and KNPII. On the lateral surface it has a an antero-ventrally sloping sutural contact with the dentary and has a large reflected lamina which extends posteriorly and ventrally as far as the ventral margin of the lower jaw. The lateral surface of the lamina is smooth and its posterior margin is rounded.

In ventral view the anterior end of the angular is wedged between the splenial medially and dentary laterally, as is evident in KNP1, KNP4 and SAM-PK-K319. The contact between the angular and the splenial continues posteromedially until the bones meet the prearticular posterodorsally about half-way along the lower jaw.

Surangular: The surangular forms most of the posterodorsal part of the mandible and makes up the coronoid eminence. On the dorsolateral surface the surangular forms a laterally projecting ridge separating it from the angular.

Splenial: The splenial (Figs. 6.32A, 6. 39A,C), as is evident on the left mandible of SAM-PK-K319, is a plate-like bone, on the medial and posteroventral surfaces of the dentary symphysis, and broadens as it extends posteriorly half way along the medial surface of the lower jaw where it meets the prearticular. Here it thins posteroventrally to a ventral spur which contacts the angular and prearticular. Strangely the splenial is not preserved in the most of the subadult skulls (AMNH

FARB 5550, 5553, KNPI, KNPII, KNPIII) except SAM-PK-0713, KNPIV. As in *Moschognathus*, but in contrast to *Tapinocaninus* and *Ulemosaurus*, the posterior margin of the splenial forms only a single spur which is equivalent to the dorsal spur in *Tapinocaninus*. The surface of splenial, in contrast to that of *Moschognathus* and *Tapinocaninus*, is not flattened and it is thick and its anterior ventral margin is subhorizontal as in *Tapinocaninus*, and does not slope posteroventrally as in *Moschognathus*.

Prearticular and articular: The prearticular is an anteroposteriorly elongated bone that covers more than half of the medial surface of the lower jaw. Anteriorly it overlies the medial surface of the dentary and has a wedged anterior contact between the dentary and splenial. It curves posteroventrally as it contacts the surangular dorsally and angular ventrally, and extends posteriorly to meet the articular and has a short contact with the dorsal surface of the angular. An elongated trough-like adductor fossa is present between the surangular and prearticular's medial surface as is evident in AMNH FARB 5550, AMNH FARB 5553 and SAM-PK-K319.

The angle of the posteroventral curve of the posterior end of the prearticular relative to the anterior end is less in subadult (AMNH FARB 5550, AMNH FARB 5553) than adult (SAM-PK-K319) specimens. Similar to SAM-PK-K319, a large angle is also present in the adult holotype specimens of *Tapinocaninus* and *Ulemosaurus*, but a smaller angle is manifest in the holotype specimens of *Moschognathus* and *Riebeeckosaurus*, which do not appear to be juveniles.

The articular is positioned between the surangular laterally, prearticular anteromedially and both the prearticular and angular along its ventral border. Its dorsal surface exposure is triangular with the apex pointing anteriorly between the medial surface of the surangular and prearticular marking the end of the slit-like fossa formed parallel to the posterior portion of the prearticular's medial surface. Posteriorly the articular expands to form two rounded articular fossae separated by a thick ridge. The hooked retroarticular process is best preserved in SAM-PK-K319 and is also preserved in AMNH FARB 5553, AMNH FARB 5550 and KNP4.

6.4.3.7 Dentition

Several *Moschops* specimens have teeth preserved *in situ*, but as most of these are preserved with occluded jaws, it is difficult to study the dentition. In most of the specimens which have upper and lower jaws separated, the teeth have either fallen out of their alveoli (eg. AMNH FARB 5550, AMNH FARB 5552, AMNH FARB 5553, SAM-PK-K319) or have only partial preservation of labial views as in SAM-PK-11582, KNPIV, KNPIII (Fig.5.41). The best preserved *Moschops* teeth are those of KNPIV (Fig. 5.41A1-A2) which manifest postcanine crown morphology in labial view.

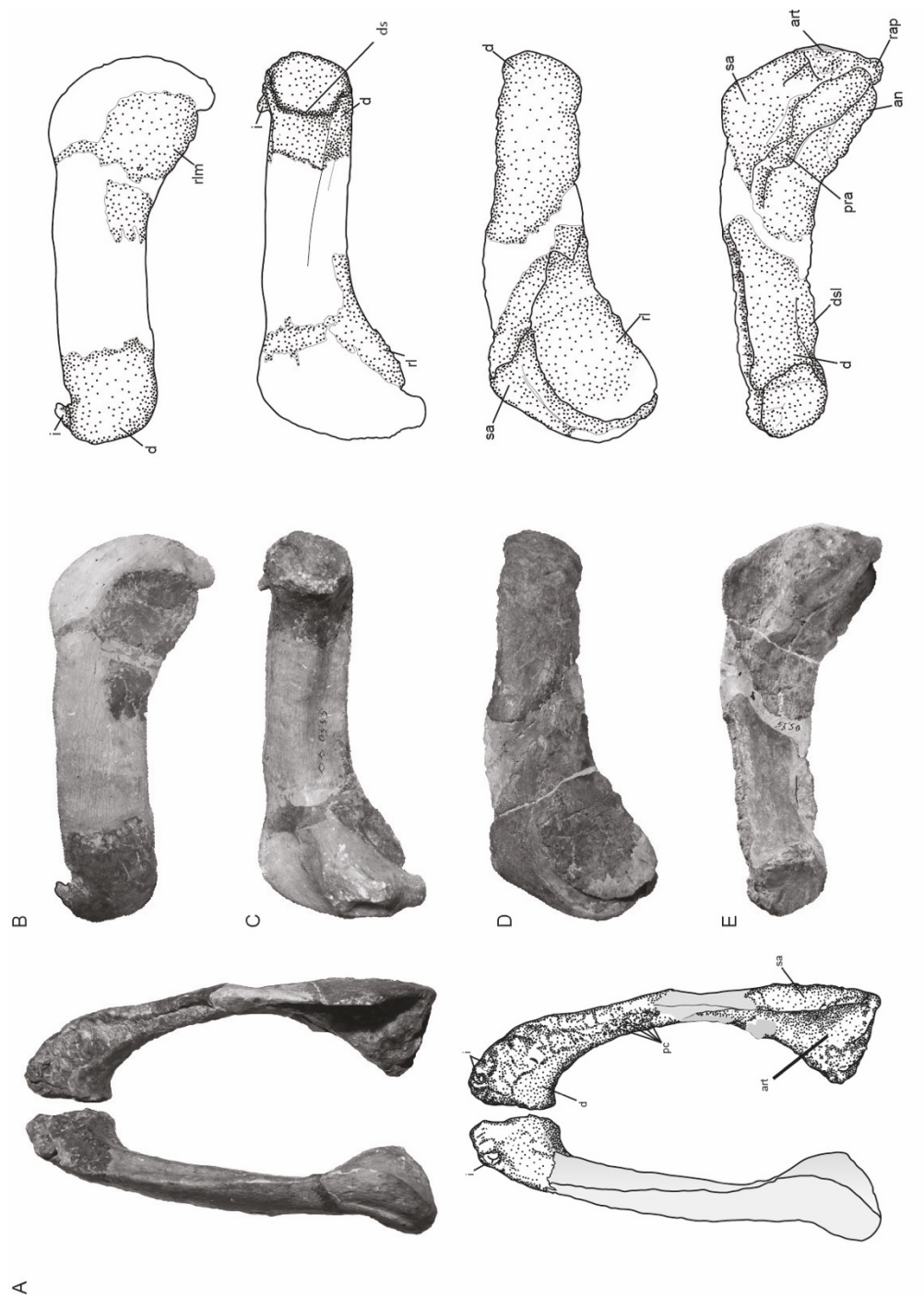


Figure 6. 36. *Moschops*: photograph and illustration of the lower jaw of AMNH FARB5550: dorsal (A), left lateral (B), medial (C), right lateral (D) and medial (E) views. Grey shaded areas indicate plaster reconstruction. Scale:10 cm.

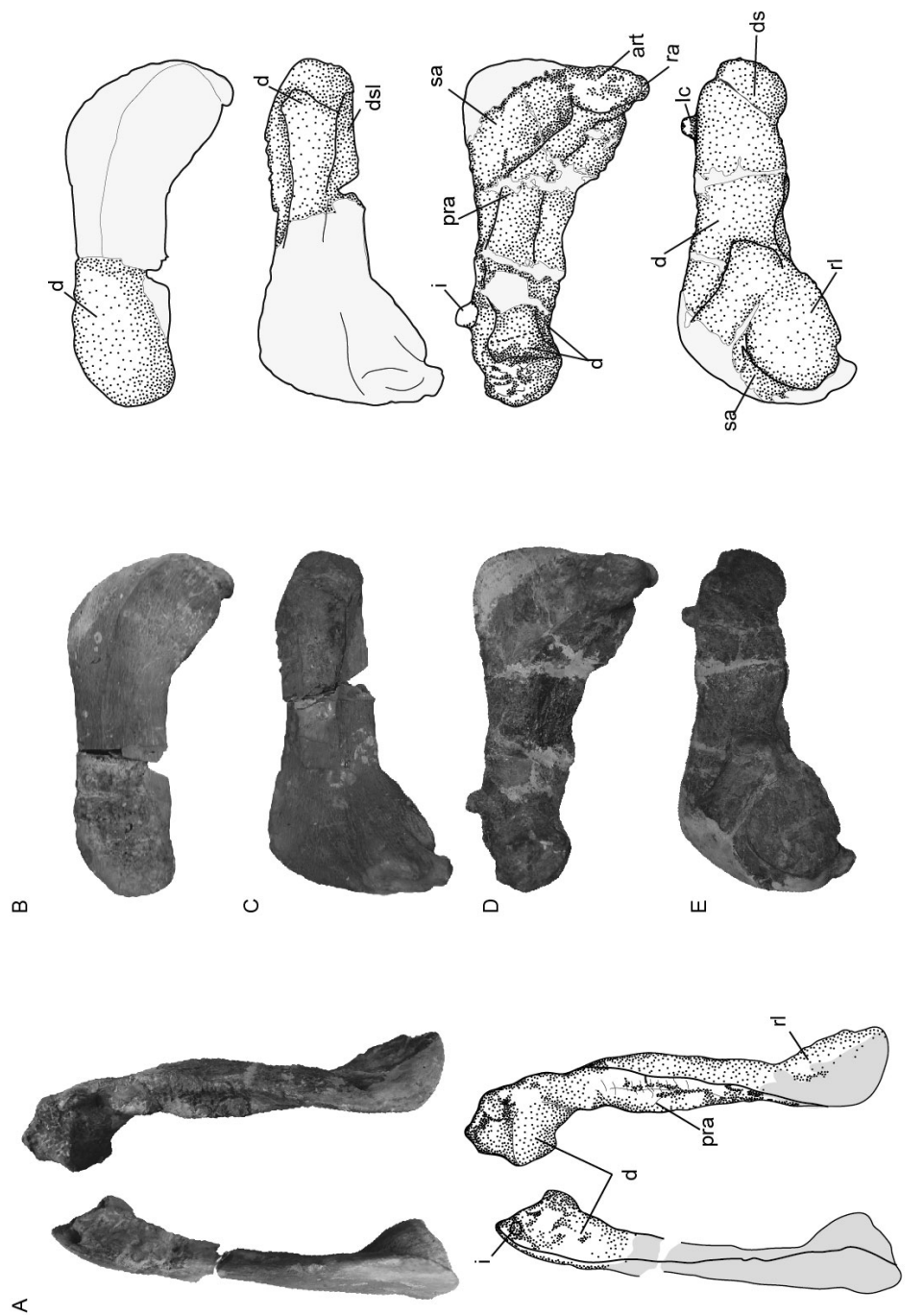


Figure 6.37. *Moschops*: photographs and corresponding illustrations of AMNH FARB 5553 lower jaw: dorsal (A), left lateral (B) medial (C), right lateral (D) and medial (E) views. Grey shaded areas indicate plaster reconstruction. Scale: 10 cm.

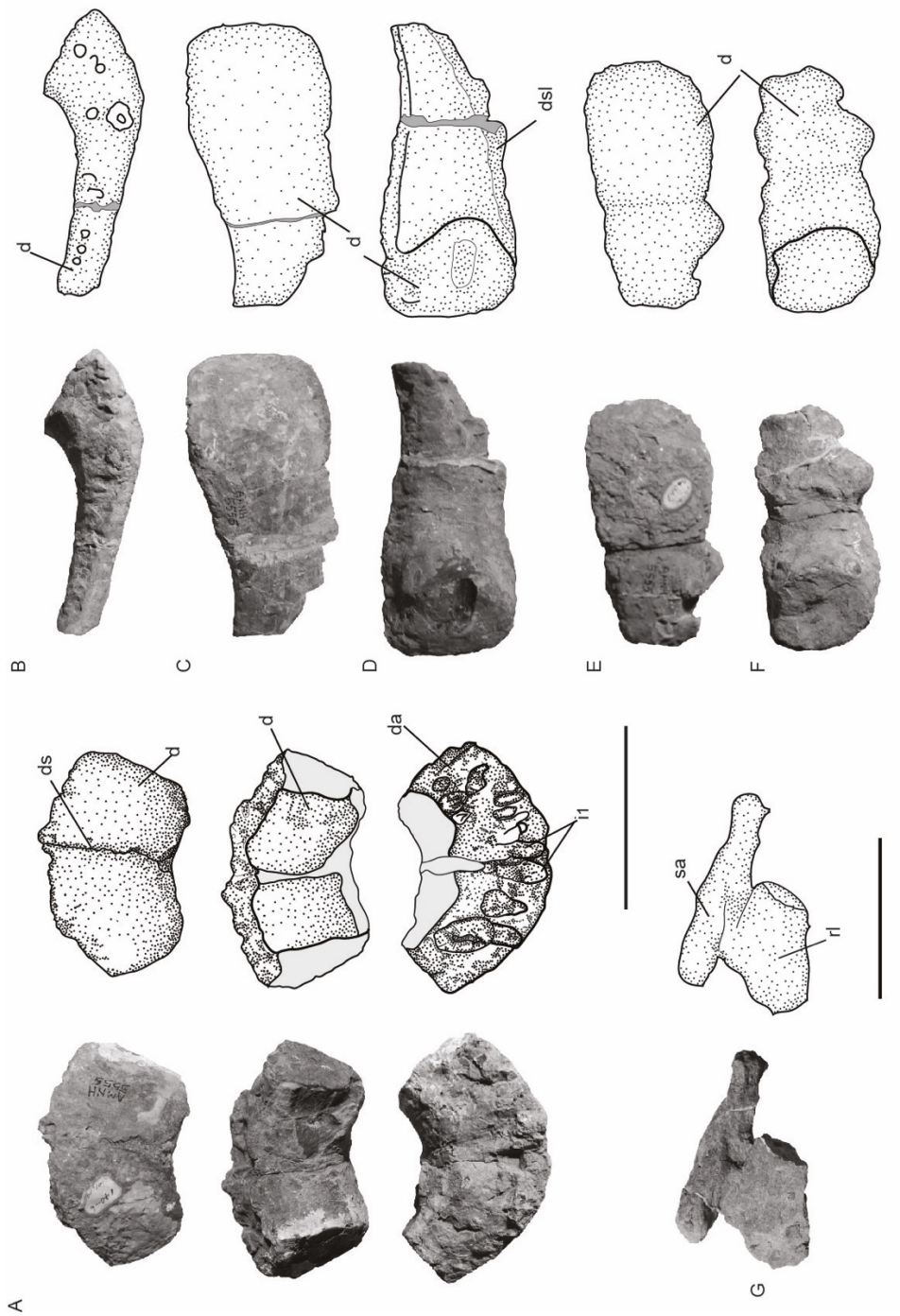


Figure 6.38. *Moschops*: photographs and illustrations of the lower jaw of AMNH FARB 5555: dorsal view of mandible (A), lateral view of left mandible (B), medial view of left mandible (C), medial view of right mandible (D) and lateral view of right mandible (E). Scale: 10 cm.

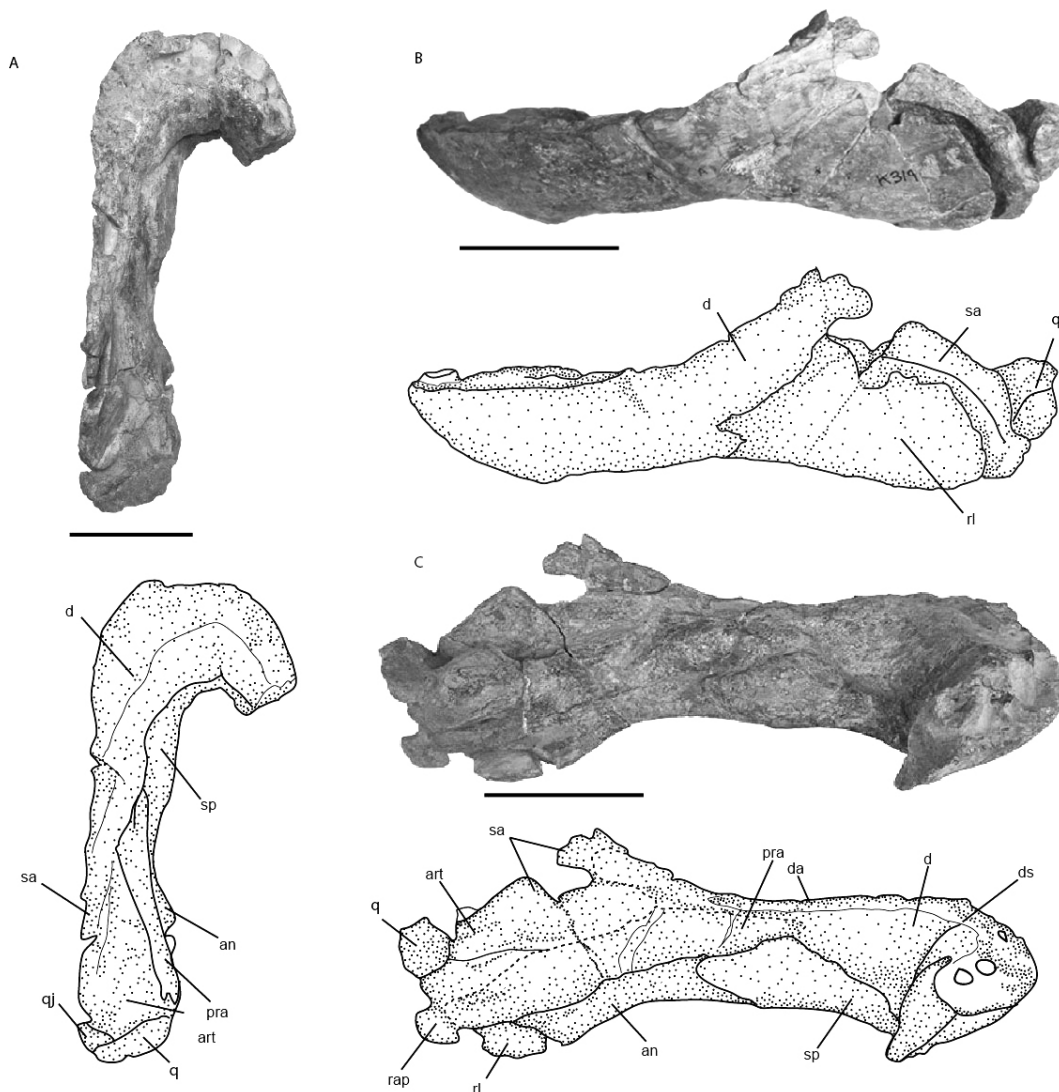


Figure 6. 39. *Moschops*: photograph and illustration of SAM-PK-K319 lower jaw: (A) dorsal, (B) lateral and medial (C) views. Scale: 10 cm.

Incisors: Four incisors are present on the premaxilla and three on the dentary as is evident in KNPIV, KNPIII and SAM-PK-11582. The morphology of the incisors is not clearly demonstrated as they are preserved in occlusion with their labial views which are also quite damaged. The first upper incisor has narrow mesiodistally elongated crown morphology. Also the alveoli of the first pair in

AMNH FARB 5550 exhibits the typical mesodistally elongated root morphology of the first incisors in tapinocephalids.

In SAM-PK-K319, a single fully erupted replacement crown (with a broken talon tip) is exposed and it is probably the replacement for the third right premaxillary tooth. The heel is inclined anteriorly and heel margins are denticled.

Postcanine: Posterior to the single canine (first tooth of the maxilla) the maxilla bears the tips of replacement teeth and/ or alveoli pits of six to eleven postcanines (six in SAM-PK-K319; AMNH FARB 5550, eight in AMNH FARB 5553 and 12 in KNPIV). The largest postcanine teeth are positioned anteriorly and they progressively decrease in size posteriorly. In this specimen while the postcanines which are positioned more anteriorly on the jaw are larger in size, they are exposed in lateral profile and show talon and heel morphology. The first five anterior maxillary teeth intermesh with the corresponding four dentary teeth. The outline of the crowns of the posterior postcanines (*see*. Teeth 8 to 12 in Fig. 6.40A1) are in leaf-like and triangular, and they are anteroposteriorly aligned.

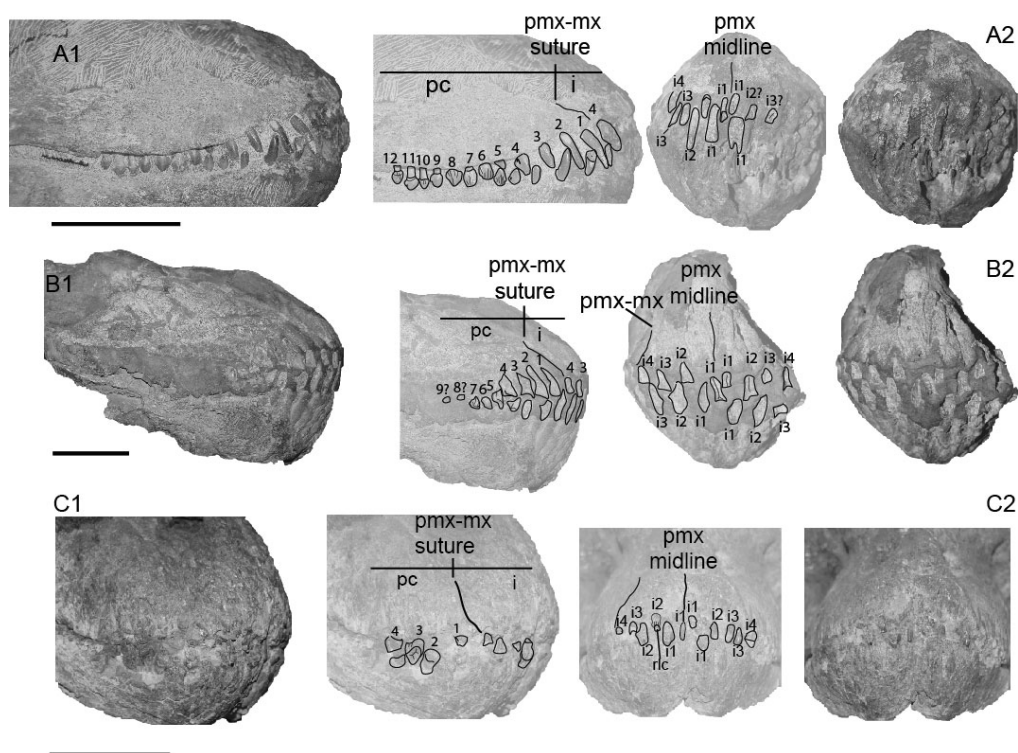


Figure 6. 40. *Moschops* skulls with upper and lower jaw occluded seen in the lateral (A1, B1, C1) and anterior view (A2, B2, C2) in KNPIV (A1-2), KNPIII (B1-2) and SAM-PK-11582 (C1-2), Scale bar: 5 cm.

6.4.4 Comparison of the holotypes of *Moschops capensis*, *Moschops koupensis*, and *Delphinognathus conocephalus*.

As a result of extensive comparative research of all available moschopid material it is concluded that *Moschops koupensis*, and *Delphinognathus conocephalus* should be synonymized with *Moschops capensis*. The following section explains why these are considered conspecific, and provides a brief comparative description of AMNH FARB 5550, the holotype of *Moschops capensis*, SAM-PK-11582 the holotype of *Moschops koupensis*, and SAM-PK-0713 the holotype of *Delphinognathus conocephalus*. For the purpose of consistency of comparison this description excludes bones which are present in only one of the skulls.

SAM-PK-0713 (*Delphinognathus*) is the smallest skull with a cranial length of 270 mm (as the specimen is incomplete the measurement was taken between the most anterior and most posterior parts of the snout). Removal of matrix sediment from the palatal area revealed that more than half of the vomer is preserved indicating that very little of the snout is missing. AMNH FARB 5550 (*Moschops capensis*) with cranial length of 292 mm is intermediate in size, and SAM-PK-11582 (*Moschops koupensis*) with a length of 325 mm is the largest. AMNH FARB 5550 and SAM-PK-11582 have short snouts, 42,5% of the skull length in AMNH FARB 5550, and 46,75 % in SAM-PK-11582. Neither the postorbital nor the preorbital portion is preserved completely in SAM-PK-0713, thus it is not possible to provide an accurate snout length ratio for this skull but the proportion is similar to that of AMNH FARB 5550.

The snout of SAM-PK-0713 is incompletely preserved which does not enable reliable comparison with the other skulls, but all three skulls have narrow and dorsoventrally deep snouts. The transition from the skull roof to the snout on the top of the skull slopes gently and is not steep in all three specimens. All three skulls have a narrow interorbital region and narrow intertemporal breadth except SAM-PK-11582 (largest skull) which has an intertemporal width broader than its interorbital width. Cranial pachyostosis of the smaller skulls AMNH FR5550 and SAM-PK-0713 is relatively light relative to that of the larger SAM-PK-11582. Pachyostosis in the latter skull is well developed on the cranial roof, postorbital bar and the zygoma. The smaller skulls (AMNH FARB 5550 and SAM-PK-0713)

have a relatively large temporal fenestra, whereas that of SAM-PK-11582 is anteroposteriorly smaller as a result of thickening of the circumfenestral bones. The position of the jaw joint, which is around the level of posterior border of the postorbital bar in the smaller skulls (SAM-PK-0713 and AMNH FARB 5550), is situated further anteriorly in the larger SAM-PK-11582.

The anterior bones of the skull roof are best preserved in AMNH FR5550 and SAM-PK-11582. SAM-PK-0713 shows partial preservation of a few premaxillary teeth.

The nasal is preserved completely in SAM-PK-11582, while only the posterior portion is preserved in AMNH FARB 5550. In SAM-PK-0713 there is partial preservation of the posterior part of the left nasal. Anteriorly the nasal forms the dorsal border of the external naris, ventrally it has a long contact with the maxilla, posterolaterally it meets the prefrontal and the frontal posteromedially. In all the skulls the nasal bifurcates at its contact with the frontal at the mid-orbital level. Posteriorly the midline of the nasal is slightly depressed in SAM-PK-11582, and is swollen in AMNH FARB 5550 and SAM-PK-0713.

The maxilla is the largest bone on the lateral surface of the skull and is a dorsoventrally deep triangular bone in both AMNH FARB 5550 and SAM-PK-11582. Only a very small portion of the left maxilla is preserved in SAM-PK-0713. In AMNH FARB 5550 and SAM-PK-11582 the maxilla has an elongated horizontal depression in the upper regions. In both these skulls the premaxilla-

maxilla suture extends from the ventrolateral margin of the external naris to the alveolar border of the snout between the last incisor on the premaxilla and the first maxillary tooth. AMNH FARB 5550 preserves the alveoli of eight maxillary teeth. The anterior teeth are transversely elongated whereas the more posterior teeth are smaller and rounded in cross section. In SAM-PK-11582 two intermeshing anterior maxillary teeth crowns are preserved and have relatively small fragmented crowns.

The small quadrangular lacrimal forms the anterior border of the orbit and is in contact with the prefrontal dorsally, the maxilla anteriorly and the jugal ventrally but is not well preserved in AMNH FARB 5550 and on the left side of SAM-PK-0713. In SAM-PK-11582 a slight depression is present along its suture with the prefrontal as a result of thickening of the prefrontal.

The jugal, which has a short anterior and long posterior extension, forms the ventral border of the orbit. The anterior extension of the jugal is not preserved in all skulls; while its posterior extension is preserved only in SAM-PK-0713 and SAM-PK-11582. The posterior portion of the jugal extends along the ventral side of the squamosal as far as the notch in the squamosal. At the posteroventral end of the skull the squamosal forms a notch where the posteriorend of the jugal and the quadratojugal meet. This notch between the posterior end of the jugal and the quadratojugal is almost lost in SAM-PK-11582. Also, the posterior end of the jugal bone in SAM-PK-0713 forms a sharp corner before it turns posterodorsally into the cut out of the squamosal. This corner is also lost in SAM-PK-11582 and

the posterior portion of the jugal bone is in the form of narrow thickened stout bone lying under the squamosal.

The remaining skull roof bones (prefrontal, frontal, postfrontal, parietal, squamosal) are preserved in all three skulls. The squamosal forms the most of the zygoma posteriorly and contributes to both the lateral and the occipital views of the skull. In AMNH FARB 5550 and SAM-PK-0713 the squamosal is thin whereas in the larger SAM-PK-11582 it is thickened. The squamosal forms the posterior margin of the temporal fenestra and is slender in AMNH FARB 5550 and SAM-PK-0713. Conversely it is very thickened and rounded in SAM-PK-11582. Also the occipital portion of the squamosal has a greater surface area in SAM-PK11582 than SAM-PK-0713 and AMNH FR5550 and is further positioned in SAM-PK-11582 than it is in SAM-PK-0713 and AMNH FARB 5550 because of the greater anteroventral slope of the occipital surface in the larger skull.

In all three skulls, the prefrontal is large and forms the anterior and anterodorsal border of the orbit. However in SAM-PK-11582 it is thickened and overhangs the lacrimal. The frontal is the largest bone of the cranial roof and has the largest surface area in SAM-PK-11582. In all three specimens the frontal makes a short contribution to the dorsal orbital border and does not form part of the dorsal border of the temporal fenestra. The midline suture in AMNH FARB 5550 and SAM-PK-11582 is depressed, but there is no sign of a depression in SAM-PK-0713.

The triangular postfrontal contributes to the dorsal border of both the orbit and temporal fenestra and is heavily pachyostosed in SAM-PK-11582, in contrast to the two smaller skulls. The parietal forms the posterior end of the cranial roof stretching between the temporal fenestrae and is preserved in all three skulls with an anterior V-shaped contact with the frontal and posteriorly it is in contact to the postparietal. Around the pineal opening the parietal surface is higher than the frontal surface in both AMNH FARB 5550 and SAM-PK-0713 (and is even higher SAM-PK-0713) but is relatively depressed in the main corpus of the bone but thickened on the dorsal border of the temporal fenestra in SAM-PK-11582.

The postorbital forms the lower two-thirds of the postorbital bar in all three specimens and turns medially into the temporal fenestra. It has a dorsal sutural contact with the postfrontal and parietal, and ventrally with the squamosal.

The palate is weathered and poorly preserved in AMNH FARB 5550 and SAM-PK-0713. The vomer is preserved completely in AMNH FARB 5550, but the anterior end is not exposed in SAM-PK-0713 and SAM-PK-11582, and in SAM-PK-0713 only the left portion of the vomer is preserved. Its ventral surface is flat in SAM-PK-0713 and AMNH FARB 5550. Posterolaterally the vomer meets the palatine and posteromedially the pterygoid. The anterior extension of the palatine which extends halfway up the choana is preserved in AMNH FARB 5550 and SAM-PK-11582 and the palatine boss is preserved only on SAM-PK-11582 as a small edentulous reniform projection which is not clearly separate from the small

pterygoid boss. The obliquely arranged transverse flange has a short posterior platform (largest in SAM-PK-11582) from which the quadrate ramus of the pterygoid (which is relatively short and thickened in SAM-PK-11582) extends posterolaterally to meet the medial surface of the quadrate. The ventral surface of the transverse flange is thin in SAM-PK-0713 and AMNH FARB 5550, but is greatly thickened in the larger SAM-PK-11582. The parabasisphenoid and basioccipital complex is well preserved in SAM-PK-11582 but is weathered in AMNH FARB 5550 and SAM-PK-0713.

The quadrate is completely preserved in SAM-PK-0713 but the surface is weathered and in AMNH FARB 5550 and SAM-PK-11582 only the dorsal process is present and is more rounded in SAM-PK-11582 whereas in the other two specimens it is longer and more slender. The quadratojugal is preserved (in SAM-PK-0713 where it is thin, and in SAM-PK-11582 where it is robust) on the lateral condyle of the quadrate and is partially overlapped dorsally by the squamosal and it has a laterally exposed strip like portion under the squamosal. Due to the more anteriorly positioned jaw joint the plane of the quadratojugal is almost parallel to the plane of the jugal's posterior end in the large specimens such as SAM-PK-11582, in the smaller specimens such as SAM-PK-0713 there is a rather large angle between the jugal and quadratojugal.

The outline of the occiput is best preserved in SAM-PK-11582, partially preserved in AMNH FARB 5550 and not preserved in SAM-PK-0713. The occiput of SAM-PK-11582 differs with its larger size and greater degree of cranial

thickening and with a depressed occipital surface. The dorsal and lateral margins of the occiput are incompletely preserved in AMNH FARB 5550 and the occipital surface is rather flat because of the lack of pachyostosis. The supraoccipital is poorly preserved in all three specimens and only the dorsal spur of the supraoccipital is well preserved in all. The dorsal spur of the supraoccipital is thus narrow in the small skulls, and wide and more rounded in SAM-PK-11582. The tabular is a semilunar bone that is best preserved in SAM-PK-11582 and only partially preserved in the rest. Its medial contact with the postparietal (preserved in all except AMNH FARB 5550) is convex in SAM-PK-0713 and forms a straight line in SAM-PK-11582. The exoccipital and opisthotic are not well preserved and the basioccipital bone is best preserved in SAM-PK-11582 and forms the ventral lobe of the tripartite occipital condyle.

Elements of the lower jaw are preserved in all three specimens. The dentary extends over half of the mandible length and contacts the surangular posterodorsally to form the coronoid eminence which is well preserved in SAM-PK-0713 and partially in AMNH FARB5550. A ridge extends on the lateral surface of the angular parallel to the dorsal horizontal suture with the surangular and is partially covered by the reflected lamina which is preserved in SAM-PK-0713 and AMNH FARB 5550. In SAM-PK-0713 a small notch is present on the anterodorsal side and a horizontal depression separates the dorsal one-thirds of the reflected lamina from the ventral two-thirds. This depression is likely caused by prefossilisation deformation. The prearticular of SAM-PK-0713 and AMNH

FARB 5550 are morphologically similar, and the articular is preserved in SAM-PK-0713 and AMNH FARB 5550 but not well exposed.

As is evident from the above description the holotype skulls of *Delphinognathus conocephalus*, *Moschops capensis*, and *Moschops koupensis* are morphologically very similar and differ mainly in the degree of skull roof pachyostosis which is greatest in the holotype specimen of *Moschops koupensis* (SAM-PK-11582) (the largest skull), slightly less developed in AMNH FARB 5550 (*Moschops capensis*), and least developed in SAM-PK-0713 the holotype and only specimen of *Delphinognathus* (the smallest skull). It is thus proposed that these three species should be synonymised and that they represent an ontogenetic growth series (see below).

6.4. 5 Results and discussion

To test the idea that *Moschops capensis*, *M. koupensis* and *Delphinognathus* are conspecific and that their differences are manifestation of ontogenetic growth, all specimens which could be securely identified as *Moschops capensis* were studied to evaluate morphological differences in the holotypes of *Delphinognathus conocephalus*, *Moschops capensis*, and *Moschops koupensis*. *Moschops capensis* skulls included in the analysis are two large specimens (one with complete mandible) and a number of smaller skulls including the type series of *Moschops capensis* which were found together at a single site (AMNH FARB 5550, 5552, 5553, 5555a&b) and the four recently discovered *Moschops* skulls (KNPI-IV) which were also found together. Worth noting is the fact that the individual skulls

(which are morphologically similar) comprising each of the AMNH and KNP groupings are of different sizes and appear to comprise individuals of different ontogenetic age as pointed out previously (*e.g.* Broom, 1911, Gregory, 1926).

Within the type series of *Moschops capensis* (AMNH FARB 5550, 5552, 5553, 5555a&b) and between the type series and the large skulls referred to *Moschops capensis* the following changes occur and are considered to be related to ontogenetic development: An increase in skull size results in thickening of the postorbital bar, zygoma, intertemporal breadth and concomitant size decrease of orbit size and the temporal fenestra. The occipital plate is more anteroventrally tilted in the larger specimens, shifting the jaw joint further anteriorly.

Morphological comparison between the small holotype skulls of *Moschops capensis* and the larger holotype skull of *Moschops koupensis* reveals that the differences are typically the result of ontogenetic cranial thickening. In the description of *Moschops koupensis* (Boonstra 1957), this specimen was considered to differ from *M. capensis* in that the cranial bones of *M. koupensis* are more robust and thickened. Both holotype specimens have a depressed midline on the dorsal surface of the frontal. This feature, while also preserved in the topotype skull of *Moschops capensis* (AMNH FARB 5553), is not observed in the two referred large skulls of *Moschops capensis* where the frontal forms a swollen surface and there is no depression along the frontal midline. Similarly, the dorsal and lateral borders of the occipital crest are much thicker and the anteroposterior diameter of the temporal fenestra relatively shorter in *Moschops koupensis* than

the two large size skulls of *Moschops capensis*. These differences between the large skulls of *Moschops* may be a manifestation of individual, possibly sexual, variation in *Moschops capensis*.

The above description shows that the type skulls of *Delphinognathus conocephalus* and *Moschops capensis* differ in the presence of the higher pineal opening and the large notch on anteroventral corner of the zygoma in *Delphinognathus*. This study of all *Moschops* specimens shows that in the larger specimens, the pineal chimney disappears because of greater cranial pachyostosis around the pineal opening. Of significance is the fact that within the small skulls in type series of *Moschops capensis* there is also a relative difference in the prominence of the pineal opening which appears to regardless of their size and could possibly be indicate to individual variation: *e.g* pineal opening chimney is more prominent in AMNH FARB 5552 than it is in AMNH FARB 5550 even though the AMNH FARB 5552 is relatively larger than the skull. This indicates that because there is less cranial thickening in the small skulls individual variation in this feature is evident which can't be observed in the large sized skulls because it is masked by cranial thickening.

Thus, the fact that the size of the pineal boss differs in the sample of *M. capensis* skulls which all come from the same site, indicates that the size of the pineal boss varies in different specimens of *Moschops capensis* and thus should not be used as a character to differentiate between *Delphinognathus* and *Moschops capensis*.

Another character cited in the literature to differentiate between *Delphinognathus*

and *Moschops capensis* is the presence of a large notch on the posteroventral edge of the squamosal in *Delphinognathus*. This portion of the zygoma is not preserved in any of the *Moschops* holotypes, but is present in the juvenile series of KNP skulls (best in KNPIV) where a large squamosal notch, similar to that in the *Delphinognathus* holotype, is present. The size of this notch becomes smaller as the jaw joint is positioned further anteriorly in larger skulls of *Moschops*, as is the situation in other large tapinocephalid skulls such as *Tapinocephalus* and *Mormosaurus*.

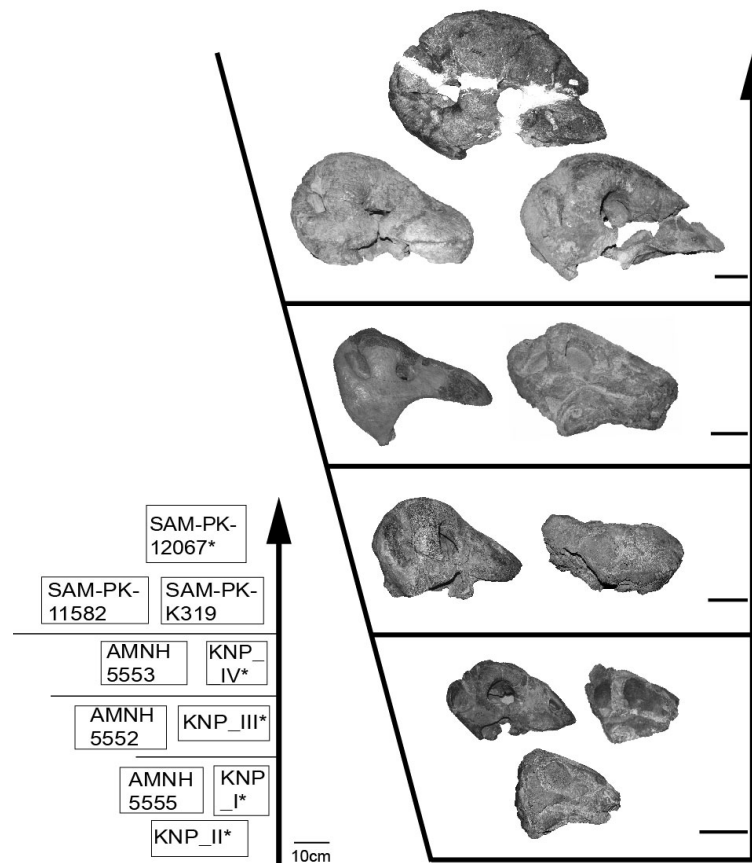


Figure 6. 41. Size and cranial variation within *Moschops capensis* skulls. Collection numbers of the specimens (left) are placed in the same order as in the figure (right). * indicates specimens which the left lateral view is preserved. The arrow indicates size increase.

Another distinguishing character cited in the literature to differentiate between *Delphinognathus* and *Moschops* is the apparently longer snout of *Delphinognathus* (Gregory, 1926, fig. 22, Zittel, 1932, fig. 357A, Boonstra, 1957). The fact that the holotype of *Delphinognathus* preserves remnants of premaxillary teeth as well as a partial dentary symphysis, indicates that the skull was not significantly longer. This conclusion is supported by the fact that the anterior part of the palate is preserved in *Delphinognathus*. The contention of Kammerer (2009) that *Delphinognathus* had a taller mandible than *M. capensis* is unlikely as the skull has suffered lateral compression and the left and right mandibles of the same specimen differ in height.

Accordingly it is proposed that the holotype skulls of *Delphinognathus conocephalus*, *Moschops koupensis* and *Moschops capensis* represent different ontogenetic stages of the same species. The synonymy of *Delphinognathus conocephalus* and *Moschops capensis* would result in *Delphinognathus* having nomenclatorial priority following the article 23.1 of the Code. However, *Moschops* is the best-known and most established dinocephalian species in both in scientific and popular literature. *Delphinognathus* does not meet all the requirements of Article 23.9 for a *nomen oblitum*, specifically Article 23.9.1.1. The name *Delphinognathus* has been in use since 1899 as a valid tapinocephalid genus. Conversely *Moschops* has been widely used and is well established in the literature as a key representative of the Tapinocephalidae and satisfies the condition in the Article 23.9.1.2 of the Code. Accordingly the author wishes to maintain the usage of *Moschops* as retaining the name *Delphinognathus* would

threaten universality of the taxon and cause confusion. ICZN Article 23.9.3 states that in this case the matter should be referred to the Commission for a ruling. Thus, it is proposed that by reversal of precedence the name *Delphinognathus* be replaced by *Moschops* (Appendix 3).

6.5 *Moschognathus whaitsi* BROOM 1914a

Holotype: AMNH FARB 5602, comprises a complete right mandible, portions of a left mandible, posterior portion of a zygoma with corresponding portion of the occiput, and associated postcranial elements from an unknown locality in the Beaufort West District (Broom, 1914a, fig. 2; Broom, 1915, pl.2, fig.24, 27).



Figure 6. 42. Skull of *Moschognathus whaitsi*, AMNH FARB 5602: photograph of the right lateral view of the holotype skull comprising the snout tip, mandible and zygoma portions. Scale bar: 10 cm.

Previous diagnosis for genus and species: Steeply angled frons and short, dorsoventrally and laterally narrow snout. Differs from the closely allied

Moschops in having a proportionally taller and shorter mandible than that of *Moschops*, with a well-developed symphysis quite unlike the weak, shallow, anteroventrally sloping symphysis of *Moschops*. It differs in snout proportions, having a dorsoventrally thinner maxilla and anteroposteriorly longer premaxilla (Kammerer, 2009).

6.5.1 Brief notes on the holotype

The preserved cranial fragments of the holotype indicate a short snouted tapinocephalid with slightly longer preorbital region than that of a similarly-sized *Moschops* skull (Fig. 6.42). Pachyostosis is very light as evidenced by the thin posterior border of the temporal fenestra and the dorsoventrally thin premaxilla. The lower jaw is one of the best preserved of a tapinocephalid, excluding those of the holotypes of *Tapinocaninus* and *Ulemosaurus*. The right mandible, which is about 269 mm. long, preserves all the bones of the lower jaw except the articular, and the mid-portion of the left ramus is missing. The well-preserved in-situ dentition of the right mandible is the best preserved for any tapinocephalid.

6.5.2 Historical background.

Broom (1914a, fig. 2, p. 137-138) briefly described the medial view of the right mandible as a dinocephalian lower jaw for which he proposed the name *Moschognathus whaitsi*, recognizing its affinities to *Moschops*. He (Broom 1914b, pl.2, fig.24, 27) also provided figures of some of the postcranial elements. This was followed up by (Broom 1915, fig. 2, p. 111) a description of the left mandible fragments, posterior border of the skull, and several postcranial

elements. Gregory (1926, fig. 25, pl. xvi-xvii(c), xviii(c), xix(a), xx(b)) provided photographs of the cranial elements of the holotype including an additional lower incisor and a pair of disarticulated premaxillae. He (Gregory 1926, p. 225) supported the validity of *Moschognathus whaitsi* which he considered to be different to *Moschops* in “the vertical shallowness of the snout, which distinctly foreshadows that of *Mormosaurus*, and in unthickened form of the zygomatic bar.” Gregory (1926, p. 225) noted “the mandible is perhaps not quite so deep as that of a full-grown *Moschops*, but this also may be an age character as all his observations on *Moschops* were based on the sub-adult individuals of the type series of *Moschops capensis*. *Moschognathus* is also distinguished from *Moschops* by the more slender character of the axis and by the other details of the postcranial skeleton.” Gregory (1926) also proposed a dental formula of three lower incisors and 12-16 postcanines for the species. Broom (1932, p. 44) emphasized that *Moschognathus* is distinctive from *Moschops* in having a much flatter snout than that of *Moschops*. Boonstra (1969) tentatively suggested synonymy of *Moschognathus whaitsi* as a species of *Moschops*. Kammerer (2009, p.227) considered *Moschognathus whaitsi* valid stating that its mandible “is proportionally taller and shorter than that of *Moschops*, with a robust, well-developed symphysis quite unlike the weak, shallow, anteroventrally sloping symphysis of *Moschops*” and its snout has a “dorsoventrally thinner maxilla and anteroposteriorly longer premaxilla” (also see. Boos et al., 2015). Kammerer (2009, p.227), based on the height of the premaxilla and maxilla, suggested that the same snout morphology is present in the holotype of *Struthionops intermedius*

Boonstra, 1952i and proposed the synonymy of *Struthionops* with *Moschognathus*.

6.5.3 Systematic Palaeontology

Moschognathus whaitsi Broom 1914a

Revised diagnosis: There are no clear autapomorphies for identification.

Moschognathus is identified on the following unique combination of characters:

Dorsoventrally shallower skull and laterally narrower and relatively elongated skull compared to that of *Moschops*, mentum of lower jaw almost vertical and does not slope anteroventrally.

6.5.4 Description

6.5.4.1 Material

AMNH FARB 5602 - The holotype of *Moschognathus whaitsi* comprises an almost complete right mandible and the portions of the left mandible, posterior portion of right zygoma and anterior portion of the snout. Unknown locality in the Beaufort West District. AM4950 - Skull with articulated lower jaw from the farm Grant 39 in Grahamstown, Eastern Cape Province. The skull roof is weathered away but the palate and dentition are well preserved.

6.5.4.2 General preservation and cranial pachyostosis

The holotype (AMNH FARB 5602) comprises a well preserved right lower jaw, posterior portion of the skull including the jaw articulation and posterior part of

the temporal opening, as well as the anterior margin of the snout. The zygoma is only slightly pachyostosed. A newly discovered referred specimen (AM 4950) comprises a dorso-laterally compressed skull with an imperfectly preserved left side, ventral and occipital views and a right mandible which is reasonably complete with well-preserved dentition. AM 4950 is about 36 cm long but this may be exaggerated by deformation as the skull has been dorsolaterally compressed. The left side of the skull has been weathered away as a result of surface exposure in the field. The dentary shifted anteriorly relative to the postdentary bones. Both the holotype and AM 4950 are medium-sized tapinocephalid skulls with a relatively narrow intertemporal bar, large temporal fenestra, and relatively weak pachyostosis compared to most tapinocephalids

6.5.4.3 Skull roof

Premaxilla: The premaxilla (Figs. 6.43, 6.44-6.46) forms the anterior extremity of the snout and the anterior margin of the external nares and, as in all tapinocephalid dinocephalians, has a posterodorsal extension between the external nares and the nasal. This extension is not preserved in the holotype but is preserved in AM 4950 where it is a laterally narrow and dorsoventrally relatively thin bone. It extends slightly more than the half-way up the preorbital portion of the skull and has a posterior transverse contact with the nasal. Only the right premaxilla is preserved in AM 4950, in AMNH FARB5602 both premaxillae are preserved but are disarticulated. Both specimens had five incisors which are separated from the first tooth of the maxilla by an obliquely positioned

premaxilla-maxilla suture which extends from the anteroventral edge of the external naris to the choanal border.

Septomaxilla: The septomaxilla (Fig.6.46B) is poorly preserved in the ventral and anterior margins of the external naris on both sides of AMNH FARB5602 and on the right side of AM 4950. In AM 4950, as in most tapinocephalids, it forms a hook-like projection (a in Fig. 6.46B) into the naris before continuing posteriorly as the facial extension (b in Fig. 6.46B). This extension, which is bordered by the nasal dorsally and the maxilla on the ventral side, tapers posteriorly to end about half-way along the preorbital length.

Nasal: As in all tapinocephalid dinocephalians, the nasal (Figs. 6.46-6.47) is an anteroposteriorly elongated paired bone that anteriorly forms the posterior margin of the external naris and contributes to the dorsal and the lateral surface of the skull roof. It is preserved only on the right side of AM 4950 where it is anterodorsally in contact with the posterior extension of the premaxilla. The nasal's posterodorsal contact with the frontal is not clearly visible in AM 4950, and tentatively considered to be half way along the orbit. Although this contact is not well preserved the posterior end of the nasal appears to be bifurcated.

Maxilla: The maxilla (Figs.6.43, 5.45A,B) is a large triangular bone that is well preserved on the right side of AM 4950. In AMNH FARB5602 only a small anterior portion of the bone is preserved where it contacts the premaxilla. The maxilla has been slightly separated from its posterior neighbouring bones by a

shear which pushed the bone anteriorly about 50 mm. The apex of the triangular maxilla is positioned posterodorsally, wedging between the prefrontal posteriorly and the nasal dorsally. The dorsal contact of the maxilla and nasal has suffered distortion resulting in the anterior end of the nasal extending into the external naris. The maxilla has anterior sutural contact with the premaxilla below the external naris, and ventrally it forms the alveolar border of the snout and extends posteriorly as a thin spur below the anteroventral border of the jugal.

Jugal: The jugal (Fig. 6. 45) is a prominent antero-posteriorly elongated bone contributing to the lateral surface of the snout and forming the ventral border of the orbit. It is preserved only in AM 4950. Dorsally the jugal contacts the lacrimal with a short straight suture and anteriorly it forms a zig-zag contact with the maxilla. Posteriorly the jugal is in contact with the squamosal and it has a very short posterodorsal contact with the postorbital.

Squamosal: The squamosal (Figs. 6.44, 6.45) forms the ventral and posteroventral border of the temporal fenestra in lateral view and it contributes to the posterolateral margin of the occiput. In AM 4950 the entire squamosal is preserved, and in the holotype (AMNH FARB 5602) only the anterior portion below the postorbital bar is not preserved. Anteriorly the squamosal extends two-thirds of the width of the postorbital bar and contacts the jugal anteriorly. Below the jugal the squamosal has a prominent indentation which accommodates the posterior end of the jugal and the lateral appendage of the quadratojugal. These two bones meet with an angle which becomes more acute in *Moschops* due to the

anterior shift of the skull and the pachyostosis of the zygoma with age in larger specimens in *Moschops*. The squamosal indentation, as in the subadults of *Moschops*, is quite large in both the holotype AMNH FARB 5602 and AM 4950 but, in contrast to *Moschops* subadults, is more anteriorly positioned.

Posterodorsally the squamosal has a long contact with the tabular on the occiput and the contact with the parietal on the dorsal border of the temporal fenestra is preserved only in AM 4950. The squamosal's contribution to the occiput is limited and only a narrow external auditory meatus is present.

The posteroventral margin of the squamosal of the holotype (AMNH FARB 5602) is gently concave in AM 4950 and not strongly concave as in adult *Moschops* and *Tapinocephalus* specimens, or angular as in the longirostrin *Mormosaurus* and *Struthiocephalus*.

Prefrontal: The prefrontal (Fig.6.45, 6.46A) is preserved in AM 4950 and contributes to the anterodorsal margin of the orbit. It has a short anterior contact with the maxilla, and dorsal contact with the nasal and frontal.

Frontal: The frontal (Fig.6.45, 6.46A) forms the largest portion of the cranial roof in AM 4950. Anteriorly it contacts the prefrontal and bifurcated nasal, while posteriorly it has a V-shaped contact with the parietal. The frontal makes a short contribution to the orbital border (preserved on the left side) but it is unclear whether it contributes to the border of the temporal fenestra posterolaterally.

Postfrontal: The postfrontal (Fig. 6.45, 6.46A) forms the posterodorsal border of the orbit, but is poorly preserved in AM 4950.

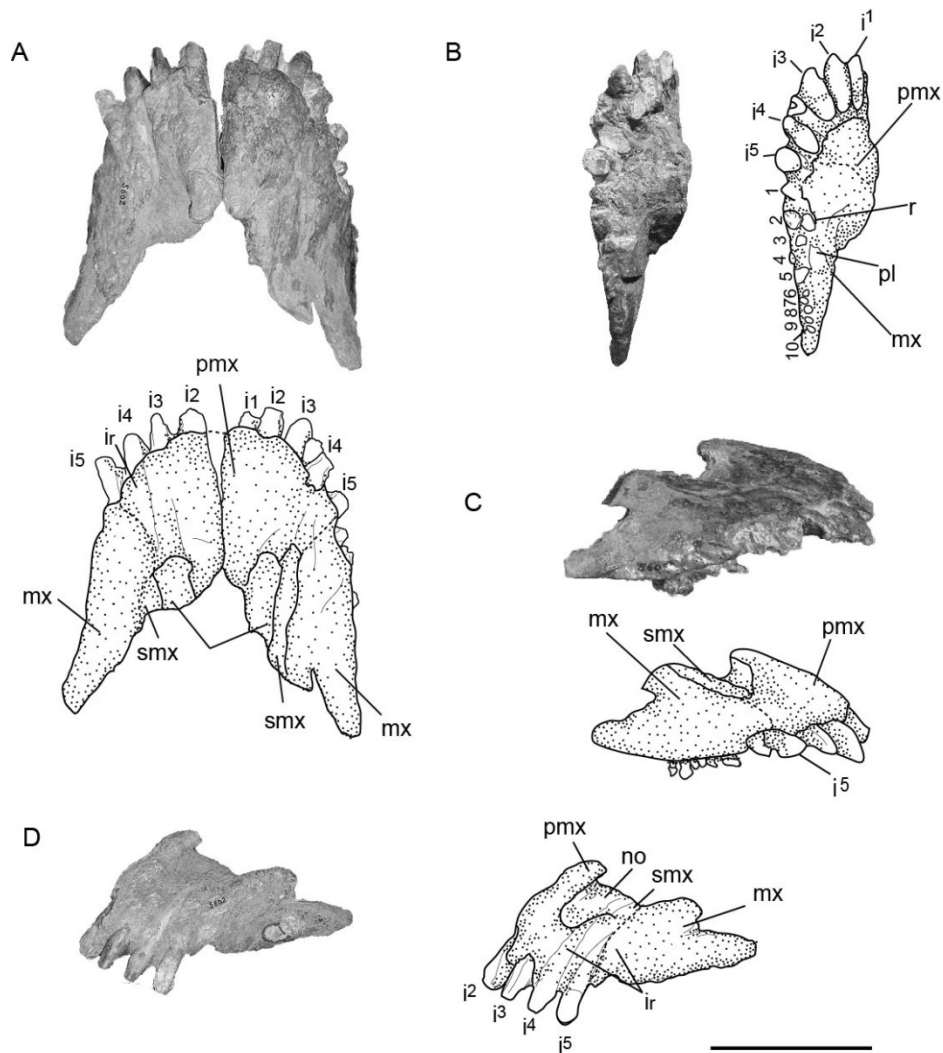


Figure 6. 43. *Moschognathus*: photograph and illustration of AMNH FARB5602 showing the anterior end of the snout; dorsal (A), ventral (B), right lateral (C), and left lateral (D). Scale. 10 cm. Photo in D is courtesy of Dr. C. Kammerer.

Parietal: The parietal (Fig.6.45, 6.46A) forms the posterior portion of the cranial roof and extends between the temporal fenestrae. Its contacts with the surrounding bones are not clear in AM 4950, except for the anterior suture with the frontal. A short longitudinal depression is present on the anteromedial surface of the parietal.

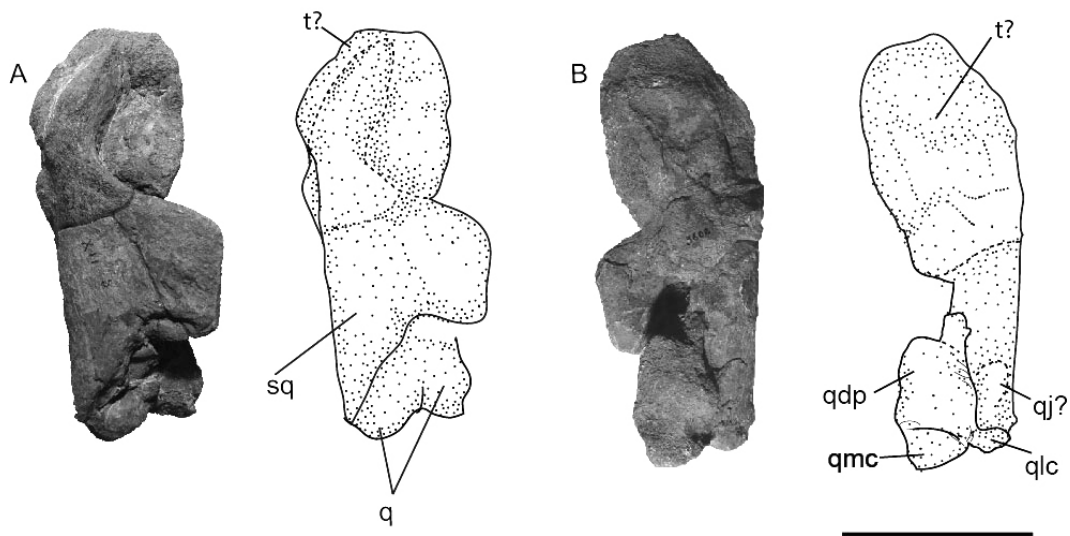


Figure 6. 44. *Moschognathus*: preserved portion of right zygoma of the holotype of *Moschognathus whaitsi* AMNH FARB5602. Scale: 10 cm.

6.5.4.4 Occiput and braincase

Parabasisphenoid: The parabasisphenoid (Fig. 6.47A) is preserved as a roughly triangular bone in AM 4950. Its surface is heavily weathered such that only the parabasisphenoidal keel, positioned on the midline of the bone, is recognisable. The anterior apex of the parabasisphenoid has a pointed contact with the pterygoid, and posteriorly it has a transverse sutural contact with the basioccipital. Posterolaterally it forms the anterior border of the fenestra ovalis.

Basioccipital: As with the parabasisphenoid, the bone surface of the basioccipital is heavily weathered allowing only the outline of the bone to be recognized. Posteroventrally it makes up the ventral lobe to the tripartite occipital condyle and extends dorsolaterally to contact the exoccipital and laterally to meet the paraoccipital process of the opisthotic. These sutural contacts are discernable in AM 4950 (Fig. 6.47)

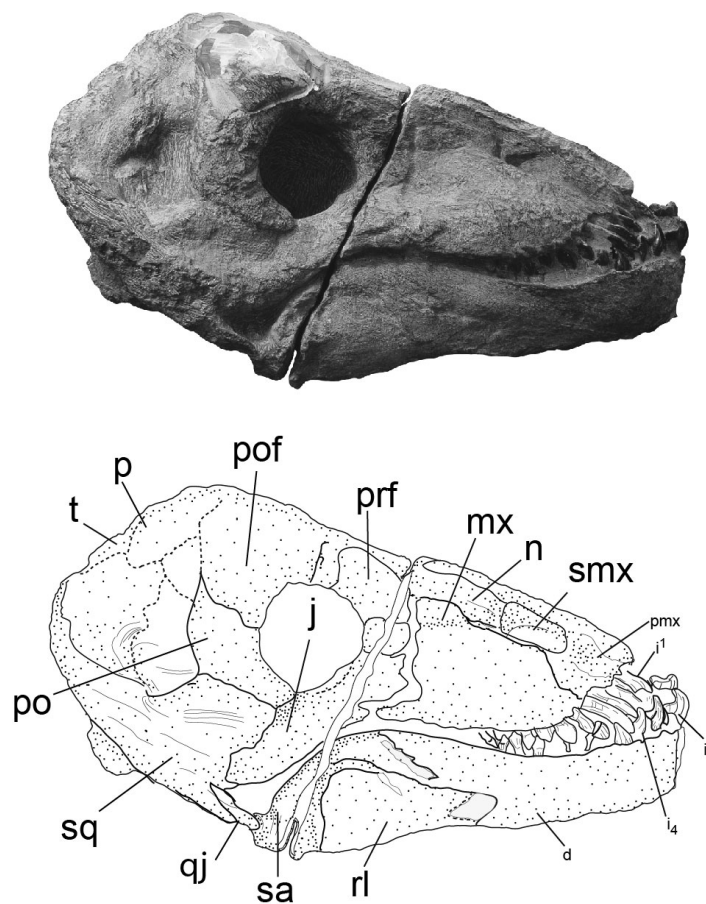


Figure 6. 45. *Moschognathus*: photograph and illustration of the right lateral view of AM 4950. Scale: 10 cm.

Postparietal: The postparietal is quadrangular bone which is dorsally in contact with the parietal and has lateral sutural contact with the tabular, and the supraoccipital ventrally. A median keel is weathered away. The remnant of this portion indicates that the keel broadened towards the midline spur of the supraoccipital.

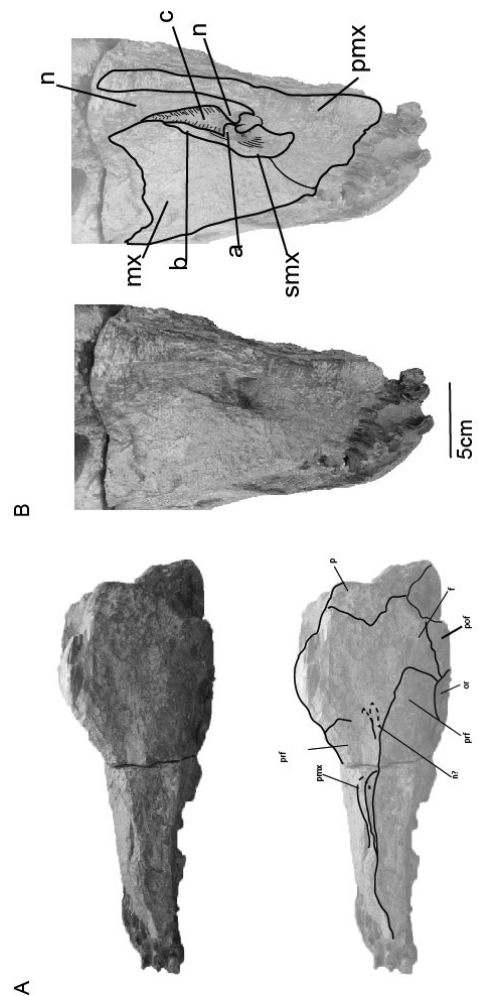


Figure 6.46. *Moschognathus*: photograph and illustration of the dorsal view of AM 4950 (A) and a close up of the septomaxillary area (B). Scale: 10 cm. B shows the relationship between the facial bones; premaxilla, maxilla, septomaxilla and nasal. Key for lettering: a, the hook-like medial projection of septomaxilla; b, facial extension of septomaxilla; c, sediment filled triangular area showing the position of the detachment between the maxilla and nasal. Note the nasal contribution to the posterior border of the external naris has been medially displaced.

Tabular: The tabular (Fig. 6.47B) is a quadrangular bone forming the dorsolateral parts of the occipital surface. In AMNH FARB5602, the tabular surface is heavily weathered and is preserved only closer to its lateral contact with the squamosal, but the right tabular in AM4950 is more completely preserved but is broken dorsomedially. Medially the tabular shares a contact with the postparietal and this bone bulges against the tabular. The tapering ventral spur of the tabular is wedged between the paraoccipital process medially and the squamosal laterally.

Supraoccipital: The supraoccipital (Fig.6.47B) is best preserved on the right side of AM 4950 and is a transversely elongate bone with a broad rounded midline spur which overlies the postparietal. Its surface is badly eroded and the sutural contacts with the paraoccipital and exoccipital are not discernable.

Exoccipital: The exoccipital (Fig.6.47B) is preserved on the right side of AM 4950 forming a wing-like bone that contributes to the lateral border of the foramen magnum. Dorsally it contacts the supraoccipital and laterally meets the opisthotic.

Opisthotic: The opisthotic (Fig. 6.47) is a prominent transversely elongate bone on the occipital surface which contacts the exoccipital medially and flares laterally to form the paraoccipital process. The dorsal portion is in contact with the tabular dorsally and laterally, and the ventral part forms the ventral border of the occiput and contacts the squamosal ventrolaterally.

Quadrate and quadratojugal: The quadrate is loosely attached to the anterior side of the ventral process of the squamosal. Dorsally it is a flat sheet-like bone, and ventrally it has relatively small lateral and medial articular condyles. In AM 4950 the medial condyle contacts the distal end of the quadrate ramus of the pterygoid and the distal end of the stapes. The quadrato-jugal is covered by matrix in AM 4950 and not preserved in AMNH FARB5602.

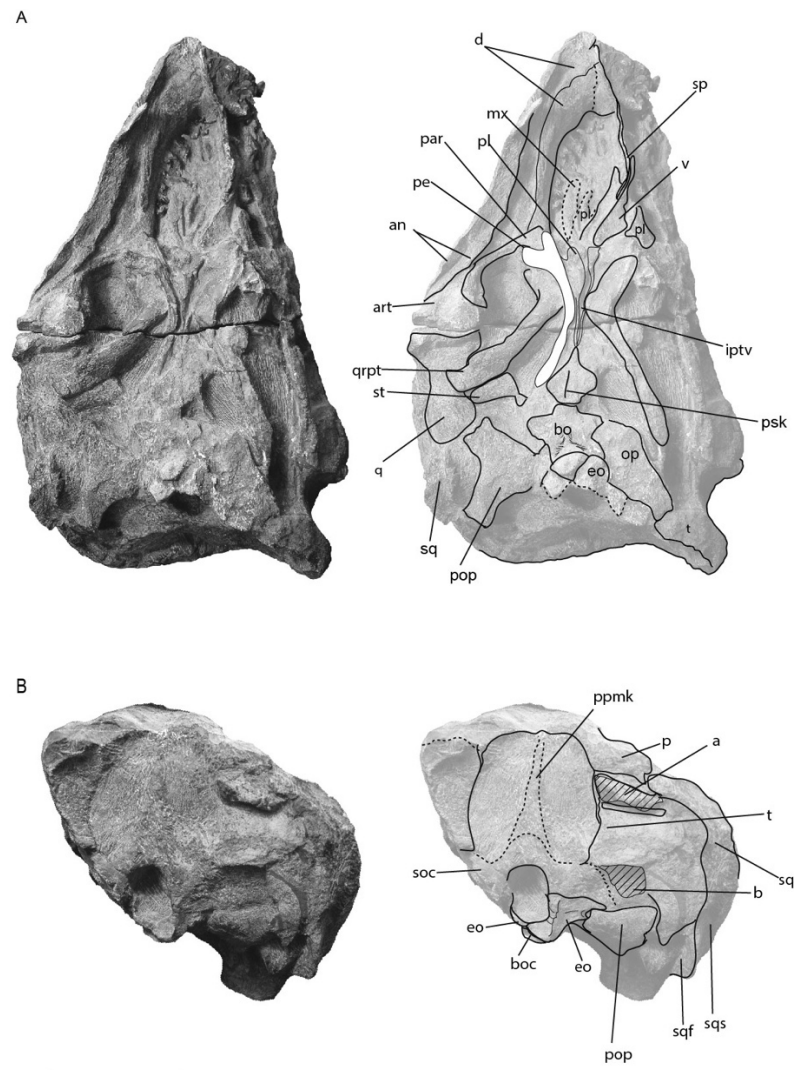


Figure 6. 47. *Moschognathus*: photograph and illustrations of the ventral (A) and occipital (B) view of AM 4950. Scale: 10 cm.

6.5.4.5 Palate

Only the anterior extremity of the premaxilla and small portions of the maxilla and palatine are preserved in the holotype, AMNH FARB5602. However the palate is relatively complete in AM 4950 but has suffered some distortion and weathering.

Premaxilla: The premaxilla (Fig. 6.43B) forms the narrow anterior tip of the ventral surface which is exposed only in the holotype. In the both specimens there are five incisors preserved and in the holotype the first four incisor teeth are preserved with labiolingually elongated crowns. Apart from the first incisor pair all have teeth have a broken talon and the crown heels are all weathered and flattened. The fifth premaxillary tooth is preserved with its rounded root.

Vomer: The paired vomer (Fig. 6.47A) is preserved in AM 4950 as an anteroposteriorly elongated bone. As a result of distortion the nature of the anterior contact of the vomer with the premaxilla cannot be determined as it is masked by the splenial of the lower jaw, but it appears that the anterior end of the left vomer is rounded. Posteriorly, the vomer broadens in ventral view and, together with its counterpart, forms a longitudinal V which extends along the entire midline. A long lateral ridge extends down the entire bone. Posterolaterally the vomer contacts the palatine and posteromedially meets the pterygoid. A thin and elongate midline keel is present on the posterior portion of the vomer.

Palatine: The right palatine (Fig. 6.43B, 6.47A) is preserved in both specimens, but only the anterior tip of the anterior process is present in the holotype, but the bone is complete in AM 4950. The anterior process is a narrow antero-posteriorly elongated bone that ventrally overlies the medial surface of the maxilla on the lateral border of the choana. The palatine boss is badly preserved but it is small and reniform without dentition as in *Moschops*.

Maxilla: The maxilla forms the alveolar border for the upper jaw and is in contact with the premaxilla anteriorly, and posteriorly should be ventrally overlain by the ectopterygoid but this is not preserved in any of the specimens. There are 10 alveoli on the maxilla on the holotype AMNH FARB5602 (Fig. 6.43B), while 6 maxillary teeth are visible on the lateral view of AM 4950 (Fig. 6. 50A).

Pterygoid: The pterygoid complex (Fig. 6.47A) is preserved only in AM 4950 and forms about half of the ventral surface of the palate. As it has suffered a great deal of distortion in AM 4950 it is difficult to recognize defining features. Typically the pterygoid corpus is situated medially and anteriorly contacts the posterior end of the vomer. The pterygoid extends laterally to form the transverse flange which has a large horizontal platform on its posterior side. From here a fairly short and robust quadrate ramus of the pterygoid extends posterolaterally to contact medial surface of the quadrate. Here the quadrate ramus of the pterygoid has contact with the expanded distal end of the stapes. An interpterygoidal vacuity is present and

extends posteriorly behind the lateral flange to the anterior end of the parabasisphenoid.

Parabasisphenoid: The parabasisphenoid (Fig. 6.47A) is a triangular bone which anteriorly has a narrow point forming a wedged contact with the pterygoid posterior to the interpterygoidal vacuity. Posteriorly the parabasisphenoid is in contact with the basioccipital. The surface of the bone is not well preserved, fairly weathered and the only distinguishable surface feature is the low median keel of parasphenoid.

6.5.4.6 Lower jaw

The lower jaw of the holotype AMNH FARB5602 comprises an almost complete right ramus which is well preserved but missing the posterodorsal portion, and a left ramus which is missing the middle portion (Figs. 6.47- 6.49). In both specimens of *Moschognathus* the anterior margin of the symphysis does not slope anteroventrally. This differs from the situation in adult *Moschops* specimens which have a shallower symphysis which slopes anteroventrally. Despite this difference the mandible of *Moschognathus whaitsi* is morphologically most similar to that of *Moschops* but is more robust than the mandibles of similar sized *Moschops* specimens (Gregory, 1926, figs.pl. xvii, Kammerer, 2009).

Dentary: In AM 4950 the dentary has been distorted but it is well preserved in AMNH FARB5602. It is evident that the dentary is the largest element of the lower jaw where it comprises approximately the two-thirds of the lateral surface

of the mandible as is the situation in *Tapinocaninus* and *Ulemosaurus*.

Posterodorsally, on the lateral side, the dentary is in contact with the surangular and ventrally meets the angular. On the ventromedial surface the dentary contacts the splenial ventrally, the angular posteroventrally and the coronoid posterodorsally (Fig.6.48). The latter bone is preserved only in the holotype and fits into a slight trough which is present on the posterodorsal end of the medial surface of the dentary (Grine 1997, fig. 2, 3). The ventral margin of the dentary, behind the symphyseal region, is mostly subhorizontal but curves posterodorsally at the angular process and has sutural contact with the angular half-way up the mandible. Behind the symphysis the dentary forms a shelf-like platform which slopes posteroventrally.

Angular: The angular (Figs. 6.48 A, D,C,F) forms the posterior portion of the lower jaw. It is exposed on both the lateral and the medial surfaces but is best preserved on the right ramus of AMNH FARB5602 and the lateral surface of AM 4950. A rounded reflected lamina which has a flat lateral surface with no ridges is present on the left ramus of the holotype and on AM 4950.

On the ventral margin of the mandible it is evident that the angular is wedged between the splenial medially and the dentary laterally. On the medial side, as is evident in the holotype, the angular and the splenial have a long contact extending horizontally half-way along the mandible and ending posteriorly close to the anterior-end of the prearticular. The contact between the angular and prearticular is relatively long and slopes posteroventrally to meet the articular at the posterior end of the lower jaw.

Surangular: The surangular forms most of the coronoid eminence and has its greatest exposure dorsally on the posteromedial surface of the mandible. On the right rami of AMNH FARB5602 and AM 4950 only the posterodorsal and posterior extent of the surangular are preserved, and its anterodorsal portion is partially preserved on the left ramus of AMNH FARB5602. The posteroventrally sloping curved suture between the surangular and angular on the lateral surface of the lower jaw is clearly visible. On the medial side of the jaw the anterodorsal surface of the surangular forms a slight trough to accommodate the posterodorsal end of the coronoid. This trough is not present in any of the *Moschops* lower jaws.

Coronoid: The coronoid is a relatively small, elongated bone which is preserved only on the holotype AMNH FARB5602 where it is positioned posterodorsally on the medial surface of the lower jaw. It is broadest anteriorly and gradually thins posteriorly. Ventrally the coronoid contacts the upward projecting prearticular. (Fig. 6.48D).

Splénial: The splénial (Figs.5.48D,E) is a plate-like bone positioned against the medial and posteroventral surfaces of the dentary symphysis, extending posteriorly with a posterodorsal slope to half-way along the medial surface of the lower jaw. In the holotype it is well preserved on the right mandible and the posterior end is missing on the left ramus. In AM 4950 only the left and rather weathered splénial is present and has been displaced anteriorly between the vomerine pair. The splénial is dorsoventrally thin close to the symphysis and becomes broader posteriorly to reach its greatest thickness below the anterior end

of the prearticular. A slight fossa is present on the dorsomedial surface of each splenial close to the symphysis. Posteroventrally the splenial overlies the medial surface of the angular and is in sutural contact with prearticular posterodorsally where it wedges between the anterior ends of the prearticular and angular bones. This is contra the condition observed in *Moschops* and *Tapinocaninus* where the posterodorsal part of the splenial ventrally underlies the anterior part of the prearticular. The splenial in the holotype, as in *Moschops*, forms a single spur on the medial surface of the angular. In *Tapinocaninus*, contra to this situation, the posterior border of the splenial forms two spurs: a narrow dorsal spur close to the meckelian fossa and a broader ventral one. The splenial of *Moschognathus* differs from that of *Tapinocaninus* and *Moschops* in being anteroposteriorly more elongated and dorsoventrally relatively narrower. The ventral margin of the anterior part of the splenial slopes posteroventrally, unlike the situation in *Tapinocaninus* and *Moschops* where the anteroventral splenial margin parallels the ventral margin of the mandible.

Prearticular: The prearticular is an elongated strap-like bone that is exposed only on the medial side of the lower jaw and extends over more than the half the length of the mandible. In AMNH 5602 (Figs. 6.48D-E, 6.49C) it is completely preserved on the right ramus and only the posterior portion of the left ramus is present. In AM 4950, the weathered and dislocated partial prearticular of the right mandible is preserved.

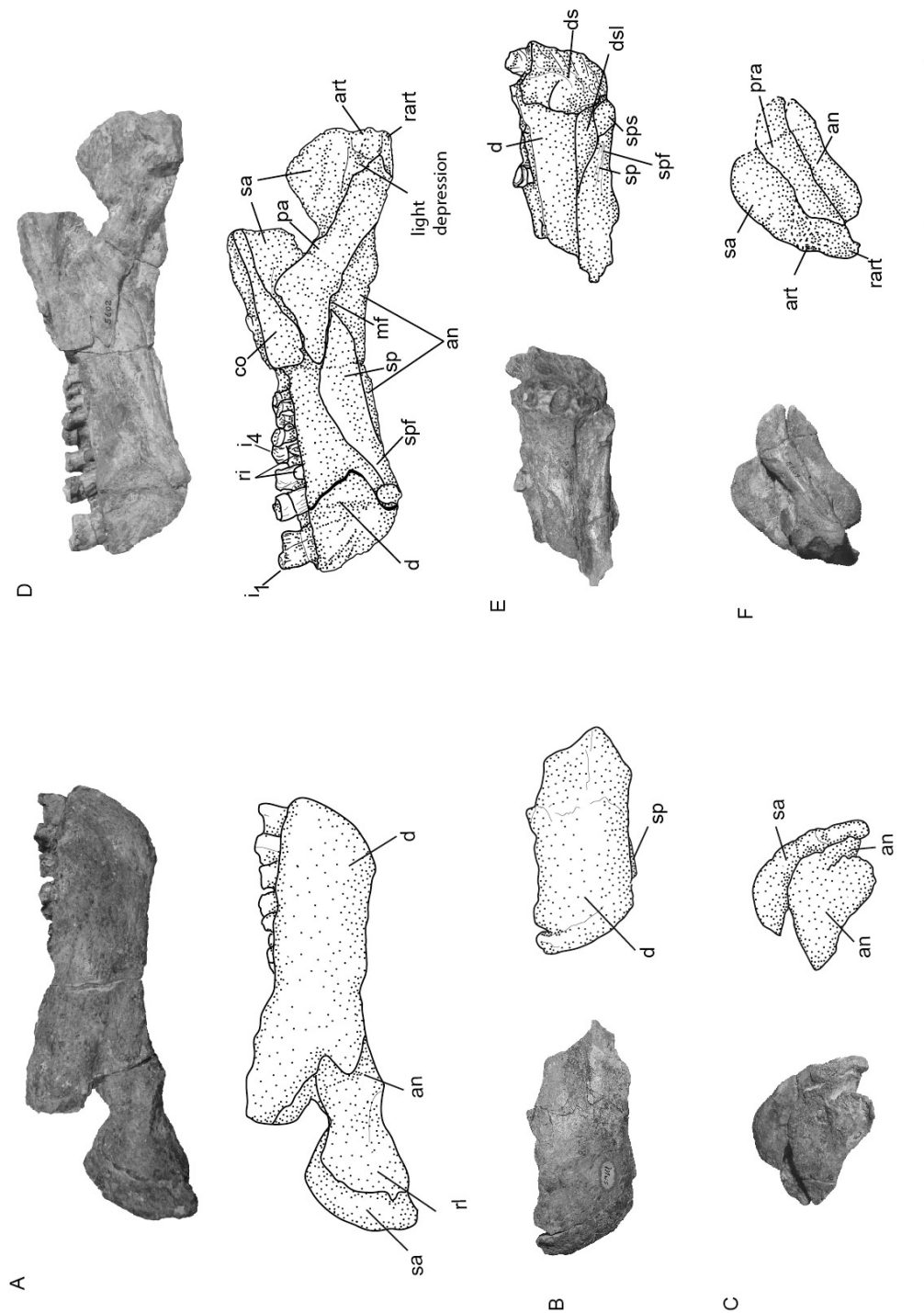


Figure 6.48. *Moschognathus*: photograph and illustration of the lateral (A) and medial (D) view of the right mandible and the lateral (B,C) and medial (E,F) views of the left mandible of AMNH FARB5602, the holotype of *Moschognathus whaitsi*. Scale: 10 cm

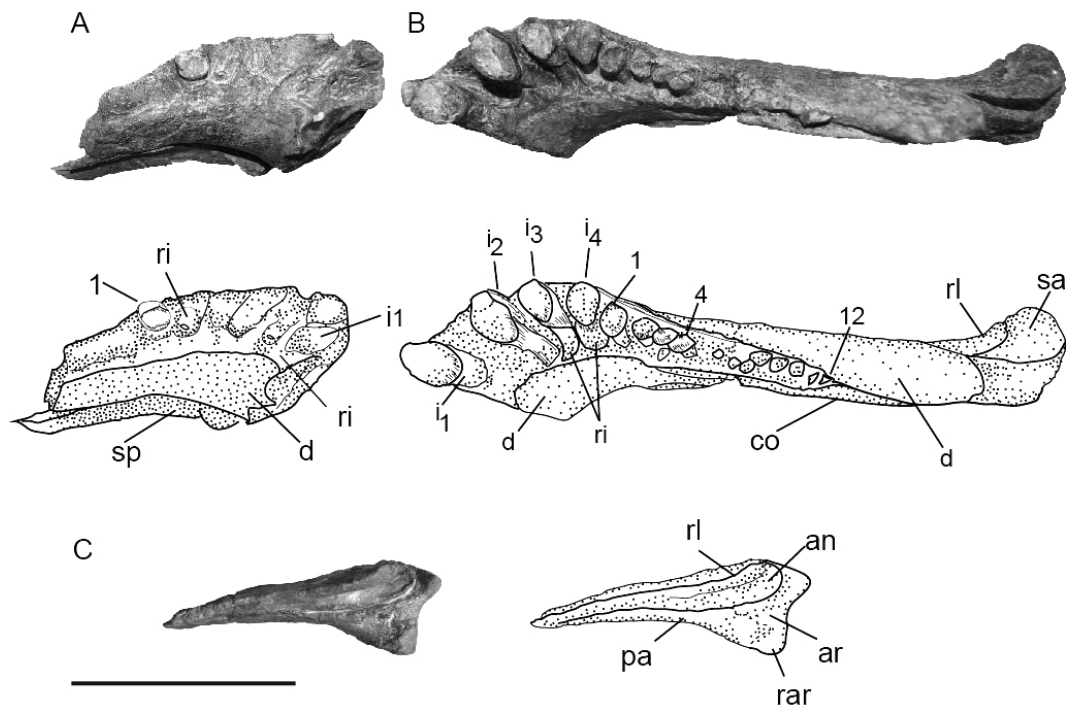


Figure 6. 49. *Moschognathus*: photograph and illustration of the dorsal views of right mandible (A) and the left dentary portion from the syphysis (B) and the ventral view of the posterior end of the left mandible (C) of AMNH FARB 5602, the holotype of *Moschognathus whaitsi*. Scale: 10 cm.

Anteriorly the prearticular is broad and contacts the coronoid dorsally and the splenial ventrally. The anterodorsal end of the prearticular is not completely preserved and this portion of the bone normally (as in *Tapinocaninus*, *Ulemosaurus* and *Moschops*) extends anteriorly as far as the highest portion of the splenial. Thus, the overall extent of the prearticular is slightly less than that of *Tapinocephalus* and *Moschops*. The prearticular slopes posteroventrally, contacts the surangular dorsally, and meets the angular ventrally as far as the articular at the posteroventral end of the mandible. Along its contact with the surangular, a

narrow shallow trough is formed along the prearticular and the medial surface of the surangular. As in the subadult *Moschops* specimens the lateral profile of the prearticular forms a rather steep slope but differs from the adult *Moschops* where the prearticular is elongated and positioned almost parallel to the longitudinal axis of the mandible.

Articular: The surface of the articular is not well preserved as a result of weathering. In dorsal view the articular is triangular with the apex pointing forward and the base being the lateral and medial articular fossae, separated by a ridge, for articulation with the quadrate condyles. Its medial and ventral surface is covered by the prearticular ventrally, while its lateral surface is covered by the angular (Fig. 6.48D-F; 6.49D).

6.5.5.7 Dentition

Both specimens of *Moschognathus* have five upper and four lower incisors, and the number of maxillary and dentary teeth varies in the two specimens. The dental formula is: the holotype specimen, AMNH FARB5602 - $I_4^5 PC_{12}^{10}$; AM 4950 - $I_4^5 PC_8^7$.

Incisors: In both specimens the incisors have the typical tapinocephalid morphology with labiolingually elongated roots and crowns with a long piercing talon and labiolingually elongated heels. The occlusal surface of the fifth incisor of the premaxilla appears to be rounded in the holotype and the crown of the first

upper incisor is significantly narrower than those of the rest. The lower incisors are labiolingually less elongated and mesiodistally enlarged compared to those of the upper incisors, and the root of the last incisor of the lower jaw, as in the upper jaw, is circular in cross section. In both specimens the talon margins and the surfaces of the heels are worn such that preserved talons have sharp edges and lingual portion of the heel is flattened.

In AM 4950 a replacement for the fourth incisor is exposed and has a well preserved talon and heel. Also the exposed vertical section of the premaxilla on the left side of the skull manifests replacement of the third upper incisor in lateral view, showing the talon and heel.

Maxillary and dentary teeth: All preserved teeth posterior to the incisors described above, with the exception of the most posterior maxillary and dentary teeth, show a similar incisiform morphology except that the talons and heels are much smaller than those of the incisors. No caniniform differentiation is present in the first tooth of the maxilla and the corresponding tooth of the dentary.

The first maxillary tooth is preserved only in AM 4950 and has a relatively shorter talon and smaller heel with respect to the last incisor. The second maxillary tooth is preserved in both the holotype and AM 4950 (Fig. 6.50A,B): Only the rounded root is visible in the holotype while in AM 4950 the complete tooth is preserved which appears smaller than the first maxillary tooth and has a smaller heel. The third maxillary tooth is preserved in AM 4950 with broken crown, while only a small portion of the root is present in the holotype. This

tooth has a relatively smaller crown and a talon relative to the second tooth and has a small heel (Fig. 6.50C). Only the crown of the fourth maxillary tooth is preserved in AM 4950. The teeth positioned posterior to this maxillary tooth have a considerably and progressively smaller crown as one proceeds posteriorly along the jaw. The and from this maxillary tooth on the crown size becomes considerably smaller posteriorly (Fig. 6.50A). The lingual views of these teeth in AM 4950 are covered by a thin matrix layer and are not visible but judging from the greatly reduced labial view concavity of the crown, it is considered that the lingual heels are greatly reduced. In the holotype these teeth are preserved as small ovoid roots in the alveoli and the maxillary teeth demonstrate a posterior decrease in size as is typical for tapinocephalids (Boonstra 1962).

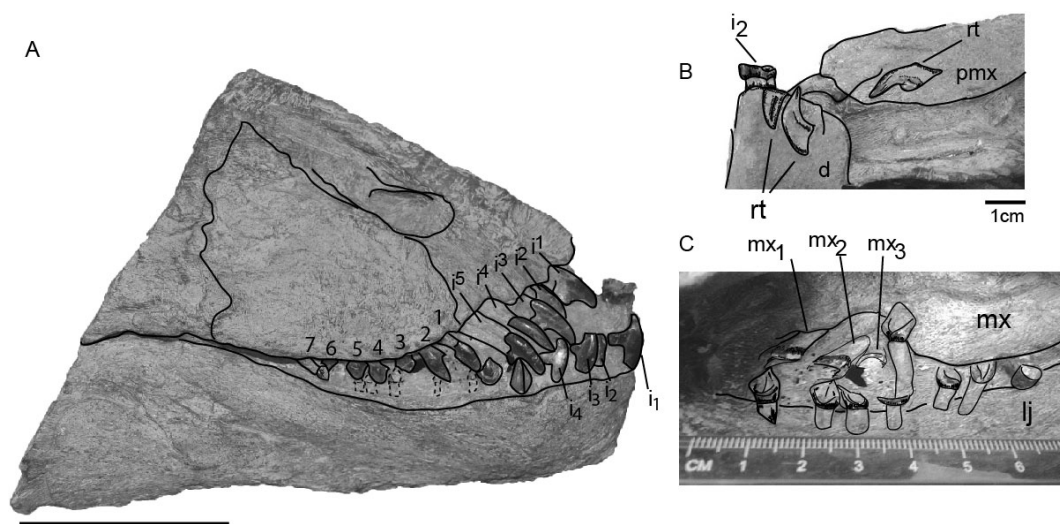


Figure 6. 50. *Moschognathus*:Dentition of AM 4950 on photos and illustration of its anterior portion: showing snout on right lateral (A), right medial (B, C). Scale: 5 cm.

The reduction in the crown size starts more anteriorly in the mandible than in the upper jaw. In AM 4950 the dentary teeth corresponding to the maxillary teeth have fallen out of their alveoli. In the maxilla these teeth are not visible in lateral view as they are still embedded on a thin layer of matrix between the right upper and lower jaw. In medial view, they show leaflike crowns with greatly reduced lingual heels. In the holotype, the first maxillary tooth on the right mandible has a small heel and a median ridge which runs from the apex of the crown down to the mid-heel margin ventrally. Backwards from the second mandibular tooth the crown and heels are greatly reduced in size and the crowns are positioned close to each other. The crowns of these teeth are positioned obliquely and partially overlap the succeeding tooth (Fig. 6.48D, 6.49A, B).

6.5.5 Results and discussion

This research supports the conclusions of Gregory (1926) and Kammerer (2009) in recognizing *Moschognathus whaitsi* as valid. The holotype is similar to the relatively recently discovered AM 4950 which is preserved with good dentition (Rubidge and de Klerk, 2007). This specimen was initially (before preparation) considered to be a juvenile *Anteosaurus* (Modesto et al., 2001) and a subadult *Moschops capensis* by Benoit et al. (2017) who noted that although many cranial roof bones were unfused, the length of AM 4950 was close to the adult size for *Moschops*.

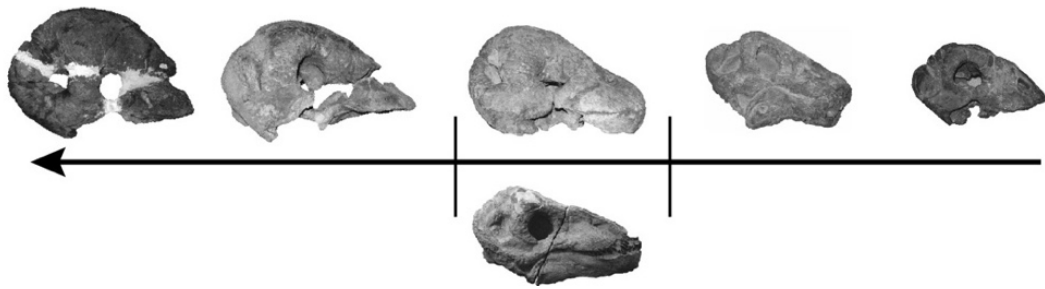


Figure 6. 51. Ontogenetic sequence of *Moschops capensis* skulls (upper row), increasing in size from right to left (collection numbers respectively: AMNH FR5550, KNPI, SAM-PK-11582, SAM-PK-K319 (reflected from left view), SAM-PK-1206). AM4950 (*Moschognathus*) is positioned in the lower row relative to a similarly-sized *Moschops* skull. This demonstrates that AM 4950 differs from similar-sized *Moschops* skulls in having; a relatively longer snout, the conical shape of the skull roof, and less cranial pachyostosis.

It is now evident that AM 4950 differs from the subadult *Moschops* skulls in having a longer snout and much less cranial pachyostosis than a similar sized *Moschops* skull (Fig. 6.51). This specimen shares the following features with the *Moschognathus* holotype: a shallow and thin zygoma, shallow snout and a lesser anteroventral slope of the lower jaw symphysis. Both the holotype and AM 4950 appear to represent different sub-adult developmental stages of a single species (Fig 6.51).

6.6 *Criocephalosaurus vanderbyli* BROOM, 1928

Holotype: MMK 5138, posterior two-thirds of a skull with partial occiput from Abrahamskraal, Prince Albert District, South Africa.

Previous diagnosis: Orbits close together, greatly enlarged frontals, greatly thickened parietal; enormous parietal canal, broad intertemporal overhanging the slit-like temporal fossa. Orbits lie further forward than *Moschops* and intertemporal region is so broad that temporal fossa cannot be seen in the dorsal ortho-projection (Broom, 1928; Boonstra, 1963b; Boonstra, 1969).

6.6.1 Brief notes on the holotype

MMK 5138 (Fig. 5.52) is a skull roof comprising right supraorbital, occiput and dorsal portion of left temporal fenestra. The skull has a round outline in dorsal view because of swelling of the frontal which extends into the temporal fenestra (Broom, 1928). The pineal canal extends almost parallel to the axis of the skull roof. The intertemporal is broad and the interorbital is unusually narrow which brings the orbits closer together, and they are positioned further anteriorly than they are in *Moschops*. This possibly enabled stereoscopic vision.

6.6.2 Historical Background

Broom (1928) described *Criocephalosus vanderbyli* from the Beaufort Group of South Africa on the basis of a poorly preserved cranial roof. Boonstra (1968b, fig. 30) introduced a second species, *C. gunyankaensis*, with line drawings of four crania from the Madumabisa mudstones of Zimbabwe. Kammerer (2009, p. 229) synonymized *C. vanderbyli* with *Moschops capensis* but made no mention of *Criocephalosaurus gunyankaensis*. Kammerer (2009, p.229) considered *Criocephalosaurus* to represent “a final stage of cranial pachyostosis in

Moschops”. With the recent discovery of new specimens of *Criocephalosaurus*’ which showed distinct differences from *Moschops*, the genus was later reinstated (Güven et al., 2012, Day et al., 2015).

6.6.3 Systematic Palaeontology

Criocephalosaurus vanderbyli Broom 1928

Revised diagnosis for genus and species: A short snouted tapinocephalid skull with a conical cranial roof in the vicinity of the intertemporal region. Long pineal canal orientated almost parallel to the long axis of the cranium. Temporal fenestra slit-like and anteroposteriorly elongated. A dorsoventrally elongated postparietal and supraoccipital midline spur.

The skull of *Criocephalosaurus vanderbyli* differs from that of *Moschops capensis* as follows: The orbits are much closer to each other resulting in a narrower interorbital region, and they are positioned further anteriorly than they are in *Moschops* skulls. The orientation of the horizontal axis of the pineal canal forms a much larger angle with the horizontal axis of the skull in *Criocephalosaurus* than it is in *Moschops*. The postparietal and supraoccipital median spur are much shorter in *Moschops*.

6.6.4 Description

6.6.4.1 Material.

This cranial description of *Criocephalosaurus* is based on the following specimens: MMK 5138 (holotype), is the posterior two-thirds of a skull with partial occiput, from Abrahamskraal, Prince Albert; NHMUK PV R 36626, well-preserved posterior two-thirds of a skull comprising a cranial roof, anterior branches of the temporal fenestra, dorsal portion of the occiput, from Gunyankaas Kraal, South of Lake Kariba, Zimbabwe. This specimen was not catalogued at the Natural History Museum, but further investigation revealed that it was purchased in 1960 from Birkbeck College in London, and it has a label stating *Criocephalus* sp. from Gunyankaa's Kraal, South of Lake Kariba, Zimbabwe. There is no collector information, neither there is an information on how Birkbeck College acquired it. The cranial outline of this specimen is similar to that of the specimens which Boonstra (1946, 1968, fig. 30) referred to *Criocephalosaurus gunyankaensis* and comes from the same locality. As the type specimens of *C. gunyankaensis* are lost, NHMUK PV R 36626 is the only *Criocephalosaurus* specimen from Zimbabwe; SAM-PK-K10888, posterior two-thirds of a cranium lacking snout, palate and a lower jaw, from Beaufort West, South Africa; BP/1/7214, posterior two-thirds of a cranium preserved with posterior circumorbital area and left temporal fenestra, from Putfontein, Beaufort West; BP/1/5445, relatively large posterior two-thirds of a skull comprising a weathered cranial roof, orbits, temporal fenestra, and partial palate, from Spitskopfontein, Laingsburg District; BP/1/1582, large posterior two-third of a cranial roof comprising the supraorbital and dorsolateral portion of the temporal fenestra from De Bad, Fraserburg District; CGP/846, small posterior third of weathered cranium, from Palmietfontein, Beaufort West.

6.6.4.2 Cranial pachyostosis and general preservation

All specimens identified as *Criocephalosaurus* have only the posterior two-thirds of the skull preserved. In BP/1/582, SAM-PK-K10888, and BP/1/7214 (Figs. 6.52-6.57) the supraorbital bones are preserved and in BP/1/582 the posterior-end of the nasal bone is present. In all specimens the intertemporal area is broad with the exception of the smallest specimens, SAM-PK-K10888 and BP/1/7214 (7-7.8 cm). The preserved parts of the temporal fenestrae show an anteroposteriorly elongated and dorsoventrally narrow opening with the long axis oriented almost parallel to the skull roof.

Cl	~210*	>200*	~235	~227	200	155	~165
Cw	~220	230	~230	210	~210	122*	193
Iob	~160 / 187	132 / 175	~134*	-	-	-	116
Itb	~200	-	172	148	~140 - 150	70	78
Pob	63	-	-	~50	40	35	37

Table 6.1. Cranial measurements of *Criocephalosaurus* in mm. Abbreviations: cl- cranial length measured between the posterior border of the orbit and anterior rim of the pineal opening, * refers to skulls in which parietal is either not preserved or preserved with only its anterior extremity- thus it is measured up to the F-P border anteromedially); cw- cranial width in postorbital region; iob- interorbital width (mid-orbital level /posterior border of the orbit); itb- intertemporal width; pob- postorbital thickening. * indicates to the measurement is estimated from preserved half of the cranium.

From the basal cranial length, measured between the areas which are preserved in all skulls, BP/1/5445, BP/1/1582 and MMK 5138 are the largest specimens,

followed by NHMUK PV R 36626 and CGP/1/846, while SAM-PK-K10888 and BP/1/7214 are the smallest (Table 6.2). The intertemporal width of the SAM-PK-K10888 and BP/1/7214 (the smallest skulls) is much narrower than the rest.

Cranial thickening is prominent on the postorbital bar and the parietal which is thickened around the pineal opening. The surface texture and degree of cranial thickening varies between the specimens; while it is swollen and sculptured in MMK 5138 and CGP/1/846, it is smoother and less rounded on the rest.

6.6.4.3 Skull roof

Nasal: The nasal (Figs. 6.53A, 6.55A,E) is a paired anteroposteriorly elongated bone of which only the bifurcated posterior end is preserved in BP/1/1582, and BP/1/5445. BP/1/5445 shows the relatively thickened nasal pair in sagittal section. Posterolaterally the nasal contacts the prefrontal, and dorsally it sutures with the frontal.

Prefrontal: The prefrontal (Figs. 6.55A- 6.57) which is best preserved in BP/1/582 is present in all specimens except NHMUK PV R36626. It is anteroposteriorly elongated, dorsoventrally relatively thin, and makes up the antero-dorsal orbital border. Anteromedially the prefrontal contacts the nasal, while posterodorsally and posterolaterally it meets frontal.

Frontal: The frontal (Figs. 6.52- 6.58) is a large, anteroposteriorly elongated bone covering most of the surface of the skull roof. It has a short contact on the orbital border, is in contact with the prefrontal and postfrontal laterally and

posteriorly has a wedged contact between the postfrontal laterally and the parietal medially. This suture between the frontal and parietal is defined by a slight elongated depression in MMK 5138 and SAM-PK-K10888. In MMK 5138, BP/1/5445 and CGP/1/846 the frontal is swollen and has a rugose surface in contrast to the smooth surface of BPI/7214, SAM-PK-K10888 and NHMUK PV R 36626. In contrast to *Moschops* the frontal of *Criocephalosaurus* is not significantly thickened, and its dorsoventral thickening is limited to the thickening in the area close to the pineal canal.

Postfrontal: The postfrontal (Figs. 6.52- 6.58) is a narrow anteroposteriorly-elongated bone oriented almost parallel to the long axis of the skull. It has a long straight medial sutural contact with the frontal and a shorter oblique lateral contact with the postorbital. The postfrontal makes a short contribution to the posterodorsal orbital border and posteriorly wedges between the parietal and postorbital forming largest portion of the dorsal border of the temporal fenestra. The postfrontal's contribution to the temporal fenestra is in an anteriorly directed spur in SAM-PK-K10888 and CGP/1/846 (Figs. 6.57B, 6.58B).

Postorbital: The postorbital (Figs. 6.52C, 6.53B,C, 6.55C,D, 6.56B,C, 6.57B, 6.58B) is short and forms the posterior orbital border. It has dorsal sutural contact with the postfrontal on the postorbital bar, it meets the squamosal posterodorsally, and makes up a large part of the medial wall of the temporal fenestra, which is evident in CGP/1/846, NHMUK PV R 36626, MMK 5138, SAM PK K10888 and BP/1/1582.

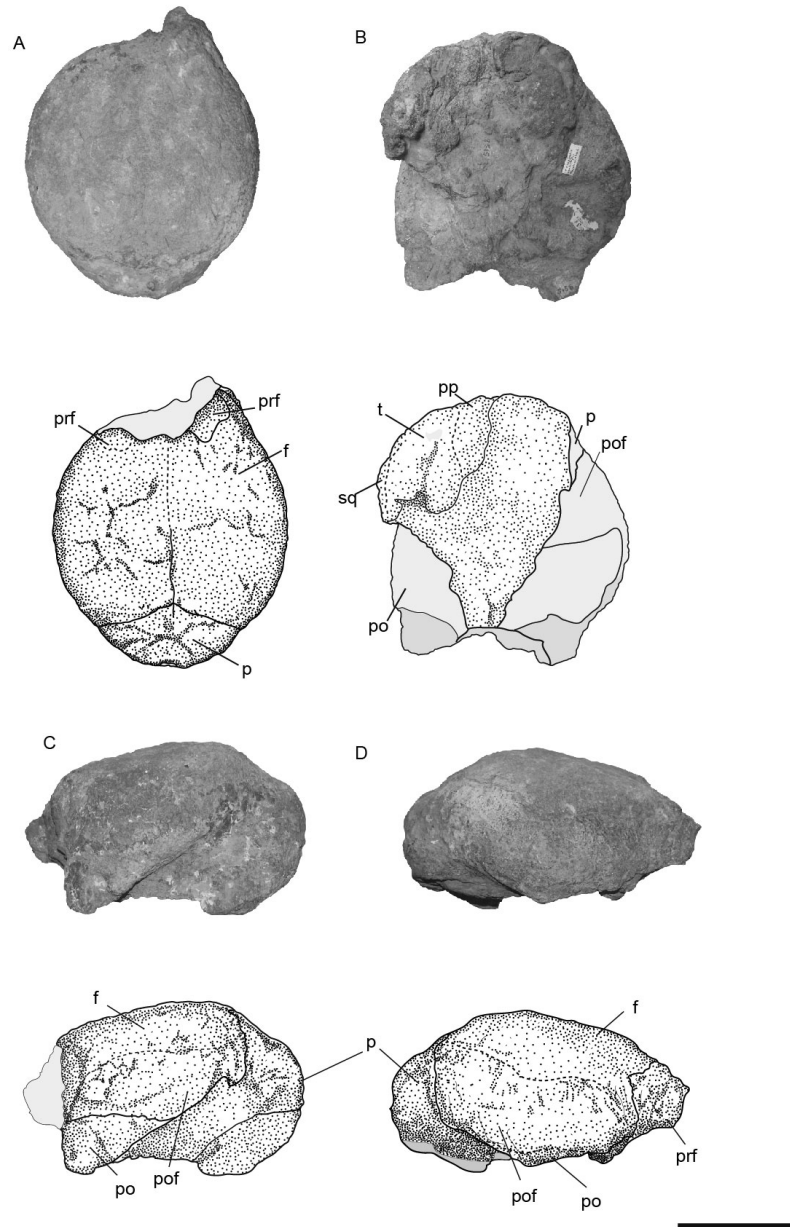
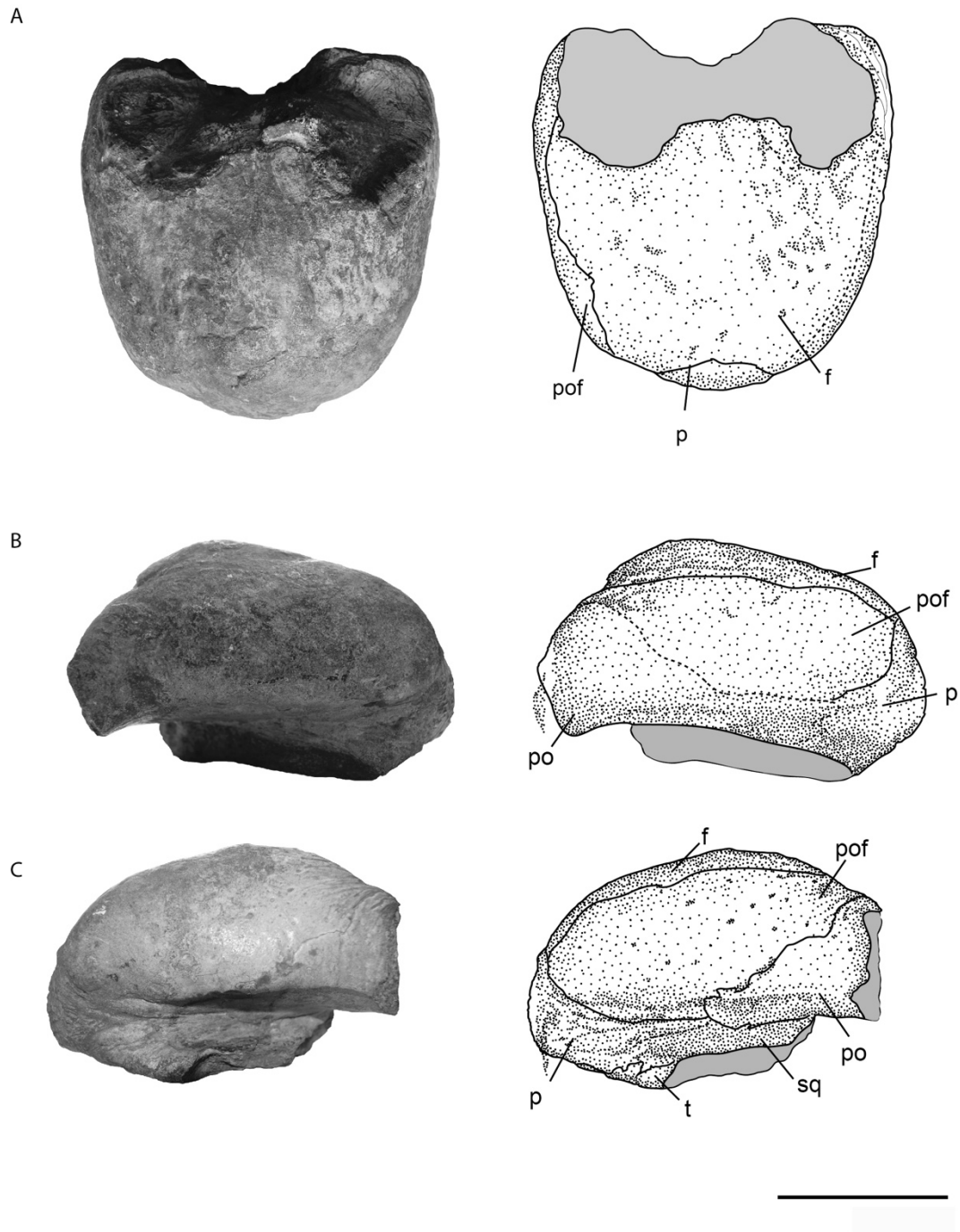


Figure 6. 52. *Criocephalosaurus*: photograph and drawing of MMK 5138 in dorsal (A), occiput (B), left lateral (C) and right lateral (D) view. Scale: 10 cm.



The ventral contact with the jugal is not preserved in any specimen. The thickness of the postorbital bar differs in the various individuals from as wide as 60 mm (BPI/1/5445) to 30 mm (SAM PK K 10888).

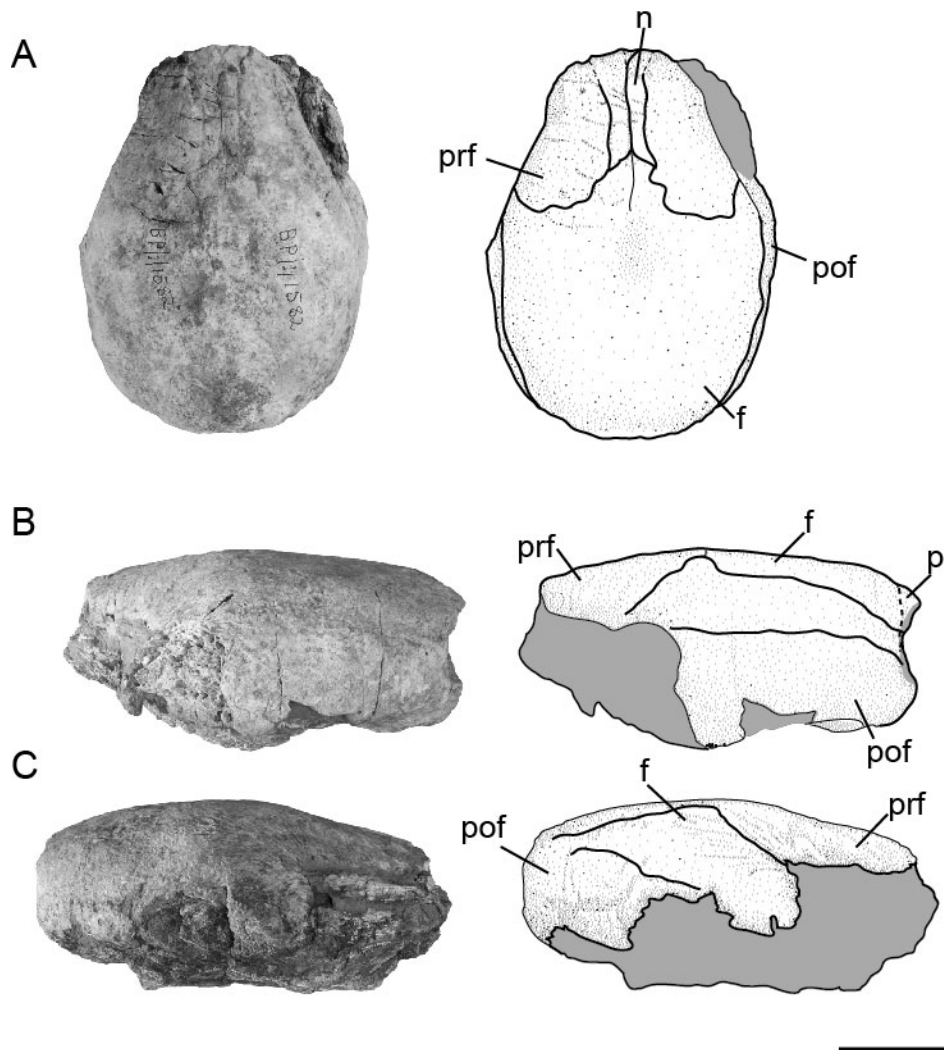


Figure 6.54. *Criocephalosaurus*: photographs and drawings of BP/1/1582 in dorsal (A), left lateral (B) and right lateral (C) view. Scale: 10 cm.

Squamosal: The squamosal (Figs. 6. 55C,D, 6.56B,C, 6.57B) is preserved only in SAM-PK-K10888 and BP/1/7214 where it is preserved as a small fragmentary

bone forming the lateral and anteroventral borders of the temporal fenestra. In both specimens it contacts the postorbital on the ventral side of the postorbital bar.

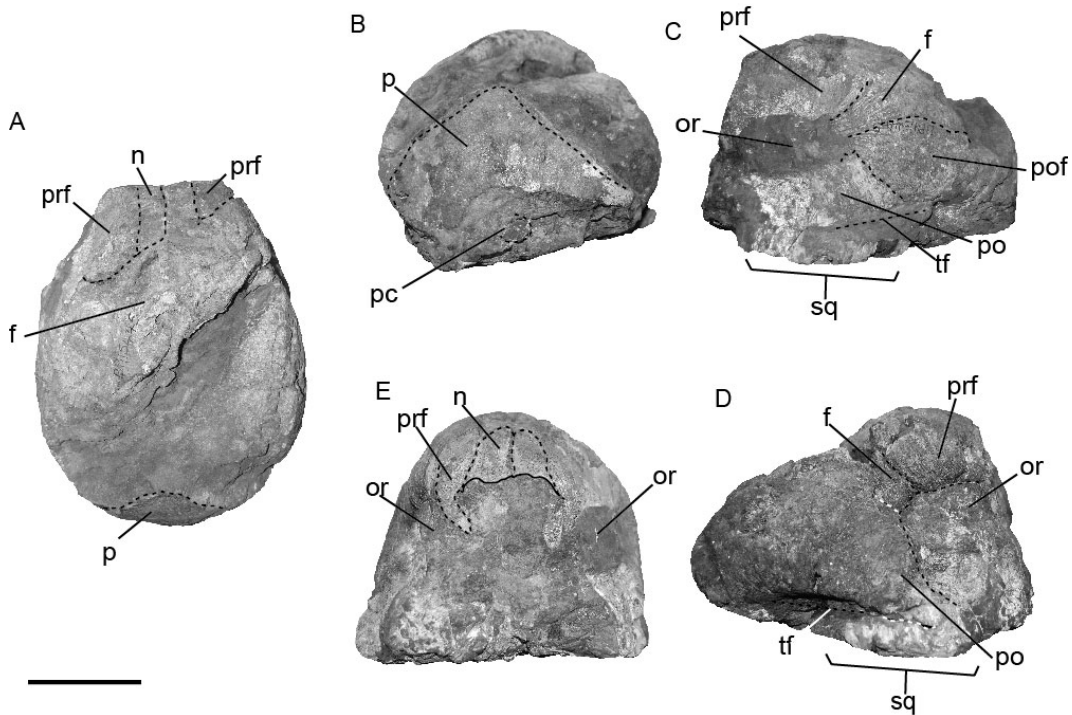


Figure 6.55. *Criocephalosaurus*: photographs and drawings of BP/1/5445 in dorsal (A), parietal (B), left lateral (C) and right lateral (D) view. E shows the natural section anteriorly going through the nasal dorsally. Scale: 10 cm.

Parietal: Compared to other tapinocephalid dinocephalians the parietal (Figs. 6.59A-F) makes up a relatively small portion of the cranial roof and surrounds the pineal foramen which is situated on a low mound. This gives the posterior part of the skull roof a conical appearance. Anteromedially the parietal is in contact with the frontal and contributes to the dorsomedial border of the temporal fenestra. Posteriorly the parietal meets the postparietal on the occipital crest. The intertemporal is wide in all specimens with the exception of SAM-PK-K10888 and BP/1/7214 (Itb, in Table 1).

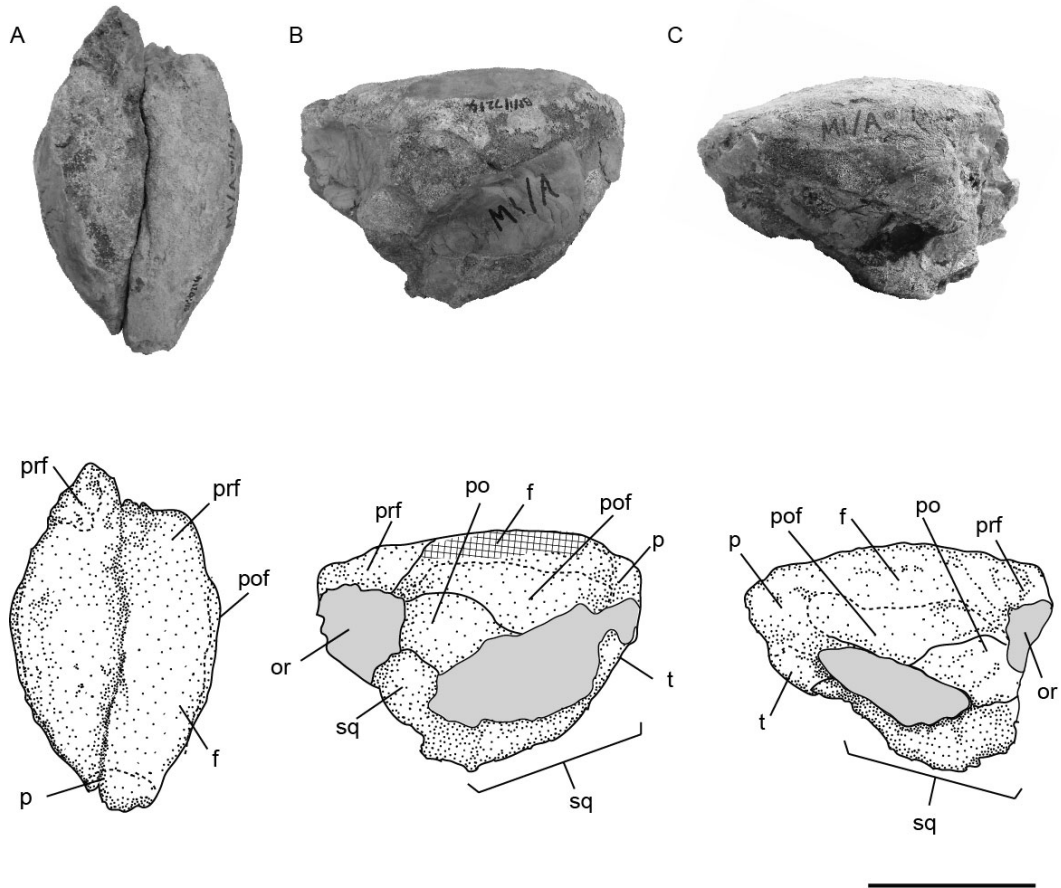


Figure 6.56. *Criocephalosaurus*: photographs and drawings of BP/1/7214 in dorsal (A), left lateral (B) and right lateral (C) view. Scale: 10 cm.

6.6.4.4 Occiput

The occiput is not well preserved in any of the specimens and only a partially preserved braincase and occiput is preserved in SAM-PK-K10888 and NHMUK PV R 36626 (Figs. 6.59). In MMK5138, CGP/1/846 and BP/1/7214 only the occipital crest is preserved (Fig. 6.59A-C, E-F).

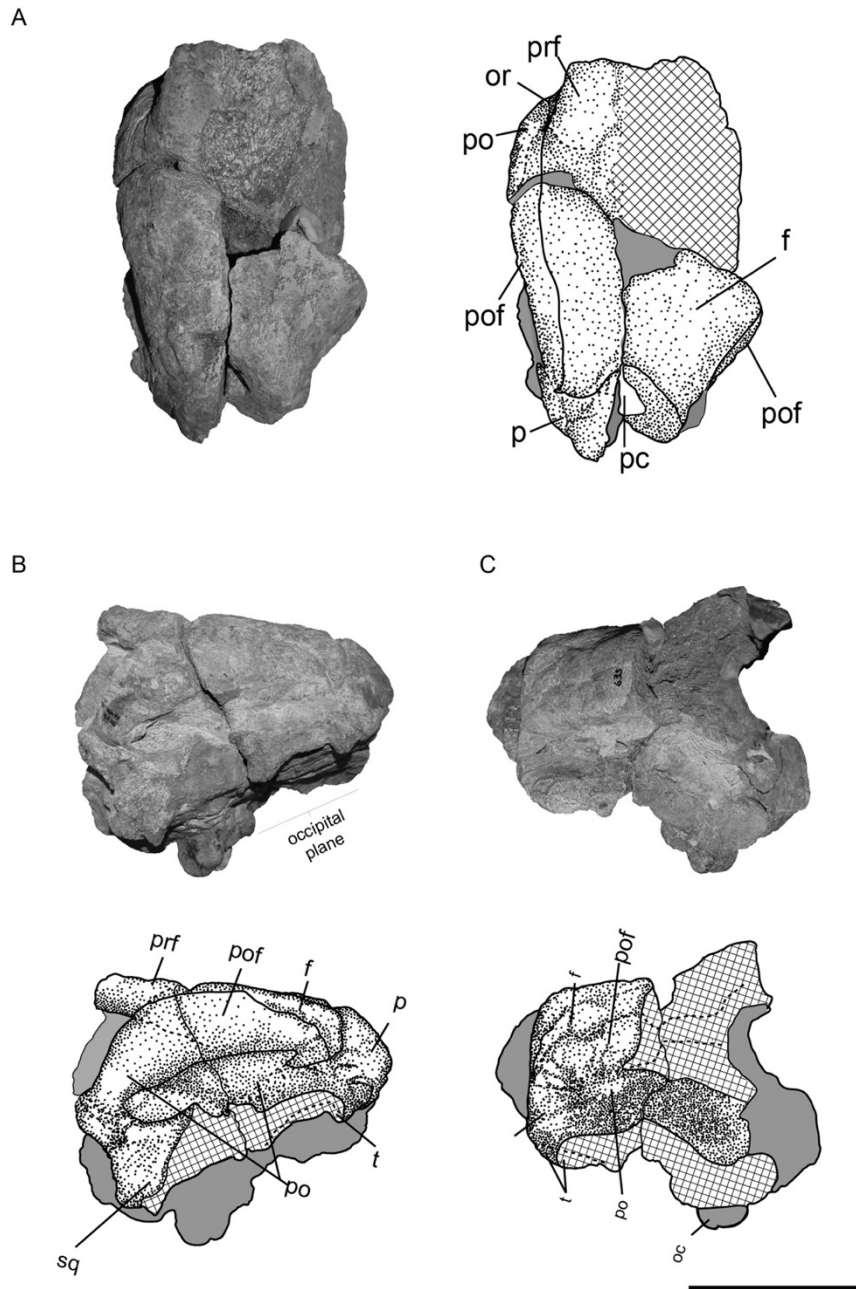


Figure 6. 57. *Criocephalosaurus*: photographs and drawings of SAM-PK-K10888 in dorsal (A), left lateral (B), and right lateral (C) view.

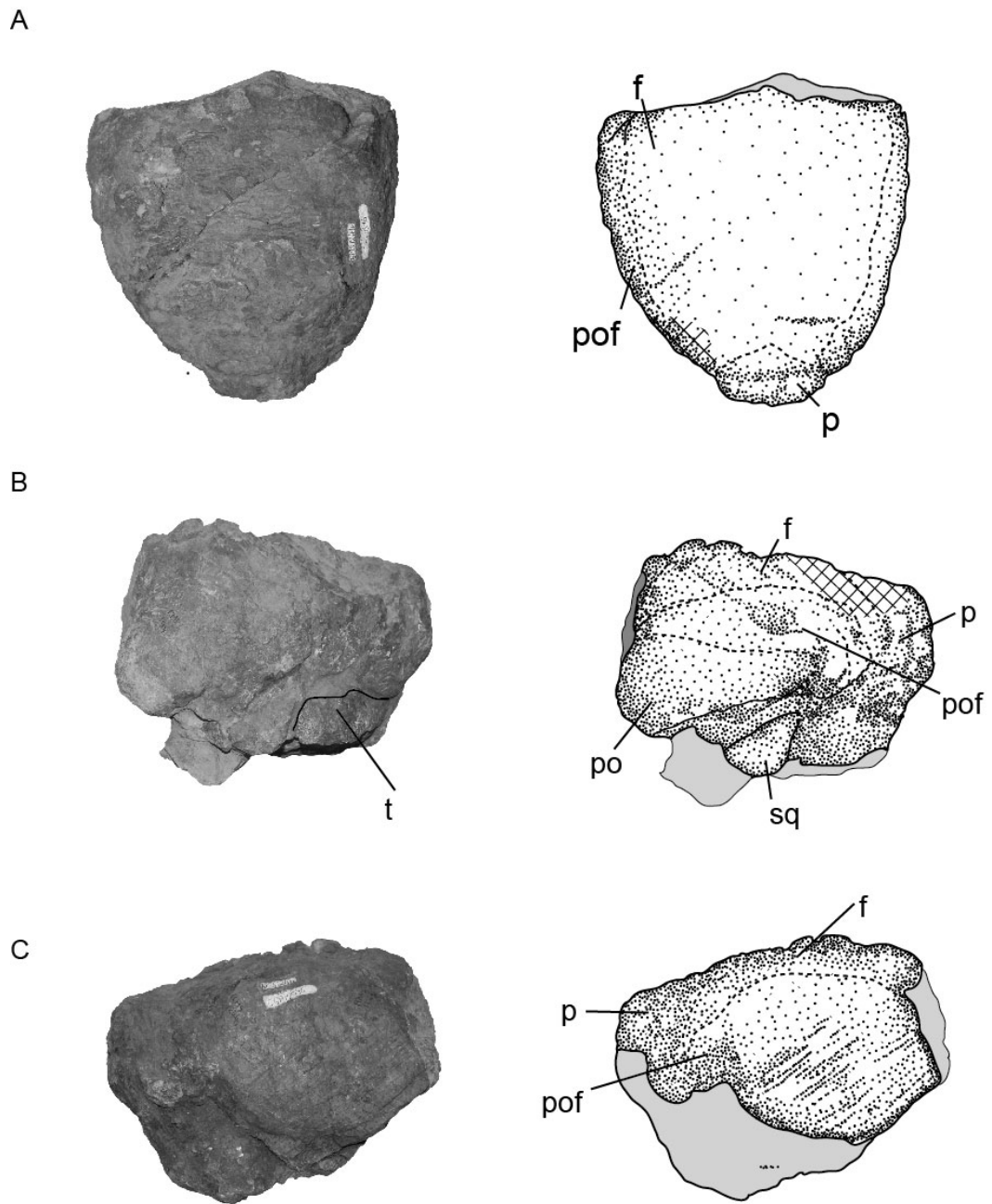


Figure 6.58. *Criocephalosaurus*: photographs and drawings of CGP/1/846 in dorsal (A), left lateral (B) and right lateral (C) view. Scale bar: 10 cm.

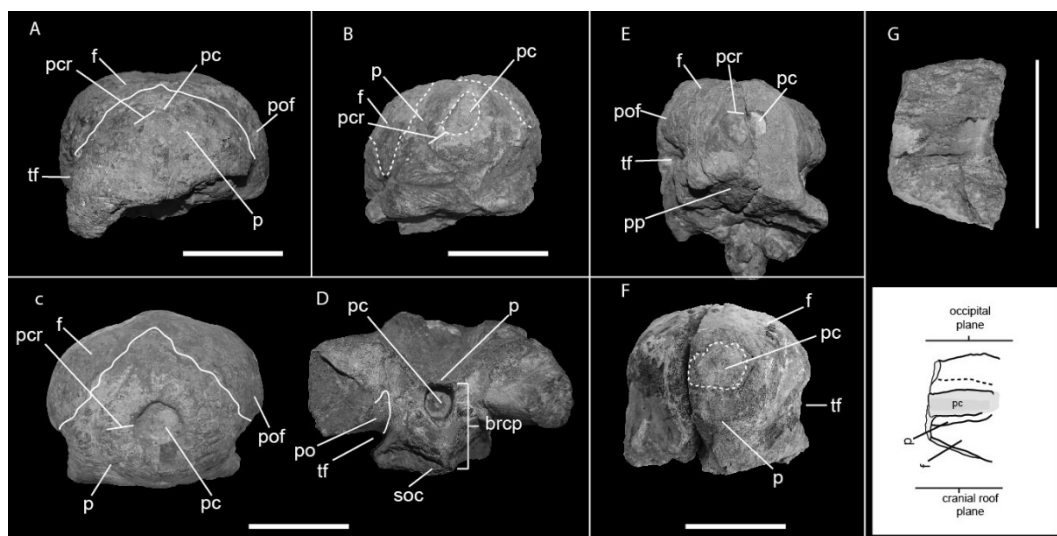


Figure 6. 59. *Criocephalosaurus*: photographs of the temporal roof showing the pineal foramen MMK5138 (A), CGP/1/846 (B), NHMUK PV R 36626 (C, D), SAM-PK-K10888 (E), BP/1/7214 (F) and photograph (G) and drawing of a cranial section through the pineal canal in SAM-PK-K10888. Scale 10cm.

Postparietal: The postparietal is an anteroposteriorly elongated rectangular bone which is situated medially on the occiput. Ventrally it has a long sutural contact with the supraoccipital, contacts the tabular laterally, while dorsally it contributes to the occipital crest forming a concave border with the parietal. The postparietal does not form a median ridge as in *Moschops* by it is overlain by a long, dorsal, and midline spur of the supraoccipital. The surface of the postparietal exhibits a series of muscle scars stretching from the median spur of the supraoccipital to the lateral and dorsal border of the postparietal (ms in Fig. 6.60).

Tabular: The tabular (Figs. 6.60) is a sheet-like bone on the either side of the postparietal and is partially preserved in NHMUK PV R36626, SAM-PK-K10888 and MMK 5138. In NHMUK PV R 36626 and SAM-PK-K10888 the dorsomedial

part of the bone is preserved and MMK5138 preserves the dorsal two-thirds of the bone. Dorsally the tabular contacts the parietal and makes a small thin contribution to the posterodorsal part of the temporal fenestra. Ventromedially the tabular is in contact with the lateral extension of the supraoccipital and the opisthotic as is evident in SAM-PK-K10888.

Supraoccipital: The supraoccipital comprises the dorsal and dorsolateral borders of the foramen magnum as is evident in SAM-PK-K10888. It extends over more than two-thirds of the height of the postparietal as is evident in NHMUK PV R 36636 which is different to the situation in any other short snouted tapinocephalid genus.

Exooccipital: The exoccipital is a relatively small bone forming the lateroventral border of foramen magnum and the lateral portions of the tripartite occipital condyle. This portion of the occiput is preserved only in SAM-PK-K10888 and as it is damaged in this specimen, it is not possible to determine sutures between the exoccipital, the opisthotic and basioccipital. A jugular foramen is present at the junction between the opisthotic and exoccipital.

Opisthotic: The opisthotic is preserved in SAM-PK-K10888 being exposed on the lateroventral part of the occiput and forms the lateral and the ventral border of the posttemporal foramen. The dorsolateral border comprises the tabular. The opisthotic laterally extends to form the paraoccipital process of the opisthotic which is not preserved completely in the specimen.

Basioccipital: The basioccipital (Figs. 6.60B- 6.61) is a relatively small bone that contributes to both the palatal and occipital surfaces. On the occipital surface it forms the occipital condyle. In palatal view the basioccipital is triangular with the apex contacting the parabasisphenoid anterior to the fenestra ovalis such that the basioccipital forms the posterior border of the fenestra ovalis. It has a very prominent and thick midline ridge which, amongst tapinocephalids, is present only in *Criocephalosaurus*. This ridge extends down the midline and diminishes in size ventrally as the basioccipital meets basisphenoid but the sutural contact between the two bones is unsure.

6.6.4.5 Palate

Parabasisphenoid: The fused parabasisphenoid (Figs. 6.60B, 6.61) is a broadly triangular bone visible on the ventral surface of SAM-PK-K10888. Posteriorly the base of this triangular bone is in contact with the basioccipital between the fenestrae ovalis but the suture is not evident. Anteriorly the parabasisphenoid has a short contact with the pterygoid complex but this area is not well preserved.

Stapes. The stapes (Figs. 6.60B, 6.61) is a robust small rod-like element that is preserved only in SAM-PK-10888. It has an expanded distal end which contacts the medial surface of the quadrate which is not preserved in this specimen, while its proximal end is preserved in articulation in the fenestra ovalis. It is positioned

relatively dorsally in respect to the axis of the parabasisphenoid in the ventral view of the skull.

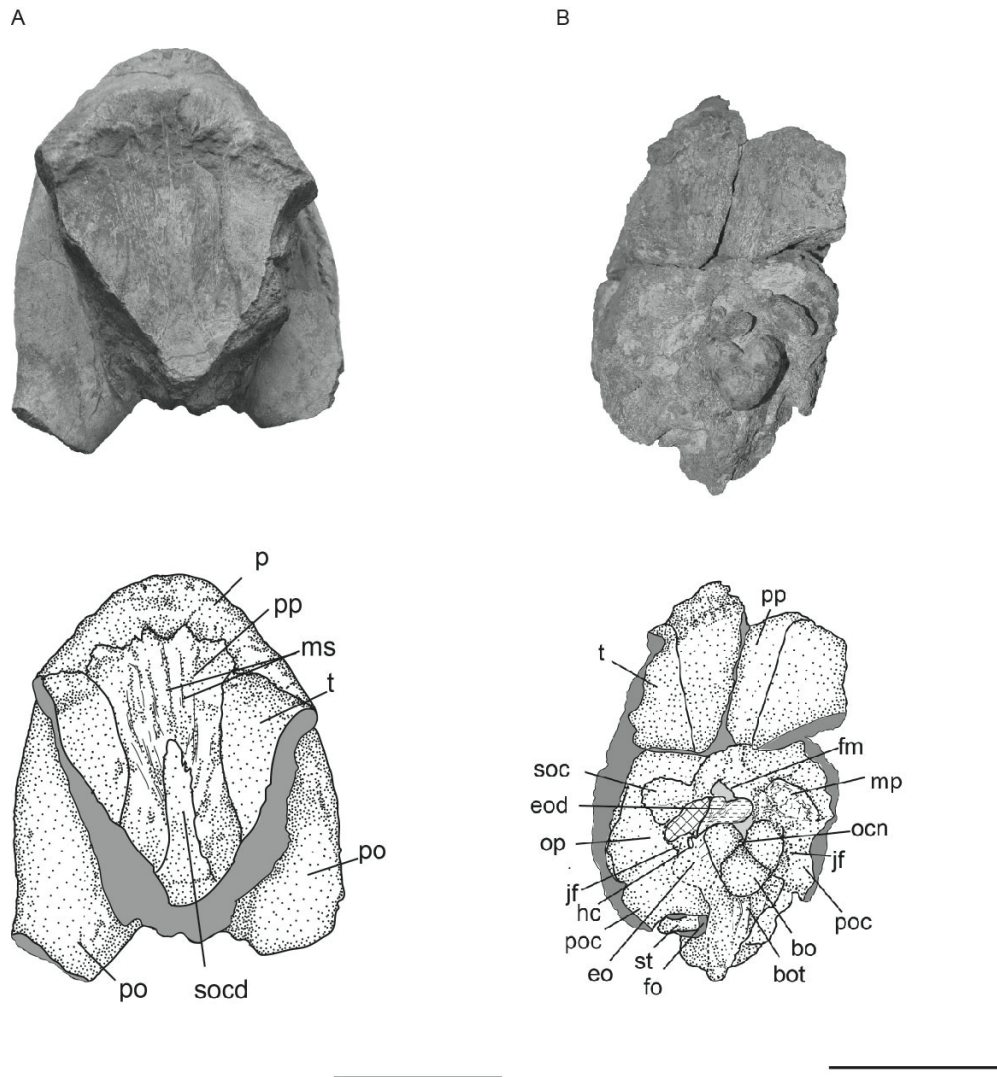


Figure 6.60. *Criocephalosaurus*: Photographs (above) and drawings (below) of the occiput of NHMUK PV R 36626 (1A) and SAM-PK-K10888 (B).

6.6.4.6 Individual variation within the species

The skulls of *Criocephalosaurus vanderbyli* which were studied here vary from each other in cranial length, width, shape of cranial roof outline, postorbital bar thickness, and intertemporal width (Table 6.1). These changes appear to be a function of size and are thus possibly ontogenetic.

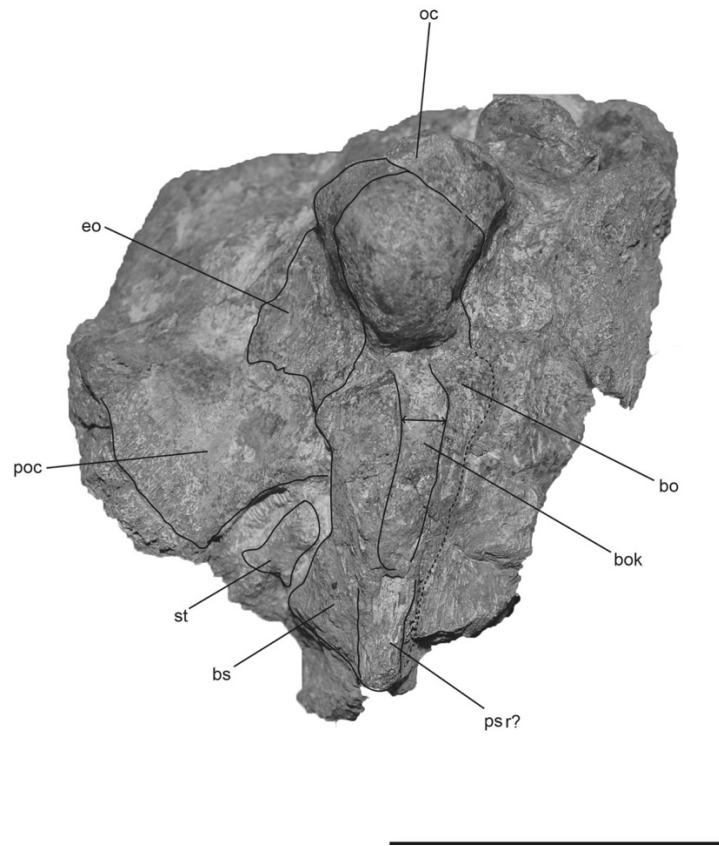


Figure 6. 61. Interpretative drawing on the photograph of the basicranium of SAM-PK-K10888.

BP/1/5445, BP/1/582, MMK5138, NHMUK PV R 36626 and CGP/1/846 are the largest skulls, as they have the greatest cranial length values. This is followed by SAM-PK-K10888, and BP/1/7214 is the smallest. As the snout of none of the specimens is preserved cranial length was measured as function of the thickening

of the parietal along the pineal canal which lies close to the anteroposterior axis of the skull. Postorbital bar thickness is one of the most important characters in *Moschops* which changes with ontogeny (see above). However in *Criocephalosaurus*, although the postorbital bar becomes thicker with an increase in cranial length, this increase in postorbital bar thickness is not as dramatic as it is in *Moschops*. Intertemporal breadth on the other hand shows a positive correlation with an increase in size and seems to be linked with ontogenetic growth.

There is also a change in the cranial outline in dorsal view. This outline is rounded (particularly along the frontals as a result of frontal swelling) in the large skulls MMK5138 and BP/1/5445 (Fig. 5.52A, 5.55A), and is gently curved in the rest of the skulls (Figs. 5.53A, 5.54A, 5.56A, 5.57A).

However, despite the fact that the seven available skulls of *Criocephalosaurus* vary in size which is possibly the result of ontogenetic growth, it is strange that the two smallest specimens (SAM-PK-K10888 and BP/1/7214) are from the *Pristerognathus* Assemblage Zone, while the rest of the specimens are from *Tapinocephalus* Assemblage Zone. Thus the current conclusion regarding ontogenetic changes in *Criocephalosaurus* should be considered tentative until further discoveries demonstrating that large and small individuals with the described characteristics occur in both biozones.

6.6.5 Results and discussion

In general outline the skull of *Criocephalosaurus* is similar to that of *Moschops* and differs in the following apomorphic features: (1) the plane of the pineal canal is almost parallel to the long axis of the skull or at an acute angle to it (Fig. 6.62 E-F), a much wider angle is exhibited in *Moschops* (Fig. 6.62 A-D); (2) extensive antero-posterior elongation of the slit-like temporal fenestra results in the orbit of *Criocephalosaurus* being further anteriorly positioned than it is *Moschops* such that the distance between the pineal opening and the orbit is much shorter in *Moschops*; (3) The postparietal and supraoccipital are dorso-ventrally elongated in *Criocephalosaurus*, and are much shorter in *Moschops*.

The recently discovered skulls which are both from *Pristerognathus* AZ, are smaller than the rest, have a very narrow intertemporal region and relatively large orbits. All these features in association in the case of *Moschops* (above) are indicative of juvenility, and the same probably applies to *Criocephalosaurus*. The difference between the skulls of *Criocephalosaurus* and *Moschops* is that the measure of age for *Criocephalosaurus* would be the width of the cranial roof and extent of the anteroposterior elongation along the postfrontal rather than the thickness of the postorbital bar.

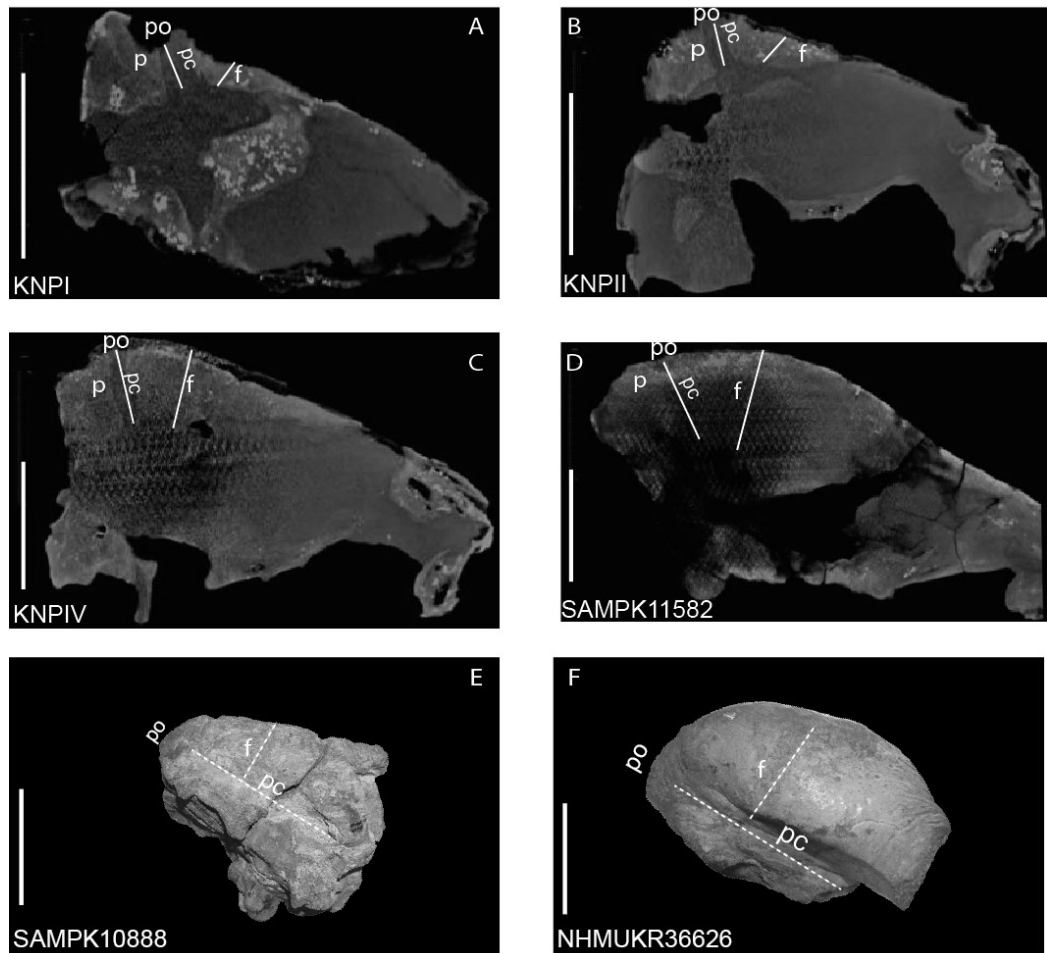


Figure 6.62. A- D. CT scans showing sagittal sections of *Moschops* skulls on an ontogenetic series (KNPI, KNPII, KNPIV, SAM-PK-11582 respectively). The images show the relative orientation between the pineal canal (**pc**) and the dorsoventral axis of the frontal thickness (**f**) in *Moschops*. E-F. Lateral view of the recently discovered *Criocephalosaurus* skulls (subadult assumed SAM-PK-K10888 and NHMUK PV R 36626 respectively). Dashed lines on the surface of the lateral profile of the cranium indicate the orientation and thickness of the pineal canal (**pc**); the frontal (**f**). **p** is for parietal and **po** is for pineal opening. Scale: 10cm.

Criocephalosaurus gunyankaensis is not a well-founded species as none of the Boonstra (1946, 1968, 1969) publications provide a diagnosis for the species. The holotype material appears to be lost and recognition of the species is reliant on the

Boonstra (1968, fig.30) line drawings of three skulls in sagittal section (Fig. 5.63A,C-D) and one cranium in coronal section (Fig. 5.63B). These figures are not very informative and only show that the skulls attributed to *Criocephalosaurus gunyankaensis* had an elongated parietal canal which is almost parallel to the horizontal axis of the skull. The specimens appear to differ in size (judging by the length of the pineal canal noted in the figure), convexity of the occipital surface, and swelling on the posterior end of the frontal. The smallest skull (fig. 5.63D) shows no postparietal concavity, no swollen frontal, and a lesser parietal rise around the pineal canal. The pineal canal in the first section is not shaded to indicate that it was preserved only as a cast.

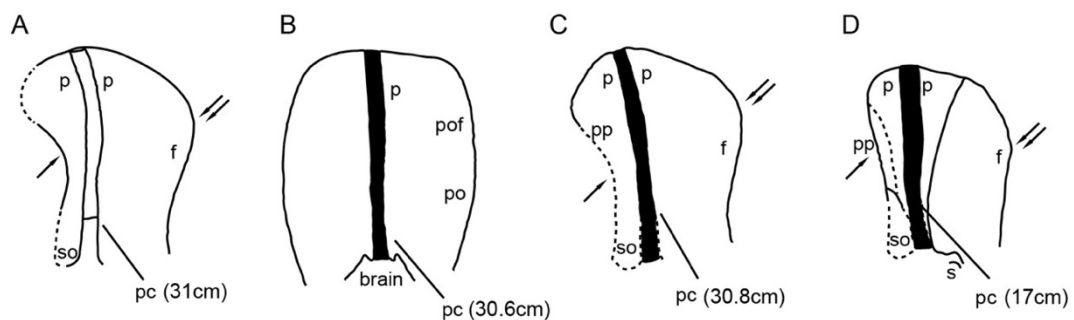


Figure 6.63. The missing “holotype” specimens of *Criocephalosaurus gunyankaensis* redrawn based on the line drawings of Boonstra (1968, fig. 30): A, C and D show skulls in sagittal section and B, in coronal section. Single arrows indicate the concavity of the surface of the the postparietal and double arrow the convexity of the frontal bone.

Boonstra (1946, 1968) did not present a holotype and the drawing of the specimen he presented are lost. Information from Boonstra (1968, fig.30), indicate that these specimens were certainly *Criocephalosaurus* (as the figures show characteristic

features such as long pineal canal parallel to the antero-posterior axis of the skull roof), but do not provide a convincing argument to justify the existence of a separate species from *Criocephalosaurus vanderbyli*. Thus, *Criocephalosaurus gunyankaensis* is considered junior synonym of *C. vanderbyli*. Accordingly *Criocephalosaurus vanderbyli* is the only valid species of the genus.

6.7 *Agnosaurus pienaari* BOONSTRA, 1952d

Holotype: SAM-PK-11832, skull with attached lower jaw from Lamerkraal, Prince Albert District.

Previous Diagnosis: “*Moschosaurus* like tapinocephalid with little pachyostosis. Great temporal fossa and narrow, long and high snout. Quadrate moderately shifted forward. Anterior teeth typical tapinocephalid but posteriorly teeth with spatulate crowns and silindiric roots” (Boonstra 1952d, 242).

6.7.1 Brief notes on the holotype. SAM-PK-11832, the only specimen of *Agnosaurus*, comprises two separate fragments, namely the postorbital and preorbital regions of the skull with associated pieces of the lower jaw attached. The overall state of preservation is poor, especially the left side of the skull, which was presumably exposed to weathering processes longer than the right. As in *Moschognathus*, the skull is only slightly pachyostosed and the preserved portion of the temporal fenestra is suggestive of a large temporal fenestra. The skull has a relatively long preorbital region. As a result of weathering the dentition is not well

preserved and there is no enlarged canine. The palate is not well preserved except for the anterior portion which includes the posterior end of a narrow vomer and a rounded palatine boss with distinct palatine teeth.

6.7.2 Historical background. Boonstra (1952d) considered *Agnosaurus pienzaari* a *Moschosaurus*-like tapinocephalid with little pachyostosis, large temporal fossa, long, high and narrow snout and moderately forward shifted quadrate, and noted the change in dental morphology with the posterior teeth having spatulate crowns and cylindrical roots. *Moschosaurus* in turn (Haughton, 1915) has been considered to be a juvenile *Struthiocephalus* or possibly *Mormosaurus* (*i.e.* a longirostrine tapinocephalid) (Boonstra, 1963b, 1969, King, 1988, Kammerer, 2009). Boonstra (1969) synonymised *Agnosaurus* with *Moschops sp.*, a sentiment later echoed by Brink (1981) and King (1988). Kammerer (2009) synonymised *Agnosaurus pienzaari* with *Moschops capensis*. No reasons were provided for the synonymy of *Agnosaurus* with *Moschops* by any of these authors.

6.7.3 Systematic Palaeontology

Agnosaurus pienzaari Boonstra 1952d

Revised diagnosis. Short snouted tapinocephalid dinocephalian with postfrontal overhanging the orbit, posterodorsally swollen nasal elevates the posterior region of snout resulting in abrupt transition to dorsal skull roof. Palatine boss rounded with marginal dentition arranged anteriorly and laterally. Narrow vomer with thin vomerine lateral ridges extending ventrally.

6.7.4 Description

6.7.4.1 Material

This description is based on the holotype specimen SAM-PK-011832 which is a skull with attached lower jaw from Lamerkraal, Prince Albert District. The surface of the skull and lower jaw are fairly weathered .

6.7.4.2 Cranial pachyostosis and general preservation

The skull of SAM-PK-011832 is badly weathered such that sutural connections between the bones are not clearly visible. The specimen was found as two separate blocks and most of the left side is weathered away. The right side is relatively well preserved but the bone surface is weathered, and the posterior regions of the temporal fenestra and zygoma are missing. The snout and most of the lower jaw are preserved in the anterior block. The anterior palate is well preserved, but the basicranium and the occiput on the left side are not present (Figs.6.64, 6.65).

The cranial roof is flat and narrow with a transition over a slight swelling on nasal to the snout. The snout dorsal outline forms a gentle slope until the tip of the premaxilla anteriorly. The skull has a thin postorbital bar and little pachyostosis (present only on the postfrontal, nasal and incipiently on the postorbital bar), and a relatively large temporal fenestra as in *Tapinocaninus* and *Avenantia*.

The following description is based on the preserved bones of the right side of the skull, as the left side is poorly preserved.

6.7.4.3 Skull roof

Premaxilla: The premaxilla forms the anterior extremity of the snout, the anterior and anterodorsal margins of the external naris (Fig. 6.64), and is best preserved posterodorsally on the snout. The bone surface is heavily eroded to the extent that the roots of the replacement incisors are revealed in dorsal view. A maxilla-premaxilla suture is not visible. Because of the eroded nature of the skull remains of the incisor dentition are mostly the roots of the replacement incisors and it is not possible to determine the number of teeth. Posterodorsally the premaxilla has a short transverse sutural contact with the nasal slightly over the mid- preorbital portion of the snout.

Septomaxilla: The septomaxilla (Fig. 6.64) which is preserved only on the right side, is very fragmented within the naris and extends posteriorly on the skull roof behind the external naris as a pointed wedge between the maxilla and nasal.

Nasal: The nasals (Fig. 6.64) are typically long strap-like bones which form most of the dorsal surface of the preorbital region and the roof of the external naris. Posteriorly they have a short contact with the prefrontal, a transverse sutural contact with the frontal and laterally have a long contact with the maxilla.

Maxilla: In lateral view the maxilla (Fig. 6.64) is a relatively high and small sub-triangular bone. The posterodorsal apex of the triangle forms a wedge between the nasal and the prefrontal, thus preventing contact between these two bones.

Posteriorly the maxilla contacts the prefrontal, lacrimal and jugal anterior to the orbit, but because of extensive weathering of the skull these contacts are not visible. Dorsally the maxilla contacts the nasal but this suture too is not visible.

Anterodorsally the maxilla meets the septomaxilla posterior to the external naris and has sutural contact with the premaxilla anteriorly, below the external naris.

Weathering on the maxillary surface reveals casts of several generations of poorly preserved replacement teeth.

Lacrimal: The lacrimal (Fig. 6.64) forms the anteroventral margin of the orbit.

Dorsally it contacts the prefrontal and ventrally has an arcuate sutural contact with the jugal, but the anterior contact with the maxilla is not evident.

Jugal: The jugal (Fig. 6.64) forms the entire ventral margin of the orbit but its anterior border with the maxilla is not preserved. Anterodorsally it contacts the lacrimal. Posterodorsally it contacts the postorbital at the base of the postorbital bar and meets the squamosal posteriorly and ventrally such that the jugal does not participate in the border of the temporal fenestra.

Prefrontal: In lateral view the prefrontal (Fig. 6.64) is an elongated quadrangular bone forming most of the dorsal margin and half of the anterior margin of the orbit, but because of extensive weathering of the skull surface none

of the surrounding sutural contacts can be precisely determined. Posterolaterally and dorsally it contacts the frontal while anterodorsally it has a short contact with the nasal and anteriorly with the maxilla. The surface of the prefrontal is slightly thickened along the dorsal orbital margin and along its border with the frontal.

Frontal: In dorsal view the frontal is an elongated quadrangular bone (Fig.5.64) that forms most of the preserved cranial roof. Anterolaterally it is in contact with the prefrontal, anteriorly with the nasal and meets the parietal posteriorly. The surface of the frontal is mostly weathered away but a crenulated midline suture is clearly visible. The frontal has a short contact with the dorsal orbital margin but its contribution to the temporal fenestra is not clear (Fig. 6.64).

Postfrontal: The postfrontal is a triangular bone (Fig. 6.64) forming the posterodorsal margin of the orbit and dorsal-most portion of the postorbital bar. A feature of the postfrontal is its anterodorsally protruding morphology which differentiates *Agnosaurus* from all other short snouted tapinocephalids perhaps with the exclusion of *Struthiocephalus* where the postfrontal forms a boss. Dorsomedially the postfrontal contacts the frontal and has an oblique ventral contact with the postorbital but its contribution to the margin of the temporal fenestra is not clear.

Postorbital: The postorbital, in lateral view, is a triangular bone with its apex having a short contact on the posterior orbital border (Fig. 6.64). Anteroventrally it contacts the jugal and has a short posteroventral contact with the squamosal.

Due to the weathering it is not possible to determine whether the postorbital contacts the margin of the temporal fenestra. Dorsally it is in contact with the postfrontal.

Parietal: In dorsal view the parietal is a relatively narrow triangular bone positioned between the temporal fenestrae with its apex pointing forward to form a midline wedge between the frontal pair (Fig. 6.64). Posteriorly it meets the postparietal but the contact is not clear as a result of weathering. Laterally the parietal contributes to the dorsal border of the temporal fenestra but contact with other surrounding bones is not preserved.

The ovoid pineal opening is situated half way along the dorsal surface of the parietal. Despite excessive weathering it appears that the surface of the parietal in the area around the pineal foramen is raised above the frontal surface on a slight chimney.

Squamosal: Only a small anterior portion of the squamosal is preserved where it contacts the postorbital anterodorsally and jugal anteriorly. The posterior part, which forms the zygomatic arch, is almost completely weathered away and does not facilitate description.

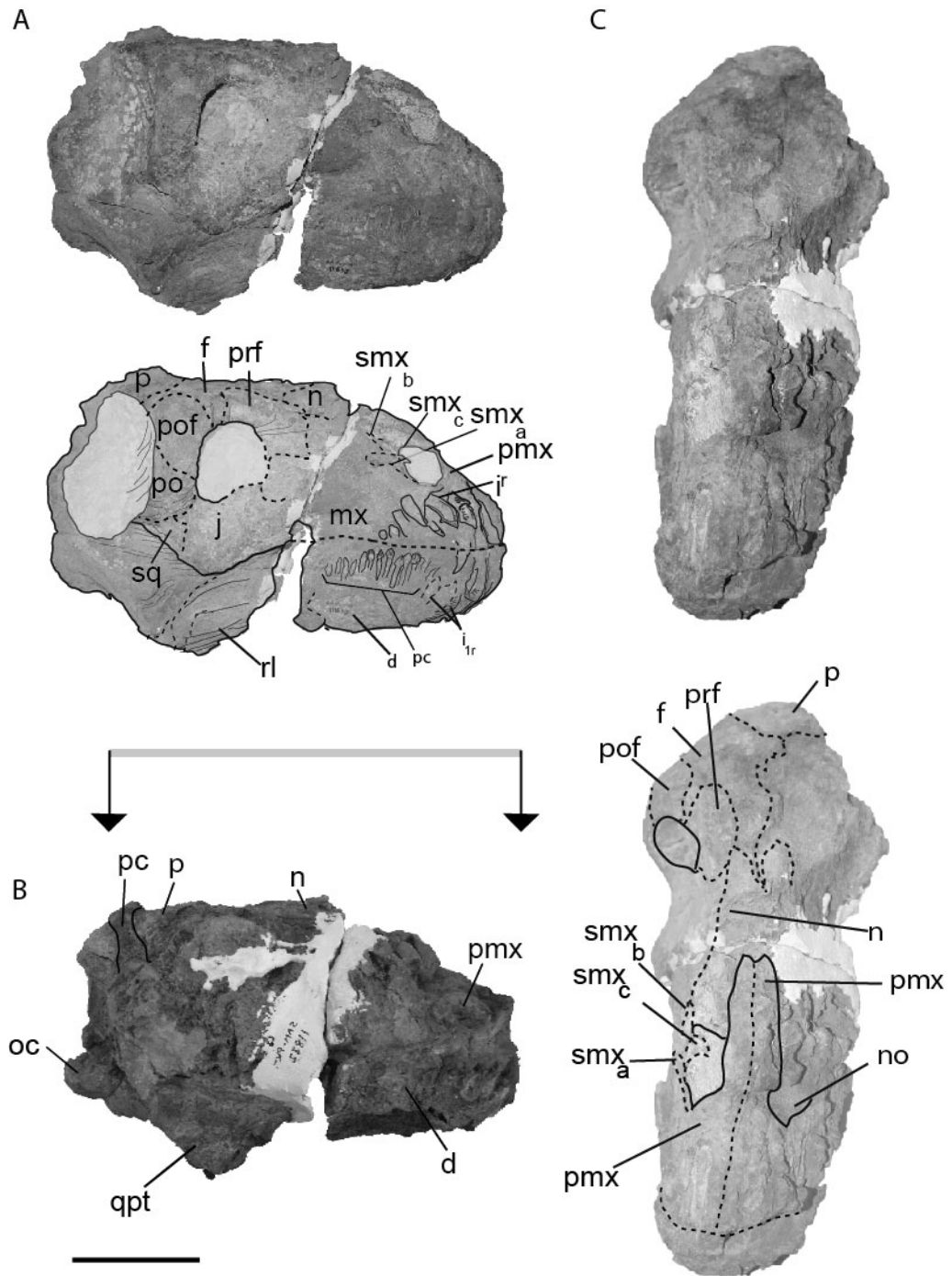


Figure 6. 64. The holotype of *Agnosaurus pienaari* (SAM-PK-11832): right lateral view (A), reflected left lateral view to facilitate comparison (B), and anterodorsal view of the skull roof (C). Scale 10 cm.

6.7.4.4 Occiput

The occiput (Fig. 6.65C) is badly preserved, particularly the left side, missing the occipital rim and showing the weathered right partial surface of the postparietal, supraoccipital, tabular and paraoccipital process. However, it appears as if the supraoccipital, opisthotic and the tabular are fused together so that the sutures in between them are not visible. The occipital condyle is tripartite as in all tapinocephalid dinocephalians, and it is preserved with the contribution of the right exoccipital dorsolaterally and the basioccipital ventrally.

Postparietal: In occipital view, the right side of the unpaired quadrangular postparietal (Fig. 6.65C) is preserved but its sutural contacts with the surrounding bones cannot be delineated. On the dorsal rim of the occiput, although the bone surface is not preserved, its contribution to the occipital rim can be deduced from a dorsal suture with the parietal. A longitudinal raised keel extends down the midline.

Supraoccipital: The supraoccipital (Fig. 6.65C) forms the dorsal margin of a small foramen magnum but neither its general shape nor its contacts are discernable on the specimen.

Tabular: Situated on the right dorsolateral side the tabular is a smooth surfaced semilunate bone which contacts the postparietal medially, but its contacts with the rest of the surrounding bones (supraoccipital, opisthotic and squamosal) cannot be delineated (Fig. 6.65C).

Opisthotic: The opisthotic forms the posteroventral portion of the occiput and its surface is weathered such that it is not possible to accurately describe its morphology.

6.7.4.5 Palate

Premaxilla: The paired premaxilla forms the anterior margin of the palate. Its alveolar border is covered by the lower jaw and is not visible. Posteromedially it meets the vomer at the anterior end of the internal naris. Normally in tapinocephalids the vomer abuts on the medioventral side of the premaxilla but this portion of the premaxilla appears to ventrally overlie the anterior end of the vomer which is here considered as secondary deformation in this specimen.

Vomer: The vomer, which forms the medial border of the elliptical chona, is a paired elongate bone with a midline groove. In ventral view it overlies the premaxilla anteriorly and is in contact with the palatine posteriorly. A lateral ridge projects ventrally along the entire bone and contacts the palatine boss posteriorly, and towards the anterior end the ridge becomes less prominent.

Palatine: The right anterior projection of the palatine (Fig. 5.65A, 5.66A) is exposed and ventromedially overlies the maxilla. It extends posteromedially to form the palatine boss which is best exposed on the left side. Anteromedially the palatine forms the posterior margin of the internal naris and is in sutural contact with the posterior end of the vomer. The anteriorly rounded and relatively large

(compared to *Moschops*) palatine boss is elevated relative to the rest of the palatine and bears a single row of marginal teeth on the anterior and lateral edges. The middle portion of the boss is slightly depressed and has a smooth surface.

Pterygoid: The pterygoid, which covers more than the half of the palatal surface, typically comprises a thin palatine process of the pterygoid anteriorly, and a posterior corpus which posterolaterally extends as a thin elongated quadrate ramus that is preserved on the right side. The transverse flanges of the pterygoid are not preserved in this specimen. An interpterygoidal vacuity appears to be absent, and the united pterygoids form a midline ridge posterior to the lateral processes and the interpterygoidal vacuity. The posterior sutural contact of the pterygoid with the parabasisphenoid is not discernable.

Parabasisphenoid: The parabasisphenoid (Fig. 6.65A) is a relatively small bone. Anteriorly it contacts the pterygoid corpus while posteriorly it meets the basioccipital, but these contacts are not discernable. A midline ridge extends down the ventral surface and is a posterior continuation of the pterygoidal midline ridge and continues posteriorly as the basioccipital keel.

Basioccipital: This bone is not well preserved. It lacks the portion that contributes to the occipital condyle and the anterior connection with the basisphenoid.

Stapes: The right stapes (Fig. 6.65) is present, but not well preserved, and extends between the medial condyle of the quadrate distally and the fenestra ovalis on the

medial side. The stapes appears to project almost vertically out from the palatal surface such that the lateral end is more ventrally positioned than the medial end which enters the fenestra ovalis.

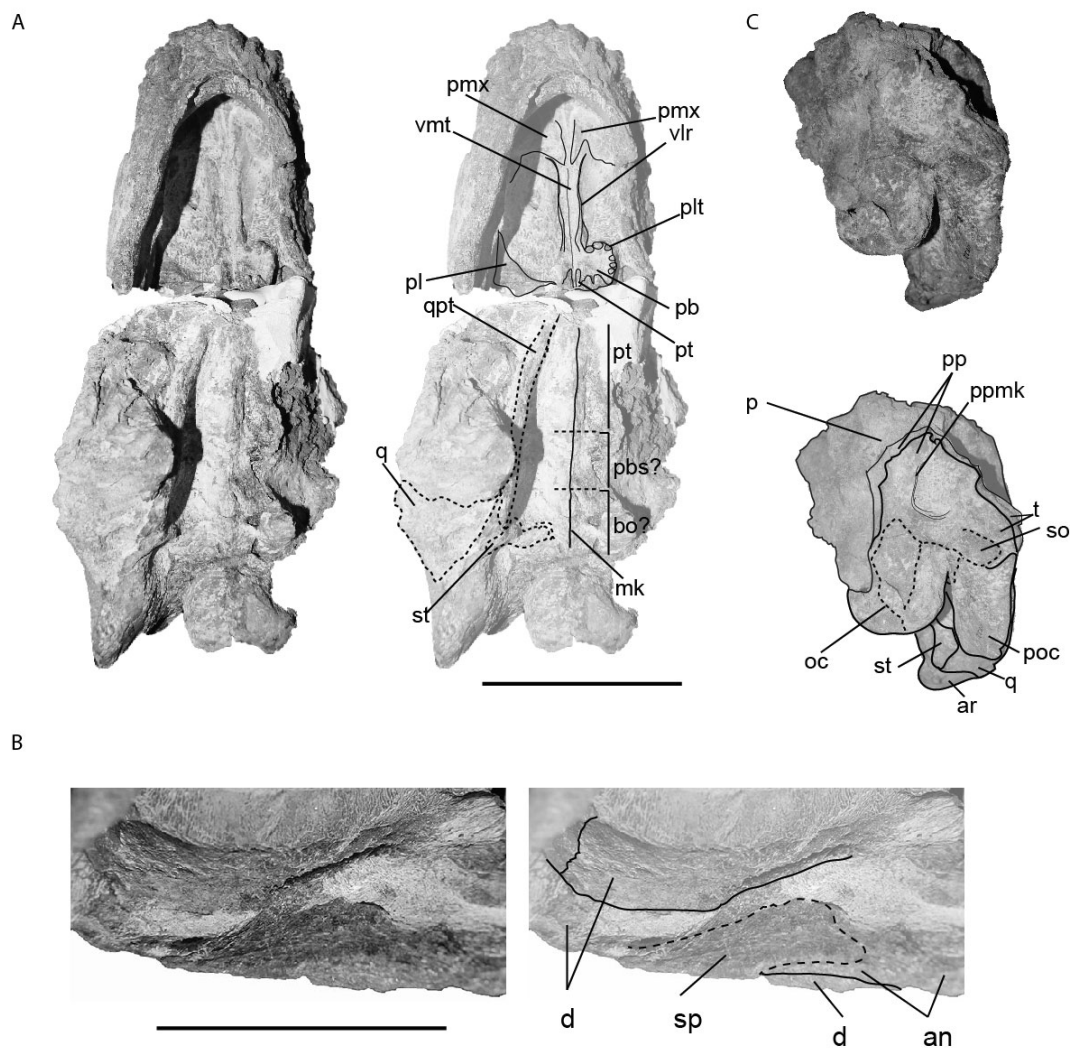


Figure 6. 65. *Agnosaurus pienaari* (SAM-PK-11832): ventral view of the palate (A); medial view of the right mandible anteriorly (B); posterior view of occiput (C). Scale: 10 cm.

Quadrate: On its dorsal side, the quadrate (Fig. 5.65A) is a relatively large sheet like bone which is poorly preserved and present only on the right side of the skull, ventrally it has two condyles which articulate with the lower jaw. The dorsal process anteriorly overlies the squamosal and the medial condyle contacts the quadrate ramus of the pterygoid and the stapes.

6.7.4.6 Lower jaw and dentition

The lower jaw of the *Agnosaurus* holotype (SAM-PK-11832) is preserved in occlusion with the upper jaw, but only the anterior and posterior ends are present and are badly weathered.

Dentary: The dentary forms most of the preserved right lateral surface of the lower jaw and has a very thick anterior symphysis. Anteriorly the lateral surface is very weathered and fortuitously reveals the crown and roots of at least seven emerged postcanines and an additional four which are in the process of emerging; as well as the weathered crowns of four incisors and an additional two teeth which are replacement incisors (Fig. 6.64A).

Splénial: The splénial is a sheet like bone that covers the anterior one third of the ventromedial surface of the lower jaw and meet its counterpart anteromedially in the symphysis. Anterodorsally its has a long contact with the dentary which continues posteriorly to meet the prearticular.

Angular: On the lateral surface of the lower jaw the angular is discernable only at its anteroventral contact with the dentary and posteriorly where it forms what

appears to be a small reflected lamina (Fig. 6.64A). Only the posterodorsal portion of this lamina is preserved. Anteriorly on the ventral margin of the lower jaw, the angular has a wedged contact between the dentary laterally and splenial on the medial side (Fig. 6.65B).

6.7.5 Results and discussion.

The holotypes of both *Agnosaurus pienaari* (SAM-PK-11832) and *Moschosaurus longiceps* (SAM-PK-3015) were prepared to remove as much matrix as possible. This resulted in exposure of the palate in both skulls which surprisingly revealed teeth on the palatine boss in both genera. In *Agnosaurus* these are arranged as a single row on the anterior and lateral edges of a rounded palatine bosses; in *Moschosaurus* the palatine bosses are reniform and the dentition is scattered and not in a single row on the boss in contrast to *Agnosaurus*.

A few aspects relating to the palatal morphology are interesting: The presence of dentition on the palatine boss in tapinocephalids is known only from one specimen of *Struthiocephalus* and a possible presence in *Tapinocaninus*. Rubidge (1994) in his description of *Tapinocaninus* recognised pitting on the relatively enlarged palatine boss of *Tapinocaninus* which he considered to possibly be the remnants of alveoli of palatal teeth but pointed out that no teeth are preserved. Boonstra (1953b, p. 4, fig.4) mentions the *Struthiocephalus* specimen, SAM-PK-11591 having a rounded palatine boss with “indications of the roots of a small number of palatine teeth”. This specimen does not manifest the rounded palatine boss of *Agnosaurus* and has irregularly separated tooth roots as depicted by

Boonstra (1953b, fig. 4). Amongst Dinocephalia palatine teeth are known in anteosaurids, estemmenosuchids (*e.g.* Orlov, 1958; Tchudinov, 1965; Rubidge, 1991; Kammerer, 2010) and Rubidge and van den Heever (1998) also described pitting on the palatine boss in *Styracocephalus*, similar to *Tapinocaninus*.

Amongst therapsids Huttenlocker and Abdala (2016) considered the presence of palatine teeth in some therocephalians to be a juvenile feature. Because of their small size, lack of cranial pachyostosis, thin postorbital bar and large orbits it is possible that the holotypes of both *Moschosaurus* and *Agnosaurus* could be juvenile or subadult individuals, and the question arises as to whether the presence of palatine teeth in these skulls could be a juvenile feature and if they could be juveniles of a known tapinocephalid genus. *Moschosaurus* and *Agnosaurus* have in the past been synonymised with *Struthiocephalus* and *Moschops* respectively (Boonstra, 1969).

The ontogeny in tapinocephalids is not well established mainly due to the lack of good representation of size in its taxa. *Struthiocephalus* is based on large size skulls, whereas *Moschops* is represented by mostly small sized skulls (incl. skulls which are similar in size to *Agnosaurus* holotype). Could *Moschosaurus* be a juvenile *Struthiocephalus*? The holotype of *Moschosaurus* has similarities with the longirostrine forms (*e.g.* *proportionally* long and slender snout and similarly angled zygoma), however, the morphology and size of the palatine boss in *Moschosaurus* is different to that of *Struthiocephalus* (Fig. 6.65B, B1, D, D1 and G). Also the palatine boss in *Struthiocephalus* is greatly reduced in comparison

with that of *Moschosaurus*. Reduction in the size of palatine boss could be ontogenetic for *Struthiocephalus* but there are not sufficient specimens to test this argument as *Struthiocephalus whaitsi* is represented by only large sized skulls. In contrast *Moschops* is represented mainly by small skulls and permit testing of this idea: It appears the palatine boss in both the juvenile and the adult *Moschops* skulls are similar in morphology and are small in *Moschops* (Fig. 5.65 E-F), thus suggesting that the same principle may apply to *Struthiocephalus* and it is thus unlikely that *Agnosaurus* is a juvenile of this genus.

This thesis has demonstrated that *Moschops* not only lacks palatal dentition in the subadults, but also its cranial morphology in both subadults and adults is quite different to that of *Agnosaurus*. The palatine boss of *Agnosaurus* in contrast is fairly large and rounded (Fig. 5.64 A,A1). The palatine boss of *Agnosaurus* appears to differ from that of all other known tapinocephalids in this aspect (Fig. 5.65A1-D1). The outline of the cranial roof of *Agnosaurus*, as seen in lateral view, also differs from that of all the other tapinocephalids as the transition from its rather flat cranial roof occurs over a nasal swelling.

Thus, based on the above mentioned differences (the unique palatine boss morphology and palatine teeth pattern) and the difference in cranial outline, *Agnosaurus pienaari* is considered to be a valid taxon which is represented by a possibly subadult holotype.

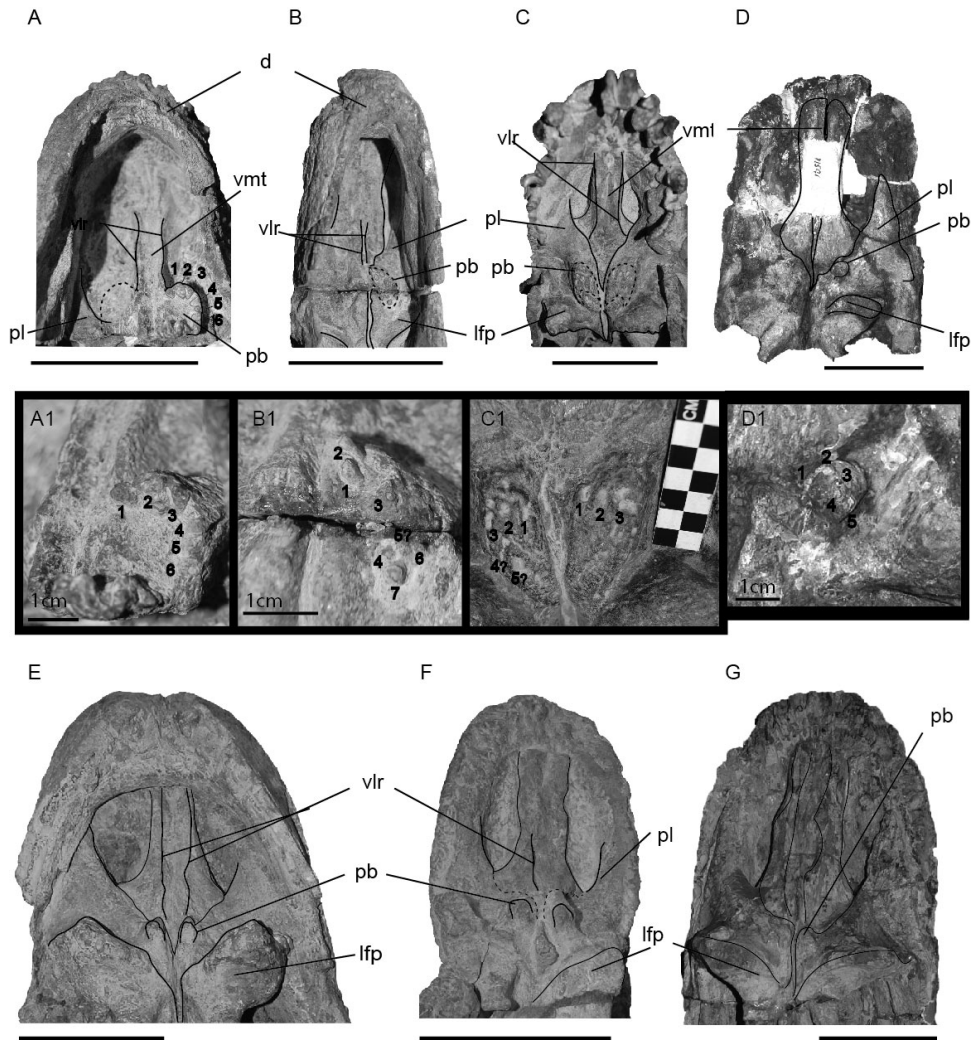


Figure 6.66. The anterior portion of the palate in the holotype of *Agnosaurus pienaari*, SAPK-11832 (A), holotype of *Moschosaurus longiceps*, SAM-PK-3015 (B), holotype of *Tapinocaninus pamela*, NMQR2987 (C), referred specimen of *Struthiocephalus whaitsi*, SAM-PK-11591 (D), referred specimen of *Moschops capensis* (holotype of *M. koupensis*) SAM-PK-11582 (E), the holotype of *Moschops capensis*, AMNH FARB5550 (F) and a referred specimen of *Struthiocephalus whaitsi*, SAM-PK-K272 (G). The upper row shows the tapinocephalids which have palatine dentition or with alveolar pits for palatine dentition. The middle row shows close-up photos of the palatine boss of the above specimens labelled A1, B1, C1 and D1 respectively. Scale: 10 cm.

6.8 *Mormosaurus seeleyi* WATSON, 1914

Holotype: NHMUK PV R 3594 a skull without lower jaw (Broom, 1909b, figs.1-2, Watson, 1914, Pl.IV., 1-2, text figs.1-4, Broom, 1932, figs. 10A-B). The locality of the specimen is unknown. Broom (1909b, p.401) assumed that it is from the “the Pareiasaurus Zone of Gough”.

Previous Diagnosis for genus. “(1) Snout short, very shallow, facial surface not exceeding posterior to the anterior orbital border, very abrupt transition from the facial to the cranial surface. (2) Dorsal cranial surface very strongly pachyostosed, with the centres of thickening coalasced, and transition on the face very abrupt along a very definite transverse line forming a transverse wall. (3) Additional pachyostosis: (a) Nasal boss laterally confluent with the thickening of the postorbital bar and the prefrontal and thus forming a transverse wall from orbit to orbit. (b) Parietal boss not very distinct, confluent with the general pachyostosis of the parietal and frontal. (c) Postorbital bar wide and massive but without distinct bulbous boss and thus flowing evenly on to the general dorsally thickened surface. (d) Posttemporal arch greatly thickened and rugose. (e) Orbits not visible in dorsal view and in dorsal view the postorbitals do not form the lateral border of the skull. (f) Antero-posterior diameter of temporal fossa small and fossa transversely oval. (g) Dorsal parietal surface fairly wide, laterally indistinctly bayed. (4) Dentition feeble, uniform. (5) Quadrate moderately far forward with the quadrate ramus of the pterygoid not extending much posterior to the plane of the quadratic condyle, not underlaying the distal end of the stapes. (6) The lateral ramus of the pterygoid does not form a prominent transverse bar and the width across the transverse rami is small. (7) The intersquamosal width is large. (8) The

basioccipital condyle is directed posteriorly. (9) The frontal appears to be small and is excluded from the orbital border, the supraoccipital is wide and low, the tabular with a moderate occipital face and apparently enters the posttemporal fossa, the lacrimal meets the nasal, the squamosal with an anterior wedge into the jugal.” Boonstra, 1953b, p. 45-46.

Previous Diagnosis for genus and species.

“ 1. The preorbital length is 57-58% of the total median length; the snout is thus fairly long (preorbital length 270-318 mm.) and fairly narrow to fairly broad (222-279 mm.) and fairly high (150-186), with the height 67-68% of the width; the facial surface of the snout is fairly short and it does not extend to the plane of the antorbital border; the transition from the facial to the cranial surface is abrupt. 2. The dorsal cranial bones are strongly pachyostosed, with the centres of thickening coalesced and the transition on to the face is by an abrupt step along a curved transverse line; the thickening extends far forward- anterior to the plane of the anterior orbital border; along the median line the pachyostotic cranial roof is 252-267 mm. In length and this is 48-55 % of the total median length of the skull; this moderate anterior extension is due to the thickened naso-frontal boss, which stands out well above the general cranial surface. On the upwardly sloping face of the posterior part of the nasals there are a pair of shallow depressions. The prefrontal is greatly thickened in its posterior three- quarters but not in its anterior one-quarter and it overhangs the orbit, but not in its anterior one-quarter and it overhangs the orbit, but the antero-dorsal orbital border is not greatly thickened. The surface around the pineal opening foramen is lower than that of the

surrounding bones. 3. The postorbital bar is fairly wide and massive. 4. The posttemporal arch is thick and the temporal fossa is small with its antero-posterior diameter small to moderate. 5. The dorsal parietal surface moderate to broad (150-200mm) and the interorbital width is 88-97% of the intertemporal width. 6. The antero-posterior length of the parietal is small (75 mm.) and the frontal is fairly large. 7. The intersquamosal width is moderate to great (438-477 mm.); and the median length is 105-115% of the intersquamosal width and skull is thus slightly to appreciably narrower than long. 8. The quadrate is situated fairly far forward; the mandibular length is 59-64% of the median length of the skull; the lateral pterygoid rami weak but fairly wide. 9. The dentition is poorly preserved, but the anterior teeth in one specimen fairly robust.” Boonstra, 1956, p. 158-159.

“*Mormosaurus* can be diagnosed by the following autapomorphy: masive frontonasal boss circular in cross-section.” Kammerer, 2009, p. 223

6.8.1 Historical background. The skull of NHMUK PV R 3594 was initially referred by Broom (1909b, figs.1,2) to *Tapinocephalus*. Watson (1914, text figs.1-4), after further preparation of the skull, described this specimen as the holotype of *Mormosaurus seeleyi*. He (Watson, 1914) did not provide a diagnosis for the species but provided information about the holotype in a composite description of the tapinocephalid skull. Gregory (1926, p. 227) (based on the illustration provided by Watson [1914] which suggests that he had not personally examined the specimen) considered *Mormosaurus* to be the most derived tapinocephalid because of the “enormous” width of the postorbital and zygomatic arches. He

stated that although *Mormosaurus* had affinities with both *Tapinocephalus* and *Struthiocephalus*, it was probably cogenetic with *Tapinocephalus*. Boonstra (1936, p.94) however determined that the affinities weighed more on the longirostrin side and grouped *Mormosaurus*, *Struthiocephalus* and *Taurocephalus* in Mormosauridae as a longirostrin family. Boonstra considered *Mormosaurus* as morphologically intermediate between the short and long snouted tapinocephalid forms. He differentiated *Mormosaurus* from *Tapinocephalus* because of the former's relatively longer snout and less pachyostosis. Boonstra (1953b, p. 45-46) presented a lengthy diagnosis for the genus *Mormosaurus* which he based in the Watson's description and figures. This diagnosis was later adapted into a specific diagnosis with contributions from a referred specimen, SAM-PK-9082 (Boonstra, 1956, p. 158-159, figs.8-10). Boonstra (1956), different to his previous works (Boonstra, 1936, 1953b), discarded Mormosauridae and grouped *Mormosaurus* with *Tapinocephalus* under Tapinocephalidae which also included *Phocosaurus*, *Keratocephalus* and *Taurops*. *Taurops* was shortly hereafter synonymised with *Tapinocephalus* by Boonstra (1969). More recently, because the holotype of *Phocosaurus megischion* was based on only postcranial elements it was considered a *nomen dubium* (Kammerer 2009). The only cranial element which was referred to *Phocosaurus* (SAM-PK-11997, comprising both cranial and postcranial material) on the basis of the similarity of the postcranium was also referred to *Mormosaurus* by Kammerer (2009). *Keratocephalus moloch* of von Huene (1931) is based on a skeleton and cranial fragments and has been synonymised with *Struthiocephalus whaitsi* by Kammerer (2009). Thus, currently

Mormosaurus and *Tapinocephalus* are left as the only members of the subfamily Tapinocephalinae of Boonstra (1969) (=Tapinocephalidae of Boonstra, 1956).

Kammerer (2009, p. 224) drew attention to the similarity between *Mormosaurus* and *Struthiocephalus* in having flattened snouts, distinct nasofrontal bosses and similar zygoma morphology. He recognised the validity of both genera stating “The frontonasal boss of *Mormosaurus* is massive and circular with a dome-like appearance in lateral view, whereas that of *Struthiocephalus* is anteroposteriorly elongate, with a somewhat blade-like appearance in lateral view.” ... “The snout of *Mormosaurus* is broader anteriorly than that of *Struthiocephalus*..”

“..*Mormosaurus* lacks the laterally flared zygoma in dorsal view present in *Struthiocephalus*”. Kammerer (2009) further regarded *Taurocephalus lerouxi* of Broom, 1928 and *Struthiocephalus rheederi* of Broom, 1937 (= *S. whaitsi* by Boonstra 1969) as synonymous with *Mormosaurus seeleyi* as well. The holotype skulls of both *Taurocephalus lerouxi* and *Struthiocephalus rheederi* are extensively reconstructed with plaster and in the process of reconstruction they gained features which made the specimens unusual (e.g. the extremely long quadrates of *S. rheederi* and the strongly projecting eyebrow like supraorbital bosses of *T. lerouxi*).

6.8.2 Systematic Palaeontology

Mormosaurus seeleyi Watson 1914

Syn. *Struthiocephalus rheederi*

Taurocephalus lerouxi

Pnigalion oweni

Revised diagnosis. *Mormosaurus* can be diagnosed by the following combination of characters: Tapinocephalid with a broad and moderately long snout, with or without nasofrontal boss which is anteroposteriorly elongated (shorter than *Struthiocephalus*) and the thickening of the nasofrontal area is in confluence with the thickening of the postorbital dorsally as in *Tapinocephalus* but not in with the prefrontal (in contrast to *Tapinocephalus*), zygoma posteroventral corner is angled and does not flare as in *Struthiocephalus*. The nasofrontal boss gently rounded in lateral view and does not forms the sharp blade-like dorsal outline of *Struthiocephalus* (after Boonstra, 1956 and Kammerer, 2009).

Remarks. As taxonomic revision and description of the longirostrin tapinocephalids is not the ambit of this thesis, in this contribution, the proposed synonymies by Kammerer (2009) and a proposed synonym of *Pnigalion oweni* in this work, are discussed through the comparative description of the holotype materials of all synonymised taxa. This is done because the holotype of *Mormosaurus* (NHMUK PV R 3594) was originally described as a short snouted tapinocephalid.

6.8.3 Comparative description of the holotype skulls of *Mormosaurus seeleyi*, *Taurocephalus lerouxi*, *Struthiocephalus rheederi* and *Pnigalion oweni*.

6.8.3.1 General preservation and cranial pachyostosis. The holotype of *Mormosaurus seeleyi*, NHMUK PV R 3594, comprises a skull lacking a lower

jaw and part of the left zygoma. The skull is moderate to large size with fairly good preservation of the cranial roof and anterior part of the palate. The occiput and basicranium portions are damaged and distorted. Dentition is very poorly preserved on the alveolar border of skull and the only remnants are alveolar pits in the premaxilla and maxilla. The cranial roof is thickened but the overall pachyostosis, for its size, is less than that of a similar-sized *Tapinocephalus* skull. The intertemporal width is also, for its size, relatively narrower than that of *Tapinocephalus*. The holotype of *Struthiocephalus rhedeeri* (TM 1484) is the largest and the most pachyostosed of the above skulls with an intertemporal width of 140 mm. The skull is relatively well preserved but lacks the basicranium and a large part of the occiput, right zygoma and lower jaw.

The holotype skull of *Taurocephalus lerouxi* (AMNH FARB 5655) is largely plaster reconstructed. It comprises portions of lower jaw which are occluded with the upper jaw, including the anterodorsal part of the left dentary and the posterior portion of the right ramus of the lower jaw. The rest of the lower jaw is reconstructed in plaster. The skull roof is not as pachyostosed as those of NHMUK PV R 3594 and TM 1484. The intertemporal width is 110 mm and, as a result of excessive surface weathering, it is difficult to determine sutres between bones of the skull roof.

The holotype of *Pnigalion oweni* (NHMUK PV R 3596) comprises an incomplete posterior two-thirds of a skull with a lower jaw and associated postcranial elements. It lacks the entire preorbital region (*incl.* the anterior border of the orbit)

and palate, and the occiput is poorly preserved. The cranial roof demonstrates moderate pachyostosis (less than most other tapinocephalids), a narrow intertemporal (110 mm) and relatively roomy temporal fenestra. Distortion twisted the vertical axis of the skull towards the left and explains the exaggerated flanking of the right zygoma. The left zygoma is incompletely preserved, mainly anteriorly, and appears to have been reconstructed from several bone fragments.

The following cranial description pertains to specimens NHMUK PV R 3594 (*Mormosaurus seeleyi* holotype), NHMUK PV R 3596 (*Pnigalion oweni* holotype), TM 1484 (*Struthiocephalus rhedeeri* holotype) and AMNH FARB 5655 (*Taurocephalus lerouxi*).

6.8.3.2 Skull roof.

Premaxilla: The premaxilla (Figs. 6.67A, 6.68A, 6.69A, 6.71, 6.73) is a paired bone which is preserved in all specimens except NHMUK PV R 3596. It forms the anterior tip of the snout and on the skull roof it borders the anterior and medial borders of the narial opening (preserved only in NHMUK PV R 3594 and TM 1484). This portion of the premaxilla is flat and is anteroposteriorly long, extending as a narrow internarial process that contacts the nasal above the level of the anterior border of the orbit as is evident in NHMUK PV R 3594, TM 1484 and AMNH FARB 5655. The premaxilla's contact with the nasal is bifurcated in NHMUK PV R 3594 and TM 1484, but is not visible in AMNH FARB 5655. The posterior end of the premaxilla curves upwards slightly as it contacts the nasal on

the anterior border of the nasofrontal boss. This upward curve is smoother in AMNH FARB 5655 than it is in NHMUK PV R 3594 and TM 1484.

The premaxilla-maxilla suture is visible on the lateral surfaces of NHMUK PV R 3594 and TM 1484 on the left side, extending from the anterolateral border of the narial opening to the alveolar margin. This appears to coincide with the alveolar border of the fifth incisor in NHMUK PV R 3594 (Fig. 6.66B).

Septomaxilla: Anteriorly the septomaxilla (Figs. 6.71A, 6.68A, 6.69A, 6.72, 6.72, 6.73) covers the base of the narial opening and posteriorly contributes to the lateral border of the narial opening. Posteriorly the septomaxilla forms a pointed facial extension which extends as far as the mid-preorbital level in NHMUK PV R 3494; while it ends slightly further forward in AMNH FARB 5655 and TM 1484.

Nasal: The nasal (Figs. 6.71A, 6.68A, 6.69A, 6.71, 6.72, 6.73) is preserved in all three specimens, but in NHMUK PV R 3596 its anterior portion is damaged where it forms the posterior border of the narial opening. It is a long triangular bone with its base against the frontal, and the apex forming the posterior border of the external naris. Posterodorsally it has a long lateral sutural contact with the maxilla, and meets the frontal posteriorly and posterolaterally as preserved in NHMUK PV R 3594 and TM 1484. A nasofrontal boss is relatively well developed in NHMUK PV R 3594 and TM 1484 but is only slightly elevated above the skull roof in the rest of the skulls. This upward turn of nasal and frontal to form the nasofrontal boss is not as pronounced as that of *Tapinocephalus* and

Struthiocephalus. The nasal is not preserved in NHMUK PV R 3596 but the morphology of its sutural contact with the frontal at its posterior end is evident.

A relatively shallow depression on the surface of the nasal pair is present anterior to the nasofrontal boss and is evident in NHMUK PV R 3594 and TM 1484, but not in AMNH FARB5655. This feature was reported by Boonstra (1956) as occurring in the short snouted taxa, but my study has demonstrated that it is also present in some *Struthiocephalus* specimens as well (e.g. SAM-PK-K272). The oval external naris has its longitudinal axis more or less parallel to the horizontal axis of the snout in NHMUK PV R 3594, TM 1484 and AMNH FARB 5655.

Maxilla: The maxilla (Figs. 6.71A, 6.68A, 6.69A, 6.71, 6.72, 6.73), which is a relatively large bone on the lateral surface of the snout, is almost completely preserved in NHMUK PV R 3594 and partially in TM 1484 and AMNH FARB 5655. It is broadly triangular with the apex at the pointed contact between the nasal and prefrontal. The maxilla forms the ventral border of the external naris, has an anterior sutural contact with the premaxilla, and meets the septomaxilla and nasal dorsally. Posteriorly it has sutural contact with the prefrontal, lacrimal, and a wavy sutural contact with the jugal. The posteroventral end of the maxilla forms a thin spur into the jugal as seen on the right side of NHMUK PV R 3594 and AMNH FARB 5655.

Jugal: The jugal (Figs. 6.71, 6.72, 6.73) is an elongate bone that forms the ventral border of the orbit and contributes to both the facial surface anteriorly and the

zygoma posteroventrally. It is almost completely preserved on the right side of NHMUK PV R 3594 and AMNH FARB 5655. The suborbital portion in all three skulls is damaged, particularly affecting the areas where it contributes to the orbital border and its connection posteriorly with the postorbital. In both NHMUK PV R 3594 and AMNH FARB 5655, the zygoma surface is weathered (particularly in AMNH FARB 5655) and the sutures of the jugal with the surrounding bones are not easily discernable. This difficulty is enhanced by the fact that presumed sutural contacts were drawn on the specimen by previous investigations. In AMNH FARB 5655 the posteroventral end of the jugal (following drawn suture lines (Broom, 1928, fig. 2; Boonstra, 1936, fig. 5)) indicates a large and unnatural exposure of the quadratojugal on the lateral surface of the skull. My research cannot positively define the sutural contacts of the quadratojugal bone of this specimen with the surrounding bones as the skull has several cracks in this area which makes it difficult to determine the real sutural contacts. NHMUK PV R 3594 also has drawn “suture” lines showing the jugal with a hook-like posteroventral end which is probably not real.

Prefrontal: The prefrontal (Figs. 6.68A, 6.69A, 6.70 B,C, 6.71, 6.73) forms the anterodorsal and dorsal border of the orbit. It is well preserved in NHMUK PV R3594, NHMUK PV R 3596 (right side), and TM 1484. The prefrontal anteriorly does not contribute to the thickening of the nasofrontal boss as in *Tapinocephalus*.

Frontal: The frontal (Figs. 6.67A, 6.69A, 6.70, 6.71, 6.73), which is a flat and slightly depressed bone on the dorsal surface, is the largest bone of the cranial

roof and it is preserved in all the specimens except AMNH FARB 5655. The main frontal surface is flat and slightly depressed except anteriorly where it rises to contribute to the nasofrontal boss as preserved in NHMUK PV R 3594 and TM 1484. Anteriorly it forms a pointed contact between the nasal pair and contributes to the nasofrontal boss in NHMUK PV R 3594 and TM 1484, and anterolaterally has a pointed contact between the prefrontal and the nasal. Posterolaterally it has a short contact with the postfrontal, and posteriorly has a long transverse sutural contact with the parietal. The frontal is excluded from the orbital border, and posterolaterally it contributes to the temporal fenestra.

The transition from the frontal's main corpus to its anterior portion which contributes to the nasofrontal boss is abrupt in NHMUK PV R 3594 and TM 1484. In these specimens the frontal, except the portion contributing to the nasofrontal boss, is not thickened and thus does not have the swollen cranial roof appearance of *Tapinocephalus* where the entire frontal is thickened. In NHMUK PV R 3596, the nasal is eroded away revealing the suture line with the frontal. This portion of the frontal is elevated to form an incipient nasofrontal thickening. In AMNH FARB 5655 this portion of the skull was covered by plaster so it is difficult to judge the connection of the frontal to the nasal but this region appears similar to NHMUK PV R 3596.

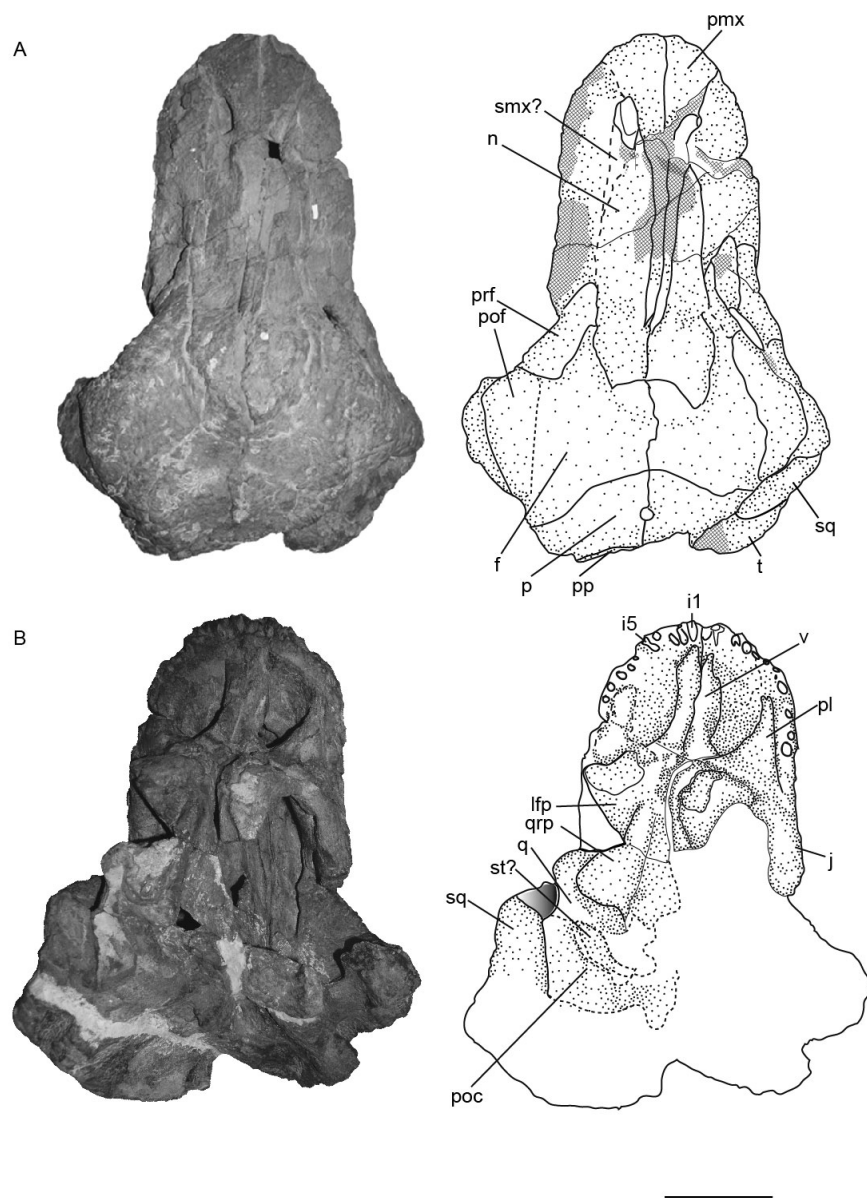


Figure 6. 67. *Mormosaurus*: photographs and interpretative drawings of NMHUK PV R 3594, the holotype of *Mormosaurus seeleyi* showing the cranial roof (A) and ventral view (B). Scale: 10 cm.

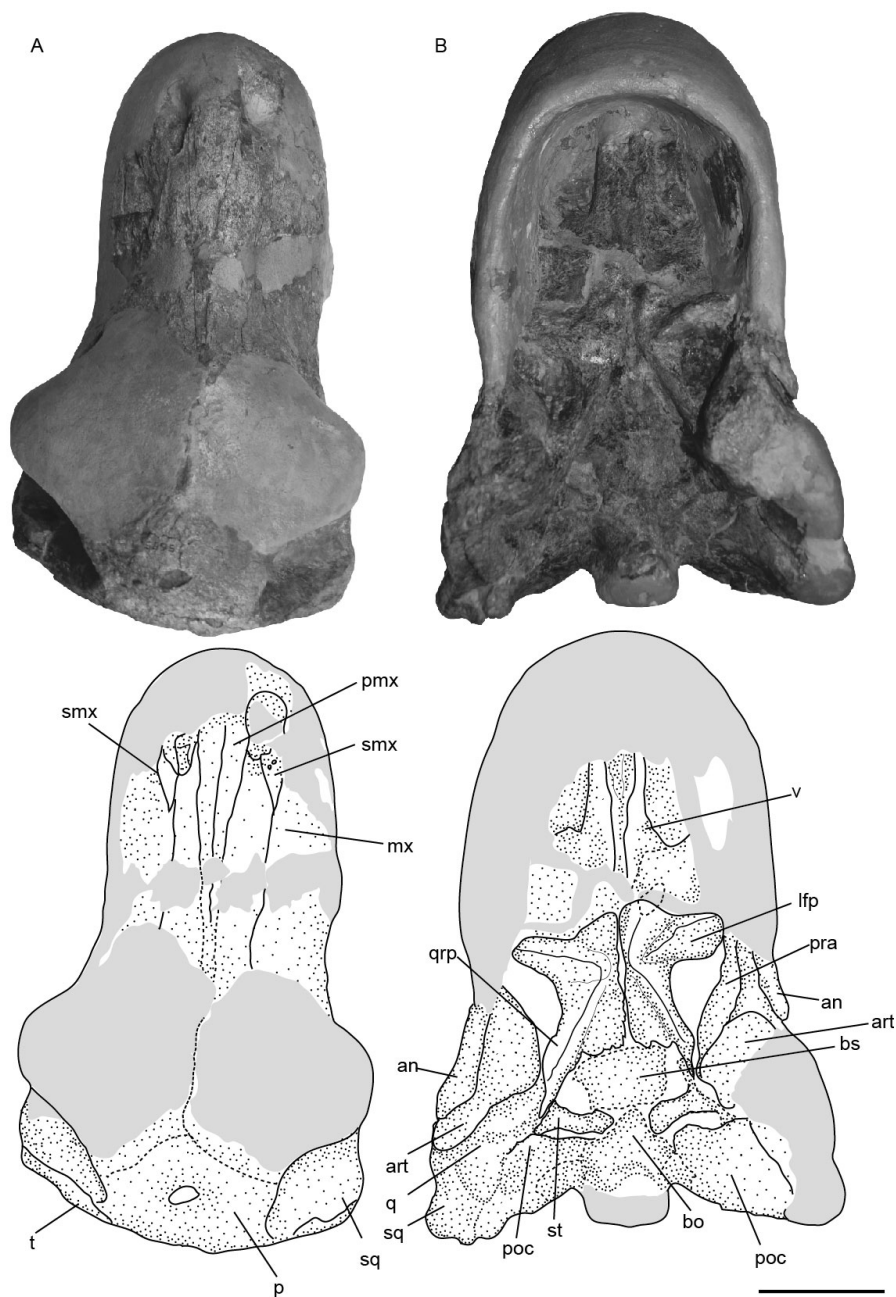


Figure 6.68. *Mormosaurus*: photographs and interpretative drawings of AMNH FARB 5655, the holotype of *Taurocephalus lerouxi* showing the cranial roof (A) and ventral view (B). Scale: 10 cm.

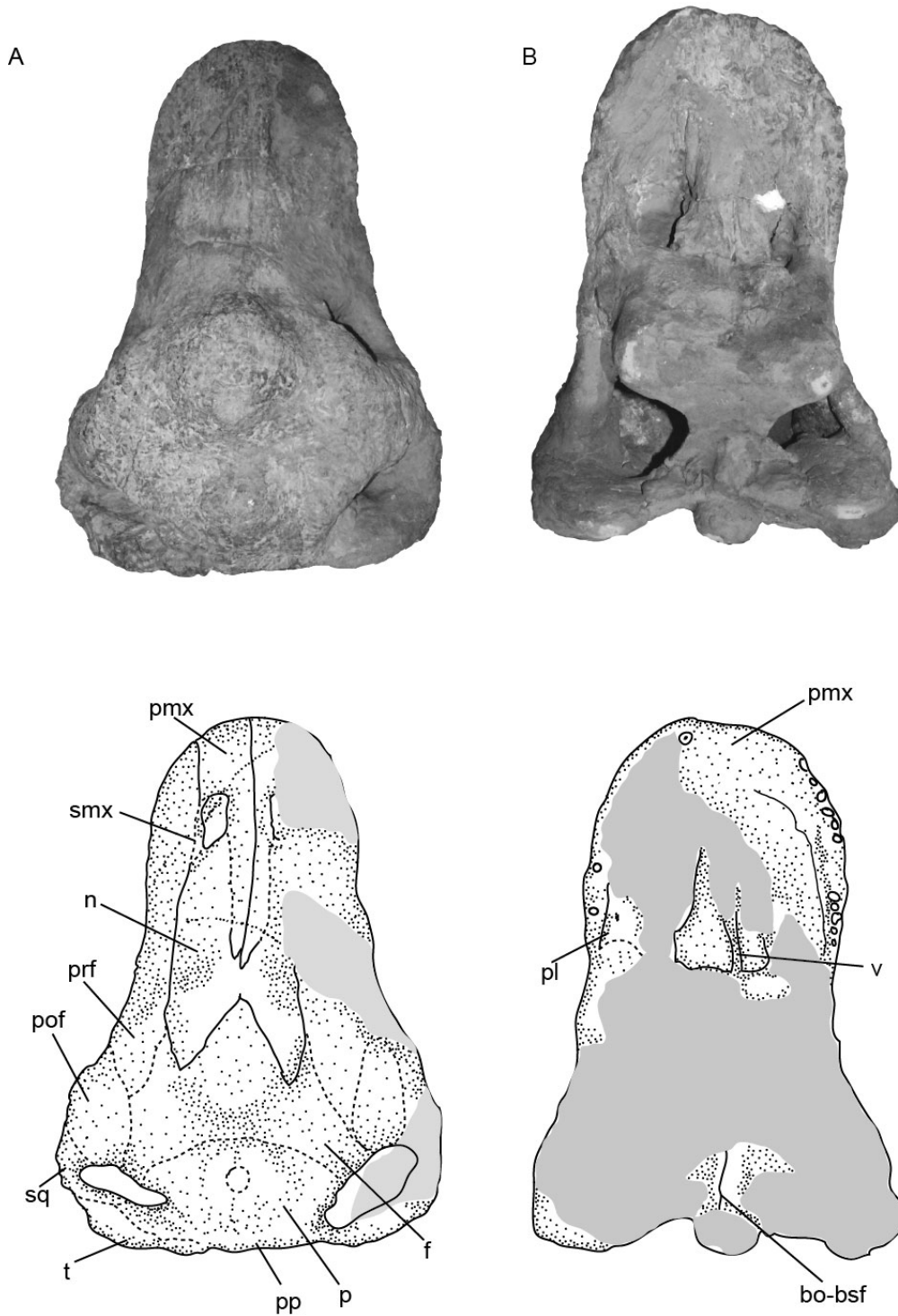


Figure 6.69. *Mormosaurus*: photographs and interpretative drawings of TM 1484, the holotype of *Struthiocephalus rheederi* showing the cranial roof (A) and ventral view (B). Scale bar: 10 cm.

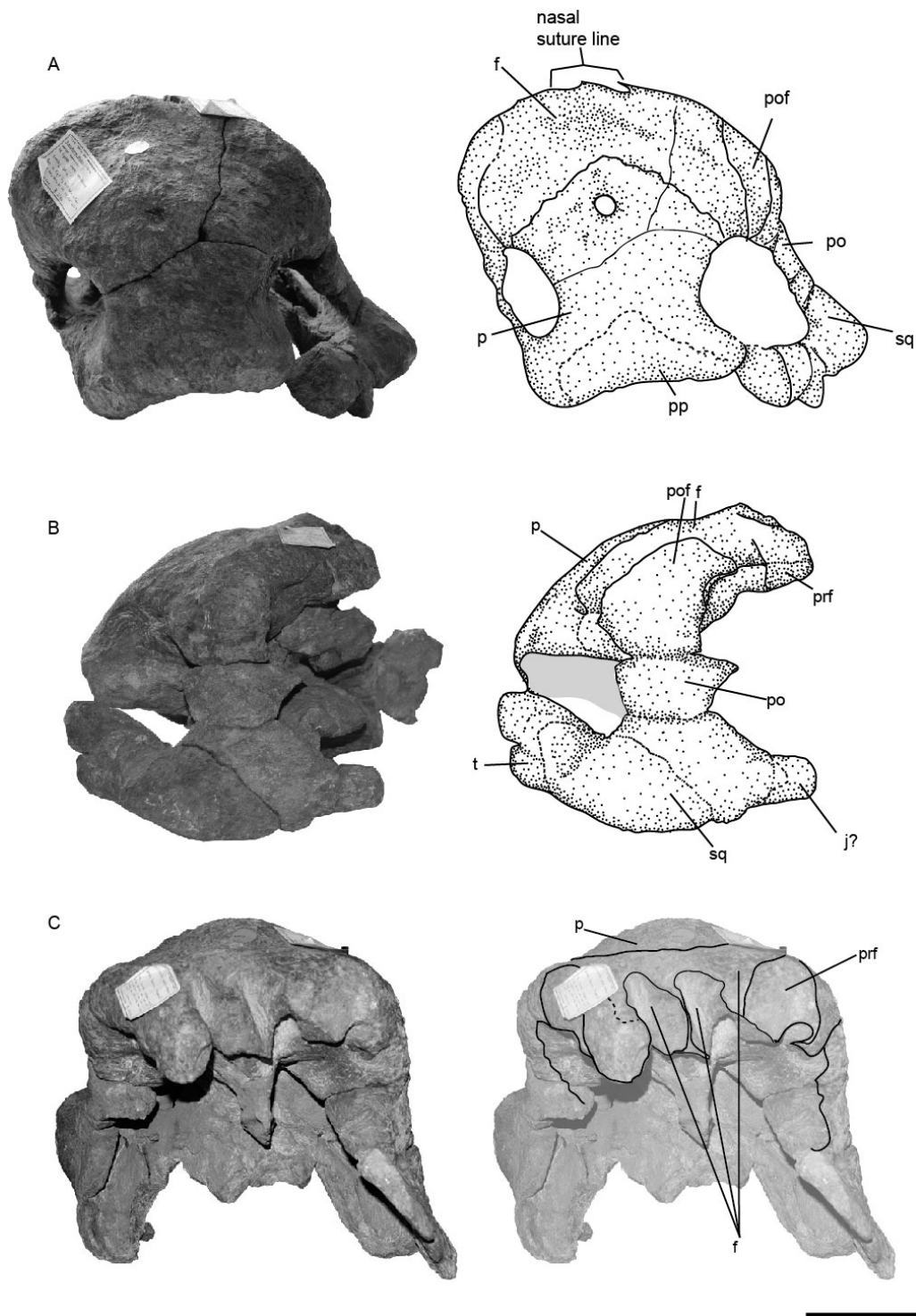


Figure 6.70. Photograph and interpretative drawings of holotype NMHUK PV R 3596, the holotype of *Pnigalion oweni* showing the parietal (A), right lateral (B) and anterior (C) views. Scale: 10 cm.

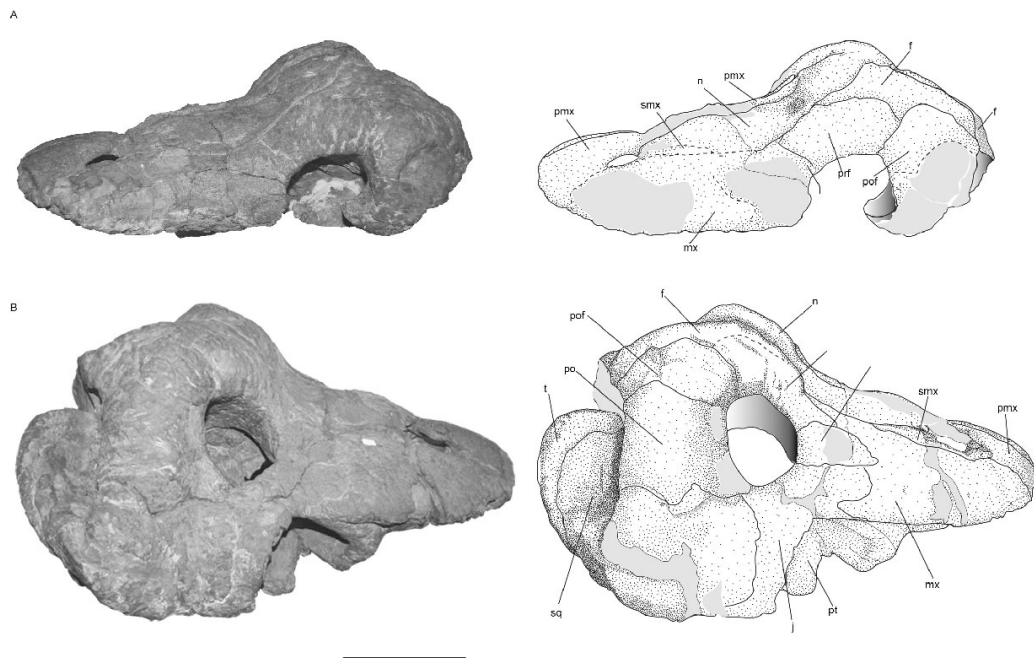


Figure 6.71. *Mormosaurus*: photographs and interpretative drawings of NMHUK PV R 3594, the holotype of *Mormosaurus seeleyi* showing the left (A) and right lateral views. Scale: 10 cm.

Postfrontal: The postfrontal (Figs. 6.67A, 6.69A, 6.70, 6.71, 6.73) is preserved in all the specimens except AMNH FARB 5655. It is an oblong bone that contributes to the posterodorsal border of the orbit and anterodorsal border of the temporal fenestra. Anterodorsally it has a short sutural contact with the prefrontal, and dorsomedially with the frontal. Ventrally it has a transverse sutural contact with the postorbital. The postfrontal is pachyostotically thickened but this is less developed in NHMUK PV R 3594. However, it is important to note that the postfrontal does not have a brow-like supraorbital thickening as was reconstructed on AMNH FARB 5655.

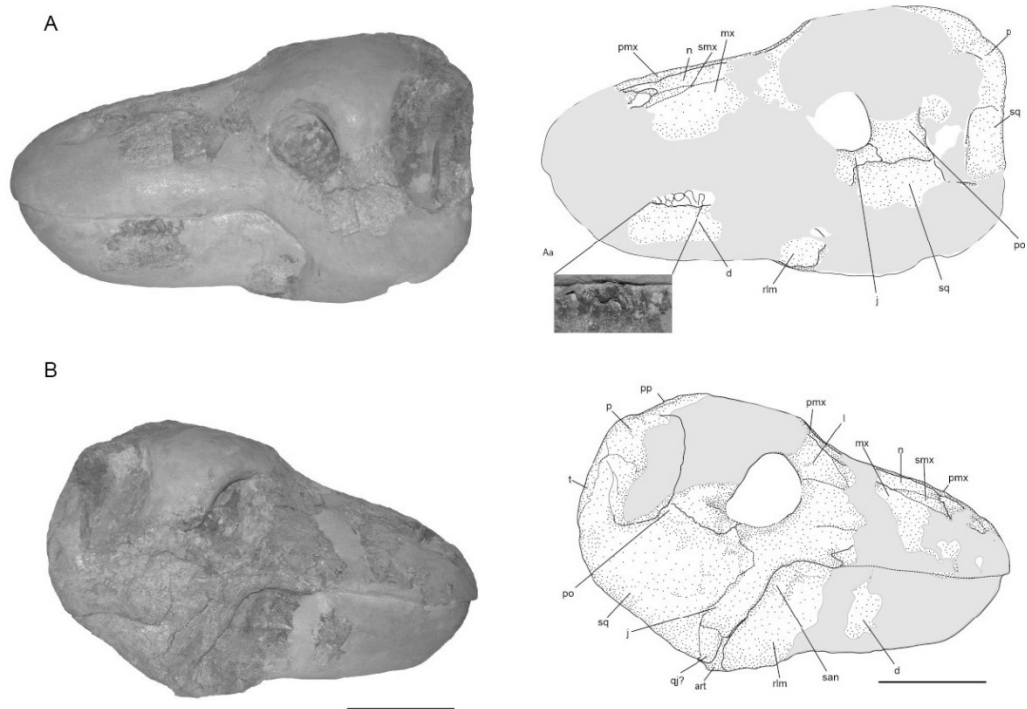


Figure 6.72. *Mormosaurus*: photographs and interpretative drawings of AMNH FARB 5655, the holotype of *Taurocephalus lerouxi* showing the left (A), right (B) lateral views and a detail from the labial views of the posterior postcanine teeth on the left (Aa).

Parietal: In dorsal view the parietal surface demonstrates more pachyostotic thickening around the pineal foramen. It is a large semi-rectangular bone which extends transversely between the temporal fenestrae and extends posteriorly to have a narrow exposure on the dorsal occipital surface. It has an anterior transverse sutural contact with the frontal and posteroventrally meets the postparietal as is evident in all specimens except NHMUK PV R 3594 where the suture could not be determined. The parietal has a short lateral contact with the squamosal and posteroventrally with the tabular. This contact is evident in AMNH FARB 5655 and TM 1484.

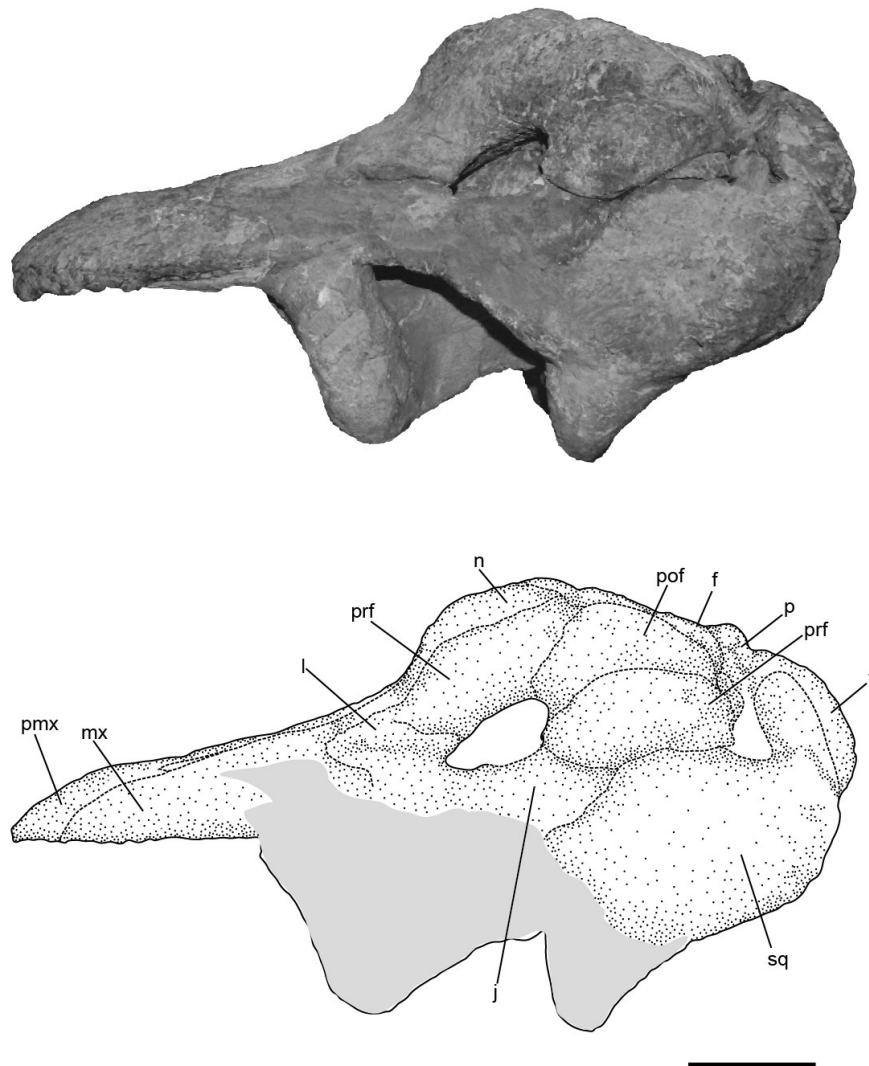


Figure 6.73. *Mormosaurus*: photograph and interpretative drawing of TM 1484, the holotype of *Struthiocephalus rheederi* showing the left lateral view. Scale: 10 cm.

Postorbital: The postorbital (Figs. 6.70B, 6.71, 6.73) is preserved in all except AMNH FARB 5655. It dorsally is in contact to the postfrontal, ventrally to the jugal and squamosal, while forms the ventrolateral border of the orbit anteriorly

and contributes to the temporal fenestra anterolateral border. The postorbital bar is heavily thickened in all except NHMUK R3596, which is the smallest cranium.

Squamosal: The squamosal (Figs. 6.67A, 6.68A, 6.69A, 6.70A-B, 6.71B, 6.72B, 6.73) is a large bone that forms most of the zygoma and is preserved on the right side of NHMUK PV R3594, AMNH FARB 5655, NHMUK PV R 3596 and left side of TM1484. In lateral view it contacts the jugal with a wavy suture below the orbit, the postorbital dorsally with a transverse suture at the base of the postobital bar, and forms the posteroventral border of the skull. It also makes up the posteroventral and ventral borders of the temporal opening, has a short posterior sutural contact with the tabular, and meets the parietal dorsally within the temporal fenestra as is evident in AMNH FARB 5655 and TM 1484. Its contribution to the occipital surface is limited (Fig. 6.74).

The posterior edge of the zygoma, which is formed by the squamosal, is angled. This feature is similar to the situation in longirostrine tapinocephalids as it was stated in Kammerer (2009) and unlike the situation in the short snouted tapinocephalids where the squamosal corner is rounded in the adults.

6.8.3.4 Occiput

None of the specimens has a fully preserved occiput and all have been exposed to severe surface weathering. NHMUK PV R3594 and NHMUK PV R3596 have suffered varying degrees of distortion and TM 1484, which is not distorted, is the best preserved (Fig. 6.74).

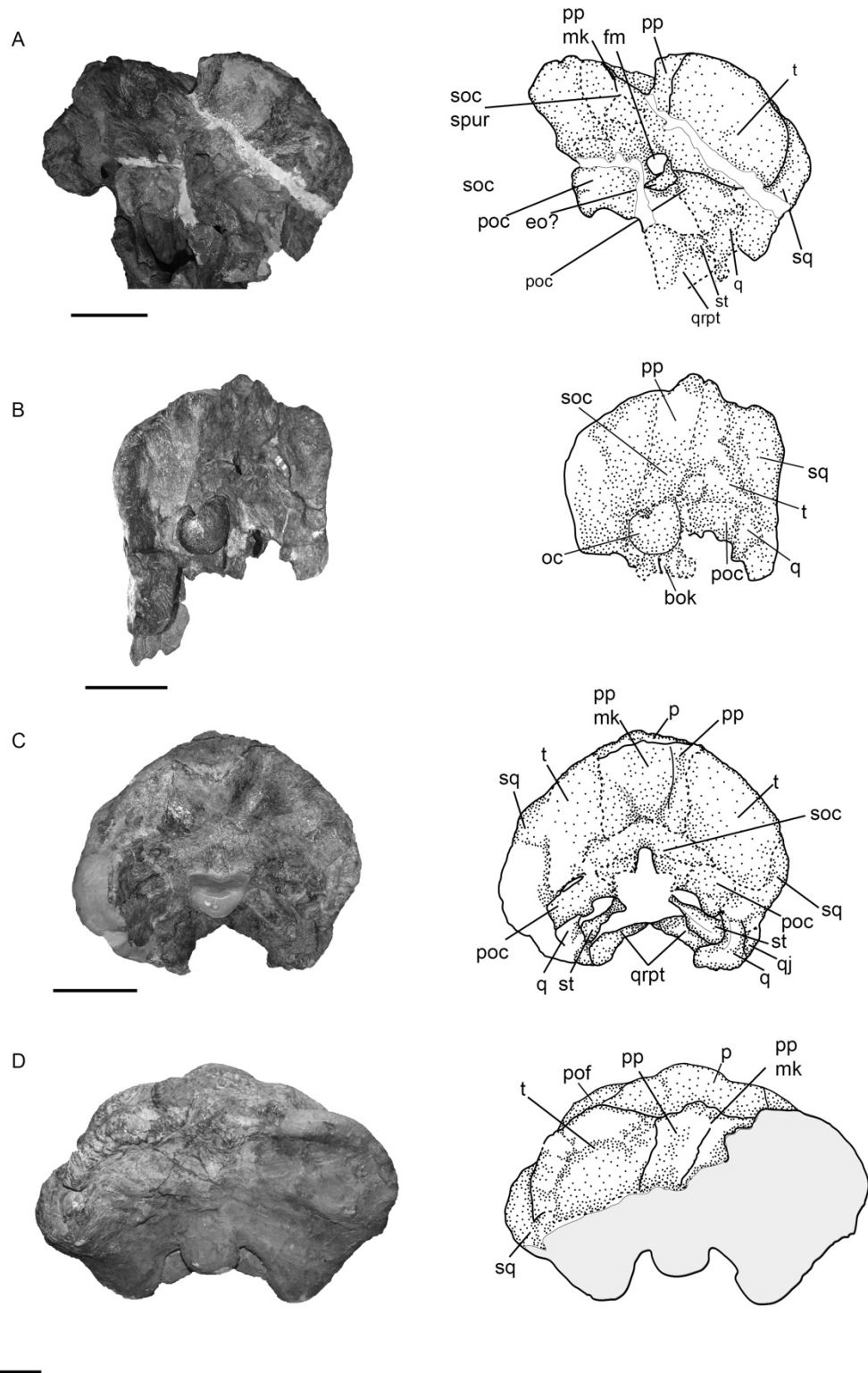


Figure 6.74. *Mormosaurus*: photograph and interpretative drawings of the occiput of NMHUK PV R3594, holotype of *Mormosaurus seeleyi* (A), NMHUK PV R 3596, holotype of *Pnigalion oweni* (B), AMNH FARB 5655, holotype of *Taurocephalus lerouxii* (C), TM 1484, the holotype of *Struthiocephalus rhedeeri* (D). Scale: 10 cm.

Postparietal: The postparietal is a quadrangular bone that is completely preserved in only AMNH FARB 5655. Dorsally it contacts the parietal with an interdigitating transverse suture which has a midline dorsal intrusion into the parietal as is evident in AMNH FARB 5655 and TM 1484. Laterally the postparietal has a vertical contact with the tabular and ventrally meets the supraoccipital but this ventral suture is not evident. The posterior surface of the postparietal has a midline keel which is best preserved in AMNH FARB 5655.

Tabular: The tabular is a semilunate bone that forms most of the occipital surface. Medially it contacts the postparietal, dorsally the parietal on the occipital crest, dorsolaterally the squamosal, and ventrally it is in contact with the supraoccipital and paraoccipital process of the opisthotic but the ventral sutural contacts are unsure.

Supraoccipital: The supraoccipital is best preserved in NHMUK PV R3596 and AMNH FARB 5655. Dorsomedially it contacts the postparietal and laterally the tabular. On the ventral side it forms the dorsal border of the foramen magnum (only preserved NHMUK PV R 3594 and AMNH FARB 5655) and ventrolaterally contacts the exoccipital and opisthotic complex.

Exoccipital: The exoccipital and opisthotic area is poorly preserved in all the specimens and sutural contacts are unclear. A posttemporal foramen could not be determined.

Basioccipital: The basioccipital is poorly preserved in all specimens. From AMNH FARB 5655 it is evident that it contributes to the occipital condyle ventrally but because of weathering its contact with surrounding bones is unclear.

6.8.3.5 Palate

Premaxilla: The premaxilla forms the anterior extremity of the ventral surface of the skull and is well preserved in NHMUK PV R 3594 (Fig. 6.67B) and only partly preserved in TM 1484 (Fig. 6.69B). Its ventral surface is relatively wide and bears the alveoli of five incisors. The premaxilla contacts the anterior end of the vomer along its posterior midline. The posterior sutural contact of the premaxilla with the maxilla, which is evident on the left side of NHMUK PV R 3594, extends medially from behind the alveolus of the fifth incisor to the lateral border of the internal naris.

Maxilla: The maxilla (Figs. 6.67B, 6.69B) forms the ventral alveolar surface which is well preserved in NHMUK PV R 3594 and TM 1484. From the left maxilla it is evident that there are seven maxillary teeth in NHMUK PV R 3594 and eleven in TM 1484. A tongue-shaped anterior process of the palatine ventrally overlies the ventromedial surface of the maxilla and is best preserved in NHMUK PV R 3594.

Vomer: The entire vomer (Figs. 6.67B) is best preserved in NHMUK PV R 3594 and the posterior portion is present in AMNH FARB 5655 (Fig. 6.68B) and TM 1484 (Fig. 6.69B). The vomer is a paired elongated bone which, with its partner,

has a bifurcated anterior contact with the premaxilla. It bears a midline groove and on either side are longitudinal ventrally extending ridges. Posteriorly the vomer broadens and contacts the palatine posterolaterally, and possibly the pterygoid posteromedially but this contact is not evident in any of the specimens.

Palatine: The palatine (Figs. 6.67B, 6.68B, 6.69B) is a broad paired bone that makes up a large proportion of the middle part of the palate. The anterior process overlies the medial surface of the maxilla. Medially it has a short contact with the vomer and posteriorly has a transverse sutural contact with the pterygoid. It is preserved in NHMUK PV R 3594, TM 1484 and AMNH FARB 5655 in varying degrees of completeness. Posterolaterally it is in sutural contact with the ectopterygoid which is evident on the right side of NHMUK PV R 3594. An obliquely positioned oval palatine-ptyerygoid boss is present medially on the palatine and is best preserved on the right side of AMNH FARB 5655.

Pterygoid: The pterygoid (Figs. 6.67B, 6.68B) is preserved only in NHMUK PV R3594 and AMNH FARB 5655 and forms almost half of the basal cranial length. Typically it comprises a robust lateral process, a medial corpus with a low edentulous pterygoid boss, and has a posterolaterally diverging quadrate ramus. Anteriorly the pterygoid is in contact with the palatine, anterolaterally the ectopterygoid (preserved in NHMUK PV R 3594), posteriolaterally with the quadrate medial surface, and posteromedially with the parabasisphenoid (preserved in AMNH FARB 5655). The quadrate ramus is relatively thick and long and extends posterolaterally to meet the medial side of the medial quadrate

condyle. Medial to the quadrate ramus the wide and flat pterygoidal platform extends between the posterior end of the quadrate ramus and the anterior border of the basisphenoid. The platform is preserved only on the right side of the NHMUK PV R3594 and is wider than it is in AMNH FARB 5655.

The ectopterygoid (Fig. 6.67B) is roughly triangular and is preserved on the right side of NHMUK PV R3594 where it is positioned medially on the anterior side of the lateral flange of the pterygoid. It has a short anterior contact with the palatine and a more dorsally positioned contact with the jugal.

Quadrate: The quadrate (Figs. 6.67B, 6.68B, 6.69B) is best preserved in AMNH FR5655, but is also present in NHMUK PV R 3594 and NHMUK PV R 3596. It has a thin plate-like dorsal process, which has a loose contact with the anterior side of the squamosal, and two ventrally positioned condyles which articulate with the lower jaw. The distal end of the stapes is positioned in the stapelial groove of the quadrate and is evident in AMNH FARB 5655.

Quadratojugal: A small quadratojugal has been tentatively identified in AMNH FARB 5655 with its small portion exposed on the lateral surface of the skull which is dorsally overlapped by the posteroventral portion of the squamosal.

Parabasisphenoid: The parabasisphenoid (Fig. 6.68B) is preserved only in AMNH FARB 5655 and is a roughly quadrangular bone. Its thin anteromedial end once contacted the pterygoid but the contact is not preserved. At its posterior end

the parabasisphenoid contacts the basioccipital but the suture in between the two bones is indistinguishable.

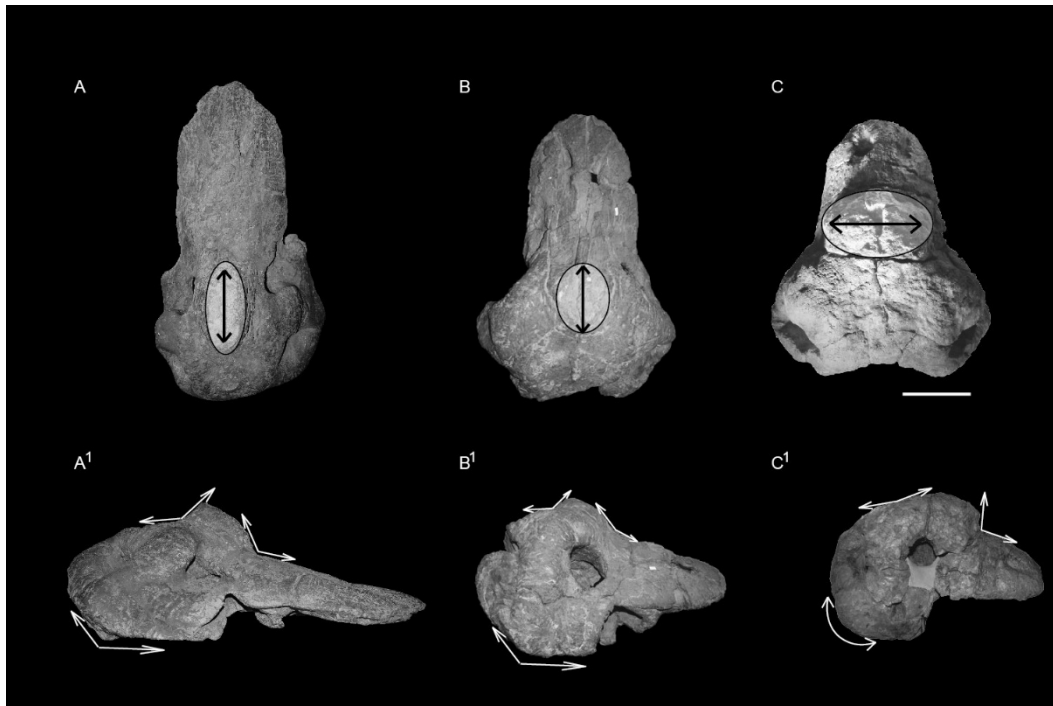


Figure 6.75 Nasofrontal boss formation in tapinocephalids shown on BP/1/284 (A), the holotype of *Struthiocephalus kitchingi*; NHMUK PV R 3594 (B), the holotype of *Mormosaurus seeleyi* and SAM-PK-2344 (C), a referred specimen of *Tapinocephalus atherstonei*. While the nasofrontal boss is developed parallel to the long axis of the skull and has an elliptic shape in the longirostrin forms *Struthiocephalus* and *Mormosaurus*, it is developed transversely in *Tapinocephalus*. Thickening on the the nasofrontal boss area in longirostrin forms excludes the prefrontal, whereas in *Tapinocephalus* the thickening occurs in confluence on the entire cranial roof. The transition from the cranial surface to the nasofrontal boss is abrupt in *Struthiocephalus* and *Mormosaurus*, and is smoother in *Tapinocephalus*. Finally the zygoma posterior corner is angled in the longirostrin forms; and is rounded in *Tapinocephalus* as stated in Kammerer (2009). Scale: 10 cm.

Stapes: The stapes (Figs.5.67B, 5.68B) is preserved on both sides of AMNH FARB 5655 and the right side of NHMUK PV R 3594. It is a relatively long rod-

like bone with a small rounded proximal end positioned in the fenestra ovalis and a greatly enlarged distal end which is positioned in the stapedial groove of the quadrate. A stapedial foramen is not evident.

6.8.3.6 Lower jaw

The lower jaw is not well preserved in any of the specimens. AMNH FARB 5655 preserves fragments of dentary, surangular, reflected lamina of the angular, posterior end of the prearticular, and ventral surface of the articular. NHMUK PV R 3596 has the dentary symphysis and thick anterior process of the angular preserved and was reconstructed in plaster in such a way that it appears wide on the anterior end. The dentary symphysis of NHMUK PV R 3594 slopes anteroventrally but is not preserved in AMNH FARB 5655.

NHMUK PV R 3596 has the emerging crowns of three anteriorly positioned narrow incisors and a larger more posteriorly positioned incisor having a large crown with talon and hell morphology.

6.8.4 Results and discussion

This study, in agreement with Kammerer (2009), recognises three tapinocephalid genera with a nasofrontal boss in adult individuals: the short snouted *Tapinocephalus*, and the longirostrin *Mormosaurus* and *Struthiocephalus*. The holotypes of *Mormosaurus seeleyi*, *Struthiocephalus rheederi*, *Taurocephalus lerouxi* and *Pinigalion oweni* all share the same cranial roof sutures, zygoma, cranial proportions and nasofrontal boss morphology (As the snout of NHMUK PV R 3596 is not preserved it is not possible to determine the last two characters

for this specimen). All specimens have flat and anteriorly wide snouts, but the snout is not preserved in the holotype of *Pnigalion* (NHMUK PV R 3596) but the wide, and thickened symphysis of the dentary suggests that this specimen also had a wide snout. The holotype skulls of all these genera have a relatively short intertemporal width and an angled posteroventral corner of the skull as in the longirostrin skulls, and not rounded as in *Tapinocephalus*. Although it is angled, this portion of the zygoma does not, as pointed out by Kammerer (2009), flare out as in *Struthiocephalus*. The nasofrontal boss is an anteroposteriorly elongated large oval in cross section due to the reduced contribution from prefrontal anteriorly to the thickening of the nasofrontal boss (but not circular as suggested by Kammerer [2009, p. 223]). The nasofrontal boss of *Mormosaurus* (*excl. Taurocephalus* and *Pnigalion* where the boss is not preserved), although it is anteroventrally elongated as in *Struthiocephalus*, does not form a narrow oval and a blade like nasofrontal boss dorsal profile as in *Struthiocephalus* as pointed out by Kammerer (2009). It also does not overhang the facial surface anteriorly as in *Tapinocephalus* (Fig. 6.75).

The degree of thickening of the nasofrontal boss varies in the different specimens and not all specimens exhibit the large boss seen in NHMUK PV R 3594 and TM 1484, which are also the largest specimens. This is similar to the situation described for *Tapinocephalus* (above) where a smaller specimen (an apparent subadult) has limited thickening on the cranial boss and large individuals have excessive thickening of this boss. As skull sizes, general cranial thickening, and the thickening of the postorbital bar of AMNH FARB 5655 and NHMUK PV R

3596 are not significantly smaller than the specimens with the nasofrontal boss this feature change cannot readily be attributed to ontogeny. However, the postorbital bar of NHMUK PV R 3596 (*P. oweni*) is thinner than the rest and the large cavity of the posterior border of the orbit suggests a large orbit. These features together (lack of strong cranial pachyostosis, thinner postorbital bar and large orbits) are strongly associated with a subadult stage in tapinocephalids.

As the palate and occiput are not well preserved in any of the skulls they will not be discussed.

My research considers *Mormosaurus seeleyi* to be valid, and follows Kammerer (2009) in synonymising *Taurocephalus lerouxi* and *Struthiocephalus rheederi* with *Mormosaurus seeleyi*. In addition I consider the holotype of *Pnigalion oweni* of Watson, 1914 to be the same as *Mormosaurus seeleyi* and propose their synonymy. *Pnigalion oweni* was previously synonymised with *Moschops* by Boonstra (1969). But the skull does not share any characteristics of *Moschops* in contrast it has the angled zygoma of *Mormosaurus* and shares the same suture patterns.

My research also indicates that the holotype skull of *Mormosaurus seeleyi* differs from *Tapinocephalus* in the morphology of its zygoma, cranial roof and with its moderately long snout. The initial description of *Mormosaurus seeleyi* and *Pnigalion oweni* appeared in the same publication (Watson, 1914, page 267) and

as *Mormosaurus* has page priority and is known from a much more complete skull, *Phigalion oweni* will be synonymised with *Mormosaurus seeleyi*.

6.9 *Keratocephalus moloch* VON HUENE 1931

Holotype: GPIT/RE/7102 (UTHuene1931T.167), anteriormost extremity of a snout, mid-dorsal portion of the cranial roof and associated postcranial elements (vertebrae, femur, tibia) found on Abrahamskraal, Prince Albert (von Huene, 1931, figs. Pl.II[X], fig.2, Pl.III[XI],fig.1-2).

6.9.1 Brief notes on the holotype. The skull of GPIT/RE/7102 comprises two pieces: anterior extremity of a large flat snout; and a portion of the cranial roof. The snout portion preserves the dorsal surface of the premaxilla and an adjacent small part of the left maxilla. The cranial roof portion includes the frontal, parietal, pineal opening and postparietal along the midline of the skull roof. The nasofrontal boss is not completely preserved, but the frontal portion of the boss is anteroposteriorly elongated and dorsally elevated at its anterior end indicating its contribution to the nasofrontal boss. The nasal is not preserved in the specimen. Judging from the preserved portion of the boss (*ie.* the elevated frontal portion) suggests a sharp transition to the rest of the boss is as the case in *Struthiocephalus*. Posteriorly the paired frontal forms a midline wedged contact with the parietal. The surface of the parietal is elevated around the pineal opening to form a thickened rim.

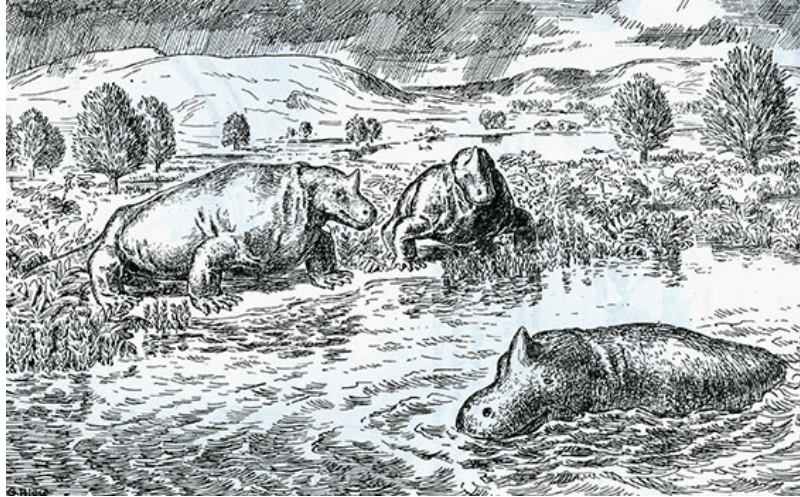


Figure 6. 76. The reconstruction of a *Keratocephalus moloch* group, in a Permian landscape by von G.Biese, fig.12 in von Huene, 1931.

6.9.2 Historical background. von Huene (1931) described GPIT/RE/7102 (which comprises both cranial and postcranial elements) as *Keratocephalus* and recognised it as a tapinocephalid because of the similarities with *Moschognathus* in dentition and *Tapinocephalus* in the postcrania. He depicted the specimen as an animal with a *Struthiocephalus*-like cranial roof and *Tapinocephalus*-like short snout (Fig. 6.76). Boonstra (1936b, 1956, 1969) grouped it with *Tapinocephalus*, but distinguished it from *Tapinocephalus* in having a narrower nasofrontal boss. Boonstra (1956) referred two additional specimens (SAM-PK-8946 and SAM-PK-10557) to *Keratocephalus moloch*. These specimens had a *Struthiocephalus*-like nasofrontal boss, but the snouts were not preserved. Kammerer (2009, p. 234, 235) considered that *Keratocephalus moloch* exhibits the same spatulate shaped snout and anteroventrally elongated nasofrontal boss morphology as *Struthiocephalus whaitsi*. Accordingly he synonymised *K. moloch* with *Struthiocephalus whaitsi* and included the two referred skulls of Boonstra (1956) in the same species.

6.9.3 Brief descriptive comparison of preserved cranial portions of the holotypes of *Keratocephalus moloch* and *Struthiocephalus whaitsi*.

This description compares the cranial roof bones and dental features of only the cranial roof bones and dental features which are preserved in both the holotypes of both *Keratocephalus moloch* (GPIT/RE/7102) and *Struthiocephalus whaitsi* (SAM-PK-2678). This includes only the following cranial bones: premaxilla, frontal, parietal and dentary. The dentary is preserved only in *Keratocephalus* and the anterior portion of the lower jaw is occluded to the corresponding portion on the upper jaw.

Premaxilla: The premaxilla (Fig.5.77A, B, D) forms both the anterior border of the snout and anterior border of the narial opening, and lacks the narrow posteromedial dorsal extension in both holotypes. The premaxilla is dorsoventrally flat and bears five incisors. The left premaxilla of *Keratocephalus* is twisted and the incisor is separated from the first maxillary tooth by the premaxilla-maxilla suture. It is not clear how many incisors were present in the holotype of *Struthiocephalus* but the following dental remains are present in the left maxilla (from anterior midline posteriorly towards the premaxilla-maxilla suture): tips of two incisor crowns (presumably first and the second incisors), one large rounded incisor root, two large rounded alveoli.

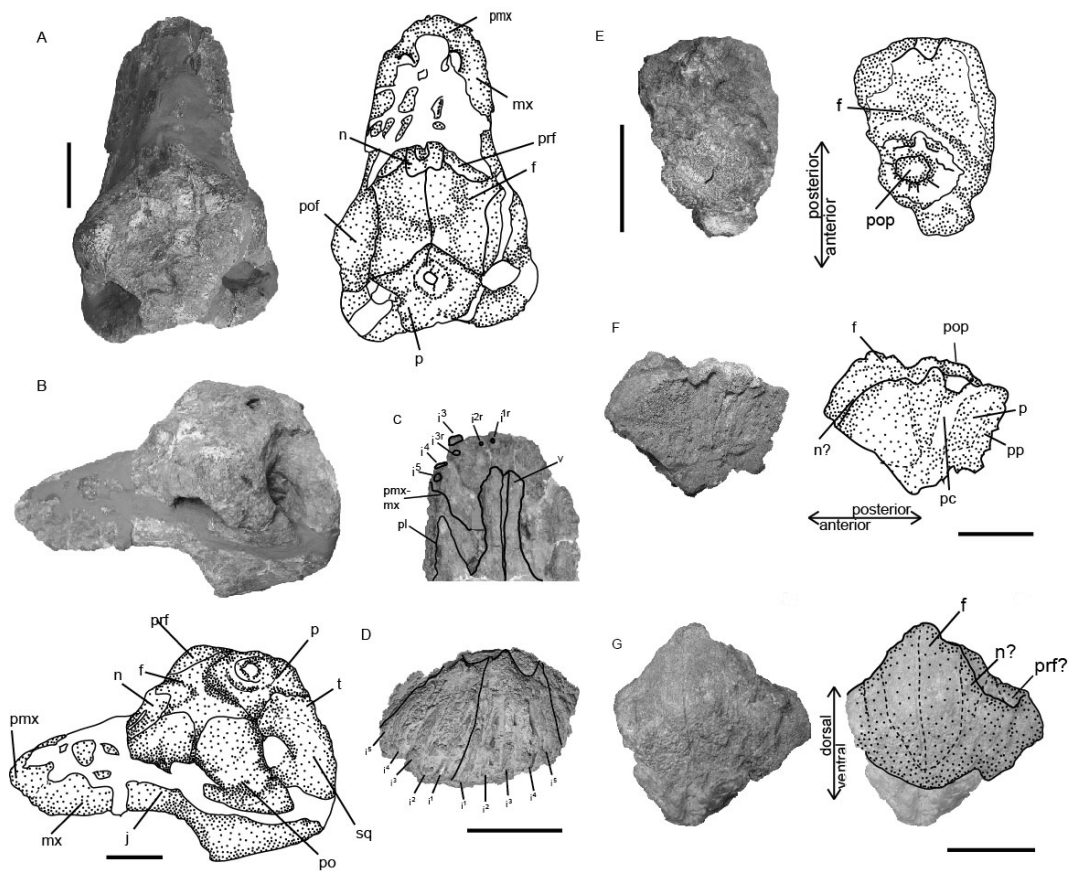


Figure 6.77. Photos and illustrations of the comparable portions of GPIT/RE/7102, the holotype of *Keratocephalus moloch* von Huene 1931 and SAM-PK-2678, the holotype of *Struthiocephalus whaitsi* Haughton 1915 showing: the skull roof (A) and left lateral view (B) and the anterior portion of the palate (C) of SAM-PK-2678; the dorsal view of the anterior tip of the snout (D), cranial roof portion which includes the pineal opening (upper right), dorsal view of the cranial roof portion of *Keratocephalus* showing the frontal boss (lower left) and lateral view of the cranial roof portion (lower right). Scale:10 cm.

Frontal: The frontal (Fig. 5.77A,B, E-G) forms the largest bone of the cranial roof which is preserved with its anterior contact with the nasal and anterolateral contact with the prefrontal only in SAM-PK-2678; posteriorly the paired frontals have a V-shaped sutural contact with the parietal. In both skulls the anteromedial

portion of the frontal is greatly elevated on an anteroposteriorly elongated axis to contribute to the nasofrontal boss.

Parietal: The parietal is an anteroposteriorly relatively narrow bone that stretches between the temporal fenestrae and is completely preserved only in *Struthiocephalus* (SAM-PK-2678). In *Keratocephalus* (GPIT/RE/7102) the right side of the bone is partly preserved but lacks the posterior sutural contact with the postparietal as well as the lateral portion which contributes to the temporal fenestra. A diagnostic character present in both specimens is the relatively large rounded pineal opening with an elevated rim.

6.9.4 Results and discussion

The skull remains of the holotype of *Keratocephalus moloch* shares the following cranial roof characteristics with *Struthiocephalus whaitsi*: anteriorly raised frontal to contribute to the nasofrontal boss; large pineal opening surrounded by an elevated rim. The thickening of the frontal area is not in confluence with the adjacent small portion of the left prefrontal bone (left side) as in *Struthiocephalus* (Boonstra, 1953b, p.46). Incomplete skulls which were previously referred to *Keratocephalus* (SAM-PK-8946 and SAM-PK-10557) by Boonstra (1956) also have an almost complete nasofrontal boss which is anteroposteriorly elongated and narrow as in *Struthiocephalus* and the postfrontal bone is distinctly thickened as in *Struthiocephalus*. Thus the only diagnostic cranial characters of *Keratocephalus*, the raised rim around the enlarged pineal foramen and the anteroposteriorly elongated frontal boss are also present in *Struthiocephalus*.

Accordingly Kammerer's (2009) synonymy of *Keratocephalus moloch* with *Struthiocephalus whaitsi* is here supported. This means that *Keratocephalus* (now *Struthiocephalus*) is a longirostrin dinocephalian and is no-longer falls within the ambit of this thesis.

There are three additional specimens that are referred as *Keratocephalus* in the literature: SAM-PK-00918, SAM-PK-11294; SAM-PK-11937 (Boonstra, 1956, figs. King, 1988). The first is the holotype of *Pelosuchus priscus* and its cranium is represented by weathereed lower jaw fragments which were synonymised by Boonstra (1955) with *Keratocephalus* on the basis of the similarity of the pasterania. This synonymy is not validified in here as it was based on postcrania (see latter in the invalid taxa section). SAM-PK-11294 does not exist in the South African Museum database and this work could not verify its existence. SAM-PK-11937 is referred to *Mormosaurus* in this work on the basis of similarities on nasofrontal boss and the zygoma.

6.10 Invalid taxa

6.10.1 *Phocosaurus megischion* SEELEY 1888

Holotype. NHMUK PV OR 43525, postcranial elements *incl.* incomplete coracoid-scapula, ulna, humeri, incomplete pelvis and proximal half of right femur.

Diagnosis. No cranial diagnosis supplied as the specimen is described on postcranium.

Brief notes on the holotype and the historical background. Seeley (1888, p. 91-92) described *Phocosaurus megischion* on the basis of postcranial material that had originally been identified as *Pareiasaurus* by Owen (1876, pl. 17, fig. 8;). Lydekker (1890, p. 775-776, fig. 13) latter referred this material to *Tapinocephalus* and declared *Phocosaurus megischion* to be a dubious taxon. Watson (1914, fig. 15) considered the name *Phocosaurus megischion* to be valid on the basis of a block containing partial pterygoid and palatine bones which was apparently associated with the holotype. This portion had not been mentioned previously before by either Seeley (1888) or Lydekker (1890). Watson (1914) did not provide illustrations or a description of this palatal fragment but mentioned that it looked very much like to the palate of NHMUK PV R 3594, the holotype of *Mormosaurus seeleyi*.

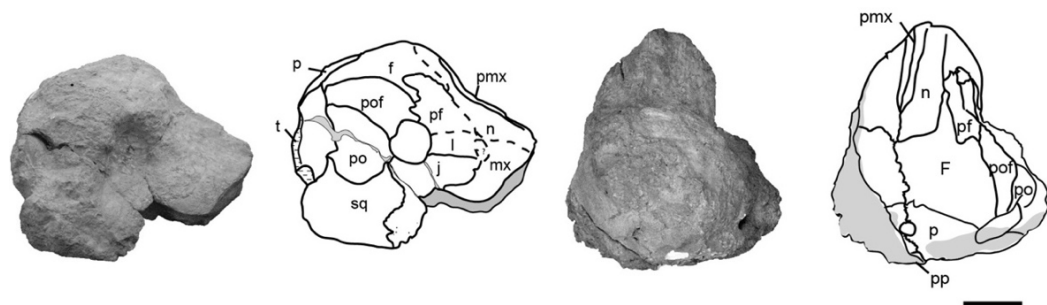


Figure 6. 78. The lateral view (left) and dorsal view (right) photos and interpretative drawings of the skull of SAM-PK-11997. Scale. 10cm. This skull on the basis of a similarity recognised by Boonstra (1956) was referred to *Phocosaurus* and treated as the cranial representative the genus. This skull was referred as *Mormosaurus* by Kammerer (2009) with which this work also agrees.

The taxonomic decision of Lydekker (1890) to synonymise *Phocosaurus* with *Tapinocephalus* was supported by Broom (1932). However the name *Phocosaurus* continued to be used in later works eg. Boonstra (1955, p. 210, 218-221, figs. 4,5,11,12,14; 1956, figs. 6, 7), Boonstra (1969), King (1988). Boonstra (1956) referred the posterior two-thirds of another large cranium and associated postcranial elements (distal end of a femur and incomplete ilium) (SAM-PK-11997, Fig. 5.78) to *Phocosaurus* based on the similarity of the postcranium of SAM-PK-11997 to that of *Phocosaurus*.

Conclusion: Resemblances in the postcrania between the holotypes of *Tapinocephalus atherstonei* and *Phocosaurus megischion* led Lydekker (1890) to refer *Phocosaurus* to *Tapinocephalus*. The only cranial element preserved of *Phocosaurus* is a fragment of palate mentioned by Watson (1914) which can no longer be traced. It is thus suggested that this fragment should be treated as a misidentification by Watson (1914). Kammerer (2009) considered this taxon temporarily *nomen dubium* as it is defined only on postcranial elements. In agreement with this decision of Kammerer, *Phocosaurus megischion* should be considered Tapinocephalid *indet.*

6.10.2 *Pelosuchus priscus* BROOM 1905b

Holotype: SAM-PK-918, collected on Boksfontein, Prince Albert, comprises a badly weathered dentary fragment (probably anterior portions close to the symphysis from right), a few vertebrae, parts of the shoulder girdle, pelvis, some ribs, a femur and other fragments. Broom (1905b) mentions a palatal portion but

this could not be located. Broom (1905b) describes the remains briefly but does not present a diagnosis.

Diagnosis: No diagnosis.

Brief notes on the holotype: The cranial portion of the holotype comprises a lower jaw fragment which appears to be portion of the left dentary. The bone surface is eroded to reveal the roots of some dentary teeth. These teeth are all labiolingually elongated and mesiodistally narrow.

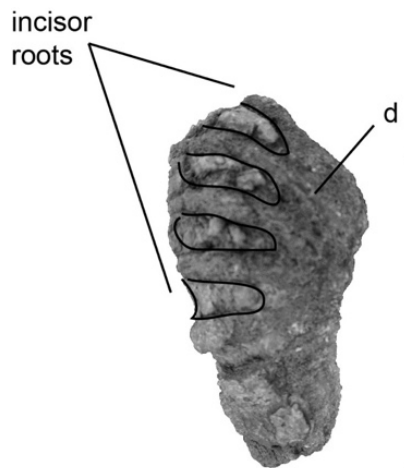


Figure 6.79. Photograph showing the dentary portion of SAM-PK-00918, left dorsal view. Scale. 10 cm.

Historical Background: Boonstra (1955, fig.7; 1969) synonymised *Pelosuchus* with *Keratocephalus moloch* (von Huene, 1931) on the basis of the resemblance between the coracoid and scapula portions of the two holotypes. Boonstra (1969) supported this decision noting that the dentary fragment provided no taxonomic information.

Conclusion: The palatal portion of the holotype has not been cited in the literature since Broom (1905b) and the present study was unable to verify the existence of the palatal fragment. The only existing cranial pieces of the holotype comprise two heavily weathered lower jaw fragments which have no diagnostic characters. Thus the identification of this specimen as a tapinocephalid is reliant on the interpretation of previous authors based on postcranial elements. Thus, in agreement with Kammerer (2009) *Pelosuchus priscus* is considered *nomen dubium* and should be set aside as *tapinocephalid indet.*

6.10.3 *Taurops macrodon* BROOM 1912

Holotype: AMNH FARB 5610, anterior extremity of a snout found at Bosmanshoek, Komsberg, Prince Albert (Broom, 1912, pl.xc, figs. 1-2).

Diagnosis: “In size it almost equals *Tapinocephalus atherstonei*, but the snout though narrower is considerably deeper, and it differs in the great degree of development of the teeth, especially of the incisors.” Broom, 1912, p. 859.

Brief notes on the holotype: AMNH FARB 5610 is the anterior tip of the snout comprising tightly occluded upper and lower jaw elements. The dorsal surface of the snout and its associated lower jaw are heavily weathered, revealing the roots of premaxillary, maxillary and dentary teeth as described by Broom (1912). The poorly preserved and paired premaxilla of AMNH FARB 5610 is a laterally wide bone as in *Tapinocephalus* and *Mormosaurus* that forms the anterior portion of the snout, and the anterior and the anteromedial borders of the external naris. The

premaxilla- maxilla suture is not visible but the number of the premaxillary teeth is estimated to be five which decrease in size posteriorly. Eight maxillary teeth are present on the left and nine on the right. The first three left maxillary teeth are preserved with crowns and partial roots while dental remains are represented only by alveoli. On the right the crowns of all the teeth are preserved, except the first, and are exposed in labial view.

The lower jaw portion of the snout comprises portion of the dentary which is eroded to reveal the crowns of four incisors (first generation?) and the succeeding generation of the dentary teeth.

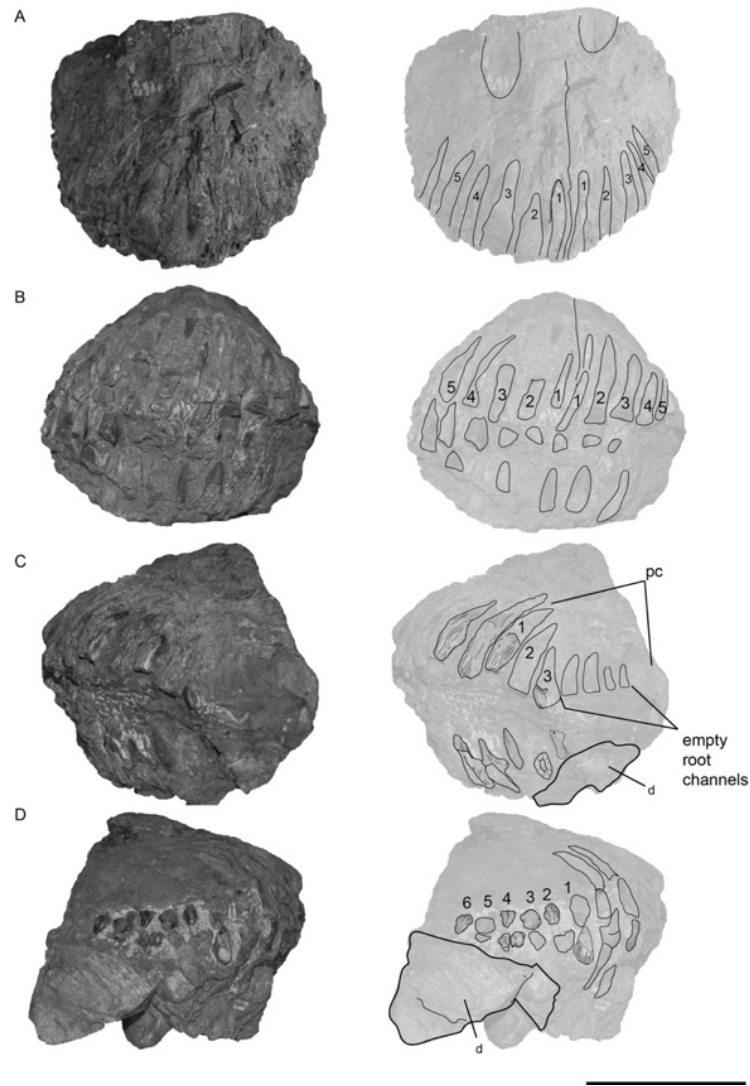


Figure 6. 80. *Taurops macrodon*: dorsal (A), anterior (B), left (C) and right (D) views of AMNH FARB 5610. Scale: 10 cm.

Historical background: *Taurops macrodon* was considered closely related to *Tapinocephalus* (Broom 1912) and was later synonymised with *Tapinocephalus* by Boonstra (1956, 1969) and later supported by Kammerer (2009). Both Boonstra (1969) and Kammerer (2009) based their synonymy on the similarity in size between the premaxillary bones of *Taurops macrodon* and *Tapinocephalus atherstonei*.

Conclusion. The holotype of *Taurops macrodon* (AMNH FARB 5610) can be confidently identified as a tapinocephalid because of the typical tapinocephalid incisor and postcanine morphology. The snout tip of *Taurops macrodon* is wide and shallow, similar to that of both *Tapinocephalus atherstonei* and *Mormosaurus seeleyi*. As the width of the premaxilla is not alone diagnostic character for *Tapinocephalus atherstonei*, it is not possible to positively synonymise *Taurops macrodon* with *Tapinocephalus* on this character and the species is considered *nomen dubium* and the status of the holotype is tapinocephalid indet.

6.10.4 *Moschoides romeri* BYRNE 1937

Holotype: FMNH UC 367, a dentary fragment and associated incomplete postcrania found on Hottentotsrivier, Beaufort West. (Byrne, 1937).

Diagnosis: “*Moschoides romeri* is an herbivorous dinocephalian closely similar, structurally, to *Moschops capensis*. *Moschoides* may be distinguished from *Moschops* by the following characters: (1) Its somewhat greater size; (2) the greater massiveness of the first sacral rib as compared with the second; (3) the relatively longer anterior process of the ilium, and (4) the more vertically placed femora.” (Byrne, 1937, p. 221).

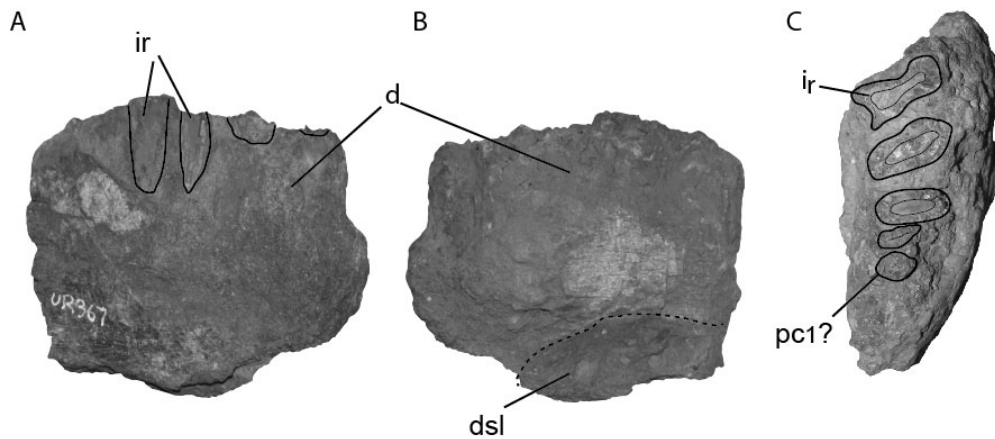


Figure 6.81. Photographs of the only cranial portion (Byrne, 1937, p. 221) of the holotype of *Moschoides romeri* (FMNH UC 367) showing the lateral (A), medial (B) and dorsal (C) views of the right dentary portion. Byrne (1937, pl. 1-3, Figs. 1-32.) described and illustrated only the postcranial elements of the holotype. The lower jaw portion manifests three labiolingually elongated incisors. Scale: 10 cm. Photo. Dr. K. Angielczyk.

Brief notes on the holotype: FMNH UC 367 (Fig. 6.81) comprises a fairly weathered right dentary fragment from behind the symphyseal line of the mandible. The lateral surface of the dentary is smooth and weathering has revealed the relatively long roots of two anterior lower incisor teeth (Fig. 6.81A). In medial view the dentary has a trough to accommodate the splenial and the dorsal surface shows the roots of three labiolingually elongated teeth and a fourth small circular one which is positioned posteriorly.

Historical background & conclusion: As the only cranial portion of the holotype is a weathered anterior dentary fragment it is evident that *Moschoides romeri* of Byrne (1937) has been retained on the basis of its postcranial remains. These comprise mostly fragmentary elements with the exception of few fused vertebral portions, most of long bones and some ribs. Byrne (1937, p.221) considered

Moschoides romeri very similar to *Moschops capensis* but differing from it because of its larger size. More recently *Moschoides romeri* has been synonymised with *Moschops capensis* (Boonstra 1969; Kammerer 2009) but no reasons were given by these authors. As the species is represented with a non-diagnostic cranial element *Moschoides romeri* is regarded as tapinocephalid indet.

6.11 Conclusion

This chapter provides a composite redescription of the skulls of the short snouted tapinocephalid subfamilies Moschopinae and Tapinocephalinae and includes illustrations of relevant material as well as detailed cranial descriptions.

Tapinocephalus atherstonei, *Moschops capensis*, *Moschognathus whaitsi*, *Agnosaurus pienaari*, and *Criocephalosaurus vanderbyli* are considered valid monospecific genera of these subfamilies.

Avenantia has been synonymised with *Riebeeckosaurus*. *Mormosaurus* and *Keratocephalus* are now considered to be longirostin tapinocephalids in the Struthiocephalinae, and *Keratocephalus* is synonymised with *Struthiocephalus whaitsi*. Because of fragmentary and nondiagnostic holotype cranial material: *Moschoides romeri* and *Pelosuchus priscus* are regarded as *nomen dubium*; and *Taurops macrodon* and *Phocosaurus megischion* should be considered tapinocephalid indet.

7 PHYLOGENETIC ANALYSIS OF TAPINOCEPHALID DINOCEPHALIA

7.1 Introduction

A cladistic approach to determine the phylogenetic relationship of dinocephalians relative to other therapsid clades was first undertaken by Hopson and Barghusen (1986) and later by Sidor (2000), and has also been applied to test phylogenetic placement of different taxa within the Dinocephalia (*e.g.* Rubidge, 1991, 1994, Rubidge and van den Heever, 1997; Cisneros et al., 2012, Liu, 2013, Fraser et al., 2019). Amongst the main dinocephalian clades the carnivorous Anteosauridae and the herbivorous Tapinocephalidae are the most speciose. An investigation of species interrelationships within Anteosauridae was undertaken by Kammerer (2011), here I investigate the phylogenetic interrelationships of tapinocephalid genera for the first time.

In the analysis the basal therapsid *Biarmosuchus*, the anteosaurian dinocephalian *Archaeosyodon*, and the deuterosaurian dinocephalian *Deuterosaurus* are used as outgroups. *Archaeosyodon* is considered the most basal member of the Anteosauridae (Kammerer, 2011) and *Deuterosaurus* has been considered in both the herbivorous and carnivorous Dinocephalia (*e.g.* Watson, 1914, Boonstra, 1965). The basal Tapinocephalia is represented by the titanosuchid *Jonkeria* (following Kammerer, 2011; S. Jirah *pers comm.*).

Tapinocephalid genera represented in the analysis follow the taxonomic revision undertaken in this thesis for the short snouted subfamilies Tapinocephalinae and Moschopinae (incl. *Riebeeckosaurus*), and for the long snouted Tapinocephalidae the taxonomy of Kammerer (2009) is applied. The taxa represented in the analysis are *Tapinocaninus*, *Ulemosaurus*, *Riebeeckosaurus*, *Tapinocephalus*, *Moschops*, *Moschognathus*, *Agnosaurus*, *Criocephalosaurus*, *Mormosaurus*, *Struthiocephalus* and *Struthionops*. Of these, *Agnosaurus*, *Moschognathus* and *Struthionops* are considered to be represented by subadult specimens.

7.2 Material and methods

The character matrix, which comprises 15 taxa and 60 cranial/dental characters (Appendix 7.1), was prepared in Mesquite version 3.51 (Maddison and Maddison, 2018). For the character list, characters used in previous analyses (Rubidge & van den Heever, 1997; Sidor, 2000; Kammerer, 2011; Cisneros et al., 2012; Fraser et al., 2019), some of them with modifications, were considered, as well as new proposed characters.

The cladistic analysis was done using TNT version 1.5 (Goloboff et al., 2008; Goloboff & Catalano, 2016) and the analyses were performed with all characters having equal weight, including and excluding the three subadult taxa (*Agnosaurus*, *Moschognathus* and *Struthionops*).

7.2.1. Specimens used in the analysis

Biarmosuchus: PIN 1758/2, PIN 1758/7, PIN 1758/8, PIN 1758/18, PIN 1758/19, PIN 1758/86 (photos are curtesy of Dr. J. Liu). *Archaeosyodon*: PIN1758/3, PIN 1758/95, PIN 1758/293, PIN 1758/294, PIN 1758/328. *Deuterosaurus*: PIN 1954/1, PIN 2629/1. *Jonkeria*: SAM-PK-4343, SAM-PK-12030. *Tapinocaninus*: NMQR 2987, NMQR 2986, NMQR 2985. *Ulemosaurus*: PIN2207/1, PIN2207/2, PIN 157/4. *Riebeeckosaurus*: SAM-PK-3400, SAM-PK11955, SAM-PK-9166. *Agnosaurus*: SAM-PK-11832. *Moschognathus*: AMNH FARB 5602, AM4950. *Moschops*: SAM-PK-11582, SAM-PK-K319, SAM-PK-12067. *Criocephalosaurus*: MMK 5138, NHMUK PV R 36626, BP/1/5445, BP/1/1582. *Tapinocephalus*: NHMUK PV R 1705, SAM-PK-2344, AMNH FARB 5626, CGP/1/2266. *Mormosaurus*: NHMUK PV R3594, NHMUK PV R 3596, TM1484, AMNH FARB 5655, CGP/1/280, CGP/1/1848. *Struthiocephalus*: SAM-PK-2678, SAM-PK-K272, BP/1/1575, SAM-PK-11591, FMNH UC 1512. *Struthionops*: SAM-PK-11947, CGP/1/26.

7.3 Results and discussion

Under the implicit enumeration search, two most parsimonious trees were recovered when all taxa were included in the analysis, and one tree was found when the subadult taxa were excluded. The tree length in the first analysis is 139 with a consistency index (CI) of 0.68 and retention index (RI) of 0.72; whereas the second analysis resulted in a tree length of 119, CI of 0.79 and RI of 0.84. The strict consensus of the first analysis and the only most parsimonious tree of the

second analysis are shown (Fig. 7.1), in which bootstrap values greater than 50 are indicated below the branches.

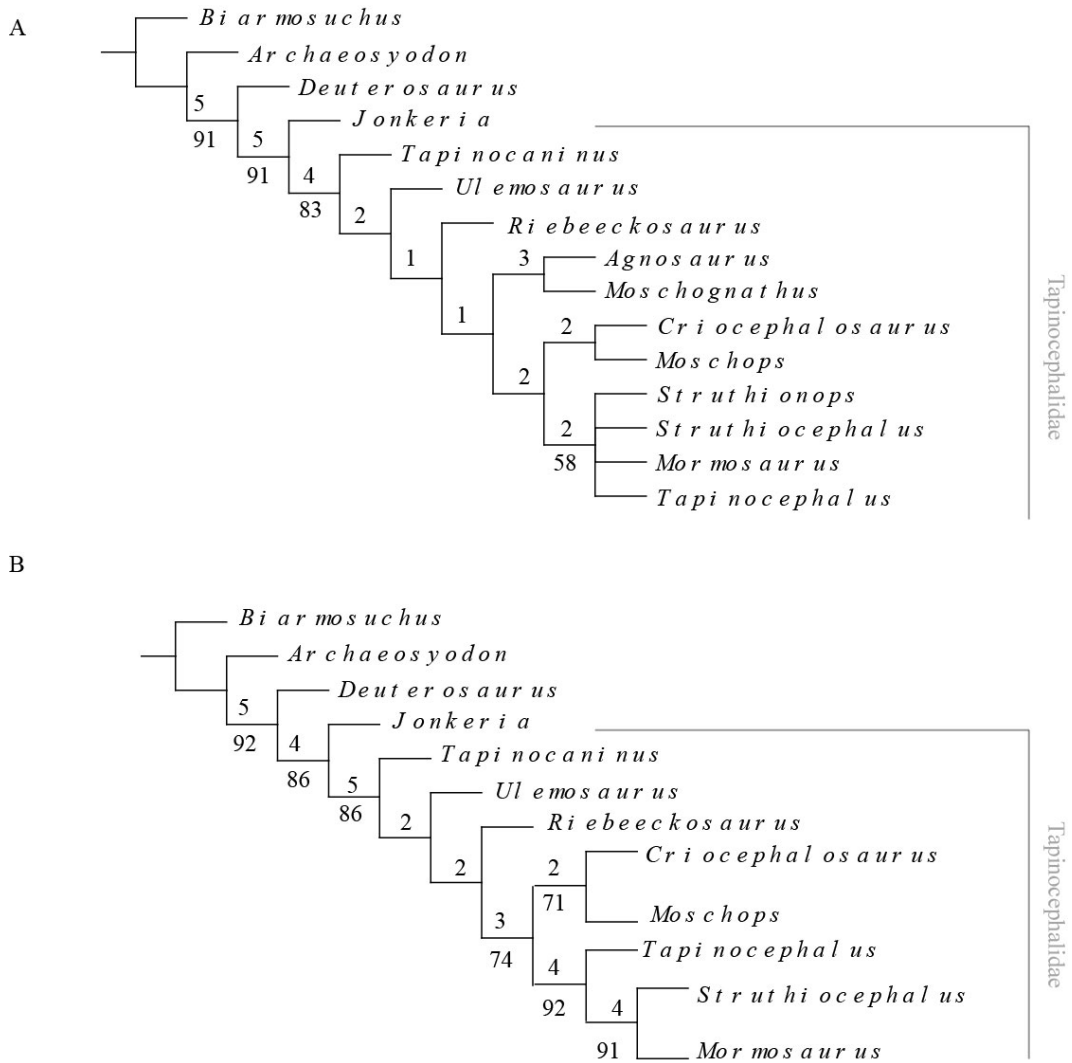


Figure 7.1. Strict consensus trees in A the result when all taxa included and single most parsimonious tree in B when three taxa represented by subadults are excluded. Bremer values and Bootstrap values (greater than 50) indicated respectively above and under the branches.

The only differences between these two analyses is the polytomy in the most nested group of tapinocephalids, *Struthionops*, *Struthiocephalus*, *Mormosaurus*

and *Tapinocephalus*. The subclade which includes *Agnosaurus* and *Moschognathus*, is positioned relatively basal in the cladogram (Fig. 7.1A). This placement is anticipated because the taxa represented by subadult specimens manifest characters of more basal taxa, for example weak cranial pachyostosis and anteroventral slope of the occiput, and thinner postorbital bar. The second analysis (Fig. 7.1B), where the subadult *Agnosaurus*, *Moschognathus* and *Struthionops* are excluded, shows complete resolution for the relationships of the Tapinocephalidae, with *Tapinocephalus* being the sister taxon of the clade formed by *Struthiocephalus* and *Mormosaurus*.

The monophyly of the herbivorous tapinocephalids plus *Jonkeria* is supported by seven synapomorphies: subhorizontal or weakly upturned premaxilla alveolar margin (1/1>0); posterior extent of the nasal process of the premaxilla more than half the preorbital length (3/0>2); long septomaxilla facial exposure (4/0>1); nonterminal external naris (5/0>1); presence of longitudinally oriented maxillary depression that extends posteriorly onto the lacrimal (16/0>1); moderately sized quadrate positioned anteriorly below temporal fossa (42/1>2); presence of horizontal shelf posterior to the lateral flanges of the pterygoid (43/0>1).

The monophyly of tapinocephalid dinocephalians is well supported with nine synapomorphies: postorbital bar ventral border is formed by jugal (one-third) and squamosal (two-thirds) (13/0>1); greatly expanded subtemporal bar (17/1>2); swollen and round zygoma lateral surface (21/0>1); parietal's posterior bends down (slightly to moderately) is present with its portion including pineal opening

(33/0>1); teeth of the maxillary tooth row decrease in size posteriorly with the canine barely differentiated (51/0>1); canine with small ridge-like lingual heels (53/0>1); size of upper canine is as large as the incisors (54/2>1); pattern of interlocking extends to canine (56/0>1); anterior end of postcanine tooth row does not extend lingual to the canine (59/0>1).

The analyses shows *Tapinocaninus* and *Ulemosaurus* respectively as the most basal tapinocephalid genera. The monophyly of *Ulemosaurus* and remaining tapinocephalids is supported by three synapomorphies: frontal contribution to the temporal fenestra margin (25/0>1); reduced reniform palatine boss ventral surface (35/0>1); lack of palatine dentition (36/3>0).

Derived tapinocephalids include two subclades namely (*Criocephalosaurus* + *Moschops*) and (*Tapinocephalus* + *Mormosaurus* + *Struthiocephalus*). The sister group relationship of the first subclade is supported by two synapomorphies: absence of frontal contribution to margin of the temporal fenestra (25/1>0); dorsoventral thickening along the pineal opening is greater than the thickening along the frontal (30/1>3). In the latter subclade, the sister group relationship of *Mormosaurus* and *Struthiocephalus* is supported in the second analysis by four synapomorphies: premaxilla distance between the anterior margin of the external naris and anterior border of premaxilla considerably longer than the long axis of the external naris (2/2>3); preorbital length longer than the half of the greatest length of the length of the skull (6/0>1); zygoma posteroventral corner is angled (20/0>1); relatively slender zygoma with a longitudinal depression formed close

to the anteroventral border (21/1>2). While bootstrap support is moderate for the higher tapinocephalid clades and for the sister group relationship of the subclade *Criocephalosaurus*+*Moschops*, values for the subclade *Tapinocephalus*+*Mormosaurus*+*Struthiocephalus* are higher.

7.4. Conclusion

This phylogenetic analysis provides the first phylogenetic analysis for Tapinocephalidae. The monophyly of the clade is well supported. The analysis shows a better relationship within the tapinocephalid taxa when the taxa with subadults (*Agnosaurus*, *Moschognathus* and *Struthionops*) are excluded from the analysis. The analysis show that *Tapinocaninus*, *Ulemosaurus* and *Riebeeckosaurus* are basal to the rest of the tapinocephalid taxa and *Tapinocaninus* is the most basal member of the group. The derived Tapinocephalidae is represented with two subclades: *Criocephalosaurus*+*Moschops* and *Tapinocephalus* + *Mormosaurus* + *Struthiocephalus*.

8 CONCLUSION

This research is part of a major project to determine tetrapod biodiversity change in the terrestrial realm during the Middle Permian. The Dinocephalia, apart from being the earliest large therapsids, comprised a major component of the middle Permian terrestrial ecosystems and despite their taxonomic diversity and apparent ecological success they went extinct at the end of the Capitanian stage of the Middle Permian thus having the dubious distinction of being the first therapsid lineage to face extinction.

The most diverse dinocephalian family in terms of both species and numbers of individuals, the Tapinocephalidae, are known from Russia, Zimbabwe, Tanzania, Zambia and Brasil and are most abundantly represented by discoveries from the South African Karoo Supergroup. A total of 31 tapinocephalid species have been described from Russia, South Africa and Zimbabwe. Later taxonomic revision by Boonstra (1969) recognized 17 species in 13 genera from South African which were considered to fall in two broad groups depending on whether they were long- or short-snouted. More recently Kammerer (2009) recognized only six species.

In this study all the previously described tapinocephalid holotypes were revisited and a taxonomic revision is proposed for the short snouted tapinocephalid dinocephalians. Only holotypes described from cranial material were considered.

The relatively large sample size enabled recognition of tapinocephalid cranial characters which modify during ontogenetic development, and identification of species which were previously erected on the basis of subadult characters. Of 23 holotypes that are described as short-snouted tapinocephalid holotypes, only nine monospecific genera are recognised as valid as a result of this study. These are *Tapinocaninus pamelae*, *Ulemosaurus svijagensis*, *Riebeeckosaurus longirostris*, *Agnosaurus pienaari*, *Moschognathus whaitsi*, *Criocephalosaurus vanderbyli*, *Moschops capensis*, *Tapinocephalus atherstonei*, and *Mormosaurus seeleyi*. A detailed description and illustration of the valid short snouted taxa is presented.

The cranial morphology of the South African *Tapinocaninus* and *Ulemosaurus* from Russia were compared for the first time. The results confirmed the findings of Rubidge (1994) that both taxa possess a combination of primitive and derived features. Plesiomorphic characters retained by them include narrow intertemporal breadth, large temporal fenestra, non-incisiform canine, and relatively anteriorly positioned jaw joint when compared with other tapinocephalids. Cladistic analysis supported the previously proposed basal position of the two genera with *Tapinocaninus* proving to be more basal.

Avenantia was synonymised with *Riebeeckosaurus* which is now considered a basal short-snouted tapinocephalid and also retains a narrow intertemporal and an enlarged caniniform tooth. However the occiput slopes further anteroventrally resulting in a more anteriorly positioned jaw joint relative to that of *Tapinocaninus* and *Ulemosaurus*. Morphological differences between the two genera, such as surface thickening of the parietal, postorbital and general cranial thickening, are interpreted to be the result of ontogenetic or sexual variation.

Following extensive archival research in the Natural History Museum in London and in line with the suggestion of Haughton (1915), it is apparent that the holotype of *Tapinocephalus* (the first described tapinocephalid dinocephalian) does not provide satisfactory diagnostic cranial characters and a neotype is suggested as *Tapinocephalus* is indeed a valid genus and is represented by several specimens in different museum collections.

Moschops capensis, *Moschops koupensis* and *Delphinognathus conocephalus* are shown to be congeneric and their cranial differences, which are mainly to do with the degree of skull roof pachyostosis, are considered a manifestation of ontogenetic development. Although *Delphinognathus* has nomenclatorial priority, the name *Moschops capensis* is so well entrenched in both scientific and popular literature that the reversal of nomenclatorial precedence in favour of *Moschops* is suggested.

Moschognathus whaitsi in accordance with Gregory (1926) and Kammerer (2009) is considered valid and its cranial description has been augmented by the discovery of the new well-preserved specimen (AM4950). Both the holotype and the new specimen appear to represent different sub-adult ontogenetic developmental stages of a single species.

Contra Kammerer (2009) the validity of *Criocephalosaurus vanderbyli* is recognized as a result of the recent discovery of new cranial material which clearly demonstrates characters distinguishing it from *Moschops*.

Further preparation of the holotype and only specimen of *Agnosaurus pienaari* revealed unique palatal characters (particularly the presence and arrangement of palatine teeth as around the outer edge of the palatine boss) which proves its difference from *Moschops* and any other tapinocephalids and warrant its recognition as a valid genus despite the holotype being subadult, as recognized from the relatively large orbit in association with reduced cranial pachyostosis and a narrow intertemporal.

Mormosaurus which is distinguished by a large antero-posteriorly oriented nasofrontal boss in adult individuals is shown to be a longirostrin (long-snouted) tapinocephalid and *Pnigalion oweni* (previously referred to *Moschops* by Boonstra [1969] and Kammerer [2009]), *Taurocephalus lerouxii* and *Struthiocephalus rheederi* are synonymised with *Mormosaurus seeleyi* in agreement with Kammerer (2009).

Keratocephalus, in line with the proposal of Kammerer (2009) is with the longirostrin *Struthiocephalus whaitsi*. As both *Mormosaurus* and *Stuthiocephalus* are long-snouted tapinocephalids they do not fall within the ambit of this thesis.

This study includes the first extensive phylogenetic analysis of the Tapinocephalidae and indicates that the lower Beaufort Group of the South Africa Karoo Supergroup, largely because its time expansive depositional sequence, hosts both the most basal and most derived tapinocephalid dinocephalians. The analysis shows that the longirostrin taxa, together with the short snouted *Tapinocephalus*, are the most derived tapinocephalid taxa.

This research recognise the following taxonomic ranking for the family:

FAMILY TAPINOCEPHALIDAE

Tapinocaninus

Ulemosaurus

Riebeeckosaurus

Agnosaurus

SUBFAMILY MOSCHOPINAE

Moschops

Moschognathus

SUBFAMILY TAPINOCEPHALINAE

Tapinocephalus

Mormosaurus

Struthiocephalus

Struthionops

Subfamily Ulemosaurinae including *Ulemosaurus*, *Tapinocaninus*, and *Riebeeckosaurus*. Subfamily Tapinocephalinae including *Tapinocephalus*, *Moschops*, *Criocephalosaurus*, *Moschognathus*, *Agnosaurus*. Struthiocephalinae including *Struthiocephalus*, *Mormosaurus*, and *Struthionops*.

Up till now research on this important group of middle Permian tetrapods has been hampered by the large unwieldy size of specimens, the difficulty in preparing them because of their hard intractable matrix, and the fragmentary nature of the specimens. Hopefully this project, which for the first time provides illustrations of the material as well as detailed cranial descriptions and proposes which characters are subject to ontogenetic change, will provide a reliable taxonomic assessment of the diversity of short snouted tapinocephalid dinocephalians. This will enhance middle Permian biodiversity studies and pave the way for future researchers to address investigations on dinocephalians relating to sexual dimorphism and ontogenetic development.

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APPENDIX 1 List of papers published during Ph.D. registration

Due to the change in my civil status during my studies different surnames are used in the articles: Atayman, Atayman- Güven, and Güven.

List of papers produced from the Ph.D.

Güven, S., Rubidge, B.S. and Abdala, F. 2013. Cranial morphology and taxonomy of South African Tapinocephalidae (Therapsida: Dinocephalia): the case of *Avenantia* and *Riebeeckosaurus*. *Palaeontologia Africana*.48: 24-33.

Day, M. O., **Güven, S.**, Abdal, F., Jirah, S., Rubidge, B., Almond, J., 2015. Youngest dinocephalian fossils extend the *Tapinocephalus* Zone, Karoo Basin, South Africa. *South African Journal of Science*, 111 (3-4): 1-5.

Other papers published during Ph.D.

Şengör, A.M.C., **Atayman, S.** & Özeren, S. 2008. A scale of greatness and causal classification of mass extinctions: Implications for mechanisms.

Proceedings of the National Academy of Sciences, 105 (37): 13736-13740.

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Cisneros, J.C., Abdala, F., **Atayman-Güven, S.**, Rubidge, B.S., Şengör, A.M.C. & Schultz, C.L., 2012. Canivorous dinocephalian from the Middle

Permian of Brazil and tetrapod dispersal in Pangea. *Proceedings of the National Academy of Sciences*, 109 (5): 1584-1588.

APPENDIX 2 List of the tapinocephalid specimens examined in this study.

¹ indicates short-snouted specimen taxa or cranial and/or dental elements from a short-snouted taxon. ² indicates specimens not personally examined and

photographs are utilised. ³ indicates skulls associated with postcranial element(s).

The current ID for the long-snouted tapinocephalids follows the revision provided by Kammerer (2009).

Specimen no	Cranial representation	Status	Original ID	Current ID
NMQR 2987 ^{1,3}	skull	holotype	<i>Tapinocaninus pamela</i>	<i>Tapinocaninus pamela</i>
NMQR 2986 ^{1,3}	skull	topotype	<i>Tapinocaninus pamela</i>	<i>Tapinocaninus pamela</i>
NMQR 2985 ^{1,3}	skull	topotype	<i>Tapinocaninus pamela</i>	<i>Tapinocaninus pamela</i>
ROZ K 95 ¹	skull		<i>Tapinocaninus pamela</i>	<i>Tapinocaninus pamela</i>
PIN 2207/2 ^{1,3}	skull	lectotype	<i>Ulemosaurus svijagensis</i>	<i>Ulemosaurus svijagensis</i>
PIN 2207/1 ¹	skull		<i>Ulemosaurus svijagensis</i>	<i>Ulemosaurus svijagensis</i>
PIN 2972/1 ¹	skull		<i>Ulemosaurus gigas</i>	<i>Ulemosaurus svijagensis</i>
PIN 157/4 ¹	skull		<i>Ulemosaurus gigas</i>	<i>Ulemosaurus svijagensis</i>
PIN 1955/3 ¹	tooth	holotype	<i>Ulemosaurus gigas</i>	<i>Ulemosaurus svijagensis</i>
PIN 1955/4-5 ¹	tooth	holotype	<i>Ulemosaurus gigas</i>	<i>Ulemosaurus svijagensis</i>
SAM-PK-3400 ¹	skull	holotype	<i>Riebeeckosaurus longirostris</i>	<i>Riebeeckosaurus longirostris</i>
SAM-PK-11955 ¹	skull		<i>Riebeeckosaurus longirostris</i>	<i>Riebeeckosaurus longirostris</i>
SAM-PK-9166 ^{1,3}	skull	holotype	<i>Avenantia kruisvleiensis</i>	<i>Riebeeckosaurus longirostris</i>
NHMK PV R1705 ^{1,3}	skull	holotype	<i>Tapinocephalus atherstonei</i>	<i>Tapinocephalus atherstonei</i>
SAM-PK-2344 ¹	skull		<i>Tapinocephalus atherstonei</i>	<i>Tapinocephalus atherstonei</i>
NHMB 1556 ¹	skull		-	<i>Tapinocephalus atherstonei</i>

AMNH FARB5626 ¹	skull		<i>Tapinocephalus atherstonei</i>	<i>Tapinocephalus atherstonei</i>
CGP/1/2266 ¹	skull		-	<i>Tapinocephalus atherstonei</i>
NHMK PV R 4094	tooth		<i>Tapinocephalus?</i>	Tapinocephalid indet.
SAM-PK-0713 ¹	skull	holotype	<i>Delphinognathus conocephalus</i>	<i>Moschops capensis</i>
AMNH FARB5550 ¹	skull	holotype	<i>Moschops capensis</i>	<i>Moschops capensis</i>
AMNH FARB5552 ^{1,3}	skull	topotype	<i>Moschops capensis</i>	<i>Moschops capensis</i>
AMNH FARB5553 ^{1,3}	skull	topotype	<i>Moschops capensis</i>	<i>Moschops capensis</i>
AMNH FARB5555a ¹	skull	topotype	<i>Moschops capensis</i>	<i>Moschops capensis</i>
AMNH FARB5555b ¹	skull	topotype	<i>Moschops capensis</i>	<i>Moschops capensis</i>
SAM-PK-11582 ¹	skull	holotype	<i>Moschops koupensis</i>	<i>Moschops capensis</i>
SAM-PK-319 ¹	skull	holotype	<i>Criocephalosaurus</i>	<i>Moschops capensis</i>
SAM-PK-12067 ¹	skull	holotype	<i>Moschops capensis</i>	<i>Moschops capensis</i>
SAM-PK-11972 ^{1,3}	skull		<i>Moschops capensis</i>	<i>Moschops</i> sp.
SAM-PK-11973 ¹	skull		<i>Moschops capensis</i>	<i>Moschops capensis</i>
SAM-PK-11974 ^{1,3}	skull		<i>Moschops capensis</i>	<i>Moschops capensis</i>
BP/1/1740 ¹	skull		<i>Moschops</i>	<i>Moschops capensis</i>
KNPI ¹	skull		-	<i>Moschops capensis</i>
KNPII ¹	skull		-	<i>Moschops capensis</i>
KNPIII ¹	skull		-	<i>Moschops capensis</i>
KNPIV ¹	skull		-	<i>Moschops capensis</i>
AMNH FARB5602 ^{1,3}	skull	holotype	<i>Moschognathus whaitsi</i>	<i>Moschognathus whaitsi</i>
AM 4950 ¹	skull		-	<i>Moschognathus whaitsi</i>
MMK 5138 ¹	skull	holotype	<i>Criocephalosaurus vanderbyli</i>	<i>Criocephalosaurus vanderbyli</i>
NHMK PV R 36626 ¹	skull		<i>Criocephalosaurus</i> sp.	<i>Criocephalosaurus vanderbyli</i>
BPI/1/582 ¹	skull		-	<i>Criocephalosaurus vanderbyli</i>
BPI/1/5445 ¹	skull		-	<i>Criocephalosaurus</i>

				<i>vanderbyli</i>
BPI/1/7214 ¹	skull		-	<i>Criocephalosaurus vanderbyli</i>
SAM-PK-K10888 ¹	skull		-	<i>Criocephalosaurus vanderbyli</i>
CGP/1/846 ¹	skull		-	<i>Criocephalosaurus vanderbyli</i>
SAM-PK-11832 ¹	skull	holotype	<i>Agnosaurus pienaari</i>	<i>Agnosaurus pienaari</i>
SAM-PK-918 ³	mandible	holotype	<i>Pelosuchus priscus</i>	Tapinocephalid indet.
AMNH FARB 5610	skull	holotype	<i>Taurops macrodon</i>	Tapinocephalid indet.
FMNH UC 367 ^{1,2,3}	mandible	holotype	<i>Moschoides romeri</i>	Tapinocephalid indet.
NHMUK PV R R3594 ³	skull	holotype	<i>Mormosaurus seeleyi</i>	<i>Mormosaurus seeleyi</i>
AMNH FARB 5655	skull	holotype	<i>Taurocephalus lerouxi</i>	<i>Mormosaurus seeleyi</i>
TM 1484	skull	holotype	<i>Struthiocephalus rheederi</i>	<i>Mormosaurus seeleyi</i>
NHMUK PV R 3596	skull	holotype	<i>Prigalion oweni</i>	<i>Mormosaurus seeleyi</i>
SAM-PK-9080 ³	skull with lower jaw		<i>Mormosaurus seeleyi</i>	<i>Mormosaurus seeleyi</i>
SAM-PK-110997 ³	skull		<i>Phocosaurus megischion</i>	<i>Mormosaurus seeleyi</i>
CGP/1/280	skull		-	<i>Mormosaurus seeleyi</i>
CGP/1/1848	skull		-	<i>Mormosaurus seeleyi</i>
SAM-PK-11947	skull	holotype	<i>Struthionops intermedius</i>	<i>Struthionops intermedius</i>
CGP/1/26	skull with lower jaw		-	<i>Struthionops intermedius</i>
SAM-PK-3015 ³	skull with lower jaw	holotype	<i>Struthiocephalus whaitsi</i>	<i>Struthiocephalus whaitsi</i> (?)
UT Huene1931 T. 167 F4,F8-F10	skull	holotype	<i>Keratocephalus moloch</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-8946 ³	skull		<i>Keratocephalus moloch</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-10557	skull		<i>Keratocephalus moloch</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-K272	skull with lower jaw		<i>Struthiocephalus whaitsi</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-3719 ³	skull		<i>Struthiocephalus whaitsi</i>	<i>Struthiocephalus whaitsi</i>

BP/1/1575	skull	holotype	<i>Struthiocephalus kitchingi</i>	<i>Struthiocephalus whaitsi</i>
FMNH UC 1512	skull	holotype	<i>Struthiocephalus milleri</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-11591	skull		<i>Struthiocephalus whaitsi</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-11693	skull		<i>Struthiocephaloides duplessisi</i>	<i>Struthiocephalus whaitsi</i>
SAM-PK-12269	teeth		<i>Struthiocephalus</i> sp.	<i>Struthiocephalus</i> sp.

APPENDIX 3 *Moschops* Broom, 1911 (Therapsida, Dinocephalia): proposed conversation by reversal of precedence with *Delphinognathus* Seeley, 1892.

[Article in preparation]

Abstract. The purpose of this application, under Article 23.9.3 and 81.2.3 of the ICZN Code, is to conserve the generic name *Moschops* Broom, 1911 (TAPINOCEPHALIDAE, DINOCEPHALIA). The name *Moschops* is threatened by its senior subjective synonym *Delphinognathus* Seeley, 1892. It is proposed that *Moschops* be given precedence over *Delphinognathus* whenever these names are considered to be synonyms. *Moschops* Broom, 1911 is the most well established tapinocephalid dinocephalian.

Keywords. Nomenclature; taxonomy; Therapsida; Dinocephalia; Tapinocephalidae; Tapinocephalinae; *Delphinognathus*; *Delphinognathus conocephalus*; *Moschops*; *Moschops capensis*; middle Permian; South Africa; Karoo.

1. *Delphinognathus* Seeley, 1892 was named based on an incomplete weathered and damaged skull with attached partial lower jaw which was collected from Middle Permian deposits of the Karoo Supergroup at an unknown locality in the Beaufort West District of Western Cape, South Africa (Seeley, 1892). The type species is by monotypy *Delphinognathus conocephalus* Seeley, 1892. The specimen was described and illustrated by Seeley (1892, fig. 1). The generic name refers to the superficial

morphological similarity of the lower jaw and dentition with the dolphin (a general name for the aquatic mammal from the infraorder Cetacea) in the initial description (Seeley, 1892, p. 474): *i.e.* Delphino is Greek for Dolphin and -gnathus is Latin for jaw. The type specimen, SAM-PK-0713 is housed in the IZIKO South African Museum in Cape Town, South Africa.

2. *Moschops* Broom, 1911 was named on the basis of a well-preserved skull with mandibles which was chosen by the author as the holotype from a series of skulls with skeletal remains found together. It was found in the farm Spitzkop, Laingsburg district in Moordenaars Karoo of South Africa. As the remains only differ from each other in size and degree of cranial thickening they were considered to represent an ontogenetic series. The type species, after the latest revisions is by monotypy *Moschops capensis* Broom, 1911. The generic name is combination of “moskhos” and “ops”, respectively Greek for “calf” and “face”. The type specimen AMNH FARB 5550 is housed in the American Natural History Museum, New York, USA. The topotypes at the museum are: AMNH FARB 5552 (skull and associated postcranium), AMNH FARB 5553 (skull with mandibles and associated postcranium), AMNH FARB 5555a (occiput with mandible portions), AMNH FARB 5555b (occiput with mandible portions). The rest of the topotypes are postcranial elements: AMNH FARB 5551 (interclavicle, scapulocoracoid, humerus, radius, ulna, pelvis, femur, tibia, fibula, pes, vertebrae), AMNH FARB 5554 (ribs and vertebrae), AMNH FARB 5556 (humerus), AMNH FARB 5557 (humerus), AMNH FARB

23922 (humerus), AMNH FARB 23923 (humerus), AMNH FARB 23924 (humerus), AMNH FARB 23925 (humerus), AMNH FARB 23926 (ulna), AMNH FARB 23927 (ulna and radius), AMNH FARB 23928 (ulna), AMNH FARB 23929 (ulna), AMNH FARB 23930 (radius), AMNH FARB 23931 (femur), AMNH FARB 23945 (scapula), AMNH FARB 23946 (coracoid), AMNH FARB 23947 (ulna and ribs), AMNH FARB 23991 (femur), AMNH FARB 23992 (femur), AMNH FARB 23992 (femur), AMNH FARB 23994 (femur), AMNH FARB 24101 (fibula), AMNH FARB 24104 (fibula), AMNH FARB 24106 (tibia), AMNH FARB 24107(fibula), AMNH FARB 24108(partial pelvis), AMNH FARB24109 (partial pelvis), AMNH FARB 24110 (partial pelvis), AMNH FARB 24112 (partial pelvis). There are numerous referred specimens of *Moschops* housed in the South African institutions: *e.g.* SAM-PK-11582 (large skull), SAM-PK-K319 (large skull with mandible), SAM-PK-11973 (incomplete medium size skull), SAM-PK-11974 (incomplete medium size skull), SAM-PK-12067, KNPI (small skull), KNPII (small skull), KNPIII (small skull), KNPI IV (small skull with complete mandibles). These last four skulls are housed in the Karoo National Park, Beaufort West, South Africa.

3. The differences between *Delphinognathus* and *Moschops* are considered to be representative of different ontogenetic stages of the same species. Following Article 23.9 of the Code, *Delphinognathus* has the priority over *Moschops*. However, *Moschops* has been universally used as a valid genus name since its description in palaeontological literature as well as other

life science related literature and popular culture, and it is the most cited dinocephalian taxon. A reversal of precedence is required to preserve *Moschops* and retain universality. A non-exhaustive list of 47 citations using the name *Moschops* as valid is being provided below of which 20 of them covers the time span of 10 years. The reversal of precedence is requested because *Delphinognathus* does not meet all the requirements of Article 23.9.1 specifically, Article 23.9.1.1. *Delphinognathus* has been in use the since 1899 solely as result of its being a valid tapinocephalid genus. *Moschops*, apart from being recognised as a valid taxon become the key representative of tapinocephalid dinocephalians in scientific and popular literature and satisfies the condition of Article 23.9.1.2 of the Code.

4. The International Commission on Zoological Nomenclature is accordingly asked:

- (1) To use its plenary power, accordingly with the Article 23.9.3 of the Code, to rule that the name *Moschops* Broom, 1911 is to be given precedence over *Delphinognathus* Seeley, 1892, whenever the two are referred as synonyms;

- (2) to place on the Official List of Generic Names in Zoology the following names:

- (a) *Moschops* Broom, 1911, type species by original designation *Moschops capensis* Broom, 1911, with the endorsement that it is to be given precedence over *Delphinognathus* Seeley, 1892, whenever the two are considered synonyms;

(b) *Delphinognathus* Seeley (1892), type species by monotypy
Delphinognathus conocephalus Seeley, 1892, whenever the two
are regarded synonyms;

(3) To place on the Official List of Specific Names in Zoology the
following names:

(a) *capensis* Broom, 1911, as published in the binomen *Moschops*
capensis (specific name of the type species of *Moschops*);

(b) *conocephalus* Seeley, 1892, as published in the binomen
Delphinognathus conocephalus (specific name of the type species
of *Delphinognathus* Seeley, 1892).

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Below is a selection of references, including articles and books, which cite *Moschops capensis*. The articles span the time period 1969-2019 as required by the Article 23.9.1.2 of the Code. The list of publications is presented according to the date published. The last 20 reference spans the last 10 years.

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APPENDIX 4 Characters used in the phylogenetic analysis.

Citations made in the following style: “author(s):character number”, “author: table.clade.character number”, “author: chapter. character number”, “author: suite. character number”, Abbreviations for the cited authors are as follow: H&B- Hopson and Barghusen, 1986; FBDR-Fraser et al., 1998; Ka- Kammerer, 2010; Ki- King, 1988; S- Sidor, 2000; R&H- Rubidge and van den Heever, 1997. The citations followed with an asterisk indicates that either the character definition and/or states are modified or a character state(s) excluded or an additional character state(s) has been included.

- 1.** Premaxilla alveolar margin is: (0) subhorizontal or weakly upturned; strongly upturned (1). (H&B*: 2.12.2; H&R: 19; Ka*:7)
- 2.** Premaxilla length between the anterior margin of external naris and the anterior border of premaxilla: (0) one-third of the long axis of the external naris; (1) half the length of the long axis of the external naris; (2) almost equal to the long axis of the external naris; (3) considerably longer than the long axis of the external naris.
- 3.** Posterior extent of the nasal process of premaxilla: (0) less than half preorbital length; (1) half of the preorbital length; (2) more than half the preorbital length; (3) close to the nasal posterior end. (FBDR*: 4; H&B*: 1.2.7; S:4.1*).
- 4.** Septomaxilla facial exposure: (0) short; (1) long. (FBDR*: 7; H&B*: 1.2.2; S*: 4.12).

5. Location of external naris: (0) terminal; (1) nonterminal. (FBDR*: 3; Ka: 6; Ki:1.2; S:4.8)
6. Preorbital length: (0) almost equal to or shorter than half of the greatest length of the skull; (1) more than half of the greatest length of the skull.
7. Snout width/height ratio: (0) height greater; (1) height equal than width; (2) width greater. (FBDR: 2; Ka*: 21)
8. Snout dorsal profile anteriorly is: (0) gradually sloping towards the tip; (1) steep slope; (2) evenly convex. (FBDR*: 1; S*: 4.15)
9. Transition from cranial roof to snout: (0) extends on an even surface; (1) extends over a swelling on the nasal posteriorly; (2) extends over a gentle slope; (3) extends over a nasofrontal boss.
10. Transition from frontal to the nasofrontal boss: (0) abrupt; (1) smooth.
11. Depression close to posterior end of each nasal: (0) absent; (1) present.
12. The area of the nasofrontal boss is: (0) laterally protruded with the contribution of the prefrontal; (1) anteroposteriorly elongated as a result of a

reduced contribution from the prefrontal; (2) anteroposteriorly elongated and narrow as a result of no contribution of the prefrontal.

13. Postorbital bar ventral border formed by: (0) jugal; (1) jugal (one-third) and squamosal (two-thirds). (R&H*: 1.15).

14. Maxilla dorsal apex wedges between the prefrontal and nasal positioned: (0) anteriorly half-way along the snout; (1) posteriorly on the snout.

15. Maxillary surface weakly to moderately swollen over the alveolar region of the canine: (0) absent; (1) present. (S*: 4.10)

16. Longitudinally oriented maxillary depression that extends posteriorly onto the lacrimal: (0) absent; (1) present.

17. Dorsoventral expansion of the subtemporal region is: (0) narrow; (1) moderately expanded; (2) greatly expanded.

18. Zygomatic process of the jugal in contact with or close to quadratojugal, which is visible in lateral view: (0) absent; (1) present. (S*:4. 27)

19. The end of zygomatic process of jugal flares laterally: (0) absent; (1) present.

20. Zygoma posteroventral corner as seen on the dorsal view of the skull: (0) rounded; (1) angled.

21. Squamosal lateral surface: (0) not thickened; (1) swollen and round; (2) slender with longitudinal depression close to anteroventral border. (FBDR*: 19; S*: 4.32)
22. Anteroposterior diameter of the temporal fossa is: (0) less than dorsoventral axis; (1) about equal to or slightly greater than dorsoventral axis. (Ki*: 1.3)
23. Frontal contribution to orbital border: (0) present; (1) absent.
24. Frontal forms lateral spur between nasal and prefrontal: (0) absent; (1) present.
25. Frontal contributes to margin of temporal fossa: (0) absent; (1) present.
26. Thickening of the prefrontal is anteriorly in confluence with the thickening of the nasal and overhang together on the lateral surface of the snout: (0) absent; (1) present.
27. Supraorbital and postorbital regions dorsoventrally thickened to form a domed cranial roof: (0) absent; (1) present.
28. Postfrontal with boss like thickening which overhangs the orbit dorsally: (0) absent; (1) present.

29. General cranial thickening: (0) absent; (1) weak; (2) moderate; (3) strong.
30. Dorso-ventral thickening along parietal and frontal: (0) no thickening; (1) parietal and frontal thickening about the same; (2) parietal thickening less than frontal thickening; (3) parietal thickening greater than frontal thickening.
31. Thickness of postorbital bar is: (0) less than 20% of the orbital diameter; (1) 20% or more of the orbital diameter; (2) 35 % or more of the orbital diameter; (3) 50 % of the orbital diameter; (4) as thick as the orbital diameter; (5) thicker than the orbital diameter. (FBDR:13; S*: 18; S:4.18)
32. Horizontal ridge exposed in the dorsal view, extending forward from contact between parietal and squamosal in temporal opening: (0) absent; (1) present.
33. Parietal posterior curvature: (0) absent; (1) include pineal opening; (2) not include pineal opening; (3) pineal opening at the apex of the curvature.
34. Pineal canal elongated on an axis almost parallel to the long axis of the cranium: (0) absent; (1) present.
35. Ventral surface of palatine boss: (0) expanded; (1) reduced.
36. Dentition on palatine boss: (0) absent; (1) randomly distributed teeth on ventral surface; (2) randomly distributed along anterior edge of ventral surface:

(3) single row of teeth along the anterior edge of ventral surface. (FBDR*: 35; R&H*:17; S*:4.45L)

37. Parietal surface: (0) slightly depressed or flat with well-defined pineal chimney; (1) slightly depressed or flat without well-defined pineal chimney; (2) swollen with pineal chimney barely differentiated; (3) swollen with well-defined pineal chimney. (FBDR*:17; H&B*: 1.2.8; S*: 4.24)

38. Intertemporal breadth is: (0) narrow, with or without sagittal crest (1) broad. (FBDR*: 18; H&B*:1.4.1; S*: 4.35)

39. Morphology of postparietal: (0) approximately square; (1) taller than wide. (FBDR*:41)

40. Median spur of supraoccipital is: (0) less than one-third of postparietal height; (1) about one-third of postparietal height; (2) great than one-third of the postparietal height.

41. Squamosal contribution to the occipital surface: (0) narrow; (1) broad.

42. Anteroventral slope of the occiput is: (0) absent; (1) weak ; (2) moderate; (3) strong. (FBDR*: 42; H&B*: 2.15.1; S*:4.55)

43. Shelf behind the lateral flanges of the pterygoid: (0) absent; (1) present.

(H&B*: 2.15.5; R&H: 7; S: 4.50)

44. Ventral margin of the quadrate ramus of the pterygoid: (0) narrow and slender;
(1) broad and thickened.

45. Interpterygoid vacuity anteriorly very short or closed (0) absent; (1) present.

(H&B*: 1.2.10)

46. Position of jaw articulation: (0) close to the posterior border of the temporal fossa; (1) in the center of the temporal fossa; (2) at the anterior border of the temporal fossa; (3) at the anterior border of the postorbital bar; (4) under the orbit.

(H&B*:2.15.1; Ka*: 35;Ki*:C.1; R&H*:25)

47. Anteroventral slope of dentary symphysis: (0) absent; (1) moderate slope; (2) strong slope.

48. Dorsal profile of the lower jaw along the symphysis is: (0) straight; (1) slightly to moderately concave. (Ka*:31)

49. Posterior coronoid bone: (0) absent; (1) present. (FBDR*: 49; S: 75)

50. Splenial posteriorly ends with two spurs: (0) absent; (1) present.

51. Maxillary dentition decreases in size posteriorly with the upper canine barely differentiated: (0) absent- clear separation into incisors, canine, postcanine; (1) present. (H&B*: 2.17.1; S*: 4.83)

52. Incisor morphology: (0) without lingual heels; (1) with weakly developed lingual heel; (2) with well-developed lingual heel. (FBDR:59; H & B: 1.5.3; R&H:1;Ki*: C.1)

53. Canines are: (0) lingually flat; (1) lingually forms small ridge like heel; (2) incisiform. (FBDR: 63; H&B*: 2.18.2; S*:4.86)

54. Size of upper canine with respect to incisors: (0) smaller; (1) as large; (2) larger. (S*:4.80)

55. Canine curvature: (0) moderate; (1) strong; (2) straight or weak curvature. (Ka*:4)

56. Pattern of interlocking extends to canine: (0) absent; (1) present. (H&B*: 2.18.2)

57. Postcanine morphology anteriorly: (0) bulbous; (1) leaf-like; (2) heeled. (H&B*: 2.12.2 and 2.15.3; R&H: 2)

58. Posterior teeth of the lower jaw superimposed, positioned obliquely on the dental tooth margin: (0) absent; (1) present.

59. Anterior end of postcanine tooth row does not extend lingual to the canine: (0) absent; (1) present. (H&B:2.15.4)

60. Pattern of interlocking extends to anterior postcanine: (0) absent; (1) present. (H&B*: 2.18.2; S:4.87).

APPENDIX 5 Character matrix used in the phylogenetic analysis

Taxon	1	111111112	222222223	333333334	444444445	555555556
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Biarmosuchus</i>	100001101-	0-00100000	0000000000	10000100??	?100?00010	0002000000
<i>Archaeosyodon</i>	100001101-	0-00100000	0000000000	10000100??	?100?00010	0102100000
<i>Deuterosaurus</i>	120000011-	0-00101100	0?0??1001?	1??003????	?100?0001?	020?202000
<i>Jonkeria</i>	032111100-	0-01111100	0100010021	200002200?	1210?11110	0202001000
<i>Tapinocaninus</i>	022110102-	0-10112100	1100010031	4110031000	1210022111	1211212?1?
<i>Riebeeckosaurus</i>	??3????2-	0-1???2??0	1100111031	4120101000	1311040000	1?1?21????
<i>Ulemosaurus</i>	022110102-	0-11102100	1000100032	4010102001	1210120011	1211212110
<i>Moschops</i>	023110102-	0-11012100	1000010033	4020101101 2	0311142100	1220212111
<i>Tapinocephalus</i>	0231102031	10110?2000	1011100031	5020101101 2	031014????	?2????????
<i>Criocephalosaurus</i>	??3????02-	0-1???????	?0000?0033	3031??2112	?3???4????	??????????
<i>Moschognathus</i>	022110102-	0-11012100	01???00021	3000101001	0310?31010	122021211?
<i>Agnosaurus</i>	022110101-	0-110?????	0?00100021	30001310??	?2?0?31?0?	1220212??1
<i>Mormosaurus</i>	0331112030	11110?2101	2001100031 1	5020101101 2	031014210?	122?2?2???
<i>Struthiocephalus</i>	0331112020 3	1211002111	2001100031 1 1	5000101111 12	0310142110	1220212??1
<i>Struthionops</i>	033?111230	021100????	??01100121	3000??31??	?3???4????	?2????2???