

# The Capitosauria (Amphibia): characters, phylogeny, and stratigraphy

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## Abstract

The phylogeny of the largest amphibians, the Triassic capitosaur, is still much debated. One key taxon for the understanding of their relationships, *Odenwaldia heidelbergensis* from the Buntsandstein of Waldkatzenbach, is restudied here. A phylogenetic analysis performed on the basis of 66 characters and 25 taxa gives a new hypothesis of relationships. It rests to a large degree on previous data matrices, but many character codings have been changed with respect to new observations as well as the discovery of new taxa. The present data indicate that all classic capitosaur taxa do form a clade.

The Capitosauria (all taxa more closely related to *Parotosuchus* than to *Trematosaurus*) excludes *Benthosuchus* and *Edingerella* but includes *Wetlugasaurus*, *Sclerothorax*, *Watsonisuchus*, *Parotosuchus*, and all other capitosaur. All capitosaur above *Watsonisuchus* are referred to as the Capitosauroida, which includes *Parotosuchus*, *Cherninia* + *Odenwaldia*, *Eryosuchus*, *Xenotosuchus*, and a vast capitosaur crown clade. The crown includes two main branches: (1) the “Eucyclotosauria” (*Cyclotosaurus*, *Kupferzellia*, *Procyclusaurus*, *Stanocephalosaurus pronus*) and (2) the “Paracyclotosauria” (*Stanocephalosaurus birdi*, *Paracyclusaurus*, *Mastodonsaurus*, and the heylerosaurids *Eocyclotosaurus* and *Quasicyclotosaurus*).

Stratigraphically, capitosaur phylogeny still reveals a rather poor match. However, the present phylogenetic hypothesis matches the stratigraphic ranges more precisely than the previous ones. The early branching between the “Eucyclotosauria” and “Paracyclotosauria” is more consistent with the fossil record than an alternative concept, in which *Cyclotosaurus* and the heylerosaurids form sister taxa (“Pancyclotosauria”). In any case, the otic fenestra and several other probably correlated features in the palate must have evolved two times independently within the crown capitosauroids.

**Key words:** Eucyclotosauria, Paracyclotosauria, Pancyclotosauria, *Odenwaldia*, phylogenetic analysis, evolution, Triassic.

## Zusammenfassung

Die Phylogenie der Capitosaurier, der größten Amphibien der Erdgeschichte, wird noch immer kontrovers diskutiert. Als entscheidendes Taxon in dieser Debatte gilt *Odenwaldia heidelbergensis* aus Waldkatzenbach, die hier neu beschrieben wird. Eine umfangreiche phylogenetische Analyse der Capitosaurier stützt sich auf 66 Merkmale und 25 Arten. Ein Großteil der Daten stammt aus früheren Analysen, die jedoch durch viele Beobachtungen korrigiert und neu beschriebene Taxa ergänzt wurden. Die Analyse bestätigt die Monophylie aller Capitosaurier.

Die Capitosauria umfassen alle Taxa, die näher mit *Parotosuchus* als mit *Trematosaurus* verwandt sind; nach der vorliegenden Analyse gehören *Benthosuchus* und *Edingerella* nicht zu dieser Linie, wohl aber *Wetlugasaurus*, *Sclerothorax*, *Watsonisuchus*, *Parotosuchus* und alle weiteren Capitosaurier. Alle Taxa oberhalb von *Watsonisuchus* zählen zu den Capitosauroida: *Parotosuchus*, *Cherninia*, *Odenwaldia* und eine “Kronengruppe”. Letztere umfasst zwei Hauptgruppen, die hier mit neuen Namen belegt werden: (1) die “Eucyclotosauria” (*Cyclotosaurus*, *Kupferzellia*, *Procyclusaurus*, “*Stanocephalosaurus*” *pronus*) und (2) die “Paracyclotosauria” (*Stanocephalosaurus birdi*, *Paracyclusaurus*, *Mastodonsaurus* und die Heylerosauriden *Eocyclotosaurus* und *Quasicyclotosaurus*).

Stratigraphisches Auftreten und phylogenetische Verzweigung der Capitosaurier sind noch immer schwer in Einklang zu bringen. Ein Abgleich der neuen Hypothese mit den stratigraphischen Reichweiten zeigt allerdings, dass die neue Hypothese auch in dieser Hinsicht sparsamer ist, als die bisherigen Stammbäume. Die frühe Aufspaltung der “Eucyclotosauria” und “Paracyclotosauria” wird durch die Stratigraphie besser gestützt, als eine alternative Hypothese, in der *Cyclotosaurus* und die Heylerosauriden Schwestergruppen bilden (Pancyclotosauria-Hypothese). Als wahrscheinlich kann gelten, dass das Ohrfenster und mehrere andere, damit wahrscheinlich korrelierende Merkmale innerhalb der höheren Capitosauroiden zweimal unabhängig entstanden sind.

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## 1. Introduction

The largest and most speciose group of amphibians, the temnospondyls, originated in the early Carboniferous and probably gave rise to salamanders and frogs (MILNER 1988, 1993; RUTA et al. 2003, 2007; ANDERSON et al. 2008). While the modern amphibians still reach a relatively large diversity with more than 6,000 surviving species, late Palaeozoic and early Mesozoic temnospondyls could have been as rich in species, although this is not adequately preserved by the patchy fossil record. In contrast to their modern relatives, their size range was much wider, with many species reaching a body length between one and two metres. But even from this perspective, one group certainly stands out: the capitosaur, which evolved some of the largest amphibians of earth history and which dominated many Mesozoic aquatic ecosystems in rivers, lakes, and swamps.

The first capitosaur to be discovered and named was *Mastodonsaurus giganteus*, the remains of which were first found in a mine near the town of Gaildorf, south of Hall in northern Württemberg (JAEGER 1828; HAGDORN 1988; MOSER & SCHOCH 2007). Despite the discovery of numerous capitosaur, *Mastodonsaurus* remains the largest well known amphibian ever since. This taxon was recognized by the “inspector” of the Royal Natural Collection at Stuttgart, G. F. JAEGER, in the first half of the 19<sup>th</sup> century, who correctly identified the first, scrappy remains of *Mastodonsaurus* as a giant salamander, stemming from the “batrachian family of the Reptilia” (JAEGER 1824, 1828). The finds, which included partial skulls of more than one metre length, attracted the attention of various famous geologists and anatomists of the time, among them ALBERTI (1834), MEYER in MEYER & PLIENINGER (1844), OWEN (1841), and QUENSTEDT (1850). OWEN

(1841) created the higher taxon Labyrinthodontes, by which *Mastodonsaurus* (= *Labyrinthodon*) and other early known capitosaur were henceforth categorized. Also within this group fell a taxon erected by MÜNSTER (1836), *Capitosaurus arenaceus*, which later formed the basis for WATSON’s (1919) family Capitosauridae and SÄVE-SÖDERBERGH’s (1935) extension of the superfamily Capitosauriidea, encompassing ever more taxa. Other milestones of capitosaur research, to name just a few, were MEYER & PLIENINGER (1844), QUENSTEDT (1850), MEYER (1855–57, 1858), FRAAS (1889, 1913), HUENE (1922), BYSTROW & EFREMOV (1940), ROMER (1947), and the extensive revision by WELLES & COSGRIFF (1965). KONZHUKOVA (1965) and OCHEV (1966, 1972) further described new taxa from the Eastern European Platform and discussed their relationships, as did PATON (1974) for English material.

Today comprising some 20 genera and 42 valid species, capitosaur form a group whose intrarelationships are not easily overlooked. Their phylogeny was discussed in depth by WATSON (1919, 1962), SÄVE-SÖDERBERGH (1935), ROMER (1947), and SHISHKIN (1964, 1980). Much of the debate on capitosaur relationships centered on a single feature expressed only within the group, the presence of completely closed otic fenestrae in the cheek. These form a pair of round openings posterior to the orbits, which may have housed a tympanum or some other structure associated with the middle ear. This feature gave also the name to *Cyclotosaurus* (‘round-eared lizard’), one of the last capitosaur from the Upper Triassic of Germany, and the bearers of a closed otic fenestra have been called ‘cyclotosaur’. After this condition had long been considered a key feature and was used in stratigraphical correlations of capitosaur-bearing beds, phylogenetic analyses found the case to be unsettled and the correlations to be questionable. First phylogenetic analyses of capitosaur, performed

without computer programmes but considering apomorphic character-states, were reported by INGAVAT & JANVIER (1981), and MILNER (1990). Based on SHISHKIN's (1980) concept of a diphyletic origin of the otic fenestra in capitosaur, MORALES & KAMPHAUSEN (1984) described a new taxon (*Odenwaldia heidelbergensis*) which appeared to confirm that hypothesis.

Only recently, however, have capitosaur formed the focus of cladistic analyses in the strict sense (SCHOCH 2000a; DAMIANI 2001a), based on larger data sets and employing the software packages PAUP and MacClade. A range of additional papers covered aspects of capitosaur phylogeny (STEYER 2003; LIU & WANG 2005; STAYTON & RUTA 2006; SCHOCH et al. 2007; RUTA et al. 2007). SCHOCH & MILNER (2000) provided a classification of capitosaur based on synapomorphies, referring largely to SCHOCH's (2000a) foregoing analysis. The two existing phylogenetic concepts are in fact based on rather complementary studies: while SCHOCH & MILNER's (2000) classification was under the impact of the recent study of *Mastodonsaurus giganteus* (SCHOCH 1999) and other European and North American capitosaur (SCHOCH 2000b), DAMIANI (2001a) expanded from his revision of Australian and South African genera (DAMIANI 1999, 2002; DAMIANI & HANCOX 2003).

In the most recent years, new taxa from around the world were reported that might fall within the capitosaur (DAMIANI 2002; SULEJ & MAJER 2005; LIU & WANG 2005; SCHOCH et al. 2007), and this by itself prompts a reconsideration of the case. Another point is the taxonomic discrepancy between the published papers, which culminated in the alternative use of two different superfamily names for much the same group – Capitosauroida versus Mastodonsauroida. Apart from nomenclature, these two names stand for rather different phylogenetic concepts that are mutually exclusive, and the present reconsideration seeks to come somewhat closer to the solution of that phylogenetic problem.

The objective of the present study is as follows: (1) re-examine the original material of *Odenwaldia heidelbergensis*, a potential keystone taxon for capitosaur relationships, (2) conduct a phylogenetic analysis of all well-known taxa, including those that have been assigned to the group by some authors only, and (3) discuss scenarios of capitosaur evolution derived from the cladistic analysis and supplemented by stratigraphical data.

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## 2. Material

The following range of specimens was studied first hand by the author:

*Benthosuchus sushkini* (PIN 9/2243/1, 9/2243, 19/2252, 32/2354, 33/2355), *Cyclotosaurus ebrachensis* (BSP 1931–X1), *Cyclotosaurus mordax* (SMNS 13014, 50008, 50009, 50059, 50063, 51102, 55112, 51435), *Cyclotosaurus posthumus* (SMNS 12988), *Cyclotosaurus robustus* (GPIT 27–1/16, 1801–1802, 1804; SMNS 4139, 4935, 5775), *Eocyclotosaurus lehmani* (SMNS 51562), *Eocyclotosaurus wellsi* (UCMP 41343, 41632, 41645, 42840, 42841, 123590, 123595, 125365, 125366), *Eryosuchus garjainovi* (PIN 104/3521, /3694–3702), *Kupferzellia wildi* (SMNS 54670–54674, 80959, 80962, 80965–80967, MHI material), *Lydekkerina huxleyi* (BPI–4638, K1421, 8089; SAM 3525, 3521, 3604), *Mastodonsaurus cappelenensis* (uncatalogued SMNK material), *Mastodonsaurus giganteus* (SMNS 740, 4194, 4698, 4706–4707, 4774, 4938, 54675, 54677–54679, 56630, 56634, 80249, 80704, 80878, 80887, 80889, 80890, MHI material), *Mastodonsaurus torvus* (PIN 415/1–4), *Odenwaldia heidelbergensis* (GPIH SMO 1), *Paracyclotosaurus davidi* (BMNH R.6000), *Parotosuchus nasutus* (SMNS 5776, 7957, 81697), *Parotosuchus orenburgensis* (PIN 951/42), *Parotosuchus orientalis* (PIN 104/222), *Procyclotosaurus stantonensis* (BMNH R.3174), *Quasicyclotosaurus campi* (UCMP 37754, 41635), *Rhineceps nyasaensis* (SAM 7866, UMZC T.259), *Sclerothorax hypselonotus* (HLD-V 607–608, GPIM–N 2045, NMK–S 117–118), *Stanocephalosaurus birdi* (AMNH 3029, UCMP 36058, many specimens from UCMP locality V3835), *Stenotosaurus semiclausus* (BMNH R.5276), *Thoosuchus yakovlevi* (PIN 3200, SMNS 81782), *Uranocentrodon senekalensis* (TM 75), *Wetlugasaurus angustifrons* (PIN 2253/6, 16–19, 3583), *Xenotosuchus africanus* (SAM 2360, UCMP 41286).

Comment. – A thorough search for the type material of *Cyclotosaurus hemprichi* KUHN, 1942 gave the result that it was probably destroyed in the war.

#### Anatomical abbreviations

|       |                          |
|-------|--------------------------|
| a     | angular                  |
| ad-fe | adductor fenestra        |
| ad-sh | adductor shelf           |
| apv   | anterior palatal vacuity |
| ar    | articular                |
| bc    | braincase                |
| ch    | choana                   |
| c1    | anterior coronoid        |
| c2    | intercoronoid            |
| c3    | posterior coronoid       |
| d     | dentary                  |
| ec    | ectopterygoid            |
| eo    | exoccipital              |
| f     | frontal                  |

|       |                                   |
|-------|-----------------------------------|
| fo    | foramen ovale                     |
| gle   | glenoid                           |
| ha-pr | hamate process                    |
| ior   | interorbital sulcus               |
| ipv   | interpterygoid vacuity            |
| ju    | jugal                             |
| ju-al | alary process of jugal            |
| la    | lacrima                           |
| las   | laterosphenoid region (braincase) |
| la-fl | lacrima flexure                   |
| m     | maxilla                           |
| me-fe | meckelian fenestra                |
| n     | nasal                             |
| ot    | otic                              |
| p     | parietal                          |
| par   | prearticular                      |
| pf    | postfrontal                       |
| pga   | postglenoid area                  |
| pin   | pineal region of braincase        |
| pl    | palatine                          |
| pm    | premaxilla                        |
| po    | postorbital                       |
| po-co | posterior coronoid teeth          |
| pp    | postparietal                      |
| pp-pl | posterior process of palatine     |
| prf   | prefrontal                        |
| pr-sp | presphenial                       |
| ps    | parasphenoid                      |
| pt    | pterygoid                         |
| q     | quadrate                          |
| qj    | quadratojugal                     |
| q-bo  | quadrate boss                     |
| sa    | surangular                        |
| se    | sphenethmoid                      |
| sm    | septomaxilla                      |
| sor   | supraorbital sulcus               |
| sp    | sphenial                          |
| sq    | squamosal                         |
| st    | supratemporal                     |
| stw   | subtemporal window                |
| sy-tu | symphyseal tusk                   |
| ta    | tabular                           |
| vo    | vomer                             |
| vo-tu | vomerine tusks                    |

|      |   |
|------|---|
| SMNS | Staatliches Museum für Naturkunde Stuttgart (Germany)             |
| TM   | Transvaal Museum Pretoria (South Africa)                          |
| UCMP | University of California Museum of Paleontology at Berkeley (USA) |
| UMZC | University Museum of Zoology Cambridge (UK)                       |

### 3. A reassessment of *Odenwaldia heidelbergensis*

*Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984 has been considered a keystone taxon for the understanding of capitosaur phylogeny (KAMPHAUSEN 1989; DAMIANI 2001a). This taxon is based on a single specimen from Waldkatzenbach near Heidelberg, located in the Odenwald mountain range, southwestern Germany. The single skull was found in the upper conglomerate horizon (Oberes Konglomerat) in the topmost section of the Middle Buntsandstein (Solling-Folge, S6, Upper Olenekian). First considered a trematosaurid (SIMON 1961), it was then shown to share a range of features with the Russian genus *Benthosuchus* (MORALES & KAMPHAUSEN 1984) and argued to have held a phylogenetically intermediate position between *Benthosuchus* and *Eocyclotaurus*, a capitosaur known from slightly younger horizons in the Upper Buntsandstein of Europe (KAMPHAUSEN 1989). This interpretation was consistent with stratigraphic ranges, but was not based on a phylogenetic analysis. The concept was accepted by some authors (MILNER 1990; DAMIANI 2001a) but questioned by others (SCHOCH 2000a; SCHOCH & MILNER 2000; RUTA et al. 2007), and the case may be viewed as unsettled, as long as no additional evidence emerges. This prompts a thorough re-examination of the material, which forms the scope of the present section.

#### 3.1. Systematic palaeontology

|                          |   |
|--------------------------|---|
| Acronyms of institutions |   |
| AMNH                     | American Museum of Natural History New York (USA)                                 |
| BMNH                     | The Natural History Museum London (UK)  |
| BPI                      | Bernard Price Institute for Palaeontological Research Johannesburg (South Africa) |
| GPIH                     | Geologisch-Paläontologisches Institut Heidelberg (Germany)                        |
| GPIM                     | Geologisch-Paläontologisches Institut Mainz (Germany)                             |
| GPIT                     | Institut für Geologie Tübingen (Germany)  |
| HLD                      | Hessisches Landesmuseum Darmstadt (Germany)                                       |
| MHI                      | Muschelkalkmuseum Hagdorn Ingelfingen (Germany)                                   |
| NMK                      | Naturhistorisches Museum Ottoneum Kassel (Germany)                                |
| PIN                      | Paleontological Institute of the Russian Academy of Sciences Moscow (Russia)      |
| SAM                      | South African Museum Cape Town (South Africa)                                     |
| SMNK                     | Staatliches Museum für Naturkunde Karlsruhe (Germany)                             |

|                |  |
|----------------|--|
| Tetrapoda      | HAWORTH, 1825 sensu GOODRICH, 1930               |
| Temnospondyli  | ZITTEL, 1888 sensu MILNER, 1990                  |
| Stereospondyli | ZITTEL, 1888 sensu MILNER, 1994                  |
| Capitosauria   | YATES & WARREN, 2000 sensu DAMIANI & YATES, 2003 |
| Capitosauroida | WATSON, 1919 sensu SCHOCH & MILNER, 2000         |

*Odenwaldia* MORALES & KAMPHAUSEN, 1984

**Diagnosis.** – Autapomorphies: (1) Median series of skull roof (frontal, parietal) wide combined with small orbits; (2) preorbital region slender, with nasals and lacrimals narrower than frontals.

**Homoplasies:** (a) anterior palatal fenestra paired (shared with many trematosaurids, metoposaurids, and some capitosauroids); (b) prearial portion of premaxilla

slightly elongated (shared with *Benthosuchus*, but not as extreme); (c) dermal ornament consists of throughout small, equal-sized polygons, lacking elongated ridges (shared with *Edingerella*, *Watsonisuchus*, *Parotosuchus*); (d) supraorbital sulcus traverses lacrimal (shared with *Benthosuchus*, all trematosaurids, *Yuanansuchus*, *Mastodonsaurus*, *Eocyclotosaurus*, *Quasicyclotosaurus*); (e) posterior quadrate boss (shared with many primitive capitosaur: *Wetlugasaurus*, *Watsonisuchus*, *Parotosuchus*).

**Plesiomorphies:** (i) tabular horns directed posteriorly, constricting otic notch only faintly; (ii) postorbital with large lateral projection, widely separated from prefrontal.

**Unclear character-state:** prefrontal and postfrontal apparently sutured (a plesiomorphic state among capitosaur, shared only with *Wetlugasaurus*, *Eocyclotosaurus*, *Quasicyclotosaurus*, and some specimens of *Cyclotosaurus mordax*).

*Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN,  
1984

Figs. 1–2

1961 “*Trematosaurus*”. – SIMON, p. 128, figs. 1–2.

\*1984 *Odenwaldia heidelbergensis* n. g. n. sp. – MORALES & KAMPHAUSEN, p. 673–683, fig. 1.

1989 *Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984. – KAMPHAUSEN, p. 26, fig. 7, pl. 6.

2000 *Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984. – SCHOCH & MILNER, p. 136, fig. 92.

2001 *Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984. – DAMIANI, p. 396, fig. 14. – [2001a]

**Holotype:** GPIH SMO 1, a natural mould of the skull, preserving most of the skull roof, the marginal dentition, parts of the braincase, and traces of the palate (Fig. 1A–D).

**Type locality:** Former construction pit, Waldkatzenbach am Katzenbuckel, Odenwald mountain range (Baden-Württemberg, Germany) (SIMON 1961: 129).

**Type horizon:** Upper Conglomerate Horizon (Oberes Konglomerat), Solling Formation (S6), top of the Middle Buntsandstein section (SIMON 1961: 129).

**Referred material:** KAMPHAUSEN & KELLER (1986) referred an isolated right quadratojugal from a roughly coeval horizon of the Spessart mountain range to *O. heidelbergensis*, which was considered indeterminate by SCHOCH & MILNER (2000), a conclusion that is followed here.

**Diagnosis.** – As for genus, as this is the only species.

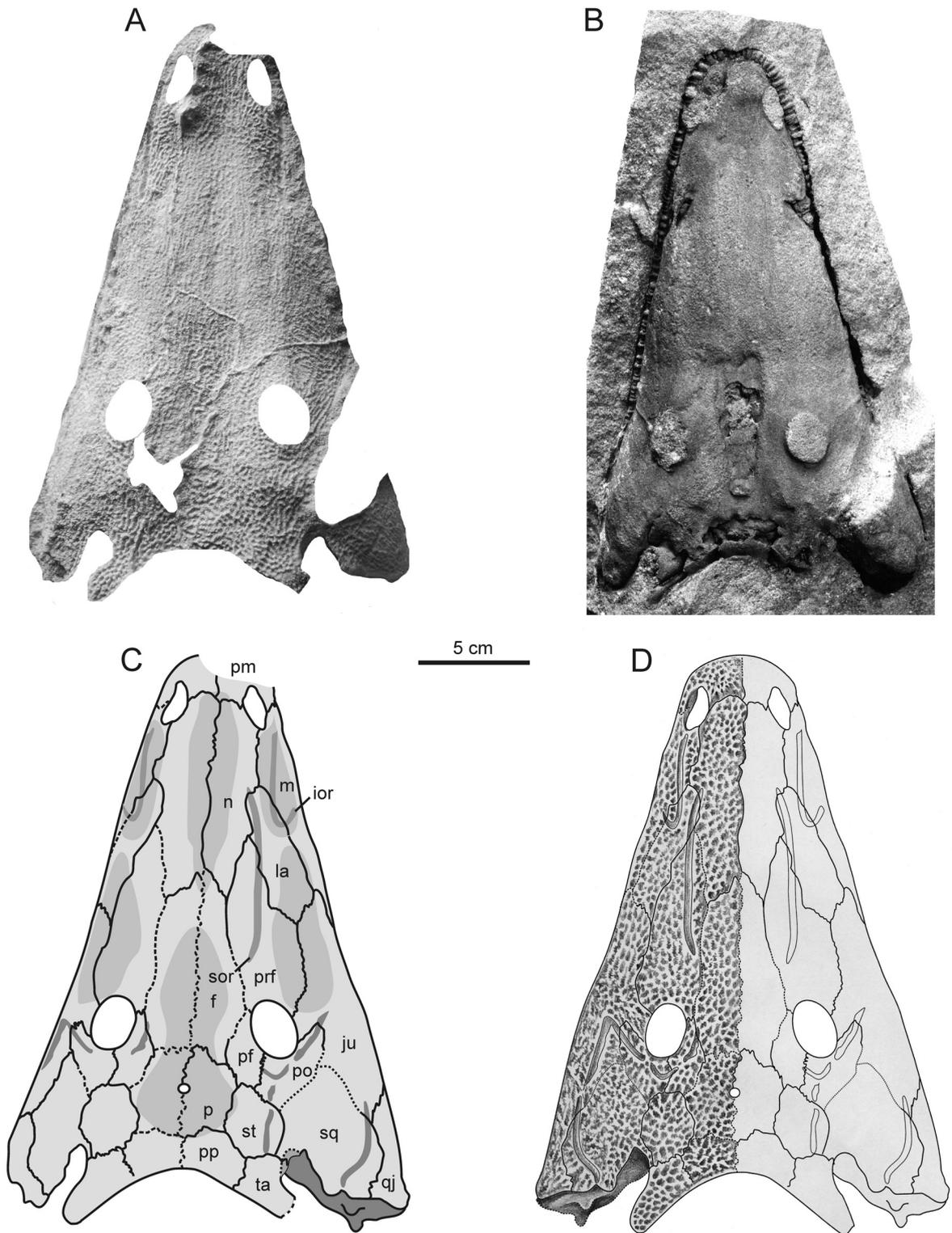
**Description.** – **Skull Roof:** MORALES & KAMPHAUSEN (1984) provided an interpretation of the skull roof with most sutures and the course of the lateral line sulci mapped onto a drawing of the skull. The present findings depart in many details from their interpretation, but I should highlight that most sutures are very difficult to identify because of the intense dermal ornament and the imperfect preservation of this mould by the rather coarse sandstone. It is probably impossible to ignore suture pat-

terns of other taxa and personal experience entirely when working on such problematic material. I have therefore mapped the sutures identified with a higher degree of certainty as continued lines, those that are more questionable as broken lines, and the inferred ones dotted. Most suture lines were traced on the dorsal side of the skull roof, supplemented by information from the ventral side as preserved on the top of the steinkern (Fig. 1B–D).

The general structure of the skull agrees in many points with that of *Wetlugasaurus* (BYSTROW & EFREMOV 1940), *Watsonisuchus* (WARREN & SCHROEDER 1995; DAMIANI 2001) *Parotosuchus nasutus* (MEYER 1858), and especially *P. helgolandiae* (SCHRÖDER 1913). *Odenwaldia* shares with all these taxa the proportions of the posterior skull table and cheeks, the posteriorly directed tabular horns, and the small, numerous polygonal ridges of its ornament. Instead, elongated, parallel ridges or large polygons like in *Mastodonsaurus*, *Eocyclotosaurus*, or *Cyclotosaurus* are entirely lacking. *Odenwaldia* agrees further with *Parotosuchus helgolandiae* and *P. haughtoni* (DAMIANI 2002) in having a relatively slender, tapering snout and small orbits. However, the orbits are only slightly raised above the level of the posterior skull table.

Unique to *Odenwaldia* is the combination of a narrow preorbital region with a broad interorbital distance and unusually small, oval orbits (Fig. 1C) the parietals and frontals are thus substantially wider than the nasals, which is only exceeded by one other potential capitosaur, the recently redescribed *Sclerothorax* (SCHOCH et al. 2007). Otherwise, however, these two Middle Buntsandstein taxa are boldly different, and *Odenwaldia* clusters with the slender-headed capitosaur in having an elongated preorbital region that is more than three times longer than the posterior skull table. The skull table is not flat but houses a central depression that continues anteriorly into the frontal region, while the orbits are located on top of an elongated, parasagittal ridge running from the tabular to the prefrontal regions.

A further difference to all derived capitosauroids (sensu SCHOCH & MILNER 2000) are the lateral line sulci, which are poorly established and much narrower than for instance in *Eocyclotosaurus*, *Cyclotosaurus*, *Mastodonsaurus*, or *Eryosuchus*. Their slender channels resemble the condition in *Wetlugasaurus* and *Parotosuchus nasutus*, but in *Odenwaldia* only the lacrimal flexure is well-developed and continuous (Fig. 1C–D). The lacrimal region is poorly preserved, but there are faint traces of a supraorbital sulcus traversing the lacrimal bone region, which is in accordance with MORALES & KAMPHAUSEN’s (1984) interpretation. The large naris has an elongated oval outline and is located at the lateral margin of the snout. The prenarial portion of the premaxilla is as long as in *Parotosuchus orenburgensis* and *P. nasutus*, but clearly longer than in most other capitosaur. However, in *Benthosuchus* the



**Fig. 1.** Morphology of *Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984. Type and only specimen (GPIH SMO1). – **A.** Cast of skull roof (dorsal view). **B.** Steinkern of skull with braincase, nares, and dentition exposed (dorsal view). **C.** Interpretation of sutures in dorsal view, showing the 3d structure of the skull. **D.** Restoration of skull in dorsal view, with ornament depicted on left side.

naris and premaxilla in general are substantially larger than in both *Odenwaldia* and capitosaurids (cf. DAMIANI 2001a).

The nasal is relatively slender, and although it has the typical stepped lateral margin anterior to the prefrontal and lacrimal, it is not as wide as in *Parotosuchus* (any species) or most higher capitosauroids, except for *Eocyclotosaurus* and *Stenotosaurus*, which have similar slender snouts. The lacrimal is located well anterior, separated from the orbit by a long prefrontal-jugal suture. The nasal, lacrimal, and frontal are covered by small, reticulate polygons not essentially different from those of the posterior skull table, but with ridges that are less pronounced. The central depression on the frontals continues into a longitudinal groove running along the symphysis of the countersided nasals, which end at about mid-level of the nasals (Fig. 1C). The anterior third of the snout is slightly raised and the ornament is somewhat more clearly established there. The prefrontal measures half the length of the preorbital region. Its anterior tip is pointed and the lateral margin is markedly stepped to accommodate the rectangular lacrimal. The suture between the prefrontal and jugal is long and convex, located in the most intensely ornamented region of the skull. There, the jugal and prefrontal are covered by large, slightly elongated polygons that are aligned radially. The laterally projecting and convex posterior portion of the prefrontal is most similar to that of *Watsonisuchus* and, to a lesser extent, *Wellugasaurus* (DAMIANI 2001a).

The interorbital region is poorly preserved, and seems to have been occupied largely by the unusually wide frontals. On the dorsal side, there appears to have been a narrow contact between the prefrontal and postfrontal, but this region is poorly preserved on both sides (Fig. 1C–D). However, on the ventral side, which is weakly impressed in the steinkern, the situation is different in that the postfrontal does not reach as far anterior as dorsally, and it is questionable whether it reached the prefrontal on the internal side of the skull.

The posterior skull table is consistent with that of *Parotosuchus*, especially *P. nasutus*, as well as *Sclerothorax* (SCHOCH et al. 2007). This includes the suture topology as well as ornament, the position of the pineal foramen, and the impression and course of the lateral line sulci. Another peculiarity is the concave, anteriorly pointed outline of the posterior skull margin, which in both *Odenwaldia* and *Sclerothorax* attains the shape of an 'A'. The postorbital appears to be rather short, but has a large anterolateral wing projecting well into the jugal, again very similar to the situation of *Sclerothorax*, but also *Parotosuchus* (all species), *Watsonisuchus*, and *Cherninia*. Like in many of these taxa, the lateral wing of the postorbital bears a well-established lateral line sulcus. The postorbital projection does not even come close to the prefrontal, in stark con-

trast to MORALES & KAMPHAUSEN's (1984) interpretation, in which there was a contact. The present interpretation rests on examination of both left and right dorsal sides and the right ventral side of the skull roof, which are all consistent.

The squamosal embayment is semilunar and deeply set into the posterior skull margin, framed anteromedially by a descending flange of the squamosal and tabular. The tabular horn is most similar to that of *Parotosuchus helgolandiae* and *Sclerothorax* in length and proportions. The lateral direction of the tabular horn, which was first mentioned (but not figured!) by MORALES & KAMPHAUSEN (1984), is not established. In fact, the condition in *Odenwaldia* is not any different from that of *Parotosuchus nasutus*, *P. haughtoni*, or *Benthosuchus*. It is therefore wrong to code it as "derived" along with the truly apomorphic states of *Eryosuchus*, *Stanocephalosaurus*, *Paracyclotosaurus*, *Mastodonsaurus*, and the cyclotosaurids sensu lato.

On the internal side of the skull roof, preserved on top of the steinkern, some interesting additional details are preserved. Apart from the internal sutures, the posterior skull table reveals faint traces of the attachment of braincase elements to the tabular, postparietal, and supratemporal. On both sides, paired impressions indicate a connection between the supratemporal (at about mid-level anteroposteriorly) and an anterolateral portion of the endocranium; by its position, this was probably a dorsal process of the epipterygoid (SCHOCH & MILNER 2000; SCHOCH 2002b).

**Palate:** The palate is only exposed in few regions, while the rest is still concealed by the infilling (steinkern) of the skull roof (Fig. 1B); as preparation would almost inevitably destroy informative parts of the steinkern, it has not been attempted. The exposed parts include the complete marginal and anterior portions of the dentition, the palatine tusks, part of the vomerine tusks, and the left side of the anterior palatal fenestra. The interpterygoid vacuities, choanae, and basicranial regions remain unknown, although some features of the concealed regions have been coded in recent cladistic analyses (e. g. DAMIANI 2001a). A tentative reconstruction of the exposed regions is given in Fig. 2B.

The premaxillary and maxillary dentition of *Odenwaldia* reveals a broad range of tooth sizes, with the anterior and anterolateral ones being the largest. The premaxilla houses 8–10 teeth, the maxilla 63–65, and the palatine-ectopterygoid arcade some 43 teeth (in each case, all sockets and teeth were counted). The anteriormost maxilla teeth are the largest and vary greatly in outline, from extremely constricted-oval to wide oval.

All marginal teeth are closely set, so that neighbouring sockets almost contact one another (Fig. 2A). Teeth and sockets alternate quite regularly. All sockets are antero-

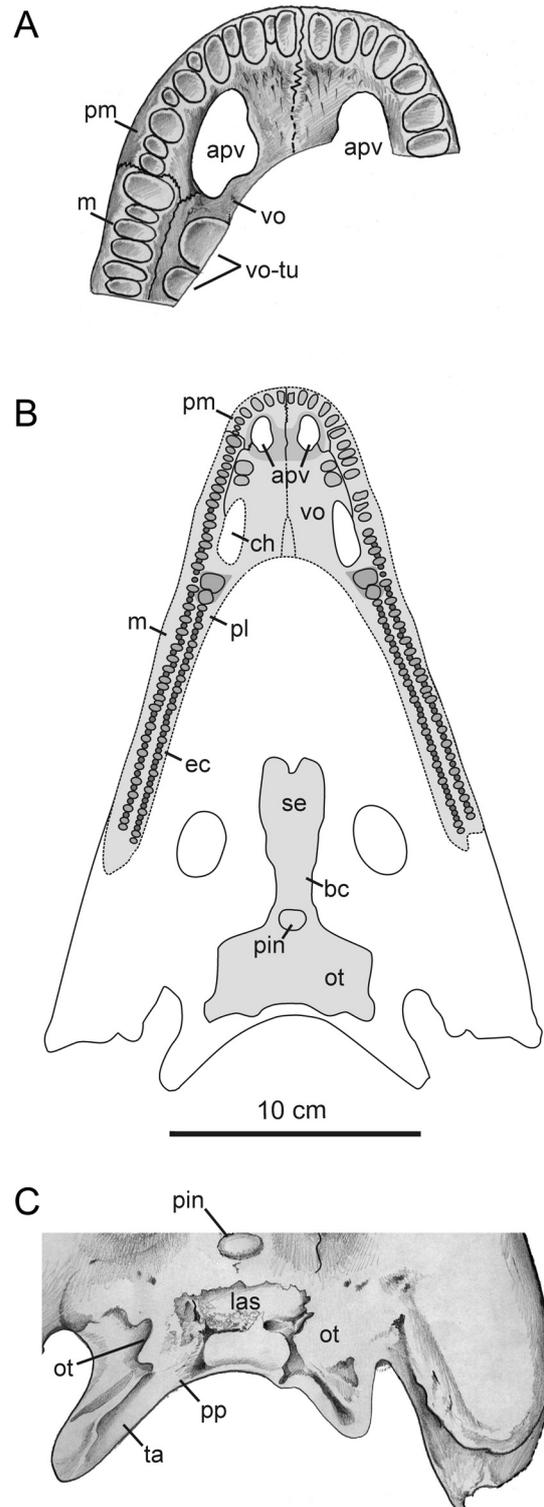
posteriorly compressed, a feature known from many steospondyls, but that is especially pronounced and consistent in capitosaurids (SCHOCH & MILNER 2000; DAMIANI 2001a).

The palatine fang pair is exposed on both sides, revealing moderately sized fangs. The anterior one is larger and transversely oval. These tusks have two to three times the diameter of the palatine marginal teeth. The vomerine tusks reveal a similar pattern, with the anterior one being larger, and there the teeth are surrounded by a lateral groove. The anterior palatal vacuities are clearly completely separated, as the left opening and its medial margin is completely exposed (Fig. 2A). The openings are parasagittally elongated and located unusually far laterally, with a broad medial subdivision. Posteromedially, the fenestrae are markedly expanded. This situation departs from that of *Eocyclotosaurus* in two aspects: (1) the medial premaxilla process is much wider in *Odenwaldia*, and (2) the posteromedial expansion is absent in *Eocyclotosaurus*, which in general has a much narrower anterior snout region.

**Braincase and occiput:** Impressions on the dorsal side of the steinkern expose a large portion of the braincase, which includes almost the complete dorsal side of the sphenethmoid, the pineal region (“laterosphenoid”), the otic ossifications on both sides, as well as the region between the otics (Fig. 2C). In the right otic notch, the stapes is preserved, exposing a cross-section of the distal portion of the shaft. In addition, small, paired pits indicate the attachment of the ?epipterygoid to the supratemporals (Fig. 2C).

The sphenethmoid ossification is well elongated and only slightly wider in its anterior half (Figs. 1B, 2B). Although the impression is weak and damaged, it is visible that the anterior end was well bifurcated. The bone appears to have been well ossified. The pineal region houses a poorly defined trace of a transversely oval structure, what probably represents the cavity that connected the dorsal part of the brain with the pineal organ. The otic regions are preserved as markedly curved dorsolateral outgrowths of the otic ossifications attached to the tabulars and supratemporals. Similar, but less curved attachment sites were described and figured by SHISHKIN (1973) in various lower temnospondyls, by WITZMANN (2006), and SCHOCH (1999, 2002a) in *Mastodonsaurus*.

The occiput is only exposed along the rim of the tabular and squamosal. The ventral side of the tabular bears two marked crests, like in *Benthosuchus sushkini* (BYSTROW & EFREMOV 1940) and many capitosauroids (DAMIANI 2001a). The anterolateral crest is deep and well-ossified, recalling the condition in rhinesuchids and some archegosauroids (personal observation). A pronounced falciform crest is present on the posterior rim of the squamosal, quite as in *Sclerothorax* (Fig. 1C–D).



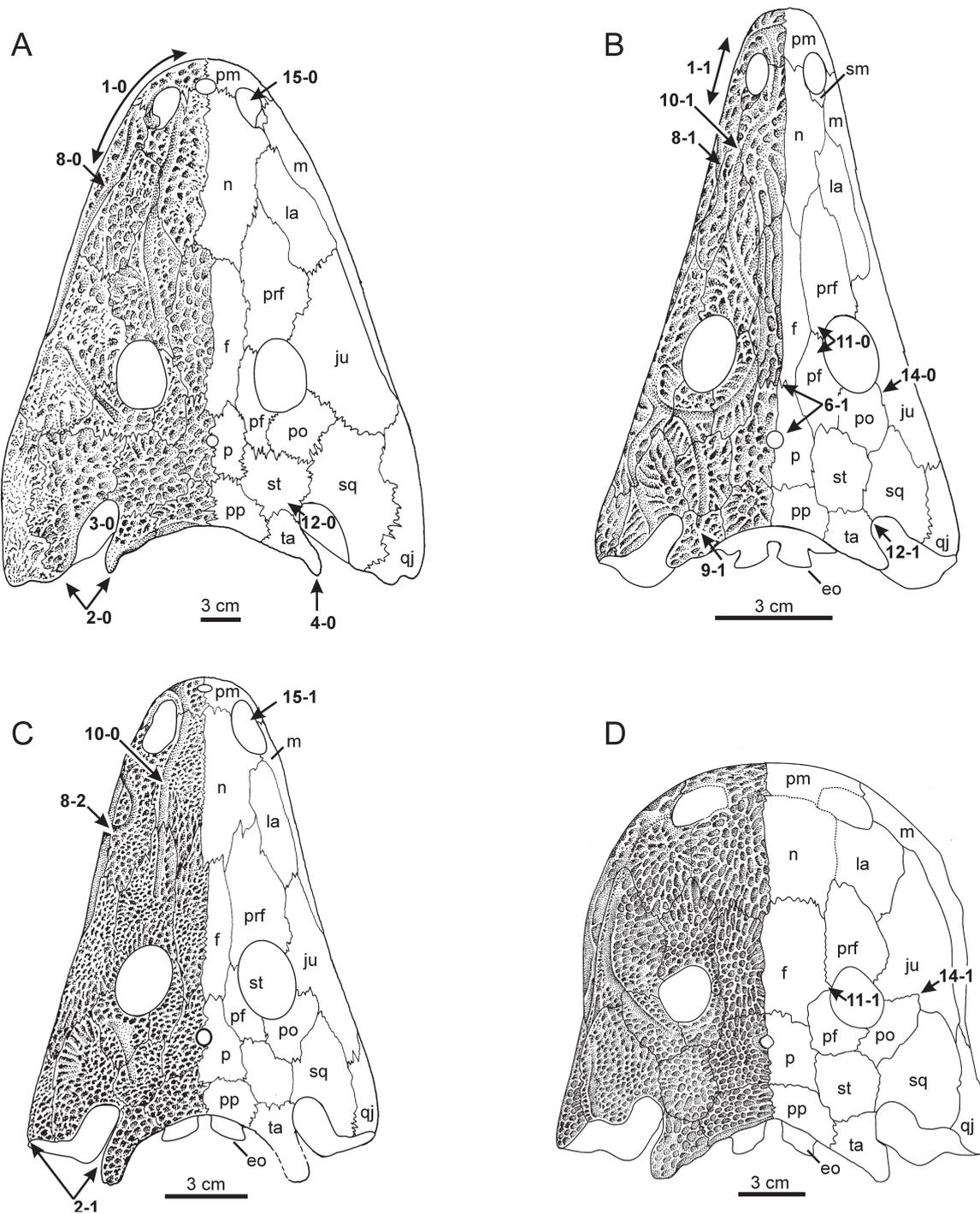
**Fig. 2.** Reconstruction of *Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984. Based on GPIH SMO1. – **A.** Anterior portion of snout with double palatal vacuities preserved. **B.** Restoration of the palate in ventral view. **C.** Posterior portion of skull, with details of braincase preserved as imprints on the steinkern.

## 4. Phylogenetic analysis

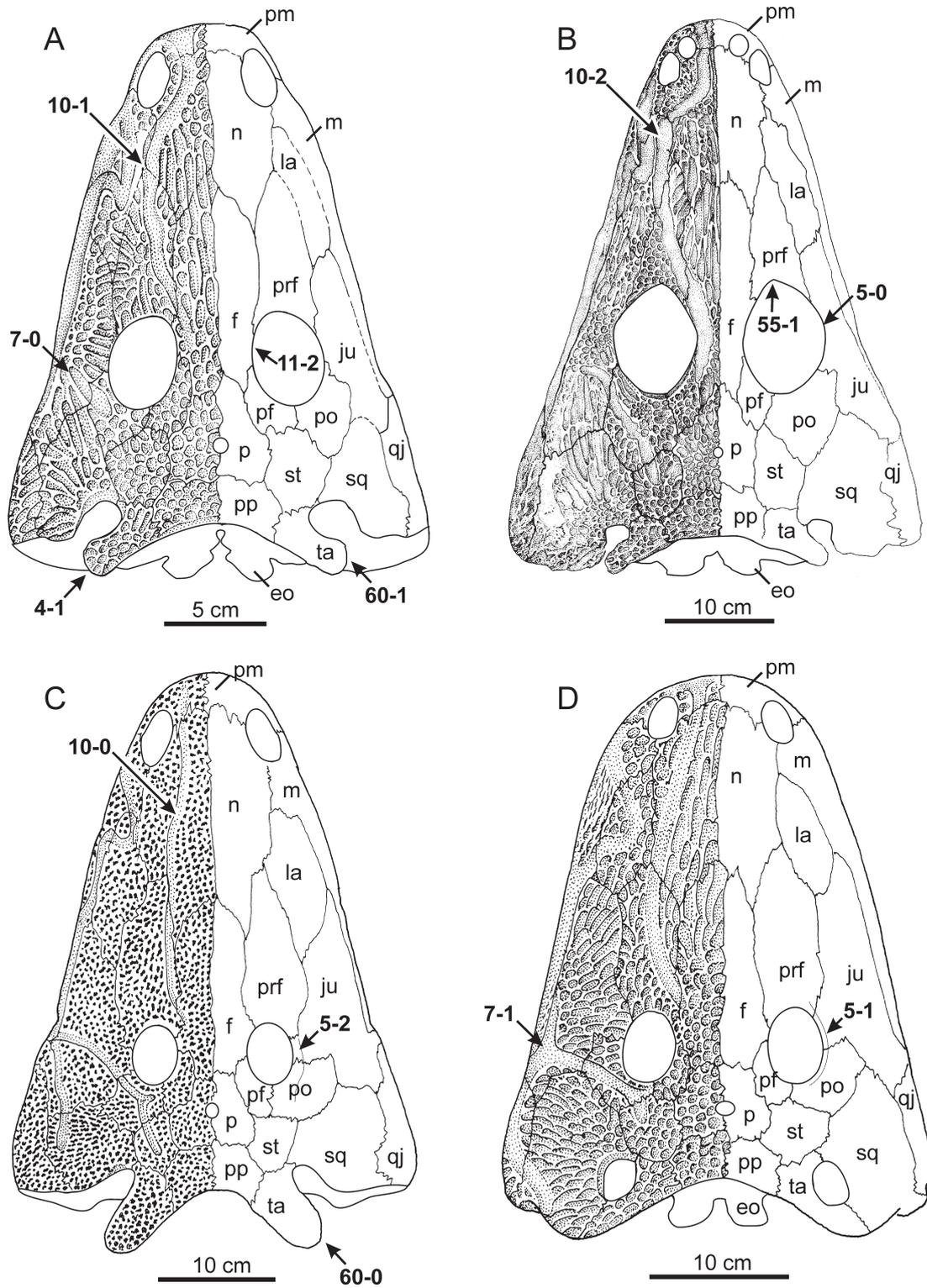
### 4.1. Description of characters

The following list of characters starts with 47 features defined and used by DAMIANI (2001a), which are retained in their original consecutive numbering. The list is complemented by characters defined by SCHOCH (2000a), SCHOCH & MILNER (2000), MORALES & SHISHKIN (2002) and other sources, as indicated. Figures 3–6 depict numerous character-states, referred to by their numbers and state-numbers (e. g., 4-1 meaning character 4, state 1).

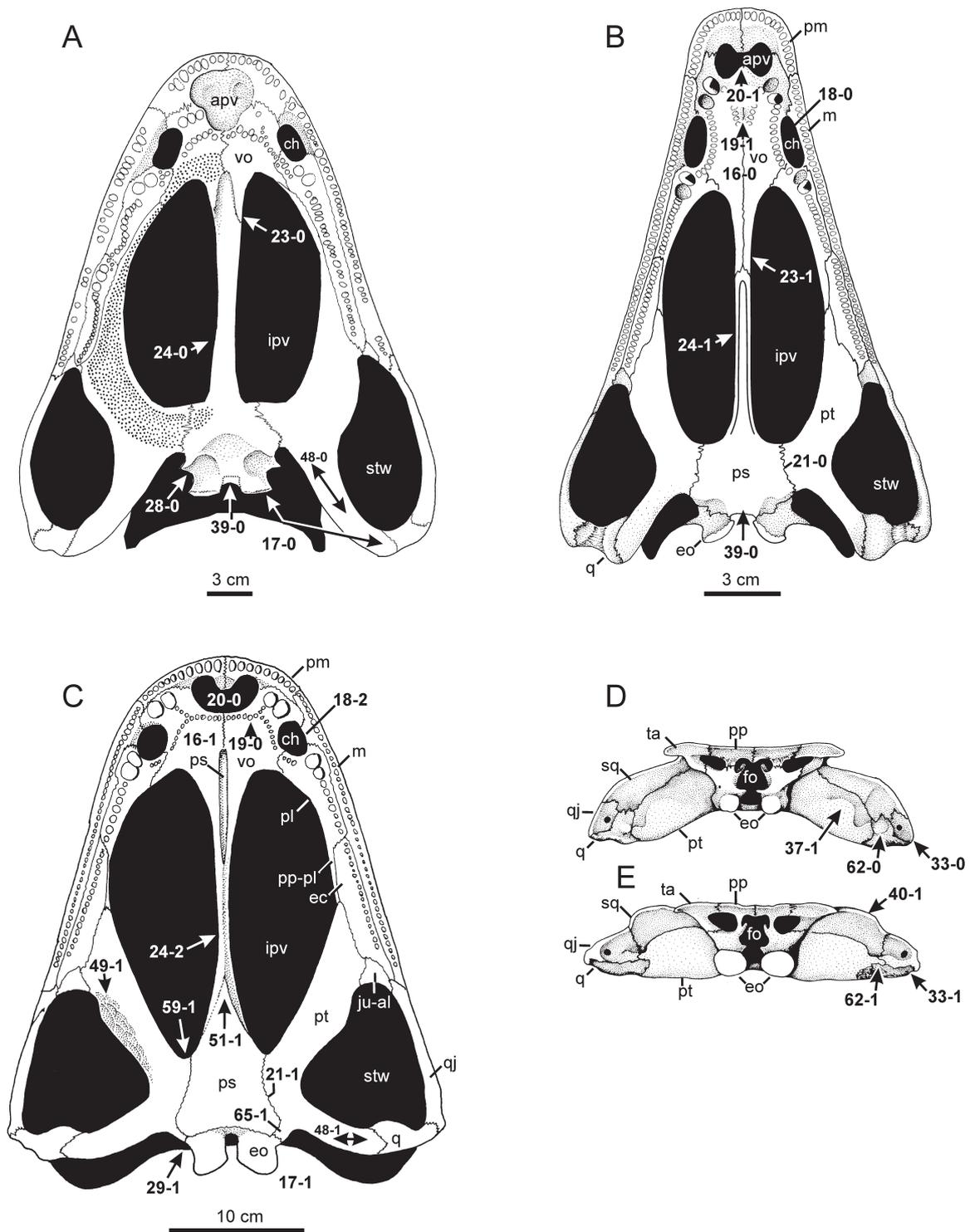
1. **Preorbital region.** Parabolic (0), or tapering (1). DAMIANI (2001a, 1, reformulated). (Fig. 3A, B).
2. **Posterolateral skull corners (quadrates).** Posterior to distal end of tabular horns (0), or anterior (1). DAMIANI (2001a, 2). (Fig. 3A, C).
3. **Otic notch.** Deeply incised into posterior skull margin (0), or reduced to an embayment (1). DAMIANI (2001a, 3). (Fig. 3A).
4. **Tabular horns.** Directed posteriorly (0), or laterally (1). DAMIANI (2001a, 4). (Fig. 3A, 4A).
5. **Orbital margins.** Flush with plane of skull roof (0), or well elevated above plane of skull roof (1), or emplaced on high sockets protruding even level of posterior skull table (2). DAMIANI (2001a, 5, reformulated and recoded). (Fig. 3B–D).
6. **Postorbital-prepineal growth zone.** Absent (0), or present (1). DAMIANI (2001a, 6). (Fig. 3B).
7. **Lateral line sulci.** Weakly impressed, discontinuous (0), or continuous, well impressed (1). DAMIANI (2001a, 7). (Fig. 4A, D).
8. **Lacrimal flexure of infraorbital canal.** Absent (0), stepped (1), or Z-shaped (2). DAMIANI (2001a, 8). (Fig. 3A–C).
9. **Occipital sensory canal.** Absent (0), or present (1). DAMIANI (2001a, 9). (Fig. 3B).
10. **Supraorbital sensory canal.** Traversing nasal (0), or nasal and lacrimal (1), or only lacrimal (2). DAMIANI (2001a, 10, reformulated and newly coded). Character-states ordered (because they form a sequence of geometric states). (Fig. 3B–C).
11. **Frontal.** Excluded from orbit (0), or entering medial margin of orbit in a narrow strip (1), or forming most of the medial margin of orbit (2). DAMIANI (2001a, 11, recoded). Character-states ordered, because they form a morphological sequence of states. (Figs. 3B, D, 4A).
12. **Supratemporal.** Entering dorsal margin of otic notch (0), or excluded from dorsal margin of otic notch (1). DAMIANI (2001a, 12). (Fig. 3A–B).
13. **Preorbital projection of jugal.** Shorter than half the length of snout (0), or as long or longer (1). DAMIANI (2001a, 13, reformulated). (Fig. 3D).
14. **Postorbital.** Laterally not wider than orbit (0), or with lateral wing projecting well beyond orbit (1). DAMIANI (2001a, 14, recoded). (Fig. 3B, D).
15. **Naris.** Oval (0), or narrow and elongated (1). DAMIANI (2001a, 15). (Fig. 3A, C).
16. **Vomerine plate.** Short, as wide as long (0), or narrow and longer than wide (1). DAMIANI (2001a, 16, reformulated). (Fig. 5B, C).
17. **Occipital condyles.** Anterior to quadrate condyles (0), or level with or posterior to these (1). DAMIANI (2001a, 17). (Fig. 5A, C).
18. **Choanal outline.** Oval-shaped (0), or narrow and slit-like (1), or circular (2). DAMIANI (2001a, 18). This character is here coded unordered, since no morphological transformation series is apparent. (Fig. 5B–C).
19. **Transvomerine tooth row.** Transverse (0), or V-shaped (1). DAMIANI (2001a, 19). (Fig. 5B–C).
20. **Anterior palatal vacuity.** Unpaired (0), or medially subdivided by anterior process (1), or completely subdivided (2). DAMIANI (2001a, 20, recoded). (Fig. 5A–C).
21. **Pterygoid-parasphenoid suture.** As long as basal plate is wide (0), or substantially longer than basal plate is wide (1). DAMIANI (2001a, 21, reformulated). (Fig. 5B–C).
22. **Posterolateral process of vomer.** Absent (0), or present (1). DAMIANI (2001a, 22). (Fig. 5A).
23. **Cultriform process extension between vomers.** Extends beyond anterior margin of interpterygoid vacuities (0), or underplated by vomers (1). DAMIANI (2001a, 23). (Fig. 5A–B).
24. **Cultriform process.** Ventrally flat (0), or flat with central ventral ridge (1), or slender with deep ventral crest (“knife-edged”) (2). DAMIANI (2001a, 24, reformulated). This character is here coded unordered, since no morphological transformation series is apparent. (Fig. 5A–C).
25. **Ectopterygoid exposure.** Excluded from the lateral margin of interpterygoid vacuities (0), or entering margin, wedged between palatine and pterygoid (1). DAMIANI (2001a, 25, reformulated). (Fig. 5C).
26. **Crista muscularis, extension.** Behind posterior border of parasphenoid-ptyerygoid suture (0), or level with that border (1). DAMIANI (2001a, 26). (Fig. 5C).
27. **Crista muscularis, midline.** Discontinuous (0), or confluent in midline (1). DAMIANI (2001a, 27). (Fig. 5B–C).
28. **Parasphenoid pockets.** Facing posterodorsally, located along the posterior rim of the plate (0), or ventrally, entirely located on the flat surface (1). DAMIANI (2001a, 28). (Fig. 5A).
29. **Exoccipital-ptyerygoid suture.** Absent (0), or present (1). DAMIANI (2001a, 29). (Fig. 5C).
30. **Marginal teeth.** Circular or moderately oval (0), or anteroposteriorly compressed and closely set (1). DAMIANI (2001a, 30).
31. **Ectopterygoid tusks.** Present (0), or absent (1). DAMIANI (2001a, 31). (Fig. 5B–C).
32. **Denticle field.** Present on parasphenoid and pterygoid (0), or absent (1). DAMIANI (2001a, 32). (Fig. 5A).
33. **Quadratojugal.** Excluded from quadrate trochlea (0), or forming lateral portion of it (1). DAMIANI (2001a, 33). (Fig. 5D–E).
34. **Cheek region, posterior view.** Rounded (0), or straight, box-like (1). DAMIANI (2001a, 34). Only state 0 is established in the taxa studied here, hence this character is uninformative for the present analysis. (Fig. 5D–E).
35. **Posttemporal fenestra.** Narrow and slit-like (0), or triangular (1). DAMIANI (2001a, 36). (Fig. 5D–E).
36. **Tabular horn.** Short, supported only by paroccipital process (0), or posteriorly extended, supported by two ventral ridges (1). DAMIANI (2001a, 36, reformulated). (Fig. 5D–E).
37. **Crista obliqua of pterygoid.** Absent (0), or present (1). DAMIANI (2001a, 37). (Fig. 5D–E).
38. **Crista muscularis of parasphenoid.** Visible in occipital view (0), or not visible (1). DAMIANI (2001a, 38). (Fig. 5D–E).
39. **Basioccipital.** Present (0), or absent (1). DAMIANI (2001a, 39). (Fig. 5A–B, D–E).
40. **Crista falciformis.** Absent (0), or present (1). DAMIANI (2001a, 40). (Fig. 5D–E).



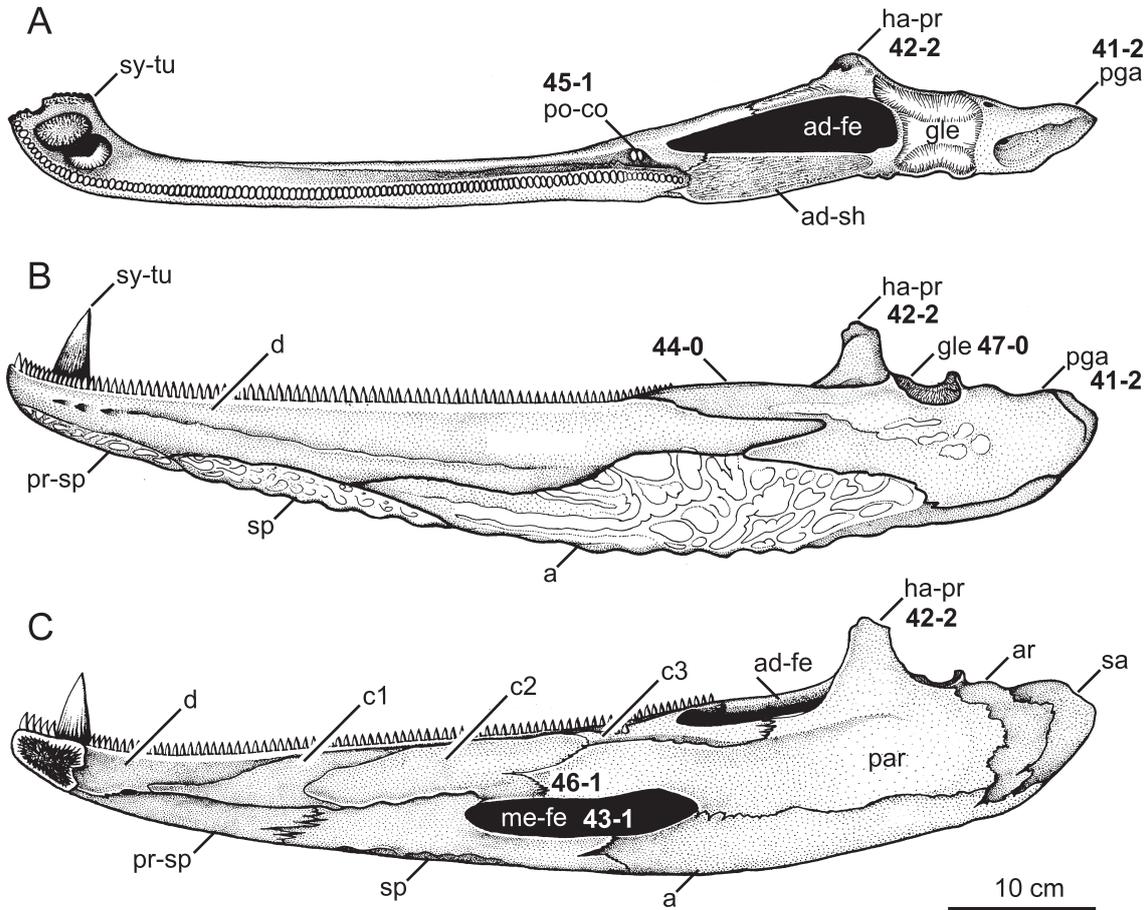
**Fig. 3.** Skulls of stereospondyls and basal capitosaur in dorsal view (after SCHOCH & MILNER 2000 and SCHOCH et al. 2007). Character-states mapped (see text for definition). – **A.** *Rhineceps nyasaensis*. **B.** *Thoosuchus yakovlevi*. **C.** *Wellugasaurus angustifrons*. **D.** *Sclerothorax hypselonotus*.



**Fig. 4.** Skulls of capitosaurs in dorsal view (after SCHOCH & MILNER 2000). Character-states mapped (see text for definition). – **A.** *Eryosuchus garjainovi*. **B.** *Mastodonsaurus giganteus*. **C.** *Parotosuchus orenburgensis*. **D.** *Cyclotosaurus robustus*.



**Fig. 5.** Skulls of stereospondyls and basal capitosaur in ventral (A–C) and occipital view (D–E) (after SCHOCH & MILNER 2000). Character-states mapped (see text for definition). – A. *Rhineceps nyasaensis*. B. *Benthosuchus sushkini*. C. *Cyclotosaurus robustus*. D. *Benthosuchus sushkini*. E. *Mastodonsaurus giganteus*.



**Fig. 6.** Mandible of *Mastodonsaurus giganteus* (after SCHOCH & MILNER 2000). Character-states mapped (see text for definition). – A. Dorsal view. B. Lateral view. C. Medial view.

- 41. **Postglenoid area.** Short boss (0), or distinct process (1), or extended, longer than glenoid facet (2). DAMIANI (2001a, 41, reformulated and recoded). (Fig. 6A–B).
  - 42. **Hamate process of prearticular.** Absent or rudimentary, forming at best an anterior margin of the glenoid facet (0), or present, raised well above glenoid and as high as quadrate trochlea (1), or substantially higher than quadrate trochlea (2). DAMIANI (2001a, 42). (Fig. 6A–C).
  - 43. **Posterior meckelian fenestra.** Small and round (0), or elongated, reaching  $\frac{1}{4}$  to  $\frac{1}{3}$  of mandible length (1). DAMIANI (2001a, 43, reformulated). (Fig. 6C).
  - 44. **Labial wall of adductor chamber.** Dorsally horizontal (0), or dorsally convex (1). DAMIANI (2001a, 44). (Fig. 6B).
  - 45. **Coronoid series.** With tooth patch (0), or single row of teeth (1). DAMIANI (2001a, 45). (Fig. 6A).
  - 46. **Prearticular.** Sutures with splenial anteriorly (0), or separated from it by dentary or coronoid 2 (1). DAMIANI (2001a, 46, reformulated). (Fig. 6C).
  - 47. **Glenoid facet.** Above level of dorsal surface of dentary (0), or below (1). DAMIANI (2001a, 47). (Fig. 6B–C).
- Additional characters.
- 48. **Quadrate ramus of pterygoid.** Parasagittally aligned (0), or laterally aligned and abbreviated (1). (Fig. 5A–C).
  - 49. **Palatine ramus of pterygoid.** Ventrally smooth (0), or ornamented (1). (Fig. 5A–B).
  - 50. **Basal plate of parasphenoid.** Short anterior to entrance foramina of carotid (0), or much elongated anteriorly (1). (Fig. 5A–C).
  - 51. **Cultriform process.** Merges continuously from basal plate (1), or forming a deltoid base (1). (SCHOCH 2000a). (Fig. 5A–C).
  - 52. **Vomerine tusks.** Posterior to anterior palatal vacuity (0), or lateral to it (1). (Fig. 5A–C).
  - 53. **Postparietals and tabular length.** Shorter than parietals (0), or as long or longer (1). (Fig. 4A–C).
  - 54. **Otic fenestra.** Tabular and squamosal separated by otic notch posteriorly (0), or separated by narrow slit (1), or sutured to encircle an otic fenestra (2). DAMIANI (2001a: character 4–2). (Fig. 4A–D).
  - 55. **Orbit anteriorly extended.** Oval or round (0), or anteriorly extended, indented into prefrontal (1). (Fig. 5A–D).
  - 56. **Tip of snout.** Pre-narial portion shorter than naris (0), or as long or longer (1). (Fig. 3A–D).
  - 57. **Snout penetrated by tusks.** Tip of snout completely ossified (0), or bearing paired openings anterior to naris to accommodate large symphyseal tusks (1). (Fig. 4B).
  - 58. **Postorbital and prefrontal.** Widely separated (0), or nearing one another by thin projections (1), or sutured, excluding jugal from orbit margin (2). (Fig. 4A–D).

59. **Interpterygoid vacuities.** Equally wide anteriorly and posteriorly (0), or tapered posteriorly (1). MORALES & SHISHKIN (2002, character 10). (Fig. 5A–C).
60. **Tip of tabular.** Equally wide throughout (0), or anterodistally broadened (1). DAMIANI (2001a, listed as a synapomorphy of *Eryosuchus garjainovi* and “*Stanocephalosaurus pronus*”). (Fig. 4A–C).
61. **Posterior margin of anterior palatal depression.** Concave (0), or straight (1). (Fig. 5A–C).
62. **Posterior boss of quadrate.** Occipital face of quadrate with prominent posterior boss (0), or smooth (1). (“hyoid tubercle” of MORALES & SHISHKIN 2002). (Fig. 5D–E).
63. **Tabular, posterior.** Wider than long (0), or posteriorly extended, as long as wide (1). (Fig. 4A–D).
64. **Epityergoid.** Short, tetrahedral (0), or anteriorly expanded with process paralleling sphenethmoid (1). SCHOCH (2000c).
65. **Posterior process of pterygoid.** Absent (0), or present, contacting exoccipital (1). (Fig. 5A–C).
66. **Snout width.** Elongate parabolic (0), or wide parabolic (1), or anteriorly expanded (2). (Fig. 3A–D).

## 4.2. Taxa

### 4.2.1. Analyzed taxa

All below-listed taxa that are marked by an asterisk (\*) were examined by the author.

#### Outgroup:

1. Rhinesuchidae, represented by *Uranocentron senekalensis* VAN HOEPEN, 1911 and *Rhineceps nyasaensis* (HAUGHTON, 1927) (VAN HOEPEN 1915).\* (Fig. 3A).

#### Ingroups:

2. *Lydekkerina huxleyi* (LYDEKKER, 1889) (SHISHKIN et al. 1996; JEANNOT et al. 2006; PAWLEY & WARREN 2005; HEWISON 2007).\*
3. *Benthosuchus sushkini* (EFREMOV, 1929) (BYSTROW & EFREMOV 1940).\* (Fig. 5B, D).
4. *Cherninia denwai* MUKHERJEE & SENGUPTA, 1998. I follow DAMIANI (2001b) in considering this taxon to be closely related to the type species, *Cherninia megarhina* (CHERNIN & COSGRIFF, 1975).
5. *Cyclotosaurus robustus* (MEYER & PLEININGER, 1844) (SCHOCH & MILNER 2000).\* This is the classic representative of the genus, which is also known from other horizons: *C. ebrachensis* (KUHN 1932), *C. mordax* and *C. posthumus* (FRAAS 1913), *C. hemprichi* (KUHN 1940, 1942) and *C. intermedius* from Poland (SULEJ & MAJER 2005), *C. cf. posthumus* from Greenland (JENKINS et al. 1996), and *C. cf. posthumus* from Thailand (INGAVAT & JANVIER 1981). Although these taxa are all relatively similar, the Greenland specimen has a completely subdivided anterior palatal opening (character 20-2) instead of a partially divided or undivided one in other species (20-0), while some specimens of *C. mordax* have a frontal excluded from the orbit margin (11-0) instead of entering it (11-2) as is the normal case for other species of the genus. (Fig. 4D, 5C).
6. *Edingerella madagascariensis* (LEHMAN, 1961) (STEYER 2003). Formerly ranked under the generic name *Parotosuchus*, it was referred to a new genus *Edingerella* by SCHOCH & MILNER (2000) and tentatively referred to the capitosauroid stem. Subsequently, DAMIANI (2001a) found *Edingerella* to nest with lydekkerinids, whereas STEYER (2003) found it to

nest with *Watsonisuchus*. Because of these uncertainties, it is not a priori attributed to *Watsonisuchus* here.

7. *Eocyclotosaurus lehmani* (HEYLER, 1969) (KAMPHAUSEN 1989).\* SCHOCH & MILNER (2000) synonymized *E. woschmidti* with *E. lehmani*, and SCHOCH (2000b) described the new species *E. wellsi* from the Anisian of Arizona. The latter is preserved with different size classes, revealing that the preorbital region became wider with age, the interorbital distance broader, and the prefrontal neared the postorbital. The otic fenestra was closed even in small juveniles.
8. *Eryosuchus garjainovi* OCHEV, 1966 (OCHEV 1972; SHISHKIN 1995).\* Among the three *Eryosuchus* species listed by OCHEV (1972), *E. garjainovi* is the best known and represented by the largest sample. However, I do not follow the assignment of taxa from outside Russia to this genus (e.g., DAMIANI 2001a) unless their close relationship with *Eryosuchus* has been demonstrated phylogenetically. (Fig. 4A)
9. *Kupferzellia wildi* SCHOCH, 1997.\* This taxon is similar in most details to *Tatrasuchus kulczyckii* (MARYANSKA & SHISHKIN 1996), but differs in one significant character, the outline of the choana, in which it is more similar to *Cyclotosaurus* than *Tatrasuchus*. Therefore, generic separation from *Tatrasuchus* is maintained here. As *Kupferzellia* is more completely known than *Tatrasuchus*, and the latter needs to be reexamined in features of the poorly described palate, only the former is considered here.
10. *Mastodonsaurus cappelensis* WEPFER, 1923 (PFANNENSTIEL 1932).\* SÄVE-SÖDERBERGH (1935) created a separate genus, *Heptasaurus*, for this species, but present evidence indicates close ties with *Mastodonsaurus giganteus*, which is why this species is here referred to *Mastodonsaurus*.
11. *Mastodonsaurus giganteus* JAEGER, 1828 (SCHOCH 1999, 2002a, b; MOSER & SCHOCH 2007).\* (Figs. 4B, 5E, 6A–C)
12. *Odenwaldia heidelbergensis* MORALES & KAMPHAUSEN, 1984 (present study).\*
13. *Paracyclotosaurus crookshanki* MUKHERJEE & SENGUPTA, 1998. The skull of this species is much better preserved than that of the type species, *P. davidi* WATSON, 1958 and that of the recently named *P. morganorum* DAMIANI & HANCOX, 2003. These three species are morphologically very close, and therefore *P. crookshanki* is here considered as representing the other two.
14. *Parotosuchus haughtoni* BROILLI & SCHRÖDER, 1937 (DAMIANI 2002).
15. *Parotosuchus nasutus* MEYER, 1858 (SCHOCH & MILNER 2000).\* Coding of this species was entirely based on personal examination of surviving specimens in various German collections.
16. *Parotosuchus orenburgensis* (KONZHUKOVA, 1965).\* (Fig. 4C).
17. *Quasicyclotosaurus campi* SCHOCH, 2000 (SCHOCH 2000b).\* The specimen on which the original description was based is considerably crushed. I have therefore relied on an additional specimen (UCMP 132022) brought to my attention by courtesy of RANDALL IRMIS (Berkeley).
18. *Sclerothorax hypselonotus* HUENE, 1932 (SCHOCH et al. 2007).\* This taxon was recently redescribed on the basis of new material and turned out in a phylogenetic analysis to nest with capitosauroids (SCHOCH et al. 2007). (Fig. 3D)
19. *Stanocephalosaurus birdi* BROWN, 1933 (WELLES & COSGRIFF 1965; “*Wellesaurus*” of DAMIANI 2001a).\* *Stanocephalosaurus* was argued by SCHOCH & MILNER (2000) to hold priority over *Wellesaurus*, after re-examination of the original material. WELLES & COSGRIFF (1965) studied this species extensively, but further undescribed UCMP material preserves juveniles showing that the snout was elongated even in small specimens.

20. “*Stanocephalosaurus*” *pronus* HOWIE, 1970 (“*Wellesaurus*” of DAMIANI 2001a). This species was originally referred to the “waste-basket” genus *Parotosuchus* (HOWIE 1970), but turned out to be more highly derived than *Parotosuchus sensu stricto* (DAMIANI 2001a). The suggestion to include “*S.*” *pronus* within the genus *Eryosuchus* as put forward by DAMIANI (2001a) is not followed here.
21. *Procyclusaurus stantonensis* PATON, 1974 (KAMPHAUSEN 1989).\* This genus was synonymized with *Stenotosaurus* by DAMIANI (2001a), but as the two genera differ with respect to the prefrontal-postorbital contact (present in *Stenotosaurus*, absent in *Procyclusaurus*), I prefer to uphold the generic separation.
22. *Thoosuchus yakovlevi* RIABININ, 1927 (GETMANOV 1986).\* Recently briefly described in English by DAMIANI & YATES (2003), this taxon is one of the best-studied trematosaur. (Fig. 3B).
23. *Watsonisuchus rewanensis* (WARREN, 1980). Based on re-examination of the South African taxon *Watsonisuchus magnus*, DAMIANI (2001a) defined that genus on the basis of autapomorphies and referred three more completely known Australian species to the genus, *W. aliciae*, *W. gunganj*, and *W. rewanensis*. As these are very similar (DAMIANI 2000, 2001a), I have here chosen *W. rewanensis* to represent the group, which is very likely to form a clade.
24. *Weilugasaurus angustifrons* RIABININ, 1930 (EFREMOV 1940; BYSTROW & EFREMOV 1940).\* (Fig. 3C)
25. *Xenotosuchus africanus* (BROOM, 1909) (MORALES & SHISHKIN 2002; DAMIANI 2008).\*

As an optional addition, two further, incompletely known taxa have been included (see extended taxon sample for details on analysis and results):

26. *Yuanansuchus laticeps* LIU & WANG, 2005.
27. *Stenotosaurus semiclausus* SWINTON, 1927 (KAMPHAUSEN 1989).

**Comment.** – I have not included *Jammerbergia formops* DAMIANI & HANCOX (2003) for two reasons. First, this taxon is very incompletely known, consisting only of the back of skull table and cheek, and second, the type and only specimen was stolen after the description and is no longer available for research (DAMIANI, pers. comm. 2007).

#### 4.2.2. Incompleteness of data sets

Emphasis was put on single species as terminal taxa that are well-known at least in the skull and mandible. The postcranium is adequately preserved only in a few species (*Sclerorhax hypselonotus*, *Mastodonsaurus giganteus*, *Paracyclusaurus davidi*), but undescribed or completely unknown in many genera (*Procyclusaurus*, *Stanocephalosaurus*, *Kupferzellia*, *Watsonisuchus*, *Xenotosuchus*, *Yuanansuchus*). Some taxa (*Cyclotosaurus*, *Eocyclotosaurus*, *Parotosuchus*) are known from fair skulls but few associated postcranial elements (e. g., interclavicles, humeri, intercentra, thoracic ribs) which appear rather poor in phylogenetically informative characters (PAWLEY & WARREN 2005; WITZMANN & SCHOCH 2006). In many cases,

the association of skulls with isolated postcranial elements is ambiguous, because many temnospondyl localities have yielded more than one taxon. Therefore, the present data set strongly leans towards cranial and mandibular characters. The knowledge of the braincase and palatoquadrate in capitosaur is in a similar situation (PFANNENSTIEL 1932; CASE 1933; WELLES & COSGRIFF 1965; DAMIANI 2002; SCHOCH 2002a, b), whereas in the visceral skeleton the stapes is much more widely known (BYSTROW & EFREMOV 1940; SCHOCH & MILNER 2000; SCHOCH 2000c).

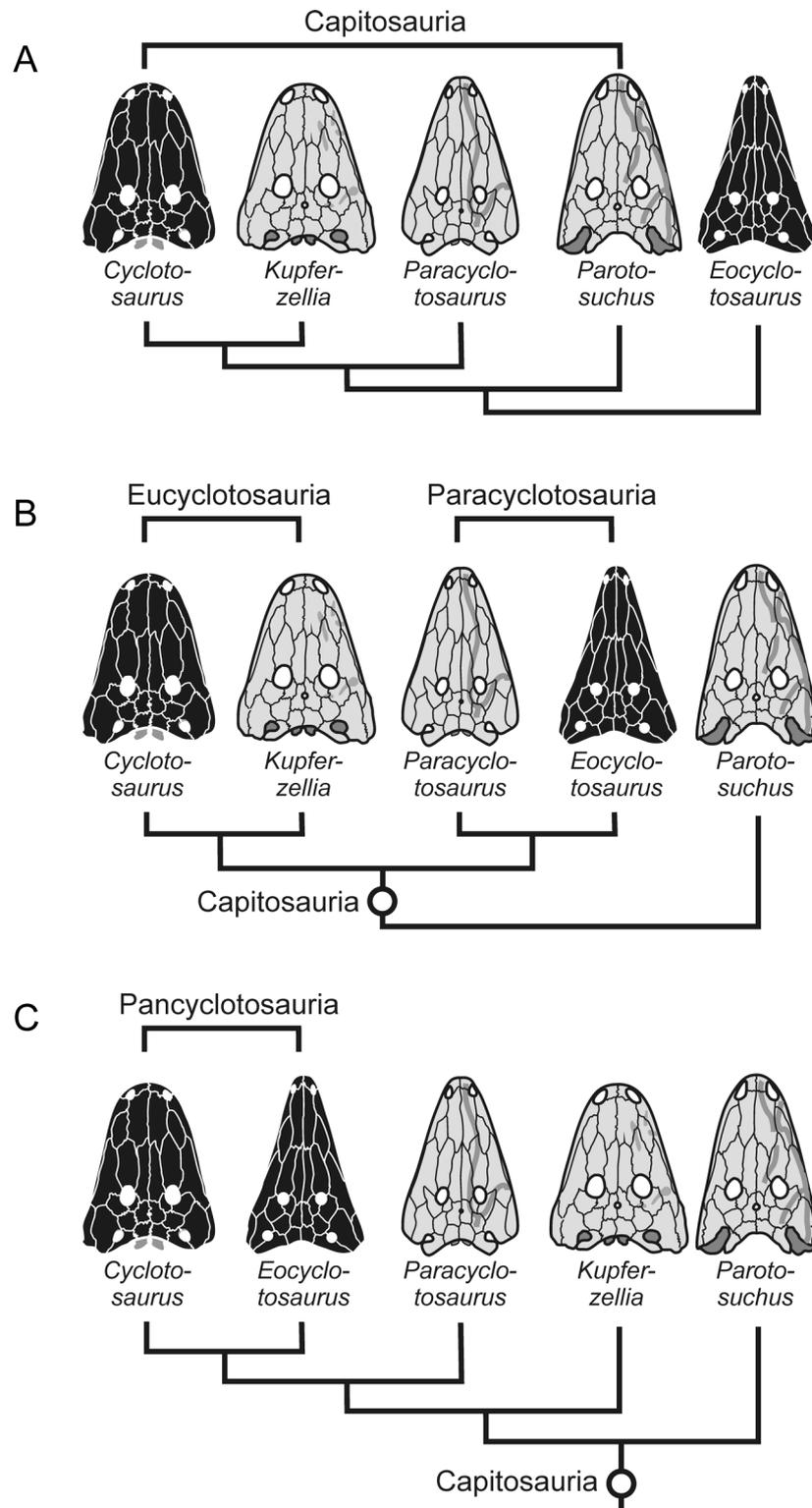
It would mean major efforts in collecting material around the world in order to fill the many gaps in capitosaur anatomy. The recent reexamination of *Sclerorhax* highlighted the importance of postcranial data, as this capitosaur has a very unusual axial skeleton and shoulder girdle; yet in the analysis many postcranial features of this taxon appeared to be convergences with *Eryops* or dissozophoids, simply because too little is known from other capitosaur, or even stereospondyls as a whole (SCHOCH et al. 2007). I have therefore treated the few more widely known postcranial characters with caution (see below).

#### 4.3. Terminology for phylogenetic concepts

Throughout the present study, the condition in which the otic fenestra is closed (character 54-2) is referred to as the ‘cyclotosaur’ condition and the taxa sharing this feature as the ‘cyclotosaur’ – without implying their close relationship. There are only a few genera which unambiguously have this character-state: *Cyclotosaurus*, *Eocyclotosaurus*, *Quasicyclotosaurus*, *Kupferzellia* (adults), and *Procyclusaurus*. Other genera (e. g., *Stanocephalosaurus*, *Paracyclusaurus*) come close to that condition in that the tabular and squamosal near each other, but they all retain a narrow gap in this region.

A deep split (extreme diphyly) between *Cyclotosaurus* and *Eocyclotosaurus* was postulated by SHISHKIN (1980) and DAMIANI (2001a). SCHOCH (2000a) and SCHOCH & MILNER (2000) instead favoured the monophyly of these two genera, nested within crown capitosaur. In order to distinguish these concepts, I coin three names which are used as labels for phylogenetic concepts on the evolution of the ‘cyclotosaur’ condition (Fig. 7).

- 1) **Convergence scenario:** *Cyclotosaurus* evolved the cyclotosaur condition independent from *Eocyclotosaurus*. This gives two names characterizing the groups that evolved the feature in parallel:
  - a) “Eucyclotosauria”: *Cyclotosaurus* and its stem-group. (Greek ‘eu’ = proper, true)
  - b) “Paracyclotosauria”: *Eocyclotosaurus* and *Quasicyclotosaurus* plus their stem-group (Greek ‘para’ = parallel, beneath)
- 2) **Monophyly scenario:** The genera *Cyclotosau-*



**Fig. 7.** Three different concepts of capitosaur relationships. Only some key taxa are mapped. – **A.** Deep diphyly as proposed by SHISHKIN (1980) and found by DAMIANI'S (2001a) cladistic analysis. **B.** Shallow diphyly as found by the present analysis (see below). **C.** Monophyly as found by SCHOCH (2000a).

*rus*, *Eocyclotosaurus* and *Quasicyclotosaurus* evolved the cyclotosaur condition just once, the whole group being referred to as “Pancyclotosauria” (Greek ‘pan’ = whole, all).

#### 4.4. Analysis

The analysis was run on a PC using a Macintosh Emulator, and employing the software packages Paup 3.1.1 (SWOFFORD 1991) and MacClade 3.0. (MADDISON & MADDISON 1992). The main analysis (25 taxa, 66 characters) was run in the Heuristic Search Mode, and gave a single tree that required 162 steps (CI=0.525, RI=0.727, RC=0.381). All characters were treated as having equal weight, and only those multistates which form a logical sequence were ordered (see 4.1.). Assessments of the robustness of nodes were carried out using Bootstrap and by calculating the Bremer Decay Index (Branch-and-Bound Mode). Various constraint trees were analyzed in MacClade, focussing on the alternatives proposed by previous studies (see below, section 4.4.3.). The first 47 characters derive from DAMIANI (2001a) and have not been altered in their sequence in order to maintain comparability; character 34 was informative in DAMIANI’S (2001a) analysis with respect to lydekkerinid affinities, but is not informative in the present analysis, as only *Lydekkerina* was considered. Therefore, only 65 characters were informative in the present analysis. See Fig. 8 for the results of the analysis.

#### 4.5. Results

The resulting tree agrees in several aspects with those of previous authors, thereby forming a compromise between the two existing extremes: with DAMIANI (2001a) in the basal branching of *Wetlugasaurus*, *Watsonisuchus*, and the higher capitosauroids, with SCHOCH (2000a) and LIU & WANG (2005) in that *Eocyclotosaurus* nests well within the higher capitosauroids. However, *Eocyclotosaurus* and *Cyclotosaurus* do not form closely related taxa, albeit both fall within the capitosaur crown (Fig. 8). A further compromise was found with respect to the positions of *Benthosuchus* and *Wetlugasaurus*: while *Benthosuchus* was found to nest with *Thoosuchus* (and by that the base of the trematosaur-clade, see SCHOCH 2008), *Wetlugasaurus* is robustly nested with the capitosaur-clade (capitosauroids sensu SCHOCH & MILNER 2000).

In the following I describe the results node by node, with reference to supporting character-states, their status, and robustness. See Figs. 9–10 for the general topology and the support for the nodes.

(1) Post-rhinesuchid Stereospondyli. (*Lydekkerina*, *Thoosuchus*, *Benthosuchus*, and the capitosaur).

This node was found by many recent analyses, including YATES & WARREN (2000), SCHOCH & MILNER (2000), SCHOCH (2006, 2008), SCHOCH et al. (2007). In the present analysis, it is supported by six synapomorphies (2, 12, 22, 35, 45, 56) and one homoplasy (8-1H).

(2) Trematosaur-capitosaur Clade ((*Benthosuchus*, *Thoosuchus*) + capitosaur). So far, only DAMIANI & YATES (2003) found evidence for this group. Whereas SCHOCH (2000a) and SCHOCH & MILNER (2000) included *Wetlugasaurus* in the trematosaur-clade as well, DAMIANI (2001a) found *Wetlugasaurus* and *Benthosuchus* to nest with capitosauroids, while YATES & WARREN (2000) suggested that *Lydekkerina* was more closely related to *Mastodonsaurus*, *Benthosuchus*, and the capitosaur than to trematosaur. Obviously, this node is more controversial than the post-rhinesuchid stereospondyls, although the quite unorthodox solution suggested by YATES & WARREN (2000) has not been found elsewhere and appears less likely than the other alternatives. However, to keep the number of taxa at an operational level, and because the specific question of this study is the phylogeny within capitosaur, the present analysis has excluded the short-faced stereospondyls (brachyopoids, rhytidosteids, plagiosaurids). These are likely to form a clade of their own that may either be closely related to (1) lydekkerinids (SCHOCH & MILNER 2000), or (2) nest between lydekkerinids and the trematosaur-capitosaur dichotomy (SCHOCH 2008, version A), or nest with trematosaur above the trematosaur-capitosaur split (YATES & WARREN 2000; SCHOCH 2008, version B). The trematosaur-capitosaur clade is here supported by two synapomorphies (37, 38) and two reversals (14R, 16R).

(3) Trematosauria. This clade includes *Edingerella*, *Benthosuchus*, and *Thoosuchus*. It has not been found before, and contrasts the hypotheses of both DAMIANI (2001a) in which *Edingerella* nested with *Lydekkerina* and that of STEYER (2003) in which *Edingerella* fell within the genus *Watsonisuchus*. In other words, the present analysis favours *Edingerella* to be a trematosaur, rather than a lydekkerinid or a capitosaur. However, the support for this is weak, no unequivocal synapomorphy and only three homoplasies (7H, 10H, 19R).

(4) Long-snouted Trematosauria. Here represented by *Thoosuchus* and *Benthosuchus*. These two genera were found by SCHOCH (2000a) to nest with *Trematosaurus*, and were consequently argued by SCHOCH & MILNER (2000) to form part of the stem-group of the trematosauroids proper. A Trematosauria of this composition was also found by DAMIANI & YATES (2003), after YATES & WARREN (2000) and DAMIANI

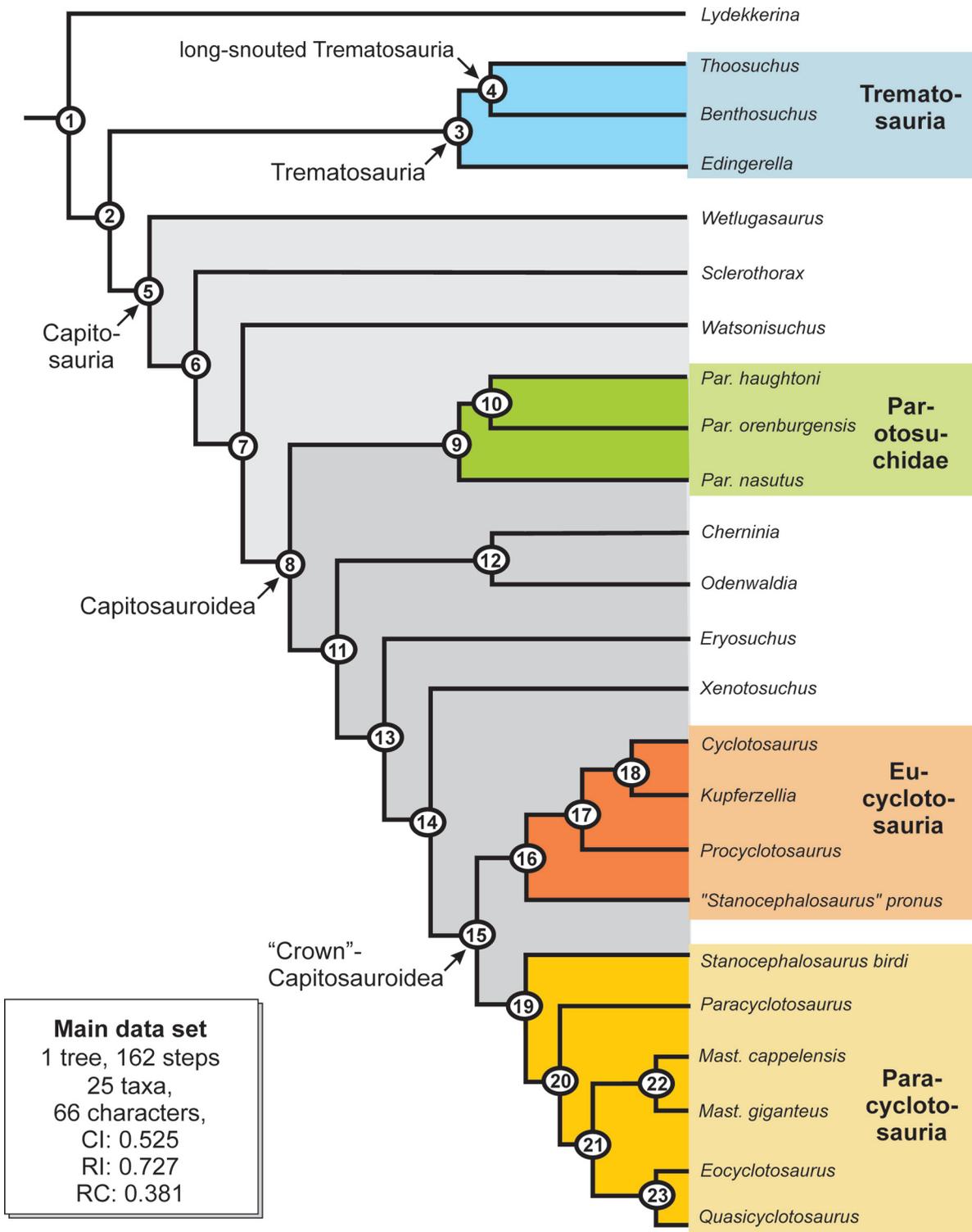


Fig. 8. Resulting topology of the main analysis. Numbers in circles refer to nodes as listed in the text.



- (2001a) had argued instead for a closer relationship between *Benthosuchus* and the capitosaurids. Trematosauria is here supported by five synapomorphies (9, 23, 44, 47, 56) and one homoplasy (8-1H).
- (5) Capitosauria. The Capitosauria was (re)defined as “all stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Trematosaurus*” (DAMIANI & YATES 2003). This is a more operational definition than YATES & WARREN’S (2000), because it involves two long-known and well-understood taxa, and it excludes brachyopoids whose inclusion added numerous problems to the already complicated debate (see recent analysis of SCHOCH 2008). The Capitosauria sensu DAMIANI & YATES (2003) includes the stem of the capitosauroids, notably *Wetlugasaurus* and *Watsonisuchus*. This clade is confirmed by the present analysis, supported by four unambiguous synapomorphies (8-2, 27, 28, 42-1) and one reversal (13R).
  - (6) Post-*Wetlugasaurus* capitosaurids (*Sclerothorax*, *Watsonisuchus*, and Capitosauroida). In this composition, the clade is reported for the first time. DAMIANI (2001a) found *Watsonisuchus* nesting as sister taxon of the capitosauroids, but *Sclerothorax* could only be considered after its recent redescription (SCHOCH et al. 2007). The position of *Sclerothorax* between *Wetlugasaurus* and *Watsonisuchus* is not surprising, as it bears numerous similarities with these genera and some species of *Parotosuchus*; in the first phylogenetic study, which analyzed a much broader range of temnospondyls (SCHOCH et al. 2007), *Sclerothorax* nested with the two only considered capitosaurids (*Mastodonsaurus* and *Paracyclotosaurus*), despite major differences in the postcranial skeleton. The post-*Wetlugasaurus* capitosaurids are supported as a clade by one synapomorphy (32).
  - (7) *Watsonisuchus* and Capitosauroida. This group, which was essentially found by DAMIANI (2001a) as well, is only supported by one reversal (11R).
  - (8) Capitosauroida (post-*Watsonisuchus* capitosauroids). The classic capitosaur clade, as defined by SCHOCH & MILNER (2000), is here supported by one unambiguous synapomorphy (61). Although not named as such, DAMIANI (2001a) found a similar clade which however excluded *Odenwaldia* and *Eocyclotosaurus*.
  - (9) Parotosuchidae (*Parotosuchus nasutus* + (*P. haughtoni* + *P. orenburgensis*)). Parotosuchidae was first named by SCHOCH & WERNEBURG (1998) and later reported as a monophylum by SCHOCH & MILNER (2000). DAMIANI (2001a) basically agreed with this by restricting the genus *Parotosuchus* to the three species here analyzed plus *P. helgolandiae*. Parotosuchidae as defined here is supported by one synapomorphy (18-1).
  - (10) *Parotosuchus haughtoni* + *P. orenburgensis*. This is the “crown” clade of *Parotosuchus*, formed by the two currently best-known species. It is supported by one synapomorphy (5-2).
  - (11) Post-*Parotosuchus* capitosauroids. A weakly supported group that lacks any unequivocal synapomorphy. In DAMIANI’S (2001a) analysis, *Cherninia* had a similar position, only that *Eryosuchus* was more basal.
  - (12) *Odenwaldia* + *Cherninia*. This potential sister group has not been found before and is supported by one homoplasy (20-2H).
  - (13) Higher capitosauroids. Cyclotosauridae, Stenotosauridae, Heylerosauridae, Mastodonsauridae and their shared stem-group taxa (*Eryosuchus*, *Xenotosuchus*). This large clade is supported by one synapomorphy (4) and one reversal (50R).
  - (14) Post-*Eryosuchus* capitosauroids. This clade includes *Xenotosuchus* and all “advanced” capitosaur families. This node is supported by one reversal (59R).
  - (15) Capitosauroid “Crown”. As such found by SCHOCH (2000a) and SCHOCH & MILNER (2000), and with the exclusion of the heylerosaurids also found by DAMIANI (2001a). This clade is supported by one reversal only (29R).
  - (16) “Eucyclotosauria”. Here found for the first time, including “*Stanocephalosaurus*” *pronus*, *Procyclotosaurus stantonensis*, *Kupferzellia*, and *Cyclotosaurus*. This group lacks support by unambiguous synapomorphies, but shares the homoplastic character 43.
  - (17) *Procyclotosaurus*, *Kupferzellia*, and *Cyclotosaurus*. Not found before, this clade is supported by one reversal (54-2R).
  - (18) Cyclotosauridae. Includes *Kupferzellia* and *Cyclotosaurus*. This was found before by DAMIANI (2001a) and also suggested by SCHOCH & MILNER (2000). It is supported by three synapomorphies (18-2, 52, 66) and one reversal (16R).
  - (19) “Paracyclotosauria” (*Stanocephalosaurus birdi*, Heylerosauridae, Mastodonsauridae, *Paracyclotosaurus*). This clade has never been found before, and is here supported by one synapomorphy (20-1).
  - (20) Heylerosauridae, Mastodonsauridae, *Paracyclotosaurus*. Again, an unorthodox clade, here supported by four homoplasies (7H, 10H, 20-2H, 21H).
  - (21) Heylerosauridae and Mastodonsauridae. A similar group was found by LIU & WANG (2005), albeit including *Yuanansuchus* which nested in between. Here, a sister-group relationship of mastodonsaurids and heylerosaurids is supported by one homoplasy (24H).
  - (22) Mastodonsauridae. This clade includes *Mastodon-*



*saurus giganteus* and *M. cappelensis*. The monophyly of the genus *Mastodonsaurus* has not been disputed since SÄVE-SÖDERBERGH (1935), despite the occasional referral of *M. cappelensis* to a separate genus *Heptasaurus*. This sister group is supported by three synapomorphies (48, 55, 57) and three ambiguous characters (6H, 13H, 14R).

- (23) Heylerosauridae. Includes only *Eocyclotosaurus* and *Quasicyclotosaurus*. This was found by SCHOCH (2000a) and LIU & WANG (2005). In the present analysis, it is supported by one synapomorphy (58-2) and two homoplasies (11R, 54-2R).

#### 4.5.1. Support and robustness of nodes

The support for the single nodes and their robustness according to Bremer Decay Index and Bootstrap are generally low. All nodes except five (2, 4, 5, 13, 22) have a Bremer index of one, and only eight reached Bootstrap values higher than 50 (2: 91, 4: 85, 5: 80, 10: 70, 13: 74, 18: 58, 21: 79, 22: 100). In sum, this indicates that apart from the Capitosauria and Trematosauria, only the Mastodonsauridae and the “crown”-capitosauroids are well-supported. Among these, the large clade formed by trematosauroids and capitosauroids, the trematosauroids proper (represented by *Benthosuchus* plus *Thoosuchus*), and the mastodonsaurids are supported by 3 steps Bremer support each. In the Bootstrap analysis, the sister group formed by *Parotosuchus haughtoni* and *P. orenburgensis*, as well as the Cyclotosauridae (*Cyclotosaurus* plus *Kupferzellia*) are still reasonably well supported.

#### 4.5.2. Constraint trees

The following constraint trees were produced in MacClade 3.0 in order to test the support for alternative phylogenetic topologies within the frame of the present data set.

- 1) The monophyly of all “cyclotosaur” capitosauroids as found by SCHOCH (2000a) (*Cyclotosaurus*, *Eocyclotosaurus*, and *Quasicyclotosaurus*) required two extra steps.
- 2) The monophyly of mastodonsaurids (*Mastodonsaurus giganteus*, *M. cappelensis*) and *Eryosuchus* as found by SCHOCH (2000a) required two extra steps.
- 3) *Odenwaldia* nesting lower, between *Watsonisuchus* and the *Parotosuchus* clade required two extra steps.
- 4) The alternative that *Stanocephalosaurus birdi* and “*Stanocephalosaurus*” *pronus* form a clade (SCHOCH & MILNER 2000) requires two extra steps.
- 5) *Eryosuchus garjainovi* and “*Stanocephalosaurus*” *pronus* forming a clade (*Eryosuchus* of DAMIANI 2001a) requires seven extra steps.

- 6) The alternative in which monophyletic *Eocyclotosaurus* and *Odenwaldia* nest below *Wetlugasaurus*, as initially suggested by MORALES & KAMPHAUSEN (1984) and later found by DAMIANI (2001a) is here found to require 13 extra steps.
- 7) A constraint tree in which *Edingerella* and *Watsonisuchus* form a clade (as found by STEYER 2003) requires seven extra steps, one with *Edingerella* and *Lydekkerina* being monophyletic having six extra steps (DAMIANI 2001a). However, a further constraint tree with *Edingerella* at the base of the Capitosauria (between Trematosauria and *Wetlugasaurus*) requires only one additional step.

#### 4.5.3. Restricted taxon sample

- 1) An exclusion of *Cherninia* from the main data set was performed in order to test the impact of this taxon on the position of *Odenwaldia*. This resulted in a substantially more basal nesting of *Odenwaldia*, between *Wetlugasaurus* and *Sclerothorax*. Morphologically, this appears to be a more sound hypothesis than the one found by analyzing the main data set. However, the exclusion of *Cherninia* also has an impact on the topology of the “crown”-capitosauroids: *Cyclotosaurus* now forms the sister taxon of the heylerosaurids, *Kupferzellia* nests in between *Eryosuchus* and *Procyclusaurus*, and the latter forms an unresolved trichotomy with “*Stanocephalosaurus*” *pronus*. In other words, the omission of *Cherninia* results in the break-up of the “Eucyclotosauria” found in the main analysis, with most of its constituents falling on a grade.
- 2) An exclusion of both *Cherninia* and *Odenwaldia* gives the same main topology as described in (1).
- 3) Exclusion of *Xenotosuchus* from the main data set resulted in a monophyletic Pancyclotosauria, with *Paracyclusaurus* and an unresolved trichotomy between *Procyclusaurus*, “*Stanocephalosaurus*” *pronus* and the rest forming successive sister groups of that clade. *Kupferzellia* assumes the position held by *Xenotosuchus* in the main analysis, between *Eryosuchus* and the rest.
- 4) Exclusion of *Xenotosuchus* and “*Stanocephalosaurus*” *pronus* gave the same topology, but only a single tree. In a variant, *Procyclusaurus* was omitted, which again resulted in the same topology.
- 5) More significant than the changes reported above was the exclusion of only “*Stanocephalosaurus*” *pronus*: this retained the Eucyclotosauria – Paracyclusauria split obtained in the main analysis.
- 6) Exclusion of *Edingerella* did not change the topology of the remaining taxa at all.

4.5.4. Extended taxon sample: *Yuanansuchus* and *Stenotosaurus*

In addition to the main analysis, which focused on the bulk of the well-preserved capitosaurids, a second data set was analyzed (see data matrix in the Appendix). The inclusion of the incompletely known Chinese taxon *Yuanansuchus laticeps* and the fragmentarily preserved *Stenotosaurus semiclausus* was tested for two reasons. (1) Both taxa combine character-states known from more than one clade found by the main analysis, apparently challenging its results on the convergent evolution of cyclotosaurids. While *Yuanansuchus* shares features with *Cyclotosaurus*, heylerosaurids, and mastodontosaurids, *Stenotosaurus* combines character-states found in heylerosaurids, *Cyclotosaurus*, and *Procyclusaurus*. (2) *Stenotosaurus* occurs in the same formation as *Eocyclusaurus* in Germany, whereas *Yuanansuchus* is the first well-known capitosaur from China, which makes both taxa potentially significant.

Despite their unusual combination of characters, both taxa did not essentially change the results of the main analysis (Fig. 11). In the following sections, I report the details of separate and combined analyses with these taxa included into the main data set.

- 1) When *Yuanansuchus* alone is added (26 taxa, 66 characters), two trees are found requiring 168 steps (CI: 0.506, RI: 0.720, RC: 0.364). The resulting consensus tree agrees with the single tree of the main analysis in all branching nodes, with *Yuanansuchus* forming an unresolved trichotomy with *Paracyclusaurus* and a clade formed by heylerosaurids plus mastodontosaurids. The two alternative trees vary in that *Yuanansuchus* either nests as sister taxon of heylerosaurids or as sister taxon of the heylerosaurid-mastodontosaurid clade.
- 2) When *Stenotosaurus* is included in addition to *Yuanansuchus*, (27 taxa, 66 characters), six trees are found requiring 167 steps (CI: 0.515, RI: 0.727, RC: 0.375). Again, the resulting consensus tree does not change the topology of the main analysis, but places the two additional taxa in polytomies: *Stenotosaurus* in a trichotomy with *Procyclusaurus* and a clade formed by *Cyclotosaurus* plus *Kupferzellia*, and *Yuanansuchus* in a trichotomy with *Paracyclusaurus* and the heylerosaurid-mastodontosaurid clade (as in 1).

Although the extended taxon sample basically confirms the findings of the main analysis, it also creates polytomies that reflect homoplastic character distributions. Interestingly, the similarity between *Stenotosaurus* and the heylerosaurids does not have a bearing on their relationships as found here, which partially confirms the thoughts of SHISHKIN (1980) and KAMPHAUSEN (1989) on the differences between *Stenotosaurus* and *Eocyclusaurus*. This shows that the different position of *Odenwaldia* as

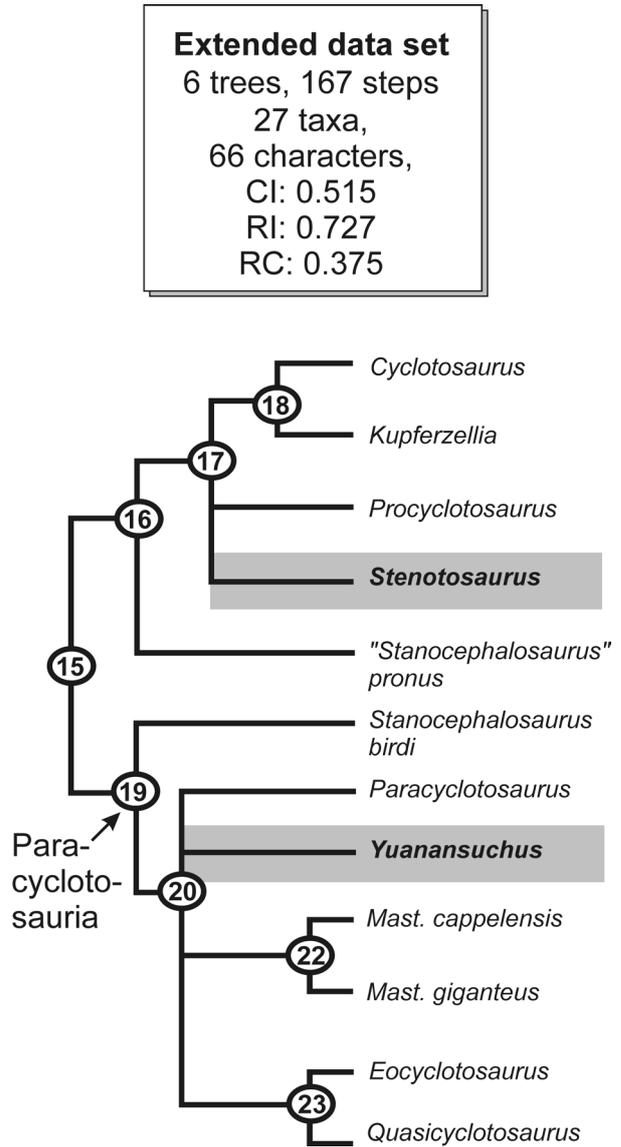


Fig. 11. Resulting topology of the extended analysis, which includes *Stenotosaurus semiclausus* and *Yuanansuchus laticeps* to the data matrix of the main set. Numbers in circles refer to nodes as listed in the text.

found here need not change the whole story, but retains another component of KAMPHAUSEN'S (1989) diphyletic scenario of cyclotosaur origins; the difference lies in the depth of the split, which by the shift of *Odenwaldia* well into the capitosauroids has become much shallower.

4.5.5. Exclusion of characters

An exclusion of key characters was performed to test their impact on the phylogenetic topology; character numbers are listed in brackets below.

- (8) Exclusion of the lacrimal flexure of the infraorbital sulcus gave the same result as the main analysis. This was interesting, because the character is not always clearly established (e. g., when the sulci are faint or discontinuous). However, this variant analysis gave the same topology as the main one.
- (11) When the contact between prefrontal and postfrontal is left unconsidered, the analysis produces a very poorly resolved tree: *Wetlugasaurus*, *Watsonisuchus*, *Sclerothorax* and *Parotosuchus nasutus* forming a bush, *Eryosuchus* and *Xenotosuchus* an unresolved trichotomy with the “crown”, and the higher capitosauroids form a nearly complete bush in which only the two *Mastodonsaurus* species are found as sister taxa. This is apparently the most important character of the whole analysis, and all former authors have agreed that it may be one of the few really significant phylogenetic signals in capitosaur evolution (HOWIE 1970; YATES & WARREN 2000; DAMIANI 2001a). This is supported by numerous observations on variation in capitosaur, which is usually wide, but never includes a variation in the states of character 11. There is only one exception, *Cyclotosaurus mordax*, which was cited by SCHOCH (2000a) as counter-evidence against the invariable significance of the character. Closer inspection, however, of the other *Cyclotosaurus* species (*C. posthumus*, *C. ebrachensis*, *C. intermedius*) suggests that this phenomenon was restricted to one particular species, and even the oldest well-known species (*C. robustus*) does not share this increased level of variation. Hence, the character may be viewed as rather robust and probably significant.
- (16) When the abbreviated vomerine plate is excluded from the analysis, *Kupferzellia* is moved away from *Cyclotosaurus* and nests between *Xenotosuchus* and *Procyclusaurus*. This shows that the absence of the potential shared-derived character of the broad-headed “cyclotosaurids” results in their dissolution, with the “Pancyclotosauria” hypothesis being supported instead. That is, there are no other significant synapomorphies shared between *Kupferzellia* and the taxa above *Xenotosuchus*.
- (20) Exclusion of the anterior palatal opening results in a reduced resolution (9 alternative trees, 141 steps), but a generally similar topology as in the main analysis. The major difference is the position of *Odenwaldia*, which is shifted from being the sister taxon of *Cherninia* towards a trichotomy with *Wetlugasaurus* and the rest. However, in contrast to most other variant analyses, the cores of the two main clades within the “crown” capitosauroids, *Cyclotosaurus-Kupferzellia-Procyclusaurus* versus Heylerosauridae-Mastodonsauridae-*Paracyclusaurus* are retained. Interestingly, *Stanocephalosaurius birdi* and “*Stanocephalosaurius*” *pronus* form a polytomy with the *Cyclotosaurus*-clade. This reveals that the morphology of the anterior palatal opening is not essential, but important to fully resolve the topology; the results also reveal that in the case that *Cherninia* and *Odenwaldia* had acquired the derived state of this character convergently, the simple consideration of character 20 would be sufficient to position *Odenwaldia* much higher within the Capitosauria. Overall morphology indeed suggests that this is the case, and *Odenwaldia* probably nested more basally.

- (58) The exclusion of the jugal from the orbit margin is found in both heylerosaurids and *Stenotosaurus semiclausus*, but not in *Cyclotosaurus*. However, exclusion of this character gave the same result as the main analysis.

#### 4.6. Problems and open questions

##### 4.6.1. *Capitosaurus arenaceus*

WATSON'S (1919) Capitosauridae (and all higher taxa derived from it) was originally based on *Capitosaurus arenaceus* MÜNSTER, 1836, a partial skull from the Benk Sandstone unit that falls within the Gipskeuper section (probably lowermost Carnian, Fig. 12) of Franconia (northern Bavaria, Germany). The type and only specimen was often considered close to or identical with *Cyclotosaurus robustus*, a better preserved species first reported by MEYER in MEYER & PLIENINGER (1844). BROILI (1915) re-described the specimen of *C. arenaceus*, highlighting its general similarity to *Parotosuchus nasutus* instead, a taxon from the Olenekian Middle Buntsandstein that was also referred to the genus *Capitosaurus* at that time. Later, JAEKEL (1922) suggested restricting the generic name *Capitosaurus* to *C. arenaceus*. The case appeared to be settled by WELLES & COSGRIFF'S (1965) outright declaration of invalidity (“nomen vanum”) for *C. arenaceus*, because it lacked the otic region. This was only consequent, because by that time the closure of the otic fenestra was regarded a key feature for advanced capitosaur, with any new find in which this region was unknown considered undiagnostic.

Concerning the otic region of *Capitosaurus arenaceus*, KAMPHAUSEN (1990) correctly stressed that MÜNSTER (1836) had given a description of the find when it was still complete, highlighting the existence of closed otic fenestrae in the posterolateral corners of the skull! Apparently, the posterior end of the skull was lost after MÜNSTER'S description, because BRAUN (1840) already figured the specimen in its present incomplete state. MÜNSTER'S original report was almost certainly unknown to workers unfamiliar with the German language, and even BROILI (1915) seems not to have taken notice of MÜNSTER'S (1836) com-

ments. I concur entirely with KAMPHAUSEN (1990) that there is no reason to doubt MÜNSTER's original report.

Most recently, KAMPHAUSEN (1990) and DAMIANI (2001a) discussed the significance and relationship of *Capitosaurus arenaceus*, and both suggested close affinities to *Cyclotosaurus*. (In fact, KAMPHAUSEN 1990 even argued that *Cyclotosaurus* was a synonym of *Capitosaurus*, a matter on which I disagree.) This correlates with a shift towards regarding the closure of the otic window of less significance, as both authors suggested that it evolved in parallel in *Eocyclotosaurus* and *Cyclotosaurus*. Indeed, although the present analysis comes to a different conclusion regarding the origin of *Eocyclotosaurus*, it concurs with the notion that the otic window is probably not a reliable phylogenetic signal. Therefore, it is not convincing to consider a taxon invalid simply because its otic region is unknown (and this is only required if one disbelieves MÜNSTER's report in the first place). Instead, if the preceding phylogenetic discussion is borne in mind, other characters emerge that are evidently more significant. For instance, the outline of the skull, and especially the choanal and vomerine regions, have a characteristic morphology in *Cyclotosaurus* and its hypothesized relative *Kupferzellia*. The abbreviated, rounded choana is not found in any other capitosaur, except *Capitosaurus arenaceus*, where it is poorly exposed, however. Hence, both the abbreviated and broadened choana and the foreshortened vomerine region is a synapomorphy shared between *Cyclotosaurus*, *Kupferzellia*, and *Capitosaurus arenaceus*, as is the wide-parabolic preorbital region, although this is slightly constricted near the tip in *C. arenaceus*.

In this light, the reexamination of *Capitosaurus arenaceus* reveals interesting details, and when compared with both *Cyclotosaurus* and *Kupferzellia*, it readily assumes an intermediate position: (1) the cultriform process lacks a ventral crest (symplesiomorphy with *Kupferzellia*), (2) the basicranial region is short (symplesiomorphy with *Kupferzellia*), and (3) the outline of the interpterygoid vacuities is posteriorly narrower due to a steeper angled pterygoids (apomorphy shared with *Cyclotosaurus*).

To sum up, *Capitosaurus arenaceus* shares the main constituent synapomorphies of the "Cyclotosauridae" as found in the main analysis (*Cyclotosaurus* plus *Kupferzellia*). (If one trusts MÜNSTER's original report, then the closed otic fenestra of *Capitosaurus* is a fact). I regard these as strong arguments not only for acceptance of *C. arenaceus* as a valid taxon (and not just a fragmentary *Cyclotosaurus*), but also for maintenance of the genus *Capitosaurus*, because it probably represents a branch somewhere below the origin of the classic *Cyclotosaurus*, regardless of the relationships with *Kupferzellia* and the heylerosaurids. Stratigraphically, the occurrence of *Capitosaurus* (Ladinian-Carnian boundary) is consistent with its phylogenetic position, slightly younger than *Kupferzel-*

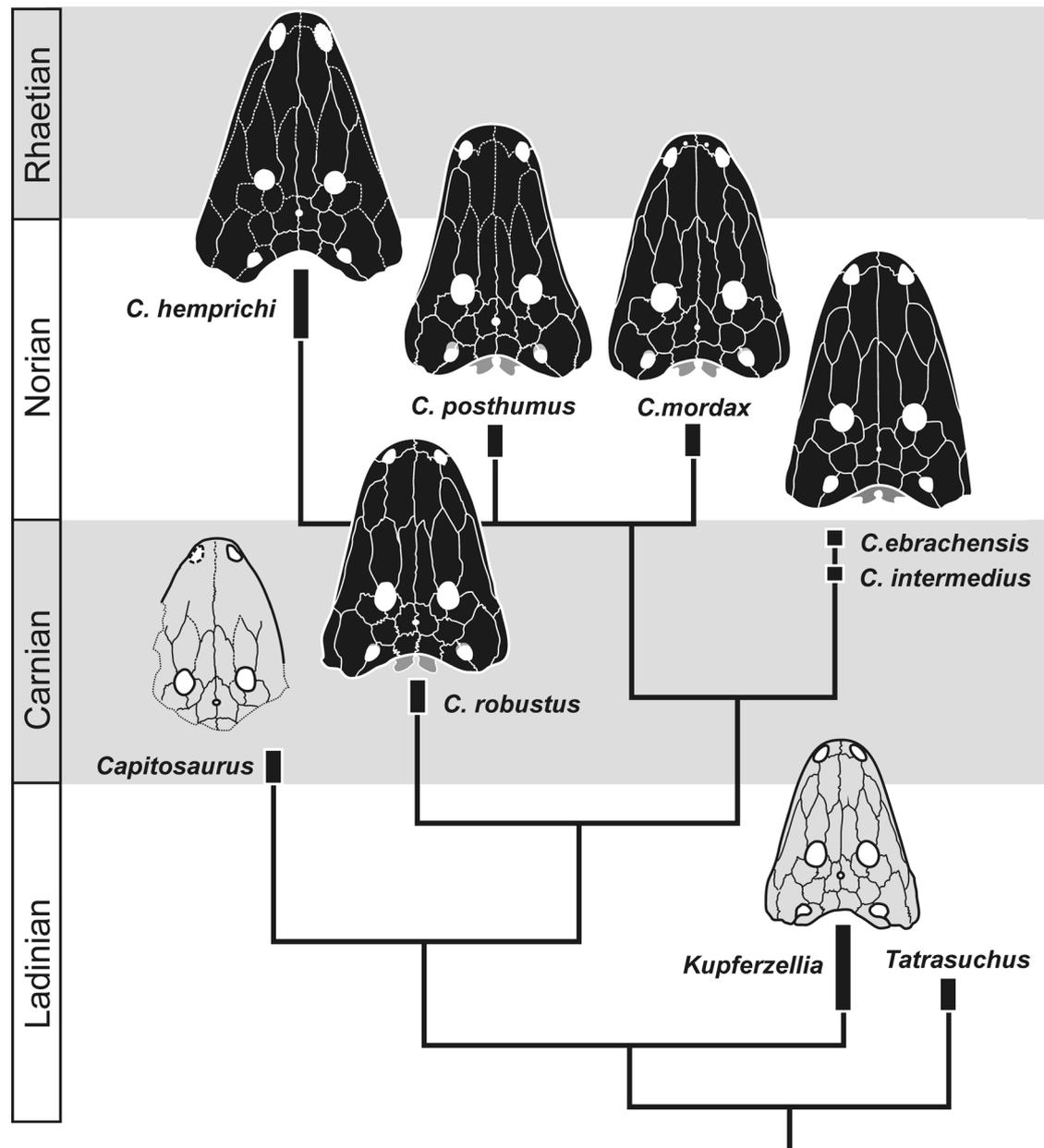
*lia* (Upper Ladinian) and clearly older than *Cyclotosaurus robustus*, the oldest unequivocal representative of the genus (Fig. 12).

#### 4.6.2. The stratigraphic range of *Cyclotosaurus*

The stratigraphic range of the genus *Cyclotosaurus* is one of the few cases in which the fossil record of capitosaur is exceptionally well-sampled across a larger stratigraphic section (Figs. 12–13). When only the unequivocal occurrences of the genus are counted, it ranges from the Middle Carnian Schilfsandstein (Julian: 225 Ma) through the Upper Norian Knollenmergel (Sevatian: 207 Ma), giving a minimal total range of at least 18 Ma. Within this sequence, *Cyclotosaurus* is known from specimens in five different stratigraphical levels (Schilfsandstein, an equivalent of Lehrbergschichten, Blasensandstein, Stubensandstein, Knollenmergel) and from four different regions in Europe – southern Germany (Württemberg, Oberfranken), Central Germany (Saxony-Anhalt), southeast Poland (Opole region), and eastern Greenland (Jameson Land).

In the last section, the putative sister taxa of *Cyclotosaurus*, *Capitosaurus arenaceus* and *Kupferzellia wildi*, were aligned in a stratigraphic sequence that correlates well with their morphological similarities. In contrast to this sequence, the stratigraphical range of *Cyclotosaurus* can also be read in a different way. This hinges upon the single find of "*Cyclotosaurus*" *papilio* and its interpretation. WEPFER (1923b) described this taxon from a posterior skull fragment that is fairly consistent with *Cyclotosaurus robustus*. Yet stratigraphically, *C. papilio* stems from the Lower Keuper, being coeval with *Kupferzellia* and by that the oldest and only unequivocally Ladinian evidence of the genus. (If truly a *Cyclotosaurus*, this would push back the range of the genus by some additional 8–10 Ma). In order to resolve this problem, it is crucial to compare *C. papilio* closely to other "cyclotosaurs", such as *Procyclotosaurus*, *Stenotosaurus*, and the heylerosaurids. Although the critical regions are not preserved (basicranium, vomer, choana), *C. papilio* differs from all these by the wide jugal, a feature consistent with all species of *Cyclotosaurus* and *Kupferzellia*. These findings suggest that "*C.*" *papilio* is at least more closely related to the *Kupferzellia-Capitosaurus-Cyclotosaurus* clade than any other group of "crown" capitosaur. Yet it does not provide sufficient evidence for the proof of the genus *Cyclotosaurus*, and therefore the stratigraphic-evolutionary scenario outlined in the last section is not critically challenged.

The first unequivocal occurrence of *Cyclotosaurus* is *C. robustus*, from the Middle Carnian Schilfsandstein of Stuttgart (Feuerbach) and other localities in southern and central Germany (Fig. 12). This is followed by Upper Carnian *C. intermedius* from the Drawno Beds of Krasiejów,



**Fig. 12.** Phylogeny and stratigraphical match of the "Eucyclotosauria", based on analysis of the main taxon sample. Particular emphasis on the genus *Cyclotosaurus*. Taxa not considered in the analysis have been mapped onto tree. Species of *Cyclotosaurus* highlighted in black.

southeast Poland (SULEJ & MAJER 2005), uppermost Carnian *C. ebrachensis* from the Blasensandstein (= Kiesel-sandstein) of Ebrach in northern Bavaria, Middle Norian *C. posthumus* and *C. mordax* from the Middle Stubensandstein of Pfaffenhofen and other localities in Württemberg, Upper Norian *C. hemprichi* from the Knollenmergel of Halberstadt in Saxony-Anhalt (central Germany), and probably roughly coeval *C. n. sp.* from the Fleming Fjord Formation of Jameson Land, eastern Greenland (JENKINS

et al. 1996). The *Cyclotosaurus* specimens from the lower and middle parts of the sections are all very similar; *C. ebrachensis* and *C. intermedius* apparently hardly differ at all. Only *C. posthumus* and *C. hemprichi* stand out, the latter more extremely so, but as the type and only specimen was lost in the last war, the many remaining problems concerning this taxon will not be resolved.

It is hard not to think of an anagenetic lineage for at least some members of this sequence, especially for those

occurrences from the same basin (Fig. 12). Especially *C. robustus* – *C. ebrachensis*/*C. intermedius* – *C. mordax* form a sound succession of similar morphologies, as demonstrated by SULEJ & MAJER (2005). However, the case becomes less clear with *C. posthumus* and especially *C. hemprichi*, which bear some resemblance to heylerosaurids and stenotosaurids. The Greenland taxon, which is still undescribed and was only figured and briefly reported by JENKINS et al. (1996), is more consistent with *C. intermedius* and *C. ebrachensis* in the proportions of the skull roof. Yet in the palate, Greenland *Cyclotosaurus* acquired an autapomorphy that parallels the situation in heylerosaurids and *Mastodonsaurus*: the anterior palatal opening is subdivided by a wide medial junction of premaxilla and vomer. In both cases, character-states known from lower Anisian heylerosaurids apparently evolved within the *Cyclotosaurus* lineage, and as both features appear not before the Middle Norian, it is very probable that they form convergences with respect to heylerosaurids. The next section will deal with a more general question, namely the origin of the *Cyclotosaurus* lineage and its relationships to other “cyclotosaur” taxa.

#### 4.6.3. The cyclotosaur paradox

The problem to be reported here is a central theme of capitosaur phylogeny and systematics ever since the first discovery of the classic genera *Mastodonsaurus*, *Capitosaurus*, *Parotosuchus*, and *Cyclotosaurus*. The last section already touched this problem, but it dealt exclusively within the framework of the Eucyclotosauria hypothesis, which found the strongest support in the performed analyses. However, the range of *Cyclotosaurus* and its morphology form a paradox, which centres at the question of how often the complete closure of the otic fenestra and the associated morphology of the occiput and posterior skull table might have evolved in capitosaurs. Although *Capitosaurus* is probably closely related to *Cyclotosaurus*, the origin of “cyclotosaurs” as a whole group is a more complicated, multifaceted issue. As well as revealing multiple character conflicts between different sets of morphological features, it is also a case where stratigraphy and morphology as a whole are in conflict.

Although the present phylogenetic analysis considered many more taxa than were known to MEYER (in MEYER & PLIENINGER 1844), FRAAS (1889), BROILI (1915), WELLES & COSGRIFF (1965), and it even added data to DAMIANI’S (2001a) very authoritative survey, it is still constrained by incomplete specimens and collecting bias. For instance, the critical “cyclotosaur” specimens were all found in Western and Central Laurussia, whereas the much vaster areas of Gondwana and East Asia have yielded tantalizingly fragmentary material that is just enough to indicate

that the story was not confined to North America and Europe at all. For instance, the find in Thailand of a posterior skull almost identical to *Cyclotosaurus posthumus* shows how widespread the genus must have been (INGAVAT & JANVIER 1981).

Having said that, it is surprising that the present analysis found one parsimonious topology with even the “cyclotosaurs” fully resolved. Given that this topology was correct, the evolution of the closed otic fenestra must have happened two times independently, albeit starting from a common ancestor in which the cheek and posterior skull table were close to the “cyclotosaur” condition. Such a primitive state is retained by *Paracyclotosaurus* and *Stanocephalosaurus birdi*. Although the closed otic window was coded as an apomorphic state here, the “cyclotosaurs” came out as two convergent clades because of the overwhelming majority of apomorphies that support a deeper split between *Cyclotosaurus* (plus *Kupferzellia*) and the rest.

The heylerosaurids *Eocyclotosaurus* and *Quasicyclotosaurus*, which appear so similar to *Cyclotosaurus* in the posterior skull table and basicranium, form the most problematic clade in this respect. Heylerosaurids have prefrontals contacting postfrontals, paired anterior palatal openings, supraorbital sulci traversing the lacrimals, and prefrontals suturing with postorbitals laterally. These are all character-states that are not found in classic *Cyclotosaurus robustus*, and they are also absent in the slightly younger *C. intermedius* and *C. ebrachensis*. In the present analysis, this clearly shifts *Cyclotosaurus* to nest with *Kupferzellia*, while heylerosaurids group with *Mastodonsaurus*, which has paired anterior palatal openings and similarly aligned supraorbital sulci. This is surprising, because otherwise the two clades are rather different, and the fact that both character-states also occur in trematosaurids weakens the argument. I shall discuss this dilemma in more detail below, and will argue that stratigraphy does contribute a crucial criterion to decide between the alternative hypotheses.

##### 4.6.3.1. Convergence scenario: Eucyclotosauria – Paracyclotosauria

The first evolutionary scenario is based on the findings of the main analysis, with *Cyclotosaurus* having evolved its closed otic fenestra convergently to heylerosaurids. In this concept, *Mastodonsaurus* and heylerosaurids are immediate sister taxa, with *Paracyclotosaurus* and *Stanocephalosaurus birdi* forming successive sister groups of the two. *Cyclotosaurus*, on the other hand, is nested with *Kupferzellia*, *Procyclotosaurus*, and “*Stanocephalosaurus*” *pronus* as sister taxa. Closest to the putative common ancestor of the whole “cyclotosaur” clade

come *Xenotosuchus* and, slightly more basal, *Eryosuchus*. These share a laterally directed tabular horn, a prominent falciform crest of the squamosal, quadrate and occipital condyles at one level, and the basicranial suture only slightly elongated, with no contact between exoccipital and pterygoid. The choana is not as long and slit-like as in *Parotosuchus*, but generally narrow. The cultriform process is ventrally flush flat, and the anterior palatal opening unpaired but anteromedially constricted. In some specimens of *Eryosuchus garjainovi*, this subdivision is quite substantial, leaving only a narrow posterior connection between the left and right part (PIN 2865/65). Such an increased level of individual variation suggests that parallel evolution of this character is likely. In the mandible, the meckelian fenestra is elongated, and a prominent hamate process is established. The symphyseal region bears rather small medial fangs and a transverse row of postsymphyseal teeth. In the following scenario, I shall refer to the branch ending in the genus *Cyclotosaurus* as “Eucyclotosauria”, and the clade encompassing the Paracyclotosauridae, Heylerosauridae, and Mastodonsauridae as “Paracyclotosauria” (Fig. 8) – these names form simple labels and do not have any taxonomic consequence at this stage of phylogenetic discussion.

In the “Eucyclotosauria” branch, *Kupferzellia* and “*Stanocephalosaurus*” *pronus* retained the relatively short basicranial suture and the notch separating the exoccipital from the pterygoid. (If we add *Capitosaurus*, it also shares the short basicranial suture). *Kupferzellia* had already acquired a broadened choana and a foreshortened vomer, with the vomerine fangs more lateral to the anterior palatal opening. This lineage had also developed a rather short and wide parabolic snout, which was retained by *Cyclotosaurus*. In contrast, “*Stanocephalosaurus*” *pronus* evolved (as autapomorphies) a long and slender snout paralleling the condition in *Paracyclotosaurus*, and a slightly foreshortened posterior skull table. Another similarity to the *Paracyclotosaurus*-Heylerosauridae lineage is the close approximation of prefrontal and postorbital, here also postulated to have evolved in parallel.

If mapped onto this scenario, *Tatrasuchus* assumes a more basal position than *Kupferzellia*, because it lacks the broadened choana shared by *Kupferzellia* and *Cyclotosaurus*. Slightly more derived than *Kupferzellia*, *Capitosaurus* had acquired posteriorly constricted interpterygoid vacuities (Fig. 12). While lower Carnian *Capitosaurus* approached the general morphology of *Cyclotosaurus*, it retained the flat ventral surface of the cultriform process. In middle Carnian *Cyclotosaurus robustus*, the oldest unequivocal species of that genus, the parasphenoid acquired a knife-edged ventral crest and the choana was completely rounded. (This is a very puzzling character-state, as it appears in parallel in the paracyclotosaurid-heylerosaurid branch.) Further evolution of the “cyclotosaurid” clade

seems straightforward within the Central European Basin, with the very similar (?conspecific) *C. intermedius* and *C. ebrachensis* succeeding *C. robustus* in the late Carnian, and *C. mordax* forming the continuation of that lineage in the middle Norian. It remains unclear whether the exclusion of the frontals from the orbital margin forms a microevolutionary trend or represents a polymorphic fluctuation just within *C. mordax*; this character is not clearly visible on KUHN’s (1942) figures of *C. hemprichi*, which was destroyed in the last war.

In contrast, middle Norian *C. posthumus* and especially upper Norian *C. hemprichi* might have evolved from a rather different ancestor than *C. robustus*, but there is currently no way to prove that. In contrast, late Norian *Cyclotosaurus* from Greenland is more consistent with *C. intermedius* and *C. ebrachensis*, but evolved the unique morphology of a completely separated anterior palatal opening. In this case, stratigraphic control indicates a convergent origin of this feature from all the other lineages (heylerosaurids, *Mastodonsaurus*).

The “Paracyclotosauria” branch of this scenario forms a more heterogenous lineage, which cladistically is largely held together by the paired anterior palatal openings; these are established in all taxa except the basalmost one, *Stanocephalosaurus birdi*. Indeed, *S. birdi* forms a plausible ancestor to both *Paracyclotosaurus* and the heylerosaurids for two reasons: (1) it shares the elongated postparietals and tabulars with all of them, and (2) the prefrontals and postorbitals come very close to each other, forming a pre-condition for the exclusion of the jugal from the orbit margin in some heylerosaurids.

Stratigraphically, this gives a consistent picture, as well: *Stanocephalosaurus birdi* is from the Olenekian of Arizona, while all undisputed heylerosaurids (*Eocyclotosaurus wellsi*, *E. lehmani*, *Quasicyclotosaurus campi*) are early Anisian, and so is the earliest record for *Mastodonsaurus cappelensis* (Fig. 13). This does not imply that evolution took place within the Moenkopi Basin (from *Stanocephalosaurus* to *Quasicyclotosaurus*, for instance), because the occurrences of heylerosaurids in France and Germany are probably of similar age and there are further, poorly understood taxa like *Meyerosuchus fuerstenberganus* from the late Olenekian of the Black Forest that may add to the picture, once it becomes more completely known.

The described scenario rests on the consistency of stratigraphy with major nodes found by the cladistic analysis, but it also requires assumptions about some substantial parallel evolution of other characters. Some of these convergences are very probable, because conflicting evidence leaves no alternative: the paired anterior palatal openings (20) certainly evolved in trematosaurids, in *Cherninia*, in *Odenwaldia*, and within the “Paracyclotosauria” in parallel, and so probably did the crest on the ventral surface of

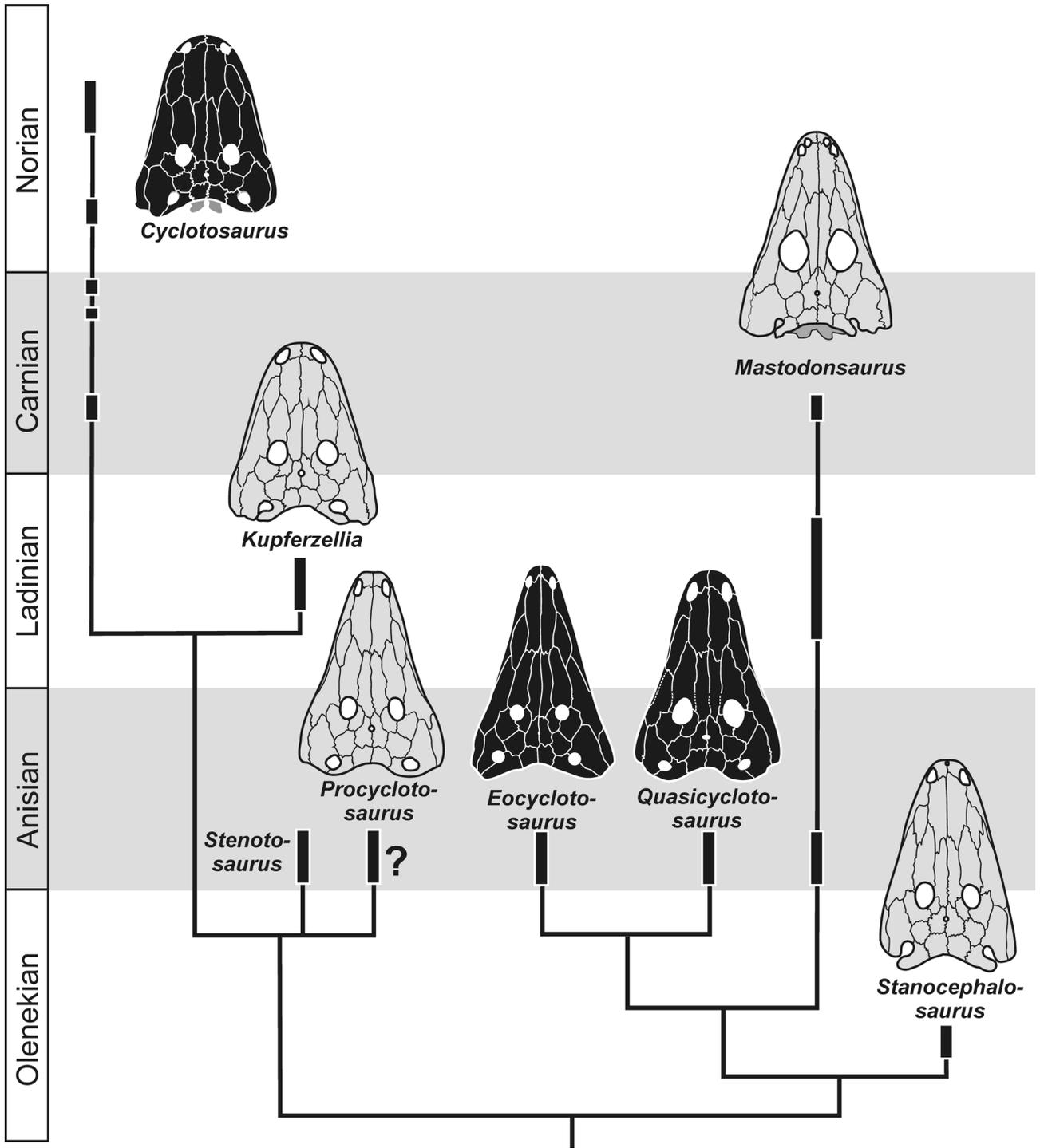


Fig. 13. Phylogeny and stratigraphical match of the higher capitosaurs, depicting selected taxa after the “Eucyclotosauria”-“Paracyclotossaur” split, based on analysis of the main taxon sample.

the parasphenoid (24), the exoccipitals contacting the pterygoids (29), the hamate process (42-2), and the elongated meckelian fenestra (43).

#### 4.6.3.2. Monophyly scenario: “Pancyclotosauria”

The addition of just two extra steps in a constraint tree (*Cyclotosaurus* nesting with heylerosaurids) substantially alters the branching of higher capitosauroids. In this topology, *Kupferzellia* and *Procyclusaurus* fall onto a grade starting with *Eryosuchus* and *Xenotosuchus* (more basal) and ending with the crown-capitosauroids. A similar tree is obtained when *Cherninia* is removed from the analysis, with the additional effect that *Odenwaldia* nests more basal between *Wetlugasaurus* and *Sclerothorax*.

In this alternative scenario, “Paracyclotosauria” as found by the main analysis is retained, only that *Cyclotosaurus* nests in its crown, far separate from what in the convergence scenario was interpreted as the stem-group of the genus *Cyclotosaurus* (*Procyclusaurus* and *Kupferzellia*). It may be worth to discuss the implications of these alternative trees, although they are not supported by any other data set.

In this scenario, features correlating with the “cyclotosaur” condition – elongated basicranial suture, ventrally crested parasphenoid, and the pterygoid suturing with the exoccipital – were essentially acquired only once. Yet even in this scenario, the closed otic fenestra must have evolved at least twice, once in *Kupferzellia* and *Procyclusaurus* and a second time in the stem-group of heylerosaurids plus *Cyclotosaurus*.

A first consequence of the “Pancyclotosauria” concept is that the features shared between *Cyclotosaurus* and *Kupferzellia* (broad choana, short vomer, broad-parabolic snout) evolved in parallel. *Kupferzellia* and the slightly less derived *Tatrasuchus* would have branched off long before the origin of the “Pancyclotosauria”, and might have formed a clade of their own. Stratigraphically, this would imply that the “cyclotosaur” characters evolved in the Olenekian at the latest, because the heylerosaurids and mastodonsaurids were already present in the Upper Anisian. This requires a ghost lineage of some 15 Ma, to bridge the gap between *Quasicyclotosaurus* and *Capitosaurus* or even 20 Ma between the former and *Cyclotosaurus robustus*. The only problem the “Pancyclotosauria” hypothesis would solve is the Ladinian age of *Cyclotosaurus papilio*, which would help to bridge the gap between heylerosaurids and *Cyclotosaurus* somewhat. The most plausible scenario within this hypothesis would be a succession like *Eocyclotosaurus wellsi* – *E. lehmani* – *Quasicyclotosaurus campi* – *Cyclotosaurus robustus*. This hypothetical phylogenetic (not anagenetic or stratophenetic) sequence would start with a slender-snouted taxon

and progress into taxa with ever wider snouts, with the prefrontal-postfrontal contact as well as the exclusion of the jugal from the orbit margin eventually lost in *Cyclotosaurus*. Such a scenario would be supported by the intraspecific variation in *Cyclotosaurus mordax*, which may have preserved the plesiomorphic state (prefrontal-postfrontal contact) occasionally. However, this does not apply for the jugal exclusion, and in the case of the anterior palatal opening only one of the stratigraphically youngest species of *Cyclotosaurus* has the same condition as the heylerosaurids. Hence, from both stratigraphic and phylogenetic points of view, a heylerosaurid origin of *Cyclotosaurus* requires a considerable range of ad hoc hypotheses. The alternative scenario (cyclotosaur-origin of the heylerosaurids) would fit much better with morphology and parsimony, but it would entirely contradict stratigraphy and result in an even longer ghost lineage. In addition, in both variants of the “Pancyclotosauria” hypothesis the apparent ‘right’ age of *Tatrasuchus* and *Kupferzellia* as potential stem-taxa of *Cyclotosaurus* would just be a coincidence. In conclusion, the “Pancyclotosauria” hypothesis may be consistent with some earlier thoughts and cladistic results (SCHOCH 2000a), but it requires too many additional assumptions and rests on too poorly resolved a phylogeny to be an attractive alternative to the “eucyclotosaur”-“paracyclotosaur” scenario. For these reasons, I lean to accept the results of the main analysis, and with these the convergent scenario, as the preferred phylogenetic hypothesis of capitosaur evolution.

#### 4.6.4. Phylogeny and higher-rank taxonomy

These results indicate that, with the inclusion of new data on hitherto poorly known taxa (*Mastodonsaurus*, *Xenotosuchus*, *Odenwaldia*, *Sclerothorax*) and newly discovered taxa (*Yuanansuchus*), the monophyly of capitosaurs sensu lato has become more likely. However, although the deep split between *Eocyclotosaurus* and the other “cyclotosaurs” as found by DAMIANI (2001a) is currently poorly supported, their strict monophyly as suggested by SCHOCH (2000a, b) is not found either by the present analysis. Rather, a “consensus phylogeny” emerges in which the higher capitosauroids encompass two main branches reflecting the here outlined “eucyclotosaur”-“paracyclotosaur” split. The real relationships may still be obscured by too many missing entries in the matrix, such as *Stenotosaurus*, *Meyerosuchus*, and *Yuanansuchus*.

Therefore, the two rather different approaches of DAMIANI (2001a) and SCHOCH & MILNER (2000) as to how these taxa may be classified still remain equally applicable: the lumpers’ preference would be to summarize them under a single family (Mastodonsauridae of DAMIANI 2001a, Capitosauridae in the present reading), while the

splitter's choice would be to include within a large Capitosauroida at least some of the well-defined taxa as separate families: Parotosuchidae (*Parotosuchus*), Mastodontosauridae (*Mastodontosaurus*), Cyclotosauridae (*Cyclotosaurus*, *Capitosaurus*, *Kupferzellia*, *Tatrasuchus*, *Procyclotosaurus*, *Stenotosaurus*), and Heylerosauridae (*Eocyclusosaurus*, *Quasicyclotosaurus*). However, the proposed taxa ("Eucyclotosauria" and "Paracyclotosauria") might form a starting point for a future convergence of these approaches, whatever the final composition of these clades will turn out.

## 5. Evolution of the Capitosauria

### 5.1. Stratigraphy

The following stratigraphical occurrences are found among the capitosaurids (SCHOCH & MILNER 2000; SCHOCH 2000a, b; DAMIANI 1999, 2001a–c, 2002; DAMIANI & HANCOX 2003). See Figs. 13–14 for stratigraphical ranges of taxa.

**Induan:** Only early capitosaurids present: *Wetlugasaurus*, *Watsonisuchus*.

**Olenekian:** Remaining early capitosaurids (aberrant *Sclerotherorax*) and primitive capitosauroids (*Parotosuchus*, *Odenwaldia*) in South Africa, Russia, Germany, Utah). Only one crown-capitosauroid: paracyclotosaur-grade *Stanocephalosaurus birdi*.

**Anisian:** By the early Anisian, most major crown clades were present: heylerosaurids (*Eocyclusosaurus*, *Quasicyclotosaurus*), mastodontosaurids (*M. cappelenensis*), stenotosaurids (*Stenotosaurus*).

**Ladinian:** *Eryosuchus*-grade capitosauroids (*Eryosuchus*, *Xenotosuchus*), cyclotosaurids (*Kupferzellia*, *Tatrasuchus*, "*Cyclotosaurus*" *papilio*), mastodontosaurids (*M. giganteus* from Europe, *M. torvus* from Russia).

**Carnian:** *Capitosaurus*, *Cyclotosaurus*, *Mastodontosaurus*.

**Norian:** Only *Cyclotosaurus* present, confined to the northern hemisphere (Greenland and Eurasia).

**Problematic ranges:** *Procyclotosaurus*, *Paracyclotosaurus*, *Cherninia*, and "*Stanocephalosaurus*" *pronus* were all referred to the "?Middle Triassic".

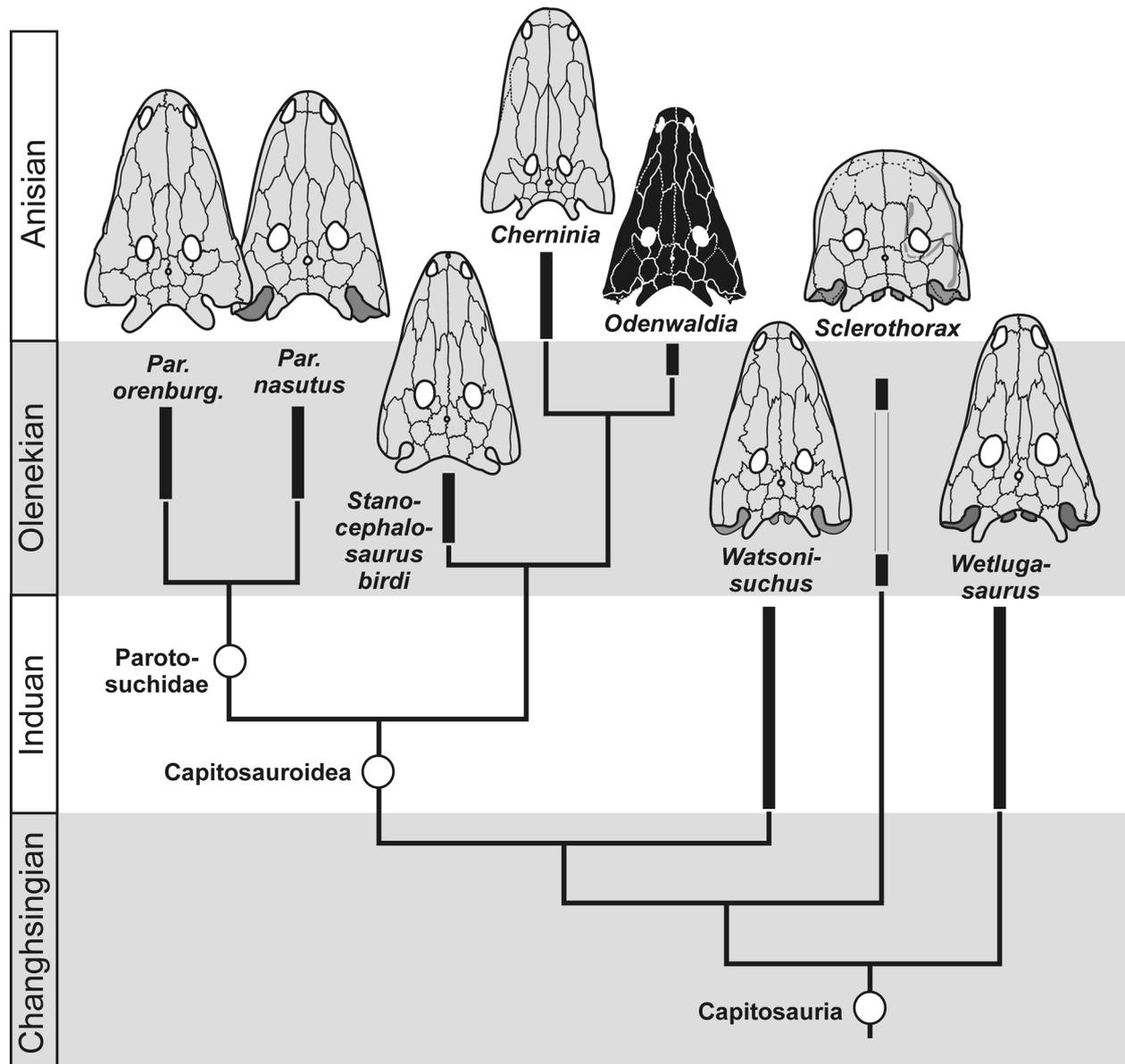
A major problem of the stratigraphical calibration is that in some formations, temnospondyls have been used as basis for the correlation; this unavoidably carries some circularity that is hard to come by (STEYER 2000). For instance, the age of the English Bromsgrove Sandstone that yielded *Procyclotosaurus* has been partially determined by what was then presumed the "evolutionary stage" of this capitosaur (PATON 1974). Similar problems emerge with the East European platform, where *Mastodontosaurus* for instance has been used as an index fossil, despite the fact that the finds of this taxon are extremely rare there (SHISHKIN 1995). Yet even the Upper Moenkopi Formation of Arizona and New Mexico was correlated with the Upper Buntsandstein sequence of the Black Forest and Vosges

partly on the occurrence of *Eocyclusosaurus*, which is at least very common in the North American deposits (LUCAS & SCHOCH 2002), although in this case there are magnetostratigraphic and other arguments pointing into the same direction. It is only fair to say that these problems may be used to counter stratigraphic "control" or "calibration" of phylogenies, and for this reason alone a "refutation" of a particular morphology-based phylogeny is not possible.

### 5.2. Mapping postcranial characters onto phylogeny

Until very recently, capitosaurids were considered rather uniform in their postcranial anatomy (WARREN & SNELL 1991; SCHOCH & MILNER 2000). This view was based on a few monographically described taxa, especially *Benthosuchus sushkini* (BYSTROW & EFREMOV 1940), *Paracyclotosaurus davidi* (WATSON 1958), "*Stanocephalosaurus*" *pronus* (HOWIE 1970), and *Mastodontosaurus giganteus* (SCHOCH 1999). Among these, only *Paracyclotosaurus* is in fact known from a complete, articulated skeleton, which revealed the number of presacral vertebrae (28), the length of the vertebral segments relative to the skull, and the proportions and size of the girdles and limbs. These data are based on a single skeleton housed in the Natural History Museum London, according to which the body was elongated, with a trunk measuring twice the length of the skull and the tail having about skull length (WATSON 1958). Despite numerous finds from various localities in southern and central Germany, *Mastodontosaurus* is only known from partially articulated specimens; the most recent reconstruction of *Mastodontosaurus* is consequently based on the anatomical features of its vertebrae and the general proportions of *Paracyclotosaurus*.

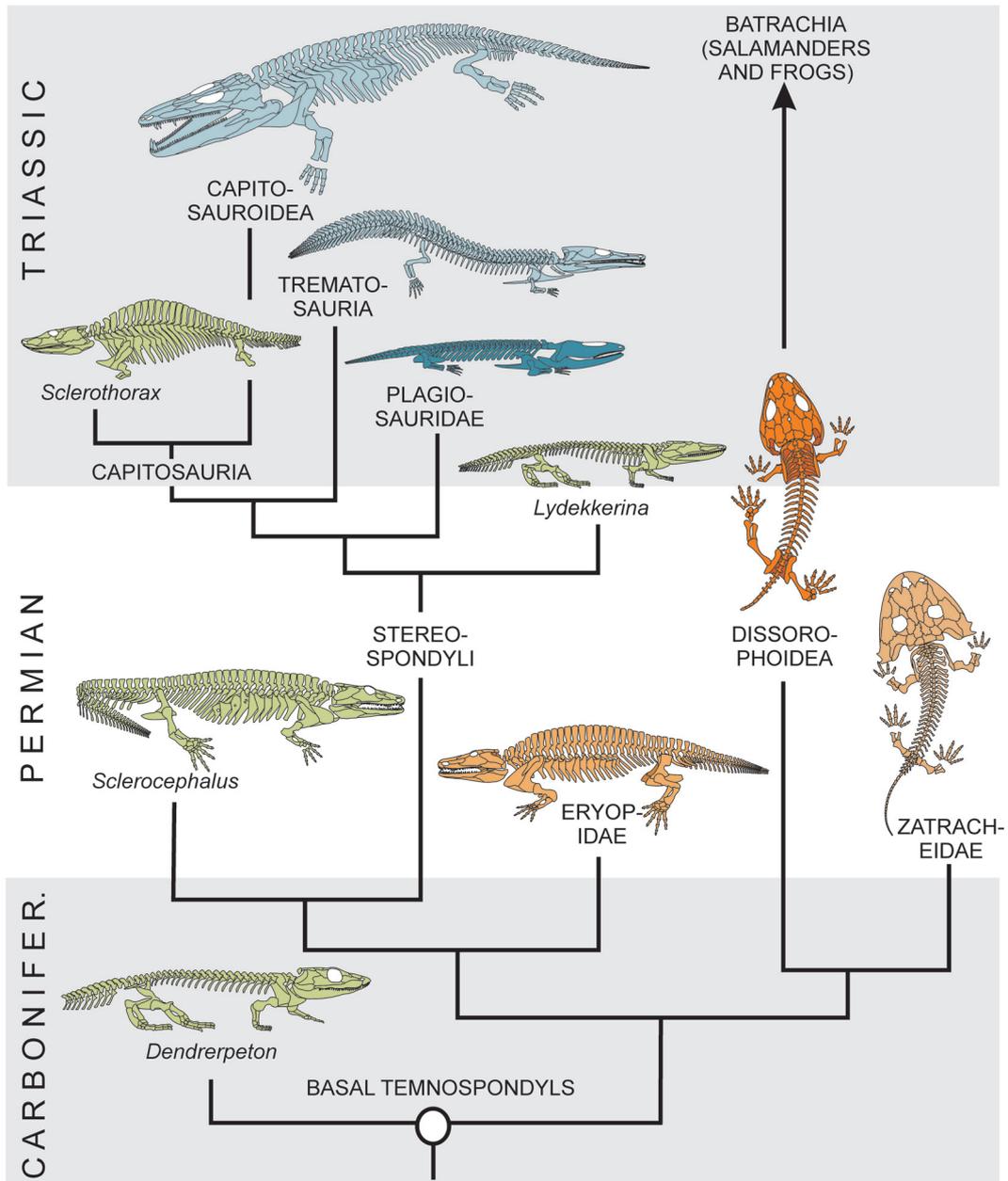
The redescription of *Sclerotherorax hypselonotus* (HUENE 1932) has quite changed the picture (SCHOCH et al. 2007). This taxon combines stereospondyl cranial characters with eryopid-like and dissorophid-like features in the axial and appendicular skeleton (Fig. 15). The present analysis has found this taxon to be a capitosaur, even close to the origin of the capitosauroids, which makes the postcranial features even more striking. Despite its resemblance to terrestrial temnospondyls (tall and robust neural spines, tall scapular blade, pronounced glenoid facet, pelvis fully ossified, ilium dorsally broadened and hooked), *Sclerotherorax* preserves well-impressed lateral line sulci, indicating that it probably spent longer phases in the water. The dentition, consistent with that of other capitosaurids, suggests focus on aquatic prey. Most unique among capitosaurids are the numerous robust and ornamented ossicles in the skin of *Sclerotherorax*. They recall the situation in *Laidleria*, *Peltobatrachus*, or the dissorophids, but differ from all these in that the ossicles must have been more numerous and much tinier in *Sclerotherorax*.



**Fig. 14.** Phylogeny and stratigraphical match of the basal capitosaurians, based on analysis of the main taxon sample. *Odenwaldia heidelbergensis* is highlighted in black.

Capitosaurians differ most clearly in the axial skeleton, and these variations are consistent with the major nodes of phylogeny. *Benthosuchus* exemplifies the primitive condition, in which the intercentrum is low and poorly ossified, well apart from the pleurocentra and the neural arch (BYSTROW & EFREMOV 1940). Yet unfortunately, in many taxa the intercentra are not known (e. g., *Watsonisuchus*, *Parotosuchus*, *Odenwaldia*). Among the capitosauroids, *Kupferzellia* and *Stanocephalosaurus birdi* share the low crescents, while *Mastodonsaurus cappelenensis*, “*Stano-*

*cephalosaurus*” *pronus*, *Paracyclotosaurus davidi*, *Eocy-clotosaurus wellsi*, and *Cyclotosaurus intermedius* have more solid intercentra with slightly higher flanks (WEPFER 1923a; WATSON 1958; HOWIE 1970; SULEJ & MAJER 2005). In *Mastodonsaurus giganteus* and *Cyclotosaurus hemprichi*, the intercentra finally have the typical stereospondylous condition, forming complete, massive discs (KUHN 1942; SCHOCH 1999; WITZMANN & GASSNER 2008). There may be a loose size correlation here, as *C. hemprichi* and *M. giganteus* rank among the largest capitosaur species,



**Fig. 15.** Probable life habits depicted in a tree of stereospondyls, showing that the Triassic taxa evolved a range of different life strategies, centered at predominantly aquatic forms (light blue). Phylogeny of the temnospondyls based on MILNER (1990), YATES & WARREN (2000) and SCHOCH (2008). Skeletons colour-coded with respect to the presumed life habits (blue = aquatic, green = amphibious, brown = terrestrial).

but recent finds indicate that juvenile *Mastodonsaurus giganteus* developed the dorsally closed discs at an early stage (SCHOCH & WITZMANN, in progress).

Apart from *Sclerothorax*, capitosaurians appear to have been throughout aquatic, which is highlighted by their poorly ossified postcranial skeletons. The interclavicles, clavicles, scapulocoracoids, and humeri are mostly very

similar (*Stanocephalosaurus*, *Paracyclotosaurus*, *Mastodonsaurus*, *Eocyclotosaurus*, *Cyclotosaurus*). An extended anterior stylus is present in the interclavicles of *Mastodonsaurus* and *Cyclotosaurus*, but not in *Paracyclotosaurus*. Compared with more basal temnospondyls, the humerus is rudimentary in all capitosaurians. The condyles are mostly unossified, and the torsion is not com-

Tab. 1. Character-taxon matrix.

|                           | 1 | 2 | 3 | 4  | 5  | 6 | 7 | 8 | 9   | 10  | 11 | 12  | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20  | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 |    |   |   |
|---------------------------|---|---|---|----|----|---|---|---|-----|-----|----|-----|----|----|----|----|----|----|----|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|
| <i>Benthosuchus</i>       | 1 | 1 | 0 | 0  | 1  | 0 | 1 | 1 | 0,1 | 1   | 0  | 1   | 0  | 1  | 1  | 1  | 0  | 0  | 1  | 1   | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 1  | 0  | 0  |   |   |
| <i>Cherninia</i>          | 0 | 1 | 0 | 1  | 1  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 2   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  |   |   |
| <i>Cyclotosaurus</i>      | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | 0,1 | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 2  | 0  | 0,1 | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1* | 1  | 1  | 1  | 1  |   |   |
| <i>Edingerella</i>        | 0 | 1 | 1 | 0  | 0  | 0 | 1 | 1 | 0   | 2   | 1  | 0,1 | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 1   | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  |   |   |
| <i>Eocyclotosaurus</i>    | 1 | 1 | 0 | 1  | 0  | 0 | 1 | 2 | 0   | 2   | 0  | 1   | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 2   | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1* |   |   |
| <i>Eryosuchus</i>         | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | 0,1 | 2  | 1   | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0,1 | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  |   |   |
| <i>Kupferzellia</i>       | 0 | 1 | 0 | 1  | 0* | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 0  | 0  | 2  | 0  | 0   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  |   |   |
| <i>Lydekkerina</i>        | 0 | 1 | 1 | 0  | 0  | 0 | 1 | 0 | 0   | 0   | 0  | 1   | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0   | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 1  | 0  | 0  |   |   |
| <i>M. cappelenis</i>      | 0 | 1 | 0 | 1  | 0  | 0 | 1 | 2 | 0   | 2   | 2  | 1   | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 2   | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |   |   |
| <i>M. giganteus</i>       | 0 | 1 | 0 | 1  | 0  | 0 | 1 | 2 | 0   | 2   | 2  | 1   | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 2   | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |   |   |
| <i>Odenwaldia</i>         | 1 | 1 | 0 | 0* | 1  | 0 | 0 | 2 | 0   | ?   | ?  | 1   | 1  | 1  | 0  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |   |   |
| <i>Pa. haughtoni</i>      | 0 | 1 | 0 | 0  | 2  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 0  | 1  | 0  | 0   | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  |   |   |
| <i>Pa. nasutus</i>        | 0 | 1 | 0 | 0  | 1  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 0  | 1  | 0  | 0   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Pa. orenburgensis</i>  | 0 | 1 | 0 | 0  | 2  | 0 | 1 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 0  | 1  | 0  | 0   | 0  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Pc. crookshanki</i>    | 0 | 1 | 0 | 1  | 0  | 0 | 1 | 2 | 0   | 1   | 2  | 1   | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 2   | 1  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Procyclotosaurus</i>   | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | ?  | 1  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Quasicyclotosaurus</i> | 0 | 1 | 0 | 1  | 0  | 0 | 1 | 2 | 0   | 1   | 0  | 1   | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 2   | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Rhinesuchidae</i>      | 0 | 0 | 0 | 0  | 0  | 0 | 0 | 0 | 0   | 0   | 0  | 0   | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0 |   |
| <i>Sclerothorax</i>       | 0 | 1 | 0 | 0  | 1  | 0 | 0 | ? | 0   | 0   | 1  | 1   | 1  | 1  | 0  | ?  | 1  | ?  | ?  | ?   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ? |   |
| <i>St. birdi</i>          | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 1   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1 |   |
| <i>"St." pronus</i>       | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Thoosuchus</i>         | 1 | 1 | 1 | 0  | 0  | 1 | 1 | 1 | 1   | 1   | 0  | 1   | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 2   | 0  | 1  | 1  | 2  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0 |   |
| <i>Watsonisuchus</i>      | 0 | 1 | 0 | 0  | 1  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0   | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1 |   |
| <i>Wetlugasaurus</i>      | 0 | 1 | 0 | 0  | 1  | 0 | 0 | 2 | 0   | 0   | 0  | 1   | 1  | 1  | 1  | 1  | 0  | 0  | 1  | 0   | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 1  | 1  | 0  | 1  | 1  | 0  | 1  | 0 | 1 |
| <i>Xenotosuchus</i>       | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | ?   | 1  | 1   | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1 | 1 |
| <i>Yuanansuchus</i>       | 0 | 1 | 0 | 1  | 0  | 0 | 1 | 2 | 0   | 2   | 0  | 1   | 1  | 1  | 0  | 0  | 1  | 0  | 0  | ?   | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1 | 1 |
| <i>Stenotosaurus</i>      | 0 | 1 | 0 | 1  | 0  | 0 | 0 | 2 | 0   | 0   | 2  | 1   | 1  | 1  | 0  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ? | ? |

|                           | 34  | 35 | 36 | 37 | 38 | 39 | 40  | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63  | 64 | 65 | 66 |   |   |   |   |
|---------------------------|-----|----|----|----|----|----|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|----|----|----|---|---|---|---|
| <i>Benthosuchus</i>       | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 |   |   |
| <i>Cherninia</i>          | 0   | 1  | 1  | 1  | 1  | 1  | 1   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? |   |   |
| <i>Cyclotosaurus</i>      | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 2  | 2  | 1  | 0* | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? |   |   |
| <i>Edingerella</i>        | 0   | 0  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 0  | 1  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? |   |   |
| <i>Eocyclotosaurus</i>    | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 2  | 2  | 1  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? |   |   |
| <i>Eryosuchus</i>         | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 2  | 2  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 |   |   |
| <i>Kupferzellia</i>       | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 1  | 0* | 1  | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 |   |
| <i>Lydekkerina</i>        | 1   | 1  | 0  | 0  | 0  | 1  | 0   | 1  | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 |   |
| <i>M. cappelenis</i>      | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 2  | 2  | 1  | 0  | 1  | 1  | 0  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 1  | 0  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 1  | 1 | 1 | 1 |   |
| <i>M. giganteus</i>       | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 2  | 2  | 1  | 0* | 1  | 1  | 0  | 1  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 1  | 1 | 1 | 1 |   |
| <i>Odenwaldia</i>         | 0   | 1  | 1  | 1  | ?  | 1  | 1   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? | ? |   |
| <i>Pa. haughtoni</i>      | 0   | 1  | 1  | 1  | 1  | 1  | 1   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? | ? |   |
| <i>Pa. nasutus</i>        | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 |   |
| <i>Pa. orenburgensis</i>  | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 | 0 |
| <i>Pc. crookshanki</i>    | 0   | 1  | 1  | 1  | 1  | 1  | 1   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? | ? | ? |
| <i>Procyclotosaurus</i>   | 0   | 1  | 1  | 1  | 1  | 1  | 1   | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? | ? | ? |
| <i>Quasicyclotosaurus</i> | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?   | ?  | ?  | ?  | ? | ? | ? | ? |
| <i>Rhinesuchidae</i>      | 0   | 0  | 0  | 0  | 0  | 0  | 0,1 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 |   |
| <i>Sclerothorax</i>       | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | ?  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | ?   | 0  | 0  | ?  | 0 | 1 | 0 |   |
| <i>St. birdi</i>          | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 1  | 0   | 0  | 0  | 0  | 0 | 0 | 0 |   |
| <i>"St." pronus</i>       | 0   | 1  | 1  | ?  | 1  | 1  | 1   | ?  | 1  | 1  | 0  | ?  | 1  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 1  | 0   | 0  | 0  | 0  | 0 | 0 | 0 |   |
| <i>Thoosuchus</i>         | 0   | 1  | 0  | 0  | 1  | 1  | 0   | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 | 0 |
| <i>Watsonisuchus</i>      | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0 | 0 | 0 | 0 |
| <i>Wetlugasaurus</i>      | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0,1 | 0  | 0  | 0  | 0 | 0 | 0 | 0 |
| <i>Xenotosuchus</i>       | 0   | 1  | 1  | 1  | 1  | 1  | 1   | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | ?  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 1   | 1  | 0  | 0  | ? | 0 | 0 | 0 |
| <i>Yuanansuchus</i>       | 0</ |    |    |    |    |    |     |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |     |    |    |    |   |   |   |   |

reached only by dissorophoids. This scenario is very gross and may even be wrong, because the skeletal features and sedimentary facies may not tell enough about the actual life habits. A good example for this problem is *Sclerocephalus*, a taxon that stands at the very beginning of stereospondyl evolution. This genus managed to exist in diverse lakes during the Carboniferous and Permian, and apparently adjusted to environmental parameters by modifying ontogeny, skeletal morphology, and life span (SCHOCH in press).

## 6. Conclusions

1. Redescription of the original material of *Odenwaldia heidelbergensis* revealed that this taxon shares numerous features with basal capitosaurids, notably *Watsonisuchus*. In contrast, there are no unequivocal derived characters shared between *Odenwaldia* and *Eocycloptosaurus*. *Odenwaldia* shares with numerous stereospondyls medially separated anterior palatal vacuities.
2. A phylogenetic analysis of the capitosaurids results in a new hypothesis of their relationships. The analysis of 66 characters from 25 taxa gave one most parsimonious tree which departs from the previous concepts of DAMIANI (2001a) and SCHOCH (2000a) in several ways: (1) the recently revised genus *Sclerorhynchus* nests at the base of the capitosaurids, (2) *Odenwaldia* forms a clade with *Cherninia* above the Parotosuchidae, and (3) the ‘cycloptosaurs’ fall into two clades, here referred to as “Eucycloptosauria” and “Paracycloptosauria”.
3. Capitosauria is here defined as all taxa sharing a closer relationship with *Parotosuchus* than with *Trematosaurus*. This group encompasses *Wetlugasaurus*, *Sclerorhynchus*, and *Watsonisuchus* as basalmost taxa, but neither *Benthosuchus* nor *Edingerella*, which instead nest with *Thoosuchus*, by that falling within Trematosauria.
4. “Eucycloptosauria” includes *Cycloptosaurus*, *Kupferzellia*, *Procyloptosaurus*, and “*Stanocephalosaurus*” *promus*. Within “Paracycloptosauria” fall the Heylerosauridae, Mastodontosauridae, *Paracycloptosaurus*, and *Stanocephalosaurus birdi* (*Wellesaurus peabodyi*). The “Eucycloptosauria”-“Paracycloptosauria” concept is supported by the stratigraphical ranges of taxa. It is slightly weakened by *Cycloptosaurus* requiring only two steps to fall within the Paracycloptosauria.

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