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Redescription and phylogenetic reassessment of *Tertrema acuta* from the Early Triassic of Svalbard

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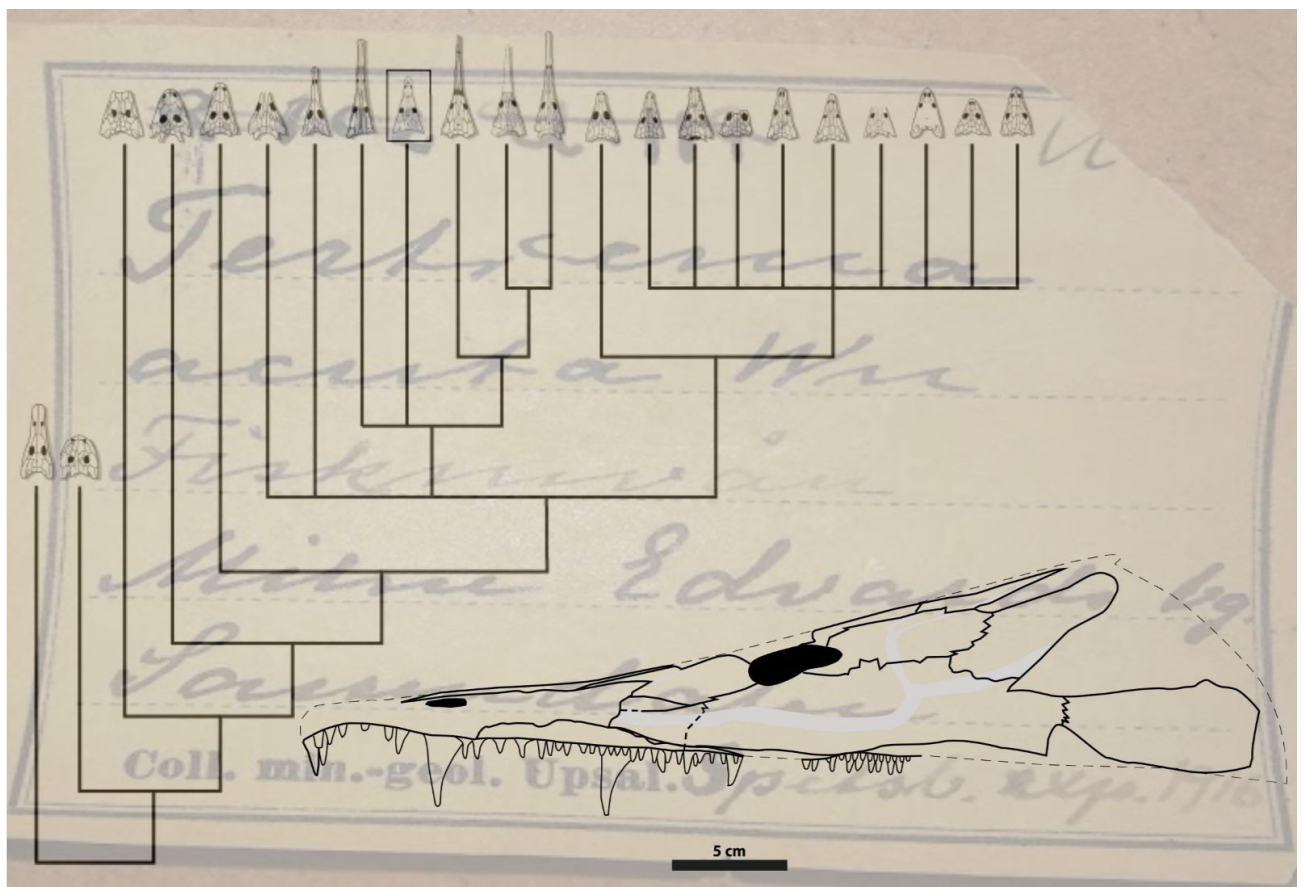
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Redescription and phylogenetic reassessment of *Tertrema acuta* from the Early Triassic of Svalbard

from

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Contents

1 Abstract

Trematosaurs represent a group of early tetrapods (Temnospondyli, Amphibia), which reached global distribution within the Early Triassic, whereas most other lineages went extinct during the Permian. Trematosaurids represent a large and diverse clade, which adapted to a fully aquatic life mode, but their palaeobiology and interspecific relationships are still not clarified. Herein, a detailed and illustrated redescription of the species *Tertrema acuta* is presented. This species is exclusively known from two specimens collected from the Olenekian of the Vikinghøgda Formation in Svalbard. Herein, skull morphology is discussed with regards to the adaptions to a fully aquatic life mode. A reassessment of the phylogenetic position of *T. acuta*, by updating a pre-existing database, causes a significant shift of its position and reveals problems of the previous analyses. Hence, we could not support the previous findings of the dichotomy of the Trematosaurids into a Lonchorhynchine monophylum and a Trematosaurinae monophylum, and suggest rather a more complex evolution.

2 Introduction

2.1 Objective

Tertrema acuta is a temnospondyl amphibian species known from two specimens of the Lower Triassic Vikinghøgda Formation in Svalbard. This material has been briefly described and illustrated by Wiman (1914, 1917) and (Säve-Söderbergh, 1937), and their work represents important research of high historical value. Nevertheless, the specimens have not received a modern anatomical description so far. The main focus of this work is to analyses the specimens with regard to their relevant morphological features in order to provide a modern and detailed description and, combined with photographic and interpretative illustrations. Furthermore, new palaeobiological implications from the skull morphology are presented and discussed.

More recently, *Tertrema acuta* was included in a series of cladistic analyses, which tested the interspecific relationships of the Trematosauridae group (Fernández-Coll et al., 2018; Fortuny et al., 2017; Steyer, 2002). These analyses were based on literature studies of the historical publications of Wiman (1914, 1917) and Säve-Söderbergh (1937), leading to misinterpretations of character states which could obscure the phylogenetic placement. Therefore, a cladistic reassessment of *Tertrema acuta* is presented herein, on the basis of first-hand anatomical observations and new character scoring.

Additionally, first-hand observations of the type material of the Australian species *Tirraturhinus smisseni* was conducted, in order to confirm or reject the hypothesis of a possible relationship to *Tertrema acuta* (Nield et al., 2006). Additionally, it is included in the updated phylogenetic analysis.

The aim of this research is to provide more information about *Tertrema acuta* for a better understanding of the palaeobiology and evolution of this diverse Triassic trematosaurid group.

2.2 Previous concepts of the phylogenetic position of *Tertrema acuta*

Temnospondyls form the largest clade of Palaeozoic and Mesozoic tetrapods, and has been studied since the beginning of the 19th century when the first findings of 'Labyrinthodont'-teeth (von Jäger, 1824, 1828) and the discovery of *Mastodonsaurus giganteus* roused the attention of palaeontologists (von Meyer and Plieninger, 1844). The first phylogenetic hypotheses were made by Watson (1919, 1926, 1940, 1958, 1962) and the first phylogenetic tree developed by Romer (1947). The first analogue phylogenetic systematics were performed by Boy (1972, 1974), Warren and Black (1985) and Milner (1988, 1990) to understand the relationship within temnospondyls accruing numerous studies about the major temnospondyl branches (see review of Schoch, 2013). Whilst temnospondyls form a robust clade, the intraspecific relationships remain topical because many phylogenetic approaches provide controversial and conflicting results.

However, a recent broad review and cladistic study by Schoch (2013) analysed the relationships of the major temnospondyl clades and their phylogenetic supports, from which a robust supertree of temnospondyls was produced (see Figure 1). Therein, the Triassic Stereospondyli form a stable monophyletic clade, as found by Milner (1990), and Yates and Warren (2000). More exclusively, the Trematosauria form a large clade which was first proposed by Warren and Black (1985), and later by Yates and Warren (2000). Within the Trematosauria, Schoch (2013) supported the clade of the Trematosauroidea, which has been found by Milner (1990), Yates and Warren (2000), Damiani and Yates (2003) and Schoch (2006, 2008), but added further groups. The Trematosauridae forms one of the most exclusive clades of the stereospondyls, and is nested within the Trematosauroidea; however, this clade, which was represented only by the taxa *Trematosaurus* and *Trematolestes*, had comparatively low statistical support in Schoch's (2013) analysis.

The intrarelationships of the Trematosauridae have been studied by many authors discussing several subdivisions. These were based on the elongation of the snout (Cosgriff and Garbutt, 1972; Säve-Söderbergh, 1935), the morphology of the palate (Hellrung, 1987), and on the elongation of the snout, the dentary, the interclavicle and the position of nostrils and choanae (Hammer, 1987; Welles, 1993). Steyer (2002) reviewed these studies, and employed only taxa which were considered taxonomically valid for the first substantial cladistic analysis of the trematosaurid group. Their results presented a subdivision which was congruent with the findings of the phenetic analysis of Hammer (1987), and the preliminary cladistic approach of Welles (1993). All three studies divide the trematosaurids into the short-snouted Trematosaurinae and the long-snouted Lonchorhynchinae. On basis of Steyer's (2002) analysis, two follow-up studies (Fernández-Coll et al., 2018; Fortuny et al., 2017) were published, which added more taxa and agreed with the dichotomy of this group. Nevertheless, Schoch (2006) found the Trematosaurinae as a paraphylum and the Lonchorhynchinae as the most derived monophylum.

The studies of Steyer (2002), Fortuny et al. (2017) and Fernández-Coll (2018) present the most inclusive trees (i.e., including the most taxa) concerning the Trematosauridae thus far, with

Tertrema acuta nested as a highly derived taxon within the Trematosaurinae. However, in the smaller phylogenetic approach of the Trematosauridae by Schoch (2006), *T. acuta* represented the sister group to a clade of (the short snouted) *Trematolestes + Tertremoides* and the Lonchorhynchinae. For the sake of completeness, *T. acuta* was also included by Damiani and Yates (2003), who presented a phylogeny of Trematosauroidea. However, *T. acuta* was shown therein merely as a highly derived taxon within the relatively unresolved Trematosauria.
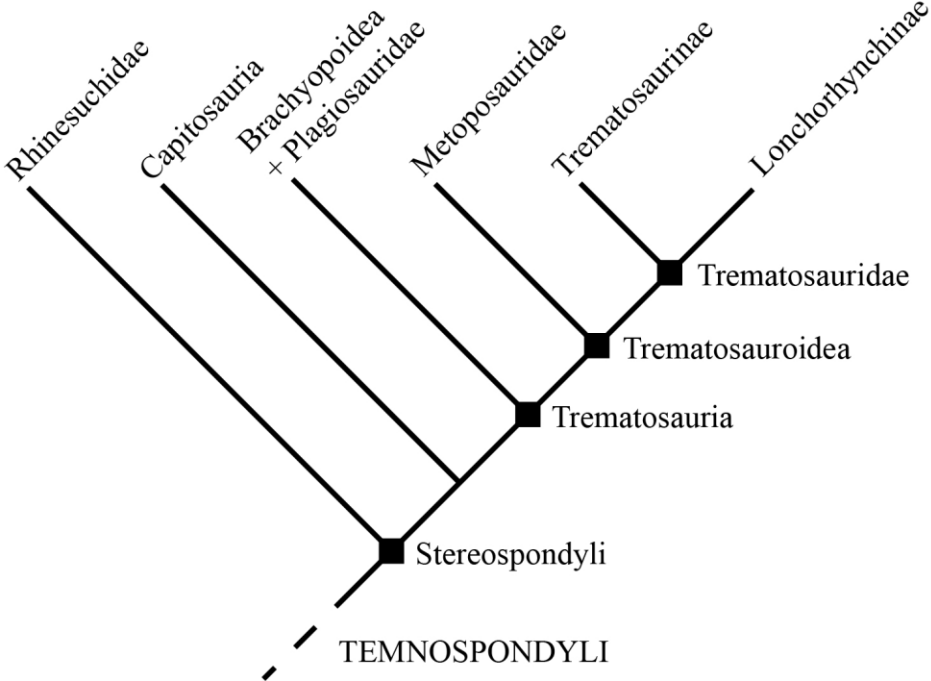

Figure 1 Schematic tree of the here relevant Temnospondyl groups simplified after the phylogenetic supertree of Schoch (2013). However, the subdivision of the Trematosauridae is not examined by Schoch (2013). The dichotomy of the Trematosauridae into Trematosaurinae and Lonchorhynchinae as in e.g. Steyer (2002) is not totally consistent as shown by Schoch (2006).

2.3 Evolutionary background of Trematosaurs

Temnospondyls represent a large and successful group of Palaeozoic and Mesozoic tetrapods alongside the amniotes (Schoch, 2013; Yates and Warren, 2000). Currently, at least 198 genera and 292 species of temnospondyls are known (Schoch, 2013). They span the entire stratigraphic record from the early Carboniferous (Visean) to the Early Cretaceous (Aptian), a duration of at least 220 Myr, with peaks of diversity in the Permian and Triassic (Milner, 1990; Schoch, 2013). During this time, the Earth's climate underwent significant climate changes (Fielding et al., 2008; Preto et al., 2010) which influenced the habitats of temnospondyls. Nevertheless, they overcame different intervals of extinction and radiation (Ruta and Benton, 2008) and changed their size, shape and feeding modes to adapt to diverse terrestrial, fluvial, littoral, coastal and marine environments (e.g. (Fortuny et al., 2011; Schoch, 2009)). Their magnificent size range, from 3–6 m long stereospondyls to miniaturised 5–10 cm long amphibamids and branchiosaurids, is just one example for their adaptability (Schoch, 2013).

Their prosperity ended during the end-Permian mass extinction (~251.9 Ma;(Burgess et al., 2014)). Whilst most lineages of temnospondyls died out during the Permian, three primarily semi-aquatic to aquatic subclades survived: The Dvinosauria and, within the clade of Stereospondyli, the Capitosauria and Trematosauria (Benton, 2014). These groups dispersed rapidly over Pangaea and showed a broad diversity in the Early Triassic (Schoch, 2013). However, the rising competition with successful amniotes (e.g., synapsids and archosaurs) in the terrestrial realm since the end-Permian event restricted the advantage of temnospondyls to aquatic habitats (Benton, 2014).

Concerning Trematosaurs, Nield et al. (2006) demonstrated that this group was already present in the Griesbachian Age (earliest Triassic), and phylogenetic analysis showed that their origin and diversification must have been much earlier, such as the late Permian (Schoch and Milner, 2000). The majority of trematosaurs are represented by secondarily-adapted aquatic species, characterised by an elongated head and slender body, and considered to be piscivorous predators (Fortuny et al., 2011). At their apex in the Early Triassic, they had a global distribution (Hammer, 1987), and are known from continental (Nield et al., 2006), deltaic (Cosgriff, 1984) and shallow marine sediments (Hammer, 1987). Their success showed an early recovery of higher trophic levels in the marine realm after the end-Permian extinction event (Scheyer et al., 2014). However, their diversity reduced significantly in the Middle Triassic, from which only the genus *Microposaurus* of South Africa and the species *Trematolestes hagdorni* of Germany are known (Schoch, 2006). So far, the only representative Temnospondyl of the Late Triassic is the trematosaur *Hyperkynodon keupernius* from Germany (Hellrung, 1987; Schoch et al., 2002). The end of the prosperity of trematosaurs and their almost complete disappearance can be roughly correlated with the emergence of marine reptiles, as ichthyosaurs and sauropterygians captured marine habitats and replaced the amphibians as more successful predators (Scheyer et al., 2014).

The Temnospondyli largely disappeared after the end-Triassic mass extinction (Benton, 2014; Schoch, 2013), except for a few examples which persisted until the Jurassic and even the Early

Cretaceous, like *Koolasuchus* from Australia, considered to be one of the last temnospondyls (Benton, 2014; Warren et al., 1997). They were probably surviving in isolated basins that were not invaded by reptiles (Benton, 2014).

Figure 2. Life reconstruction of Trematosaurus brauni*, a representative of a marine trematosaur species. Picture by Vladislav Egorov (2016).*

2.4   Localities, geology and palaeogeography

The species *Tertrema acuta* was reportedly found on two mountains: Sticky Keep, where the holotype was discovered (Wiman, 1914), and Millne Edwarsfjellet, the origin of the later found specimen (Wiman, 1917). These are located on the southern side of the Sassendalen, a giant valley in central eastern Spitzbergen, the main island of the Svalbard archipelago.

The rounded and plateau-shaped mountains in this area expose flat-lying rock beds of the Triassic, which represent uplifted parts of the extensive, but otherwise submerged, Barents Sea Shelf (Mørk, 2015). During the Early Triassic, this area was a shallow marine depositional basin in the boreal zone, which underwent a transgression during the Middle Triassic. It was surrounded by the Norwegian mainland to the south, the Canadian Arctic Islands to the northwest and Greenland to the southwest (Mørk, 2015).

The stratigraphy of the area of Central Spitzbergen is mainly composed of Lower Triassic to lower Upper Triassic marine sediments representing varying sea depths. Because of the fossil-richness, it has a long history of geological and palaeontological research, which provided complex lithostratigraphic subdivisions, summarised by Mørk et al. (1999a). Firstly, Wiman (1910, 1928) divided the strata into several discrete informal units, based on fossil contents: the lowermost is the 'Fish Level', followed by the '*Grippia* Level', which is overlain by the 'Lower Saurian Level' and 'Upper Saurian Level'. Continual re-examinations (Buchan et al., 1965; Gregory, 1921; Mørk et al., 1999a; Mørk et al., 1999b; Mørk et al., 1982; Pčelina, 1980, 1983; Späth, 1921) gave different subdivisions. However, Mørk et al. (1999a) correlates the 'Fish Level' (Wiman, 1910b) to the Lusitaniadalen Member, the lower Olenekian section of the Vikinghøgda Formation, and represents the most recent subdivision. Reportedly, both specimen of *Tertrema acuta*, presumably originating from the 'Fish Level', which is composed of dark grey oil shales(Wiman, 1914). The lower part of the Lusitaniadalen member shows the transgressive development from the towards a moderately deep shelf depositional environment (Mørk et al., 1999b). It is distal to the main clastic sediment input from the west, which is indicative of the concurrent deltaic systems exposed on western Spitzbergen (Figure 3 B) (Mørk, 2015).

Table 1 Comparison of the first nomenclature (Wiman, 1910,1928) with one of the most recent stratigraphical subdivisions (Mørk et al., 1999b) of Central eastern Spitzbergen according to Mørk (2015). Tertrema acuta *originates from the 'Fish-Level' strata.*

Epoch	Age	Wiman (1910, 1928) lithostratigraphy	Mørk et al. (1999b) lithostratigraphy	
Early Triassic	Olenekian	Unteres Saurier-Niveau	Vikinghøgda Formation	Vendomdalen Member
		Grippia-Niveau		Lusitaniadalen Member
		Fisch-Niveau		
				Deltadalen Member
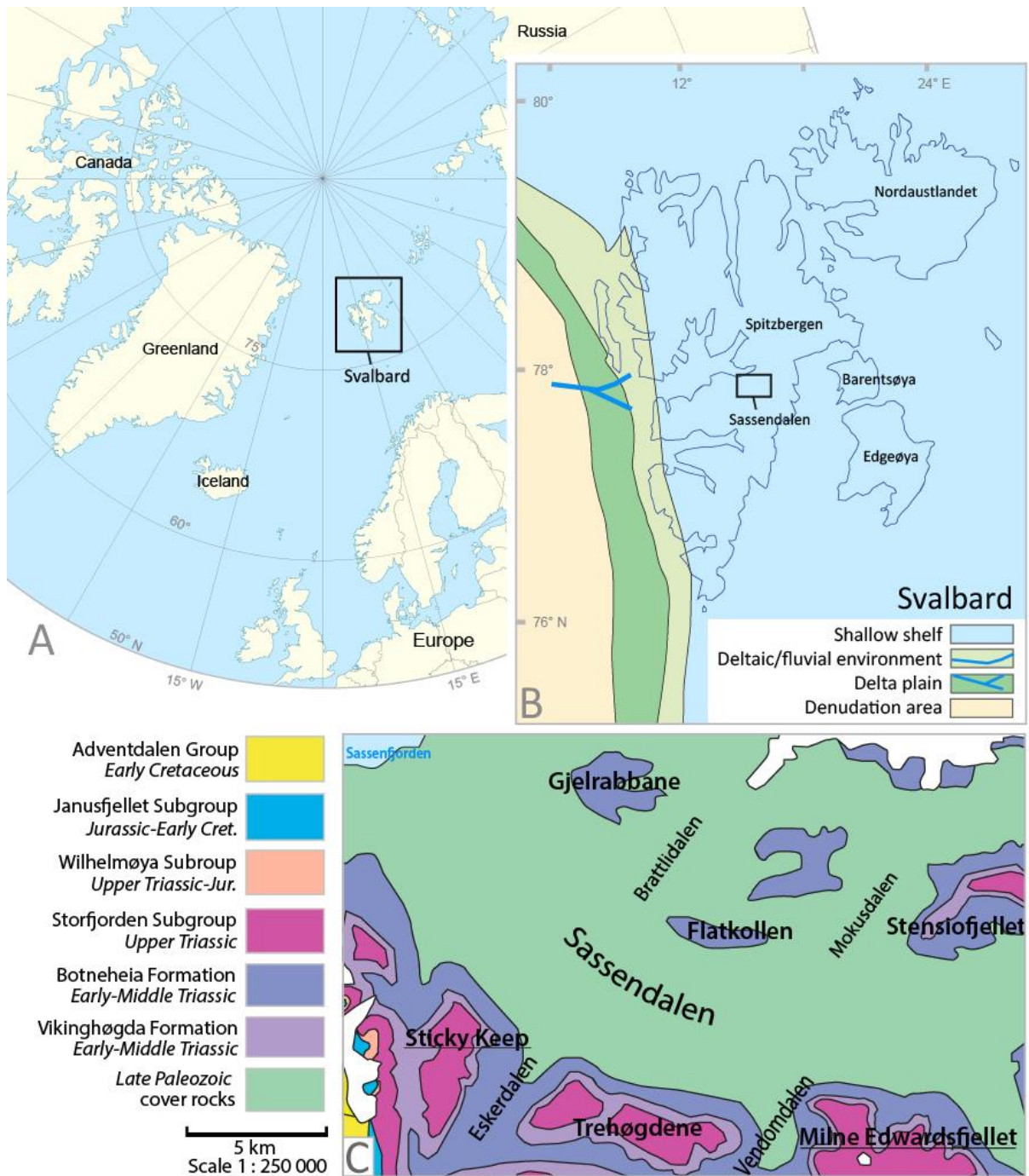
Figure 3 A: Geographical Map showing the location of the Svalbard archipelago. Modified from Wikimedia Commons (2018). ; B: Paleogeographic reconstruction of Svalbard's sedimentary basin during the Early Triassic. The Sassendalen area is located distal to the deltaic clastic input from the west, the boxed shows the Sassendalen area. Modified from Mørk (2015).; C: Geological map of the Mesozoic of the Sassendalen of Central eastern Spitzbergen. Modified from Mørk et al. (1999a). The two localities of Tertrema acuta*, the mountains Sticky Keep and Milne Edwardsfjellet, are underlined.*

2.5 Temnospondyli fauna of Svalbard and fossil record of the Vikinghøgda Formation

The Svalbard archipelago yields a Triassic stratigraphic succession, producing a rich marine vertebrate fauna, which has been studied mainly in the first half of the 20th century (see Kear et al. (2016) for review) This represents an historically important fossil locality which has only recently been gaining renewed attention during the last years (Kear et al., 2016).

Particularly interesting is the diversity of Triassic temnospondyl species which has been summarised by Kear et al. (2016) (Figure 4): in addition to *Tertrema acuta* (Säve-Söderbergh, 1935; Wiman, 1914, 1917), *Aphaneramma rostratum* (Woodward, 1904)*, Boreosaurus thorslundi* (Nilsson, 1943a)*, Lyrocephaliscus euri* (Nilsson, 1943b; Wiman, 1914)*, Peltostega erici* (Wiman, 1914)*, Platystega depressa* (Wiman, 1914)*, Sassenisaurus spitzbergensis* (Nilsson, 1942; Wiman, 1914) are known from the Olenekian (late Early Triassic) from different sites belonging to the Vikinghøgda Formation. Furthermore, cf. *Plagiosternum* sp. (Cox and Smith, 1973; Lowy, 1949) occurs from the Olenekian to the end of the Ladinian (Middle Triassic) in the Urd Formation, and cf. *Plagiosuchus* sp. (Cox and Smith, 1973) from Ladinian to the early Carnian (Late Jurassic) in the Tschermakfjellet Formation. The youngest species from Svalbard is *Cyclotosaurus* sp. (Cox and Smith, 1973; Kear et al., 2016) from the late Carnian of the De Geerdalen Formation.
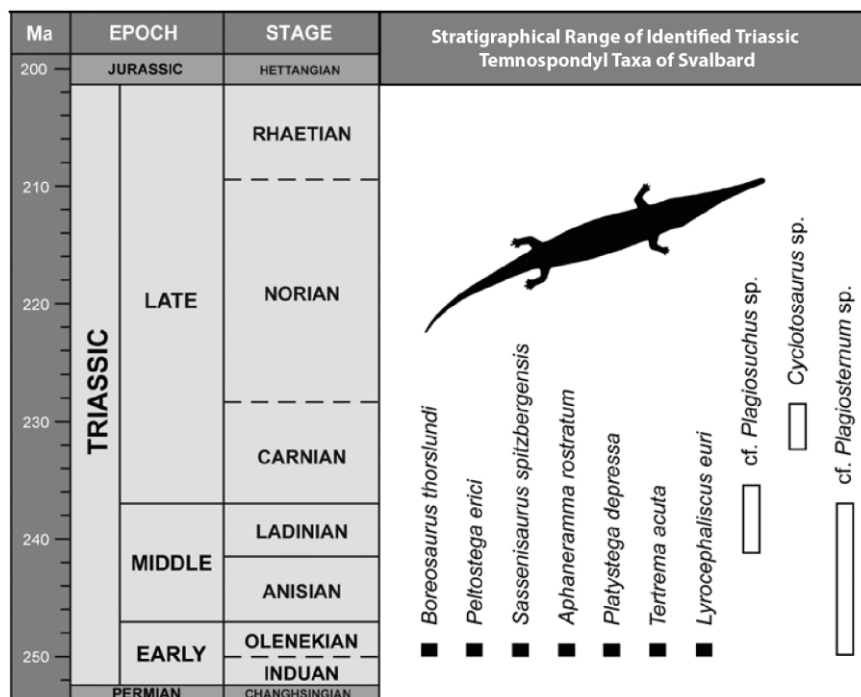
Figure 4. Stratigraphic distribution of the temnospondyl taxa of Svalbard. Geological timescale after (Gradstein et al., 2012). Black filled taxon bars: named species; unfilled taxon bars: indeterminate occurrences assigned to probable genus level. Figure after Kear et al. (2016).

Concerning the Lusitaniadalen Member, a remarkably high diversity of marine invertebrates and vertebrate fossils in nearly all layers (Mørk et al., 1999b) has been explored. Their remains are exceptionally well preserved often within calcareous concretions (Mørk et al., 1999b; Wiman, 1914). Ammonites and bivalves are common invertebrates (Mørk et al., 1999b; Späth, 1921). The vertebrate fauna is represented by sharks and bony fishes (Birkenmajer and

Jerzmańska, 1979; Błażejowski, 2004; Stensiö, 1918, 1921, 1925), marine reptiles (Wiman, 1910b, 1916b) and other temnospondyl amphibians in addition to *Tertrema acuta* (Nilsson, 1942, 1943a, b, 1946; Säve-Söderbergh, 1935, 1936, 1937; Wiman, 1910a, 1913, 1914, 1916a, 1917)

3   Material and methods

This study focusses on the redescription and cladistic analysis of the species *Tertrema acuta* using two specimens including the holotype. Furthermore, additional material of the Australian trematosaurine *Tirraturhinus smisseni* was included into the phylogeny to increase the palaeobiogeographical taxon coverage and possible implications because of the suggested close relationship to *Tertrema acuta* (Nield et al., 2006).

3.1   Material

3.1.1   *Tertrema acuta*

The apparently monospecific *Tertrema* is represented by well-preserved fragments of two skulls of *T. acuta*: 1) the holotype (PMU24148); and 2) the Edwardsfjellet specimen (PMU 24157)*.* They were found during the Spitzbergen expeditions of Erik Andersson Stensiö between 1914 and 1916 at the mountain Sticky Keep (PMU24148), and at the Milne Edwardsfjellet (PMU 24157). Both of these localities are in the Sassendalen, a valley on Spitzbergen, the main island of the Svalbard-Archipelago (Wiman, 1914, 1917). The fossils found on Stensiö's expeditions were subsequently donated to the Museum of Uppsala, whereupon they were first examined and described by Carl Wiman (1914, 1917). Nowadays, the fossils are part of the historical collections at the University of Uppsala.

According to the explorer Stensiö (Wiman, 2014), the two specimens were found *ex situ* as part of a scree deposit and fragmented through frost weathering. He reported that they were probably eroded from the 'Fish-Level' strata, which was recently correlated by Mørk (2015) to the Lusitaniadalen Member of the Vikinghøgda Formation (Olenekian, Lower Triassic).

The fossils are preserved in ironstone nodules in negative relief. The bones themselves were removed by Wiman since they were bituminous and therefore soft and unstable (Wiman, 1914). They left behind a highly detailed, three-dimensional impression of the bone surface in the hard rock of the nodule. Thereby, the holotype consists of three, non-contacting nodule fragments representing parts of the skull roof (Figure 5). The more complete Edwardsfjellet specimen is represented by nine merging fragments showing parts of the skull roof, occiput and palate (Figure 6, Figure 8, Figure 9).

Carl Wiman, who conducted the first descriptions of *Tertrema acuta,* merged the fragments together, produced a mould of each specimen, then modelled the missing skull parts, with assumptions based on the anatomy of different fossil temnospondyl taxa (Wiman, 1914). Unfortunately, the nodule fragments incorporating the holotype are permanently embedded into the mould constructed by Wiman (1914) and cannot be removed without damage, even though their relative position to each other may be not completely accurate (Figure 5A). The nodule fragments of the skull roof of the Edwardsfjellet specimen are merged as well (Figure 6A), while the counterparts, which include the palate and occiput, are loose (Figure 8A; Figure 9A).

The plastotypes resulting from the moulds preserve the morphological characters from the nodule and allow an easier observation of the anatomy of the specimens (Figure 5B; Figure 6B, Figure 8B ;Figure 9B). All plastotypes were labelled with the same collection numbers as the corresponding fossils. However, the old plastotypes show a relatively low degree of detail compared to the rock impression, and degradation because of mechanical damage. Therefore, the original rock impressions, combined with the plastotypes were used for the observations.

3.1.2   *Tirraturhinus smisseni*

Tirraturhinus smisseni is represented by the holotype (QMF 44093), a fragment of the anterior part of the rostrum (Nield et al., 2006). The specimen originates from the Arcadia Formation (Rewan Group, Bowen Basin) from an outcrop at the Duckworth Creek locality in southern central Queensland, Australia (Nield et al., 2006). Because the Arcadia Formation is regarded to be Griesbachian in age (earliest Triassic) (Warren et al., 2006), *Tirraturhinus smisseni* is probably the oldest known trematosaurine (Nield et al., 2006). The fossil is housed in the holotype collection of the Queensland Museum in Brisbane, Australia. *Tirraturhinus* was first described and recognised as a new monospecific genus by Nield et al. (2006). However, the authors also suggest *Tertrema acuta* to be a close relative to *Tirraturhinus* based on its morphology.

The specimen mainly represents the prenarial part of the snout, including the skull roof, as well as the palate. The fossilised bones show a three-dimensional preservation, which also provides the structure of the bone surface.

3.2 Methods

3.2.1 Description and documentation

To record anatomical features of the skull bones, the fossil impressions and plastotypes of *Tertrema acuta* and the fossilised bones of *Tirraturhinus smisseni* were studied macroscopically. In this respect, former studies of Wiman (1914, 1917) and Säve-Söderbergh (1936) regarding *Tertrema acuta* and of Nield et al. (2006) regarding *Tirraturhinus smisseni* were consulted. In the scope of the phylogenetic re-assessment, the description was focused on the anatomical features of the character list of Steyer (2002).

However, Wiman's reconstructions of the holotype were not completely accurate regarding the position of the fragments. Thereby, lateral lines of the two posterior fragments were not accurately merged together, which resulted in an asymmetrical skull reconstruction and a slightly too small size estimation. Since the fragments were permanently merged together by Wiman's mould construction, their relative position was corrected by manipulating photographs of the plastotype with the software Adobe Photoshop CC, version 2015.5. Specifically, the bone portions were cropped with the clipping tool, and moved to more accurate positions, relative to each other. Finally, the results were visualised with the program Adobe Illustrator CC, version 2015.3.

Finally, the *Tertrema acuta* specimen and the here resulting interpretations were visualised with the following methods. All specimens were photographed under low-angle lateral light conditions to visualize the three-dimensionality and textural characteristics of the bone surface. Photos were captured with a Canon EOS 700D Camera together with a 1:3,5-5,6 IS STM zoom lens. Further processing of the photographs was made with the Adobe Lightroom CC software package, version 2015.12, to increase the sharpness and contrasts when necessary, as well as to turn the photographs into monochrome.

3.2.2 Phylogenetic reassessment

To determine the effects of the character state changes on the phylogenetic placement of *Tertrema acuta* within the Trematosauroidea, cladistic analyses were conducted by using and updating a pre-existing morphological database.

The data matrix was originally developed by Steyer (2002), who incorporated taxa from different localities of the whole world, and derived the character states mainly on literature studies of the specimens. Fortuny et al. (2017) and Fernández-Coll et al. (2018) complement this data matrix with further taxa based partly on literature, and partly first-hand observed specimen, whilst excluding problematic (incomplete) fossil taxa of Steyer's (2002) analysis. The study herein employs the newest data matrix by Fernández-Coll et al. (2018), but added *Tertrema acuta* and *Tirraturhinus smisseni* based on our own, first-hand specimen observations (see supplemental material). replaced the literature-based character states of Steyer (2002). Furthermore, we use the analysis parameter stipulated by Fortuny et al. (2017) as followed:

In all our analyses, *Onchiodon frossardi* (Werneburg and Steyer, 1999) and *Archegosaurus decheni* (Witzmann, 2006) were defined as most basally branching outgroups. We treated *Angusaurus* as a generic hypodigm in all our analyses. In total, 69 characters were analysed (see supplemental material for modified data matrix). All characters were defined as equally weighted and unordered. Furthermore, the following eight parsimony-uninformative identified characters were excluded: 16 (frontal contact orbit), 17 (interfrontal), 28 (vomer contact maxilla), 46 (paraquadrate foramen), 56 (stapes morphology), 62 (parasymphysial tooth row), 63 (denticles on coronoids) and 67 (crista articularis). A standard parsimony analysis was undertaken in PAUP* v.4.0b10 for Macintosh (Swofford, 2002)with the 'amb-' option implemented to eliminate ambiguous zero length branches (creating polytomies) (Kearney and Clark, 2003). A heuristic search with tree-bisection reconnection (TBR) branch swapping, a simple addition sequence with only a single tree saved at each step and 10,000 replicates was conducted.

The following analysis steps were performed:

1) Simulation of the analysis from a) Fortuny et al. (2017) and b) Fernandez-Coll et al. (2018) employing their unmodified matrices and similar settings.

2) Analysis with our first-hand character scores of *Tertrema acuta* replacing Steyer's (2002) literature-based character states using the matrix of a) Fortuny et al. (2017) and b) Fernández-Coll et al. (2018).

3) As per step 2, with the addition of *Tirraturhinus smisseni*.

4) Screening for wildcard taxa using semi-strict Adams consensus, where wildcards do not obscure adequately supported nodes (Wilkinson, 1995, 2003).

5) Bootstrapping (1,000 replicates) and Bremer decay indices calculated using TreeRot v. 3 (Sorenson and Franzosa, 2007) were used to test node support.

6) Testing accelerated transformation (ACCTRAN) vs delayed transformation (DELTRAN) character state optimisation on the deduced phylogeny. Unequivocal synapomorphies were deemed to be those shared by both DELTRAN and ACCTRAN. Thereby, only 'global' character changes were considered, which were equal at the same nodes of all resulting MPTs (large arrows [==>] in the apomorphy list in the supplemental material**Fehler! Verweisquelle konnte nicht gefunden werden.**). Thereby, 'global' means not, that reversals of the character states along the branch are not possible.

The visualisation of the tree was undertaken with Adobe Illustrator CC, v. 2015.3.

3.2.3 Development of the 'Systematic Palaeontology'

This systematic ranking is arranged within a Linnean classification framework, which groups closely related taxa in hierarchal order together (Carroll, 1988). Hereby, the classification is based on the most recent reviews of Schoch (2015) and Steyer (2002), who employed cladistic analysis methods. The synonymy list is coded according to the standardised method of nomenclature introduced by Matthews (1973).

3.3 Abbreviations

3.3.1 Institutional abbreviations

The casts and fossil impressions of *Tertrema acuta* are labelled with the institutional prefix **PMU**: Museum of Evolution (Palaeontological Museum), Uppsala, Sweden. The fossil bones representing *Tirraturhinus smisseni* are labelled with prefix **QMF**: Queensland Museum Fossil, Brisbane, Australia. These prefixes are then followed by the respective collection specimen numbers.

3.3.2 Anatomical abbreviations

apalv, anterior palatal vacuity; **cc**, carotid canal; **ch**, choana; **co**, crista obliqua; **cp**, cultriform process; **cv**, *columna verticalis*; **ect**, ectopterygoid; **eo**, exoccipital; **f**, frontal; **fm**, foramen magnum; **fsm**, fossa subostralis media; **ipv**, interpterygoid vacuity; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **oc**, occipital condyle; **p**, parietal; **pal**, palatine; **pap**, paroccipital process; **prf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pt**, pterygoid; **ptf**, posttemporal fenestra; **psp**, parasphenoid; **qj**, quadratojugal; **slg**, sensory line groove; **sq**, squamosal; **st**, supratemporal; **stv**, supratemporal vacuity; **v**, vomer.

4 Results

4.1 Systematic Palaeontology

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ORDER Temnospondyli Zittel, 1888

SUBORDER Stereospondyli Zittel, 1888

Clade **Trematosauria** Romer, 1947 *sensu* Yates & Warren, 2000

SUPERFAMILY Trematosauroidea Säve-Söderbergh, 1935 *sensu* Schoch, 2013

FAMILY Trematosauridae Watson, 1919

SUBFAMILY Lonchorhynchinae Säve-Söderbergh 1935 *sensu* Steyer, 2002

Tertrema acuta Wiman, 1914

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Synonymy:	v.1914, Wiman: Bull. Geol. Instit. Upsala 13; p. 21, pl. 7.
	v.1917, Wiman: Bull. Geol. Instit. Upsala 14; pp. 229-233, text-fig. 1-2, pls 6-8.
	v.1937, Säve-Söderbergh: Bull. Geol. Instit. Upsala 27; pp. 112-114, text-figs 50-51.
Material:	**Holotype:** PMU24148, three unconnected fragments of the skull roof. **Additional material:** PMU 24157: Three unconnected fragments of the skull roof, partly preserved occiput and almost complete palate.
	Both specimens are preserved in ironstone nodules as negative reliefs. 3-D plastotypes made by Wiman (1914, 1917) are necessary for the detailed description.
Type horizon and locality:	'Fisch-Niveau' (Wiman, 1910b, 1928), Lusitaniadalen Member, Vikinghøgda Formation (Mørk et al., 1999b), Sticky Keep (PMU24148), Sassendalen, central eastern Spitzbergen.
Stratigraphic range:	Olenekian, Lower Triassic (Mørk et al., 1999b).
Diagnosis:	See description of Wiman (1914).
Comments:	According to Lehman (1979), p. 36-38 , *Tertrema* sp. may be present in Madagascar, on the basis of a fragment of the snout tip. Later on, this specimen was regarded as indeterminate (Cosgriff, 1984; Janvier, 1992; Welles, 1993).
	Furthermore, *Tirraturhinus smisseni* from Queensland, Australia, also represented by the snout tip, was already by Nield et al. (2006) suggested to be a close relative to *T. acuta* on basis of the

morphology of the snout tip. This study confirms the similarity of *T. smisseni* to *T. acuta.*

The genus *Tertrema* was established by Wiman 1914 and so far, *Tertrema acuta* is the only known species represented by two specimens.

4.2 Description of Tertrema acuta

In this redescription, we summarise and complement the first descriptions of the holotype (PMU24148) (Wiman, 1914) and the Edwardsfjellet specimen (PMU24157) (Wiman, 1917) of *Tertrema acuta*. Thereby, the focus of the description lies on the most important aspects for the phylogenetic analysis.

4.2.1 Preservation

The two large skulls are of approximately the same size and preserved in limestone nodules. The bones themselves were bituminous and soft and were therefore removed by Wiman soon after recovery. Nevertheless, the surrounding limestone preserved a detailed and three-dimensional impression of exceptional resolution of the bone surface.

The holotype (PMU24148) is represented only by three non-contacting fragments of the skull roof. They form a large part of the tip of the snout and smaller parts of the pre- and postorbital region. Thereby, the premaxilla, maxilla, nasal, the nostril and parts of the frontal, lacrimal and prefrontal are preserved from the postorbital region. Further, parts of the postfrontal, postorbital, parietal, supratemporal and squamosal are preserved on the postorbital components of the fossil. Nevertheless, large parts of the region between the orbits and postorbital region up to the terminal margin are missing.

The Edwardsfjellet specimen (PMU24157) provides a more complete skull, complementing important parts of the skull roof, palate and occiput which are largely missing from the holotype. The preserved parts of the skull roof are almost the same as those of the holotype, but provide additional parts of the mandible, frontal, jugal, quadratojugal and parietal. Two fragments of the palate show the entire posterior part including premaxilla, maxilla, vomer, choana, palatine and ectopterygoid. Furthermore, the parasphenoid and parts of the pterygoid are preserved, forming the posterior margin of the interpterygoid vacuity. Only the medial margin of the subtemporal vacuity is present. The centre of the occiput is well-preserved, showing the occipital condyles, paroccipital processes and *columna verticalis*. Furthermore, parts of the exoccipital and pterygoids are preserved, forming most of the foramen magnum and post-temporal fenestra.

4.2.2 Skull

The skull of *Tertrema acuta* presents an elongated, triangular shape with a narrow and slightly constricted rostrum. The skull length of the holotype (Figure 5) is estimated to be at least 37.5 cm. The width of the skull at the posterior end is approximately 20.5 cm, and approximately 14.3 cm at the level of the centre of the orbits. The skull of the Edwardsfjellet specimen (Figure 6) measures approximately 34.5 cm in length. It is about 19.3 cm wide at the posterior end of the skull, and about 11.5 cm at the level of the centre of the orbits. Hence, due to our reconstructions, the holotype is slightly larger than the Edwardsfjellet specimen and both are estimated to be larger than the size suggested by Wiman's original reconstructions (Wiman, 1914, 1917).

The skull width reduces progressively from posterior to anterior and measures approximately 6 cm at the level of the nostrils for the holotype, and approximately 5.2 cm for the Edwardsfjellet specimen. The height of the skull can be only reconstructed from to the more complete preservation of the Edwardsfjellet specimen: the height at the level of the nostrils is smaller than 2 cm and higher than 8.5 cm at the posterior end. Thereby, vertical shortening of the nodule because of compression cannot be totally excluded. Nevertheless, the skull roof between the orbits and the posterior margin between the eyes are not preserved in the specimens representing *Tertrema acuta.*

The distance between the centre of the nostrils and the tip of the snout measures about 5.7 cm for the holotype and 6.5 cm in the Edwardsfjellet specimen. Hence, the prenarial part of the skull is slim and slightly elongated. The nostrils are long [8(2)], slightly bean-shaped and facing dorsolaterally [9(1)].

According to the here refined skull reconstructions, the orbits are situated close to halfway between the posterior and anterior ends of the skull, but slightly towards the posterior half: in the holotype, the distance of the centre of the orbit and the snout tip measures approximately 23 cm and in the Edwardsfjellet specimen approximately 21 cm. The orbits are oval [6(1)] and facing dorsolaterally [5(1)]. According to the character definition of Steyer (2002), the orbits are small compared to the skull size, since they are measuring less than 14% of the estimated skull length (PMU24148: ~12%; PMU24157: ~9.6%) [4(1)].

4.2.3　Skull roof

4.2.3.1　Dermal bone ornamentation

The surface of the skull roof bones of *Tertrema acuta* show the typical morphology for temnospondyls (Figure 5, Figure 6). It presents the characteristic fine ornamentation with ridge rows or rounded pits forming a reticular pattern, radiating from the centre of the bone surface to the periphery or along elongated bones (compare e.g. (Rinehart and Lucas, 2013)). Pits are especially present at the tip of the snout and on the premaxilla, maxilla, prefrontal, postfrontal, postorbital and the medial part of the supratemporal. The ridges are mainly visible at the nasal, frontal, parietal, jugal, quadratojugal and squamosal. However, the holotype shows more of the reticular pattern than the Edwardsfjellet specimen, which generally shows more ridges. The jugal and quadratojugal are represented only by the Edwardsfjellet specimen and show especially wide ridges.

4.2.3.2　Lateral line system

In both specimens, the sensory-line grooves are clearly visible, (Figure 5, 6). Two channels are symmetrically on each side of the skull. They are present in front of the orbits [13(1)], as well as behind [14(0)]. The depth of the lateral lines is relatively constant but varies irregularly in width.

The supraorbital grooves extend rearward of the orbits on the postfrontal, proceed anteriorly in curves along the midlines over the frontals, prefrontals, and nasals, between the nostrils to the tip of the snout on the premaxillae, where they divide into two branches. One branch bends laterally along the margin, and the other is less prominent, extending towards the midline.

The infraorbital grooves extend ventrolaterally at the maxilla and the lacrimal. At the lacrimal, it bifurcates: the lower branch extends posteriorly over the squamosal, while the upper one continues medial on the postorbital. This latter branch divides into three parallel subbranches on the holotype and two in the Edwardsfjellet specimen. Thereby, the outermost of the parallel grooves is longer than the inner ones and continues over the supratemporal. On the holotype, the inner branches continue probably onto the supratemporal as well, but the position of the postorbital-supratemporal suture cannot be identified with full certainty. On the Edwardsfjellet specimen, the inner branch ends on the postorbital.

4.2.3.3 Bones of the skull roof

The visibility of the suture lines varies across the skull roof and between both specimens (Figure 5, 6) The suture lines are poorly visible where the bone ornamentation is strongly reticular, and better visible where it does not reach the sutures, or the ornamentation pattern changes between bones. In addition, they are relatively difficult to trace among the lateral-line grooves. Therefore, the suture lines are harder to recognize on the holotype and more recognizable on the Edwardsfjellet specimen.

The premaxillae are large and represent most of the area anterior of the nostrils. The premaxilla-nasal suture is anteriorly directed [24(2)] and ends at the nostrils. The premaxilla-maxilla suture is not visible in dorsal view (Figure 5, 6).

The nasals extend anteriorly to the nostrils. They are broad compared to the slim snout but become progressively narrower posteriorly to the width of the frontals. The contact with the frontals presents a short jagged suture situated approximately in the middle between the nostrils and the orbits.

The nostrils are mainly bordered by the nasals and the premaxilla. Since the premaxilla-maxilla suture is not visible, it is unclear if the maxilla is contacting the nostrils. Due to the preservation as a negative relief, the inner lying bones, such as the septomaxillae, are unknown [19(?)].

The maxillae are narrow bones and represent the lateral margins of the skull. Their preservation is poor, so the positions of the anterior and medial sutures cannot be identified for certain. Nevertheless, they are contacting anteriorly the premaxillae, medial the lacrimals and posteriorly the prefrontals and jugals.

The lacrimals are small, very slim and located dorsolaterally on the skull roof. Only anteriorly do they contact the nasals and are bounded medially by the prefrontals and laterally by the maxillae.

The prefrontals are large and represent parts of the anterodorsal and -lateral skull roof. They broaden from posteriorly. Laterally, they extend approximately to the level of the centre of the orbits, where they contact the jugals; the suture to the lacrimals has about the same length as the suture to the jugals. Posteriorly, they represent the anterior margin of the orbits.

The frontals are long and narrower than the nasals. Laterally, they contact the pre- and postfrontals, and posteriorly they contact the parietals. They extend posteriorly to the orbits [15(1)]. The mid-orbit area of both specimens is mostly not preserved. However, the large prefrontals and postfrontals reach far along the medial margins of the orbits, that it is most likely, that the frontals not contacting the orbits [16(0)]. Furthermore, it is not possible to identify the presence of the interfrontals [17(?)].

The postfrontals have an elongated shape. The anterior part is not completely preserved but extends further anteriorly than the level of the centre of the orbits. It is posteriorly elongated and narrows towards the short suture to the supratemporal.

The postorbitals have the approximate shape of an elongated triangle. Medially, they end at the same level as the postfrontal, while laterally they extend more posteriorly. The lateral suture is semicircular; the postorbital-supratemporal suture is almost indiscernible due to the overlying lateral groves and the reticular dermal bone pattern overprinting the suture.

The parietals are elongated. Their shape is anteriorly slim and broadening in the posterior direction. The lateral margin formed by the postorbital-parietal and the supratemporal-parietal suture is relatively straight. Since the medial posterior part of the parietals is not preserved, it is not possible to determine the presence of a centroparietal [18(?)] and the anatomical characters of the pineal foramen [11(?), 12(?)].

The poor preservation of the supratemporals and the squamosal does not facilitate full anatomical description. However, the supratemporals face dorsally and broaden posteriorly in the preserved anterior half. The squamosal faces dorsolaterally and only the anterior and centre parts are preserved.

The jugals and the quadratojugals form the posterolateral part of the skull roof and the lateral margin of the subtemporal vacuities. The jugal is long and widens posteriorly. The sutures to the squamosal and the quadratojugal are only partly preserved.

Despite the anterior contact with the jugal, only the centre of one of the quadratojugals is preserved. Nevertheless, it represents the most posterior part of the preserved skull roof and is preserved to the level of the occipital condyle. The exoccipital extends behind the occipital condyle, however the quadrate condyle is not preserved and their relative positions to each other cannot be confidently identified [22(?)].

Because of the missing posterior region of the skull roof, several characters cannot be described: the bulging if the skull roof between the orbits [10(?)], the posterior margin of the skull roof [7(?)], the morphology of the tabular [21(?)], otic notches [20(?)], and the 'temporal fossae' [26(?)].
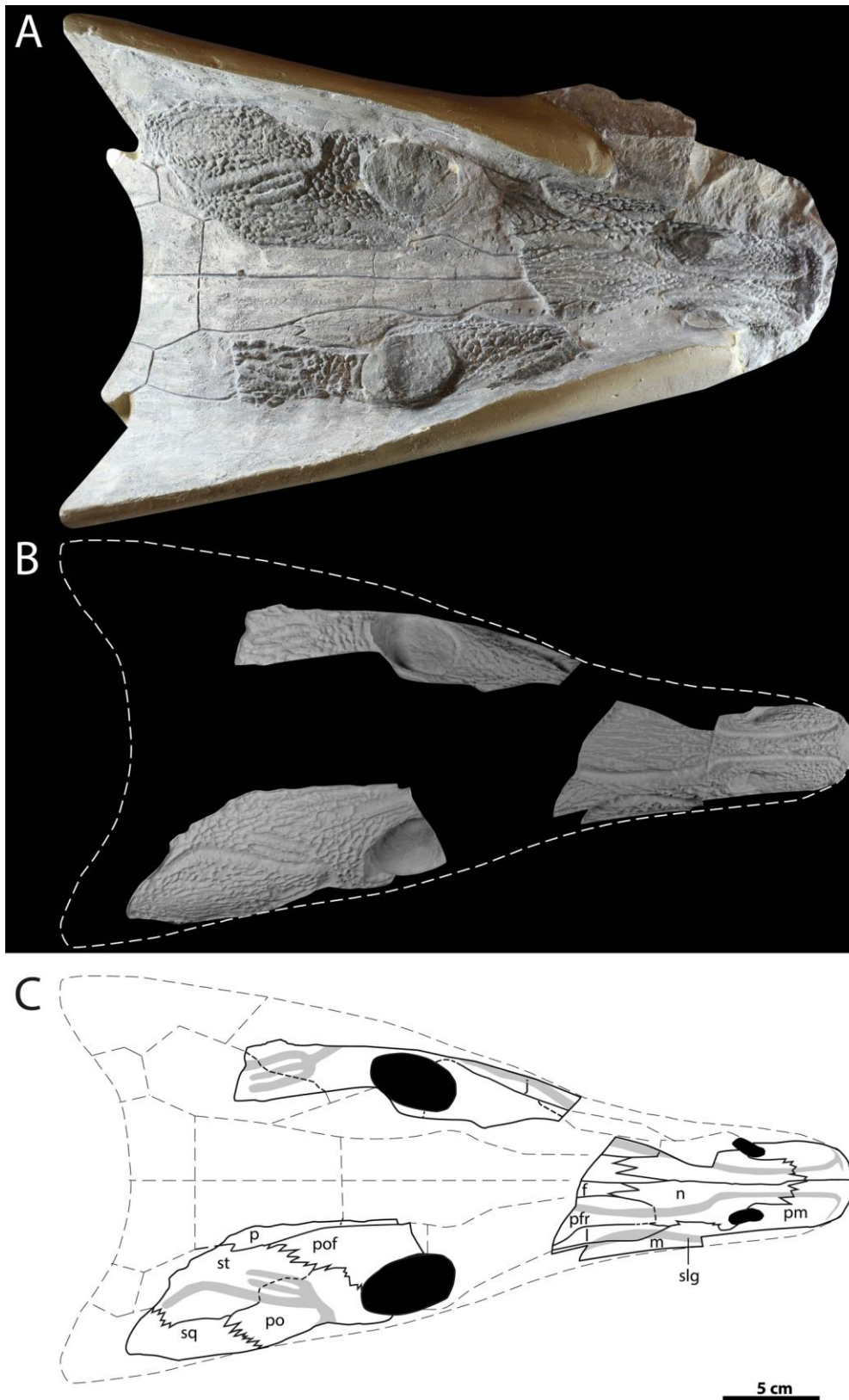
Figure 5. Tertrema acuta, *holotype (PMU24148), Lower Triassic of Spitzbergen, dorsal view. A: photograph of the rock impression, merged together by Wiman (1914) into a mould. B: photograph of the plastotype. The actual bone casts are cropped out with image editing software and their relative positions are corrected. C: interpretative drawing. Broad grey lines: sensory-line grooves. Small dashed lines: simplification of indiscernible suture lines. Large dashed lines: simplified skull reconstruction. Abbreviations: **f,** frontal; **j,** jugal; **l,** lacrimal; **m,** maxilla; **n,** nasal; **p,** parietal; **prf,** prefrontal; **pm,** premaxilla; **po,** postorbital; **pof,** postfrontal, **slg,** sensory line groove; **sq,** squamosal; **st,** supratemporal; **v,** vomer.*

Figure 6. Tertrema acuta*, Edwardsfjellet specimen (PMU24157), Lower Triassic of Spitzbergen, dorsal view. A: photograph of the rock impression, merged together by Wiman (1917) into a mould. B: photograph of the plastotype. The actual bone casts are cropped out with image editing software. C: interpretative drawing. Broad grey lines: sensory-line grooves. Small dashed lines: simplification of indiscernible suture lines. Large dashed lines: simplified skull reconstruction. Abbreviations: **f**, frontal; **j**, jugal; **l**, lacrymal; **m**, maxilla; **n**, nasal; **p,** parietal; **prf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **qj**, quadratojugal; **slg**, sensory line groove; **sq**, squamosal; **st**, supratemporal; **v**, vomer.*

Figure 7 Tertrema acuta, *Edwardsfjellet specimen (PMU24157), Lower Triassic of Spitzbergen, lateral view. A: Photographs of the plastotype. The actual casts were consisting of two parts (palate and skull roof). They were cropped and merged together out with image editing software. B: interpretative drawing. Broad grey lines: sensory-line grooves. Small dashed lines: simplification of indiscernible suture lines. Large dashed lines: simplified skull reconstruction. On A and B: For illustrative reasons, only the dentition of the left side of the palate is showed. Abbreviations: j, jugal; l, lacrymal; m, maxilla; n, nasal; prf, prefrontal; pm, premaxilla; po, postorbital; pof, postfrontal; qj, quadratojugal; slg, sensory line groove; sq, squamosal; st, supratemporal; v, vomer.*

4.2.4   Palate

4.2.4.1   Bones and vacuities of the palate

The visibility of the suture lines on the palate is very poor because of the fine ornamentation and high number of teeth in the narrow snout, which obscures the ornamentation. Furthermore, the palate is characterised by very slim and elongated bones especially in the anterior part of the snout and by large vacuities.

The premaxilla-maxilla suture is not visible in palatal view but it is suggested by (Säve-Söderbergh, 1936) to be approximately located between the nostrils and the choanae. The premaxilla-vomerine suture is located between the anteropalatal vacuities [32(1)]. Close to the tip of the snout fossa subostralis media is visible, which is formed by the medial sutures between the premaxillae. It forms a teardrop-shaped rise, with the tip pointing posteriorly and a concave surface.

Paired anteropalatal vacuities are present at the tip of the snout [31(2)]. They are large and have an oval, slightly elongated shape. They are primarily bordered by the premaxilla and posteriorly contacted by the vomers.

The vomers are elongated and represent most of the anterior part of the palate. Anteriorly, they are contacting the premaxillaries and maxillaries [28(1)]; posteriorly, they narrow where they contact the cultriform process of the parasphenoid.

The choanae are also oval, but slimmer and more elongated [29(1)] than the anteropalatal vacuities. They are located posteriorly of the ventral opening of the nostrils. Whilst both openings are in close proximity, they do not overlap each other [30(0)]. The choanae are bordered posteriorly by the vomers, laterally by the maxillae and anteriorly by the palatine.

The palatine bones are slim and elongated. Medially they contact the cultriform process of the parasphenoid and form the anterior margin of the interpterygoid vacuities. However, the palatine-ectopterygoid and palatine-pterygoid sutures are very short [39(1)].

The ectopterygoid is relatively broad and constant in width. It presents an ectopterygoidal tusk in the anterior part [44(0)]. The ectopterygoid-pterygoid suture is long and almost reaches the anterior end of the interpterygoid vacuities. The posterior end is not preserved.

The anterior branch of the pterygoid is relatively narrow [35(2)]. It forms the lateral posterior margin of the interpterygoid vacuity and the medial margin of the supratemporal vacuity. At the anterior branch of the pterygoid, the area asparta *sensu* Bystrow and Efremov (1940), a region of a shagreened and granulous pattern of the bone surface is visible [37(1)]. Furthermore, the pterygoid shows a peculiar elongated bulge in the centre of the bone. The pterygoid-parasphenoid suture is long [40(1)], roundly bend towards the parasphenoid and follows posteriorly along the carotid canal. The lateral parts of the posterior bones are not completely preserved [36(?)]. Moreover, the pterygoid-exoccipital suture is indiscernible [45(?)]. Hence it is not possible to evaluate the relationship of the position of the crista obliqua to the pterygoid [34(?)].

The interpterygoid vacuities are relatively narrow, elongated and widening anteriorly [33(1)]. The supratemporal vacuities are mostly not preserved. Small parts of the medial margin are preserved shown by the lateral margin of the pterygoid. However, they are mostly estimated through skull reconstruction.

The parasphenoid plate is anteriorly slimmer and widens posteriorly [41(0)]. The cultriform process is narrow [38(1)] and extends posteriorly towards the vomers. The carotid canal is visible at the margins of the parasphenoid plate [43(1)]. The crista muscularis of the parasphenoid is absent [42(0)].

4.2.4.2 Dentition

The palatal dentition is heterodont, symmetrical and regularly placed in two tooth rows, represented by 129 teeth and empty sockets counted from the preserved palatal fragments of the Edwardsfjellet specimen of *Tertrema acuta* (Figure 8). The full number of teeth cannot be reconstructed, since not all missing parts of the palate can be reconstructed. However, mirroring the parts of the more complete left side of the palate, the animal must have had at least 175 teeth plus the teeth of the missing middle part of the palate.

All preserved teeth have round bases, conical tips, and are variable in size and shape depending in their positions. The dentition is characterized by small marginal teeth and an inner row of large tusks in the anterior part, as well as smaller teeth in the posterior part of the palate.

The anterior premaxillary teeth are relatively large and tilted slightly anteriorly. From anterior to posterior, the marginal teeth show a gradual decrease in size. Thereby, the largest teeth at the premaxillary have a basal diameter of 5.5 mm and height of 23.5 mm. The smallest teeth on the posterior end of the jugals show teeth with a basal diameter of 1 to 2 mm and 3 to 4 mm height.

Moreover, the palate shows four exceptionally big tusks on each side, borne by the vomer and palatine. In total, four tusks are preserved and four are represented by empty bases. They have a maximum diameter of 18 mm and a maximum height of 37 mm. The vomer tusks are lined-up between the anteropalatal vacuity and the choana. The two preserved vomer tusks are slightly bent and tilted slightly medial-anteriorly.

The palatines bear two big tusks each, lining up to the inner tooth row. Additionally, the palatine bears two middle-sized teeth posterior of the tusks. The palatal tusks are generally straight, but the right is tilted slightly laterally, and the left tilted posteriorly. As such, it cannot be determined with complete certainty if these structures are a natural pattern or the result of differential compaction within the nodule.

The ectopterygoid contains a row of teeth parallel to the marginal teeth. The fourth tooth is middle-sized and probably represents the ectopterygoidal tusk [44(0)]. It is preserved on the left side and represented by an empty base on the right side. The tusk measures 17 mm diameter at the base and 7.5 mm in height. However, the third ectopterygoidal tooth is shown only by a base measuring 8 mm in diameter and represents therefore probably an even bigger tusk. Posteriorly, the ectopterygoid dentition is represented by small teeth which have a maximum basal diameter of 5 mm and an approximate height of 10 mm and so, they are generally bigger than the marginal teeth.
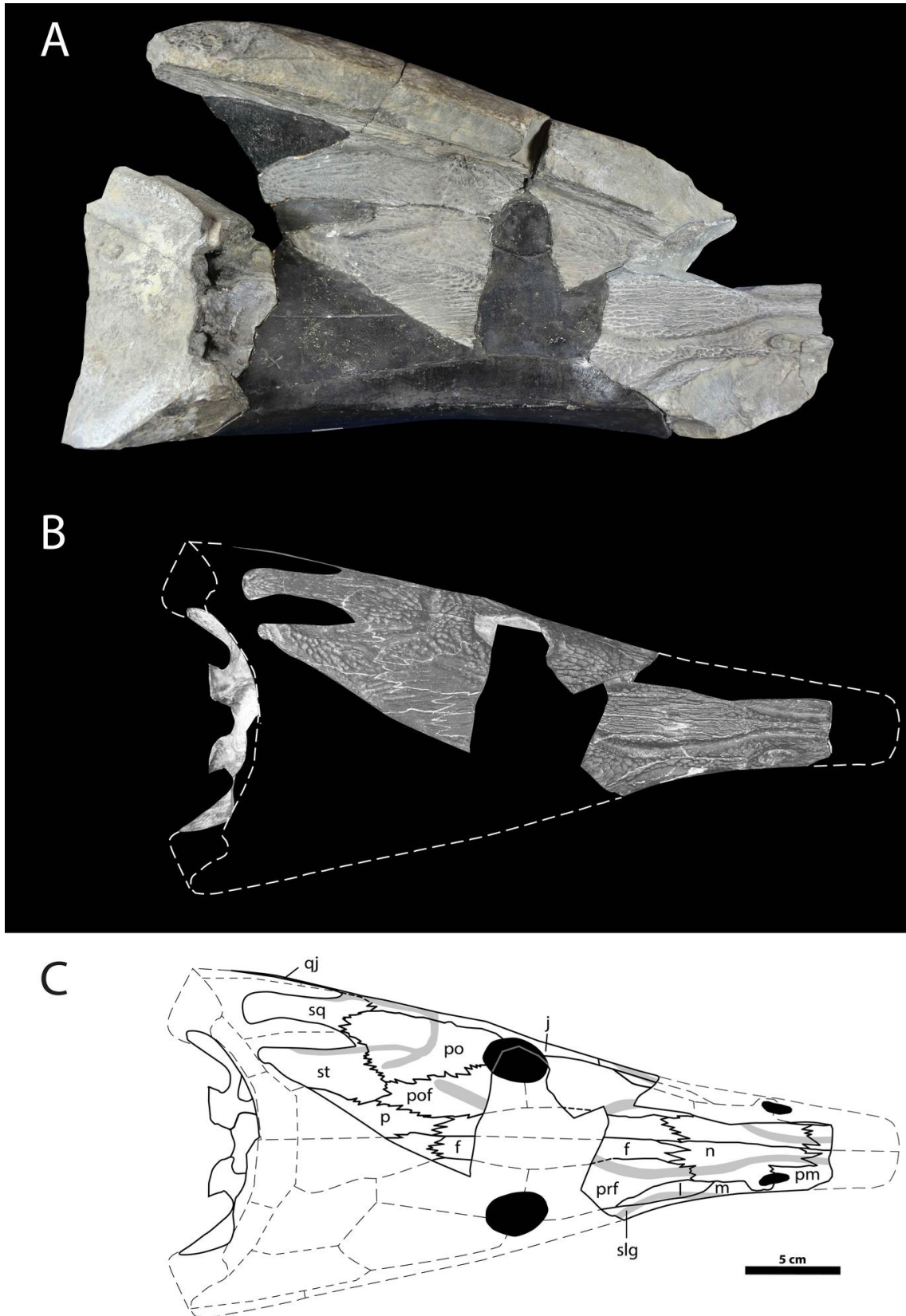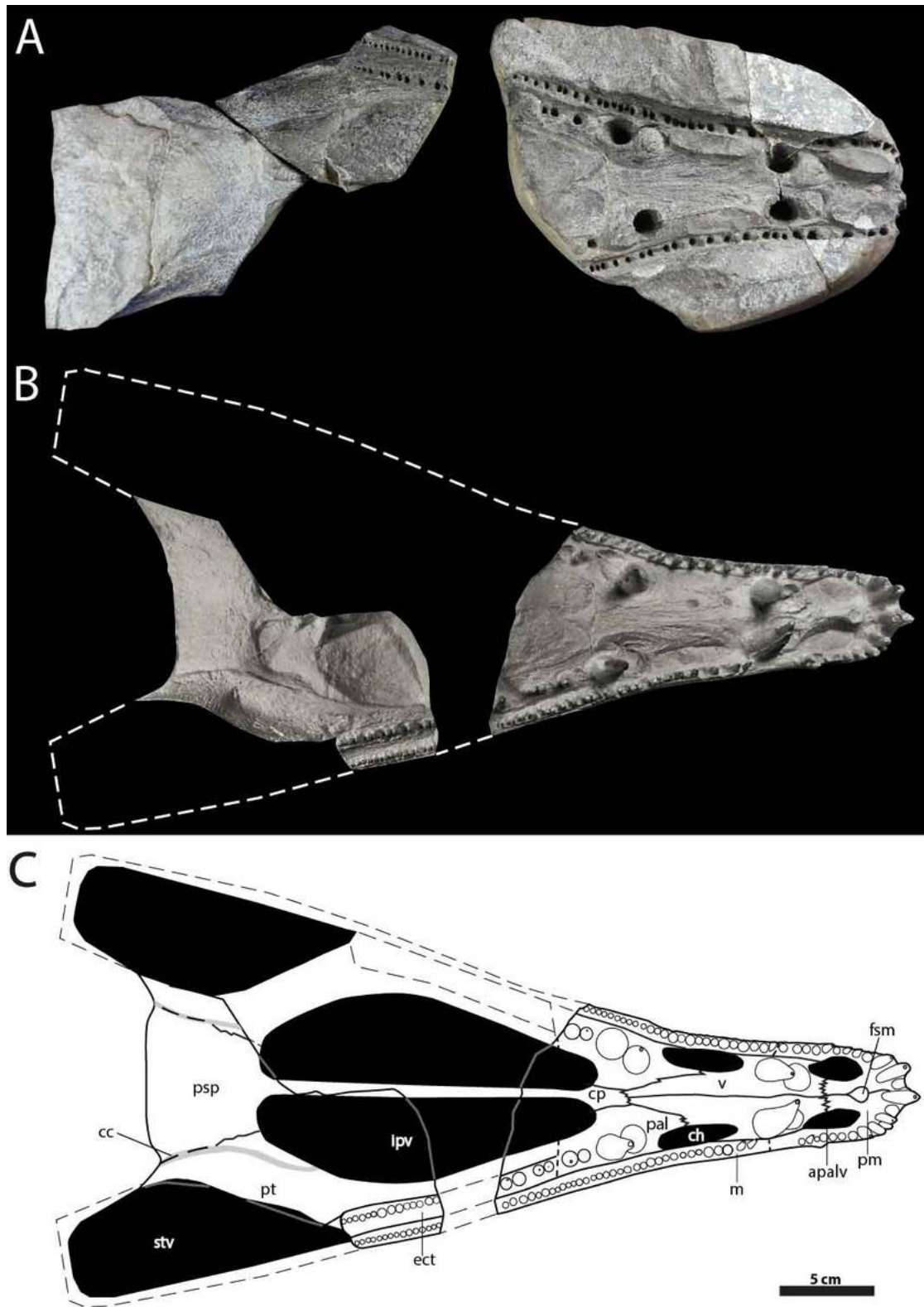
Figure 8. Tertrema acuta*, Edwardsfjellet specimen (PMU24157), Lower Triassic of Spitzbergen, palatal view. A: photograph of the rock impression, merged together by Wiman (1917). B: photograph of the plastotype. The actual bone casts are cropped out with image editing software. C: interpretative drawing. Broad grey lines: carotid canals. Small dashed lines: simplification of indiscernible suture lines. Large dashed lines: simplified skull reconstruction. Note that the supratemporal vacuities are mostly reconstructed. Abbreviations: **apalv**, anterior palatal vacuity; **ch**, choana; **cp**, cultriform process; **ect**, ectopterygoid; **fsm**, fossa subostralis media; **ipv**, interpterygoid vacuity; **m**, maxilla; **pal**, palatine; **pm**, premaxilla; **pt**, pterygoid; **psp**, parasphenoid; **stv**, supratemporal vacuity.*

4.2.5 Occiput

In occipital view (Figure 9), the skull of *Tertrema acuta* is vaulted, narrow and deep [47(1)]. The dorsal and lateral margins are not preserved, but their approximate positions can be estimated from the fragments of the nodule forming the skull roof. However, the tabular [48(?)] and parts of the quadratojugal bearing the paraquadrate foramen [46(?)] and the squamosal with the crista falciformis [53(?)] are not preserved. Due to the preservation as a mold, the inner structures and the stapes are also not discernible [56(?)].

The centre of the occiput is formed by the exoccipital delimiting three openings. The foramen magnum is ventrally constricted and forms a keyhole shape [51(1)], although the shape of the dorsal margin is not preserved [52(?)]. The columna verticalis and paroccipital process border the post-temporal fenestra, which is deep [54(1)] and forming the shape of a triangle [55(1)] with unequal sides.

The occipital condyles are large, approximately 1 cm in length in dorsal view, and approximately 3 cm maximum diameter in occipital view [49(1)]. They are narrow [50(1)], having a distance of approximately 1.5 cm and extending laterally in dorsal view. In occipital view, the right occipital condyle has a triangular and the left one an oval shape.
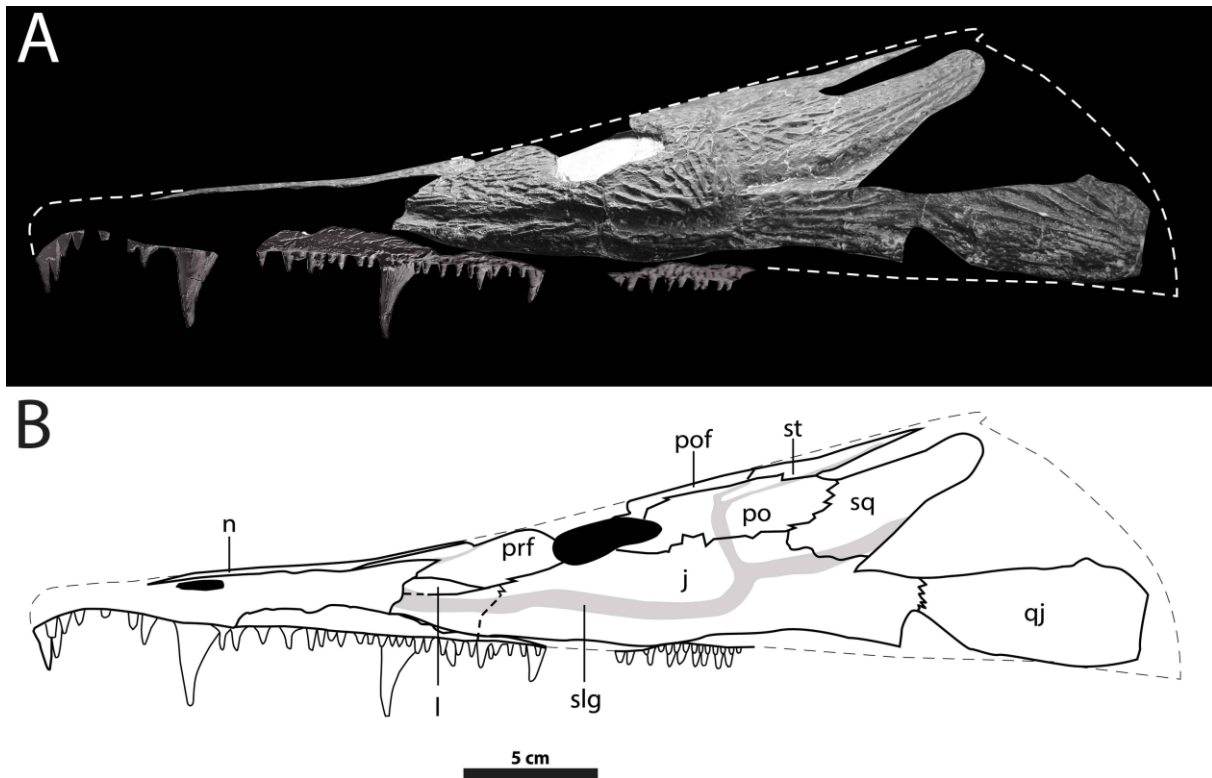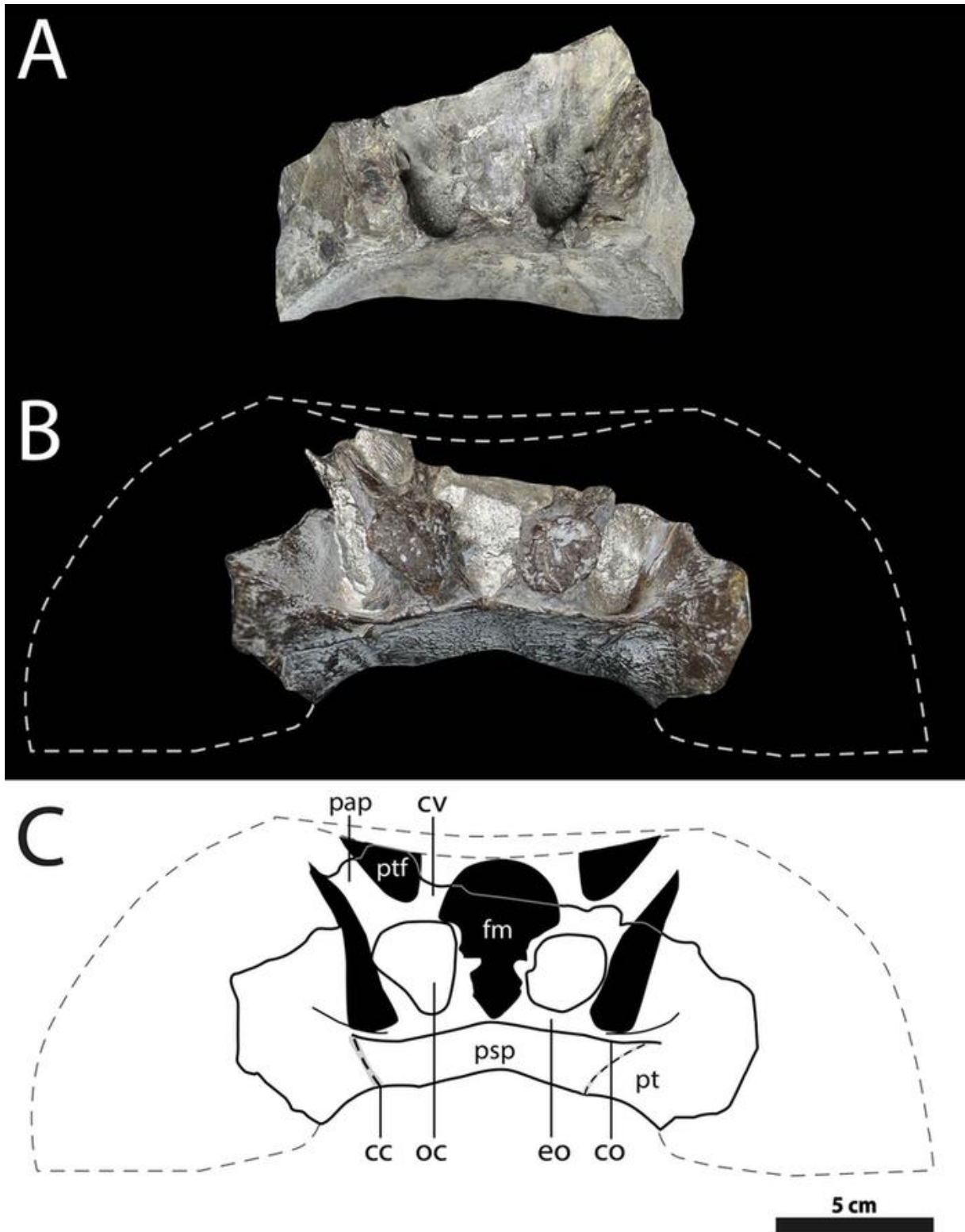
Figure 9. Tertrema acuta*, Edwardsfjellet specimen (PMU24157), Lower Triassic of Spitzbergen, occipital view. A: photograph of the rock impression. B: photograph of the plastotype. The actual bone casts are cropped out with image editing software. C: interpretative drawing. Broad grey lines: carotid canal. Small dashed lines: simplification of indiscernible suture lines. Large dashed lines: simplified skull reconstruction. Abbreviations: **cc**, carotid canal; **co**, crista obliqua, **cv**, columna verticalis; **eo**, exoccipital; **fm**: foramen magnum; **oc**, occipital condyle; **pap**, paroccipital process; **psp**: parasphenoid plate; **pt**: pterygoid; **ptf**: posttemporal fenestra.*

4.3   Character states of *Tirraturhinus smisseni*

The observation of the *Tirraturhinus smisseni* specimen showed that 89.9% of the required characters for the phylogenetic analysis are missing. However, the preserved tip of the snout allowed to identify 8 characters, as described as followed:

The nostrils are elongated [8(2)] and in lateral position [9(1)]. The sensory-line groves are present in front of the orbits [13(1)]. The premaxilla-nasal suture is anteriorly directed [24(2)]. The prenarial part of the snout is not extremely elongated and shows therefore no prenarial growth zone [25(0)]. The vomer contacts the palate [28(1)]. Paired anteropalatal vacuities are present [31(2)]. The premaxilla-vomerine suture lies between the anteropalatal vacuities [32(1)].

Noteworthy, all character states of *Tirraturhinus smisseni* are similar to those observed on *Tertrema acuta.*
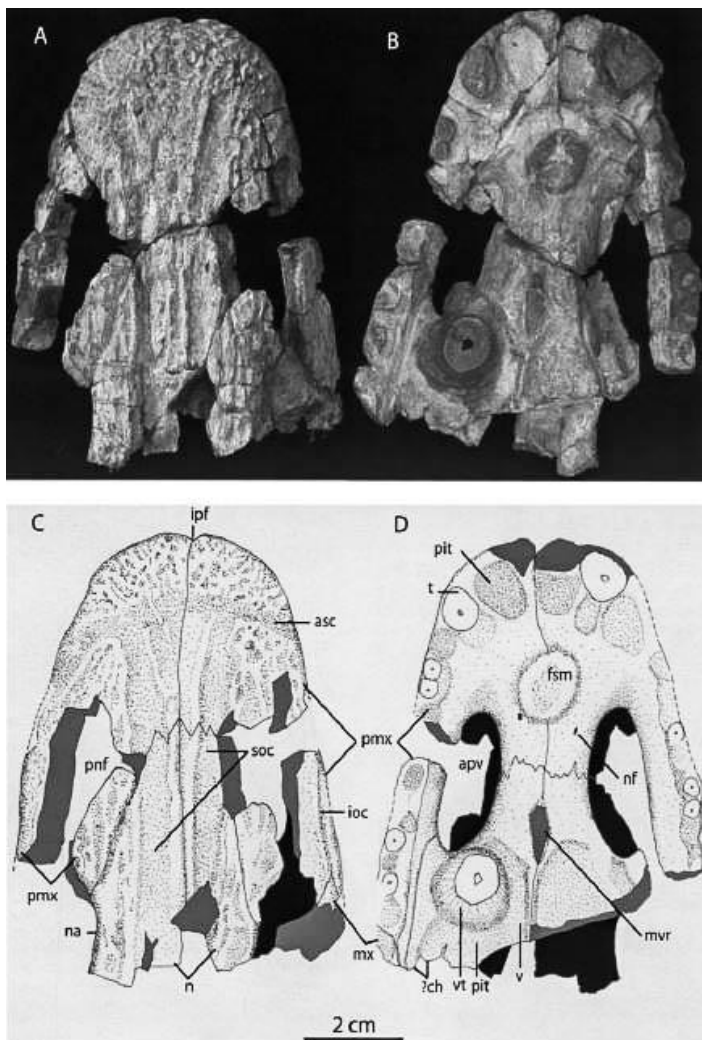
← *Figure 10* Tirraturhinus smisseni *holotype (QMF 44093), Lower Triassic, Queensland, Australia. Photograph of A: the dorsal and B: the palatal view. Interpretative drawing of C: the dorsal and D: palatal view. Figure from Nield et al. (2008) using the following abbreviations:* **apv:** *anterior palatal vacuity,* **asc:** *anterior transverse sensory canal,* **ch:** *choana,* **fsm:** *fossa subrostralis media,* **ioc:** *infraorbital sensory canal,* **ipf:** *interpremaxillary foramen,* **mx:** *maxilla,* **mvr:** *mid-vomerine ridge,* **n:** *nasal,* **na:** *naris,* **nf:** *nutritive foramina,* **pit:** *tooth replacement pit (alveolus),* **pmx:** *premaxilla,* **pnf:** *prenarial foramen for dentary tusk,* **soc:** *supraorbital sensory canal,* **t:** *tooth,* **v:** *vomer,* **vt:** *vomerine tusk.*

4.4 Reassessment of the phylogeny

In this chapter, we present the results of the procedure of analysing the position of *Tertrema acuta* within the Trematosaurid clade in a stepwise fashion. These steps follow those laid out in chapter 4.2.2, and elaborated below:

1) **Simulation of former analyses.** The initial simulation of the Fortuny et al. (2018) analysis yielded a topology comparable to their published strict consensus tree (Fortuny et al. 2018, p. 683, fig. 3), but with a basal trematosaurid polytomy incorporating Trematosaurinae + Lonchorhynchinae + *Trematolestes hagdorni* + *Stoschiosaurus nielseni* (Most Parsimonious Trees [MPTs] = 4; [L]ength = 192; Consistency Index [CI] = 0.3802; Rescaled Consistency Index [RCI] = 0.1717). The addition of *Syrtosuchus samarensis* and *Prothoosuchus blomi*, as prescribed by Fernández-Coll et al. (2018), produced similar results (see Fernández-Coll et al. 2018, p. 9, fig. 4a). However, these exhibited poor resolution amongst lonchorhynchine taxa, except for species of *Aphaneramma*, which persistently formed a monoplyletic clade (MPTs = 5; L = 196; CI = 0.3724; RCI = 0.1741). Significantly, the placement of *T. acuta* as a derived trematosaurine (*sensu* Steyer 2002) was unaffected by either of these analyses.

2) **Analysis with our first-hand character scores of *Tertrema acuta.*** The substitution with the modified first-hand scores of *T. acuta* shifted its position radically. In both Fortuny et al.'s (2017) and Fernández-Coll et al.'s (2018) datasets, *T. acuta* is shifted within a lonchorhynchine clade, which contains *Cosgriffius campi* and the species of *Aphaneramma.*

3) **Analysis with our first-hand character scores of *Tertrema acuta + Tirraturinus smisseni.*** The inclusion of *Tirraturhinus smisseni* returned *Tertrema acuta* again outside of Trematosaurinae in both datasets. This time, both of these taxa collapsed into a polytomy also comprising all other long-snouted taxa (*Cosgriffius campi, Stoschiosaurus nielseni, Wantzosaurus elongatus, and Aphaneramma* spp.). Thereby, Fortuny et al. (2018) yielded MPTs = 30, L = 189, CI = 0.3915, RCI = 0.1811 and Fernández-Coll et al. (2018) MPTs = 152, L = 193, CI = 0.3814, RCI = 0.1789.

4) **Screening for wildcard taxa using semi-strict Adams consensus.** The Adams consensus showed a basal trematosaurid polytomy incorporating Trematosaurinae + Lonchorhynchinae + *Tirraturhinus smisseni* + *Stoschiosaurus nielseni* + *Wantzosaurus elongatus.* Therefore, the latter three taxa are identified as wildcards, i.e. that their position is not stable within this clade and might obscure the most parsimonious trees. This confirms that the 89.9% missing data recorded for *T. smisseni* creates instability. Nevertheless, the 50% majority-rule consensus showed, that *T. acuta* forms in 53% of the MPT's a clade with *C. campi + Aphaneramma* spp.

5) **Bootstrapping and Bremer decay indices.** The bootstrap and Bremer index values were also extremely weak (bootstrap: <50%/Bremer index: 1), except for basal resolution of the trematosaurid ingroup (61%/3 without *T. smisseni*; 58%/3 with inclusion of *T. smisseni*), suggesting that character state conflicts, rather than missing data (which would not conflict), are driving our placement of *T. acuta* as a non-trematosaurine.

Since it was shown that the inclusion of *Tirraturhinus smisseni* causes more statistical instability because of missing data, we exclude this taxon in order to evaluate the position of *Tertrema acuta* within the Trematosauridae. Thereby, our modified dataset *sensu* Fernández-Coll (2018) was applied, because it incorporates most terminal taxa and our analysis did not show significant differences compared to the smaller dataset *sensu* Fortuny (2017). Here we present the strict consensus tree resulting from our analysis (Figure 11).

Our modifications caused less resolution within the Trematosauridae compared to the previous studies. The long-snouted taxa *Stoschiosaurus nielseni* and *Wantzosaurus elongatus* now form a trematosaurid polytomy with the clades Lonchorhynchinae and Trematosaurinae, whereas previous studies united all long-snouted taxa within one clade. The Lonchorhynchinae itself consists of a polytomy of *Tertrema acuta* + *Cosgriffius campi* + *Aphaneramma* spp. The Trematosaurinae include the same taxa, however, with no resolution except of *Trematolestes hagdorni* as a basal sister group.

6) **Analysing synapomorphies resulting from ACCTRAN and DELTRAN**. This analysis was focused on only the clades which were important to the placement of *Tertrema acuta*. Under both ACCTRAN and DELTRAN, the Benthosuchidae clade (here represented by *Benthosuchus sushkini*) is supported by six equivocal synapomorphies: ovoid nostril [8(1)], absence of an ectopterygoidal tusk [44(1)], mandible shallow in lateral view [58(0)], presence of a parasymphysial tusk [61(1)], interclavicle not narrow [68(0)], and interclavicle with dorsal crest(s) [69(0)]. *Tertrema acuta* is not a benthosuchid, because it has elongated nostrils [8(2)] and presents ectopterygoidal tusks [44(0)]. However, the other characters which represent unambiguous synapomorphies for *Benthosuchus sushkini* were not preserved in *T. acuta.*

Under ACCTRAN, the Trematosauridae clade is not supported by global synapomorphies, but under DELTRAN this clade was supported by the following character states: a laterally facing orbit [5(1)], the presence of paired anteropalatal vacuities [31(2)], a knife edged cultriform process of the parasphenoid plate [38(2)], and the absence of the crista muscularis of the parasphenoid [42(0)]. *Tertrema acuta* as a trematosaurid is supported by the characters [5(1)], [31(2)], and [42(0)], but not by character [38], because it shows a narrow cultriform process of the parasphenoid plate (2).

In either ACCTRAN and DELTRAN, the Trematosaurinae clade is supported by the following unequivocal synapomorphies: ovoid nostrils [8(1)], large pineal foramen [11(1)] and absence of the crista falciformis of the squamosal [53(0)]. *Tertrema acuta* is not a trematosaurine, because it has elongated nostrils [8(1)]. However, the two other synapomorphies for this clade are not preserved in *T. acuta.* Finally, the ACCTRAN analysis did not produce unambiguous synapomorphies for the Lonchorhynchinae, but the DELTRAN analysis created the following three unambiguous synapomorphies: small orbit [4(1)], large occipital condyles [49(1)] and occipital condyles not widely separated from each other [50(1)]. The placement of *Tertrema acuta* is supported by all three of these synapomorphies.
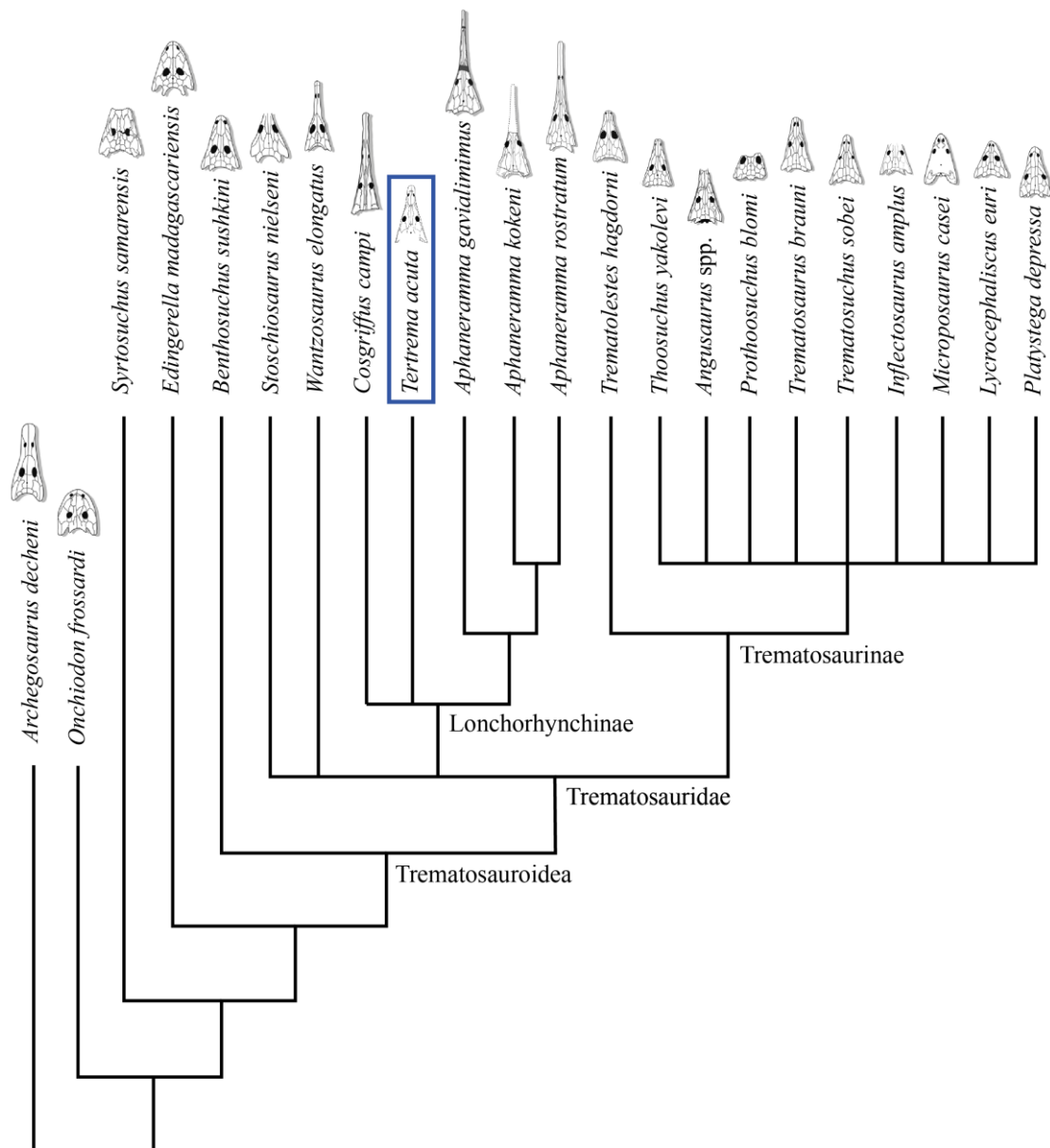
Figure 11 Phylogenetic position of Tertrema acuta *within the Trematosauroidea clade. Strict consensus of 19 trees of the here performed cladistic analysis (see text) using the database of Steyer (2002) as modified by Fernández-Coll (2018) but with our first-hand character coding of* T. acuta*. Node numbers refer to the clades (see apomorphy list in Supplemental material). Illustrations of the terminal taxa from Fernández-Coll et al. (2018), except* Tertrema acuta, *which is modified from Kear et al. (2016).*

5 Discussion

5.1 Palaeobiological implications

The morphology of *Tertrema acuta* allows interpretations about the ontological state, life mode and habitat, whilst providing important constraints concerning the phylogeny of Triassic temnospondyls.

5.1.1 Ontological stage

The ornamentation development of *Tertrema acuta* is typical within temnospondyls and allows the determination of the ontological stage of the specimens. Juvenile temnospondyls show a radial, ridge-like pattern. During ontogeny, they developed successively transverse septa between these ridges beginning from the growth centre until they reached the periphery. Thereby, the pattern is reticular with more and more rounded pits in adult fossil specimens (Figure 12) (Bystrow, 1935; Morkovin, 2015; Shishkin, 1973; Witzmann et al., 2010).

In both specimens, the reticular ornamentation pattern reaches the periphery, which implies that they were fully or almost fully-grown adult animals. However, the morphological observations herein revealed differences of the dermal skull bone ornamentation between the holotype and the Edwardsfjellet specimen. The preserved bones of the holotype show a well-developed reticular pattern with rounded pits. In the Edwardsfjellet specimen, this pattern is slightly less developed, since the pits are elongated or distinctively ordered in rows. Therefore, the Edwardsfjellet specimen probably represents a young adult while the holotype is most likely relatively older.

Exceptions to this pattern are the very elongated bones on both specimens. They clearly show ridges mainly following the long axis of the bone. This especially concerns large parts of the preorbital region and (only preserved on the Edwardsfjellet specimen) the lateral and medial bones in the postorbital region. This heterogeneity of ornamentation is suggestive of bones which had an extreme growth rate during ontogeny (Bystrow, 1935; Morkovin, 2015). In other words, these long, parallel ridges are a direct result of skull elongation during maturation, and the lack of transverse septa in these areas suggest the elongation occurred during the later stages of ontogeny. This model of development predicts the absence of elongated snouts in juvenile individuals of this species (compare (Schoch, 2009)).
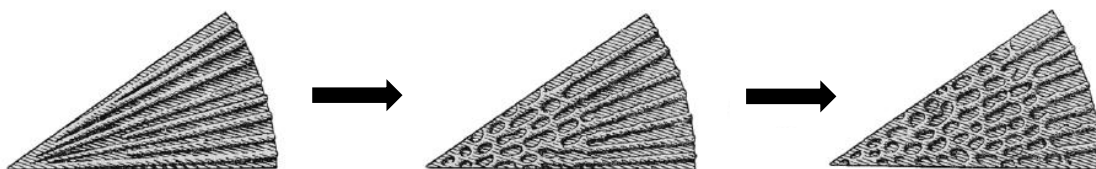
Figure 12 Scheme of the typical change of dermal ornamentation through ontogeny in Temnospondyli. A radial ridge like pattern (left) develops into a pitted ornamentation (right) starting from the growth centre to the periphery (figure from Shishkin, 1973).

To conclude, *Tertrema acuta* is represented by two specimens which reached adulthood and might have changed proportions through ontogeny, shown by the ridged-patterned areas of

extreme growth. This is important for further phylogenetic assessments since observations on immature specimens might lead to misinterpretations concerning the relationship to other species. When comparing specimens of different temnospondyl taxa, juvenile specimens tend to have greater morphological similarity than adults (Schoch, 2009). Because of this, morphological similarities between taxa, especially regarding the skull proportions, might be better explained by similar ontogenetic pathways rather than homology.

5.1.2 Variations between specimens

Tertrema acuta shows an interesting distinction in the lateral line system compared to most temnospondyls: a bi- or trifurcation of the infraorbital grooves on the postorbital and supratemporal. The genus *Trematosaurus* shows a comparable structure concerning the infraorbital grooves, but these furcating grooves reunite again posteriorly. However, *Trematosaurus* shows a trifurcation within the species *T. brauni* (Bystrow, 1935) (Figure 13, A) and a bifurcation within *T. galae* (Novikov, 2010) (Figure 13, B). Hence, the differences in the lateral lines of both *Tertrema* specimens might be an indicator, that the specimens belong to different species within that genus. Nevertheless, no other distinct differences were observed between the specimens and intraspecific variation cannot be excluded until further, and more complete, *Tertrema* specimens are found. As discussed previously (chapter 6.1.1), we can deduce that, in the case of *T. acuta*, differences through ontology are a less likely explanation for lateral line variation since both specimens represent adult individuals.
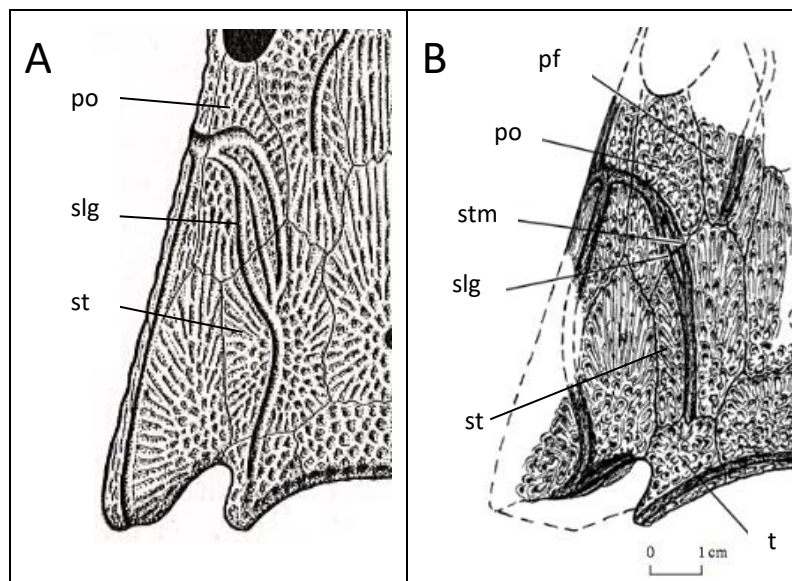
Figure 13 A: Trematosaurus brauni *(modified after (Bystrow, 1935), without scale) and B:* Trematosaurus galae *(modified after (Novikov, 2010)) showing interspecific variation concerning the furcation of the lateral line grooves on the postorbital and supratemporal. This interspecific variance is comparable to the variations found between the* Tertrema acuta *specimens. Used abbreviations:* **pf:** *postfrontal,* **po**: *postorbital,* **slg**: *sensory line groove,* **st**: *supratemporal,* **stm**: *sulcus temporalis medialis,* **t**: *tabular.*

5.1.3   Aquatic life mode and habitat

The skull of *Tertrema acuta* has morphological characters, which are typical for animals with a fully aquatic life mode, such as the lateral line system, conical teeth and an elongated, slim skull shape.

The lateral line system is well-developed, as shown by broad grooves on the pre- and postorbital external surface of the skull roof bones. The lateral line system is a tactile sense organ which enables the detection of movements (e.g., of prey) and pressure changes in the surrounding water (Dijkgraaf, 1963; Wright, 1951). This organ is unique to aquatic vertebrates, such as fossil and recent fish and amphibians. In recent amphibians, the development of the lateral line system is directly connected to their habitats: The line system is disappearing when the animal leaves the aquatic nursery ground for a mainly terrestrial life, as seen in many modern salamanders, frogs and toads (Dijkgraaf, 1963). However, some fully aquatic species keep their lateral line system throughout life, as for example newts (Wright, 1951). The fossil record of temnospondyls shows a similar pattern: Most species with lateral lines in adulthood are believed to be at least semi-aquatic (Dijkgraaf, 1963; Schoch, 2009), whereas some terrestrial temnospondyl forms lost their lateral lines through ontogeny associated with the habitat shift (Schoch, 2009). To conclude, the evidence of the remaining lateral lines in the adult specimens of *Tertrema acuta* implies that this species was adapted for a perpetual life in the water.

Aquatic lifestyle and diet can also be deduced from the shape of the teeth (Fortuny et al., 2011). The palate of *T. acuta* presents two dense rows of conical, slender and pointy teeth. The outer row is relatively homodontic with smaller teeth, while the inner row shows middle-sized teeth and large tusks. This tooth pattern is usually linked with a piscivorous feeding, because it is an effective way of capturing fish by piercing it on a long row of pointed teeth (Massare, 1987). This dentition has evolved independently in many aquatic predators of different groups. Famous fossil and recent examples are marine reptiles like ichthyosaurs, plesiosaurs, crocodiles and gharials (Massare, 1987), the toothed birds *Ichthyornis* and *Hesperornis* (Dumont et al., 2016) and dolphins within the mammals (Werth, 2000). The shape, size and function of the dentition of temnospondyl amphibians shows another case for this convergent evolution and therefore enables the interpretation of *T. acuta's* diet. The small pointed teeth are not effective for cutting, but optimal for grappling fish and possibly other slippery prey, which could be swallowed in one piece. The bigger tusks probably allowed this species to prey on bigger fish as well. The recurved shape of these tusks might had the function to help manoeuvring the prey towards the throat (Massare, 1987).

The skull shape of *Tertrema acuta* is characterised by an elongated, narrow and constricted snout, and small, oval orbits. An ecomorphological study on bite stress of various temnospondyl snout morphotypes by Fortuny et al. (2011) showed that these characteristics are an adaption for a fast lateral movement of the head to catch fast, agile and small prey, such as fish, supporting a fully aquatic feeding mode. This was previously considered for temnospondyls with similar skulls (e.g. (Witzmann, 2006)), and has been also observed in

various recent semi-aquatic or aquatic animals (Taylor, 1987), for example long-snouted crocodiles and gharials (Cleuren and de Vree, 2000), the slender fish *Lepisosteus* (Lauder and Norton, 1980) or in aquatic mammals such as river dolphins (Werth, 2000). In contrast, Fortuny et al. (2011) considers skulls characterised by broad and short snouts and round orbits to be characteristics of terrestrial or amphibious feeders, a feature particularly common amongst basal temnospondyl forms. Thus, the gradual elongation from short, broad snouts to constricted and elongated snouts within Temnospondyli seems to be an evolutionary trend from a generalist to specialist feeding strategy (Fortuny et al., 2011). Based on the highly adapted skull morphology of *T. acuta* we consider this species as a fully aquatic predator.

The morphology of *T. acuta* indeed reflects a fully aquatic life mode, however does not answer the question: in which habitat did the species live? Wiman (1914) suggested a marine habitat of the temnospondyls from the 'Fish-Layer', because it is characterised by shales which produced a rich and clearly marine fossil fauna. He argued that the absence of land plant fossils supported autochthonous deposition rather than a distally transported assemblage of the temnospondyls. Nevertheless, only temnospondyl skull fossils were reported from Svalbard, with no articulated skeletons preserved which would reinforce Wiman's (1914) hypothesis and western Spitzbergen exposes a close, concurrent deltaic system (Mørk, 2015). Also, a prior isotopic analysis of $^{87}Sr/^{86}Sr$ ratios on bones and coprolites of Svalbard temnospondyls compromises on the 'marine' hypothesis, which recovered values which were typical for fresh water (Lindemann et al., 1991). Indeed other, comparable palaeocommunities to this of Svalbard (Kear et al., 2016), as for example from the Sakamena Formation of Madagascar are clearly deposited in littoral sediments (Lehman, 1979). Moreover, *Tirraturhinus smisseni* has been found in fluvial deposits (Nield et al., 2006; Warren et al., 2006). A close relationship between *T. acuta* and *T. smisseni* is predicted, which would reinforce the littoral or even anadromous lifestyle interpretation for *T. acuta* and other Svalbard temnospondyls. However, neither the marine life hypothesis, nor the relationship of the two species can be verified here, until more fossils are found in the respective depositional settings within Svalbard.

5.2   Phylogenetic position of Tertrema acuta within trematosaurid temnospondyls

Our simulations of the datasets of Fortuny et al. (2017) and Fernández-Coll et al. (2018) showed comparable results to the previous studies, however, both expressed lower resolution, resulting in two (Fortuny et al. database) or four (Fernández-Coll et al. database) unresolved single taxa. Nevertheless, our analysis resulted in both cases with at least seven steps shorter trees and comparable CI and RCI values. Since the analyses were undertaken as described by the authors with the same version of PUAP* (but for Macintosh herein instead of Windows), these differences cannot be explained herein. Nevertheless, these discrepancies had no relevance for the position of *Tertrema acuta*, which was placed both times within the Trematosaurine clade. Hence, it was shown that our character state changes were the reason for a drastic repositioning of *T. acuta* into the Lonchorhynchinae clade.

In order to interpret the node support, only global synapomorphies (3.2.2, 6) for the particular nodes were taken into account. Other (non-global) synapomorphies are variable between the different (but statistically equally robust) MPTs, and therefore have no informative value. Furthermore, ACCTRAN and DELTRAN are two algorithms which do not change the tree itself, but push the distributions of character changes to the most possible extremes: Under ACCTRAN, changes are assigned as close to the root of the tree as possible (Agnarsson and Miller, 2008). This algorithm is in more common use, because it is believed to preserve the 'stronger' hypothesis of homology, rather than an independent gain of complex traits and accepts reversals of primitive states (Agnarsson and Miller, 2008). In contrast, under DELTRAN changes are assigned as close to the tips of the trees as possible. Hence, DELTRAN favours homoplasy, or in other words, independent gains of complex traits (Agnarsson and Miller, 2008). Although favouring homology over homoplasy might be a case of philosophy, there are theoretical reasons to favour one over the other optimization process depending on the input data. For instance, a distinguishing property of ACCTRAN is that it distributes the character changes more monotonically over the branches, while DELTRAN does the opposite (Agnarsson and Miller, 2008). Hence, ACCTRAN is more appropriate where consistency in character changes can be expected (as for example in molecular mutations)(Agnarsson and Miller, 2008). In contrast, if consistency is unlikely, as it is often the case in morphological characters, DELTRAN might be more appropriate (Agnarsson and Miller, 2008). Because of our morphological database and the probable evolutionary pressure towards the adaption to aquatic habitats, we would favour DELTRAN over ACCTRAN, as opposed to the prior studies (Steyer, 2002; Fortuny et al. 2017; Fernández-Coll, 2018). However, Agnarsson and Miller (2008) demonstrated that the explanations of homology with ACCTRAN or homoplasy with DELTRAN might be problematic to apply as a generic rule, but may be possible on the branch scale. Because of this controversy, we considered synapomorphies which are shared by both ACCTRAN and DELTRAN at the same node as non-contentious ('unequivocal') within the resulting tree. Interpretations based on these unequivocal synapomorphies should be considered the most robust for the phylogenetic placement of *Tertrema acuta*.

Our analysis showed low bootstrap values and Bremer indices, supporting previous findings (Fernández-Coll et al., 2018; Fortuny et al., 2017). This raises doubts regarding the tree

stability on the basis of the compiled database. We found the following points as problematic in our analysis. The low bootstrap and Bremer support as shown in this study as well as in the previous studies (Fernández-Coll et al., 2018; Fortuny et al., 2017) suggested a high amount of character conflict within the database. Furthermore, the character scores of many taxa have been based on literature studies by Steyer (2002), Fortuny et al. (2017) and Fernandez-Coll (2018). This study has shown that first-hand observations of the original material are required, since historical and interpretative illustrations especially might lead to misidentifications of character states which are able to provoke radical changes within the tree morphology. Indeed, an adequate character coding turns out to be impeded by many equivocal formulated character definitions concerning mostly proportions without a standardisation. Unfortunately, even comparisons with other taxa of the database could not clarify the ambiguities, because past interpretations did not seem to be consistent (Fernández-Coll et al., 2018; Fortuny et al., 2017; Steyer, 2002).This might also be crucial in terms of the position shift of *Tertrema acuta*, since those ambiguities concern some of the unequivocal synapomorphies of the relevant clades. For example, within our analysis the Trematosauridae clade is among others supported by a 'knife-edged' cultriform process of the parasphenoid and the Lonchorhynchinae (under DELTRAN) supported by 'large' and 'widely separated' condyles. These are not well-defined character states, and hence, there is a possibility that the position of *Tertrema acuta* is driven by subjective and inconsistent interpretations. A further problem represents the absence of evidence: four of six unequivocal synapomorphies of the Benthosuchidae, and two of five unequivocal synapomorphies supporting the Trematosauridae clade, could not be identified because of missing remains of *Tertrema acuta.* To conclude, inadequate character scoring because of literature-based observations, misinterpretations because of subjective character definitions and missing data are crucial factors for the position of *T. acuta* and possibly also other taxa within the database.

Nevertheless, the phylogenetic reassessment of *Tertrema acuta* revealed a closer relationship to the long-snouted *Cosgriffius campi* and *Aphaneramma* spp. than a highly derived position within the short-snouted trematosaurines. At the same time, two other long-snouted species, *Wantzosaurus elongatus* and *Stoschiosaurus nielseni*, could not be fit either into the Lonchorhynchinae or the Trematosaurinae. This raises the question about the validity of the monophyletic origin of the long-snouted species, which was shown by the analyses of Steyer (2002), Fortuny et al. (2017) and Fernández-Coll et al. (2018). Furthermore, Schoch (2006) found the taxon *Trematolestes hagdoni* resembling Lonchorhynchines in some characters, whereas the entire snout length of the adult form is indeterminable because the anterior part of the specimen is incomplete. Schoch (2006) presents a phylogenetic tree with a gradual evolution from short- to long-snouted species, with *Tertrema acuta* more derived than the short-snouted *Platystega depressa,* but as a sister group of *Trematolestes hagdorni* + the long-snouted Lonchorhynchinae clade. However, Schoch (2006) points out that the understanding of the phylogeny and functional morphology of this diverse group is still problematic, especially because of the lack of post-cranial remains. Hence, we must conclude, that more complete data is necessary to resolve the problems of the intrarelationships of the

Trematosauridae clade. So far, neither the monophyletic origin nor the gradual evolution of the long-snouted trematosaurs could be confirmed and might me more complex, considering their worldwide distribution, broad diversifications and often varied habitats and life modes. Specifically, the long and slender skull-shape might have evolved multiple times, in response to similar evolutionary pressure towards a fully aquatic and piscivorous lifestyle. Such evolutionary convergences could explain the severely destabilised phylogenetic interpretations presented here.

6   Conclusions and outlook

The aim of this thesis was to provide modern anatomical descriptions and illustrations of the holotype and the Edwardsfjellet specimens of the taxon *Tertrema acuta,* a trematosaurid temnospondyl from the Olenekian of the Vikinghøgda Formation of Svalbard.

From the skull morphology, palaeobiological features of this species were derived. The development of the reticular pattern of the dermal skull ornamentation revealed that both specimens must have reached adulthood. Thereby, the reticular pattern of the holotype is stronger developed than in the Edwardsfjellet specimen and therefore probably reached an older age. The lateral line system of the holotype shows a distinctive trifurcation of the infraorbital grooves, whereas the Edwardsfjellet specimen shows a bifurcation at the same place. However, more fossils are necessary in order to specify, if this represents inter- or intraspecific variation. In addition to the retained lateral line system in adulthood, *T. acuta* shows further adaptations for a piscivorous feeding mode as a long and slender head and rows of small conical teeth.

Furthermore, we compared the Australian trematosaurid *Tirrathurhinus smisseni* to *T. acuta* which were considered to be closely related (Nield et al., 2006). Our first-hand observations on both type materials confirmed the similarity, but the poor preservation of *T. smisseni* did not allow further interpretations concerning the relationship.

By utilising and updating the pre-existing character matrix of former studies (Steyer, 2002; Fortuny et al., 2017; Fernández-Coll et al.;2018), the phylogenetic reassessment of *Tertrema acuta* examined the interrelationships of trematosaurids resulting in a radical position change. The replacement of the literature-based scores with our first-hand data shifted *Tertrema acuta* from the Trematosaurinae into a Lonchorhynchinae clade. Furthermore, the two long-snouted taxa *Stoschiosaurus nielseni* and *Wantzosaurus elongatus* were moved into a basal trematosaur polytomy. Hence, the dichotomy of the Trematosauridae into a long-snouted lonchorhynchine monophylum and a short-snouted trematosaurine monophylum as shown by Steyer (2002), Fortuny et al. (2017) and Fernández-Coll et al. (2018) could not be supported by our analysis.

In order to optimise the character scores of *Tertrema acuta*, the subjective character interpretations must be improved by first hand comparisons with the reference material of the original data matrix (Steyer, 2002). However, to improve the informative value of the analysis, literature-based character scores should be replaced with first-hand observed scores, in order to avoid misinterpretations. Furthermore, more complete fossils are necessary to fill data gaps.

A better understanding of the interspecific relationships of this group will facilitate further palaeobiogeographical interpretations and hence contribute to the understanding of the origin and rapid, global-wide dispersal of the group after the end-Permian mass extinction.

7 Acknowledgements

8 References

Agnarsson, I., Miller, J.A., 2008. Is ACCTRAN better than DELTRAN? Cladistics 24, 1032–1038.

Benton, M., 2014. Vertebrate Palaeontology, 4th ed Wiley-Blackwell.

Birkenmajer, K., Jerzmańska, A., 1979. Lower Triassic shark and other fish teeth from Hornsund, south Spitsbergen. Studia Geologica Polonica 60, 7–37.

Błażejowski, B., 2004. Shark teeth from the Lower Triassic of Spitsbergen and their histology. Polish Polar Research 25, 153–167.

Boy, J.A., 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland) Hessisches Landesamt für Bodenforschung.

Boy, J.A., 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon–Trias); The larvae of rhachitomous amphibia (Amphibia: Temnospondyli; Carboniferous–Triassic). Paläontologische Zeitschrift 48, 236–268.

Buchan, S., Challinor, A., Harland, W., Parker, J., 1965. The Triassic Stratigraphy of Svalbard. Oslo: Norsk Polarinstitutt Skrifter.

Burgess, S.D., Bowring, S., Shen, S.-z., 2014. High-precision timeline for Earth's most severe extinction. Proceedings of the National Academy of Sciences 111, 3316–3321.

Bystrow, A., 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. Acta Zoologica 16, 65–141.

Bystrow, A., Efremov, J., 1940. *Benthosuchus sushkini* Efr.—a labyrinthodont from the Eotriassic of Sharzhenga River. Trudy Paleontologicheskogo Instituta 10, 1–152.

Carroll, R.L., 1988. Vertebrate Paleontology and Evolution. New York: W.H. Freeman and Company.

Cleuren, J., de Vree, F., 2000. Feeding in crocodylians, in: Schwenk, K. (Ed.), Feeding. New York, Boston, and London: Academic Press, 337–358.

Cosgriff, J., Garbutt, N., 1972. *Erythrobatrachus noonkanbahensis*, a trematosaurid species from the Blina Shale. Journal of the Royal Society of Western Australia 55, 5–18.

Cosgriff, J.W., 1984. The temnospondyl labyrinthodonts of the earliest Triassic. Journal of Vertebrate Paleontology 4, 30–46.

Cox, C., Smith, D.G., 1973. A review of the Triassic vertebrate faunas of Svalbard. Geological Magazine 110, 405–418.

Damiani, R.J., Yates, A.M., 2003. The Triassic amphibian *Thoosuchus yakovlevi* and the relationships of the Trematosauroidea (Temnospondyli: Stereospondyli). Records of the Australian Museum 55, 331–342.

Dijkgraaf, S., 1963. The functioning and significance of the lateral-line organs. Biological Reviews 38, 51–105.

Dumont, M., Tafforeau, P., Bertin, T., Bhullar, B.-A., Field, D., Schulp, A., Strilisky, B., Thivichon-Prince, B., Viriot, L., Louchart, A., 2016. Synchrotron imaging of dentition provides insights into the biology of *Hesperornis* and *Ichthyornis*, the "last" toothed birds. BMC Evolutionary Biology 16, 178.

Fernández-Coll, M., Arbez, T., Bernardini, F., Fortuny, J., 2018. Cranial anatomy of the Early Triassic trematosaurine *Angusaurus* (Temnospondyli: Stereospondyli): 3D endocranial insights and phylogenetic implications. Journal of Iberian Geology, 1–18.

Fielding, C.R., Frank, T.D., Isbell, J.L., 2008. The late Paleozoic ice age—A review of current understanding and synthesis of global climate patterns. Geological Society of America Special Papers 441, 343–354.

Fortuny, J., Gastou, S., Escuillié, F., Ranivoharimanana, L., Steyer, J.-S., 2017. A new extreme longirostrine temnospondyl from the Triassic of Madagascar: Phylogenetic and palaeobiogeographical implications for trematosaurids. Journal of Systematic Palaeontology 16, 675–688.

Fortuny, J., Marcé-Nogué, J., De Esteban-Trivigno, S., Gil, L., Galobart, À., 2011. Temnospondyli bite club: Ecomorphological patterns of the most diverse group of early tetrapods. Journal of Evolutionary Biology 24, 2040–2054.

Gregory, J.W., 1921. Note on the sequence across central Spitsbergen from Advent Bay to Agardhs Bay. Geological Magazine 58, 295–296.

Hammer, W., 1987. Paleoecology and phylogeny of the Trematosauridae. American Geophysical Union, Geophysical Monograph Series 41, 73–83.

Hellrung, H., 1987. Revision von *Hyperokynodon keuperinus* Plieninger (Amphibia: Temnospondyli) aus dem Schilfsandstein von Heilbronn (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde Serie B (Geologie unad Paläontologie) 136, 1–28.

Janvier, P., 1992. Les écailles des Trématosaures (Tetrapoda; Temnospondyli): nouvelles données sur les Trématosaures du Trias Inférieur de Madagascar. Bulletin du Muséum national d'histoire naturelle 4, 3–13.

Kear, B.P., Poropat, S.F., Bazzi, M., 2016. Late Triassic capitosaurian remains from Svalbard and the palaeobiogeographical context of Scandinavian Arctic temnospondyls. Geological Society, London, Special Publications 434, 113–126.

Kearney, M., Clark, J.M., 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. Journal of Vertebrate Paleontology 23, 263–274.

Lauder, G., Norton, S., 1980. Asymmetrical muscle activity during feeding in the gar, *Lepisosteus oculatus*. Journal of Experimental Biology 84, 17–32.

Lehman, J.-P., 1979. Nouveaux trématosaures de Madagascar: les stégocéphales malgaches et leur paléoécologie par. Annales de Paléontologie Vertébré 65, 35–53.

Lindemann, F., Kielan-Jaworowska, Z., Heintz, N., 1991. Temnospondyls and the Lower Triassic paleogeography of Spitsbergen, Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota Contributions from the Paleontological Museum, University of Oslo, 39–40.

Lowy, J., 1949. A labyrinthodont from the Trias of Bear Island, Spitsbergen. Nature 163, 1002.

Massare, J.A., 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7, 121–137.

Matthews, S., 1973. Notes on open nomenclature and on synonymy lists. Paleontology 16, 713–719.

Milner, A.R., 1988. The relationships and origin of living amphibians, in: Benton, M.J. (Ed.), The Phylogeny and Classification of the Tetrapods. Oxford: Clarendon Press, 59–102.

Milner, A.R., 1990. The radiation of temnospondyl amphibians, in: Taylor, P.D., Larwood, G.P. (Eds.), Major Evolutionary Radiations. Oxford: Clarendon Press, 321–349.

Mørk, A., 2015. Historical Geology: Triassic. Geoscience atlas of Svalbard, Norwegian Polar Institute, report series 148, 114–117.

Mørk, A., Dallmann, W., Dypvik, H., Johannessen, E., Larssen, G., Nagy, J., Nøttvedt, A., Olaussen, S., Pchelina, T., Worsley, D., 1999a. Mesozoic lithostratigraphy. Tromsø: Norsk Polarinstitutt.

Mørk, A., Elvebakk, G., Forsberg, A.W., Hounslow, M.W., Nakrem, H.A., Vigran, J.O., Weitschat, W., 1999b. The type section of the Vikinghogda Formation: A new Lower Triassic unit in central and eastern Svalbard. Polar Research 18, 51–82.

Mørk, A., Knarud, R., Worsley, D., 1982. Depositional and diagenetic environments of the Triassic and Lower Jurassic succession of Svalbard. CSPG Special Publications 8, 371–398.

Morkovin, B., 2015. On the development of surface ornamentation of skull bones in the ontogeny of Early Triassic benthosuchids (Amphibia, Temnospondyli). Paleontological Journal 49, 57–69.

Nield, C.M., Damiani, R., Warren, A., 2006. A short-snouted trematosauroid (Tetrapoda, Temnospondyli) from the Early Triassic of Australia: the oldest known trematosaurine. Alcheringa 30, 263–271.

Nilsson, T., 1942. *Sassenisaurus*, a new genus of Eotriassic stegocephalians from Spitsbergen. Bulletin of the Geological Institution of the University of Upsala 30, 91–102.

Nilsson, T., 1943a. On the morphology of the power jaw of "stegocephalia" with special reference to Eotriassic stegocephalians from Spitsbergen, part 1. Kungslinga Svenska Vetenskapsakademiens Handlingar 20, 1–46.

Nilsson, T., 1943b. Über einige postkraniale Skelettreste der triassischen Stegocephalen Spitzbergens. Bulletin of the Geological Institution of the University of Upsala 30, 227–272.

Nilsson, T., 1946. On the genus *Peltostega* Wiman and the classification of the Triassic stegocephalians. Kungliga Svenska vetenskapsakademiens handlingar 23, 1–55.

Novikov, I., 2010. New data on trematosauroid labyrinthodonts of Eastern Europe: 2. *Trematosaurus galae* sp. nov.: Cranial morphology. Paleontological Journal 44, 457–467.

Pčelina, T., 1980. Novye dannye po pograničnym slojam triasa i jury na arhipelage Svalbard (New data on the Triassic/Jurassic boundary beds in the Svalbard Archipelago), in: Semevskij, D. (Ed.), Geologija osadočnogo čechla arhipelaga Svalbard (Geology of the sedimentary cover of Svalbard), . Leningrad: NIIGA, 4–60.

Pčelina, T., 1983. Novye dannye po stratigrafii mezozoja archipelaga Špicbergen (New data on the Mesozoic stratigraphy of the Spitsbergen Archipelago). Leningrad: PGO Sevmorgeo.

Preto, N., Kustatscher, E., Wignall, P.B., 2010. Triassic climates—state of the art and perspectives. Palaeogeography, Palaeoclimatology, Palaeoecology 290, 1–10.

Rinehart, L.F., Lucas, S.G., 2013. The functional morphology of dermal bone ornamentation in temnospondyl amphibians. Albuquerque: New Mexico Museum of Natural History and Science.

Romer, A.S., 1947. Review of the Labyrinthodontia. Bulletin of the Museum of Comparative Zoology Harvard 99, 1–367.

Ruta, M., Benton, M.J., 2008. Calibrated diversity, tree topology and the mother of mass extinctions: the lesson of temnospondyls. Palaeontology 51, 1261–1288.

Säve-Söderbergh, G., 1935. On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia, with special reference to Eotriassic stegocephalians from East Greenland. Meddelelser om Grønland 98, 1–211.

Säve-Söderbergh, G., 1936. On the morphology of Triassic stegocephalians from Spitsbergen, and the interpretation of the endocranium in the Labyrinthodontia. Kungliga Svenska vetenskapsakademiens handlingar, series 3 16, 1–181.

Säve-Söderbergh, G., 1937. On the dermal skulls of *Lyrocephalus*, *Aphaneramma*, and *Benthosaurus*, labyrinthodonts from the Triassic of Spitsbergen and N. Russia. Bulletin of the Geological Institution of the University of Uppsala 27, 189–208.

Scheyer, T.M., Romano, C., Jenks, J., Bucher, H., 2014. Early Triassic marine biotic recovery: The predators' perspective. PLoS One 9, e88987.

Schoch, R.R., 2006. A complete trematosaurid amphibian from the Middle Triassic of Germany. Journal of Vertebrate Paleontology 26, 29–43.

Schoch, R.R., 2008. A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae. Zoological Journal of the Linnean Society 152, 79–113.

Schoch, R.R., 2009. Evolution of life cycles in early amphibians. Annual Review of Earth and Planetary Sciences 37, 135–162.

Schoch, R.R., 2013. The evolution of major temnospondyl clades: An inclusive phylogenetic analysis. Journal of Systematic Palaeontology 11, 673–705.

Schoch, R.R., Milner, A.R., 2000. Stereospondyli. Munich: Pfeil.

Schoch, R.R., Milner, A.R., Hellrung, H., 2002. The last trematosaurid amphibian *Hyperokynodon keuperinus* revisited. Stuttgarter Beiträge zur Naturkunde. Serie B, Geologie und Paläontologie 321, 1–9.

Shishkin, M., 1973. The morphology of the early Amphibia and some problems of the lower tetrapod evolution. Trudy Paleontologicheskogo Instituta 137, 1–260.

Sorenson, M., Franzosa, E., 2007. TreeRot, version 3. Boston, Massachusetts: Boston University.

Späth, L., 1921. On ammonites from Spitzbergen. Geological Magazine 58, 347–356.

Stensiö, E.A., 1918. Notes on some fish remains collected at Hornsund by the Norwegian Spitzbergen Expedition in 1917. Norsk Geologisk Tidsskrift 5, 75–78.

Stensiö, E.A., 1921. Triassic fishes from Spitzbergen Part 1. Vienna: A. Holzhausen.

Stensiö, E.A., 1925. Triassic fishes from Spitzbergen Part 2. Kungliga Svenska vetenskapsakademiens handlingar, series 3 2, 1–261.

Steyer, J.S., 2002. The first articulated trematosaur 'amphibian' from the Lower Triassic of Madagascar: Implications for the phylogeny of the group. Palaeontology 45, 771–793.

Swofford, D., 2002. PAUP* version 4.0 b10, Sunderland, Massachusetts Sinauer.

Taylor, M.A., 1987. How tetrapods feed in water: A functional analysis by paradigm. Zoological Journal of the Linnean Society 91, 171–195.

von Jäger, G.F., 1824. De ichthyosauri sive proteosauri fossilis speciminibus in agro Bollens in Würtembergia repertis.

von Jäger, G.F., 1828. Über die fossile reptilien: welche in Würtemberg aufgefunden worden sind. Stuttgart: JB Metzler.

von Meyer, H., Plieninger, T., 1844. Beiträge zur Paläontologie Württemberg's: enthaltend die fossilen wirbelthierreste aus den triasgebilden mit besonderer rücksicht auf die Labyrinthodonten des Keupers. Stuttgart: E. Schweizerbart.

Warren, A., Black, T., 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia, and the relationships of Triassic temnospondyls. Journal of Vertebrate Paleontology 5, 303–327.

Warren, A., Damiani, R., Yates, A., 2006. The South African stereospondyl *Lydekkerina huxleyi* (Tetrapoda, Temnospondyli) from the Lower Triassic of Australia. Geological Magazine 143, 877–886.

Warren, A., Rich, T.H., Vickers-Rich, P., 1997. The last last labyrinthodonts. Palaeontographica Abteilung A 247, 1–24.

Watson, D.M.S., 1919. The structure, evolution and origin of the Amphibia. The" Orders' Rachitomi and Stereospondyli. Philosophical Transactions of the Royal Society of London, Series B 209, 1–73.

Watson, D.M.S., 1926. Croonian lecture: The evolution and origin of the Amphibia. Philosophical Transactions of the Royal Society of London, Series B 214, 189–257.

Watson, D.M.S., 1940. VII—The origin of frogs. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 60, 195–231.

Watson, D.M.S., 1958. A new labyrinthodont (*Paracyclotosaurus*) from the Upper Trias of New South Wales. Bulletin of the British Museum of Natural History, London (Geology) 3, 233–263.

Watson, D.M.S., 1962. The evolution of the labyrinthodonts. Philosophical Transactions of the Royal Society of London, Series B 245, 219–265.

Welles, S.P., 1993. A review of the lonchorhynchine trematosaurs (Labyrinthodontia), and a description of a new genus and species from the Lower Moenkopi Formation of Arizona. PaleoBios 14, 1–14.

Werneburg, R., Steyer, J.-S., 1999. Redescription of the holotype of *Actinodon frossardi* (Amphibia, Temnospondyli) from the Lower Permian of the Autun basin (France). Geobios 32, 599–607.

Werth, A., 2000. Feeding in marine mammals, in: Schwenk, K. (Ed.), Feeding: Form, Function and Evolution in Tetrapod Vertebrates. San Diego: Academic Press, 475–514.

Wilkinson, M., 1995. Arbitrary resolutions, missing entries, and the problem of zero-length branches in parsimony analysis. Systematic Biology 44, 108–111.

Wilkinson, M., 2003. Missing entries and multiple trees: Instability, relationships, and support in parsimony analysis. Journal of Vertebrate Paleontology 23, 311–323.

Wiman, C., 1910a. Ein paar Labyrinthodontenreste aus der Trias Spitzbergens. Bulletin of the Geological Institution of the University of Upsala 9, 36–40.

Wiman, C., 1910b. Ichthyosaurier aus der Trias Spitzbergens. Bulletin of the Geological Institution of the University of Upsala 10, 124–148.

Wiman, C., 1913. Über das Hinterhaupt der Labyrinthodonten. Bulletin of the Geological Institution of the University of Upsala 12, 1–8.

Wiman, C., 1914. Über die Stegocephalen aus der Trias Spitzbergens. Bulletin of the Geological Institution of the University of Upsala 13, 1–34.

Wiman, C., 1916a. Neue Stegocephalenfunde aus dem posidonomyaschiefer Spitzbergens. Bulletin of the Geological Institution of the University of Upsala 13, 209–222.

Wiman, C., 1916b. Notes on the marine Triassic reptile fauna of Spitzbergen. University of California Publications, Bulletin of the Department of Geology 10, 63–73.

Wiman, C., 1917. Über die Stegocephalen *Tertrema* und *Lonchorhynchus*. Bulletin of the Geological Institution of the University of Upsala 14, 229–240.

Wiman, C., 1928. Eine neue Reptilien-Ordnung aus der Trias Spitzbergens. Bulletin of the Geological Institution of the University of Upsala 22, 183–196.

Witzmann, F., 2006. Cranial morphology and ontogeny of the Permo-Carboniferous temnospondyl *Archegosaurus decheni* Goldfuss, 1847 from the Saar-Nahe Basin, Germany. Earth and Environmental Science Transactions of The Royal Society of Edinburgh 96, 131–162.

Witzmann, F., Scholz, H., Mueller, J., Kardjilov, N., 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. Zoological Journal of the Linnean Society 160, 302–340.

Woodward, A.S., 1904. On two new labyrinthodont skulls of the genera *Capitosaurus* and *Aphaneramma*. Journal of Zoology 74, 170–176.

Wright, M.R., 1951. The lateral line system of sense organs. The Quarterly Review of Biology 26, 264–280.

Yates, A.M., Warren, A.A., 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. Zoological Journal of the Linnean Society 128, 77–121.

Zittel, K.A., 1888. Paläozoologie Band III, Vertebrata (Pisces, Amphibian, Reptilia, Aves). München: Oldenbourg.

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Wikimedia Commons (username: Tentotwo), "Arctic Ocean location map", under: https://commons.wikimedia.org/wiki/File:Arctic_Ocean_location_map.svg , (accessed 15.10.2018)

9   Supplemental material

9.1   Character list

Character list developed by Steyer (2002), 0 is the plesiomorphic state.

Characters of the skull roof

1. Skull roof elongate (midline length > maximum width; 1) or not (0).

2. Position of the centre of the orbit along the dorsal midline of the skull: orbit posteriorly (0) or anteriorly (1) situated.

3. Short (0), constricted (1), or elongated (2) snout (preorbital part of the skull twice longer than the postorbital one; 2).

4. Large (0) or small orbit (maximum size < 14 per cent of the dorsal midline length; 1).

5. Orbit facing laterally (1) or dorsally (0).

6. Rounded (0) or oval (1) orbit.

7. Slightly concave (0) or semicircular (1) posterior margin of the skull roof.

8. Nostril rounded (0), ovoid (1), or elongate (2).

9. Nostril in lateral position (1) or not (0).

10. Skull roof bulged (1) or not (0) at the level of the orbits.

11. Pineal foramen small (0) or large (1) relative to the size of the skull roof.

12. Pineal foramen rounded (0) or not (1).

13. Presence (1) or absence (0) of sensory-line grooves in front of the orbits.

14. Presence (0) or absence (1) of sensory-line grooves behind orbits.

15. Frontal extended behind orbit (1) or not (0).

16. Frontal in contact with orbit (1) or not (0).

17. Presence (1) or absence (0) of the interfrontal.

18. Presence (1) or absence (0) of the centroparietal.

19. Septomaxilla visible (0) or not (1) on the dorsal side of the skull.

20. Otic notch deep and narrow (0), or deep and open (1), or shallow and open (2).

21. Tabular rounded (0), pointed (1), or hook-shaped (2).

22. Quadrate condyle posterior (0) or anterior (1) to the occipital condyle.

23. Presence (1) or absence (0) of an anterodorsal dentary foramen.

24. Premaxilla/nasal suture posteriorly directed (the premaxilla is partly extended posterior to the nostril; 0), straight (1), or anterior directed (2).

25. Presence (1) or absence (0) of a prenarial growth zone.

26. Presence (1) or absence (0) of a `temporal fossa' (sensu Damiani 1998; a slight depressed region of the skull roof anteriorly to the otic notches).

27. Ventral opening of the orbit at the level of the posterior half (0), in the mid part (1), or in the anterior half (2) of the interpterygoid vacuity.

Characters of the palate

28. Vomer in contact (1) or not (0) with the maxilla.

29. Choana rounded (0) or elongate (1).

30. Choana overlapping the nostril (1) or not (0).

31. Absence (0) or presence of a single (1) or of a paired (2) anteropalatal vacuity.

32. Anteropalatal vacuity(ies) posterior (0), between (1), or anterior (2) to the premaxilla/vomerine suture.

33. Interpterygoid vacuity posteriorly (0) or anteriorly (1) widened, or not widened at all (2).

34. Presence (1) or absence (0) of a crista obliqua on the ventral surface of the pterygoid.

35. Anterior branch of the pterygoid laterally extended (0), entirely wide (1), or narrow (2).

36. Posterior branch (quadrate ramus) of the pterygoid narrow and elongate (0), or short and wide (1).

37. Presence (0) or absence (1) of an area asparta of the pterygoid.

38. Wide (0), narrow (1) or knife-edged (2) cultriform process of the parasphenoid.

39. Elongate (0) or very short (or absent) (1) suture between the palatine and the pterygoid.

40. Very short (0) or elongate (1) suture between the pterygoid and parasphenoid.

41. Wide (width>length; 0) or narrow (length > width; 1) parasphenoid plate.

42. Presence (1) or absence (0) of the crista muscularis of the parasphenoid.

43. Carotid canal visible (1) or not (0) on the ventral surface of the parasphenoid.

44. Presence (0) or absence (1) of ectopterygoidal tusks.

45. Suture between the exoccipital and the pterygoid visible (1) or not (0) in ventral view.

Characters of the occiput

46. Presence (1) or absence (0) of the paraquadrate foramen (foramen for the chorda tympani).

47. Flattened (0) or deep (1) occiput, in occipital view.

48. Dorsally (0) or ventrally (1) directed tabular, in occipital view.

49. Small (0) or large (1) occipital condyle.

50. Occipital condyles widely separated (0) or not (1) from each other.

51. Foramen magnum ventrally constricted (1) or not (0).

52. Curved (0) or straight (1) dorsal margin of the foramen magnum.

53. Presence (1) or absence (0) of the crista falciformis of the squamosal, in occipital view.

54. Shallow (0) or deep (1) posttemporal fenestra.

55. Elongate (0), triangular (1) or rounded (2) posttemporal fenestra.

56. Wide (0) or narrow (1) proximal part of the stapes.

Characters of the mandible

57. Posterior end of the mandible situated at the same level (0) or behind (1) the quadrate condyle.

58. Mandible deep (0) or shallow (1) in lateral view.

59. Presence (1) or absence (0) of an anterior constriction of the ventral outline of the mandible, in lateral view.

60. Reduced (0) or extended (1) dentary symphysis.

61. Presence (1) or absence (0) of a parasymphysial tusk.

62. Presence (0) or absence (1) of a parasymphysial tooth row.

63. Presence (1) or absence (0) of denticles on coronoids 2 and 3.

64. Presence (1) or absence (0) of sensory-line grooves on the mandible.

65. Meckelian foramen short (0) or elongate (1).

66. Poorly developed or absent (0), or well-developed (1) crista medialis (sensu Damiani 1998); a vertical blade on the midline of the postglenoid area (PGA sensu Jupp and Warren 1986).

67. Presence (1) or absence (0) of the crista articularis (sensu Damiani 1998); a vertical blade on the postero-lingual border of the PGA.

Characters of the postcranial skeleton

68. Interclavicle narrow (1) or not (0).

69. Interclavicle with (0) or without (1) dorsal crest(s) (trabeculae sensu Bystrow and Efremov 1940; i.e. relatively wide and flat walls posteriorly and antero-laterally directed on the dorsal surface of the interclavicle).

9.2 Terminal taxa of the phylogenetic analysis

Institutional Abbreviations

NHMUK: The Natural History Museum, London, UK; **MGUH**: Museum Geologicum Universitatis Hafniensis, Kobenhavn, Denmark; **MNB**: Museum für Naturkunde, Berlin, Germany; **MNHN**: Muséum national d'Histoire naturelle, Paris, France; **MSNM**: Museo di Storia Naturale di Milano, Italy; **PIN**: Paleontological Institute, Moscow, Russian Federation; **PMU**: Museum of Evolution (Palaeontological Museum), Uppsala, Sweden; **SMNS**: Staatliches Museum für Naturkunde in Stuttgart, Germany; **UA**: Université d'Antananarivo, Madagascar. **QMF**: Queensland Museum Fossil, Brisbane, Australia.

Terminal taxa	Specimens	Literature
Angusaurus dentatus	PIN 4196/1	Getmanov 1989; Damiani and Yates, 2003
Angusaurus succedaneus		Getmanov, 1989
Angusaurus tsylmensis	PIN 4333/6	Novikov, 1990
Aphaneramma gavialimimus	UA-Amb007, MNHN-6703	Fortuny et al. in press
Aphaneramma rostratum	MNHN 20-IBSEN 1969, MNHN Rotunda 1964, MNHN St 62, MNHN Tr A 64	Säve-Söderbergh 1936, 1937; Welles 1993; Smith-Woodward 1904; Wiman 1916
Aphaneramma kokeni		Huene 1920; Welles, 1993
Archegosaurus decheni	MNB Am 114-119, 121-131, 137 MNHN 1868-1-4 1870-479-480, MNHN 1884-10, 21-25;	Gubin 1997; Jaeckel 1896; Witzmann 2006
Benthosuchus sushkini	PIN 2424/4, PIN 2424/10, PIN 2-19-2252, PIN 2252/41	Bystrow and Efremov, 1940
Cosgriffius campi		Welles 1993
Edingerella madagascariensis	MNHN MAE3000-3009; MSNM V2992	Damiani 1998; Lehman 1961; Warren 1980; Maganuco et al. 2009; Steyer 2003
Inflectosaurus amplus		Jaeckel 1922; Shishkin 1960; Novikov 2007
Lyrocephaliscus euri	MNHN F SVT 520	Säve-Söderbergh 1935, 1936, 1937; Mazin and Janvier 1983
Micropsaurus casei		Damiani 2004
Onchiodon frossardi	MNHN 1908-20-26	Werneburg and Steyer 1999
Platystega depressa		Säve-Söderbergh 1936; Wiman 1916
Prothoosuchus blomi		Getmanov, 1989
Stoschiosaurus nielseni	MGUH At. 6, 7, 9, 12, 23, 43, 45, 46	Säve-Söderbergh 1935
Syrthosuchus samarensis		Novikov, 2016
Thoosuchus yakovlevi	SMNS 58880	Damiani and Yates, 2003; Novikov, 2007

Tertrema acuta	PMU 24148, PMU 24157	Säve-Söderbergh 1936; Wiman 1914, 1916
Tirraturhinus smisseni	QMF 44093	Nield et al 2006
Trematolestes hagdorni	SMNS 81790-91, SMNS 90022,	Schoch 2006
Trematosaurus brauni	BMNH 30270, 36354-75, 40042 MNB Am943 1/3 MNHN AC9573	Burmeister 1849; Drevermann 1920; Lehman 1966, 1979;
Trematosuchus sobeyi		Haughton 1915; Shishkin and Welman 1994
Wantzosaurus elongatus	MNHN MAE 3030, 3034;	Lehman 1961; Steyer 2002

9.3 Character states of *Tertrema acuta* and *Tirraturhinus smisseni*

Table 2 List of previous and rescored character states of Tertrema acuta *and* Tirraturhinus smisseni *for the phylogenetic reassessment. Changes in T. acuta are marked orange. Number codes refer to the character list (see 8.1).*

Character number	Tertrema acuta		Tirraturhinus smisseni	Character number	Tertrema acuta		Tirraturhinus smisseni
	Steyer (2002)	This study	This study		Steyer (2002)	This study	This study
1	1	1	?	36	?	?	?
2	0	0	?	37	1	0	?
3	0	1	?	38	?	1	?
4	1	1	?	39	1	1	?
5	1	1	?	40	1	1	?
6	1	1	?	41	1	0	?
7	0	?	?	42	0	0	?
8	2	2	2	43	0	1	?
9	1	1	1	44	0	0	?
10	0	?	?	45	0	?	?
11	?	?	?	46	?	?	?
12	?	?	?	47	1	1	?
13	1	1	1	48	0	?	?
14	0	0	?	49	1	1	?
15	1	1	?	50	1	1	?
16	?	0	?	51	0	1	?
17	?	?	?	52	1	?	?
18	?	?	?	53	1	?	?
19	1	1	?	54	?	1	?
20	?	?	?	55	1	1	?
21	?	?	?	56	1	?	?
22	?	?	?	57	?	?	?
23	?	?	?	58	?	?	?
24	2	2	2	59	?	?	?
25	0	0	0	60	?	?	?
26	?	?	?	61	?	?	?
27	1	1	?	62	?	?	?
28	1	1	1	63	?	?	?
29	1	1	?	64	?	?	?
30	0	0	?	65	?	?	?
31	2	2	2	66	?	?	?
32	2	1	1	67	?	?	?
33	1	1	?	68	?	?	?
34	1	?	?	69	?	?	?
35	0	1	?				

9.4 Matrix

Updated character matrix after Steyer (2002), Fortuny et al. (2017) and Fernandez-Coll et al. (2018). Number codes refer to the character states (see

```
Aphaneramma_gavialimimus
10211101100010100011121?2102110??2?2?02?11?11????????????????????????
Aphaneramma_kokeni
1???11???000101001?1????1?2??????0?2102111???????????????????????????
Aphaneramma_rostratum
10211101000010100111121?1101110??212102111111011111101111110????11??11
Archegosaurus_decheni
10210112001001000010100200111010012000000111010011 0?00??0100010000011
Benthosuchus_sushkini
10200101000010000011010200011111211000110111010100101101100111 0001000
Cosgriffius_campi
10?111?210??10100?????121?21100-2?????21????0????????????????????????
Edingerella_madagascariensis
10100112100010010010110101011010111000111100010101101101111101 1000111
Inflectosaurus_amplus
1011010000??10100??111??0?1???222110021110000 10?101??100001111 0111?0?
Lyrocephaliscus_euri
00001100000110100002100000210022110102110110110110111121???????????10
Microposaurus_casei
1111110201??1??????110??1?2100210?10021110?001??10?????????????????????
Onchiodon_frossardi
000000000000000000000000000000-000000000000000000000?00000000000000
Platystega_depressa
101111?00111??00?001???200110021110102111??10??????????????????????
Tertrema_acuta_MS
101111?21???1010??1????20?1110211?1?01110010??1?111??11?????????????
Tertrema_acuta_ST
1001110210??101??10????20?111022110?1?1110000?101011?11?????????????
Tirraturhinus_smisseni
???????21???1?????????2???1??21??????????????????????????????????????
Thoosuchus_yakovlevi
10201101101010100001000101011022211002110100010100100 11?0001010?1??00
Trematolestes_hagdorni
11001101101110100001101010021102110110211101001010010010?111101001??11
Trematosaurus_brauni
10011101001010100012010100211020211002111000110000 10111?100????0???0?
Trematosuchus_sobeyi
1001100000100110100200020021102?2000021110?011??????????????????????
Stoschiosaurus_nielseni
????11???000?00000?1?1??10???????110121100 1?0???????????????????????
Syrtosuchus_samarensis
10?1010??0001000001100????01?????2?00001101?00?????????????????????
Wantzosaurus_elongatus
10201112101010000012001210111 12?0?20?2?100??01100 10111?1101???00??11
Angusaurus_dentatus
1011110110101010000110020011110212??0?2110??00101?010011?????????????
Angusaurus_tsylmensis
1011110??01010100001 10??001110??2111021100001010010011?????????????
Angusaurus_succedaneus
101111???010??????????????111?21211?02110?000?0??0??????1001?10?1????
Angusaurus_spp
1011110110101010000110020011 1021211(01)021100000101001 0011?1001?10?1????
Prothoosuchus_blomi
1011110??010100000?110????1?????2111?2?10????1010010?11?????????????
```

9.5 Apomorphy list

Apomorphy lists of the analysis including *Tertrema acuta,* by using the data matrix of Fernnández-Coll (2018).

Under ACCTRAN:

```
/------------------------------------------------------------------ Archegosaurus de
|
|      /----------------------------------------------------------- Onchiodon frossa
|      |
|      |      /-------------------------------------------------- Edingerella mada
\----29      |
       |     |      /------------------------------------------- Benthosuchus sus
       |     |      |
       \----30      |                                    /------ Stoschiosaurus n
             |      |       /------------------------------32
             |      |       |                            \------ Wantzosaurus elo
             \----31       |
                    |      |                    /--------------------- Tertrema acuta M
                    |      |                    |
                    |      |      /--------------42      /----------------- Cosgriffius camp
                    \----33      |              |      |
                          |      |              \----43      /----------- Aphaneramma gavi
                          |      |                    |      |
                          |      |                    \----44      /------ Aphaneramma koke
                          |      |                          \----28
                          \----41                                \------ Aphaneramma rost
                                |
                                |      /-------------------------------- Trematolestes ha
                                |      |
                                |      |      /-------------------------- Thoosuchus yakov
                                \----40      |
                                      |      |      /--------------------- Angusaurus spp
                                      \----39      |
                                            |      |              /------ Trematosaurus br
                                            \----38      /----------36
                                                  |      |              \------ Trematosuchus so
                                                  |      |
                                                  \----37      /----------- Inflectosaurus a
                                                        |      |
                                                        |      +----------- Microposaurus ca
                                                        \----35
                                                              |      /------ Lyrocephaliscus
                                                              \----34
                                                                    \------ Platystega depre
```

Apomorphy lists:

Branch	Character	Steps	CI	Change
node_29 --> node_30	4	1	0.250	1 --> 0
	11	1	0.250	1 --> 0
	14	1	0.500	1 --> 0
	27	1	0.222	1 --> 0
	43	1	0.250	1 --> 0
	44	1	0.250	1 --> 0
	49	1	0.333	1 --> 0
node_30 --> node_31	13	1	0.500	0 --> 1
	22	1	0.200	0 --> 1
	35	1	0.333	2 --> 1
	39	1	1.000	0 --> 1
	40	1	1.000	0 --> 1
	48	1	0.500	0 --> 1
	51	1	1.000	0 --> 1
	53	1	0.333	0 --> 1
	54	1	1.000	0 --> 1
	57	1	0.333	0 --> 1
	60	1	1.000	0 --> 1
node_31 --> node_33	20	1	0.500	0 --> 1
	21	1	0.400	1 --> 0

```
                                   30              1  0.500  0 --> 1
                                   43              1  0.250  0 --> 1
                                   50              1  0.333  1 --> 0
node_33 --> node_41                5               1  0.500  0 --> 1
                                   9               1  0.250  0 --> 1
                                   31              1  0.667  1 --> 2
                                   32              1  0.400  0 --> 1
                                   38              1  1.000  0 --> 2
                                   42              1  0.200  1 --> 0
                                   66              1  1.000  0 --> 1
node_41 --> node_42                15              1  0.500  0 --> 1
                                   27              1  0.222  0 --> 1
                                   30              1  0.500  1 --> 0
                                   33              1  0.250  0 --> 1
                                   55              1  0.500  0 --> 1
node_42 --> node_43                4               1  0.250  0 --> 1
node_43 --> node_44                7               1  0.333  1 --> 0
                                   25              1  0.333  0 --> 1
                                   33              1  0.250  1 --> 2
                                   47              1  0.500  0 --> 1
                                   49              1  0.333  0 --> 1
                                   50              1  0.333  0 --> 1
                                   65              1  1.000  0 --> 1
node_44 --> Aphaneramma gavi 8                     1  0.286  2 --> 1
                                   21              1  0.400  0 --> 2
                                   27              1  0.222  1 --> 2
                                   35              1  0.333  1 --> 2
                                   41              1  0.200  0 --> 1
                                   44              1  0.250  0 --> 1
node_44 --> node_28                8               1  0.286  2 --> 1
                                   9               1  0.250  1 --> 0
                                   18              1  1.000  0 ==> 1
                                   21              1  0.400  0 --> 2
                                   24              1  0.286  2 --> 1
                                   35              1  0.333  1 --> 2
                                   36              1  0.500  0 --> 1
                                   41              1  0.200  0 --> 1
                                   42              1  0.200  0 --> 1
                                   44              1  0.250  0 --> 1
                                   64              1  0.500  0 --> 1
node_28 --> Aphaneramma koke 27                    1  0.222  1 --> 2
                                   33              1  0.250  2 ==> 0
node_43 --> Cosgriffius camp 23                    1  0.500  0 --> 1
                                   25              1  0.333  0 --> 1
                                   27              1  0.222  1 --> 2
                                   31              1  0.667  2 --> 0
                                   33              1  0.250  1 --> 2
node_42 --> Tertrema acuta M 3                     1  0.286  2 ==> 1
                                   4               1  0.250  0 --> 1
                                   38              1  1.000  2 ==> 1
                                   47              1  0.500  0 --> 1
                                   49              1  0.333  0 --> 1
                                   50              1  0.333  0 --> 1
node_41 --> node_40                7               1  0.333  1 --> 0
                                   8               1  0.286  2 ==> 1
                                   11              1  0.250  0 ==> 1
                                   15              1  0.500  0 --> 1
                                   24              1  0.286  2 --> 1
                                   27              1  0.222  0 --> 2
                                   30              1  0.500  1 --> 0
                                   33              1  0.250  0 --> 1
                                   53              1  0.333  1 ==> 0
                                   65              1  1.000  0 --> 1
node_40 --> node_39                19              1  0.333  1 ==> 0
                                   22              1  0.200  1 ==> 0
                                   33              1  0.250  1 --> 2
                                   43              1  0.250  1 ==> 0
                                   55              1  0.500  0 --> 1
                                   58              1  0.333  1 ==> 0
                                   68              1  0.250  1 ==> 0
                                   69              1  0.333  1 ==> 0
node_39 --> node_38                3               1  0.286  2 ==> 1
```

```
                                    4              1  0.250  0 ==> 1
                                    21             1  0.400  0 --> 1
                                    24             1  0.286  1 --> 2
                                    61             1  0.500  0 --> 1
node_38 --> node_37                 8              1  0.286  1 --> 0
                                    9              1  0.250  1 ==> 0
                                    41             1  0.200  0 ==> 1
                                    53             1  0.333  0 ==> 1
node_37 --> node_35                 12             1  0.500  0 --> 1
                                    29             1  0.500  1 ==> 0
                                    49             1  0.333  0 ==> 1
                                    52             1  1.000  0 --> 1
                                    55             1  0.500  1 --> 0
                                    57             1  0.333  1 --> 0
                                    59             1  0.333  0 --> 1
                                    64             1  0.500  0 --> 1
node_35 --> Inflectosaurus a       5              1  0.500  1 ==> 0
                                    22             1  0.200  0 ==> 1
                                    27             1  0.222  2 --> 1
                                    32             1  0.400  1 ==> 2
node_35 --> node_34                 33             1  0.250  2 ==> 1
                                    35             1  0.333  1 ==> 0
                                    36             1  0.500  0 ==> 1
                                    42             1  0.200  0 --> 1
                                    43             1  0.250  0 --> 1
                                    55             1  0.500  0 --> 2
                                    68             1  0.250  0 --> 1
node_34 --> Lyrocephaliscus        1              1  0.500  1 ==> 0
                                    3              1  0.286  1 ==> 0
                                    4              1  0.250  1 ==> 0
                                    11             1  0.250  1 ==> 0
                                    20             1  0.500  1 ==> 2
                                    24             1  0.286  2 ==> 0
                                    32             1  0.400  1 ==> 2
                                    41             1  0.200  1 ==> 0
                                    45             1  0.500  0 ==> 1
node_34 --> Platystega depre       10             1  0.500  0 ==> 1
                                    15             1  0.500  1 ==> 0
                                    27             1  0.222  2 --> 1
                                    44             1  0.250  0 ==> 1
node_35 --> Microposaurus ca       2              1  0.500  0 ==> 1
                                    8              1  0.286  0 ==> 2
                                    10             1  0.500  0 ==> 1
                                    25             1  0.333  0 ==> 1
                                    33             1  0.250  2 ==> 0
node_37 --> node_36                 3              1  0.286  1 ==> 0
                                    20             1  0.500  1 ==> 2
                                    21             1  0.400  1 --> 0
                                    32             1  0.400  1 --> 0
                                    45             1  0.500  0 ==> 1
                                    48             1  0.500  1 --> 0
node_36 --> Trematosaurus br       8              1  0.286  0 --> 1
                                    19             1  0.333  0 ==> 1
                                    22             1  0.200  0 ==> 1
                                    24             1  0.286  2 ==> 1
node_36 --> Trematosuchus so       6              1  0.500  1 ==> 0
                                    13             1  0.500  1 ==> 0
                                    14             1  0.500  0 ==> 1
                                    34             1  0.333  1 ==> 0
                                    35             1  0.333  1 ==> 0
node_38 --> Angusaurus spp         27             1  0.222  2 --> 1
node_39 --> Thoosuchus yakov       26             1  0.500  0 ==> 1
                                    27             1  0.222  2 ==> 0
                                    32             1  0.400  1 ==> 2
                                    42             1  0.200  0 ==> 1
                                    57             1  0.333  1 ==> 0
node_40 --> Trematolestes ha       2              1  0.500  0 ==> 1
                                    3              1  0.286  2 ==> 0
                                    12             1  0.500  0 ==> 1
                                    34             1  0.333  1 ==> 0
                                    36             1  0.500  0 --> 1
                                    41             1  0.200  0 ==> 1
```

63

```
                                     59              1  0.333  0 ==> 1
node_33 --> node_32                   5              1  0.500  0 --> 1
                                      9              1  0.250  0 --> 1
                                     23              1  0.500  0 --> 1
                                     25              1  0.333  0 ==> 1
                                     27              1  0.222  0 --> 1
                                     31              1  0.667  1 --> 2
                                     37              1  1.000  0 --> 1
                                     38              1  1.000  0 --> 2
                                     42              1  0.200  1 --> 0
                                     47              1  0.500  0 --> 1
                                     55              1  0.500  0 --> 1
node_32 --> Wantzosaurus elo 11       1  0.250  0 ==> 1
                                     20              1  0.500  1 ==> 2
                                     22              1  0.200  1 ==> 0
                                     35              1  0.333  1 ==> 2
node_31 --> Benthosuchus sus  7       1  0.333  1 --> 0
                                      8              1  0.286  2 ==> 1
                                     20              1  0.500  0 --> 1
                                     21              1  0.400  1 --> 0
                                     30              1  0.500  0 --> 1
                                     32              1  0.400  0 --> 1
                                     33              1  0.250  0 --> 2
                                     43              1  0.250  0 --> 1
                                     44              1  0.250  0 ==> 1
                                     50              1  0.333  1 --> 0
                                     58              1  0.333  1 ==> 0
                                     61              1  0.500  0 ==> 1
                                     66              1  1.000  0 --> 1
                                     68              1  0.250  1 ==> 0
                                     69              1  0.333  1 ==> 0
node_30 --> Edingerella mada  3       1  0.286  2 ==> 1
                                      9              1  0.250  0 --> 1
                                     13              1  0.500  0 --> 1
                                     22              1  0.200  0 --> 1
                                     24              1  0.286  2 ==> 1
                                     26              1  0.500  0 ==> 1
                                     33              1  0.250  0 --> 1
                                     35              1  0.333  2 --> 1
                                     39              1  1.000  0 --> 1
                                     40              1  1.000  0 --> 1
                                     41              1  0.200  0 ==> 1
                                     48              1  0.500  0 --> 1
                                     51              1  1.000  0 --> 1
                                     53              1  0.333  0 --> 1
                                     54              1  1.000  0 --> 1
                                     57              1  0.333  0 --> 1
                                     59              1  0.333  0 ==> 1
                                     60              1  1.000  0 --> 1
node_29 --> Onchiodon frossa  1       1  0.500  1 ==> 0
                                      3              1  0.286  2 ==> 0
                                      4              1  0.250  1 --> 0
                                      6              1  0.500  1 ==> 0
                                      7              1  0.333  1 --> 0
                                      8              1  0.286  2 ==> 0
                                     11              1  0.250  1 --> 0
                                     14              1  0.500  1 --> 0
                                     19              1  0.333  1 ==> 0
                                     21              1  0.400  1 --> 0
                                     24              1  0.286  2 ==> 0
                                     27              1  0.222  1 --> 0
                                     29              1  0.500  1 ==> 0
                                     31              1  0.667  1 ==> 0
                                     34              1  0.333  1 ==> 0
                                     35              1  0.333  2 --> 0
                                     42              1  0.200  1 ==> 0
                                     43              1  0.250  1 --> 0
                                     44              1  0.250  1 --> 0
                                     49              1  0.333  1 --> 0
                                     50              1  0.333  1 --> 0
                                     58              1  0.333  1 ==> 0
                                     68              1  0.250  1 ==> 0
```

64

```
69              1  0.333  1 ==> 0
```

Under DELTRAN:

```
/------------------------------------------------------------------- Archegosaurus de
|
|      /------------------------------------------------------------ Onchiodon frossa
|      |
|      |    /------------------------------------------------------- Syrtosuchus sama
\---29  |    |
     |   |    |   /--------------------------------------------------- Edingerella mada
     \---30  |    |
         |   |    |   /---------------------------------------------- Benthosuchus sus
         |   |    |   |
         \---31  |    |                                    /----- Stoschiosaurus n
             |   |    |   /------------------------------------33
             |   |    |   |                                \----- Wantzosaurus elo
             \----32  |    |
                 |   |                          /------------------ Tertrema acuta M
                 |   |                          |
                 |   |    /------------------44      /-------------- Cosgriffius camp
                 \---34   |    |                |     |
                     |   |    |                \----45     /---------- Aphaneramma gavi
                     |   |    |                     |    |
                     |   |    |                     \---46     /----- Aphaneramma koke
                     |   |    |                          \---28
                     \---43   |                               \----- Aphaneramma rost
                         |    /------------------------------ Trematolestes ha
                         |    |
                         |    |    /-------------------------- Thoosuchus yakov
                         \---42   |
                             |    |    /---------------------- Angusaurus spp
                             \---41   |
                                 |    +---------------------- Prothoosuchus bl
                                 |    |
                                 \---40    /------------------- Inflectosaurus a
                                     |    |
                                     |    |                /----- Trematosaurus br
                                     \---39    /--------37
                                         |    |        \----- Trematosuchus so
                                         |    |
                                         \----38    /---------- Microposaurus ca
                                             |    |
                                             \---36    /----- Lyrocephaliscus
                                                 \---35
                                                     \----- Platystega depre
```

Apomorphy lists:

Branch	Character	Steps	CI	Change
Archegosaurus de --> node_29	7	1	0.333	1 ==> 0
	11	1	0.250	1 ==> 0
	14	1	0.500	1 ==> 0
	21	1	0.400	1 ==> 0
	27	1	0.250	1 ==> 0
	35	1	0.333	2 ==> 0
	44	1	0.250	1 ==> 0
	49	1	0.250	1 ==> 0
node_29 --> node_30	13	1	0.500	0 ==> 1
	39	1	1.000	0 ==> 1
	40	1	1.000	0 ==> 1
node_30 --> node_31	4	1	0.200	1 --> 0
	22	1	0.200	0 ==> 1
	35	1	0.333	0 ==> 1
	48	1	0.500	0 --> 1
	51	1	1.000	0 --> 1
	53	1	0.333	0 --> 1
	54	1	1.000	0 --> 1
	57	1	0.333	0 --> 1
	60	1	1.000	0 --> 1
node_31 --> node_32	20	1	0.400	0 --> 1
	50	1	0.333	1 --> 0
	66	1	1.000	0 ==> 1
node_32 --> node_34	5	1	0.500	0 ==> 1
	9	1	0.250	0 --> 1
	31	1	0.667	1 ==> 2
	38	1	1.000	0 ==> 2

```
                                  42              1   0.200   1 ==> 0
node_34 --> node_43               15              1   0.333   0 ==> 1
                                  32              1   0.400   0 --> 1
                                  33              1   0.250   0 --> 1
                                  65              1   1.000   0 ==> 1
node_43 --> node_44               4               1   0.200   0 ==> 1
                                  27              1   0.250   0 --> 1
                                  47              1   0.500   0 --> 1
                                  49              1   0.250   0 ==> 1
                                  50              1   0.333   0 ==> 1
                                  55              1   0.500   0 --> 1
node_44 --> node_45               25              1   0.333   0 ==> 1
                                  33              1   0.250   1 --> 2
node_45 --> node_46               8               1   0.286   2 ==> 1
                                  21              1   0.400   0 --> 2
                                  35              1   0.333   1 --> 2
                                  41              1   0.200   0 --> 1
                                  44              1   0.250   0 ==> 1
node_46 --> Aphaneramma gavi      27              1   0.250   1 --> 2
node_46 --> node_28               18              1   1.000   0 ==> 1
                                  36              1   0.400   0 --> 1
node_28 --> Aphaneramma koke      27              1   0.250   1 --> 2
                                  33              1   0.250   2 ==> 0
node_28 --> Aphaneramma rost      9               1   0.250   1 --> 0
                                  24              1   0.286   2 --> 1
                                  42              1   0.200   0 --> 1
                                  64              1   0.500   0 --> 1
node_45 --> Cosgriffius camp      23              1   0.500   0 --> 1
                                  27              1   0.250   1 --> 2
                                  31              1   0.667   2 --> 0
node_44 --> Tertrema acuta M      3               1   0.286   2 ==> 1
                                  38              1   1.000   2 ==> 1
node_43 --> node_42               8               1   0.286   2 ==> 1
                                  11              1   0.250   0 ==> 1
                                  53              1   0.333   1 ==> 0
node_42 --> node_41               19              1   0.333   1 ==> 0
                                  22              1   0.200   1 ==> 0
                                  33              1   0.250   1 --> 2
                                  43              1   0.250   1 ==> 0
                                  55              1   0.500   0 --> 1
                                  58              1   0.333   1 ==> 0
                                  68              1   0.250   1 ==> 0
                                  69              1   0.333   1 ==> 0
node_41 --> node_40               3               1   0.286   2 ==> 1
                                  4               1   0.200   0 ==> 1
                                  21              1   0.400   0 ==> 1
                                  27              1   0.250   0 --> 1
node_40 --> node_39               8               1   0.286   1 ==> 0
                                  9               1   0.250   1 ==> 0
                                  41              1   0.200   0 ==> 1
node_39 --> Inflectosaurus a      5               1   0.500   1 ==> 0
                                  22              1   0.200   0 ==> 1
                                  32              1   0.400   1 ==> 2
                                  49              1   0.250   0 --> 1
                                  55              1   0.500   1 ==> 0
                                  57              1   0.333   1 ==> 0
                                  59              1   0.333   0 ==> 1
                                  61              1   0.500   0 --> 1
                                  64              1   0.500   0 ==> 1
node_39 --> node_38               27              1   0.250   1 ==> 2
                                  53              1   0.333   0 --> 1
node_38 --> node_36               29              1   0.500   1 ==> 0
                                  49              1   0.250   0 --> 1
node_36 --> node_35               12              1   0.500   0 --> 1
                                  33              1   0.250   2 --> 1
                                  35              1   0.333   1 ==> 0
                                  36              1   0.400   0 ==> 1
node_35 --> Lyrocephaliscus       1               1   0.500   1 ==> 0
                                  3               1   0.286   1 ==> 0
                                  4               1   0.200   1 ==> 0
                                  11              1   0.250   1 ==> 0
                                  20              1   0.400   1 ==> 2
                                  24              1   0.286   2 ==> 0
                                  32              1   0.400   1 ==> 2
                                  41              1   0.200   1 ==> 0
                                  42              1   0.200   0 --> 1
                                  43              1   0.250   0 --> 1
```
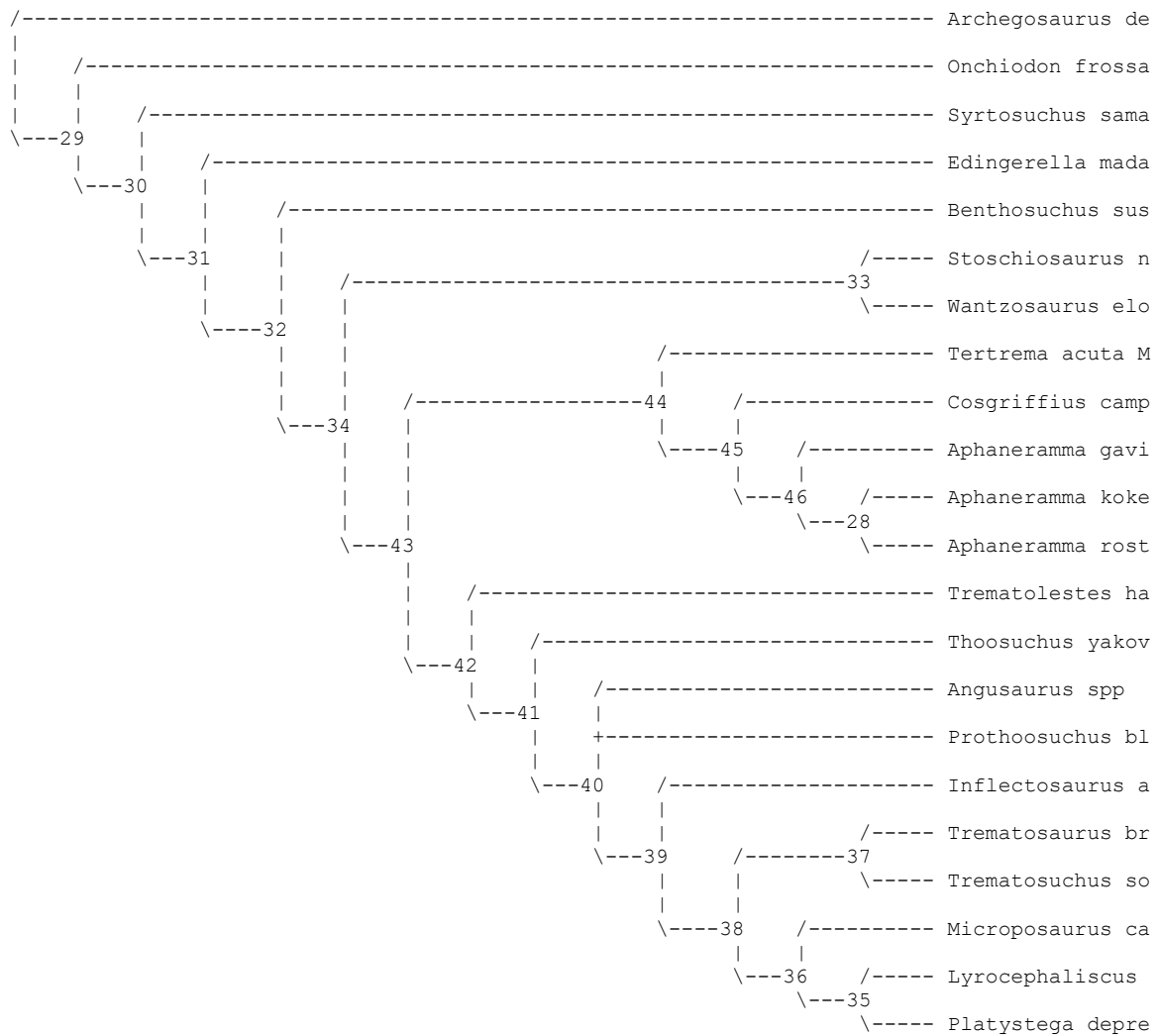
67

```
                                45          1  0.500  0 ==> 1
                                52          1  1.000  0 --> 1
                                55          1  0.500  1 --> 2
                                68          1  0.250  0 --> 1
node_35 --> Platystega depre 10             1  0.500  0 --> 1
                                15          1  0.333  1 ==> 0
                                27          1  0.250  2 ==> 1
                                44          1  0.250  0 ==> 1
node_36 --> Microposaurus ca 2              1  0.500  0 ==> 1
                                8           1  0.286  0 ==> 2
                                10          1  0.500  0 --> 1
                                25          1  0.333  0 ==> 1
                                33          1  0.250  2 --> 0
node_38 --> node_37          3              1  0.286  1 ==> 0
                                20          1  0.400  1 ==> 2
                                21          1  0.400  1 ==> 0
                                45          1  0.500  0 ==> 1
node_37 --> Trematosaurus br 8              1  0.286  0 ==> 1
                                19          1  0.333  0 ==> 1
                                22          1  0.200  0 ==> 1
                                24          1  0.286  2 ==> 1
                                32          1  0.400  1 --> 0
                                48          1  0.500  1 --> 0
node_37 --> Trematosuchus so 6              1  0.500  1 ==> 0
                                13          1  0.500  1 ==> 0
                                14          1  0.500  0 ==> 1
                                34          1  0.333  1 ==> 0
                                35          1  0.333  1 ==> 0
node_40 --> Prothoosuchus bl 15             1  0.333  1 ==> 0
                                36          1  0.400  0 --> 1
node_41 --> Thoosuchus yakov 24             1  0.286  2 --> 1
                                26          1  0.500  0 ==> 1
                                32          1  0.400  1 ==> 2
                                42          1  0.200  0 ==> 1
                                57          1  0.333  1 ==> 0
node_42 --> Trematolestes ha 2              1  0.500  0 ==> 1
                                3           1  0.286  2 ==> 0
                                12          1  0.500  0 ==> 1
                                24          1  0.286  2 --> 1
                                27          1  0.250  0 ==> 2
                                34          1  0.333  1 ==> 0
                                36          1  0.400  0 --> 1
                                41          1  0.200  0 ==> 1
                                59          1  0.333  0 ==> 1
node_34 --> node_33          25             1  0.333  0 ==> 1
node_33 --> Stoschiosaurus n 37             1  1.000  0 --> 1
node_33 --> Wantzosaurus elo 7              1  0.333  0 --> 1
                                11          1  0.250  0 ==> 1
                                20          1  0.400  1 ==> 2
                                22          1  0.200  1 ==> 0
                                23          1  0.500  0 --> 1
                                27          1  0.250  0 --> 1
                                30          1  0.500  0 --> 1
                                35          1  0.333  1 ==> 2
                                47          1  0.500  0 --> 1
                                55          1  0.500  0 --> 1
node_32 --> Benthosuchus sus 8              1  0.286  2 ==> 1
                                30          1  0.500  0 --> 1
                                32          1  0.400  0 --> 1
                                33          1  0.250  0 --> 2
                                44          1  0.250  0 ==> 1
                                58          1  0.333  1 ==> 0
                                61          1  0.500  0 ==> 1
                                68          1  0.250  1 ==> 0
                                69          1  0.333  1 ==> 0
node_31 --> Edingerella mada 3              1  0.286  2 ==> 1
                                7           1  0.333  0 ==> 1
                                9           1  0.250  0 --> 1
                                21          1  0.400  0 ==> 1
                                24          1  0.286  2 ==> 1
                                26          1  0.500  0 ==> 1
                                33          1  0.250  0 ==> 1
                                41          1  0.200  0 ==> 1
                                43          1  0.250  1 --> 0
                                59          1  0.333  0 ==> 1
node_30 --> Syrtosuchus sama 20             1  0.400  0 --> 1
                                33          1  0.250  0 --> 2
```

```
node_29 --> Onchiodon frossa 1       1  0.500  1 ==> 0
                             3       1  0.286  2 ==> 0
                             4       1  0.200  1 --> 0
                             6       1  0.500  1 ==> 0
                             8       1  0.286  2 ==> 0
                             19      1  0.333  1 ==> 0
                             24      1  0.286  2 ==> 0
                             29      1  0.500  1 ==> 0
                             31      1  0.667  1 ==> 0
                             34      1  0.333  1 ==> 0
                             42      1  0.200  1 ==> 0
                             43      1  0.250  1 --> 0
                             50      1  0.333  1 --> 0
                             58      1  0.333  1 ==> 0
                             68      1  0.250  1 ==> 0
                             69      1  0.333  1 ==> 0




node_29 --> Onchiodon frossa 1       1  0.500  1 ==> 0
                             3       1  0.286  2 ==> 0
                             4       1  0.200  1 --> 0
```