A new species of pantylid ‘microsaur’ from the Carboniferous of Nova Scotia and implications for its ecology

by

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A thesis submitted to the Faculty of Graduate and Postdoctoral Affairs in partial fulfillment of the requirements for the degree of

Master of Science

in

Earth Sciences

Carleton University
Ottawa, Ontario

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Abstract

‘Microsaurs’ are a group of terrestrial, limbed vertebrates unearthed in North America and Europe, spanning the Late Carboniferous to the Early Permian. Once considered monophyletic, recent studies have revealed their polyphyletic nature, necessitating further investigation into the relationships within this diverse early tetrapod group. A recently discovered, near-complete ‘microsaur’ skull (NSM 017GF020.002) from Sydney Mines Formation of Nova Scotia fuels this inquiry. Utilizing micro-CT scanned data, I present a full description of the anatomy, investigate its phylogenetic relationship with other “microsaurs”, and explore the possible ecological role and diet by comparing its dental morphology with extant reptiles. The morphological disparity of NSM 017GF020.002 with other pantylids, coupled with phylogenetic analysis results, support the recognition of a new genus and species. Its unique palatal dentition not only provide strong evidence rooting the origin of herbivory in Late Carboniferous, but also showcase considerable diversity within the family Pantylidae.
Chapter 1 Introduction

1.1 A synopsis of the ‘microsaurs’ and the well-known *Pantylus*

‘Microsaurs’ are a group of small terrestrial, limbed vertebrates that lived in parts of North America and Europe, from the Late Carboniferous to the Early Permian. United by common features such as small size, holospondylous vertebrae, absence of an otic notch, short and feeble limbs, etc., ‘microsaurs’ exhibit a wide range of morphological diversity indicative of various ecological roles (Carroll and Gaskill 1978). Few decades ago, ‘microsaurs’ were widely considered to be members of a monophyletic group (i.e., a natural group that contains the common ancestor and all descendants), nested within the non-amniote group Lepospondyli (Romer 1950; Carroll and Baird 1968; Carroll and Gaskill 1978). However, this idea has been recently challenged by new phylogenetic studies (Anderson 2001; Pardo et al. 2017), resurrecting a long history of taxonomic debate concerning the group.

The Order Microsauria was first established by William Dawson to contain the non-nectridean, non-aistopod lepospondyls found at the Joggins Fossil Cliffs, Nova Scotia (Carroll and Gaskill 1978). The placement of microsaurian specimens and their relationship to other tetrapods underwent a convoluted history, subjected to many revisions by different scholars, and for a long time, the definition of the group remained ambiguous. It was not until the 1950s that Alfred Romer published a monograph to provide a systematic review of the group and delineate a list of characteristics unique
to ‘microsaurs’ (Romer 1950). Subsequently, Carroll and Gaskill (1978) published a monograph that included detailed descriptions of all 25 microsaur genera known at the time, and classified them into two suborders, Tuditanomorpha and Microbranchomorpha; this division was based on the pattern of skull roof bones in the temporal region.

However, studies in the past few decades have started to question the monophyly of ‘microsaurs’ (Anderson 2001; Ruta et al. 2003; Vallin and Laurin 2004; Anderson 2007). ‘Microsaur’ was first proposed to be paraphyletic by Anderson (2001), and later, the therein-named clade Recumbirostra (a core group within Tuditanomorpha) was hypothesized to be the sister taxon to all other lepospondyls (Anderson 2007). More recently, Pardo et al. (2017) recovered recumbirostran microsaurs as reptilian amniotes, reviving the old hypothesis that at least some ‘microsaurs’ are reptiles (Vaughn 1962). The now polyphyletic status of ‘microsaurs’, wherein some members (recumbirostrans) are considered amniotes and others remain non-amniote lepospondyls, reveals much work is needed on the anatomy and relationships of these animals to understand both amniote and non-amniote evolution.

The clade Pantylidae, one of the best-known groups of recumbirostrans, was first included in the order Microsauria by Romer in his 1950 monograph. Previously, the
clade occupied a position among reptilian cotylosaurs, specifically within the Captorhinidae, due to its relatively large size and superficial similarities (Cope 1892).

Figure 1.1 Historical reconstruction of the skull of Pantylus cordatus. A, dorsal view of the skull roof; B, ventral view with lower jaw removed showing the palate; C, left lateral; D, dorsal view of the left jaw ramus; E, posterior view of the occiput; F, ventral view of the left jaw ramus. Images from Romer (1969).

The type species *Pantylus cordatus* is a large ‘microsaur’, with a broadly triangular skull reaching lengths of up to 90 mm, with orbits located anterior to the mid-length of the skull, and powerful dentition with large spaces for temporal muscles interpreted as indicating a durophagous or herbivorous diet (Romer 1969). Its palate
is equipped with numerous teeth possibly for crushing hard food, and it also has an opposing battery of coronoid teeth on the lower jaw that appears to occlude with the palatal dentition (Romer 1969). The wide rib cage is furthermore suspected to house large digestive tracts that are needed by animals that consume large amounts of plants (Romer 1969: 19; Sues and Reisz 1998). The limb articulations and the ventral armour of *Pantylus* might represent adaptations to a burrowing lifestyle (Carroll and Gaskill 1978). Additionally, the recumbent snout, the namesake feature of Recumbirostra, is seen in other vertebrates that are known to burrow (e.g., caecilians, uropeltid snakes, amphisbaenians) and/or consume vegetation as part of its diet (e.g., captorhinids, caseids, edaphosaurids).

### 1.2 Evolution of herbivory

The origin of herbivory is an important step in vertebrate evolution that allowed tetrapods to tap into the vast resources provided by terrestrial plants (Reisz and Fröbisch 2014), which eventually led to the diversification of terrestrial tetrapods and influenced the evolution of plant communities (Brocklehurst et al. 2020). Herbivory has been independently acquired in several lineages of amniote tetrapods, including caseids, edaphosaurs, diadectids, captorhinids, and possibly bolosaurids (Reisz and Fröbisch 2014). The earliest evidence of high-fibre herbivory originated in the Late Carboniferous, some 30 million years after the terrestrialization of tetrapods (Sues and Reisz 1998; Reisz and Fröbisch 2014; Brocklehurst et al. 2020).
It is difficult, and almost impossible, to know exactly the diet of extinct organisms, but paleontologists make comparisons to extant taxa with known dietary habits to infer functions and behaviours of fossilized animals (Sues and Reisz 1998; Benton 2010). There are certain craniodental and postcranial features unique to herbivorous animals, which reflect the anatomical and physiological adaptations needed for a high-fibre diet. The breakdown of plant cell walls requires mechanical and chemical actions in synergy. The mechanical breakdown of plant matter takes place shortly after the seizing of food and is reflected in the dentition: early herbivores often possess marginal teeth that are shaped for puncturing/shredding (i.e., leaf-shaped, spatulate and forward projecting), or occluding teeth that are intended for crushing/grinding (i.e., expanded crowns, dental batteries) (Sues and Reisz 1998; Reisz and Fröbisch 2014). Modifications to the jaw joints and/or jaw muscles are also present, which increase the mechanical advantage for biting and grinding (Reilly et al. 2001). Postcranially, herbivores tend to have a bulky trunk region to house large digestive tracts where endosymbiotic microbes perform cellulysis to break down otherwise tough to digest plant material (Sues and Reisz 1998). It is the combination of craniodental and postcranial features that allow paleontologists to postulate herbivorous diets in fossil taxa with a certain degree of confidence.

1.3 Inferring diet from quantitative dental complexity

Dentition is an important source of information for making inferences when interpreting possible diets in extinct taxa. Historically most comparisons of dentition
are descriptive and qualitative (as described above). The application of geometric morphometrics has emerged as a quantitative method of measuring and comparing tooth shapes among animals. However, even that approach has its weaknesses when dealing with teeth, including the requirement of homologous landmarks and the lack of sensitivity to nuanced surface shapes (Adams et al. 2004; Melstrom 2017). A homology-free technique, called the Orientation Patch Count Rotated (OPCR), presents an unique opportunity to quantify and compare the surface complexity of 3-dimensional tooth shapes across different taxa, both extinct and extant (Evans et al. 2007).

The OPCR method has been used to investigate the relationship between dental surface complexity and feeding strategies (Evans et al. 2007; Melstrom and Irmis 2019; Shipps et al. 2023). The orientation patch count technique groups pixels in the 3D scan by their individual orientations, where neighbouring pixels with similar orientations are grouped together into a ‘patch’. Higher patch count values indicate higher surface complexity (Evans et al. 2007). Past studies (Figure 1.2) have demonstrated OPCR values (an indicator of surface complexity) are correlated with diet, with distantly related taxa of similar diet yielding similar complexity values, and a trend of increasing complexity and OPCR values from carnivores to herbivores (Evans et al. 2007; Melstrom 2017; Christensen and Melstrom 2021). Thus, by applying the OPCR method to fossil taxa and compare with extant taxa (Melstrom and Irmis 2019), we can gain new insights into the preferred diet in animals that are long extinct.
1.4 Research question(s) and hypotheses

Recently, a near-complete skull of a ‘microsaur’ (NSM 017GF020.002) was discovered in the Carboniferous strata of Nova Scotia. The new specimen was found in a fossilized lycopsid tree stump in the Sydney Mines Formation on Cape Breton Island, Nova Scotia, dated to the Pennsylvanian of Late Carboniferous (Gibling et al. 2004; Allen et al. 2014). It was micro-CT (μCT) scanned and found to possess an
extensive palatal-coronoid dental complex, suggesting the animal may have been an herbivore, similar to the Permian-aged species *Pantylus*, but unexpected in an animal from as early as the middle Pennsylvanian of the Carboniferous. The new specimen is also superficially similar to *Pantylus* in its possession of a triangular-shaped skull and robust cranial construction. Given these similarities, it is suspected this new specimen may have occupied a similar ecological niche as has been proposed for *Pantylus* – i.e., a herbivorous and fossorial animal – grounding the origin of those behaviours within ‘microsaurs’ firmly within the Carboniferous. This new specimen, therefore, has great potential to shed light on ‘microsaur’ evolution from both phylogenetic and ecological perspectives.

The goal of this thesis is to, first, describe in detail the newly discovered specimen NSM 017GF020.002 and obtain its phylogenetic position to see whether it is indeed a pantylid, and to second, investigate the potential diet of NSM 017GF020.002, using quantitative (OPCR). I predict NSM 017GF020.002 would have similar dental surface complexity to taxa with known herbivorous diet. To achieve these goals, this thesis is divided into three chapters. In Chapter 2, I describe the external and internal cranial anatomy of NSM 017GF020.002 via segmentation of high-resolution μCT data and provide a virtual reconstruction of the skull. With the anatomical details in hand, Chapter 3 includes NSM 017GF020.002 in a phylogenetic analysis using maximum parsimony. In Chapter 4, I quantify the surface complexity of the dental features of NSM 017GF020.002’s using the Oriented Patch Count Rotated
method and attempt to compare its values to those from a living reptile dataset in order to infer the diet of the animal.

1.5 References


Chapter 2 Anatomical description of NSM 017GF020.002

2.1 Introduction

The problems concerning the taxonomy of phylogeny of ‘microsaurs’ has become increasingly clear over the past several decades. As such, considerable efforts have been dedicated to revising the description of some older ‘microsaurs’ through re-examination of existing specimens (Mann et al. 2018; Pardo and Mann 2018; Mann et al. 2020) or through detailed investigations of new μCT data (Maddin et al. 2011; Pardo et al. 2015; Szostakiwskyj et al. 2015; Pardo and Anderson 2016; Gee et al. 2021; MacDougall et al. 2021). Additionally, new specimens have been discovered and described (Anderson et al. 2009; Huttenlocker et al. 2013; Glienke 2015; Gee et al. 2019; Mann et al. 2019; Mann and Maddin 2019; Mann et al. 2021). Together, all of these studies share the same overarching aim of collecting new anatomical information that can aid in resolving the confusion surrounding the phylogenetic affinities and intrarelationships of ‘microsasurs’, as well as shed light on their lifestyle and ecological diversity (Gee et al. 2019; Jansen and Marjanović 2022).

In 2007, Anderson proposed the name Recumbirostra, which groups some ‘microsaurs’ that share a common feature: an overturned (or recumbent) snout. He defined Recumbirostra as “the clade descended from the most recent common ancestor of Pantylus, Cardiocephalus stembergi, Rhynchonkos, and Micraroter, but not including Tuditanus of Microbrachis” (Anderson 2007: 206). The recumbirostrans
garnered attention because some taxa revealed adaptations to a fossorial lifestyle with cranial morphology suited for head-first burrowing, suggesting possible diversification and specialization into the fossorial world as early as the Early Permian (Maddin et al. 2011; Szostakiwskyj et al. 2015). More controversially, based on the overall similarity to caecilian morphology, recumbirostran ‘microsaurs’ were proposed to be the sister taxon to caecilians, implying a polyphyletic hypothesis of lissamphibian origins (Anderson 2007; Huttenlocker et al. 2013). However, the similarities between recumbirostrans and caecilians were later deemed to be more likely due to convergences resulting from miniaturization and the evolution of fossoriality than to common ancestry (Maddin et al. 2011; Szostakiwskyj et al. 2015; Pardo et al. 2017).

On the other hand, the relatively large-bodied ‘microsaur’ group Pantylidae had received less heated attention, despite its own suite of interesting morphological features and its similarly labile placement in the phylogeny as that of other ‘microsaurs’. Following the first description by Cope (1881), the holotype species *Pantylus cordatus* has been revisited and redescribed several times, changing in its initial placement from within the batrachians (old term for amphibians) to the cotylosaurians (old name for early amniotes), and finally to the ‘Microsauria’ (Romer 1969). Today, the family Pantylidae constitutes the namesake taxon *Pantylus* from the Lower Permian beds of Texas, along with *Trachystegos* from the Upper Carboniferous of Joggins, Nova Scotia, and *Sparodus* from the Upper Carboniferous of Nýřany, Czech Republic being possible relatives (Carroll and Gaskill 1978).
discovery of *Stegotretus* from the Permo-Pennsylvanian-aged Cutler Formation in New Mexico is the most recent addition to the group (Berman et al. 1988).

Recently, the discovery of NSM 017GF020.002, a virtually complete skull, from a lycopsid tree stump at Point Aconi (Figure 2.1), on Cape Breton Island, Nova Scotia (Maddin et al. 2018), represents the newest potential addition to Pantylidae. If this assignment is indeed correct, NSM 017GF020.002 represents the first record of pantylids from Cape Breton, and adds new potential diversity, both morphological and taxonomic, to the group.

![Figure 2.1](image)

Figure 2.1 Discovery site of the lycopsid tree stump at Point Aconi, Sydney Mines Formation, Cape Breton Island, Nova Scotia, where several specimens representing various taxa were found, including NSM 017GF020.002. Site map in A and B from Lang (2006). Photos in C and D show the cliff, and the in situ location of the fossil-bearing stump.
Here I use μCT data to provide a detailed account of the anatomy of NSM 017GF020.002, which can be used to determine the identity of the specimen (i.e., new taxon or member of a known taxon) as well as score it in a phylogenetic analysis (Chapter 3) to determine its placement among early tetrapods. The features of NSM 017GF020.002 are discussed as they relate to those of other known pantylids.

### 2.2 Material and methods

#### 2.2.1 Specimen

The specimen (NSM 017GF020.002) studied here was discovered by Brian L. Hebert at Point Aconi, on Cape Breton Island, Nova Scotia, Canada (46°20'N, 60°17'W). The fossil forest assemblage, where specimen NSM 017GF020.002 was recovered from a lycopsid tree stump, occurs within the Sydney Mines Formation, a unit of the Sydney Basin of Nova Scotia (Gibling 1995). The strata within which Point Aconi is located is assigned to Sequence 14, dating to the Pennsylvanian of the Late Carboniferous (Gibling et al. 2004). The specimen was located within a lycopsid “tree” stump. It consists of a nearly complete skull, only missing parts of the nasal region, the occipital region, and the posterior right portion of the mandible and skull table (Figure 2.2). Most of the skull roof and jaw elements are in full articulation, with the exception of some braincase and otic-region related elements, which have fallen out of place post-mortem but remain within the matrix of the specimen.
2.2.2 μCT-scanning and analysis

The specimen (NSM 017GF020.002) was μCT scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility, with the following parameters: NSI scanner, Fein Focus Microfocal source, voltage 170 kV, current 0.28 mA, brass filter, Perkin Elmer detector, 0.25 pF gain, 1 fps, 1x1 binning, no flip, source to object 230.0 mm, source to detector 1109.0 mm, continuous CT scan, 2 frames averaged, 0 skip frames, 3000 projections, 6 gain calibrations, 5 mm calibration phantom, data range \([-1.0, 30.0]\) (grayscale adjusted from NSI defaults), beam-hardening correction \(= 0.1\). Post-reconstruction ring correction was applied using the following parameters:
oversample = 2, radial bin width = 17, sectors = 32, minimum arc length = 8, angular bin width = 9, angular screening factor = 4. The final image stack consisting of 1789 slices with a voxel size of 41.2 μm and a slice resolution of 1981 x 966 pixels in 8-bit format.

The μCT scan of the specimen showed mostly good contrast between the matrix and bone. Segmentation of the bones was performed manually in Dragonfly (v2022.2.0.1399) to isolate each individual element. Interpolation between no more than three slices was conducted. Measurements were acquired using the ruler annotation tool in Dragonfly. All segmented materials were then converted to mesh objects (.ply) and imported into Blender (v3.4) for reconstruction. Figures were prepared in Inkscape (v1.3).

2.2.3 Three-dimensional reconstruction

The elements isolated during the segmentation of the μCT data were manipulated and rearranged in Blender to restore the skull as closely as possible to its original condition. The protocol of reconstruction largely followed Porro et al. (2022). First, the parasphenoid, basioccipital and the centrum were aligned along the Z-axis and this axis was treated as the midline, then palatal elements were assembled around the parasphenoid. Next, I aligned the quadrate to the quadrate ramus of the pterygoid, followed by the addition of quadratojugal and jugal to form a closed perimeter of the adductor chamber, this establishes a rough basis for the remaining reconstruction. Skull roofing elements were added to the assemblage, then the lower jaws were
reconstructed so that it fits under the skull, aligning the jaw articulation and the palatal
dentition. Cracked bone fragments were aligned and pieced together by judging the
relative edge shape, length, thickness, and texture between two fragments. This
reconstruction only restored the brittle fractures of the bones, but did not attempt to
deal with any plastic deformation that may have led to distortion of the skull or any
elements (e.g. Demuth et al. 2022). The latter would require manual editing of the
faces and vertices between all fragments, which is more labour intensive than this
project permits given the degree of fragmentation in NSM 017GF020.002.

2.3 Anatomical description

2.3.1 General morphology

The skull roof is overall broadly triangular in shape, approximately equal in maximum
width and length, much like that of Pantylus (Romer 1969). Preservation is good
enough such that sutures of the main skull roof bones are mostly visible to the naked
eye. The skull roof is mostly flat and individual bones are ornamented with pits and
crenulated ridges. The posterior margin of the skull is preserved on the left side, where
the skull roof can be seen to sharply downturn at a nearly right angle. The orientation
of the preserved portion of the posterior margin of the skull roof indicates it would be
nearly straight, rather than concave or convex, again much like that of Pantylus. The
skull roof is slightly compressed dorsoventrally, and most of the skull roof bones are
fractured likely as a result of this, and other, post-mortem disturbances.
The external naris is incompletely preserved. What is present is bordered dorsally by the nasal, ventrally by the maxilla, and posteriorly by the lacrimal. Presumably, the premaxilla formed the anterior margin of the naris, as it does in most if not all tetrapods. From what is preserved, it appears that the external naris faces laterally. The oval shaped orbits are located at about one third the length of the skull and face laterally. The orbit is bounded anterodorsally by the prefrontal, dorsally by the postfrontal, anteroventrally by the lacrimal, posteroventrally by the postorbital and jugal. Around the orbit margin is a raised orbital rim that is especially visible along the anteroventral and posteroventral margins, occurring on the lacrimal, jugal and the postorbital. On the palatal surface, choanal openings are bordered medially by the tooth-bearing vomers, posteriorly by the anterior margin of the palatine, laterally by the maxilla, and probably anteriorly by the missing premaxilla.

The cheek region is broad and overlaps the posterior portion of the lower jaw in lateral view. The temporal region is also broad and robust, forming a large adductor chamber that occupies roughly the posterior one third of the skull laterally. Most of the occipital surface and posterior right lower jaw is missing due to a large obliquely transverse break in the skull. The palate is largely intact, revealing an extensive dental battery. This palatal battery opposes a similarly extensive dental battery on the lower jaw, which is in tight articulation with the skull roof. Internally, much of the braincase has been either lost, broken, or severely displaced. Most of the otic and occipital elements are disarticulated and incomplete.
Just like the skull, the lower jaw has a robust build and is broad and stout. The outer surface of the lower jaw is lightly ornamented, like the skull roof. The symphysis of the lower jaw is superficially similar to that of *Pantylus* in that the fusion is of modest extent for such a stoutly-built jaw. Formed by the dentary and the splenial, the fused part of the symphysis is approximately oval in shape, and the dentary contributes to two-thirds of the symphysis. Each jaw ramus somewhat has the shape of an inverted triangle in cross-section. The lateral surface of the jaw is formed by the dentary, surangular and angular, and the medial surface is formed by, from anterior to posterior, the splenial, postsplenial, and prearticular, with two coronoids (anterior and posterior) wedged between the lateral and medial walls of each jaw ramus, forming a dental plate at approximately the same level as the dentary teeth. At the lateral and medial ends, the coronoids turn vertically to press against the side walls of the lower jaw, forming the roof of the subcircular Meckelian canal that runs from the jaw symphysis to the adductor fossa.

There is a sizable adductor fossa on the medial surface of the lower jaw. It is an oval opening bounded anteriorly by the posterior coronoid, medially by the prearticular, laterally by the dentary and surangular, and posteriorly by the articular. The length of the adductor fossa is about one half the total length of the jaw, which would have housed the insertion of adductor musculature (Romer 1976). The jaw articulation is located in the posteriormost portion of the dorsal jaw margin, the level of articulation is slightly lower than the level of the dentary tooth row and coronoid tooth plate. Here it receives the articulation of the upper jaw formed by the quadrate and quadratojugal.
Its surface is a concave trough oriented mediolaterally, formed by the surangular and articular, similar to that of *Pantylus*. The articulating surfaces of the upper and lower jaws seem to fit snugly, and the jaw joint likely acts as a simple hinge. It is unclear whether or not there is a retroarticular process on the lower jaw due to the preserved state of the articular in this region.

### 2.3.2 Skull roof

*Premaxilla*. Although the premaxilla is mostly missing, an impression of the premaxilla is somewhat visible on the anterior end of the specimen. A portion of the premaxilla and several incomplete premaxillary teeth were able to be segmented from the CT data. Four equal-sized teeth are on the left premaxilla, the impressions of which are visible on the specimen; the same is expected for the right. The actual shape of the snout is unknown due to the incomplete nature of the premaxilla, loss of the left nasal, and part of the maxilla. However, judging from the presence of premaxillary tooth crowns, a premaxilla that extended beyond the preserved portion suggests a recumbent or overhanging snout was present in life. The preserved length of the snout (i.e., distance from the end of the snout to the anterior-most point of the orbit) is rather short, between one quarter and one third the length of the entire skull.
Figure 2.3 Surface models of NSM 017GF020.002 showing elements isolated from the matrix material (left), side by side with the 3D-reconstructed model in matching views (right). Individual bones are shown in different colours and labelled. A, dorsal; B, left lateral; C, posterior. Anatomical abbreviations: a - angular; aa.c - atlas centrum; art - articular; d - dentary; e - epipterygoid; f - frontal; j - jugal; l - lacrimal; m - maxilla; n - nasal; p - parietal; paf - parietal/pineal foramen; part - prearticular; pf - postfrontal; pm - premaxilla; po - postorbital; prf - prefrontal; pt - pterygoid; q - quadratojugal; qj - quadratojugal; sa - surangular; so - supraoccipital; sp - splenial; t - tabular. Scale bar equals 1 cm.
Figure 2.4 Surface models of NSM 017GF020.002 showing elements from the lower jaw isolated from the matrix material (left), side by side with the 3D-reconstructed model in matching views (right). Individual bones are shown in different colours and labelled. A, lower jaw in dorsal view; B, lower jaw in ventral view; C, left jaw ramus in medial view; D, left ramus in lateral view. Anatomical abbreviations: a - angular; art - articular; co.a - anterior coronoid; co. p - posterior coronoid; d - dentary; part - prearticular; sa - surangular; sp - splenial; spp - postsplenial. Scale bar equals 1 cm.
Nasal. Only the right nasal is preserved in the specimen. It has an overall rectangular shape, with a thickened, concave anterior margin, which appears to be the posterior margin of the external naris. The nasal is bounded medially by the frontal, laterally by the lacrimal and posteriorly by the prefrontal.

Maxilla. The maxilla is nearly completely preserved on both sides of the skull. It has a roughly arc shape, being slightly concave in the ventral direction. The resulting downturned shape of the maxilla contributes to the appearance of a recumbent snout. In extent, the maxilla spans the distance from the external naris to just posterior to the orbit. The maxilla is bounded dorsally by the lacrimal in its anterior half and by the jugal in its posterior half, precluding its contribution to the orbital margin. Unlike Pantylus, there is no dorsal expansion overlapping the lacrimal, meaning that the dorsal margin of the maxilla is relatively smooth. The anterior portion of the maxilla expands both dorsoventrally and mediolaterally to house a set of enlarged, possibly caniniform teeth (bases can be seen in the CT data). Only five of the posterior-most teeth, conical in shape and slightly compressed labiolingually, were preserved on the right maxilla; however, judging by the dental alveoli from the scan data, there may be 11–12 maxillary tooth positions present.

Septomaxilla. The septomaxilla, which is expected to reside within the narial opening, seems not to have been preserved or may not have been ossified.

Frontal. Both the left and right frontals are preserved, albeit broken. Each frontal is narrow and long, and roughly the same length to slightly longer than the exposed
portion of the parietal (the frontal overplates the anteriormost portion of the parietal). The frontal narrows anteriorly to insert in a space between the paired nasals. The posterior end of the frontal is somewhat concave in outline, overlying the parietal. The frontal is bordered laterally by, from anterior to posterior, the nasal, prefrontal, and postfrontal. Each of these bones is in contact with the frontal for approximately one third of its length. The frontal is excluded from the orbital margin by the prefrontal and postfrontal. The contacts between the frontal and nasal, prefrontal, and postfrontal seem to be mostly simple butt-type joints, except for the prefrontal, where there seems to be a segment of an internally interdigitated joint (Figure 2.6C). The thickness of the frontal varies greatly. It decreases in thickness from anterior to posterior, and varies also in the lateromedial direction. The suture between the two frontals seems to have a somewhat tongue-and-groove type morphology (Figure 2.6D). Ventrally, at about two thirds of its length, the frontal bears a small, obliquely oriented wedge/flange (Figure 2.5B) that likely articulates with the sphenethmoid.

Parietal. Both parietals are preserved but are broken into several pieces. The parietal is a large element that is longer and slightly wider than the frontal, and overall has a trapezoidal shape. It is bordered laterally by the postfrontal and tabular. The parietal contacts the postfrontal at a step-shape suture and the tabular at a butt-type joint changing to stepped posteriorly. The tabular and parietal suture is fairly straight and terminates near the posterior margin of the skull roof. Heavy fragmentation presents near the midpoint between the two parietals, which was initially thought to be an artefact of post-mortem damage, however, upon reconstructing the parietal bone,
there seems to be a pineal foramen slightly anterior to the midpoint of the shared parietal suture. Slight thickening of bones around the apparent “hole”, when viewed ventrally, increases the credibility of identifying this feature as a pineal foramen (Figure 2.5B).

Figure 2.5 Selected cross sections of NSM 017GF020.002 from the 3D-reconstructed model. Individual bones are shown in different colours and labelled. A. sagittal section through midline, looking to the left (sphenethmoid hidden for clarity); B, transverse section showing ventral view of the dermal skull roof; C, same cutting plane as B, but showing the dorsal surface of the palatal complex; D. transverse section showing ventral view of the palate. Anatomical abbreviations: a - angular; aa.c - atlas centrum; art - articular; e - epipterygoid; eo - exoccipital; f - frontal; j - jugal; l - lacrimal; m - maxilla; n - nasal; p - parietal; pal - palatine; part - prearticular; pbs - parabasisphenoid; pf - postfrontal; pm - premaxilla; po - postorbital; prf - prefrontal; pt - pterygoid; q - quadratojugal; qj - quadratojugal; sa - surangular; so - supraoccipital; sp - splenial; st - stapes; t - tabular. Scale bar equals 1 cm.
Postparietal. The postparietal does not appear to have been preserved; however, the posterior margin of the parietal has a small triangular-shaped incision at the midline where the postparietal likely resided. Underneath, the now exposed supraoccipital would have been covered by the postparietal.

Lacrimal. Left and right lacrimals are preserved, with the right appearing slightly more complete than the left. The lacrimal is long, spanning the distance between the orbit and external naris. Its anteriormost extent contributes to the posterior margin of the naris and then it increases in height posteriorly. Dorsally, the lacrimal is contacted by the nasal and prefrontal. Its posterior margin forms the anteroventral margin of the orbit. The lacrimal is overplated by the maxilla along most of its ventral margin. The lacrimal contacts the jugal posteriorly, excluding the maxilla from the orbital margin. Two small foramina are clearly visible on the lacrimal along the thickened anterior orbital wall (Figure 2.3B). They are positioned near the exterior edge of the rim, at approximately one third the height of the orbit, and likely represent the posterior openings of the lacrimal duct (Carroll and Gaskill 1978; Anderson et al. 2009). There might be a third foramen that occurs more medioventrally, and probably served as the opening for the palatal branch of the facial nerve (Anderson et al. 2009), but the fragmentation of the lacrimal in this area makes this interpretation less certain. Medially, the lacrimal bears a flange that contacts the lateralmost anterior process of the palatine.
Prefrontal. Both prefrontals are preserved and the left seems somewhat more complete. The prefrontal is well developed and bears a thickening along its posterolateral margin that contributes to the anterodorsal margin of the orbit. The prefrontal likely extends anteriorly between the frontal and lacrimal to contact the nasal. Posteriorly the prefrontal contacts the postfrontal at roughly the midpoint of the orbit. Together, the pre- and postfrontal exclude the frontal from the orbital margin. Anterior to the orbital rim, the prefrontal sends a long, narrow process ventrally into the choanal opening, which seems like a broken and dislodged anterior portion of the prefrontal.

Postfrontal. Left and right postfrontals are preserved in nearly equal completeness. The postfrontal is roughly rectangular in dorsal view, and similar to slightly greater in length than the prefrontal. The postfrontal contributes to roughly the posterior half of the dorsal orbital rim, and its contact with the prefrontal anteriorly excludes the frontal from the orbital margin. The postfrontal contacts the frontal and parietal medially, and the postorbital ventrally. It terminates at a contact with the tabular.

Postorbital. Both postorbitals are also nearly equal in their degree of completeness. Lateral to the postfrontal, the postorbital is extensive and somewhat square to rectangular in shape. Anteriorly, it bears a curved flange that overlaps the jugal along the posterior orbital margin. This flange is very close to meeting the opposing flange of the lacrimal. Similar to the postfrontal, the postorbital is thickened along the orbital
margin, then decreases in thickness further away from the orbit. It is bounded by the jugal along its ventral margin and contacts the tabular posteriorly.

**Jugal.** Ventral to the postorbital is a large jugal. It contributes to a portion of the ventral orbital margin and also forms most of the cheek region. Anteriorly, the jugal sends an extension that is wedged between the lacrimal and the maxilla. Posterior to the orbit, the jugal expands rapidly to form a broad triangular plate covering the cheek portion. Along its ventral margin, the jugal overlaps the maxilla slightly, and posteriorly, it overlaps the squamosal and quadratojugal to a slight extent. The expansion of the ventral margin of the jugal creates a chipmunk-like appearance of the cheeks, seen also in *Pantylus* (Romer 1969).

**Palpebral.** Within the right orbit, an element representing a possible palpebral ossification is present. Unfortunately, the poor contrast of this feature in the CT-scan hindered confident segmentation.

**Tabular.** The homology of the temporal bone in ‘microsaurs’ has been quite debatable, for all described ‘microsaurs’ only have one temporal bone with no intermediate forms. Romer (1950) proposed the single temporal bone be called the supratemporal, deduced from a similar temporal bone reduction pattern in labyrinthodons. Carroll and Gaskill (1978) suggested otherwise: the element is more appropriately identified as a tabular given its marginal position at the skull roof and support of the braincase at the otic region, a condition seen in labyrinthodonts and primitive reptiles. However, as Szostakiwskyj et al. (2015) pointed out, supratemporal may also have occipital
exposure (i.e., sending a dermal roof flange to sheath the occipital surface) when tabular is fully lost or partially reduced, which is seen in some reptiles and temnospondyls. A third possibility remains that the relatively large element is a fusion of both supratemporal and tabular. In absence of a precise solution, we follow the interpretation of Carroll and Gaskill (1978) to minimize confusion, since many of the recent ‘microsaur’ descriptions followed this terminology (e.g. Gee et al. 2019). Nonetheless, the homology of this temporal bone calls for a thorough investigation as it evidently affects the coding of character states that are used in phylogenetic analyses, which in turn, may result in different tree topology and thus, our understanding of the evolution ‘microsaurs’ and early tetrapods (Szostakiewskyj et al. 2015).

The left tabular is more complete than the right, though it is likely missing a portion of its medial occipital exposure due to the transverse fracture in the skull. The tabular is of considerable size. It contacts the parietal medially with a fairly straight edge. It is overlapped anteriorly by the postfrontal and postorbital, and underlapped laterally by the squamosal. The tabular thickens considerably at the posterior skull roof margin. The articulation of the tabular with the otic region remains uncertain due to the absence and disarticulation of bones associated with this area.

Squamosal. The left squamosal is preserved. There it can be seen to be a large element, occupying the posterior portion of the cheek region. It is contacted anteriorly by the jugal and possibly by the postorbital, dorsally by the tabular, and ventrally by
the quadratojugal, the latter two of which it slightly overlaps. Its overall curved shape cups the quadratojugal and quadrate posteriorly.

**Quadratojugal.** The quadratojugal is preserved on the left side only. The exposed portion of the quadratojugal is roughly rectangular in shape. Its anteriormost margin is overlapped by the jugal, and the squamosal overlaps most of its dorsal margin. The ventral margin of the quadratojugal forms the ventral margin of the skull roof. Posteriorly, it bears a downward projecting knob that may have contributed to the lower jaw joint, as described for *Pantylus* (Romer 1969).

**Quadrate.** The quadrate, only preserved on the left side, is fragmented and mostly disarticulated except for the portion forming the jaw joint. The quadrate likely extended as a thin flange from the quadrate ramus of the pterygoid and continued posteroventrally, where it can be seen to thicken ventrally to sit on the medial half of the lower jaw articular surface (Figure 2.5A, C; Figure 2.6F).

**2.3.3 Palate**

**Vomer.** Both vomers are preserved in the anteriormost region of the palate. Paired at the midline, the vomers form the medial margin of the internal nares (or choanal) openings. The right vomer is better preserved and less fragmented than the left. There it can be seen that the vomer is a long, narrow, trough-like element, with its length approximately four times the average width. The width of the vomer remains fairly consistent throughout its length, tapering to a somewhat pointy anterior end. The two vomers seem to come into contact anteriorly, while being separated by the anterior
extent of the pterygoid posteriorly (Figure 2.5C,D). The nature of a contact with the premaxilla is unclear, as the premaxilla is largely missing. The ventral surface of the vomer bears denticles along a pair of ridges. The denticles are small and similar in size to those on the anterior pterygoid process, but there are slightly larger ones at the anterior end of the vomerine fields.

**Palatine.** The palatine is preserved on both sides, where it can be seen to be a large, elongate, robust bone on the palatal surface. The anterior margin of the palatine contributes to the posterior margin of the choanal opening. The palatine is overlapped posterodorsally by the main portions of the anterior processes of the pterygoid (Figure 2.5A,C); however, the medialmost portion of the palatine is underlapped by a thin, sliver-like extension of the medial anterior process of the pterygoid. In medial view of the midsection of the palate, the nature of the palatine-pterygoid integration can be well visualized (Figure 2.5A). Lateral to the choana, the palatine bears an anterolaterally-directed process that makes contact with the lacrimal at an interdigitated suture (Figure 2.6A,B). Midway down the length of the palatine another, more pointed, laterally oriented process extends to meet the jugal just posterior to the orbit. On the medial margin of the palatine, also approximately midway down the length of the bone, there is a possible foramen, but contrast is weak in this region. If indeed real, as suspected due to its symmetry on both palatines, this foramen possibly served as a point of passage for the palatal branch of the internal carotid artery (Figure 2.5A). The ventral surface of the palatine is almost entirely covered by a dental field. The teeth are bulbous to somewhat pointed in shape, mostly around 1-2 mm wide at
the base, and tightly packed. The larger teeth are concentrated around the lateral periphery of the field, their widths ranging from 1.8–2.6 mm, with the largest one reaching 3.6 mm and located near the posterolateral end of the palatal dental field. Beyond this point, the widths of the teeth diminish to less than 1 mm in width (Figure 2.5D). Smaller teeth are present outside of the main dental field as well, for example on the dorsomedially extending flange that meets the pterygoid. These are much smaller denticles (e.g. 0.4–0.7 mm) than those of the main dental field.

**Ectopterygoid.** Similar to *Pantylus*, there is no evidence of an ectopterygoid. It is unclear if it was not preserved or never formed.

**Pterygoid.** Left and right pterygoids are preserved, though the posterior portion of the right one is missing due to the large, posterior break. The pterygoid is a large and well-developed bone forming a substantial portion of the palate. In dorsal view, the pterygoid can be seen to be composed of three prominent processes. A medial, anteriorly directed process extends ventral to the palatines to meet the vomer along its midline. More posteriorly, this process overplates the medial portion of the palatine (Figure 2.5C). A lateral anteriorly directed process extends along the palatine to reach, but not articulate with, the jugal. Posteriorly, a well-developed quadrate process extends posterolaterally and twists vertically to form a curved plate, which, at its end, likely presses against the dorsomedial surface of the quadrate. The interpretation of this contact is based on conjecture due to the disruption between quadrate and pterygoid, but would be consistent with the condition seen in *Pantylus*. The
interpterygoid vacuity, the medial opening between the pterygoids, is narrow in size and short anteroposteriorly, occupying only the space from the posteriormedially projecting basal articulations to slightly more anterior than the half point of the palatine (Figure 2.5C,D). On the ventral surface of the pterygoid, anterior to the basal articulations, there are many small, peg-like denticles along a medial ridge that continues to the anteriormost extent of the pterygoid. (Figure 2.5D). Towards the end of the dental field, the medial ridge rises to form a paired mediodorsally projecting process with a flat articulating surface. This process, in turn, receives the equally flat articulating surface of the basal articulation on the parabasisphenoid. The construction here is entirely different from that of Pantylus, which had a round-headed basal articulation that fits into a socket formed by the pterygoid and epipterygoid (Romer 1969).

**Epipterygoid.** The epipterygoid, partially preserved on the left but not much on the right, is an elongate, narrow, plate-like element. It appears to have fallen out of place on the right, but may be close to its original articulation on the left. There, its base is closely applied to the pterygoid, from the basal articulation onward, extending along almost the entire length of the quadrate process. From there, the epipterygoid is oriented with its long axis pointed dorsally towards the skull roof.
Figure 2.6 Sliced views from the original CT data: A, transverse slice showing interdigitated suture between the lacrimal and the anterolateral process of the right palatine; B, transverse slice showing the same feature on the left; C, coronal slice showing interdigitated joint between frontal and prefrontal; D, coronal slice showing tongue and groove joint between frontals; E, sagittal slice showing the jaw articulation between quadratojugal and surangular; F, sagittal slice showing the jaw articulation between quadrate and articular. Bones of interest are coloured and labelled. Anatomical abbreviations: art - articular; l - lacrimal; f - frontal; pal - palatine; prf - prefrontal; pt - pterygoid; qj - quadratojugal; sa - surangular. All scale bars equal to 1cm.
2.3.4 Braincase

*Sphenethmoid.* The sphenethmoid is a large, trough-like, V-shape bone that partly sits on top of the cultriform process of the parasphenoid portion of the parabasisphenoid (Figure 2.7A-C). It extends from the anterior end of the palate to, approximately, the middle of the interpterygoid vacuity. The sphenethmoidal cavity (brain cavity) likely opened widely both anteriorly and posteriorly. The dorsal portion of the sphenethmoid is very thin and plate-like. As a result, it is very fragmented due to deformation under dorsal compression. Even though reconstruction was attempted, identifying the location of foramina within the sphenethmoid was not possible to do confidently. The sphenethmoid is presumed to have extended, in parallel, from the anterior end of the orbit to the midpoint of the interpterygoid vacuity.

*Parabasisphenoid.* The parasphenoid and portions of the basisphenoid appear to be indistinguishably fused. Thus, the structure representing both ossifications is referred to as the parabasisphenoid, as it is in other taxa with the same condition. The parabasisphenoid is disarticulated and rotated 180 degrees to face posteriorly. The cultriform process of the parasphenoid portion of the structure (or parasphenoidal rostrum) extends anteriorly from the base of the basal articulation, and bears a dorsal groove to receive the ventral keel of the sphenethmoid. The well-developed basal articulations can be clearly seen to be rather robust, extending anterolaterally. Posteriorly to the basal articulations, the parasphenoid portion expands into a broadly triangular basal plate. The posterior margin of the basal plate is deeply incised at the
midline, which appears to be its natural shape. This incision, seems to match the pointy anterior extension of the basioccipital, suggesting a possible suture between the two. On top of the parasphenoid portion of the structure is the endochondral ossification representing the basisphenoid; however, probably due to poor contrast and the spongy nature of endochondral bones, the basisphenoid is not clearly discernible and/or incomplete. The extensive wings of the basisphenoid that are present in *Pantylus* (Romer 1969) are not found in this specimen. However, a tiny wing seems to be rising upwards on both sides starting past the end of the sella turcica/pituitary fossa (a pit at the end of the cultriform process, lodging the pituitary body on the dorsal surface), but do not extend very far in dorsally. Medially, these wings are joined by a transverse bone shelf, the dorsum sellae, that forms the posterior wall for the sella turcica. Unfortunately, the lack of otic elements in articulation makes it impossible to evaluate the nature of the contact between the parabasisphenoid and otic capsules.

*Prootic.* A prootic could not be confidently identified in the specimen. It's unclear if it was poorly ossified or damaged in preservation rendering it difficult to locate.

*Opisthotic.* An opisthotic could similarly not be identified in the specimen. As with the prootic, it’s unclear if this element was unossified or distorted beyond recognition.
Figure 2.7 Isolated braincase and occiput elements of NSM 017GF020.002 from the 3D-reconstructed model. Individual bones are shown in different colours and labelled. A, ventral view; B, left lateral view; C, dorsal view; D, posterior view; E, dorsal view of the occiput elements in articulation with the atlas centrum; F, same configuration as E but in right lateral view. Anatomical abbreviations: aa.c - atlas centrum; bart - basal articulation; bo - basioccipital; ds - dorsom sellae; eo - exoccipital; pbs - parabasisphenoid; se - sphenethmoid; set - sella turcica; so - supraoccipital; st - stapes. Scale bar equals 1cm; the smaller scale bar applies to panels A-D, the larger scale bar applies to panels E and F.

**Supraoccipital.** The preserved portion of the supraoccipital reveals it to be a paired bone at the posterior midline of the skull, with a tapering anterior process projecting deep under the skull roofing bones (e.g. parietal and postparietal, if the latter were preserved). There is a slight depression on the ventral side of the parietal that roughly outlines the shape of the paired supraoccipital, this outline gets more pronounced around the anterior projecting process of the supraoccipital. The lateral extension of
the supraoccipital travels past the edge of the parietal and continues underneath into the tabular. Each preserved half is roughly crescent shaped in dorsal view, giving an overall roughly triangular shape to the entire supraoccipital (Figure 2.7C). The supraoccipital turns ventrally to form a thickened wall. Beyond this point, missing pieces hinder the full interpretation of this element.

**Basioccipital.** A basioccipital was found near the rear end of the 180-degree-rotated parabasisphenoid, suggesting the posterior region of the braincase likely experienced violent displacement during preservation, hence heavy disarticulation of the elements. The basioccipital has a broadly teardrop shape in dorsal view (Figure 2.7E), and is thickened significantly anteroposteriorly (Figure 2.7B,F). Its dorsal surface is deeply concave representing the floor of the brain cavity. The posterior end of the element bears a shallow pit that served as the central region of the occipital articulation. This surface would receive the protruding cotyle of the first cervical vertebra, the atlas, as in *Pantylus*. The paired troughs on the dorsolateral sides of the articular surface probably hosted the paired exoccipitals to complete the occipital articulation surface.

**Exoccipital.** A possible exoccipital was located in the CT dataset, severely disarticulated. Its potential location is illustrated in the 3D reconstructed model (Figure 2.5A, Figure 2.7E,F); the right side seems to be rather complete whereas only half of the anterior portion is found for the left exoccipital. In typical 'microsaurs', the posterior end of the exoccipital forms the strap-shaped articulation surface together with the basioccipital, where the odontoid (the knob-like anterior process) of the first cervical
vertebrate (atlas) sits (Carroll and Gaskill 1978); the condition in NSM 017GF020.002 seems to match this description. The structure of the exoccipital itself is quite complicated (Figure 2.7E,F), it is a rod-like structure with a dual-head configuration at both the anterior and posterior ends, these heads all point to different directions, one of which broadens to form the occipital articulation with the basioccipital.

2.3.5 Lower jaw

*Dentary.* The dentary is the largest element of the lower jaw that forms most of the lateral surface of the ramus. Viewed laterally, it has a roughly long, triangular shape, which tapers towards the anterior end. The walls reach their maximum thickness at the anterior end, forming the jaw symphyssis with the splenial. The medial face of the dentary wall applies right against the two coronoids. Significant contribution of the dentary forming more than half of the medial surface of the jaw ramus, where it contacts with, from anterior to posterior: the splenial, postsplenial, and angular. There are 17 tooth positions on the dentary, which bear 16 marginal teeth on the left and 17 on the right. The dentary teeth are attached in a pleurodont style, meaning the attachment occurs largely on the medial surface of the dentary, instead of apically (acrodont) or in a socket (thecodont). The alignment of the teeth in the vertical axis is tilted slightly outward (from an angle of 35° to 25°, decreasing anteroposteriorly), the anteriormost teeth also tilt forward at about 35°, the tilting roughly follows the slope of the dentary exterior. The second and third dentary teeth are considerably enlarged, reaching almost twice the size of the largest remaining marginal teeth (Figure 2.4).
After the third tooth, the marginal teeth are much reduced in height. From the fourth tooth onwards, they tend to increase in size posteriorly, up to tooth position 14, then, after a short diastema (a gap in the tooth row), decrease again in size.

**Angular.** The angular is a thick and long, triangular shaped element that covers most of the ventrolateral surface of the posterior part of the jaw. On both sides, the angular is fragmented. The left side exhibits nearly complete preservation of the pieces, while the right side is only partially preserved, with approximately half of the posterior portion missing. On the anterolateral end, it makes contact with and is overlapped slightly by the dentary. On the medial side, it touches the postsplenial in the anterior half, and meets with the prearticular in the posterior half. Posterolaterally, it contacts the surangular in an overlapping connection.

**Surangular.** The surangular, although quite fragmented, is well developed and forms about one third of the posterolateral wall of the jaw. It contacts anteriorly the dentary, but due to heavy fragmentation in this area, the exact construction of this joint is unknown. The ventral margin of the surangular is covered slightly by the angular. Towards the posterior end, it forms the posterior margin of the lower jaw, however, it might not be fully preserved or the bone is simply too porous. The posterior end of the surangular turns medially to form an articular condyle that contributes to the jaw articulation, much like the arrangement observed in *Pantylus* (Romer 1969).

**Articular.** The articular is incomplete likely due to poor preservation or high porosity in the bone itself making it difficult to distinguish in the CT data. The dorsal portion
associated with the articular condyle is somewhat detectable, whereas the ventral portion that forms the retroarticular process is lost. From what was possible to isolate from the matrix, the articular can be seen residing between the surangular and the prearticular. The dorsal portion of the articular is saddle shaped, which contributes to the medial half of the jaw articulation.

Coronoids. On the dorsal surface of the jaw ramus, two coronoids bound the medial margin of the dentary. The coronoids bear a dorsoventrally oriented surface that extends medially to support a robust dental battery. This dental battery occludes closely with the palatal dental battery. The coronoid teeth are generally bulbous, tightly packed, and varying in size (1.4–2.2 mm at the base). Similar to the palatal dental field, the larger teeth are typically found near the lateral periphery. An enlarged conical tooth (about 4 mm at the base) is present on the posterior end of the posterior coronoid, just anterior to the adductor fossa (Fig 2.4A, 2.5A). The extent of the main coronoid dental battery ends approximately parallel to the last dentary marginal tooth. Along the medial exposure of both coronoids, there is a secondary dental field with smaller denticles (0.6–0.9 mm at the base), that is more densely packed on the anterior coronoid than the posterior. There could be a coronoid process at the end of the tooth plate, but the details of this feature remain uncertain due to bone fragmentation in the area (Figure 2.4D).

Splenial. The anterior part of the splenial forms the posterior one-third of the symphysial region. The splenial forms the medial wall of the jaw ramus, covering most
of the coronoid and meets the dentary at the ventral midline, the cross section of the splenial in the anterior end is rather thick and C-shaped.

*Postsplenial.* Preserved on both sides but largely fragmented, the thin postsplenial overlaps with the splenial anteriorly, contacts ventrally with, first the dentary, then the angular. Medially, it seems to be bordered by the surface formed by the prearticular and coronoid along its entire length. The postsplenial has a medial flange but is not very well preserved.

*Prearticular.* The prearticular starts as a thin plate at the posterior end of the splenial, overlapping tightly to the medial surface of the coronoid, and thickens posteriorly to form the medial wall of the adductor fossa. The prearticular rises to form a medial dorsal process (or adductor crest), with the highest point located approximately halfway along the length of the adductor fossa, where the prearticular swells dorsally to create a small, elongated platform at the top (Figure 2.4C), a configuration differing from that of *Pantylus.* Beyond this point, the prearticular is bounded posteriorly by the curved articular that completes the posterior boundary of the adductor fossa. Ventral to the medial dorsal process, the prearticular features a notch that forms the dorsal margin of a subrounded Meckelian foramen. This foramen opens into the adductor fossa and is bordered ventrally by the angular (Figure 2.4C). The Meckelian canal presumably runs from the jaw symphyseal region to the adductor fossa.
2.3.6 Other elements

Stapes. A stapes is preserved on the right posterior end of the skull that is not in articulation. The element bears features that resemble a footplate and columella that are mostly intact. A stapedial foramen is absent or unclear in the scan. Presumably the stapes’ footplate fits in the cup-like depression on the basioccipital (Figure 2.7F), and the columella of the stapes points posterolaterally. The preserved stapes in NSM 017GF020.002 looks fairly different from that of Pantylus (if the identification is correct), but quite similar to the one in Captorhinus laticeps (Heaton 1979:fig. 29).

Figure 2.8 The right stapes in A, dorsal and B, posterior views. Anatomical abbreviations: fp - footplate of the stapes; clm - columella of the stapes. Scale bar equals to 5mm.

Atlas. The first cervical vertebrae, the atlas, was disarticulated and found near the parabasisphenoid. Only the centrum portion is preserved (Figure 2.9). If the condition is similar to Pantylus, there should be a neural arch that attaches and fuses tightly to the dorsal side of the centrum (Carroll 1968). The depressions on either side of the centrum’s dorsolateral surface could potentially support a neural arch, while the deep medial trough on the dorsal surface likely forms the ventral part of the vertebral foramen. The articular surface (or odontoid) on the anterior face of the centrum is
knob-like and fits within the concave occipital articulation formed by the basioccipital and, presumably, paired exoccipital. Laterally, there is a downward projection on each side that may articulate with the capitulum of the rib, as in *Pantylus* (Carroll 1968). In dorsal or ventral views, the centrum maintains a relatively consistent width, suggesting that the second vertebra did not undergo a substantial reduction in size. The posterior end of the centrum has a deep, hemispheric concavity for articulating with the second cervical vertebrae (the axis).

Figure 2.9 Views of the centrum of the first cervical vertebrae, atlas. A, anterior; B, posterior; C. dorsal; D. ventral. Scale bar equals to 5mm.

**Ossicles/scales.** Similar to *Pantylus*, NSM 017GF020.002 possesses numerous subrounded pieces measuring 0.5–0.75mm in diameter, on the ventral side between the jaw rami (Figure 2.10C), a condition also found in *Tuditanus* and *Crinodon* (Romer 1969). These structures, termed scales or ossicles, are likely embedded within the ventral skin of the head in a single layer, since no overlapping of ossicles was
observed. Slightly bigger, more tightly packed ossicles (about 1 mm in diameter) are found at the end of the left jaw ramus covering the surangular in ventral view and inside the jaw ramus. The latter likely got dislodged from somewhere else (Figure 2.10A). This type of ossicle is similar in size, shape, and density, to the polygonal plates/ventral armour found in *Pantylus* in the shoulder girdle area (Carroll and Gaskill 1978). At the posterior end of the skull, a third type of scale (Figure 2.10B) has larger units and an irregular pebble shape, their analogue in *Pantylus* or other ‘microsaurs’ seems unclear.

![Figure 2.10 Ventral view of the lower jaw with various types of scales at: A, ventral surface between the jaw rami, small polygonal ossicles; B, the end of the left jaw ramus covering the surangular, slightly larger polygonal ossicles; C, the posterior end of the skull, irregular pebble shaped scales. Scale bar equals to 1cm in the overall view, and 5mm in the enlarged views.](image-url)
Unidentifiable elements. In addition, there are several elements that could not be identified due to disarticulation and/or incomplete preservation. These are included in Appendix A with figures and their postulated identification.

2.4 Discussion

2.4.1 Anatomical comparisons with members of Pantylidae, and other ‘microsaurs’

Figure 2.11 Phylogenetic relationships of recumbirostran ‘microsaurs’ according to the latest phylogenetic analysis from Mann et al. 2023, relationship within Pantylidae as per Anderson 2007. (Modified from Mann et al. 2023)
Sufficient descriptive information (Carroll 1968; Romer 1969; Berman et al. 1988; Carroll 1988) is available for the species of ‘microsaur’ confidently placed within Pantylidae (Pantylus, Stegotretus, and maybe, Trachystegos, Sparodus) such that a list of shared, derived characters could be generated (Berman et al. 1988). The anatomical data from the newly discovered specimen, NSM 017GF020.002, revealed it shares these features with other pantylid species, bearing a particular stark resemblance to Pantylus, and, to a lesser degree, Stegotretus. This suggests, NSM 017GF020.002 could indeed be the newest member of Pantylidae.

The following is the list of derived characters shared among members of Pantylidae, with new insights and clarifications provided by the anatomy preserved in NSM 017GF020.002.

(1) Overlapping lacrimal-jugal contact at the ventral margin of the orbit: in Stegotretus, Pantylus, and NSM 017GF020.002, there is a considerable overlap formed by a narrow lacrimal process lying on top of the anterior extension from the jugal, with the posterior tip of the lacrimal ending just about at the middle of the orbit. Most non-pantylid ‘microsaurs’ seem to display a simple butt-type joint at the contact between the lacrimal and jugal, with the exception of ‘tuditanids’ (e.g., Asaphestera, Crinodon; Carroll and Gaskill 1978), putative gymnarthrid Pariotichus, and some members of Ostodolepidae (e.g., Pelodosotis, Nannaroter Anderson et al. 2009). In ‘tuditanids’, the posterior tip of the lacrimal ends near the anterior end of the orbit, whereas in the aforementioned Ostodolepidae, the location of the lacrimal-jugal contact is similar to
that of *Pantylus*. Interestingly, the other ostodolepid *Micraroter*, as well as gymnarthrid *Cardiocephalis*, display a different condition where the lacrimal and jugal are separated by a gap. Both conditions (i.e., overlapping and gapped lacrimal-jugal contact) could represent derived states, as Berman et al. (1988) suggested; however, the occurrence of similar overlapping lacrimal-jugal contacts in Ostodolepidae precludes it from being a unique apomorphic state to Pantylidae.

(2) Ventral expansion of the postorbital cheek region by the jugal bone: in *Stegotretus*, *Pantylus*, and NSM 017GF020.002, there is a pronounced ventral expansion of the jugal, so far down that it conceals the maxillary posterior teeth, making a chipmunk-like appearance of the cheek. This seems to be a condition unique among the affirmative pantylids and not seen in other ‘microsaurus’, except for a modest version in *Crinodon*. However, it is not seen in the putative pantylid *Sparodus* based on Carroll’s reconstruction (1988), might be due to lack of preservation in that taxon. The functional significance of the jugal expansion remains ambiguous; it is plausible that could arise from the jugal being reinforced to provide support to the palatal complex.

(3) Enlarged choanal opening: the choanal opening seems to be quite enlarged when compared to other ‘microsaurus’, and the enlarged dentary teeth fit well in the anterior end of the choanal opening when jaws are closed. This condition is present in *Stegotretus*, *Pantylus*, and NSM 017GF020.002. The medial margin of the choanal opening is fairly close to and almost parallel to the midline of the skull, a condition that
seems to be unique to *Pantylus* and NSM 017GF020.002, as it is less so the case in *Stegotretus*. *Rhynchonkos* and *Odontopteron* also seem to have a considerably enlarged choanal opening, based on reconstructions (see Carroll and Gaskill 1978), but not quite as extensive as that seen in pantylids.

(4) Enlarged choanal opening leading to a narrow vomer: the paired vomers in *Stegotretus*, *Pantylus*, and NSM 017GF020.002 are long, narrow, tooth-bearing, trough-like elements butting against the premaxilla and palatine, separated posteriorly by the pterygoids, though the one in *Stegotretus* seems to have a wider posterior portion and be notched at its posterior contact with the palatine.

(5) Absence of ectopterygoid: This bone is not found in the palate of *Stegotretus*, *Pantylus*, and NSM 017GF020.002. Berman et al. (1988) did not find sutures indicating the presence of ectopterygoid on the palate of *Stegotretus*, but also noted that the palates of many microsaurs are subject to heavy interpretation. At least in *Pantylus*, where the reconstruction is based on several serially sectioned specimens, and in NSM 017GF020.002, which has high quality CT-data, the absence of a discrete ectopterygoid can be confirmed. It remains possible, however, that the ectopterygoid is fully fused with the palatine. For other ‘microsaurs’, past reconstructions (e.g. Carroll and Gaskill 1978) have noted a tendency toward reduction in the size of the ectopterygoid, many are illustrated to be smaller than the palatine, but recent redescriptions based on CT data revealed different proportions than historical construction. For example, *Euryodus dalaee* (Gee et al. 2021) was
shown to have a larger ectopterygoid than palatine, vastly different from historical 
construction. The validity of this shared character is probably pending more thorough 
tomographic analyses across ‘microsaurs’.

(6) Reduced tooth count in marginal dentition: Berman et al. (1988) noted both 
_Pantylus_ and _Stegotretus_ exhibit some of the lowest tooth counts in ‘microsaurs’, 
arguing marginal dentition reduction is a derived state, a statement I find difficult to 
concur with. _Pantylus_ has 3 premaxillary teeth, 9 to 10 maxillary teeth, and 9 dentary 
teeth. _Stegotretus_ has 2 premaxillary teeth, 11 to 12 maxillary teeth, and 10 to 12 
dentary teeth. The tentative pantylid _Trachystegos_, has 2 premaxilla (putative), 8 
maxillary, and 7 dentary teeth. _Sparodus_ had 4 premaxillary teeth, 11 maxillary teeth, 
and maybe 13 dentary teeth. NSM 017GF020.002 has 4 premaxillary teeth, 11 to 12 
maxillary teeth (deduced from tooth sockets in a CT scan), and 17 dentary teeth. 
NSM 017GF020.002 has less reduced dentition, especially in the dentary. Given 
pantylids’ most recent phylogenetic placement, they are considered the most basal 
recumbirostrans (Mann et al. 2023), which contrasts with Berman et al. (Carroll 
1988)’s proposition of marginal tooth reduction being a derived trait. Marginal 
dentition reduction could be a general trend in pantylids, but tooth count is probably 
less reliable as a diagnostic character, after all, in extant taxa, even species of the 
same genus can have vastly different tooth counts. Note that odontogenesis, the 
process of tooth development, is highly conserved across Tetrapoda (LeBlanc and 
Reisz 2015), therefore, making inferences from extant taxa is not totally unreasonable.
Marked size heterodonty in marginal dentition: All of *Stegotretus*, *Pantylus*, and NSM 017GF020.002 exhibit size heterodonty of the marginal teeth, but not without differences. *Pantylus* has the first premaxillary, first maxillary, and second dentary teeth greatly enlarged, reaching at least twice the height of the tallest remaining teeth. In *Stegotretus*, the first premaxillary, mid-row maxillary, and second dentary teeth are greatly enlarged, again, twice the height as other marginal ones. The putative pantylid *Trachystegos* has consistently large marginal dentition but does not exhibit size heterodonty. *Sparodus* has enlarged maxillary teeth at position 4. NSM 017GF020.002 has the first two maxillary, and the second and third dentary teeth enlarged. The extent of maxillary enlargement is unknown due to taphonomic loss; the largest dentary teeth are at least twice as tall as other ones. As seen in extant animals, enlarged teeth may be associated with their foraging and feeding behavior (e.g. Hotton 1955; Taylor 1987) or may even be a sexually selected trait (e.g. Gittleman and Valkenburgh 1997). In cases of exceptional preservation, feeding behavior can also be inferred from extinct taxa (Reisz et al. 2020), which will be attempted for NSM 017GF020.002 in Chapter 4 here.

Extensive occluding palatal-coronoid dental apparatus: This is likely the most characteristic feature of pantylids. In *Stegotretus*, *Pantylus*, NSM 017GF020.002, the putative pantylid *Trachystegos*, and *Sparodus*, an extensive palatal-coronoid apparatus is found on the palatine and coronoid, packed with marginal-sized teeth, except for those in *Trachystegos* that are always smaller than marginals. NSM 017GF020.002 seems to have a more densely packed dental field than that in
Pantylus and Stegotretus (e.g. judging from the schematic reconstructions; Carroll and Gaskill 1978), where virtually no space remains between denticles on the palatine. In Stegotretus, the palatal dental field appears to span both the palatine and the pterygoid. Except for Trachystegos, the larger palatal teeth (not including the greatly enlarged teeth) of pantylids and NSM 017GF020.002 are concentrated along the lateral periphery. Some gymnarthrids have also developed palatal and coronoid dentition. Leiocephalikon is the gymnarthrid with the most extensive palatal-coronoid apparatus: the vomer is packed with multiple rows of small denticles, the palatine has densely packed denticles, and there is a distinct row of larger teeth at the lateral periphery. Its coronoid dental plate, which consists of three coronoid bones, bears three rows of large teeth; this dental field extends beyond the marginal teeth. It is worth noting, however, that the Leiocephalikon is in need of revision and also occurs at Joggins, where Trachystegos is found.

The integration of the pterygoid and palatine forms a robust and thickened complex in NSM 017GF020.002 (Figure 2.5A) that is much more intense than Pantylus. The height of this complex, on average, is comparable to the height of the entire lower jaw ramus. This robust integration likely had a biomechanical advantage that is specific to the lifestyle of NSM 017GF020.002’s (discussed below). The extent of integration in other species is less known due to lack information; however, from the image of Sparodus (Marjanović and Laurin 2019: fig 3,4), it may have had a considerable thickened palatine.
(9) Enlarged teeth of the palatal-coronoid apparatus: *Pantylus*, *Stegotretus*, *Sparodus*, and NSM 017GF020.002 all have at least one pair of occluding, greatly enlarged teeth on the palatal-coronoid apparatus, but differ in details of construction. The ones seen in *Pantylus* are located somewhat lateral to the center of the palatine and coronoid. When the jaws are closed, the one on the coronoid occludes medially to the one on the palatine. In *Stegotretus*, a circular fenestra located posterolateral to the centre of the palatine receives the enlarged coronoid tooth when the jaws are closed. Additionally, there is at least one enlarged palatal tooth at the lateral margin in *Stegotretus*. *Sparodus*, on the other hand, has two enlarged crushing teeth at the posterior end of the palatine, matching the two on the coronoid bone. In NSM 017GF020.002, the enlarged teeth are found near the posterolateral end of the palatal plate, and the posterior end of the coronoid plate; the coronoid one lies posteromedial to the palatine one when the jaws are closed. The putative pantylid *Trachystegos* has no enlarged palatal teeth, but did have a general trend of increasing in size towards the lateral margin of the plates, like all the other pantylid taxa.

The dental lamina, an odontogenic organ, is consistently found on the medial side of the multi-toothrow dentary of *Captorhinus* (LeBlanc and Reisz 2015), and is seems to be associated with lager teeth in a multi-toothrow situation (Gee et al. 2021) By the same principle, the dental lamina, might have been placed on the lateral side of the palatine and coronoid, hence the consistent pattern of larger lateral teeth. The placement of dental lamina on the palate in ‘microsaur’ (lateral) is suggested to be different from other Paleozoic tetrapods (medial), which warrants further investigation.
into the homology of the trait and will likely have major implications for phylogeny (Gee et al. 2021).

It is unclear why the different configurations of palatal-coronoid dentition exist and what ecological implications they have. Nonetheless, they contribute to a diverse interspecific morphology, even in such a highly apomorphic trait. Naturally, such a characteristic dental apparatus would be the most informative to infer diet, which is discussed in further detail below.

(10) Polygonal dermal ossicles/scales: Small, polygonal, dermal plates are found on the ventral side of the shoulder girdle in Stegotretus, Pantylus, and maybe NSM 017GF020.002 (e.g., the ones covering the left surangular). Both NSM 017GF020.002 and Pantylus additionally have a layer of small, polygonal infradentary ossicles. Similar plates can be found between the lower jaw in non-pantylid taxa such as Tuditanus, Crinodon, and Saxonerpeton, but seems to be more rounded than those seen in pantylids (Carroll and Gaskill 1978).

2.4.2 Morphological diversity among Pantylidae

Despite the superficial resemblance between Pantylus and NSM 017GF020.002, major anatomical differences exist. These differences, along with those seen among the other pantylid species in general, add to the known morphological diversity of the group. Features potentially unique to NSM 017GF020.002 could be used to diagnose it as a new taxon, either at the genus or species level. This diversity and potentially diagnostic features of NSM 017GF020.002 are summarized below.
Skull. In pantyliids for which it is known, e.g., *Pantylus* and *Sparodus*, a prominent dorsal expansion of the maxilla into the overlying lacrimal is present. However, this is not seen in NSM 017GF020.002, which has an overall smooth, uninterrupted dorsal profile of the maxilla in lateral view. The cause of this expansion is not clear, but it does not appear to be associated with the enlarged maxillary teeth, because NSM 017GF020.002 also has enlarged teeth.

*Stegotretus*, *Trachystego*, *Sparodus*, and NSM 017GF020.002 all had a pineal foramen between the parietal, which is not found in *Pantylus*. *Stegotretus*, *Sparodus*, NSM 017GF020.002 had different proportional contributions of the prefrontal and postfrontal than that of *Pantylus*, where the prefrontal and postfrontal meet at the mid-dorsal point on the orbit; in *Pantylus*, the prefrontal occupies an extended portion of the anterodorsal and dorsal margins of the orbit, and the postfrontal occupies a short rim on the posterior.

The size of the orbit is quite similarly small in *Pantylus* and NSM 017GF020.002, in terms of the percentage of the skull length (21% and 20%, respectively), when the value for NSM 017GF020.002 is estimated after accounting for the missing premaxilla and occiput. *Sparodus* had, based on reconstruction by Carroll (1988), a slightly larger orbit (23%) and *Stegotretus* seems to have the largest orbit by proportion, reaching 26%.

The location of the orbit is rather anteriorly oriented in *Pantylus*, *Stegotretus*, NSM 017GF020.002, and *Sparodus*, but is fairly central in *Trachystegos*. 
In *Pantylus* the prefrontal sends a strong medial flange to meet ventrally with the sphenethmoid, but in NSM 017GF020.002, it is the frontal that sends a modest flange that may be interacting with the sphenethmoid. Interestingly, this descending flange from the roofing elements is quite variable among recumbirostrans, in terms of shape and bone participation, which could range from the sole participation or a combination of, frontal, parietal, and prefrontal. (see Szostakiwskyj et al. 2015).

**Braincase region.** On top of the parasphenoid, *Pantylus* had a distinguishable basisphenoid, whereas in NSM 017GF020.002 these elements were fused forming a parabasisphenoid. In *Pantylus*, the basisphenoid has a significant dorsal extension towards the skull roof, representing ossification of the pila antarctica of the embryonic braincase, ending just below the skull roof. In NSM 017GF020.002 paired, tiny wings rise dorsally, but are not comparable in size with the dorsal extensions seen in *Pantylus*. The basal plate of the parasphenoid of *Pantylus* and NSM 017GF020.002 has an overall similar width and posterior extent that ends at the level of the occiput. However, the basal plate of the parasphenoid of *Stegotretus* extends beyond the posterior margin of the skull and is extremely broad, being almost as wide as the skull, much wider than that of *Pantylus* and NSM 017GF020.002. In addition, the basal plate of *Stegotretus* has very small, tightly packed denticles covering it from the basal articulation to the tip of the cultriform process. These denticles are not seen in NSM 017GF020.002 or *Pantylus*. 
Basal articulation. The contacts of the basal articulation are vastly different among pantylids. *Pantylus* had a ball and socket type joint and NSM 017GF020.002 had flat articulating surfaces. The detailed construction of the basal articulation also varies. In *Pantylus*, the ball (basipterygoid process) is formed by the parasphenoid and basisphenoid, and the socket is contributed by the pterygoid and epipterygoid, similar to *Rhynchosphonos* (Carroll and Gaskill 1978) and *Euryodus dalae* (Gee et al. 2021). The basal articulation in NSM 017GF020.002, on the other hand, consists of paired anterolaterally directed projections from the fused parabasisphenoid butting against projections formed solely by the pterygoid. In both configurations, the epipterygoid seems to reach far dorsally towards the skull roof; however, in NSM 017GF020.002 the medioventral extent of the epipterygoid does not reach as far anteriorly as that in *Pantylus*, hence no participation in the basal articulation from the epipterygoid in NSM 017GF020.002. In *Stegotretus*, the basal articulation has no apparent socket on the pterygoid, and the basal articulation process from the parasphenoid simply contacts the ventromedial margin of the pterygoid. The process on the pterygoid is triangular, but not much could be deduced from its articulating surface based on the description of Berman et al. (1988). However, it is enough to tell that the configuration in *Stegotretus* is different from both NSM 017GF020.002 and *Pantylus*.

Romer (Romer 1969: 31) pointed out that *Pantylus*, like many primitive “amphibians”, had narrow interpterygoid vacuity and a movable basal articulation of the braincase and palate, but did not describe the movement in detail. Based on the types of basal articulation, if any movement was permitted, all three taxa would have exhibited this
phenomenon differently. The ball and socket joint in *Pantylus* would have restricted any anteroposterior or dorsoventral translation, but allowed rotation along the mediolateral axis. The less-restrained basal articulation contact in *Stegotretus* would probably have allowed “free” movement in all three axes, but this interpretation cannot be confirmed until tomographic data is available. The flat surface contact in NSM 017GF020.002 may allow sliding action parallel to the plane of contact, depending on the orientation of the contact plane; however, this movement may be restricted in one direction. As Carroll and Gaskill (1978) state, the basal articulation in many ‘microssaur’ seems to be a movable joint. This mobility may be associated with the functionality of the major tooth bearing elements of the palate, something that will be discussed further below.

*Supraoccipital*. The supraoccipital is quite different in morphology between *Pantylus* and NSM 017GF020.002 in its anterior construction: the supraoccipital in *Pantylus* sends a dual-rod structured anterior process (median ascending process) that descends downward and terminates at the level of the pituitary, whereas in NSM 017GF020.002, a paired tapering process runs parallel underneath the skull roof to the level of the parietal. Lateral expansion of the supraoccipital is also markedly different. In *Pantylus* lateral expansion of the supraoccipital descends ventrally to contact, from anterior to posterior, the prootic, opisthotic, and exoccipital. In addition, the supraoccipital encloses the dorsal vertical canals of the internal ear and the crus commune (Romer 1969). In NSM 017GF020.002, this robust lateral extension seems to wrap around a curved channel, given its concave anterior profile, which is possibly
a semicircular canal. The median ascending process of supraoccipital in NSM 017GF020.002 is somewhat similar to *Captorhinus laticeps* (Heaton 1979: 49) in that it also has a tapering anterior process that projects parallel under the skull roof and each “half” (supraoccipital is not actually paired) has a roughly crescent shape, though the curvature in *Captorhinus laticeps* is stronger, approaching almost a V-like appearance. In *Stegotretus*, the supraoccipital is described as being arch like, spanning between the exoccipital and dorsomedial margins of the otic capsules, again, a configuration that seems entirely different from *Pantylus* and NSM 017GF020.002, and is believed to be the ossification of the tectum posterius (as suppose to the tectum synoticum - another possible embryonic origin of the supraoccipital) that spanned the embryonic occipital arch (Berman 2000). Many ‘microsuars’ had a single ossification of the supraoccipital (Romer 1969; Berman 2000; Huttenlocker et al. 2013), but the homology and morphology are not clearly resolved. The single median ossification has been suggested as a potential convergence between recumbirostrans and amniotes (Szostakiwskyj et al. 2015). In NSM 017GF020.002 we are seeing a paired supraoccipital, which is the only case, along with *Pantylus*, among recumbirostrans.

Supraoccipital is not uncommon in early tetrapods, but in varying degrees, e.g. it is present in *Captorhinus*, *Petrolacosaurus*, paired in *Ophiacodon*, *Limnocelis*, but missing in *Seymouria*, *Dimetrodon*, all of the temnospondyls. This ossification could exhibit great diversity even among the same family (e.g., Rhynchonkos; Szostakiwskyj et al. 2015). The diversity in this ossification and its mosaic pattern of
presence/absence in early tetrapods suggest it could have the potential to help resolve the phylogeny problem among stem- and crown-amniotes (Szostakiwskyj et al. 2015). However, the fact that it ossifies late during ontogeny may present a potential confounding factor: if a taxon is missing this ossification, is it paedomorphic, immature, or simply missing.

**Dentition.** The differences in size heterodonty, palatal-coronoid apparatus, and enlarged palatal teeth of pantylid species and NSM 017GF020.002 were discussed above. The marginal teeth of *Trachystegos* are fairly large in proportion, and more interestingly, they bear fluting at the base. This is a condition shared with *Sparodus*, but is seen also in gymnarthrids and not other pantyilds. This resulted in Carroll’s (Carroll 1966) placement of *Trachystegos* within what group, but it was later allied with *Pantylus* (Carroll et al. 1998), though the rationale behind these moves is not clear.

**Lower Jaw.** The lower jaw of *Trachystegos* is quite shallow, but very thick mediolaterally, differing from other pantyilds whose width and height of the lower jaw are roughly equal. There seems to be a different arrangement of the splenial, postsplenial, and prearticular in *Trachystegos*, that makes it more gymnarthrid-like than pantylid (Carroll 1966). The coronoid process is quite prominent in *Pantylus*, with contributions from both the coronoid, dentary, and surangular. This feature is not found in *Sparodus*, and is uncertain in *Stegotretus* and NSM 017GF020.002. Opposite the coronoid process, there is a medial dorsal process, or adductor crest,
on the medial wall of the adductor fossa. This is differently shaped in *Pantylus* (a peaking summit) and in NSM 017GF020.002 (a raised platform). The contribution to the boundary of the meckelian foramen is formed by the angular, prearticular, and postspenial in *Pantylus*, and by the angular and prearticular (without postsplenial) in *Stegotretus* and NSM 017GF020.002. The Meckelian foramen is smaller and more anteriorly positioned than NSM 017GF020.002. *Sparodus* seems to not have a meckelian foramen or any medial foramen on the lower jaw. The foramen may have permitted an accessory vein to exit the jaw (Romer 1976), but appears to be lost in *Sparodus*. Vertically, the jaw articulation is at the level of the occipital articulation in *Pantylus*, *Stegotretus*, and NSM 017GF020.002. In *Sparodus*, it is much anterior to the skull margin, about halfway between the posterior orbital rim and the posterior limit of the skull, possibly a paedomorphic state given the small size of the animal (Carroll 1988). *Pantylus* has a prominent articular process at the posterior end of the lower jaw, and a modest one seems to present on *Sparodus*, whereas the feature is not found in *Stegotretus*, and is uncertain in NSM 017GF020.002 due to damage to the articular.

**Centrum.** The only preserved centrum of the cervical vertebrae in NSM 017GF020.002 is somewhat different from that of *Pantylus* in that there is no posterior constriction evident in the atlas centrum of NSM 017GF020.002 to receive a significantly reduced second cervical vertebrae like that in *Pantylus*. 
2.4.3 Dental apparatus and its function

*Pantylus*, *Stegotretus*, *Sparodus*, and NSM 017GF020.002 all share the same specialized dentition: heterodont marginal teeth and a palatal-coronoid apparatus with enlarged teeth on it. Such dentition was suggested by Romer (1969) to be an adaptation to a highly specialized diet and feeding behaviour, such as a durophagy or herbivory, in *Pantylus*. Given the similarities among *Pantylus*, *Stegotretus*, and NSM 017GF020.002, this interpretation could be extended to all three taxa.

The dental apparatus of NSM 017GF020.002 is especially specialized, represented by at least two enlarged anterior dentary teeth, one enlarged maxillary tooth, with palatal and coronoid dental fields that are densely and fully packed. In addition, there are several secondary dental fields with smaller, non-occluding teeth along the medial surface of the coronoid, palatine, and ventral side of the pterygoid, vomer. It is unclear what the function of these non-occluding secondary dental patches is, as they do not seem to come in contact with food. One possibility is that these smaller denticles on the palatine and coronoid may be the older teeth that got shifted as new teeth are formed on the lateral side, where the dental lamina possibly resides (Gee et al. 2021). An ontogenetic series of any of these taxa would confirm or refute this possibility.

Upon jaw closure, the upper and lower dentitions come in contact to act on the food, possibly producing a more crushing action than a shearing action. Unlike some herbivore which has blade-like, leaf-shaped, and mediolaterally compressed marginal teeth that are suitable for shearing and cropping plants (Sues and Reisz 1998), NSM
017GF020.002 retained the simple conical-shaped teeth. Also, there is no evidence of a propalineal jaw system (i.e. with longitudinal movements) in NSM 017GF020.002, which would have allowed some grinding action to further reduce food and facilitate chemical and mechanical processing down the road (Reilly et al. 2001).

The robust integration of palatine and pterygoid in NSM 017GF020.002 is considered impressive even among pantylids, and such development is not seen in any other ‘microsaur’. The height of the complex, on average, is comparable to the height of the lower jaw. The palatal complex is buttressed against the dermatocranium at two locations: the extensive interdigitating suture between the anterolateral process of the palatine and the lacrimal anterior to the orbit; and the broad butting connection between the posterolateral process of the palatine/pterygoid and the jugal just behind the posterior orbital rim.

The occluding palatal-coronoid dentition suggests a possible crushing mechanism associated with during durophagy or herbivory. Considering the hypothesized diet, such robust integration of the palatine and pterygoid could indicate a structural reinforcement strategy. The strong supporting joints ensure the palatal complex can transfer such high loading (i.e., due to repeated impact of hard food) onto the skull roof. The wide joints would allow the loads to be distributed evenly over a wider area. Interdigitating sutures have been shown to mitigate compressive forces (Markey et al. 2006). When jaws close to crush food, the interdigitating joint between the palatal complex and the skull transmits forces to the supporting lacrimal, which is thickened
and expanded at the connection, likely as a reinforcement to resist incoming loads. The same thickening/expansion/reinforcement could be seen at the joint with the jugal, where the palatal complex buttresses against it and the same principles apply. The supports, in turn, distribute the loads from the side walls to the stoutly built skull roof. How the loads distribute among the skull roofing bones, the magnitude and type of forces (e.g., tension, compression, torsion, shear, bending moment) could be only further assessed with a proper biomechanical modelling (e.g., finite element analysis).

In response to an intensive palatal-coronoid apparatus, the lower jaw of NSM 017GF020.002 is quite stoutly built. Large adductor muscles are needed to provide the powerful bites for the postulated diet, and in fact, the size of the adductor chamber in *Pantylus* and NSM 017GF020.002 are exceptionally enlarged compared to other ‘microsaurs’ that share a similar shape and size proportion relative to the skull length. This supports the presence of particularly large, and thus strong adductor muscles in both *Pantylus* and NSM 017GF020.002.

Jaw articulation modifications are sometimes associated with herbivory, such as moving the adductor muscle attachment point further away from the jaw joint, attaching the adductor muscle to a raised, long coronoid process, or depressing the level of the jaw joint (Reilly et al. 2001). Such modifications function to increase the moment arm (i.e. perpendicular distance between the line of action of the adductor muscle and the jaw articulation), hence increasing the jaw closing force and improving the biomechanical efficiency in jaw closure (Gould 1970; Reilly et al. 2001). However,
modification of the jaw joint is not evidently the case in NSM 017GF020.002. The jaw articulation seems no different from that of Pantylus, both are at a level merely lower than the marginal tooth row and coronoid tooth plate. In both taxa, the interpreted movement of the lower jaw appears to have been limited to rotation around the transverse axis at the level of the occiput, resembling a simple hinge.

Judging by how the palatal complex contacts the skull, and the overlapping and tongue-and-groove joints between the skull roofing elements, it seems unlikely that rotation can happen along any line of joint between the two components. Thus, there is no evidence of cranial kinesis in NSM 017GF020.002. The flat articulating surfaces at the basal articulation, as discussed previously, could potentially allow infrapalatal kinesis. However, even though the flat articulation surfaces could have allowed sliding movement along the plane, because the parasphenoid-sphenethmoid structure butts against the skull roof, there is probably little room for movement. Hence, infrapalatal kinesis also appears to be unlikely in NSM 017GF020.002, though it may have developed in later diverging pantylids, such as Pantylus.

2.5 References


Chapter 3 Phylogenetic analysis

3.1 Introduction

Since the creation of the Order Microsauria by Dawson (Dawson 1863)(1863), its monophyletic status had largely been the consensus view for over 100 years. Recent phylogenetic analyses, however, have challenged this view (e.g., Ruta et al. 2003; Vallin and Laurin 2004; Anderson 2007) and as of today, most studies agree that ‘microsaurs’ are likely a polyphyletic and/or a paraphyletic assemblage of early tetrapods. Further complicating matters, different groups of researchers now hold different opinions on where ‘microsaurs’ reside within Tetrapoda – i.e., as lepospondyls on the amniote stem or actually true members of Amniota (Ruta and Coates 2007: 207; Pardo et al. 2017, etc.). In fact, in Marjanovic and Laurin’s (2019: 138) original words: “It is not an overstatement to say that ‘microsaur’ phylogeny is a mess. No two analyses, usually even if based on successive versions of the same matrix, have recovered the same topology or nearly so.”

Although much recent research attention has been focused on ‘microsaurian’ groups such as Rhychonkidae and Molgophidae for their roles in important questions like the origin of lissamphibians (Carroll 2001; Carroll 2007; Szostakiwskyj et al. 2015; Pardo and Anderson 2016) and the origin and evolution of limblessness (Pardo and Mann 2018; Mann et al. 2022), respectively, the uncertain phylogenetic placement of Pantylidae has received comparatively little attention. This is despite the fact that its
namesake member, *Pantylus*, is one of the best known ‘microsaurs’ and that the group has potentially much to say about the origin and evolution of a key tetrapod innovation – herbivory (Romer 1969).

Cope’s classification of *Pantylus*, and thus Pantylidae, jumped from being within the Stegocephali of Batrachia (old name for amphibians; Cope 1881) to Cotylosauria (old name for early amniotes; Cope 1892). The latter placement was agreed upon by many subsequent workers (see Romer 1969 for a detailed account). Almost one hundred years after the discovery of *Pantylus*, its taxonomic position has largely settled to be within the Order Microsauria (Romer 1950; Gregory 1965; Carroll and Gaskill 1978), albeit now-defunct, although not without dissent (Vaughn 1962).

In his original description of *Pantylus cordatus*, Romer (Romer 1969: 26) suggested it is closely related to the gymnarthrid ‘microsaurs’ and opposed the idea of ‘microsaurs’ being reptiles or ancestors of reptiles. He instead noted that features of the otic bones and position of the fenestra ovalis are somewhat similar to ‘seymouriamorphs’, which are currently considered to be stem amniotes (Ruta et al. 2003: 2007; Ruta and Coates 2007; Pardo et al. 2017; Klembara et al. 2020). This would be consistent with the consensus view at the time that *Pantylus* and other ‘microsaurs’ should be included within the stem-amniote clade Lepospondyli (e.g., Carroll et al. 1998).

In the seminal monograph “The Order Microsauria”, Carroll and Gaskill (1978) placed Pantylidae within Tuditanomorpha, one of the two major groups of ‘microsaur’, the
other being Microbranchomorpha. This relationship is no longer valid in the context of results obtained by modern phylogenetic analyses (Ruta et al. 2003; Anderson 2007; Ruta and Coates 2007; Sigurdsen and Green 2011; Marjanović and Laurin 2013; Pardo et al. 2017), for ‘microsaur’ no longer form a monophyletic group, and the monophyly of Tuditanomorpha has not been supported in any later study.

In Ruta et al. (2003), *Pantylus* was found to be the sister taxon to *Stegotretus*, and together they nested among the other ‘microsaur’. However, ‘Microsauria’ was found to be paraphyletic with respect to the other lepospondyls (namely adelogyrinids, nectridians, and aistopods). In their subsequent analysis (Ruta and Coates 2007), ‘microsaur’ were again retrieved as a paraphyletic assemblage, this time with the pantylid clade jumping to a more crownward position being the sister taxon to a clade consisting of Molgophidae (or Lysorophia), Nectridae, and Aïstopoda.

Vallin and Laurin (2004), who adopted the matrix of Laurin and Reisz (1999) and added new data, found *Pantylus* to be united with *Cardiocephalus* (a gymnarthrid), brachystelechids, molgophids (lysorophians), and lissamphibians. Shortly after, Anderson (2007) obtained a monophyletic group of ‘microsaur’ within Lepospondyli sharing the same iconic character of a downturnning (recumbent) snout, a clade he later named Recumbirostra, of which Pantylidae (represented by *Pantylus*, *Stegotretus*, and *Sparodus*) is nested deep within. Similar placement of *Pantylus* was again obtained in Anderson et al. (2008). In later works that adapted the Anderson matrix, *Pantylus* shifted to an increasingly basal position within Recumbirostra upon
adding new data and taxa (Maddin et al. 2012; Pardo et al. 2017; Gee et al. 2021; Mann et al. 2023).

Sigurdsen and Green (2011) assembled matrices from Vallin and Laurin (2004), Ruta and Coates (2007), and Anderson et al. (2008) in an attempt to merge differences in these independently developed character matrices. Their modified matrix had found, in the Bayesian inference tree, *Pantylus* nested among the ‘microsaurs’ included in the analysis, which formed a clade sister to a clade formed by Adelospondyli and Holospondyli (i.e., Nectridea and Aistopoda). This clade (roughly representing Lepospondyli) was the sister taxon to a clade formed by *Limnoscelis* and *Seymouria*, which indicated it was on the amniote stem.

More recently, Marjanovic and Laurin (2019) made the effort to clean up and identify misscores in the Ruta and Coates (2007) matrix and added important taxa to improve taxon sampling. The result of their analysis revealed that, in most cases, pantylids (represented by *Pantylus* and *Stegotretus*) and ‘tuditanids’ were consistently falling out as sister groups forming a clade. In general, ‘microsaurs’ were nested within Lepospondyli (depending on the constraint of the analysis), but never within Amniota. Moreover, Marjanovic and Laurin (2019) were not able to recover Tuditanomorpha, Microbrachomorpha (both were proposed suborders within ‘Microsauria’ in Carroll and Gaskill 1978), or Recumbirostra in any of their analyses.
The recent discovery of NSM 017GF020.002 revealed an overall stark resemblance to *Pantylus* in many ways: the overall robust build of the skull and mandible, the broadly triangular shape of the skull, the extensive dental plates on the palatine and coronoids, and the enlarged anterior marginal teeth, among others. I will test the hypothesis that NSM 017GF020.002 is a member of Pantylidae using phylogenetic methods. If this is the case, the excellent preservation of the specimen and detailed anatomy presented in Chapter 2 mean NSM 017GF020.002 has the potential to clarify the composition of Pantylidae, and potentially shed light on the position of this group with respect to other 'microsaurs' and tetrapods in general.

### 3.2 Materials and methods

#### 3.2.1 Specimen

Specimen NSM 017GF020.002 consists of a nearly complete skull with articulated lower jaws. Its provenance and the nature of its discovery were described in Chapter 2.

#### 3.2.2 Phylogenetic analysis

The matrix used in this study was adapted from Mann et al. (2023), which was based on Pardo et al. (2017). It includes the most updated coding for recumbirostran ‘microsaurs’ and was used in previous studies to resolve relationships within recumbirostrans. Character matrix coding for NSM 017GF020.002 and modifications to previous coding was performed in Mesquite (v3.81 Maddison and Maddison 2023).
Symbols represent uncertainty (?) and inapplicable (-). Additionally, three new characters were added to the original matrix considering new anatomical data observed in NSM 017GF020.002. These are:

375 Massively enlarged teeth on the palatal-coronoid apparatus: absent (0), present (1).

376 Single or paired massively enlarged teeth on palatal-coronoid apparatus: coronoid only (0) or equally large teeth opposing on both the coronoid and palatine (1).

377 Interdentary and pectoral ossicles: absent (0), present (1)

Pardo et al. (2017) introduced many new characters pertaining to the braincase. However, since most of the characters are defined as soft tissue structures (e.g., cartilages of the chondrocranium), many cannot be scored in this fossil specimen. As such, most of the braincase characters in the matrix added in Pardo et al. (2017) were left as “?”.

Other pantyliid members discussed in Chapter 2, e.g., *Stegotretus*, *Sparodus*, and *Trachystegos*, are not scored in this matrix. For *Stegotretus* and *Sparodus* have been included in previous phylogenetic studies (e.g., Anderson 2001; Anderson 2007; Huttenlocker et al. 2013; Marjanović and Laurin 2019), and there has been no new information since their original descriptions (*Stegotretus*: Berman et al. 1988; *Sparodus*: Carroll 1988). *Trachystegos*, on the other hand, have not been included in
any phylogenetic analysis, its pantylid placement is largely speculative. The description in available literature is limited due to the fragmentary nature of the specimens, therefore no scoring attempt has been made. However, we should soon be able to reveal new information upon receiving the μCT-scan data of *Trachystegos* (see Chapter 4 discussion).

The final character-taxon matrix had a total of 70 operational taxonomic units (OTU) and 377 characters. See Appendix B for the full character list and scoring of NSM 017GF020.002, and Appendix C for final character-taxon matrix.

A parsimony analysis of the matrix was carried out in PAUP* v4.0a (Swofford 2003). *Eusthenopteron foordi* was set as the outgroup. All characters were equally weighted and unordered. Maxtrees was set to 10000, with an auto increase set to 100. Multistate taxa were treated as polymorphic and characters were optimized using the accelerated transformation (ACCTRAN) option. A heuristic search was conducted using the branch swapping algorithm (TBR; tree bisection-reconnection) and 1000 random sequence addition replicates. Tree support metrics were also calculated in PAUP (consistency index [CI], homoplasy index [HI], retention index [RI], and rescaled consistency index [RC]).

The resulting most parsimonious trees (MPTs) were visualized as a strict consensus tree and a 50% majority-rule consensus tree. Lists of apomorphies were obtained for each consensus tree using PAUP's describetrees command for nodes of interest (i.e., Pantyliidae, Recumbirostra).
The trace character tool in Mesquite was used to map and observe character transformations on the resulting tree using the accelerated transformation (ACCTRAN) option.

3.3 Results

The PAUP analysis revealed 17 characters that are constant and 13 variable characters were parsimony-uninformative. The total number of parsimony-informative characters was thus 347 out of 377. The PAUP analysis resulted in 100 most parsimonious trees (MPTs), each with 1886 steps (consistency index [CI] = 0.304; retention index [RI] = 0.655; rescaled consistency index [RC] = 0.199; homoplasy index [HI] = 0.748). The strict consensus of all 100 MPT is given in Figure 3.1 (Tree Length = 2005, CI = 0.2863; RI = 0.6235; RC = 0.1785; HI = 0.7631), referred to as the “All Trees Topology (ATT)” hereafter. The 50% Majority-rule consensus of the 100 MPTs is given in Figure 3.2 with nodal support values (Tree Length = 1889, CI = 0.3039; RI = 0.6540; RC = 0.1987; HI = 0.7013), referred to as the “Majority-Rule Topology” (MRT) hereafter. Strict consensus trees for each of the nine optimal tree islands were also calculated and are described below.
Figure 3.1 Strict consensus tree (ATT) of the 100 most parsimonious trees (MPTs). Recumbirostran ‘microsaur’ groups are coloured as: blue - Pantylidae; red - Gymnarthridae; magenta - Ostodolepidae; green - Brachystelechidae; purple - Molgophidae; brown - Odeonterpetidae; olivegreen - Rhynchonkidae.
Figure 3.2 Majority-rule (50%) consensus tree (MRT) of the 100 MPTs with percent nodal support. Recumbirostran ‘microsaur’ families are coloured as: blue - Pantylidae; red - Gymnarthridae; magenta - Ostodolepidae; green - Brachystelechidae; purple - Molgophidae; brown - Odonterpetidae; olivegreen - Rhynchoonkidae.
In all of the consensus tree topologies, a monophyletic grouping of the recumbirostran ‘microsaur’ taxa is recovered, nested within captorhinid reptiles (Figure 3.1 and Figure 3.2). The captorhinid *Opisthodontosaurus* is recovered as the sister taxon to the ‘microsaur’ clade. Among the ‘microsaur’ taxa, a clade formed by *Pantylus* and NSM 017GF020.002 is the basalmost branch, and thus represents the sister clade to all remaining “microsaur” included in this analysis.

The strict consensus trees of the nine individual tree islands differ in the patterns of relationships among the non-pantylid recumbirostrans. These variations result in a polytomy in the ATT among Gymnarthridae, *Pariotichus*, *Proxilodon*, *Huskerpeton*, Ostodolepidae, and a monophyletic group consisting of Brachystelechidae + Molgophidae, Odonterpetidae + *Listrofus*, and Rhynchonkidae.

The clade Chthonosauria, previously recognized in Mann et al. (2023), consisting of Molgophidae + Brachystelechidae in a sister group relationship, is supported here in all trees. Another previously recognized clade *Listrofus* + Odonterpetidae (*Joermungandr* + *Odonterpeton*) is again resolved here to be monophyletic in all trees (as in Mann et al. 2023). It is positioned within a clade that forms a polytomy with Chthonosauria and Rhynchonkidae (*Rhynchonkos*, *Aletrimyti*, and *Dvellecanus*), suggesting the interrelationships among major groups of non-pantylid recumbirostrans is still not settled.

All of the polytomies within Recumbirostra are resolved using a less stringent consensus tree (i.e., the 50% majority-rule). In the MRT (Figure 3.2), Pantylidae is the
basalmost lineage, with the next crownward branch being *Pariotichus*, then the remaining recumbirostran assemblage splits into two clades, one containing (Ostodolepidae, (Gymnarthridae, (Huskerpeton, Proxilodon))), and the other containing (Odonerpetidae+*Listrofus*, (Rhynchonkidae, (Molgophidae, Brachystelechidae))). Support values for this topology are thus modest, as they range from 54% to 82%.

### 3.4 Discussion

The results of the phylogenetic analysis performed here that are also reported by Pardo et al. (2017) (i.e., strict consensus of all 100 most parsimonious trees and the 50% majority-rule consensus tree) are consistent with their results. All ‘microsaurs’ included in the current analysis form a monophyletic group, nested among captorhinid reptiles. This may at first be unsurprising given this analysis was conducted upon the matrix used by Pardo et al. (2017). The ‘microsaur’ taxa included here are those that are considered to comprise the group Recumbirostra (*sensu* Anderson 2007). However, the exact arrangement of taxa within Recumbirostra differs slightly from that obtained in its original conception. Here, and like in Pardo et al. (2017), Pantylidae forms the basalmost branch of the clade. This position is interpreted as remaining within Recumbirostra proper, rather than becoming the sister taxon to it, as the taxa within Pantylidae still match the diagnosis of the group: i.e., possess a recumbent snout and includes most recent common ancestor of *Pantylus*, *Cardiocephalus*.
sternbergi, Rhynchonkos, and Micraroter, but not including Tuditanus of Microbrachis (sensu Anderson 2007).

The clade Recumbirostra in the ATT is supported by 16 transformations, of which: seven are unambiguous synapomorphies (characters 4(1), 48(1), 98(2), 111(1), 115(1), 165(2), 169(1)); six are unambiguous reversals (characters 32(0); 79(0), 92(0), 139(0), 163(0), 373(0)); two are ambiguous synapomorphies (characters 288(3), 374(1)), and one is an ambiguous reversal (character 249(0)).

The unambiguous synapomorphies supporting Recumbirostra are: character 4, intertemporal bones (state 1: replaced by anterior extension of supratemporal or tabular); character 48, parietal foramen (state 1: present); character 98, jaw articulation relative to tooth row (state 2: below); character 111, trunk neural arch to centrum (state 1: sutured); character 115, neural spine shape in lateral view (state 1: non-parallel, triangular); and character 165, radius to humerus ratio (state 2: 0.5).

The sister relationship of Pantylus and NSM 017GF020.002 is supported by 26 transformations, of which: nine are unambiguous synapomorphies (characters 67(2), 81(1), 259(1), 270(1), 325(1), 344(1), 345(1), 375(1), 377(1)), four are unambiguous reversals (characters 91(0), 102(0), 273(0), 293(0)); eight are ambiguous synapomorphies (characters 113(1), 138(1), 157(2), 193(2), 195(2), 217(1), 245(1), 263(1)); and five are ambiguous reversals (characters 25(0), 59(0), 103(0), 143(0),152(0)).
The unambiguous synapomorphies supporting Pantylidae are: character 67, number of premaxillary teeth (state 2: <5); character 81, palatal teeth size (state 1: equal to marginals); character 259, ectopterygoid (state 1: absent); character 270, prefrontal (state 1: three times as long as broad); character 325, splenial, rearmost extension of medial lamina (state 1: equidistant); character 344, nature of dermal ornament (state 1: fairly regular pit and ridges); character 375, enlarged teeth on the palatal-coronoid apparatus (state 1: present); and character 377, interdentary and pectoral ossicles (state 1: present).

This large number of characters supporting the relationship between NSM 017GF020.002 and *Pantylus* supports the hypothesis that the new specimen is indeed a pantylid. Within this framework, the most characteristic features of the pantylids are probably their extensive palatal-coronoid dental apparatus and the associated changes, namely characters 81 (palatal tooth size) and 375 (enlarged teeth on the palatal-coronoid apparatus; new character). When these characters are mapped onto the strict consensus tree, the first is seen to be non-unique to pantylids whereas the second is unique (Figure 3.3A,B). However, the combination of these two characters is unique to Pantylidae within Recumbirostra, and among all taxa included in this analysis. Note character state 1 for *Brachypectes newberryi* was probably a misscore, because it was explicitly stated that “neither teeth nor denticles are present on the palatines” in the revised description by Pardo and Anderson (2016: 16). The ecological implications of the uniquely pantylid dental apparatus will be discussed more in depth in Chapter 4.
Another character that is unique to Pantylidae among recumbirostrans is character 217 (supraoccipital ossification within the synotic tectum). Both *Pantulus* and NSM 017GF020.002 are scored as 1: supraoccipital paired at some point during ontogeny whereas most other recumbirostrans have unpaired supraoccipital (2) or have a synotic tectum coossified with otic capsules (0). As discussed in Chapter 2, the morphology of the supraoccipital exhibits exceptional diversity even among members of the same group (e.g., *Pantulus* and NSM 017GF020.002). The supraoccipital of NSM 017GF020.002 is distinct among pantylids in its fully paired configuration. A deeper understanding of the variation in supraoccipital structure could probably add resolution to the ‘microsaur’ phylogeny, and potentially, to early limbed terrestrial vertebrates.

The supraoccipital has also been proposed as one of the possible features uniting recumbirostrans and amniotes (Huttenlocker et al. 2013; Szostakiwskyj et al. 2015). However, the homology of supraoccipital (i.e. whether it is an ossification of the tectum synoticum or tectum posterius) has been debated (Berman 2000), insofar such that Heaton (1980) had proposed to use the name ‘supraoccipital’ strictly for ossification of the tectum posterius, and ‘synotic’ for the tectum synoticum. The inclusion of the supraoccipital as a character has been contentious due to its late ontogenic ossification, and the absence of this ossification in some lepospondyls and putatively all seymouriamorphs (Berman 2000; Szostakiwskyj et al. 2015).
updated, comprehensive, and comparative review on the origin and evolution of the occipital elements, like the one by Berman (2000), is much needed given the wealth of new data on the internal cranial anatomy of early tetrapods, generated from tomographic methods over the past two decades.

Furthermore, the difference in morphology (discussed in Chapter 2) between *Pantylus* and NSM 017GF020.002 warrants the recognition of NSM 017GF020.002 as a taxon distinct from *Pantylus*, and thus a new genus and species. This notion is supported by the presence of several unique features including difference in dentition (i.e. location of enlarged teeth in marginal and palatal-coronoid dentition), morphology of the supraoccipital, configuration of the basal articulation, fused parabasisphenoid, coronoid process, medial dorsal process (i.e. adductor crest), and morphology of the centrum. Together with the results of this phylogenetic analysis, a new genus and species of pantylid 'microsaur' will be named in the peer-reviewed publication of this research.

### 3.5 References


Chapter 4 Inferring the diet of NSM 017GF020.002

4.1 Introduction

Extensive research has been conducted on dental morphology and its relationship with diet within extant saurian taxa. Certain morphological features of teeth are known to be associated with dietary preferences (Hotton 1955; Montanucci, Richard R. 1968; Estes and Williams 1984; Herrel et al. 2004). For example, carnivores typically have simple teeth, often conical in shape, with varying degrees of sharpness and recurvature. Herbivorous taxa may vary in dental specialization: teeth can be labiolingually compressed, and feature multiple cusps or serrations. Durophagous taxa tend to have transversely expanded molariform teeth with features such as wrinkled enamel (Melstrom 2017). Tooth morphology among insectivorous and omnivorous taxa shows great diversity, ranging from simple conical teeth to multicusp teeth.

The dental apparatus of NSM 017GF020.002 is highly specialized, evidenced by the presence of well developed and densely packed dental plates on both the palatine and the occluding coronoid bones. This distinct feature closely resembles that of Pantylus, its putative sister taxon (see Chapter 3), that has been proposed to possess herbivorous or molluscivorous tendencies (Romer 1969). The marginal teeth of NSM 017GF020.002, on the other hand, exhibit simplicity with their conical shape and relatively obtuse apex. However, there is a clear size heterodonty, highlighted by the greatly enlarged anterior teeth on both the dentary and maxilla. This morphology in
marginal dentition bears similarities to those observed in extant squamates and crocodylians.

The distinct dentition observed in NSM 017GF020.002 strongly suggests the possibility of it being an herbivorous individual. Aside from the occluding palatal-coronoid apparatus, the robust build of the skull and mandible and the large adductor chambers all seem to be suitable for an herbivorous diet. However, inferring the dietary habits of extinct taxa can present challenges, particularly when modern analogues do not exist, as is the case here. In recent decades, methods in dental topographic analysis have developed to allow quantitative examination of the relationship between diet and dental morphology. One such method is the Orientation Patch Count (OPC).

OPC was originally developed as a quantitative tool to measure landscape complexity in Geographic Information System (GIS) software using a raster-based approach (Jernvall and Selänne 1999; Evans et al. 2007). It, and its modified version, OPC Rotated (OPCR), were later employed in the complexity analysis of dental surfaces and were effective in detecting relationships between diet and dental morphology in major taxonomic groups, including extant carnivorans, rodents (Evans et al. 2007), chiropterans (Santana et al. 2011), squamates (Christensen and Melstrom 2021), saurians (squamates, tuatara, and crocodylians; Melstrom 2017), and even in edentulous (tooth-less) turtles (Shipps et al. 2023). OPCR is a modified version of the original Oriented Patch Count (OPC) method (Evans and Jernvall 2009; Wilson et al. 2012), which calculates the OPC score eight times while rotating the model 5.625° at
each iteration to account for score variation due to model orientation (Evans and Janis 2014). Furthermore, the application of OPCR has been extended to extinct taxa belonging to groups such as crocodilyforms (Melstrom and Irmis 2019), equids (Evans and Janis 2014), and multituberculates (Wilson et al. 2012).

4.1.1 Dental surface complexity in different diets

In their study, Maelstrom and Irmis (2019) were able to infer the diets of extinct crocodilyform by comparing OPCR values with those of extant saurians (Figure 4.1). In living saurians, carnivorous taxa tend to have the lowest complexity indices. The dental surface complexity increases as diets shift towards insectivory, omnivory and herbivory. Insectivorous taxa have an overlapping range of OPCR values with omnivorous ones, therefore distinguishing between the two is usually difficult using OPCR value alone, but both insectivorous and omnivorous taxa have more complex dentition than carnivores. Herbivorous taxa can be distinguished from others by their high complexity values. Molluscivore individuals are special in having the highest complexity indices (Melstrom 2017), although the sample size for this category remains very small. Coupled with certain discrete morphological traits, it was possible to provide ecological reconstructions of the extinct crocodilyforms and glimpse into their possible dietary lifestyle (Melstrom and Irmis 2019).

Recognizing the promising aspect of OPCR as a tool for inferring diet on extinct taxa, here I employ this method to analyze the dentition of NSM 017GF020.002. The objective is to reveal its possible diet through comparison with an OPCR dataset encompassing extant saurians (Melstrom and Wistort 2021).
Figure 4.1 Comparison of dental complexity of extinct crocodyliforms with extant reptiles from Melstrom and Irmis (2019). A diet versus average OPCR value (OPCR_a); B, diet versus the most complex tooth OPCR value (OPCR_c). OPCR values from the living saurians are plotted in the background in grey. (Melstrom and Irmis 2019)

4.2 Methods

The tooth-bearing elements with preserved dentition, consisting of the dentary, palatine, and coronoid bones, were segmented in Dragonfly (v2022.2.0.1399) and then exported as “.ply” meshes. This turns the collection of segmented voxels (i.e., representing a bone or fragment of a bone) into a polygon mesh made of vertices, edges, and faces that define the surface geometry of the element; each face will have its own normal vector that intersects the face at a right angle and indicates the orientation of the face. OPCR uses the directions of these normal vectors to group adjacent faces with similar orientations into a patch (Melstrom 2017).

Upon export the polygon meshes, I used Meshlab (v2022.02) to apply Laplacian Smoothing at three iterations, followed by a Quadratic Edge Collapse Decimation to reduce the mesh count by 75%. I then applied basic mesh cleaning, such as removing...
duplicate faces, vertices, and non-manifold faces. This step aims to reduce the noise of manual segmentation, smooth out the effects of voxelization from CT scanning, and also reduce the mesh size to limit the operation lag of the software.

The resulting “.ply” files were imported into Blender (v3.4.1) for mesh editing. Any remaining scanning or segmentation artifacts were manually removed or corrected in Blender to reflect the true dental surface landscape as closely as possible. Occasional spikes or irregular protrusions on the mesh file (likely a result of matrix material of similar density being segmented with the tooth) were flattened using the “Draw” or “Smooth” tool in Blender’s Sculpt Mode.

To prepare for Oriented Patch Count Rotated (OPCR) analysis, I followed the procedure outlined in Melstrom and Wistort (2021). First, each individual tooth was detached from the tooth-bearing bone at the basalmost boundary of the tooth. This worked for the dentary teeth. For the palatal and coronoid dental fields, mesh polygons below the basalmost boundary of the denticles were removed. Next, I standardized the number of faces of each dentary tooth model to be 1000; for the palatal and coronoid tooth plates, I applied quadric decimation until the individual “tooth” on the dental field was around 1000 faces. Finally, I oriented the tooth or the dental fields so that the Z-axis was aligned to the apical-basal axis of the tooth.

Preservation of the teeth is not always perfect. A broken tooth would introduce an additional patch count (i.e. increase the OPCR value) due to its irregular surface. Therefore, broken dentary teeth were discarded from the analysis. On the palatal-coronoid apparatus, severely broken denticles were removed from the mesh, and less
severely broken ones were replaced by copy-and-pasting the mesh of another palatal-coronoid denticle of similar basal diameter and connecting it with the main dental field mesh. This conserves the individual tooth surfaces as well as the overall completeness of the dental fields.

The premaxilla, maxilla, vomer, and pterygoid were not included in the OPCR analysis. The premaxilla and maxilla teeth were mostly incompletely preserved or very small, seemingly immature, making them unsuitable for analysis. The vomer and pterygoid teeth are very small, resembling a shagreen of teeth, and do not seem to occlude with other teeth. The first coronoid on the left was broken into several pieces, making it difficult to repair via mesh editing, which would involve too much subjective interpretation and therefore was excluded from the analysis.

The completed dentary tooth and palatal-coronoid dental field models were then subjected to OPCR analyses using the molaR package (Pampush et al. 2016) in R Studio (R Studio Team 2020). Several options are available for performing OPCR analyses: Surfer Manipulator (Evans et al. 2007), MorphoTester (Winchester 2016), and molaR (Pampush et al. 2016). molaR was chosen here for its easy access through the CRAN (The Comprehensive R Archive Network) repository, and its batch processing ability, which does not require installing proprietary GIS software and simplifies the workflow by batch running mesh files. Melstrom and Wistort (2021) have investigated the results produced from all of the above methods and have noted that although molaR may be more sensitive to model preparation and threshold parameters, it is still possible to detect relationships between diet and dental surface
complexity. These drawbacks could be avoided by following a recommended set of guidelines, as outlined by Melstrom and Wistort (2021) we followed here. In addition, model quality can greatly affect OPCR results, as noise and scanning artifacts can contribute to a higher patch count. It is thus necessary to ensure the mesh is created from high resolution scans, and proper preprocessing (i.e., mesh smoothing, polygon count standardization) is applied prior to analysis.

I calculated the OPCR values of the models using three and five minimum mesh count thresholds. This is recommended to evaluate the effect of threshold change (Melstrom and Wistort 2021). A two-sample t-test was conducted to see if the OPCR values generated by the two threshold counts (three vs. five) are significantly different from each other. The mean OPCR values of left and right dentary dentition were then compared with those in a dataset of extant saurian taxa (Melstrom and Wistort 2021) in an attempt to resolve the dietary category of NSM 017GF020.002. This was deemed an appropriate comparison as NSM 017GF020.002 has relatively simple marginal dentition resembling living saurians (i.e., crocodylians, squamates). Raw OPCR outputs cannot be directly compared due to the method’s sensitivity to model preparation and threshold setting; therefore, I could only compare my results with data that were calculated using 1000 face standardization and a minimum three and five minimum mesh count thresholds. A one sample t-test was performed to test whether the average marginal tooth OPCR value of NSM 017GF020.002 is similar (non-significant) or different (significant) to the mean OPCR value of each diet category in Melstrom and Wistort (2021).
All OPCR analyses, statistical analyses, and plot generation were performed in R Studio (R Studio Team 2020).

4.3 Results

The resulting OPCR values of the dentary teeth of NSM 017GF020.002 are given in Table 4.1. There are 15 and 12 valid (i.e., mature, non-broken) teeth on the left and right dentary, respectively, see Figure 4.2 for a summary of the patch assignment on each tooth. The mean OPCR values, combining the left and right teeth, are 9.18 for the 3-patch analysis, and 8.48 for the 5 patch analysis. A quick two-sample t-test shows the mean OPCR values calculated using 3-patch and 5-patch thresholds are significantly different (p < 0.001)

![Figure 4.2 Dentary and the oriented patches for each valid tooth: A, left dentary; B. right dentary.](image)

The resulting OPCR values of the palatal-coronoid dental fields are given in Table 4.2. In the 3-patch analysis, the OPCR for the left and right palatine is 877.9 and 1172.6, respectively. The OPCR value for anterior coronoid on the right is 220. The OPCR value for posterior coronoid is 548.8 on the left and 545.1 on the right. In the 5-patch analysis, the OPCR for the left and right palatine is 706.6 and 880.5, respectively. The
OPCR value for anterior coronoid on the right is 180.9. The OPCR value for posterior coronoid is 400.9 on the left and 405.0 on the right.

Table 4.1 OPCR values for the left and right dentary teeth, using the same tooth models but different minimum patch count thresholds, i.e., 3 versus 5.

<table>
<thead>
<tr>
<th>Tooth position</th>
<th>Min. patch = 3</th>
<th>Min. patch = 5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OPCR - Left</td>
<td>OPCR - Right</td>
</tr>
<tr>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>10.12</td>
<td>9.88</td>
</tr>
<tr>
<td>3</td>
<td>10.88</td>
<td>9</td>
</tr>
<tr>
<td>4</td>
<td>9.5</td>
<td>8.62</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>9.12</td>
<td>8.38</td>
</tr>
<tr>
<td>7</td>
<td>9.75</td>
<td>8.38</td>
</tr>
<tr>
<td>8</td>
<td>10</td>
<td>9.25</td>
</tr>
<tr>
<td>9</td>
<td>8.75</td>
<td>8.75</td>
</tr>
<tr>
<td>10</td>
<td>8.62</td>
<td>8.38</td>
</tr>
<tr>
<td>11</td>
<td>10.25</td>
<td>10</td>
</tr>
<tr>
<td>12</td>
<td>8.75</td>
<td>8.62</td>
</tr>
<tr>
<td>13</td>
<td>8.38</td>
<td>8.75</td>
</tr>
<tr>
<td>14</td>
<td>-</td>
<td>9.38</td>
</tr>
<tr>
<td>15</td>
<td>9.25</td>
<td>-</td>
</tr>
<tr>
<td>16</td>
<td>8.62</td>
<td>-</td>
</tr>
<tr>
<td>17</td>
<td>8.62</td>
<td>-</td>
</tr>
<tr>
<td>Mean</td>
<td>9.37</td>
<td>8.95</td>
</tr>
<tr>
<td>Mean (L&amp;R)</td>
<td>9.18</td>
<td>8.48</td>
</tr>
</tbody>
</table>

The raw OPCR values obtained from the palatal-coronoid dental fields are limited in that they cannot be compared directly with living saurian taxa because most do not possess palatal teeth. If they do, only sparsely arranged teeth are present in a few rows or discrete patches (Mahler and Kearney 2006). However, in order to attempt a comparison of OPCR values for the palatal-coronoid teeth with those of the diet categories presented in Melstrom and Wistort (2021), I divided the patch count by the number of visible teeth on each dental plate. The resulting OPCR/tooth values are
summarized in Table 4.2. Additionally, the coloured patch orientation assignment of all dental fields is shown in Figure 4.3.

Table 4.2 OPCR values and OPCR/tooth for palatine and coronoids, using the same tooth plate models but different minimum patch count thresholds

<table>
<thead>
<tr>
<th>Bone type</th>
<th>“Tooth” count</th>
<th>Min. patch = 3</th>
<th>Min. patch = 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palatine (L)</td>
<td>81</td>
<td>877.9</td>
<td>706.6</td>
</tr>
<tr>
<td>Palatine (R)</td>
<td>89</td>
<td>1172.6</td>
<td>880.5</td>
</tr>
<tr>
<td>Anterior</td>
<td>23</td>
<td>220</td>
<td>180.9</td>
</tr>
<tr>
<td>Coronoid (R)</td>
<td>39</td>
<td>548.4</td>
<td>400.9</td>
</tr>
<tr>
<td>Coronoid (L)</td>
<td>36</td>
<td>545.1</td>
<td>405.0</td>
</tr>
</tbody>
</table>

Table 4.3 One-sample t-test results comparing the average dentary tooth OPCR values with the OPCR values in each diet category from Melstrom and Wistort 2021, by minimum mesh count threshold.

<table>
<thead>
<tr>
<th>Diet Category in MW2021</th>
<th>3-patch (p-value)</th>
<th>5-patch (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carnivore (n=12)</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td>Herbivore (n=18)</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Omnivore (n=23)</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Insectivore (n=17)</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Molluscivore (n=2)</td>
<td>0.455</td>
<td>0.441</td>
</tr>
</tbody>
</table>

The results of the comparison of the average dentary tooth OPCR values with the living saurian dataset (Melstrom and Wistort 2021), using one sample t-tests for each category, are summarized in Table 4.3 and visualized in Figure 4.4. The mean OPCR value from NSM 017GF020.002 is different from all dietary categories, except for molluscivore. However, due to the extremely small sample size of the molluscivore subset (n=2) and the wide range ([11.7, 44.9] in 3-patch versus [10.0, 24.8] in 5-patch), the insignificant p values may be the result of not enough evidence to reject the null hypothesis (i.e., $H_0$: sample mean does not differ from 9.18 (3-patch) or 8.48
(5-patch). Thus this result needs to be interpreted with caution given the sample size and data range of molluscivore in Melstrom and Wistort (2021).

Figure 4.3 Palatal-coronoid dental fields coloured by their respective oriented patches (min. patch = 5). A, left palatine; B, right palatine; C, right anterior coronoid; D, left posterior coronoid; E, right posterior coronoid. Colours indicate the orientation bin each patch identified on each tooth is assigned to. Discarded patches are coloured in black. Scale bar equals to 5mm.
Figure 4.4 Plotting the average marginal teeth OPCR value of NSM 017GF020.002 with extant saurian data from Melstrom and Wistort (2021), calculated using molaR with individual tooth standardized to 1000 triangles and a minimum patch count of: A, three and, B, five. The red dash line indicates the OPCR average of NSM 017GF020.002 from left and right marginal teeth: 9.18 (3-patch, 1000 polygon mesh) and 8.48 (5-patch, 1000 polygon mesh).
4.4 Discussion

4.4.1 Interpreting the diet of NSM 017GF020.002 from OPCR

The dentary teeth of NSM 017GF020.002 have a simple conical but blunt shape, with some variation in size but overall the same shape along the tooth row. Therefore, it is unsurprising that the OPCR values are close to the baseline eight patches of a perfectly conical tooth (Melstrom and Wistort 2021), reflecting simple teeth typical to taxa with a carnivorous or insectivorous diet (e.g., in living iguanids; Hotton 1955). The enlarged anterior dentary teeth in positions two and three had, in general, OPCR values on the higher end. In the maxillary tooth row, there are at least two missing enlarged anterior teeth, evidenced by the expanded alveoli. They possibly functioned with the enlarged teeth on the dentary to contribute to grasping food, according to modern analogue with similar dentition (Hotton 1955).

The simple shape and low OPCR values obtained from the remaining dentary teeth failed to result in a prediction of diet based on similarity with modern saurian values (Table 4.3, Figure 4.4). The average OPCR values obtained from NSM 017GF020.002 were found to be significantly different from the carnivore, herbivore, insectivore, and omnivore diet categories, thus can not be confidently associated with these diet categories. Interestingly, no significant difference was found between the dentary OPCR values and the molluscivore category. However, it is important to exercise caution when interpreting this outcome, since the Melstrom and Wistort (2021) data only had two entries in the molluscivore category. This limited sampling
does not offer strong support for interpreting the diet of NSM 017GF020.002 as molluscivore.

Figure 4.5 Enlarged posterolateral view of the occluding left palatal-coronoid dental apparatus, showing the enlarged teeth from both dental fields. Blue - palatine, lavender - posterior coronoid.

Moreover, food processing behaviour (hence dietary inference) of NSM 017GF020.002 must be considered in conjunction with the palatal apparatus, which is seen in many early tetrapods with little to no modern analogue. The OPCR values of the palatal-coronoid apparatus dentition reflect the high number of teeth on each dental field. However, when normalized by the tooth count, each tooth is found to have average values between 9.56–15.14 (for 3-patch) and 7.86–11.25 patches (5-patch). Variation in the OPCR/tooth count likely stems from the slightly varying shape and size of the teeth, and additional patches attributed to the troughs between the teeth. The larger and more bulbous teeth are lined along the lateral margin of the palatal and coronoid plates, whereas the smaller teeth with a smooth pyramidal shape pack the remainder of the dental surface. At the medial end of posterior coronoid,
there is a greatly enlarged tooth, at least twice as high as the other coronoid teeth, that occludes and possibly shears with a slightly enlarged tooth on the palatal plate (see Figure 4.5).

It is evident that the diet of NSM 017GF020.002 requires a large processing surface, consisting of pointed to slightly bulbous palatal/coronoid teeth. Together with strong muscles that would occupy the large adductor chamber/fossae, these features point to an herbivorous diet.

4.4.2 Dental wear and OPCR results

During manual segmentation of the specimen, it was noted that the right palatine seems to have higher dental wear than the left. Many palatal teeth on the right tooth plate did not have the distinct “teeth-like” apexes, making the segmentation more challenging, which probably reflected the higher OPCR/tooth values on the right side.

4.4.3 Comparison with other pantylids, recumbirostrans, ‘microsaurs’, and other early tetrapods

The extensive palatal-coronoid apparatus is unique to Pantylidae within the Recumbirostra clade, seen in *Pantylus*, *Stegotretus*, *Sparodus*, and now NSM 017GF020.002 (but see Chapter 2 for a detailed discussion on the different configurations on the palatal and coronoidal dental fields). *Trachystegos* (Carroll 1966) might be another potential pantyliid given its bulbous marginal teeth and palatal tooth plate. The CT-scan of *Trachystegos* (BM(NH) R.4563) is expected to be available soon, which will provide valuable information for testing its phylogenetic
position and comparative dental complexity analysis. If more CT-scans could be acquired, it would be immensely helpful to compare the quantified complexity of the palatal-coronoid apparatus across the group Pantylidae (*Pantylus*, NSM 017GF020.002, *Stegotretus*, *Sparodus*, and potentially, *Trachystegos*), for they all have extensive palatal-coronoid dentition but differ in many ways. However, one challenge is standardizing the raw OPCR values across taxa, and how this can be effectively done requires further sensitivity analysis.

A more modest palatal dental apparatus is present in some other recumbirostrans and ‘microsaurs’. For example, *Steenerpeton* (previously *Asaphesteira*), *Crinodon*, *Rhynchonkos* (previously *Goniorhynchus*), *Micraroter*, *Pelodosotis*, and *Leiocephalikon* all have some teeth on the palatine and ectoterygoid, but these teeth are either in loose patches or formed a single row. None have reached the intensity that resembles those seen in pantylids, except for one taxon, *Leiocephalikon*, which is also found at Joggins, where fragmentary specimens of *Trachystegos* come from (see Chapter 2 discussion). *Tuditanus* and *Hapsidopareion* have higher counts of palatal teeth mostly on the pterygoid and parasphenoid, but their small size might make it more appropriate to be call them denticles rather than teeth (definition of dentine followed that of Lombard and Bolt 2003: tooth-like protrusion with no more than 20% of the average maximal basal diameter and/or height of adjacent marginal teeth).

Other inferred herbivorous lineages have also developed extensive palatal apparatus and occluding tooth plate on the lower jaw, such as *Edaphosaurus* (Modesto 1995),
Labidosaurikos (Modesto and Dodick 1995), Captorhinikos (Modesto et al. 2014), which, in their arrangement, seem superficially similar to the apparatus of pantylids, i.e. palatal teeth comparable size with marginal, tooth plate covering an extensive area of the palate, occluding tooth plate of similar extent on the mandible, etc.

Palatal dentition is not uncommon in early sarcopterygians and tetrapods, in fact, there is astounding morphological diversity in the palatal dentition (Warren and Davey 1992; Matsumoto and Evans 2017), differing in tooth size, tooth arrangement, bone proportion participating in the palatal dentition, etc. Matsumoto and Evans (2017) provided a thorough review of the evolution of palatal dentition across a large phylogenetic scale. On the other hand, the coronoid dentition, which in NSM 017GF020.002 occludes with the palatal dentition extensively, should probably receive a similar review, as they certainly seem to have functional significance. The tooth bearing coronoid bones are lost rapidly when heading into the reptile lineages, going from the three coronoid bones with teeth in primitive tetrapods to a single coronoid bone forming the coronoid process in later reptiles (Romer 1976). Moreover, the difference in palatal tooth pattern could also signify a difference in soft tissue arrangement. Matsumoto and Evans (2017) proposed that an extensive palatal dentition might be associated with a dexterous and maybe strong, muscular tongue, working in unison to process food items. In NSM 017GF020.002, the occlusion of palatal and coronoid teeth plates left little room for a tongue, and probably limited its role in food manipulation to simply pushing food to the left or right.
Based on the highly iconic dental morphology of NSM 017GF020.002, we can confidently infer that it actively engaged in herbivory, and this inference could likely be extended to Pantylidae in general and other tentative species in the group. Thus, pantylid NSM 017GF020.002, along with some other members of the family, bear important implications, providing additional evidence to document the origin of herbivory in tetrapods, as previously postulated to be in the Late Carboniferous from fossil evidence and modelling (Sues and Reisz 1998; Brocklehurst et al. 2020). The variation in the palatal-coronoid apparatus configurations (see Chapter 2 discussion) of pantylids also indicates diversification of herbivores within this highly specialized family, as early as the Late Carboniferous.

There is great potential for using OPCR comparatively on a wide range of taxa, especially on extinct taxa where direct observation of behaviour is impossible. In combination with other techniques such as stable isotope analysis and 3D finite element modelling, it is possible to reconstruct robust diet inferences that are supported by multiple lines of evidence. For NSM 017GF020.002, the specimen is lined up for stable isotope analysis by the Maddin Lab which allows reconstruction of dietary habits by using a small fraction of the fossil tooth sample; a 3D reconstruction is partially completed (Chapter 2), which serves as a starting point of, if desired, finite element modelling to investigate potential biomechanical advantage of the skull during food processing.
4.5 References


Chapter 5 Conclusion and future directions

5.1 Conclusions

This thesis aimed to investigate the recently discovered taxon NSM 017GF020.002 utilizing tomography data. The primary goals were to determine its affinity with the well-established yet phylogenetically controversial family Pantylidae through phylogenetic analysis, and explore dietary implications based on quantified dental complexity methods.

Chapter 2 presented a comprehensive description of NSM 017GF020.002 based on μCT data. This newly discovered specimen expands the tetrapod assemblage from Point Aconi within the Sydney Mines Formation in Cape Breton Islands, Nova Scotia. Careful segmentation of the tomography data was undertaken to isolate distinct elements, followed by three-dimensional virtual reconstruction to approximate the skull morphology before post-mortem damage. Specimen NSM 017GF020.002 was revealed to have a roughly triangular, stoutly built skull, ornamented with pit and ridges. The layout of the dermatocranium roofing bones and the lower jaw bones matches closely to that of Pantylus cordatus. In addition, the most interesting feature was the palatal apparatus, which consists of extensive dental fields on both the palate and the coronoids, suggesting an herbivorous or durophagous diet. This unique feature has mostly been found in Pantylidae among ‘microsaurs’, though a modest version of such development can also be found in some gymnarthrid ‘microsaurs’.
Based on the palatal dentition and other similarities with Pantylus, NSM 017GF020.002 is proposed as a potential pantylid.

In chapter 3, I tested this taxonomic proposition using an updated character matrix, adapted from previous studies of recumbirostran ‘micosaur’ phylogeny. The parsimony analysis result places NSM 017GF020.002 as a sister taxon to Pantylus, and together they form the basalmost clade relative to all other recumbirostran ‘microsaurs’, and nested within reptilian amniotes. This placement is consistent across both strict consensus and majority-rule trees, supporting NSM 017GF020.002 as the newest addition to the family Pantylidae. Furthermore, a series of unique features distinguishing NSM 017GF020.002 from Pantylus support the erection of a new taxon, thereby enriching the diversity of this small family. While the internal placement of NSM 017GF020.002 among recumbirostran ‘microsaurs’ is established, relationships within Recumbirostra remain fluid, yielding several most parsimonious topologies located in distinct optimal islands in tree space during the heuristic searches. Additionally, alternate, independently developed character matrices have led to disputes regarding the Recumbirostra clade and its status as reptilian amniote, proposing some ‘microsaurs’ within lepospondyl as stem-amniotes. These divergent hypotheses underscore the necessity for further research and collaborative efforts to achieve a consensus on the evolution of early limbed vertebrates.

Chapter 4 employed the Oriented Patch Count Rotated method to analyze NSM 017GF020.002’s dentition - a technique designed to quantify dental surface complexity and has been shown effective in revealing dietary habits in extant and
extinct taxa. However, the analysis returned inconclusive results solely based on marginal dentition, likely due to the simplistic shape of these teeth. The study suggests that investigating NSM 017GF020.002’s diet requires examination beyond marginal dentition. The extensive palatal dental apparatus likely plays a pivotal role in food processing and offers more informative insights. Unfortunately, the absence of modern analogue for such palatal dentition hinders quantitative comparative analysis. While palatal dentition displays high occurrence and diversity in early tetrapods, no comprehensive comparative quantitative analysis has been undertaken. This remains a window for future exploration.

5.2 Future directions

Recent sampling efforts (e.g., Gee et al. 2021) using CT tomography have notably improved our understanding of new ‘microsaurs’ and the internal anatomy of some existing specimens, adding valuable new data to improve the phylogeny of ‘microsaurs’ and relationships among early tetrapods. However, some historical ‘microsaur’ groups (non-recumbirostran) are still less represented (e.g., ‘tuditanids’). It has been repeatedly shown that CT-scans could yield drastically different morphological details from historical reconstructions based on traditional methods (e.g., Szostakiwskyj et al. 2015; Gee et al. 2021). Therefore, it is pivotal nowadays, given the computing ability of PC hardware and accessibility of CT-scanning facilities, to compose paleontological description based on CT-data to supplement of traditional
methods, such that we can avoid misinterpretation and limit subjective speculation as much as possible.

There is much work to be done to resolve the relationship among 'microsaurs', and more importantly, reach consensus across the different streams of matrices. Matrices that have been developed over a long time may be riddled with potential glitches that could lead to different analytical results. Examples include, but are not limited to: biased taxon or biased character sampling, redundant characters, correlating characters (i.e., ontogeny, convergence), misscoring. Even methods of analysis (i.e., Bayesian inference versus maximum parsimony) or software used (TNT versus PAUP) may lead to different topologies. A detailed account of the possible sources of errors are elaborated in Marjanovic and Laurin (2019).

In conclusion, this study confirms the addition of a new pantylid, highlighting the value of combining tomography data and virtual construction methods to facilitate taxon description. This approach proves invaluable in reconstructing natural bone outlines and their assemblage, which is particularly beneficial when specimens are fragmented due to post-mortem damage. The discovery of NSM 017GF020.002 add yet another solid evidence anchoring the origin of herbivory in the Late Carboniferous, not long after terrestrialization of tetrapods.

### 5.3 References


Appendix A Unidentifiable elements from NSM 017GF020.002

This appendix supplements to Chapter 2 and documents some of the segmented elements that were not able to be identified. Many smaller fragments were in the matrix but are not listed here, for there are no unique feature that could help identify those elements. All scales bars equal to 1mm in the following figures.

Figure A.1 Various views (A-E) of an unidentifiable element with complex shape at the posterior end of the skull, at the same level as the lower jaw. It is suspected to be an otic element, but I could confidently identify. The outline show here is highly interpretive due to the porous interior and the ambiguous outline in the original scan. Letters in panel A indicate the viewing angle of the following panels.
Figure A.2 Various views (A-D) of an unidentifiable element in mid-skull, at the same level as the lower jaw. It is suspected to be an otolith similar to that of *Captorhinus leticeps*, but no further information was able to assist identification. This element has a slightly concaved disk shape, with a trough running in the middle. Letters in panel A indicate the viewing angle of the following panels.
Figure A.3 Various views (A-D) of an unidentifiable element found in the right posterior end, at the same level as the lower jaw. It has a very interesting articulating surface, almost looking like a knob with two flattened heads for articulation. I suspect this is one of the phalanges, by comparing with similar element in *Pantylus*. Letters in panel A indicate the viewing angle of the following panels.

Figure A.4 Various views (A-C) of an unidentifiable element found in the left adductor fossa. It is a long thin plate, with a raised edge at one end. It was suspected to be part of the dentary, surangular, or fallen above from the tabular, however, it could not be fitted to any of those bones. Letters in panel A indicate the viewing angle of the following panels.
Figure A.5 Various views (A-D) of an unidentifiable element found in the left adductor fossa, at the posterior end of the coronoid. It is suspected to be the peak of the coronoid process, but couldn’t fit with any surrounding bones, i.e. coronoid, surangular, dentary. Letters in panel A indicate the viewing angle of the following panels.
Figure A.6 Various views (A-D) of an unidentifiable element found at the posterior end of the jaw, slightly above the lower jaw. It is probably part of a rod like structure that is flattened in one of the transverse axes. One of the ends is expanding into an oval cross section where as the other end becomes relatively flattened. Letters in panel A indicate the viewing angle of the following panels.
### Appendix B Character matrix scoring using matrix from Mann et al. 2023

HPSA: Huttenlocker, Pardo, Small, and Anderson (2013)
MA: Maddin & Anderson (2012)
CABF: Clack, Ahlberg, Blom, and Finney (2012)
N: Neurocranial character by Pardo et al. 2017
C: Composite character by Pardo et al. 2017

1. Basal Skull Length (HPSA 001): (0) >70mm; (1) 50-70mm; (2) 30-50mm; (3) <30mm.
2. Skull:trunk ratio (HPSA 002): (0) 0.45; (1) 0.30-0.45; (2) 0.20-0.29; (3) 0.20.
   [Code as “?”]
3. Skull proportions (HPSA 003): (0) longer than wide; (1) wider than long.
4. Intertemporal (C 01): (0) present; (1) Replaced by anterior extension of supratemporal or tabular;
5. Supratemporal (HPSA 005): (0) present; (1) absent.
6. Supratemporal exposure on occiput (HPSA 006): (0) absent; (1) present. [Code as “-”]
7. Postfrontal shape (HPSA 009): (0) broadly quadrangular; (1) falciform.
8. Squamosal-Tabular contact (HPSA 010): (0) absent; (1) present; (2) fused.
9. Lacrimal-prefrontal suture (HPSA 012): (0) simple butt joint; (1) interdigitating; (2) prefrontal broadly underplates lacrimal
10. Lacrimal (HPSA 013): (0) present; (1) absent.
11. Lacrimal extends to naris (HPSA 014): (0) present; (1) absent.
12. Lacrimal extends to orbit (HPSA 015): (0) absent; (1) present.
13. Lacrimal orbital processes (HPSA 016): (0) only ventral present; (1) dorsal and ventral present; (2) neither present
14. Lacrimal-jugal contact (HPSA 017): (0) present; (1) absent.
15. Quadratojugal (HPSA 018): (0) present; (1) absent.
16. Quadratojugal-Jugal contact (HPSA 019): (0) present; (1) absent.
17. Quadratojugal-Maxillary contact (HPSA 020): (0) present; (1) absent.
18. Frontals (HPSA 021): (0) paired; (1) fused.
19. Frontal into orbital margin (HPSA 022): (0) no; (1) yes.
20. Anterior laterally flaring frontals (HPSA 023): (0) absent; (1) present.
21. Nasals (HPSA 024): (0) present; (1) absent.
22. Narial flange (HPSA 025): (0) absent; (1) present.
23. Alary processes of premaxilla (HPSA 026): (0) absent; (1) present. [Code as “?”]
24. Septomaxilla (HPSA 028): (0) ossified; (1) unossified. [Code as “?”]
25. Prefrontal into external narial margin (HPSA 029): (0) distant from; (1) near; (2) present.
26. External naris in dorsal view (HPSA 030): (0) exposed; (1) not exposed.
27. External naris shape (HPSA 031): (0) circular; (1) posteriorly extended, along lacrimal-prefrontal suture; (2) posteriorly extended excavation of lacrimal only. [Code as “?”]
28. Dorsal exposure of premaxilla (HPSA 032): (0) broad pars dorsalis anteromedial to external naris; (1) pars dorsalis limited, but nasopremaxillary suture exposed dorsally (2) none. [Code as “?”]
29. Dorsal shape of skull (HPSA 033): (0) triangular; (1) diamond; (2) rounded.
30. Posterior skull margin (HPSA 034): (0) concave; (1) straight; (2) convex; (3) undulating.
31. Snout shape (HPSA 035): (0) blunt; (1) pointed.
32. Snout length (HPSA 036): (0) less than ¼ total skull length; (1) greater than ¼ total skull length
33. Quadrato articulates along internal flange of squamosal (HPSA 037): (0) absent; (1) present.
34. Otic/spiracular notch (HPSA 038): (0) present; (1) absent.
35. Large otic notch approaching orbit (HPSA 039): (0) more than ½ postorbital length of skull; (1) between ¼ and ½ postorbital length of skull; (2) less than ¼ postorbital length of skull. [Code as “-”]
36. Otic notch structure (HPSA 040): (0) open posteriorly; (1) closed posteriorly. [Code as “-”]
37. Semilunar flange of supratemporal (HPSA 041): (0) absent; (1) present.
38. Supratympanic flange (HPSA 042): (0) absent; (1) present
39. Supratympanic shelf (HPSA 043): (0) absent; (1) present.
40. Raised orbital rim (HPSA 044): (0) absent; (1) present;
41. Postorbital (HPSA 045): (0) present; (1) absent.
42. Jugal-postorbital interfingered processes (HPSA 046): (0) absent; (1) present.
43. Postorbital participates in orbital margin (HPSA 047): (0) present; (1) absent.
44. Shape of postorbital (HPSA 048): (0) irregular trapezoid; (1) triangular, apex caudal.
45. Palpebral ossifications (HPSA 049): (0) absent; (1) mosaic of bony plates in orbit (new state); (2) Single large plate above orbit (new state).
46. Parietal-tabular contact (HPSA 052): (0) absent; (1) present.
47. Postparietals (HPSA 053): (0) paired; (1) fused; (2) absent.
48. Parietal foramen (HPSA 054): (0) present; (1) absent.
49. Postparietal size (HPSA 055): (0) much smaller than parietals; (1) approximately as large or larger than parietals.
50. Postparietal squamosal contact (HPSA 056): (0) absent; (1) present.
51. Postparietal length (HPSA 057): (0) large, quadrangular; (1) abbreviated anteroposteriorly, elongate lateral rectangle.
52. Squamosal-jugal contact (HPSA 058): (0) present; (1) absent.
53. Tabular (HPSA 059): (0) present; (1) absent.
54. Posterolateral projection from lateral margin of tabular above squamosal embayment (HPSA 060): (0) absent; (1) present. [Code as “-”, no squamosal embayment]
55. Tabular horns (HPSA 061): (0) absent; (1) present.
56. Tabular horns shape (HPSA 062): (0) parallel or slightly divergent; (1) widely divergent. **[Code as "-"]**
57. Squamosal forms base of tabular horn (HPSA 063): (0) absent; (1) present. **[Code as "-"]**
58. Lateral line canal grooves (HPSA 064): (0) present; (1) absent.
59. Dermal sculpturing (HPSA 065): (0) circular pits; (1) shallow ridges and grooves; (2) little to none; (3) tuberculate.
60. Premaxilla anterior margin (HPSA 066): (0) vertical; (1) overturned.
61. Maxilla into external naris (HPSA 068): (0) present; (1) absent.
62. Maxilla entire ventral naris (HPSA 069): (0) absent; (1) present.
63. Maxilla (HPSA 070): (0) longer than palatine; (1) shorter than palatine.
64. Marginal teeth orientation (HPSA 071): (0) vertical; (1) turned medially.
65. Marginal teeth largest anterior (HPSA 072): (0) absent; (1) present.
66. Marginal teeth shape (HPSA 073): (0) pointed pegs; (1) blunt pegs; (2) large cones.
67. Number of premax teeth (HPSA 074): (0) 10-20; (1) 5-9; (2) <5; (3) 20 or more.
68. Number of max teeth (HPSA 075): (0) 30-40; (1) 20-29; (2) 15-19; (3) <15; (4) >40.
69. Teeth laterally compressed (HPSA 076): (0) no; (1) yes.
70. Enlarged teeth mid toothrow (maxillary) (HPSA 077): (0) absent; (1) present. [See note on 68]
71. Teeth (HPSA 078): (0) simple points; (1) multiple cusps.
72. Multiple cusp orientation (HPSA 079): (0) Labio-lingual; (1) antero-posterior. **[Code as "-"]**
73. Enamel fluting (HPSA 080): (0) absent; (1) present.
74. Labyrinthine infolding (HPSA 081): (0) present; (1) absent.
75. Jaw articulation (HPSA 087): (0) posterior to occiput; (1) even with occiput; (2) anterior to occiput; (3) far anterior (>20% basal skull length).
76. Internal nares (HPSA 088): (0) widely separated; (1) narrowly separated.
77. Lateral exposure of the palatine (LEP) (HPSA 091): (0) absent; (1) present.
78. Anterior palatine (HPSA 092): (0) short anteromedial process articulating with vomer at choana; (1) long anteromedial process more medial than lateral; (2) palatine absent.
79. Teeth on pterygoid (HPSA 098): (0) absent; (1) present.
80. Tooth pedicely (HPSA 099): (0) absent; (1) present.
81. Palatal teeth size (HPSA 103): (0) larger than marginal teeth; (1) equal to marginal; (2) smaller than marginal.
82. Paraphaenoid (HPSA 104): (0) medial of stapes; (1) under footplate of stapes. **[Code as "?"]**
83. Interpterygoid vacuities (HPSA 115): (0) narrow or closed; (1) wide; (2) fused at midline.
84. Anterior extent of pterygoids (C 02): (0) Pterygoids contact anteriorly; (1) Pterygoids exclude vomer from interpterygoid vacuity but excluded from
median contact by parabasaloid; (2) pterygoids contact vomer but do not exclude vomer from interpterygoid vacuity; (3) pterygoids reach anteriorly only as far as palatine; (4) pterygoids reach ectopterygoid only; (5) pterygoids do not contact lateral palatal bones at all. Note: This character serves as a replacement for HPSA 116, 118, and 119.

85. Lateral process of pterygoid into posttemporal fossa (HPSA 120): (0) absent; (1) present. [there is no ptf]

86. Ectopterygoid palatine width (HPSA 122): (0) wider than maxilla; (1) narrower than maxilla.

87. Pharyngeobranchial pouches (HPSA 123): (0) absent; (1) present.

88. Dentary (HPSA 124): (0) tooth row greater than 50% of total jaw length; (1) tooth row less than 50% of total jaw length.

89. Dentary forms coronoid process (HPSA 125): (0) absent; (1) present.

90. Surangular (HPSA 126): (0) subequal in size to angular; (1) substantially smaller than angular (2) absent.

91. Angular (HPSA 127): (0) approximately as deep as the dentary mid-tooth-row, or less; (1) deeper than dentary mid-toothrow.

92. Number of splenials (HPSA 128): (0) 2; (1) 1; (2) 0.

93. Splenial exposed laterally (HPSA 129): (0) present; (1) absent.

94. Meckelian fossae (HPSA 130): (0) 2 or more; (1) 1; (2) 0.

95. Ventral border of Meckel's fossa (HPSA 131): (0) splenial; (1) angular.

96. Retroarticular process presence (HPSA 132): (0) absent; (1) present.

97. Retroarticular process shape (HPSA 133): (0) straight; (1) hooked.

98. Vertical position of jaw articulation relative to tooth row (HPSA 134): (0) above; (1) equal; (2) below.

99. Extent of angular in lateral view (HPSA 135): (0) posterior tooth row; (1) middle of tooth row.

100. Number of coronoids (HPSA 136): (0) 3; (1) 2; (2) 1; (3) 0.

101. Splenial participates in symphysis (HPSA 139): (0) yes; (1) no.

102. Symphysis: (0) dentary and splenial; (1) dentary alone.

103. Jaw sculpture (HPSA 140): (0) present; (1) absent.

104. Ossified hyoids (HPSA 141): (0) present; (1) absent. [Code as “?”]

105. Gill osteoderms (HPSA 142): (0) absent; (1) present noninterdigitating; (2) toothed interdigitating rakers.

106. Parahyoid (HPSA 143): (0) absent; (1) present. [Code as “?”]

107. Number of accessory articulations (HPSA 144): (0) 0; (1) 1; (2) 2 or more. [Code as “?”]

108. Number of presacrals (HPSA 145): (0) 25-35; (1) 20-24; (2) >35; (3) <20. [Code as “?”]

109. Vertebral development (HPSA 146): (0) arches then centra; (1) centra and arches simultaneously. [Code as “?”]

110. Caudal processes between depressions (HPSA 147): (0) absent; (1) present. [Code as “?”]

111. Trunk intercentra (HPSA 148): (0) present; (1) absent. [Code as “?”]
111. Trunk neural arch to centrum in adults (HPSA 149): (0) loosely articulated; (1) sutured; (2) fused. [Code as “?”]
112. Base of neural spine (HPSA 150): (0) equal to or wider than haemal; (1) smaller than haemal spine. [Code as “?”]
113. Height of neural spines (HPSA 151): (0) even; (1) alternating. [Code as “?”]
114. Dermal armor associated with neural arches (HPSA 152): (0) Absent; (1) Present [Code as “?”]
115. Neural spine shape in lateral view (HPSA 153): (0) anterior and posterior sides parallel, forming a rectangular surface; (1) non-parallel, triangular [Code as “?”]
116. Neural spine lateral surface (HPSA 154): (0) smooth; (1) crenulated. [Code as “?”]
117. Pleurocentra (HPSA 155): (0) paired rhachitomous; (1) closely approaching ventrally; (2) fused dominant weight bearing element; (3) embolomerous (new state). [Code as “?”]
118. Haemal arch presence (HPSA 156): (0) present; (1) absent. [Code as “?”]
119. Haemal arch fusion (HPSA 157): (0) loosely articulated to intercentra; (1) fused to mid length of centrum. [Code as “?”]
120. Haemal arch length (HPSA 158): (0) longer than or equal to neurals; (1) shorter than neurals. [Code as “?”]
121. Haemal accessory articulations (HPSA 159): (0) none; (1) one; (2) two. [Code as “?”]
122. Haemal arch shape (HPSA 160): (0) non parallel triangular; (1) parallel rectangular. [Code as “?”]
123. Tail termination in skeleton (HPSA 161): (0) tapers; (1) deep with sudden end. [Code as “?”]
124. Tail length (HPSA 162): (0) elongate equal to or exceeding trunk and skull length; (1) foreshortened markedly shorter than trunk. [Code as “?”]
125. Trunk arches (HPSA 163): (0) paired; (1) fused. [Code as “?”]
126. Spinal nerve foramina (HPSA 164): (0) absent; (1) present. [Code as “?”]
127. Extended transverse processes (HPSA 165): (0) absent; (1) present. [Code as “?”]
128. Transverse process (HPSA 166): (0) on arch pedicle; (1) on centrum. [Code as “?”]
129. Atlas axis intercentra (HPSA 167): (0) present; (1) absent. [Code as “?”]
130. Atlas Anterior centrum (HPSA 168): (0) same size as posterior; (1) laterally expanded. [Code as “?”]
131. Atlas centrum (HPSA 169): (0) multipartite; (1) single notochordal; (2) single odontoid. [Code as “?”]
132. Atlas neural arch centrum fusion (HPSA 170): (0) loosely articulated; (1) sutured to centrum; (2) fused to centrum. [Code as “?”]
133. Atlas parapophyses (HPSA 171): (0) on centrum; (1) on transverse process; (2) absent. [Code as “?”]
134. Atlas neural arch midline fusion (HPSA 172): (0) paired; (1) sutured at midline; (2) fused at midline. [Code as “?”]
135. Atlas accessory articulation (HPSA 173): (0) absent; (1) zygosphene; (2) zygantra. [Code as “?”]
136. Proatlantes (HPSA 174): (0) present; (1) absent. [Code as “?”]
137. Second cervical arch (HPSA 175): (0) more expanded to subsequent; (1) equal to subsequent; (2) shorter than subsequent. [Code as “?”]
138. Atlas ribs (HPSA 176): (0) one pair; (1) two pairs; (2) absent. [Code as “?”]
139. Cervical rib distal shape (HPSA 177): (0) spatulate; (1) pointed. [Code as “?”]
140. Ribs anterior to sacrum (HPSA 178): (0) short; (1) long. [Code as “?”]
141. Ribs (HPSA 179): (0) elongated and sometimes curved; (1) straight; (2) short simple rod. [Code as “?”]
142. Costal process at rib head (HPSA 180): (0) absent; (1) present. [Code as “?”]
143. Number of sacrals (HPSA 181): (0) 1; (1) 2; (2) 3. [Code as “?”]
144. Sacral parapophysis (HPSA 182): (0) on centrum; (1) on transverse process. [Code as “?”]
145. Number pairs of caudal ribs (HPSA 183): (0) 5 or more; (1) 4; (2) 3; (3) 2 or fewer. [Code as “?”]
146. Interclavicle posterior stem length (HPSA 184): (0) no or short; (1) long. [Code as “?”]
147. Interclavicle posterior stem breadth (HPSA 185): (0) wide; (1) narrow. [Code as “?”]
148. Interclavicle shape (HPSA 186): (0) diamond shaped; (1) T-shaped. [Code as “?”]
149. Interclavicle anterior plate (HPSA 187): (0) broad; (1) narrow. [Code as “?”]
150. Interclavicle shape (if diamond present) (HPSA 188): (0) broad diamond; (1) narrow diamond. [Code as “?”]
151. Interclavicle anterior fimbriation (HPSA 189): (0) present; (1) absent. [Code as “?”]
152. Interclavicle sculpture (HPSA 190): (0) present; (1) absent. [Code as “?”]
153. Cleithrum head dorsal extent (HPSA 191): (0) aligned along anterior rim of scapula; (1) posterodorsally enlarged head wrapping around dorsal scapula. [Code as “?”]
154. Cleithrum head size and shape (HPSA 192): (0) dorsally greatly expanded much wider than shaft; (1) simple rod without or slight dorsal expansion. [Code as “?”]
155. Cleithrum ossification (HPSA 193): (0) ossified; (1) unossified. [Code as “?”]
156. Cleithrum overall shape (HPSA 194): (0) rounded or pointed dorsally; (1) T or Y shaped. [Code as “?”]
157. Proximal clavicle blades (HPSA 195): (0) widely separate; (1) articulate medially; (2) interdigitate. [Code as “?”]
158. Supraglenoid foramen (HPSA 196): (0) present; (1) absent. [Code as “?”]
159. Number coracoid foramina (HPSA 197): (0) none; (1) 1; (2) 2. [Code as “?”]
160. Scapulocoracoid ossification (HPSA 198): (0) both; (1) scapula only; (2) absent. [Code as “?”]
161. Torsion in humerus (HPSA 200): (0) absent; (1) less than 80 degrees; (2) more
than 80 degrees. [Code as “?”]
162. Deltapectoral crest (HPSA 201): (0) weak or absent; (1) intermediate; (2) prominent. [Code as “?”]
163. Supinator process (HPSA 202): (0) absent; (1) present. [Code as “?”]
164. Humerus length (HPSA 203): (0) long (~4 trunk centra); (1) short. [Code as “?”]
165. Radius-humerus ratio (HPSA 204): (0) > 0.7; (1) 0.5 - 0.7; (2) < 0.5. [Code as “?”]
166. Olecranon process (HPSA 205): (0) unossified; (1) ossified. [Code as “?”]
167. Carpals (HPSA 206): (0) fully or partially ossified; (1) unossified. [Code as “?”]
168. Basale commune (HPSA 207): (0) absent; (1) present. [Code as “?”]
169. Number digits manus (HPSA 208): (0) 5; (1) 4; (2) 3; (3) >5. 170. Pelvis (HPSA 209): (0) fused; (1) sutured; (2) poorly ossified. [Code as “?”]
171. Anteriorly inclined ilium (HPSA 210): (0) absent; (1) present. [Code as “?”]
172. Iliac blade (HPSA 211): (0) 2 dorsal processes; (1) narrowly bifurcate; (2) single
blade. [Code as “?”]
173. Internal trochanter articulation (HPSA 212): (0) distinct; (1) continuous. [Code as “?”]
174. Femoral shaft (HPSA 213): (0) robust; (1) slender. [Code as “?”]
175. Femur (HPSA 214): (0) long; (1) short. [Code as “?”]
176. Tarsals (HPSA 215): (0) ossified; (1) unossified. [Code as “?”]
177. Elongate tibiale and fibulare (HPSA 216): (0) absent; (1) present. [Code as “?”]
178. Number of distal tarsals (HPSA 217): (0) 6; (1) 5 or fewer. [Code as “?”]
179. Astragalus (HPSA 218): (0) absent; (1) present. [Code as “?”]
180. Number of digits pes (HPSA 219): (0) 5; (1) 4 or less; (2) >5. [Code as “?”]
181. Dorsal margin of splenial only contacts first coronoid (HPSA 220): (0) absent; (1)
present.
182. Postparietal lappet (HPSA 224): (0) mostly exposed posteriorly; (1) equal
posteriorly and dorsally; (2) mostly exposed dorsally. [Code as “?”]
183. Cheek emargination (HPSA 225): (0) absent; (1) present.
184. Parietal anterior waisting (HPSA 226): (0) absent; (1) present.
185. Parietal width relative to frontal (HPSA 227): (0) greater; (1) equal or less.
186. Trabecula cranii (N 01): (0) Without significant median fusion posterior to solum
nasi (platytrabic); (1) fused medially posterior to solum nasi to form elongate
trabecula communis (tropitrabic). [Code as “?”]
187. Dorsal trabeculae (N 02): (0) dorsal trabeculae provide dorsolateral bridge
between sphenoid region and nasal capsule; (1) dorsal trabeculae absent or
incomplete, no dorsolateral bridge between sphenoid region and nasal
capsule. [Code as “?”; Same as above]
188. Ossification between optic foramen and pila antotica (N 03): (0) ossification
complete between optic foramen and pila antotica; (1) pila metoptica and
associated cartilaginous taenia unossified. [Code as “?”]
189. Ossification within columella ethmoidalis (N 04): (0) absent; (1) present. [Code as “?”; JP char]
190. Path of profundus branch of trigeminal nerve (N 05): (0) enclosed in lateral wall of sphenoid region of braincase and exits separately from maxillomandibular branch via series of small foramina; (1) extramural, exits antotic fissure with other branches of trigeminal. [Code as “?”]
191. Foramina for optic nerve and trigeminal nerve (N 06): (0) confluent; (1) widely separate. [Code as “?”]
192. Lateral head vein (N 07): (0) No distinct foramen for lateral head vein; (1) Distinct foramen within the antotic fissure serving the lateral head vein. [Code as “?”]
193. Anterior extent of cultriform process of parasphenoid (N 08): (0) cultriform process extends to anterior margin of sphenethmoid; (1) cultriform process extends far anterior to sphenethmoid; (2) cultriform process does not reach anterior margin of sphenethmoid.
194. Olfactory bulbs (N 09): (0) narrow; (1) endocasts swollen, leaving considerable impressions in lateral and ventral wall of sphenoid region and in ventral surface of frontal.
195. Flange from skull roof articulating with sphenethmoid (modified from HPSA 223): (0) absent; (1) present on frontal and parietal; (2) present on frontal only.
196. Descending lamina of parietal invades medial orbital wall between 'pleurosphenoid' and 'sphenethmoid' elements (N 10): (0) no; (1) yes.
197. Foramen for oculomotor nerve (N 11): (0) exits braincase far dorsal to foramen for optic nerve; (1) exits braincase at or below optic nerve. [Code as “?”]
198. Intermaxillary fossa (modified from HPSA 095): (0) present; (1) absent.
199. Intermaxillary fossa (N 12): (0) paired; (1) unpaired. [Code as “-”]
200. Sphenethmoid forms interorbital septum (N 13): (0) no; (1) yes.
201. Anterior extent of cultriform process along palate (N 14): (0) cultriform process extends anteriorly to level of posterior margin of choana; (1) cultriform process dramatically shortened, barely reaching the level of the posterior margin of the orbit.
202. Sutural contact between cultriform process of parasphenoid and vomer (N 15): (0) no; (1) yes.
203. Lateral wall of the nasal capsule underplated by lateral processes of the vomer and palatine (N 16): (0) no; (1) yes. [Code as “?”]
204. Cultriform process vaulted high above palatal surface (N 17): (0) no; (1) yes.
205. Posterior extent of parasphenoid beneath braincase (N 18): (0) floors sphenoid region only; (1) floors sphenoid and otic region; (2) floors sphenoid, otic, and occipital regions. [Code as “?”]
206. Basal tubera (N 19): (0) present, with significant endochondral contribution; (1) present, with contribution of parasphenoid only; (2) absent
207. Path of common internal carotid artery (N 20): (0) does not run alongside braincase, enters braincase directly in region of sella turcica; (1) follows vidian sulcus along posterior surface of basal plate of parasphenoid, enters parasphenoid via vidian canal in basal plate of parasphenoid, divides into
cerebral and palatal branches after entering parasphenoid; (2) follows vidian sulcus along posterior surface of basal plate of parasphenoid or lateral wall of braincase, divides into cerebral and palatal branches prior to entering the skull [Code as “?”]

208. Buccohypophyseal foramen in parasphenoid (N 21): (0) open; (1) absent.

209. Morphology of pila antotica (N 22): (0) pila antotica is a thin, broad sheet; (1) pila antotica is a robust dorsoventral pillar bracing the skull roof against the palate. [Code as “?”]

210. Basicranial fissure (N 23): (0) present; (1) absent.

211. Location of vidian sulcus (N 24): (0) along ventral surface of braincase; (1) along lateral surface of braincase. [Code as “?”]

212. Basipterygoid joint (N 25): (0) epipterygoid comprises entire conus recessus; (1) substantial contribution to conus recessus by pterygoid; (2) conus recessus comprised entirely of pterygoid without epipterygoid participation; (3) pterygoid and parasphenoid broadly sutured without development of a conus recessus.

213. Hypophyseal fossa (N 26): (0) single unpaired sulcus; (1) paired sulci divided medially by ridge originating on dorsum sellae.

214. Bone flanking the dorsum sellae (N 27): (0) concurrent with fully ossified lateral braincase; (1) subparallel with sagittal plane ('pleurosphenoid'); (2) strongly oblique to or perpendicular to sagittal plane ('laterosphenoid'); (3) restricted to dorsum sellae only. [Code as “?”]

215. Basal plate of parasphenoid (HPSA 105): (0) roughly quadrangular, basipterygoid articulations narrowly spaced; (1) rectangular laterally, anteroposteriorly narrow, basipterygoid articulations distant.

216. Sphenethmoid (HPSA 114): (0) ossified; (1) unossified.

217. Ossification within the synotic tectum (N 28): (0) synotic tectum massively co-ossified with otic capsules; (1) supraoccipital paired at some point in ontogeny; (2) supraoccipital unpaired throughout ontogeny; (3) no supraoccipital bone; synotic tectum invaded by dorsal processes of exoccipitals. [? char cartilage, state 1 cuz paired]

218. Median ascending process of supraoccipital (N 29): (0) absent; (1) present.

219. Lateral ascending processes of the supraoccipital (N 30): (0) absent; (1) present.

220. Margin of fenestra vestibuli (N 31): (0) parasphenoid excluded by neurocranial elements (basisphenoid and basioccipital); (1) parasphenoid contributes to anteroventral margin of fenestra vestibuli; (2) parasphenoid floors entire fenestra vestibuli; (3) Ossification of otic capsule surrounds entire fenestra vestibuli. [Code as “?”]

221. Crista intervestibularis (N 32): (0) crista intervestibularis absent; (1) crista intervestibularis present. [Code as “?”]

222. Morphology of crista parotica (N 33): (0) crista parotica meets exoccipitals only, forming lateral wall of posttemporal fossa but not bracing against dermal skull; (1) crista parotica drawn out dorsolaterally into paroccipital process that
contacts the tabular; (2) crista parotica drawn out laterally into paroccipital process that contacts the cheek and/or suspensorium. [Code as “?”]

223. Dorsal process of stapes (HPSA 111): (0) absent; (1) present. [Code as “?”]

224. Facets on dorsal surface of supraoccipital (N 34): (0) absent; (1) present. [Code as “?”]

225. Otoccipital fissure (N 35): (0) present; (1) absent. [Parietooccipital fissure?; not preserved, fissure between otic capsule and occiput;] [Code as “?”]

226. Crista parotica (N 36): (0) Descends posteriorly; (1) Horizontal along the extent of its length. [Code as “?”]

227. Position of quadrate with respect to otic capsules (modified from HPSA 82): (0) quadrates ventral and lateral to otic capsules; (1) quadrates mostly lateral to and greater or equal to twice the width of the otic capsules; (2) quadrates ventral to otic capsules; (3) quadrates approaching or abutting lateral wall of otic capsules. [Code as “?”]

228. Size of otic capsules (N 37): (0) otic capsules comprise less than 2/3 the width of otoccipital region; (1) otic capsules comprise greater than 2/3 total width of otoccipital region. [Code as “?”]

229. Otic trough (N 38): (0) absent; (1) present. [Code as “?”]

230. Articulation between the epipterygoid and prootic (N 39): (0) none; (1) elongate facet on anterior surface of prootic for articulation of epipterygoid.

231. Opisthotic obscures occipital in lateral view (N 40): (0) no; (1) yes [Code as “?”]

232. Fenestra vestibularis at end of broad, winglike lateral extension of the otic capsule (N 41): (0) no; (1) yes. [Code as “?”]

233. Cristae in otoccipital region (N 42): (0) comprised primarily of ascending flanges from braincase; (1) comprised primarily of descending flanges from skull roof [Code as “?”]

234. Opisthotic excluded from the occipital surface by tabular process of the exoccipital (N 43): (0) no; (1) yes. [Code as “?”]

235. Insertion of epaxial musculature on occiput (N 44): (0) deep within post-temporal fossae; (1) in broad, shallow fossae along occipital surface of postparietals. [Code as “?”]

236. Foramen for internal jugular vein (N 45): (0) between supraoccipital and exoccipital; (1) between opisthotic and exoccipital; (2) through exoccipital; (3) Posterior notch of fenestra vestibule. [Code as “?”]

237. Foramina for hypoglossal nerve (N 46): (0) multiple; (1) single; (2) none. [Code as “?”]

238. Occipital condyle shape (modified from HPSA 085): (0) round; (1) U-shaped; (2) paired. [Code as “?”]

239. Ventral process of exoccipital reaches basipterygoid joint along palatal surface (N 47): (0) absent; (1) present. [Code as “?”]

240. Occipital condyle shape (HPSA 084): (0) Concave; (1) Convex. [Code as “?”]

241. Columella of stapes (modified from HPSA 108): (0) perforate; (1) imperforate. [Code as “?”]
242. Orientation of stapes (modified from HPSA 109): (0) Dorsal, towards tabular or otic notch; (1) anteroventral, towards quadrate. [Code as “?”]
243. Stapedial footplate shape (HPSA 110): (0) oval; (1) round; (2) palmate. [Code as “?”]
244. Dorsal sinus between [ossified] synotic tectum [(supraoccipital)] and skull roof (modified from HPSA 222): (0) absent; (1) present.
245. Ossification within septum internasale (N 48): (0) absent; (1) present, sphenethmoid; (2) present, mesethmoid.
246. Ossification of septum internasale invades nasal tectum (N 49): (0) absent; (1) present. [Code as “?”]
247. Insertion of hypaxial musculature (N 50): (0) sphenoid; (1) otic; (2) basioccipital. [Code as “?”]
248. Prootic supported by pedicel extending from basisphenoid lateral to prootic foramen (N 51): (0) no; (1) yes. [Code as “?”]
249. Position of pineal foramen with respect to hypophyseal foramen (N 52): (0) anterior to; (1) approximately the same; (2) far posterior to. [Code as “?”]
250. Pineal foramen or fossa (N 53): (0) well anterior to posterior margin of cerebral fossa; (1) at or behind posterior margin of cerebral fossa. [Code as “?”]
251. Median wall of otic capsule (N 54): (0) completely unossified; (1) ossification of opisthotic; (2) ossification of supraoccipital and basioccipital. [Code as “?”]
252. Conical recess in basioccipital (N 55): (0) absent; (1) present. [Code as “?”]
253. Semicircular canals (N 56): (0) separated from utricular region by bone; (1) not separated from utricular region by bone. [Code as “?”]
254. Basioccipital (N 57): (0) Robust ossification ventral to foramen magnum present; (1) absent.
255. Accessory articulation processes with proatlantal facet on exoccipitals (N 58): (0) absent; (1) prominent. [Code as “?”]
256. Exoccipital proatlantal facets incorporated into occipital joint (N 59): (0) no; (1) yes. [Code as “?”]
257. Anterior tectal (modified from CABF 001): (0) anterior tectal present; (1) absent.
258. Ectopterygoid/palatine exposure (CABF 002): (0) more or less confined to tooth row; (1) broad medial exposure additional to tooth row; (2) reduced to thin sliver.
259. Ectopterygoid: (0) Present; (1) Absent.
260. Ectopterygoid as long or longer than palatines (CABF 003): (0) yes; (1) no. [Code as “-”]
261. Ectopterygoid reaches subtemporal fossa (CABF 004): (0) no; (1) yes. [Code as “-”]
262. Frontal (CABF 005): (0) absent; (1) present.
263. Jugal (CABF 007): (0) does not extend anterior to orbit; (1) extends anterior to orbit.
264. Lateral rostral present (CABF 009): (0) yes; (1) no.
265. Maxilla makes interdigitating suture with vomer (CABF 010): (0) no; (1) yes.
266. Maxilla external contact with premaxilla (CABF 011): (0) narrow contact point, not interdigitated; (1) interdigitating suture
267. Maxilla extends behind level of posterior margin of orbit (CABF 012): (0) yes; (1) no.
268. Median rostral (CABF 013): (0) single; (1) paired; (2) absent.
269. Opercular (CABF 014): (0) present; (1) absent.
270. Prefrontal (CABF 015): (0) twice as long as broad, or less; (1) three times as long as broad.
271. Prefrontal (CABF 016): (0) transverse anterior suture with tectal; (1) tapers to a point anteriorly. [Checked Greererpeton burkemorani (coded 0)]
272. Preopercular (CABF 017): (0) present; (1) absent.
273. Pterygoid quadrate ramus margin in subtemporal vacuity (CABF 018): (0) concave; (1) with some convex component.
274. Vomers separated by parasphenoid > half length (CABF 019): (0) yes; (1) no.
275. Vomers (CABF 022): (0) as broad as long or broader; (1) about twice as long as broad or longer.
276. Basipterygoid process (CABF 023): (0) not strongly projecting with concave anterior face; (1) strongly projecting with flat anterior face.
277. Ethmoid (CABF 024): (0) fully ossified; (1) partly or wholly unossified.
278. Hypophyseal region (CABF 025): (0) solid side wall pierced by small foramina for pituitary vein and other vessels; (1) single large foramen. [Code as “?”]
279. Lateral commissure of otic capsule bearing hyomandibular facets (CABF 026): (0) present; (1) absent. [Code as “?”]
280. Parasphenoid (CABF 027): (0) does not overlap basioccipital; (1) overlaps basioccipital.
281. Denticulate field of parasphenoid (CABF 028): (0) present; (1) absent.
282. Sphenoid (CABF 029): (0) fully ossified, terminating posteriorly in intracranial joint or fused to otoccipital; (1) separated from otoccipital by unossified gap.
283. Ectopterygoid fang pairs (CABF 030): (0) present; (1) absent. [Code as “-”]
284. Ectopterygoid row (3+) of smaller teeth (CABF 031): (0) present; (1) absent. [Code as “-”]
285. Ectopterygoid/palatine shagreen field (CABF 032): (0) absent; (1) present.
286. Palatine row of smaller teeth (CABF 034): (0) present; (1) absent.
287. Pterygoid shagreen (palatine ramus) (modified from CABF 035): (0) dense; (1) organized radiating rows of denticles; (2) disorganized patches or absent.
288. Dentition of transverse flange of pterygoid (new character): (0) Denticle field indistinct from palatine denticle field; (1) distinct raised denticle field; (2) organized tooth row; (3) absent.
289. Premaxillary tooth proportions (CABF 036): (0) all approximately same size; (1) posteriormost teeth at least twice height of anteriormost teeth; (2) Anteriormost teeth largest.
290. Vomerine fang pairs (CABF 037): (0) present; (1) absent.
291. Vomerine fang pairs noticeably smaller than other palatal fang pairs (CABF 038): (0) no; (1) yes. [Code as “-”]
292. Vomer anterior wall forming posterior margin of palatal fossa bears tooth row meeting at midline (CABF 039): (0) yes; (1) no.
293. Vomerine row of teeth (CABF 040): (0) present; (1) absent.
294. Vomerine shagreen field (CABF 041): (0) absent; (1) present.
295. Adductor fossa (CABF 042): (0) faces dorsally; (1) faces medially.
296. Adductor crest (CABF 043): (0) absent; (1) peak anterior to adductor fossa, dorsal margin of fossa concave; (2) peak above anterior part of adductor fossa, dorsal margin of fossa convex.
297. Angular-prearticular contact (CABF 044): (0) prearticular contacts angular edge to edge; (1) absent; (2) medial lamina of angular sutures with prearticular.
298. Coronoid (anterior) contacts splenial (CABF 045): (0) no; (1) yes.
299. Prearticular extends between infradentaries and middle coronoid (modified from CABF 046): (0) Yes; (1) No. [Code as “-”]
300. Coronoid (middle) contacts postsplenial (CABF 047): (0) no; (1) yes. [Score as “-”]
301. Coronoid (posterior) posterodorsal process (CABF 048): (0) no; (1) yes.
302. Coronoid (posterior) posterodorsal process visible in lateral view (CABF 049): (0) no; (1) yes.
303. Dentary external to angular & surangular, with chamfered ventral edge and no interdigitations (CABF 050): (0) no; (1) yes.
304. Dentary ventral edge (CABF 051): (0) smooth continuous line; (1) abruptly tapering or "stepped" margin.
305. Dentary suture with splenial & postsplenial marked by deep furrow (CABF 052): (0) no; (1) yes.
306. Mandibular sensory canal (CABF 053): (0) present; (1) absent.
307. Mandibular canal exposure (CABF 054): (0) entirely enclosed, opens through lines of pores; (1) mostly enclosed, short sections of open grooves; (2) mostly open grooves, short sections opening through pores; (3) entirely open. [Code as “-”]
308. Oral sulcus/surangular pit line of mandible (CABF 055): (0) present; (1) absent.
309. Meckelian bone floors precoronoid sulcus (CABF 056): (0) yes; (1) no.
310. Meckelian bone ossified in middle part of jaw (CABF 057): (0) yes; (1) little or no ossification.
311. Meckelian bone exposure in middle part of jaw (CABF 058): (0) depth much less than prearticular; (1) depth similar to prearticular. [Code as “-”]
312. Meckelian foramina/fenestrae, dorsal margins (CABF 059): (0) Meckelian bone; (1) prearticular; (2) infradentary
313. Meckelian foramina/fenestrae height (CABF 060): (0) much lower than adjacent prearticular; (1) equal to or greater than depth of adjacent prearticular.
314. Parasymphysial lateral foramen present (CABF 061): (0) no; (1) yes.
315. Parasymphysial mesial foramen present (CABF 062): (0) no; (1) yes.
316. Postsplenial with mesial lamina (CABF 063): (0) no; (1) small; (2) expanded, contacting precoronoid.
317. Postsplenial pit line present (CABF 064): (0) yes; (1) no.
318. Postsplenial suture with prearticular present (modified from CABF 065): (0) no; (1) yes.
319. Prearticular sutures with surangular (CABF 066): (0) no; (1) yes.
320. Medial lamina of splenial (modified from CABF 067): (0) absent; (1) present.
321. Prearticular with longitudinal ridge below coronoids (CABF 068): (0) no; (1) yes.
322. Prearticular with mesially-projecting flange on dorsal edge along posterior border of adductor fossa (CABF 069): (0) no; (1) yes.
323. Prearticular centre of radiation of striations (CABF 070): (0) level with posterior end of posterior coronoid; (1) level with middle of adductor fossa; (2) level with posterior end of adductor fossa. [Code as “?”]
324. Splenial has free ventral flange (CABF 071): (0) yes; (1) no.
325. Splenial, rearmost extension of medial lamina (CABF 072): (0) closer to anterior end of jaw than to adductor fossa; (1) equidistant; (2) closer to anterior margin of adductor fossa than to the anterior end of the jaw. [character incomplete in .nex file (w/out state 1 and 2); issue fixed]
326. Coronoids; at least one has fang pair recognizable because at least twice the height of coronoid or marginal teeth (CABF 073): (0) yes; (1) no.
327. Coronoids; at least one has fangs recognizable because noticeable lingual to vertical lamina of bone and to all other teeth (CABF 074): (0) yes; (1) no.
328. Coronoids; at least one has organized tooth row (CABF 075): (0) yes; (1) no.
329. Coronoids; at least one carries shagreen (CABF 076): (0) no; (1) yes.
330. Coronoids; size of teeth (excluding fangs) on anterior and middle coronoids relative to dentary tooth size (CABF 077): (0) about the same; (1) half the height or less.
331. Dentary tooth row (CABF 078): (0) homodont; (1) markedly heterodont.
332. Dentary with parasymphysial fangs internal to marginal tooth row (CABF 079): (0) yes; (1) no.
333. Dentary teeth (CABF 080): (0) same size as maxillary teeth; (1) larger than maxillary teeth; (2) smaller than maxillary teeth.
334. Dentary with a row of very small teeth or denticles lateral to tooth row (CABF 081): (0) yes; (1) no.
335. Parasymphysial plate tooth plate (CABF 082): (0) present; (1) absent.
336. Parasymphysial plate dentition (CABF 083): (0) shagreen or irregular tooth field; (1) organized dentition aligned parallel to jaw margin; (2) no dentition. [Code as “-”]
337. Parasymphysial plate has fang pair (CABF 084): (0) no; (1) yes. [Code as “-”]
338. Parasymphysial plate has tooth row (CABF 085): (0) no; (1) short tooth row, separated from coronoid row by diastema; (2) long tooth row reaching coronoid. [Code as “-”]
339. Prearticular shagreen field distribution (CABF 086): (0) gradually decreasing from dorsal to ventral; (1) well-defined dorsal longitudinal band; (2) scattered patches or absent.
340. Anterior palatal fenestra (CABF 087): (0) single; (1) double; (2) absent.
341. Dorsal fontanelle on snout (CABF 088): (0) absent; (1) present.
342. Interpterygoid vacuities (CABF 089): (0) absent; (1) at least 2x wider than long; (2) 2x longer than wide.
343. Intracranial joint (CABF 090): (0) present in dermal skull roof; (1) absent in dermal skull roof
344. Nature of dermal ornament (CABF 091): (0) tuberculate; (1) fairly regular pit and ridge; (2) irregular; (3) absent or almost absent
345. Nature of ornament: starbursts of radiating ornament on at least some bones (CABF 092): (0) no; (1) yes
346. Anocleithrum (CABF 093): (0) oblong with distinct anterior overlap area; (1) drop-shaped with no anterior overlap area; (2) absent. [Code as “?”]
347. Cleithrum (CABF 094): (0) ornamented; (1) not ornamented.[Code as “?”]
348. Cleithrum, postbranchial lamina (CABF 095): (0) present; (1) absent.[Code as “?”]
349. Autopod (modified from CABF 096): (0) radials; (1) digits.[Code as “?”]
350. Humerus (CABF 097): (0) narrow tapering entepicondyle; (1) square or parallelogram-shaped entepicondyle.[Code as “?”]
351. Ilium, iliac canal (CABF 098): (0) absent; (1) present.[Code as “?”]
352. Ilium, posterior process (CABF 099): (0) oriented posterodorsally; (1) oriented approximately horizontally posteriorly.[Code as “?”]
353. Interclavicle (CABF 100): (0) small and concealed or absent; (1) large and exposed.[Code as “?”]
354. Interclavicle shape (CABF 101): (0) ovoid; (1) kite shaped; (2) with posterior stem.[Code as “?”]
355. Lepidotrichia in paired appendages (CABF 102): (0) present; (1) absent.[Code as “?”]
356. Posttemporal and supracleithrum (CABF 103): (0) present; (1) absent.[Code as “?”]
357. Radius and ulna (CABF 104): (0) radius much longer than ulna; (1) approximately equal in length.[Code as “?”]
358. Ribs, trunk (CABF 107): (0) all cylindrical; (1) some or all bear flanges from posterior margin which narrow distally; (2) some or all flare distally.[Code as “?”]
359. Scapular blade (CABF 108): (0) absent; (1) small with narrow top; (2) large with broad top.[Code as “?”]
360. Scapulocoracoid (modified from CABF 109): (0) small and tripodal; (1) large plate.[Code as “?”]
361. Subscapular fossa (CABF 110): (0) broad and shallow; (1) deeply impressed posteriorly.[Code as “?”]
362. Squamation (CABF 111): (0) complete body covering of scales, all similar; (1) ventral armour of gastralvae.[Code as “?”]
363. Pectoral process (CABF112): (0) absent; (1) present.[Code as “?”]
364. Proximal limb of oblique ridge (CABF 113): (0) present, separated from anterior margin of humerus by prepectoral space; (1) absent, replaced by deltopectoral crest.[Code as “?”]
365. Latissimus dorsi attachment (CABF 114): (0) diffuse ridged area; (1) distinct process.[Code as “?”]
366. Foramina piercing oblique ventral ridge (CABF 115): (0) many; (1) one moderately large foramen in addition to entepicondylar foramen; (2) entepicondylar foramen is the only large opening, other foramina are pinpricks or absent; (3) none.[Code as “?”]
367. Humerus with well-developed anterior plate (new character): (0) yes; (1) no.[Code as “?”]
368. Subclavicular ossifications (new character): (0) Absent; (1) Sometimes present.[Code as “?”]
369. Radial capitulum (new character, modified from Sigurdsen & Green, 2011): (0) approximately same size as ulnar facet; (1) greatly enlarged and rounded, >2x size of ulnar facet.[Code as “?”]
370. Lissamphibian inner ear sensu Maddin and Anderson (2012) (MA 220): (0) no; (1) yes. [Code as “?”]
371. Enlarged cranial foramina on supraorbital region: (0) absent, (1) present.
372. Distribution of enlarged cranial foramina on supraorbital region: (0) lateral margins of frontals and postfrontal, (1) only on lateral margins of frontals, (2) lateral margins of frontals and extending onto prefrontals. [Code as “-”]
373. Transverse flange (process) of the pterygoid: (0) absent, (1) present.
374. Orientation of the transverse flange (process) of the pterygoid: (0) posterolateral orientation of the transverse flange, (1) anterolateral orientation of the transverse flange. [Code as “-”]
375. Single or paired massively enlarged crushing teeth on the palatal apparatus. Absent (0) Present (1).
376. Single or paired massively enlarged teeth on the palatal apparatus that are either restricted to the (0) coronoid only or (1) equally large teeth opposing on both the coronoid and palatine.
377. Interdentary–pectoral ossicles. Absent (0) Present (1).
Appendix C Character-taxon matrix in Nexus file format

```nexus
#NEXUS
[written Tue Aug 29 17:34:08 EDT 2023 by Mesquite  version 3.61 (build 927) at DESKTOP-QL29RAT/192.168.2.11]

BEGIN TAXA;
  TITLE Taxa;
  DIMENSIONS NTAX=70;
  TAXLABELS
    Archeria_craspidisca Crassigyrinus_scoticus Acanthostega_gunnari Eusthenopteron_Foordi
    Ichthyostega_spp. Panderichthys_Furmani Rhombolepis Pednerus_finnyae Tiktaalik_rooseveldti
    Ymeria_denticulata Proterogyrus_scheelei Balanerpeton_woodi Dendrerpeton_acadianum
    Pantylus_cordatus Cardiiceps_peabodyi Cardiiceps_sternbergii Pariotichus_brachyops 'Euryodus_dalyae (composite)'
    Euryodus_prinus Proxilodon_bonneri Huskerpeton_mckinzei Microrhynchocephalus Eocacaelia_micropagia
    Carrolla Crudaddi Quasiacaelia_texasa Listerosaurus_pricei Aletricymium_chaukii
    Dvelicus_carrolli Rhynchospongos_stevanmai Diaporosaurus_stowii
    Seymouria_baylorensis Cruciter_erythrogeios

BEGIN CHARACTERS;
  CHARSTATELABELS
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    DIMENSIONS NCHAR=377;
    TITLE 'Matrix in file "Tyrannorotermatrix-2x-Final.nex"';
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        DIMENSIONS NTAX=70;
        TAXLABELS
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          Ichthyostega_spp. Panderichthys_Furmani Rhombolepis Pednerus_finnyae Tiktaalik_rooseveldti
          Ymeria_denticulata Proterogyrus_scheelei Balanerpeton_woodi Dendrerpeton_acadianum
          Pantylus_cordatus Cardiiceps_peabodyi Cardiiceps_sternbergii Pariotichus_brachyops 'Euryodus_dalyae (composite)'
          Euryodus_prinus Proxilodon_bonneri Huskerpeton_mckinzei Microrhynchocephalus Eocacaelia_micropagia
          Carrolla Crudaddi Quasiacaelia_texasa Listerosaurus_pricei Aletricymium_chaukii
          Dvelicus_carrolli Rhynchospongos_stevanmai Diaporosaurus_stowii
          Seymouria_baylorensis Cruciter_erythrogeios
      END;
      BEGIN CHARSTATELABELS
        BEGIN TAXA;
          TITLE Taxa;
          DIMENSIONS NTAX=70;
          TAXLABELS
            Archeria_craspidisca Crassigyrinus_scoticus Acanthostega_gunnari Eusthenopteron_Foordi
            Ichthyostega_spp. Panderichthys_Furmani Rhombolepis Pednerus_finnyae Tiktaalik_rooseveldti
            Ymeria_denticulata Proterogyrus_scheelei Balanerpeton_woodi Dendrerpeton_acadianum
            Pantylus_cordatus Cardiiceps_peabodyi Cardiiceps_sternbergii Pariotichus_brachyops 'Euryodus_dalyae (composite)'
            Euryodus_prinus Proxilodon_bonneri Huskerpeton_mckinzei Microrhynchocephalus Eocacaelia_micropagia
            Carrolla Crudaddi Quasiacaelia_texasa Listerosaurus_pricei Aletricymium_chaukii
            Dvelicus_carrolli Rhynchospongos_stevanmai Diaporosaurus_stowii
            Seymouria_baylorensis Cruciter_erythrogeios
      END;
    END;
  END;

BEGIN DATA;
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  DIMENSIONS NCHAR=377;
  TITLES  'Matrix in file "Tyrannorotermatrix-2x-Final.nex"';
  TAXLABELS
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    'Ichthyostega_spp.' 'Panderichthys_Furmani' 'Rhombolepis' 'Pednerus_finnyae' 'Tiktaalik_rooseveldti'
    'Ymeria_denticulata' 'Proterogyrus_scheelei' 'Balanerpeton_woodi' 'Dendrerpeton_acadianum'
    'Pantylus_cordatus' 'Cardiiceps_peabodyi' 'Cardiiceps_sternbergii' 'Pariotichus_brachyops'
    'Euryodus_dalyae (composite)' 'Euryodus_prinus' 'Proxilodon_bonneri' 'Huskerpeton_mckinzei'
    'Microrhynchocephalus' 'Eocacaelia_micropagia' 'CarrollaCrudaddi' 'Quasiacaelia_texasa'
    'Listerosaurus_pricei' 'Aletricymium_chaukii' 'Dvelicus_carrolli' 'Rhynchospongos_stevanmai'
    'Diaporosaurus_stowii' 'Seymouria_baylorensis' 'Cruciter_erythrogeios'

  CHARACTER 
    1. Basal_skull_length / '<=70mm' '50-70mm' '30-50mm' '<=30mm';
    2. Skull_trunk / 0.45 0.30 0.45 0.20 0.29 0.20;
    3. Head_proportions / long_enough_to_square, long_enough_to_square, long_enough_to_square, long_enough_to_square, long_enough_to_square, long_enough_to_square;
    4. Intertemporal / present Replaced_by_anterior_extension_of_supratemporal_or_tabular;
    5. Supratemporal / present absent;
    6. ST_exposure_on_occiput / present absent;
    7. Frontal_shape / broad_quadrangular, falciform, squamospalatum, tabular, long_enough_to_square, Lacrimal _prefrontal_suture / simple_butt_joint, interdigitating;
    8. squamosal_tabular / present absent;
    9. Supratemporal / present absent;
    10. Squamosal_tabular / present absent;
    11. Squamosal_tabular / present absent;
    12. Squamosal_tabular / present absent;
    13. Squamosal_tabular / present absent;
    14. Squamosal_tabular / present absent;
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    65. Squamosal_tabular / present absent;
    66. Squamosal_tabular / present absent;
    67. Squamosal_tabular / present absent;
    68. Squamosal_tabular / present absent;
    69. Squamosal_tabular / present absent;
    70. Squamosal_tabular / present absent;

END;
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138
67 number_of_premax_teeth / '30-20' '5-9' '5' 20_or_more, 68 number_of_max_teeth / '30-40' '20-29' '15-19' '5-15' >40, 69 teeth_laterally_compressed / no yes, 70 enlarged_teeth_mid_toothrow / absent present, 71 teeth / simple_points multiple_cusps, 72 Multiple_Cusp_Orientation / labio-lingual 'antero-posterior', 73 enamel_fluting / absent present, 74 labrinthine_in_folding / present absent, 75 jaw_articulation / posterior_to_occiput even_with_occiput anterior_to_occiput 'far anterior (>20% BSL)', 76 internal_nares / widely_separated narrowly_separated, 77 LEP / absent present, 78 Anterior_palatine / short_antememedial_process_articulating_with_vomer_at_channa long_antememedial_process_more_medial_than_lateral_palatine_absent, 79 teeth_on_pterygoid / absent present, 80 tooth_pedically / absent present, 81 Palatal_teeth_size / larger_than_marginals equal_to_marginals smaller_than_marginals, 82 parasphenoid / medial_of_stapes_under_footplate_of_stapes, 83 interpterygoid_vacuities / narrow_close Widely_fused_at_midline 84 Anterior_extent_of_Pterygoids / Pterygoids_contact_anteriorly Pterygoids_exclude_vomer_from_interpterygoid_vacuity_only_as_far_as_palatine Pterygoids_reach_anteriorly_only_as_far_as_palatine Pterygoids_reach_ectopterygoid_only, 85 lat_process_of_pt_into_posttemp / absent present, 86 pterygoid_palatine_width / wider_than_maxilla narrower_than_maxilla, 87 pharangeal_branchial_pouches / absent present, 88 dentary / long short, 89 dentary_form_coronoid_process / absent present, 90 surangular / normal reduced absent, 91 angular / narrow deep, 92 number_of_splenial / 2 1 0, 93 splenial_exposed_laterally / present absent, 94 meckelian_fossae / 2 more 1 0, 95 ventral_border_of_meckelian_fossae / splenial_angular, 96 retroarticular_process_presence / present absent, 97 retroarticular_process_shape / straight hooked, 98 articulation_to_tooth_row / above equal below, 99 angular_extends_to_lat_view / posterior_tooth_row middle_of_tooth_row, 100 number_of_coronoids / 3 2 1 0, 101 symphysis / dentary_and_splenial dentary_alone, 102 jaw_sculpture / present absent, 103 ossified_hyoids / present absent, 104 GillSTDOUTsmoth / absent present nonintertdigitating_toothed_interdigitating_rakers, 105 parahyoid / absent present, 106 number_of_accessory_articulation / 0 1 2 3, 107 number_of_presacras / 25 35 20 24 35 20, 108 vertebral_development / arches_then_centra_centra_and_arches_simultaneously, 109 caudal_processes_btw_depression / present absent, 110 trunk_intercentra / present absent, 111 trunk_neural_arch_to_centrum / loosely_articulated sutured fused, 112 base_of_neural_spine / equal_to_or_wider_than_haemal_smaller_than_haemal_spine, 113 height_of_neural_spines / even_alternating, 114 Dermal_armor_associated_with_neural_arches / absent present, 115 neural_spine_shape_lat / ant_post_sides_parallel_rect non_parallel_triangular, 116 neural_spine_lateral_surface / smooth crested, 117 Pleurocentra / paired_rhachotous closely_approaching_ventrally fused_dominant_weight_bearing_element_embryonorous, 118 haemal_arch_presence / present absent, 119 haemal_arch_fusion / loosely_articulated_intercentra_fused_to_mid_length_of_centrum, 120 haemal_arch_length / longer_than_or_equal_to_neurals shorter_than_neurals, 121 haemal_accessory_articulations / none one two, 122 haemal_arch_shape / non_parallel_triangular parallel_rectangular, 123 tail_termination / tapers deep with_sudden_end, 124 tail_length / elongate_equal_to_or_exceeding_trunk_and_skull_length shortener_markedly_shorter_than_trunk, 125 trunk_arches / paired fused, 126 spinal_nerve_formina / present absent, 127 extended_transverse_processes / present absent, 128 transverse_process / on_arch_pedicle on_centrum, 129 atlas_axis_intercentra / present absent, 130 atlas_centrum / same_size_as_posterior_laterally_expanded, 131 atlas_centrum / multipartite single_notochordal single_odontoid, 132 atlas_neural_arch_centrum_fusion / loosely_articulated_to_centrum_fused_to_centrum, 133 atlas_interparapophyses / on_centrum_on_transverse_process_fused, 134 atlas_neural_arch_midline_fusion / paired_sutured_at_midline_fused_to_midline, 135 atlas_accessory_articulation / absent present, 136 Proatlanites / present absent, 137 second_cervical_arch / expanded_to_more_posterior equal_to_more_posterior shorter_than_more_posterior, 138 anterior_ridge / one_pair_two_pairs absent, 139 cervical_rid_distal_shape / spathulate pointed, 140 ribs_anterior_toSacrum / short long, 141 ribs / elongated and sometimes_curved straight simple_rod, 142 costo_process_at_rhoid / absent present, 143 number_of_sacra / 1 2 3, 144 sacral_interparapophyses / on_centrum_on_transverse_process_fused, 145 number_pairs_of_caudal_ribs / 5 more 4 3 2 1, 146 interclavicle_posterior_stem_length / no_or_short_long, 147 interclavicle_posterior_stem_breadth / wide narrow, 148 interclavicle_shape / diamond_shaped t_shaped, 149 interclavicle_posterior_plate / broad_narrow, 150 interclavicle_shape_diamond / broad_diamond narrow_diamond, 151 interclavicle_interclavicle_fimbria / present absent, 152 interclavicle_sculpture / present absent, 153 Cleithrum_head_dorsal_extens / aligned_along_anterior_rim_of_scapula posteroanterodorsally_posteriordorsally_enlarged_head_wrapping_around_dorsal_scapula, 154 Cleithrum_head_size_and_shape / dorsi_laterally_greatly_enlarged_through_wide_than_shaft, 155 Cleithrum_ossification / ossified absent, 156 With_overall_shape / rounded_or_pointed_dorsally_t_or_y-shaped, 157 proximal_clavicle BLades / widely_separate articulate_medially_interdigitate, 158 supraglenoid_formina / present absent, 159 number_coracoid_formina / none 1 2, 160 scapulocoracoid_occurrence / both_scapula_only absent, 161 collar_of_humerus / absent less_than_80_degrees more_than_80_degrees, 162 deltasternal_crest / weak intermediate_prominent, 163 supinator_process / present absent.
Otic trough / absent present,
229
Articulation_between_the_epiptyerygoid_and_prootic / none
230
elongate_facet_on_anterior_surface_of_prootic_for_articulation_of_epiptyerygoid,
231
Osteitic_contact_with_orbital_wall_of_prootic / no yes
232
'Fenestra vestibularis at end of broad, winglike lateral extension of the otic fossa' / no yes,
233
Cristae_in_otocapital_region / comprised_principally_of_ascending_flanges_from_braincase
234
comprised_principally_of_descending_flanges_from_skull_roof;
235
Osteitic_contact_with_orbital_wall_of_prootic / no yes
236
posteriormost_teeth_at_least_twice_height_of_anteriomost_teeth Anteriormost_teeth_largest,
237
disorganized_patches_or_absent,
238
separated_from_otoccipital_by_unossified_gap,
239
approximately_the_same_far_posterior_to,
240
orientation_of_stapes / 'Dorsal, towards tabular or otic notch' 'anteroventral, towards quadrate',
241
Meckelian_bone_exposure_in_middle_part_of_jaw / depth_much_less_than_prearticular
242
Meckelian_bone_floors_precoronoid_sulcus / yes no,
243
'Oral sulcus/surangular pit line of mandible' / present absent,
244
Mandibular_canal_exposure / 'entirely enclosed, opens through lines of pores' 'postly enclosed,
245
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
246
Coronoid (posterior) contacts postsplenial / yes no
247
Coronoid (anterior) contacts splenial / no yes
248
Angular / no yes
249
Adductor_crest / absent 'peak anterior to adductor fossa, dorsal margin of fossa concave' 'peak
250
above anterior part of adductor fossa, dorsal margin of fossa convex'
251
Angular-prearticular contact / prearticular_contacts/angular_edge_to_edge absent
252
Medial_lamina_of_anterior_sutures_with_premaxilla / no yes
253
Coronoid (anterior) contacts splenial / no yes
254
Posteriormost_teeth_at_least_twice_height_of_anteriormost_teeth Anteriormost_teeth_largest,
255
Coronoid (middle) contacts postsplenial / no yes
256
Coronoid (posterior) posterosdorsal_process / no yes
257
Dentary_external_to_anterior_suture_with_splenial / no yes
258
Dorsal_sinus_between_synotic_tectum_and_skull_roof / absent present,
259
Ectopterygoid/palatine_exposure / more_or_less_confined_to_tooth_row reduced_to_thin_sliver,
260
broad_mesial_exposure/additional_to_tooth_row reduced_to_thin_sliver;
261
Ectopterygoid / Present Absent,
262
Ectopterygoid_reaches_subtemporal_fossa / no yes,
263
Frontal / absent present,
264
Jugal / does_not_extend_anterior_to_orbit extends_anterior_to_orbit,
265
Lateral_rostral / yes no,
266
Maxilla_extends_behind_level_of_posterior_margin_of_orbit / yes no,
267
Maxilla_extends_between_infradentaries_and_middle_coronoid / yes no
268
Premaxillary_tooth_proportions / all_approximately_same_size
269
Dentition_of_transverse_flange_of_pterygoid / present absent,
270
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
271
Maxilla_makes_interdigitating_suture_with_vomer / no yes,
272
Vomerine_shagreen_field / present absent,
273
Vomerine_row_of_small_teeth / present absent,
274
Vomer_anterior_wall_forming_posterior_margin_of_palatal_fossa_bears_to / no yes
275
Vomerine_fang_pairs_noticeably_smaller_than_other_palatal_fang_pairs / no yes
276
Vomerine_fang_pairs / present absent,
277
Premaxillary_tooth_proportions / all_approximately_same_size
278
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
279
Maxilla_makes_interdigitating_suture_with_vomer / no yes,
280
Maxilla_external_contact_with_premaxilla / narrow_contact_point_not_interdigitated
281
interdigitating_suture,
282
Maxilla_extends_behind_level_of_posterior_margin_of_orbit / yes no,
283
Median_rostral / single paired absent,
284
Opercular / present absent,
285
Prefrontal / twice_as_long_as_width / three_times_as_long_as_broad,
286
Preopercular / present absent,
287
Premaxilla_fang_pairs / no yes
288
Vomer / present absent,
289
Vomerine_fang_pairs / no yes
289
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
290
Preopercular / present absent,
291
Premaxilla_fang_pairs / no yes
292
Vomer / present absent,
293
Vomerine_fang_pairs / no yes
294
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
295
Preopercular / present absent,
296
Premaxilla_fang_pairs / no yes
297
Vomer / present absent,
298
Vomerine_fang_pairs / no yes
299
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
300
Preopercular / present absent,
301
Premaxilla_fang_pairs / no yes
292
Sphenoid / 'fully ossified, terminating posteriorly in intracranial joint or fused to otocapital'
separated_from_otocapital_by_unossified_gap
303
Ectopterygoid / Present Absent,
304
Ectopterygoid_reaches_subtemporal_fossa / no yes,
305
Premaxillary_tooth_proportions / all_approximately_same_size
306
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
297
Vomer / present absent,
298
Vomerine_fang_pairs / no yes
299
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
300
Preopercular / present absent,
301
Premaxilla_fang_pairs / no yes
292
Sphenoid / 'fully ossified, terminating posteriorly in intracranial joint or fused to otocapital'
separated_from_otocapital_by_unossified_gap
303
Ectopterygoid / Present Absent,
304
Ectopterygoid_reaches_subtemporal_fossa / no yes,
305
Premaxillary_tooth_proportions / all_approximately_same_size
306
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
297
Vomer / present absent,
298
Vomerine_fang_pairs / no yes
299
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
300
Preopercular / present absent,
301
Premaxilla_fang_pairs / no yes
292
Sphenoid / 'fully ossified, terminating posteriorly in intracranial joint or fused to otocapital'
separated_from_otocapital_by_unossified_gap
303
Ectopterygoid / Present Absent,
304
Ectopterygoid_reaches_subtemporal_fossa / no yes,
305
Premaxillary_tooth_proportions / all_approximately_same_size
306
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
297
Vomer / present absent,
298
Vomerine_fang_pairs / no yes
299
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
300
Preopercular / present absent,
301
Premaxilla_fang_pairs / no yes
292
Sphenoid / 'fully ossified, terminating posteriorly in intracranial joint or fused to otocapital'
separated_from_otocapital_by_unossified_gap
303
Ectopterygoid / Present Absent,
304
Ectopterygoid_reaches_subtemporal_fossa / no yes,
305
Premaxillary_tooth_proportions / all_approximately_same_size
306
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
297
Vomer / present absent,
298
Vomerine_fang_pairs / no yes
299
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
300
Preopercular / present absent,
301
Premaxilla_fang_pairs / no yes
292
Sphenoid / 'fully ossified, terminating posteriorly in intracranial joint or fused to otocapital'
separated_from_otocapital_by_unossified_gap
303
Ectopterygoid / Present Absent,
304
Ectopterygoid_reaches_subtemporal_fossa / no yes,
305
Premaxillary_tooth_proportions / all_approximately_same_size
306
Dentary_suture_with_splenial_&_postsplenial_marked_by_deep_furrow / no yes
297
Vomer / present absent,
298
Vomerine_fang_pairs / no yes
299
Frontal / 'twice as long as broad, or less' three_times_as_long_as_broad,
314 Parasymphysial, lateral foramen present / no yes,
315 Parasymphysial, mesial foramen present / no yes,
316 Postsymphysial, mesial lamina / no small, expanded, contacting precoronoid,
317 Postsymphysial, pit line present / yes no,
318 Postsymphysial, suture with prearticular present / yes no,
319 Postsymphysial, sutures with surangular present / yes no,
320 Medial lamina of splenial / absent present,
321 Prearticular, with longitudinal ridge below coronoids / no yes,
322 Prearticular, with mesially projecting flange on dorsal edge along posterior border of adductor fossa / no yes,
323 Prearticular, centre of radiations of striations / level with posterior end of coronoid level with middle of adductor fossa / level with posterior end of adductor fossa
324 Splenial, has free ventral flange / yes no
325 'Splenial, rearmost extension of medial lamina'
closer-to-anterior-end_of_jaw_than_to_adductor_fossa
326 'Coronoids: at least one has fang pair recognizable because at least twice the height of coronoid teeth' / yes no
327 'Coronoids: at least one has fangs recognizable because noticeable mesial to vertical lamina of bone and to all other teeth' / yes no
328 'Coronoids: at least one has organized tooth row' / yes no,
329 Leporidae: at healed apposition / present absent
330 'Coronoids: size of teeth (excluding fangs) on anterior and middle coronoids relative to dentary tooth size, about the same half the height of the longest tooth
331 Dentary, tooth row / homodont markedly heterodont,
332 Dentary, with parasymphysial fangs internal to marginal tooth row / no yes
333 Dentary teeth / same size as maxillary teeth larger than maxillary teeth smaller_than_maxillary_teeth
334 Dentary, with a row of very small teeth or denticles lateral_to_tooth_row / yes no,
335 Parasymphysial, plate / present absent,
336 Parasymphysial, plate dentition / shagreen or irregular tooth field
337 Organized dentition aligned parallel to jaw margin / no dentition,
338 Parasymphysial, plate has fang pair / yes no,
339 Parasymphysial, plate has tooth row / no short tooth row separated from coronoid row by diastema
340 Long tooth row reaching coronoid / yes no,
341 Prearticular, shagreen field distribution / gradually decreasing from dorsal to ventral 'well-defined dorsal longitudinal band' scattered patches or absent,
342 Prearticular, shagreen field distribution / gradually decreasing from dorsal to ventral 'well-defined dorsal longitudinal band' scattered patches or absent,
343 Prearticular, shagreen field distribution / gradually decreasing from dorsal to ventral 'well-defined dorsal longitudinal band' scattered patches or absent,
344 Prearticular, shagreen field distribution / gradually decreasing from dorsal to ventral 'well-defined dorsal longitudinal band' scattered patches or absent,
345 Prearticular, shagreen field distribution / gradually decreasing from dorsal to ventral 'well-defined dorsal longitudinal band' scattered patches or absent,
346 Prearticular, shagreen field distribution / gradually decreasing from dorsal to ventral 'well-defined dorsal longitudinal band' scattered patches or absent,
347 Cleithrum / ornamented not ornamented,
348 Cleithrum, postbranchial lamina / present absent,
349 Digits / absent present
350 Humerus / narrow tapering entepicondyle 'square or parallelogram-shaped entepicondyle',
351 'Ilium, iliac canal' / present absent,
352 'Ilium, posterior process' / oriented posterodorsally
353 'Ilium, iliac canal' / present absent,
354 'Ilium, iliac canal' / present absent,
355 'Ilium, iliac canal' / present absent,
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466 'Ilium, iliac canal' / present absent,
toggleShowBoldCellsText off;
toggleMove不限on;
toggleColorsPanel off;
toggleDiagonal on;
setDiagonalHeight 80;
toggleLinkedScrolling on;
toggleScrollLinkedTables off;
endTell;
showwindow;
getWindow;
tell It;
forceAutosize;
endTell;
getEmployee #mesquite.charMatrices.AlterData.AlterData;
tell It;
toggleBySubmenus off;
endTell;
getEmployee #mesquite.charMatrices.ColorByState.ColorByState;
tell It;
setStateLimit 9;
toggleUniformMaximum on;
endTell;
getEmployee #mesquite.charMatrices.ColorCells.ColorCells;
tell It;
setColor Red;
removeColor off;
endTell;
getEmployee #mesquite.categ.StateNamesEditor.StateNamesEditor;
tell It;
makeWindow;
tell It;
setExplanationSize 30;
setAnnotationSize 20;
setFontIncAnnot 0;
setFontIncExp 0;
setSize 1178 1240;
setLocation -3 0;
setFont SanSerif;
setFontSize 10;
getToolPalette;
tell It;
setTool

mesquite.categ.StateNamesEditor.StateNamesWindow.ibeam;
endTell;
rowsAreCharacters on;
toggleConstrainChar on;
toggleConstrainCharNum 3;
togglePanel off;
toggleSummaryPanel off;
endTell;
showwindow;
getWindow;
tell It;
togglePanel off;
endTell;
getEmployee #mesquite.categ.StateNamesStrip.StateNamesStrip;
tell It;
showStrip off;
endTell;
getEmployee #mesquite.charMatrices.AnotPanel.AnotPanel;
tell It;
togglePanel off;
endTell;
getEmployee #mesquite.charMatrices.CharReferenceStrip.CharReferenceStrip;
tell It;
showStrip off;
endTell;
getEmployee #mesquite.charMatrices.QuickKeySelector.QuickKeySelector;
tell It;
autotabOff;
endTell;
getEmployee #mesquite.categ.SmallStateNamesEditor.SmallStateNamesEditor;
tell It;
panelOpen true;
endTell;
endTell;
getEmployee #mesquite.charMatrices.ManageCharacters.ManageCharacters;
tell It;
showcharacters #6605800557590130524 #mesquite.lists.CharacterList.CharacterList;
tell It;
setData 0;
getWindow;
tell It;
useTargetValue off;
setTargetValue
newAssistant #mesquite.lists.DefaultCharOrder.DefaultCharOrder;
newAssistant #mesquite.lists.CharlistInclusion.CharlistInclusion;
newAssistant #mesquite.lists.CharlistPartition.CharlistPartition;
newAssistant
#mesquite.parsimony.CharlistParsModels.CharlistParsModels;
newAssistant #mesquite.lists.CharlistUniqueID.CharlistUniqueID;
setExplanationSize 30;
setAnnotationSize 20;
setFontIncAnnot 0;
setFontIncExp 0;
setSize 1178 1240;
setLocation -3 0;
setFont SanSerif;
setFontSize 10;
getToolPalette;
tell It;
endTell;
showwindow;
getWindow;
tell It;
getEmployee #mesquite.lists.CharlistAnnotPanel.CharlistAnnotPanel;
tell It;

togglePanel off;
endTell;
endTell;
endTell;
endTell;
end;
endTell;
endTell;
endTell;
endTell;
end;