A new capitosaur from the Middle Triassic of Spain and the relationships within the Capitosauria

JOSEP FORTUNY, ÀNGEL GALOBART, and CARLES DE SANTISTEBAN

Capitosaurs were the largest and homogeneous group of Triassic temnospondyl amphibians with cosmopolitan distribution. However, their interrelationships are debated. The first capitosaur cranial remains found in the Iberian Peninsula were assigned to *Parotosuchus*; herein, a re-description of this material, together with information on other remains recovered from the same site, enables us to classify them as a new genus: *Calmasuchus acri* gen. et sp. nov. (Amphibia: Temnospondyli) from the early-to-middle Anisian (early Middle Triassic). This capitosaur had a combination of plesiomorphic and non-plesiomorphic characters, such as posterolaterally directed tabular horns, paired anterior palatal vacuities, and unique morphology of the lower jaw. By cladistic analysis, we propose a new phylogeny for the monophyletic capitosaurs. In the analysis, Capitosauria is supported by seven synapomorphies. *Wetlugasaurus* is the most basal member of the clade. The score of the Russian taxon *Vladlenosaurus alexeyevi* resulted in a clade including *Odenwaldia* and the latter taxa. The Madagascarian *Edingerella* is the sister taxon of *Watsonisuchus*. Finally, *Calmasuchus acri*, the new taxon described here, appears as a more derived form than *Parotosuchus*. The new genus is the sister taxon of the *Cyclotosaurus–Tatrasuchus* and *Eryosuchus–Mastodonsaurus* clades.

Key words: Temnospondyli, Capitosauria, Mastodonsauroidea, phylogeny, computed tomographic scanning, Anisian, Triassic, Spain.

Josep Fortuny [josep.fortuny@icp.cat] and Ángel Galobart [angel.galobart@icp.cat], Institut Català de Paleontologia, Universitat Autònoma de Barcelona, Edifici ICP, Campus de Bellaterra s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain;
Carles de Santisteban [carlos.santisteban@uv.es], Departament de Geologia, Universitat de València, C/o Dr. Moliner 50, 46100 Burjassot, València, Spain.

Introduction

Capitosaurs constituted one of the most abundant groups of Triassic temnospondyl amphibians. Despite their cosmopolitan distribution, fossil records in the Iberian Peninsula are scarce, with only three reported sites: Rocha da Pena, Portugal (Witzmann and Gassner 2008); and La Mora and Riera de Sant Jaume, Spain (Gaete et al. 1993; JF unpublished data).

The wide distribution of temnospondyls, especially capitosaurs, has been used in biostratigraphy (Cosgriff and Defauw 1987) to correlate Triassic tetrapod faunas (Lucas 1998). These faunas are well known in the Eastern European platform (e.g., Ochev and Shishkin 1989; Shishkin and Ochev 1994) and Beafourt Group of South Africa (Karoo Basin) (e.g., Hancox et al. 1995; Shishkin et al. 1995; Damiani 2004). However, the phylogenetic relationships of capitosaurs have remained controversial since the first discoveries, even with the more recent studies (e.g., Watson 1962; Welles and Crosgriff 1965; Ochev 1966; Schoch 2000; Schoch and Milner 2000; Damiani 2001; Steyer 2003; Schoch 2008; Maganuco et al. 2009).

The first revision of the group (Welles and Cosgriff 1965) focused on the evolution of the otic notch (open in primitive forms and closed in derived forms) in an attempt to establish the taxonomy of the "Capitosauridae". The revision by Ochev (1966) was markedly different: a large number of genera and species were recognised by using the shape of the tabular horn as a criterion for determining taxonomic relationships. The most recent revisions (Schoch 2000; Damiani 2001; Schoch 2008; Maganuco et al. 2009) demonstrate that the evolution of the group involves more cranial characters than those regarded previously.

On the other hand, recent papers include new descriptions of old and new specimens recovered from the Central European Basin, providing crucial information to understand the evolution of the clade; especially, capitosaur remains have been described in detail (Maryańska and Shishkin 1996; Schoch 1997, 1999; Sulej and Majer 2005; Shishkin and Sulej 2009). The first capitosaur cranial remains recovered in Spain were assigned to *Parotosuchus* (Gaete et al. 1993, 1994, 1996). Here, we present a revised description of the original and new materials, enabling us to establish a new genus—*Calmasuchus acri* gen. et sp. nov. (Amphibia: Temno-
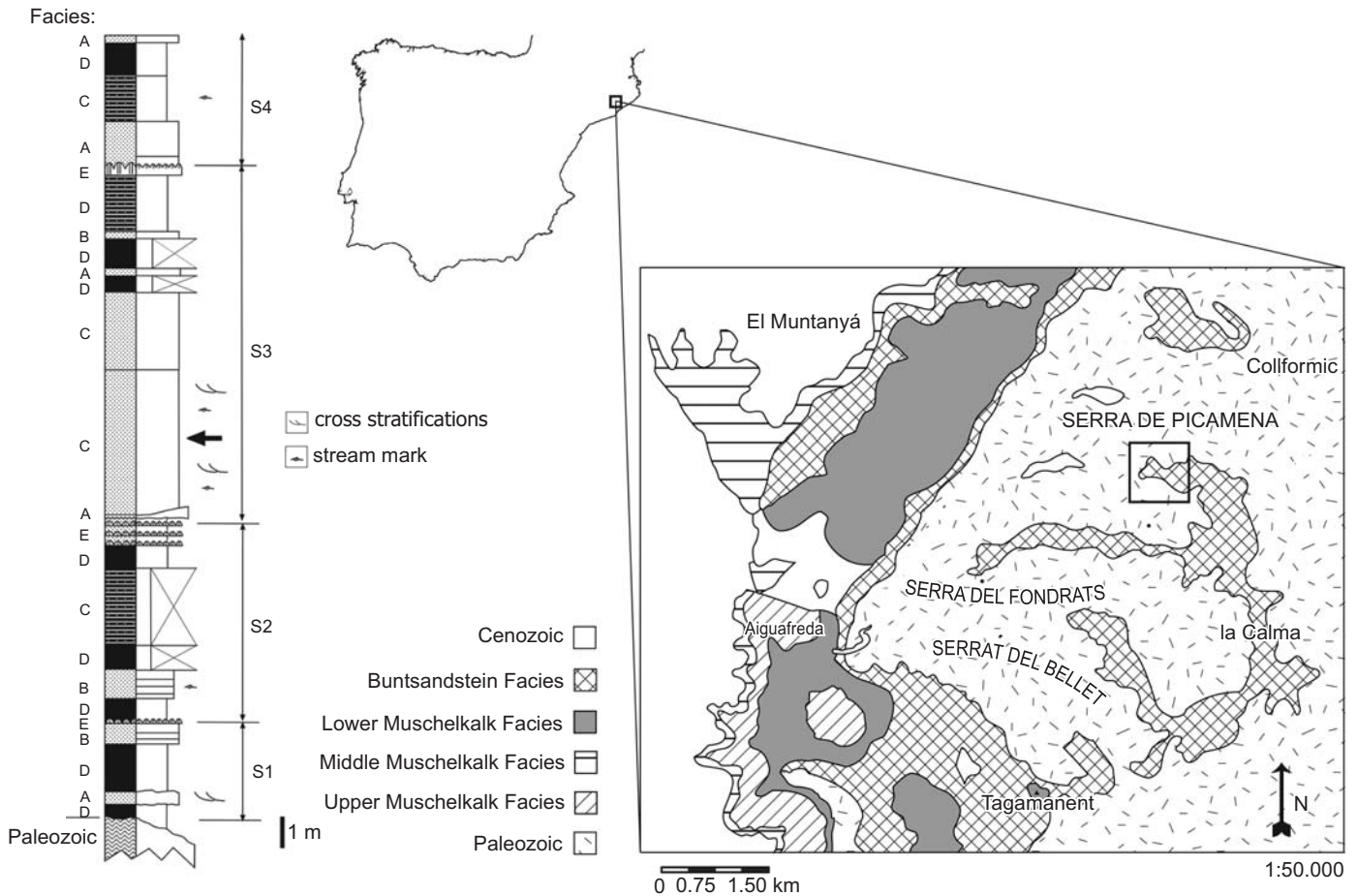
Fig. 1. Geographic and geologic location of the capitosaur *Calmasuchus acri* gen. et sp. nov. from the Anisian at the La Mora site, Spain, with a stratigraphic cross-section containing the vertebrate locality (arrow). See text for facies interpretation.

spondyli)—and providing new data to resolve the evolution of the group. In this regard, new data acquired by computed tomography, including complete skull reconstruction of this taxon, have been added to the previous information obtained by mechanical preparation of the matrix. Cladistic analysis including the new taxa performed by using an updated version of the previous matrix of Damiani (2001) for the group has enabled us to propose a new phylogeny.

Institutional abbreviations.—IPS, Institut Català de Paleontologia, Sabadell, Spain; MB, Museum für Naturkunde, Berlin, Germany; MNHN, Muséum National d'Histoire Naturelle, Paris, France; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Geological setting

The Triassic outcrops of the La Mora site (Catalonia, Spain, northeast of the Iberian Peninsula) belong to the Montseny-Llobregat domain (Calvet and Marzo 1994) of the Catalonian basin. This palaeogeographic unit has been identified as one of the eastern-most sub-basins of the Iberian plate. The Buntsandstein facies in this area (Fig. 1) is formed by

continental deposits (Calvet and Marzo 1994). These materials are derived from the erosion of the Iberian Massif and they show thickness increment from northeast (145 m) to southwest (310 m).

The sedimentary deposits of this sub-basin are mainly composed of sandstone, mudstone, and red clay (Areniscas y Lutitas del Figaró unit); these materials are interpreted as fluvial deposits and distributed from northwest-northeast to southeast-southwest (Calvet and Marzo 1994).

At the La Mora site, the Buntsandstein facies deposits belong to the lower part of the Areniscas y Lutitas del Figaró unit. This unit is unconformable on Paleozoic metamorphic rocks. The section is 25 m thick and is composed of intercalations of red clay, mudstone, and sandstone in four sedimentary sequences with five different facies bound by caliche-type palaeosols (Fig. 1). The materials are interpreted as infilling of a channel body with an erosional base and a topping plane. Facies A represents the first deposits that formed the base of the level and deposits B are enclosed by the margin of the channel. Both are interpreted as point bars. In relation to these point bars, the sandstone from facies C fills the central part of the channel and its equivalent to the lower part of the deposits of the point bar. Facies C yields the vertebrate locality. The clay and silt from facies D constitute the final infill-
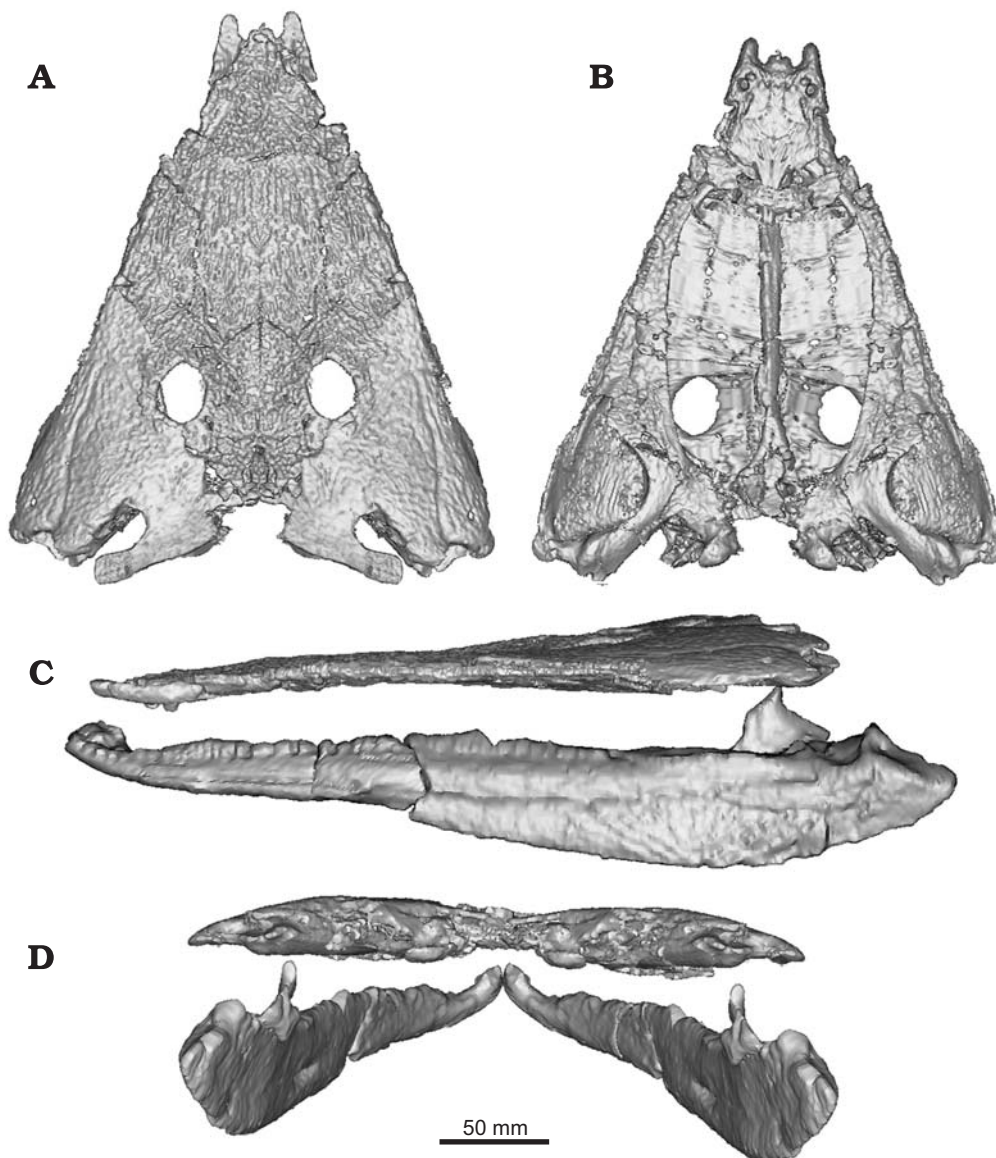
Fig. 2. Computed tomographic reconstruction of the capitosaur *Calmasuchus acri* gen. et sp. nov. from the Anisian at the La Mora site, Spain, in dorsal (**A**), ventral (**B**), lateral (**C**), and occipital (**D**) views.

ing of the abandoned fluvial channel and extend beyond the boundary of the channel as flood-plain deposits. In facies E, the sediments show a concentration of calcium carbonate nodules.

The age of the Areniscas y Lutitas del Figaró unit remains uncertain. The first palynological work in this Buntsandstein facies (Solé de Porta et al. 1987) dated the unit as Anisian. A recent palaeomagnetostratigraphic study excludes the possibility of an Olenekian stage (Dinarès-Turell et al. 2005) and biostratigraphic analysis of the overlying lower Muschelkalk facies indicates an age of middle-to-upper Pelsonian to upper Illyrian (middle-to-upper Anisian), on the basis of the presence of the conodonts *Paragondolella bulgarica*, *P. hanbulogi*, *P. bifurcata*, *Neogondolella constricta*, *N. cornuta*, *N. excentrica*, and *N. basisymetrica*. In addition, the brachiopod *Spiriferina* (*Mentzelia*) *mentzeli* is recognised at the base

of this facies and the ammonite *Paraceratites* fauna is located in the middle part of the lower Muschelkalk facies (see Márquez-Aliaga et al. 2000; Dinarès-Turell et al. 2005 for further details). All these data restrict the La Mora site to an Aegean-to-middle Pelsonian age (early-to-middle Anisian).

Materials and methods

The La Mora site was discovered in 1989 by local hikers Emili Ramon and Pere Font. A year later, palaeontological fieldwork was undertaken by the Institut de Paleontologia de Sabadell (Spain), extracting hundreds of cranial and postcranial bones. Most of these bones were identified as belonging to capitosaurs. Other elements were postcranial elements of archosauromorphs and cranial remains of procolopho-

noids noted in previous studies and currently under study (Gaete et al. 1993, 1994, 1996; JF unpublished data). In addition, tetrapod ichnites were recovered close to the site, including the ichnogenera *Rhynchosauroides*, *Chirotherium*, and *Synaptichnium* (see Calzada 1987 for further details).

The hard matrix and high density of bones (often in contact) hindered their preparation for a long time and made description of the osteology of these materials and identification of diagnostic characters difficult (Gaete et al. 1994). Nevertheless, after several years of mechanical preparation, cranial remains were sufficiently prepared for description. Moreover, computed tomographic scans were performed to understand the morphology of some areas better, and as a useful tool to enable skull reconstruction by using cranial remains (Fig. 2). This reconstruction shows the mandible and the major part of the skull roof and palatal regions. All the cranial remains were scanned by multidetector computer tomography (Sensations 16; Siemens) at Hospital Universitari Mútua Terrassa (Barcelona, Spain). Each cranial specimen was scanned at 140 kV and 220 mA with an output of 512 × 512 pixels per slice, with an interslice space of 0.2 mm, and processed by using the Mimics software (Materialise, Leuven, Belgium), obtaining an almost complete skull reconstruction from the partial fossil material.

Systematic palaeontology

Temnospondyli Zittel 1890 (sensu Milner 1990)

Stereospondyli Zittel 1890 (emend. Fraas 1889)

Capitosauria Yates and Warren 2000 (emend. Damiani and Yates 2003)

Genus *Calmasuchus* nov.

Etymology: After Pla de la Calma, the Catalan toponym for the type locality.

Type and only known species: *Calmasuchus acri* sp. nov.; see below.

Diagnosis.—Same as for the type and only species.

Stratigraphic and geographic range.—Early–middle Anisian, Tagamanent, Barcelona, Spain.

Calmasuchus acri sp. nov.

Figs. 2–6.

1993 *Parotosuchus* sp.; Gaete et al. 1993.

Etymology: From the Latin *acre*, defined as hard or strong and referring to the hardness of the matrix that surrounds the fossils and makes preparation of the material difficult.

Type material: Holotype: IPS-37401 (LM-83) has a partial skull roof and palate (Fig. 3). Paratypes: IPS-37401 (LM-63, LM-101, L, and M1) consists of skull fragments and IPS-42407 (LM-4) is a complete hemimandible (Figs. 4, 5).

Type locality: All the specimens were collected from the La Mora site of the Catalonian basin, Barcelona, Spain. All were collected by Àngel Galobart, Rodrigo Gaete, and Xavier Ros in 1990.

Type horizon: Catalonian basin, Catalan Coastal Ranges, Buntsandstein facies from the Montseny-Llobregat Domain, included in the Areniscas

y Lutitas del Figaro unit, and dated as early-to-middle Anisian (Middle Triassic).

Diagnosis.—Distinguished from all other capitosaurs by a combination of the following characters: posterolaterally directed tabular horns, orbital margins flush with the plane of the skull, the postorbital and prefrontal near each other by thin projections, paired anterior palatal vacuity, long choanal outline, the frontal enters the medial border of the orbit, presence of a transversely oriented transvomerine tooth row, cultriform process of the parasphenoid extends beyond the anterior border of the interpterygoid vacuities, absence of the denticle field in the pterygoid and parasphenoid, elongated and well developed postglenoid area.

Preservation.—Fossil bone remains from the La Mora site are well preserved despite the hard matrix that wraps parts of the bones and the action of sedimentary compaction and tectonic stress that slightly crushed some anatomical structures, making assessment of some cranial characters difficult. To resolve this problem, other cranial fragments are described when the characters are poorly or not preserved in the holotype. Here, we focus on the study of some incomplete skulls recovered from the La Mora site. All the cranial remains display well-fused sutures, indicating that they belong to adult animals. The partial cranial fragments recovered and the computed tomographic reconstruction allowed description of the skull.

Description

Skull roof.—The skull roof is nearly complete in IPS-37401 (LM-83) (Fig. 3). The length of the skull roof, as preserved, is 30.9 cm from the posterior margin of the skull to the external nares (anterior margin). The tip of the snout anterior to the external nares is not preserved in the dorsal view. The posterolateral region of the skull roof is incomplete in IPS-37401 (LM-83), but it is well preserved in IPS-37401 (LM-63, L, and M1) (Figs. 4, 6). The sutures of the skull elements in IPS-37401 (LM-83) are firmly fused and discernible. The bone ornamentation is well developed and corresponds to the typical temnospondyl pitted sculpture pattern. In the dorsal view, the overall shape of the skull roof displays a convex snout. The tabular sutures the squamosal at the level of the anterior margin of the otic notch. The tabular horns are posterolaterally directed where the apex of the horn is in close proximity to the squamosal posteriorly, without suturing it posteriorly. The posterior tip of the tabular is nearly equally expanded mediolaterally but only slightly expanded anterodistally. The tabular horns are complete and well preserved in IPS-37401 (L and M1). IPS-37401 (LM-63) preserves the tabular–squamosal and tabular–supratemporal sutures. In this fragment, the tabular horns are not completely preserved, preventing description of its postparietal–tabular margin, which shows an unpreserved suture. On the other hand, *Calmasuchus acri* lacks the long processus lateralis present in the tabular of some capitosaurs. The posterior margin of the squamosal is slightly convex dorsally, with a narrow falciform crest.

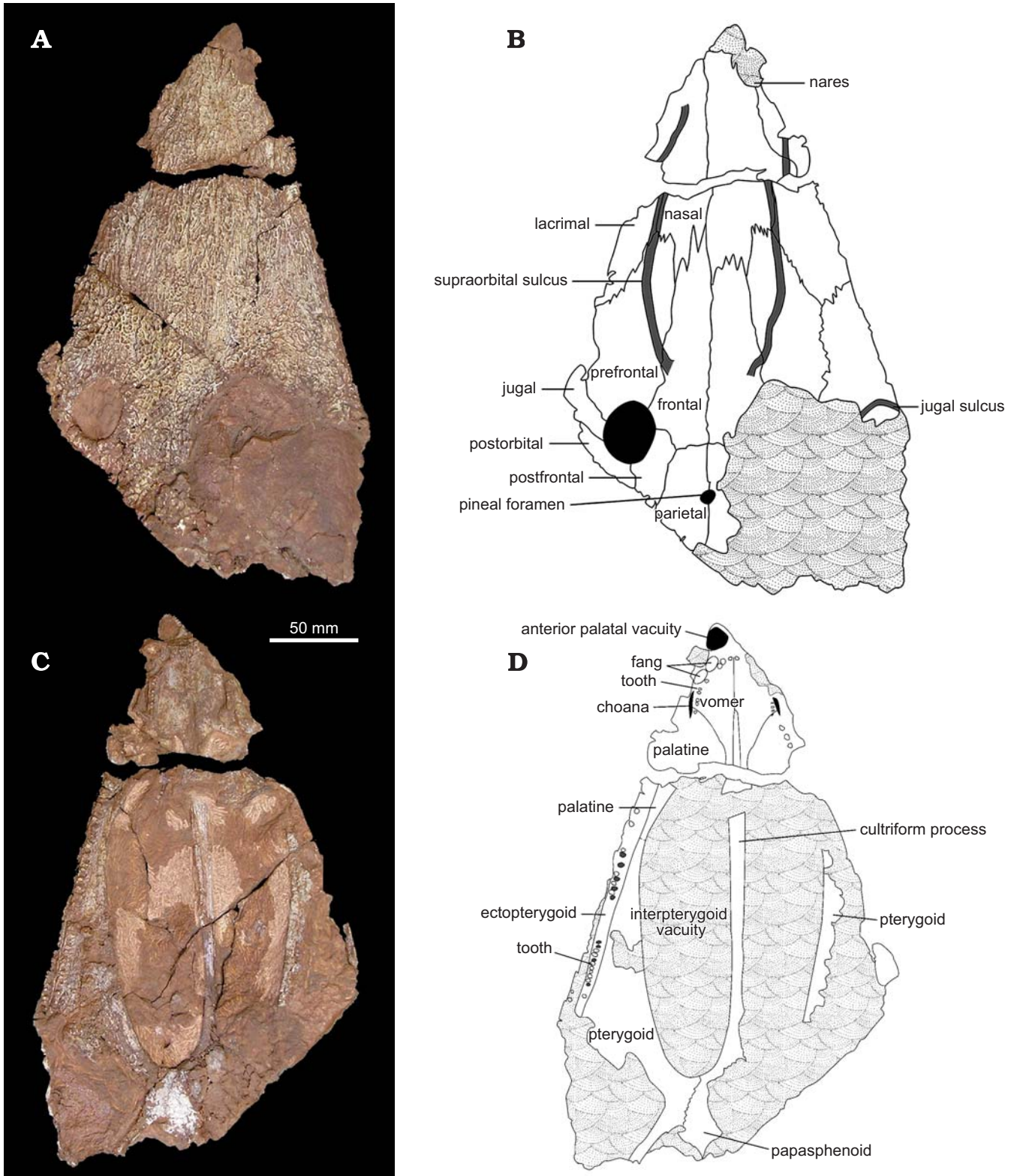The parietal is longer than the supratemporal, which is

Fig. 3. Remains of the capitosaur *Calmasuchus acri* gen. et sp. nov. IPS-37401 (LM-83) from the Anisian at the La Mora site, Spain, in dorsal (**A**, **B**) and ventral (**C**, **D**) views. Photographs (A, C) and explanatory drawings (B, D).

slightly longer than the postparietal. The supratemporal is excluded from the otic notch. The frontal enters the medial border of orbit. The morphology of the orbit is slightly sub-circular, and in IPS-37401 (LM-63), it is 35 mm in length and

30.3 mm in width. The orbital margin lies in the same plane of the skull roof. Apart from this, the interorbital area is flattened and moderately broad (55.2 mm in width) in comparison with other capitosaurs (e.g., *Stanocephalosaurus pro-*
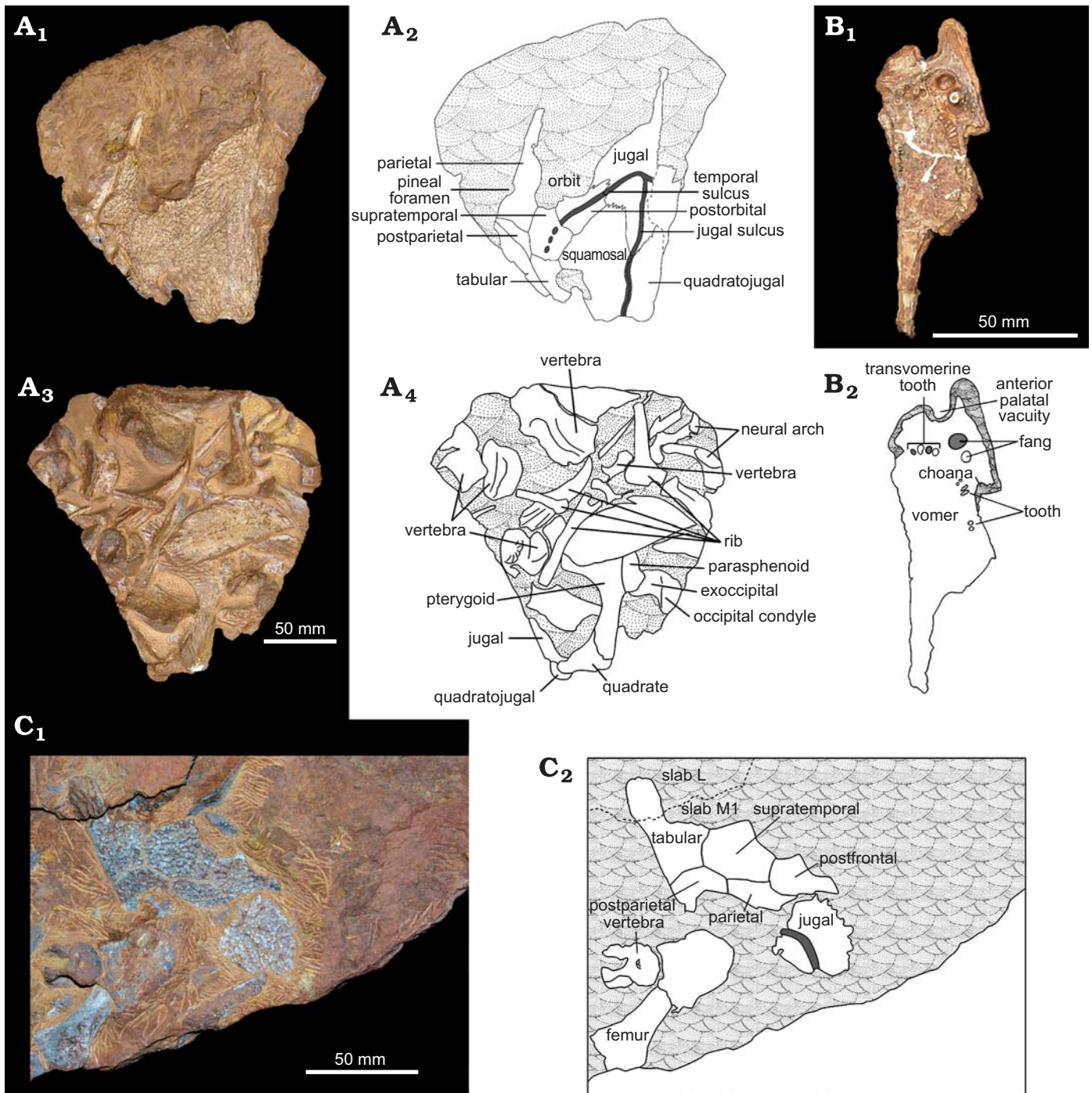
Fig. 4. Photographs and drawings of paratypes of the capitosaur *Calmasuchus acri* gen. et sp. nov. from the Anisian at the La Mora site, Spain. **A**. Cranial remains IPS-37401 (LM-63), in dorsal (A_1, A_2) and ventral (A_3, A_4) views. **B**. Palatal fragment IPS-37401 (LM-101), in dorsal (B_1, B_2) view. **C**. Posterior skull roof fragments of IPS-37401 (L and M1), in dorsal (C_1, C_2) view. Note that fragments L and M1 are in contact. Photographs (A_1, A_3, B_1, C_1) and explanatory drawings (A_2, A_4, B_2, C_2).

nus) with narrow interorbital distance. The postorbital is moderately expanded anterolaterally because it occupies less than half of the orbital border. The postorbital and prefrontal are not in contact. A thin projection of the jugal reaches the orbital margin. The external nares are not completely preserved; therefore, the morphology of this structure is uncertain.

Sensory sulci.—The lateral line sensory canals are discontinuous. The supraorbital sensory canal passes across the posterior section of the suture between the lacrimal and the nasal. It follows the nasal anteriorly, similar to that in some specimens of *Eryosuchus garjainovi* or *Cyclotosaurus robustus* as observed by Schoch (2008). On the other hand, the lacrimal flexure of the infraorbital sensory canal is partially pre-
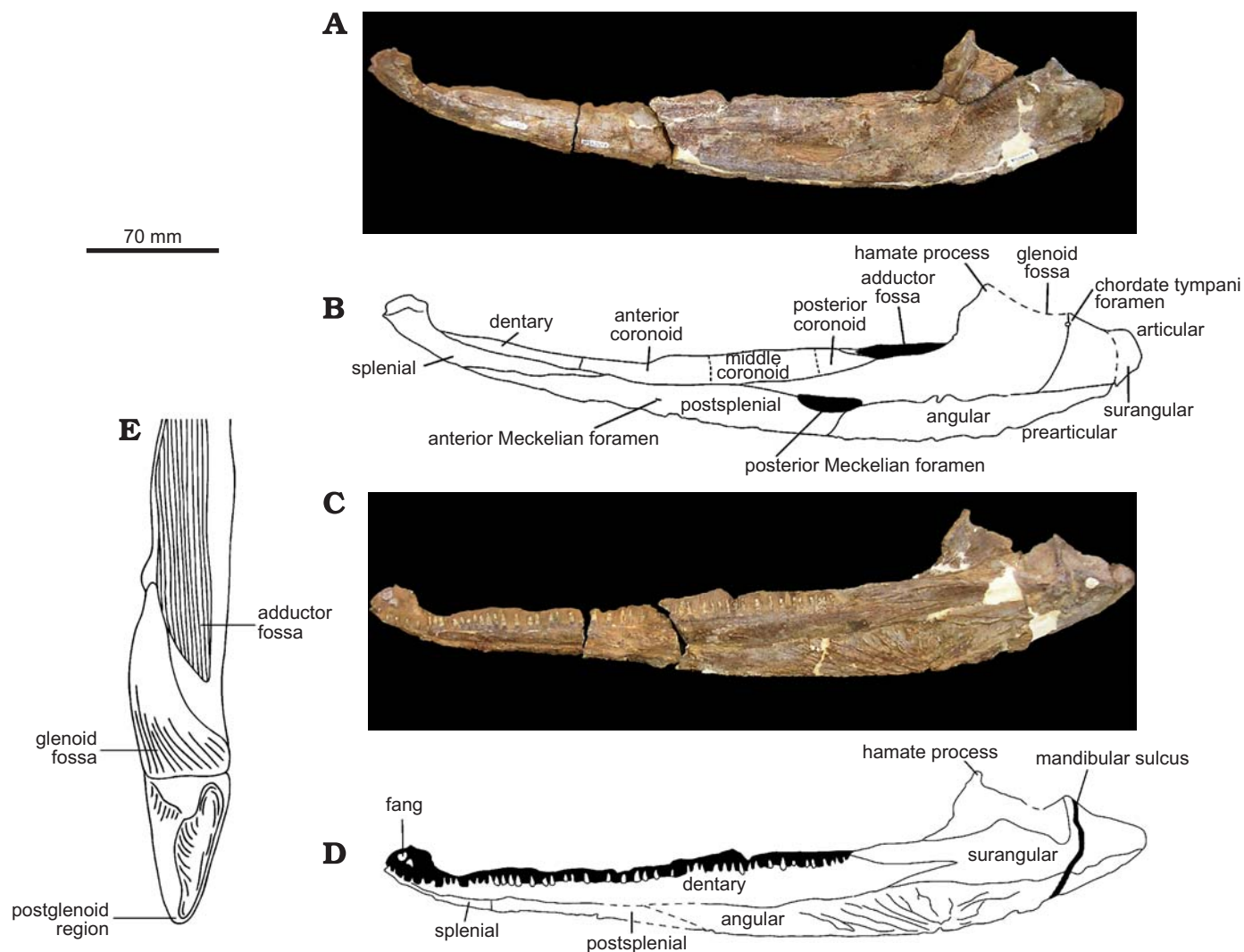
Fig. 5. Photographs and drawings of lower jaws of the capitosaur *Calmasuchus acri* gen. et sp. nov. from the Anisian at the La Mora site, Spain; specimen IPS-42407 (LM-4). Photograph (**A**) and drawing (**B**) of the hemi-mandible in lingual view. Photograph (**C**) and drawing (**D**) of the hemi-mandible in labial view. **E**. Postglenoid area.

served, preventing observation of any Z-shaped morphology. The occipital sensory canal is absent.

Palate.—The palate is partially preserved in IPS-37401 (LM-83), enabling the various palatal vacuities to be outlined (Figs. 3, 6). The vomerine plate is elongated. The transvomerine tooth is oriented transversely. The choanal outline is long but its preservation prevents discrimination between narrow choanae as in *Parotosuchus orenburgensis* or oval-shaped choanae as in *Wetlugasaurus angustifrons*. Nevertheless, the circular-subcircular outline of the choanae is rejected. Paired anterior palatal vacuities are present.

The palatal fragment in IPS-37401 (LM-101) (Fig. 4) shows both the major part of the vomer and the maximal outline of the choanae, although as in the case of IPS-37401 (LM-83) its preservation prevents discernment of the narrow or oval choanal morphology. Postfenestral teeth can be clearly outlined and placed. The distance between the postfenestral teeth and the posterior part of the anterior palatal vacuity is 5 mm. IPS-37401 (LM-101) also shows the anterior process of

the palatal vacuity. Although not well preserved, the presence of an anterior process closing the vacuity on the right side of the palatal view allows us to reject an unpaired vacuity or a medially subdivided one, as is the case in *Benthosuchus shushkini*. The ectopterygoid does not contact the interpterygoid vacuities. The interpterygoid vacuities are equally wide along their extension.

The cultriform process of the parasphenoid is preserved in IPS-37401 (LM-83). It extends beyond the anterior border of the interpterygoid vacuities to the level of the choanae. In contrast, in the posterior region of the cultriform process, there is no evidence of a deltoid base. The participation of the palatine at the margin of the interpterygoid vacuities prevents the palatine ramus of the pterygoid from contacting the vomer. The pterygoid is slender. The posterior half of the palatine ramus curves medially, where it forms the corpus of the pterygoid; then, this corpus curves laterally, forming the quadrate ramus. The pterygoid displays a pronounced sculpture in the palatine region and corpus. The palatine ramus and most of the corpus
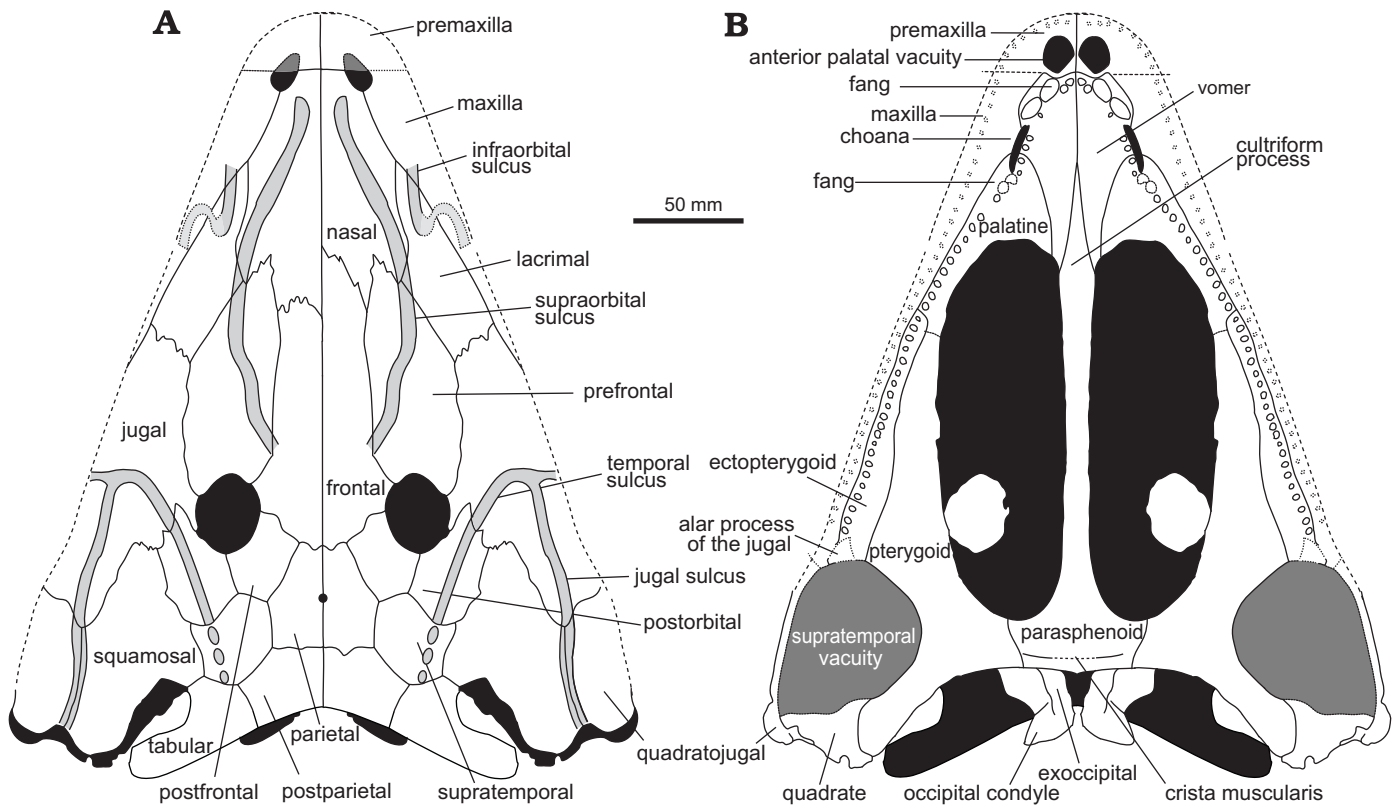
Fig. 6. Cranial reconstruction in dorsal (**A**) and ventral (**B**) views of the capitosaur *Calmasuchus acri* gen. et sp. nov. from the Anisian at the La Mora site, Spain.

of the pterygoid are present in IPS-37401 (LM-83), but the quadrate ramus of the pterygoid is damaged and badly preserved. This region is well preserved in IPS-37401 (LM-63), displaying a parasagittally oriented quadrate ramus and preserved quadrate–pterygoid suture. The suture between the pterygoid and the parasphenoid is anteroposteriorly short. The parasphenoid prevents the exoccipital from contacting the pterygoid ventrally. As revealed in IPS-37401 (LM-83), the parasphenoid plate, with a rectangular shape, is flattened without any depression or sculpturing. The crista muscularis of the parasphenoid is poorly preserved and can be discerned only at the level of the pterygoid–parasphenoid suture. The occipital condyles are located slightly anterior to the quadrate condyles.

Occiput.—Most of the occiput is not preserved and only a few characters are available for description, because of the use of computed tomographic scans (Fig. 2). Structures of the occiput are recognisable only in IPS-37401 (LM-63). Matrix deletion and virtual repositioning of the cranial structures allowed us to confirm that the quadratojugal contributes to the upper jaw condyle, whereas the post-temporal fenestra displays a triangular morphology, as is the case of almost all capitosaurs and trematosaurs.

Mandible.—At least seven well-preserved hemi-mandibles were recovered in the type locality. The general description is based on IPS-42407 (LM-4) (Fig. 5), which is complete and well preserved, at a total length of 39.5 cm. The hemi-mandible is low except for its posterior area, which is

dorsally straight along the posterior two-thirds and slightly curved in the anterior part. In the labial view, the angular shows well-defined ornamentation that becomes less evident in the postsplenial. In the posterior part of the hemi-mandible, a weakly developed mandibular sulcus is present. The dentary shows two anterior tusks and 47 teeth with moderately compressed bases. Both the dentary and the splenial form part of the symphyseal region, as is typical in temnospondyls. The postglenoid area is elongated and contains the articular and surangular, without any sign of the prearticular. The angular lies ventrally to the articular. The foramen chorda tympani lies in the posterior region of the glenoid fossa, separating the articular and prearticular.

Although Jupp and Warren (1986) discuss the lower jaw anatomy of temnospondyls, the morphology of the postglenoid area cannot be clearly placed in any of the two types described by these authors. It shares with type I the following features: the prearticular does not extend into the postglenoid area, the articular is the major component of the postglenoid area, the angular lies ventral to the articular, and the foramen chorda tympani separates the articular and prearticular. On the other hand, as in type II, the angular lies labial to the articular and the postglenoid area is elongated.

Moreover, the prearticular does not suture the splenial because it is separated by the coronoid. Although the mandibular sutures are not clearly discernable because of taphonomic reasons, the major part of the middle coronoid probably does not reach the prearticular or the posterior Meckelian fora-

men. The posterior Meckelian foramen is short, being less than half the size of the adductor fossa (Damiani 2001) and less than 25% of the total length of the mandible (Schoch 2000).The anterior Meckelian foramen is poorly preserved, but it is situated slightly in an anterior position in comparison with that in other capitosaurs.

The prearticular shows a well-developed, high, and massive hamate process. The quadrate trochlea is shorter than the hamate process. Comparisons of the postglenoid area with that of other capitosaurs allowed us to classify the mandible of *Calmasuchus acri* as type IV of Maryańska and Shishkin (1996), with an elongated postglenoid area and a depressed dorsal surface. The crista articularis is poorly preserved but is displaced and continuous with the crista medialis. The glenoid fossa lies above the dorsal surface of the dentary. The adductor fossa is short. As in most capitosaurs, the labial wall of the adductor fossa is straight and horizontal.

Phylogenetic analysis

In order to investigate the phylogenetic relationships of the new taxon, we incorporated its characters into a data matrix. We also scored *Vladlenosaurus alexeyevi* in a cladistic analysis, for the first time. This form was recovered from the late Vetlugian of Russia and confined to lacustrine habitats, and it shows an outline very similar to benthosuchids (Bystrow 1940; Getmanov 1989; Novikov 1990), although some cranial characters are similar to *Wetlugasaurus* (Morkovin and Novikov 2000; Shishkin et al. 2006). The data matrix was an updated version of Damiani (2001), with new characters and different coded taxa. Recent capitosaur findings (Morales and Shishkin 2002; Steyer 2003; Damiani 2008; Schoch 2008; Maganuco et al. 2009) provided new information on the cranial characters of the group; therefore, an upgrade of the Damiani (2001) matrix was required. From the original matrix, two characters were deleted because they were uninformative (characters 22 and 34; see Damiani 2001 for character details). In addition, eight characters were added to the matrix (see Appendix 1). These characters were previously used in cladistic analysis and provided informative data (Schoch 2000, 2008; Maganuco et al. 2009).

The analysis was performed by using PAUP 4.0 beta 1.0 for PC (Swofford 2001). The data matrix consisted of 53 characters and 26 terminal taxa, with three terminal taxa as an outgroup taxon (*Rhineceps nyasaensis*, *Uranocentrodon senekalensis*, and *Lydekkerina huxleyi*). The taxa analysed (see Appendix 2) are considered at the species level, except for *Angusaurus*, *Eocyclotosaurus*, and *Watsonisuchus*; for these taxa, we preferred to use the characters of the genus rather than those of the species, as exemplified by Damiani (2001), Damiani and Yates (2003), or Maganuco et al. (2009). Characters were scored by using information from the literature and JF personal observations (see Appendix 2). All characters were equally weighted and left unordered, except character 4 (tabular horn), because it forms a clear transformational
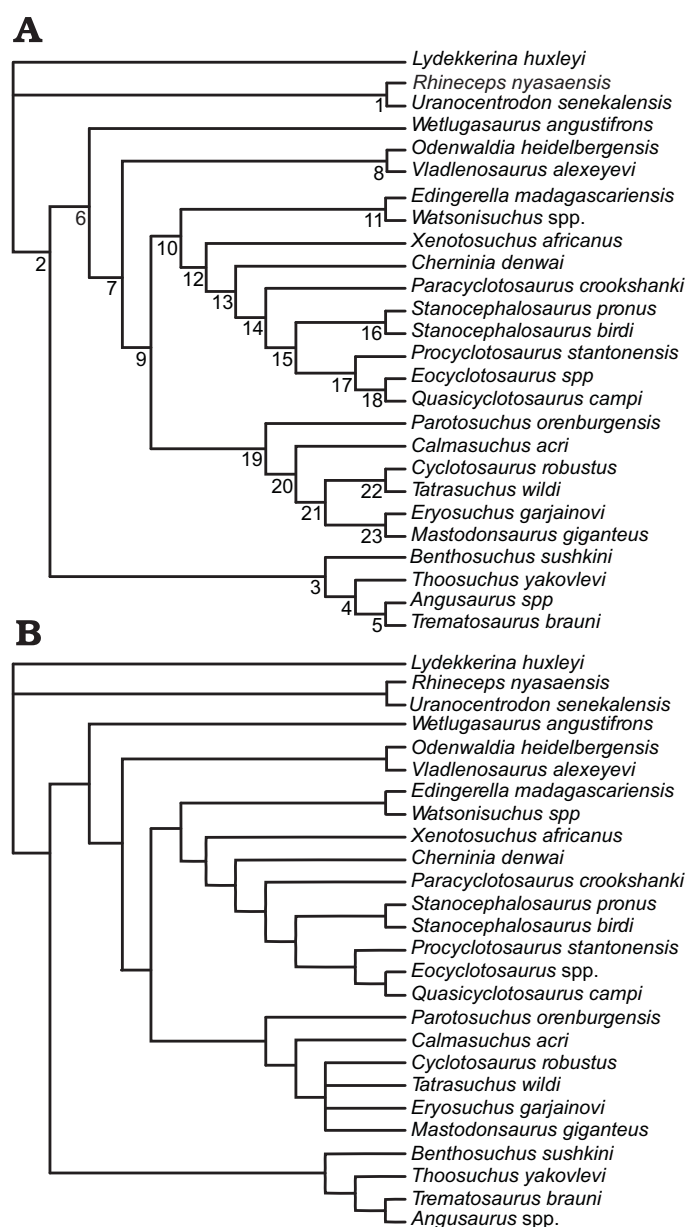

Fig. 7. Cladogram of the capitosaurs analysed in the data matrix. **A**. One of the two most parsimonious trees. **B**. Consensus trees (strict and majority rule show identical topology) of the two most parsimonious trees.

series in which the otic notch is gradually closed posteriorly, as indicated by Damiani (2001). Delayed transformation (DELTRAN) and Accelerated transformation (ACCTRAN) were selected to optimize the character transformation. Taxa coded as having multiple states were treated as polymorphic. We used a heuristic search with simple addition sequence and only one tree at each step during stepwise addition and 10,000 replicates. Tree-Bisection-Reconnection branch swapping was performed and zero-length branches were collapsed to yield polytomies. See Appendix 3 for further details.

Our phylogenetic analysis resulted in two most parsimonious trees of 141 steps each (CI = 0.41, RI = 0.70, RC = 0.29). As reported by Damiani (2001) and Maganuco et al.

(2009), a high amount of homoplasy was suspected in the evolution of the group, resulting in a low CI value. The strict and majority-rule consensus trees of the two most parsimonious trees were identical (Fig. 7) and showed one unresolved polytomy at the level of the clade composed of *Cyclotosaurus robustus*, *Tatrasuchus wildi*, *Mastodonsaurus giganteus*, and *Eryosuchus garjainovi*.

The support for the single nodes and their robustness according to bootstrap were low. Only seven nodes reached bootstrap values higher than 50% (1, 100%; 2, 93%; 4, 71%; 5, 94%; 9, 69%; 16, 77%; 18, 94%). In brief, this indicated that, apart from the Capitosauria and Trematosauria, only the trematosaurs and few capitosaur clades are well supported. The clade notation used in the paper (taxon X + taxon Y) refers to the least inclusive clade in the resolved cladogram comprising the two given taxa and does not imply that these taxa share a direct sister-taxon relationship. Node numbers are indicated in Fig. 7. The phylogenetic discussion is based on most parsimonious tree number 1, whose topology is congruent to that of the consensus trees. See Appendix 4 for the apomorphy list and more details about the character evolution.

Discussion

Previous morphological studies.—Previous studies on some of the already described material suggest close affinities to *Parotosuchus* sp. (Gaete et al. 1993, 1994, 1996). These authors published a preliminary reconstruction of the material and referred it to the genus *Parotosuchus*, reporting the presence of paired anterior palatal vacuities as a rather distinctive morphology from this genus. However, this is not the only difference between *Parotosuchus* sp. and *Calmasuchus acri*: the tabular morphology differs, being posteriorly directed in all the specimens of *Parotosuchus* and posterolaterally directed in those of *Calmasuchus acri*. The relative orbital size of *Parotosuchus* sp. and *Calmasuchus acri* is similar, but they differ in their orbital margins, which are elevated in *Parotosuchus* specimens and flushed in the same plane in *Calmasuchus acri*. Differences are also present in the mandibles, especially in the postglenoid area. *Parotosuchus orenburgensis* resembles type III of Maryańska and Shishkin (1996) whereas *Calmasuchus acri* belongs to type IV.

More recently, some authors, based on the descriptions and drawings supplied from the first papers, suggested that the La Mora specimens could be referred to as a stenotosaurid indet. (Shishkin 2000) or *Eryosuchus* sp. (Damiani 2001). However, the material described here cannot be attributed to stenotosaurids because it does not display the prefrontal–postorbital contact, typical of stenotosaurids (and heylerosaurids). Its supraorbital sensory canal is slightly displaced laterally in *Calmasuchus acri* and contacts the lacrimal–nasal suture, as in some specimens of *Cyclotosaurus robustus* and other capitosaurs such as *Eryosuchus garjainovi*; its interpterygoid vacuities are equally wide along their extension, as in *Stanocephalosaurus pronus* (Howie

1970) but unlike those of stenotosaurids, where the interpterygoid vacuities are tapered posteriorly. In addition, the otic notch and tabular horns appear to be more primitive in *Calmasuchus* than in stenotosaurids and related forms, where the squamosal usually contacts the tabular to create an embayment that is not found in *Calmasuchus*.

Regarding the affinities of the material described here with *Eryosuchus*, as suggested by Damiani (2001), we compared *Calmasuchus acri* with the eryosuchids sensu Schoch and Milner (2000) from the Eastern European platform. In the case of the capitosaur described here, the tip of the tabular is relatively wide throughout its length, with a slight anterodistally expansion. This morphology differs from *Eryosuchus garjainovi*, because the anterodistal expansion is well developed in the latter taxon. In *Calmasuchus*, the orbital size is reduced compared with that of *Eryosuchus* and resembles the medium-sized orbits of *Parotosuchus* or *Tatrasuchus wildi*. The outline of the orbits in *Eryosuchus garjainovi* is slightly more elongated and suboval than in *Calmasuchus acri*. The proportional interorbital distance is smaller in *Calmasuchus acri* than in *Eryosuchus garjainovi*; the position of the orbits in the skull roof in both genera is similar. Damiani (2001) used the position of the occipital condyles in relation to the quadrate condyles as one of the characters to group the Russian *Eryosuchus* species with the Gondwanian ones: in *Eryosuchus*, the occipital condyles are slightly anterior to the quadrate condyles. This is also the case in *Calmasuchus acri*, whereas some Gondwanian species such as *Stanocephalosaurus pronus* and *Xenotosuchus africanus* differ, with the occipital condyles at the same level (or posterior) as the quadrate condyles.

In the lower jaw, the postglenoid form of *Calmasuchus acri* is well extended and slightly concave without a medial ridge aligned sagitally as it is possible to observe in *Eryosuchus*. On the other hand, the morphology of the posterior Meckelian foramen is short, differing from the elongated morphology found in *Eryosuchus* species.

Comparisons with other taxa.—Posterolaterally directed tabular horns are considered by Schoch and Milner (2000) and Damiani (2001) as a derived character for the following capitosaurs: *Cherninia denwai*, *Eryosuchus*, *Xenotosuchus africanus*, *Mastodonsaurus giganteus*, *Stanocephalosaurus pronus*, *Paracyclotosaurus crookshanki*, and *Tatrasuchus wildi*. The tabular horns in *Calmasuchus acri* are slightly anterodistally broadened, and this expansion is more distinct in *Eryosuchus*. Further, *Calmasuchus acri* lacks a long processus lateralis in the tabular horns (present in *Tatrasuchus wildi* and *Stanocephalosaurus pronus*). Altogether, these are indications of a more derived condition in the horn morphology of *Eryosuchus*, *Tatrasuchus*, and *Stanocephalosaurus pronus* than of *Calmasuchus*.

The orbital size, in proportion to the skull, is smaller than that of *Mastodonsaurus giganteus* and similar to those of *Parotosuchus orenburgensis* and *Tatrasuchus kulczyckii*. The relative position between the postorbital and the prefrontal varies in capitosaurs. This character is also considered derived

when these bones are near each other by thin projections (Schoch 2008). This is the case of *Calmasuchus acri* and differs from other advanced capitosaurs, where the bones are widely separated, such as in *Eryosuchus*, *Tatrasuchus*, or *Xenotosuchus*, and resemble the condition found in *Paracyclotosaurus* and *Stanocephalosaurus*.

In the palatal view, the region between the anterior palatal vacuity and the anterior border of the interpterygoid vacuities (occupied by the two vomerine plates) is elongated as in *Parotosuchus orenburgensis* and *Stanocephalosaurus pronus*, and considered a derived character (Damiani 2001; Schoch 2008). The same authors considered oval or narrow slit-like choanae as plesiomorphic (e.g., *Calmasuchus acri* or *Benthosuchus sushkini*) and subcircular or circular choanae as apomorphic (Liu and Wang 2005; e.g., *Yuanansuchus laticeps* or *Mastodonsaurus giganteus*). In *Tatrasuchus wildi*, the snout is very short and broad with foreshortened vomerine plates and subcircular choanae. *Calmasuchus acri* lacks a ventral exoccipital–pterygoid contact, a character also present in *Tatrasuchus wildi* and *Xenotosuchus africanus*, differing from *Eryosuchus garjainovi* and *Tatrasuchus wildi*.

Although the presence of unpaired or paired anterior palatal vacuities is often considered a diagnostic character in trematosaurs (Welles and Cosgriff 1965; Damiani 2001), this character is also phylogenetically informative in capitosaurs. *Calmasuchus acri* has a paired anterior palatal vacuity, as does *Mastodonsaurus giganteus*. In most specimens of *Eryosuchus*, this character represents the primitive condition, but it was referred by Schoch and Milner (2000) from a gigantic undescribed specimen.

Pronounced sculpturing in the palatine region of the pterygoid is present mainly in trematosaurs, but this character is variable in capitosaurs. Basal and "advanced" forms such as *Wetlugasaurus angustifrons*, *Tatrasuchus wildi*, *Cyclotosaurus robustus*, *Eocyclotosaurus lehmani*, and the capitosaur described herein show ornamentation, whereas other forms such as *Cherninia denwai*, *Eryosuchus garjainovi*, *Mastodonsaurus giganteus*, *Paracyclotosaurus crookshanki*, and *Stanocephalosaurus pronus* display the ventrally smoothed palatine without any sign of ornamentation.

Maryańska and Shishkin (1996) recognised four patterns in the postglenoid area of capitosaurs. They referred to the plesiomorphic condition in *Wetlugasaurus angustifrons*. The postglenoid area of eryosuchids, mastodonsaurids, and tatrasuchinids was considered as the most derived one, with the retroarticular process markedly elongated and depressed in the dorsal surface (Maryańska and Shishkin 1996). This morphology is also recognised in *Calmasuchus acri*, being more derived than the morphology present in *Xenotosuchus africanus*.

The morphology of the posterior Meckelian foramen in *Calmasuchus acri* represents the primitive condition (Schoch 2000; Damiani 2001), differing from the derived condition found in *Eryosuchus garjainovi* and *Mastodonsaurus giganteus*. Moreover, the type mandible of *Tatrasuchus kulczyckii* is incomplete, but it is inferred that its posterior Meckelian foramen is elongated (Maryańska and Shishkin 1996). This is not the case of *Xenotosuchus africanus*, which displays a short posterior Meckelian foramen.

The length of the adductor fossa is short in *Calmasuchus acri* and, when compared with the total length of the mandible, similar to that of *Mastodonsaurus giganteus* and *Eryosuchus garjainovi*. On the other hand, the outline morphology of *Calmasuchus acri* resembles the Tatrasuchinae. This group combines parotosuchid-like features with other features usually found in cyclotosaurs (Schoch and Milner 2000). *Calmasuchus acri* differs from the tatrasuchinids in several characters, as already discussed: less separated postorbital and prefrontal, supraorbital sensory canal traversing the nasal and lacrimal, more elongated prefenestral division of the palate, narrower choanae, divided anterior palatal vacuity (it is undivided in the two species of *Tatrasuchus*), equally wide interpterygoid vacuities anteriorly and posteriorly (they are tapered posteriorly in *Tatrasuchus wildi* and unpreserved in *T. kulczyckii*), no sculptured ventral surface of the parasphenoid basal plate, shorter posterior Meckelian foramen, and postglenoid area longer than the glenoid facet.

The inclusion of *Calmasuchus acri* in any of the capitosaur families recognised in the literature (see Schoch and Milner 2000 for further details) is controversial because the combination of characters present in this new genus is not in agreement with the synapomorphies used to define the different families (sensu stricto Schoch and Milner 2000). Therefore, a re-definition of some capitosaur families (i.e., Parotosuchidae, Tatrasuchidae, Eryosuchidae) will be necessary. Nevertheless, as some aspects of *Calmasuchus acri* remain undiscovered, we prefer to be conservative, discarding its inclusion in any capitosaur family or even creating a new one, until additional material allows accurate assessment of the characters that remain unclear.

Phylogenetic remarks

The dichotomy between the Trematosauria and the Capitosauria was recognised in previous studies (Yates and Warren 2000; Damiani 2001; Steyer 2002; Damiani and Yates 2003; Schoch et al. 2007; Schoch 2008; Maganuco et al. 2009). Herein, the capitosaur clade is also recognised and well supported by seven unambiguous synapomorphies.

Benthosuchus sushkini was previously included in the capitosaur clade (Yates and Warren 2000; Damiani 2001; Steyer 2003). However, Damiani and Yates (2003) indicated that three characters (the lacrimal flexure of the infraorbital sensory canal, morphology of the marginal teeth, and oblique ridge of the pterygoid) were incorrectly coded in the revision by Damiani (2001). This problem is resolved here and confirms the basal position of *Benthosuchus sushkini* in the trematosaurian clade.

The Trematosauroidea (node 4) were defined as the last common ancestor of *Thoosuchus yakovlevi* and *Trematosaurus brauni* and all its descendants (Yates and Warren 2000). This was confirmed by Damiani and Yates (2003),

Maganuco et al. (2009), and the present study. *Tremato-saurus brauni* is included in the trematosaurian clade as the sister taxon of *Angusaurus*, yet considered a more primitive form (Damiani and Yates 2003).

The more recent update of the Capitosauria (node 6) (Damiani and Yates 2003) defined the group as stereopondyls that share a more recent common ancestor with *Parotosuchus* than with *Trematosaurus*. *Wetlugasaurus* was included in the trematosaurian group (Schoch 2000; Schoch and Milner 2000), although other authors consider it as a basal capitosaur or sister group to them (Ochev 1966; Kamphausen 1989; Maryańska and Shishkin 1996; Damiani 2001; Damiani and Yates 2003). A recent analysis (Schoch 2008; Maganuco et al. 2009) indicated *Wetlugasaurus* as a member of the Capito-sauria. In the present study, *Wetlugasaurus* appears as the most basal member of the Capitosauria. Therefore, we define the Capitosauria as stereopondyls that share a more recent common ancestor with *Wetlugasaurus* than with *Trematosaurus*.

The position of *Vladlenosaurus alexeyevi* within the Capitosauria is controversial. This taxon was suggested to be a species of *Wetlugasaurus* (Shishkin et al. 2006) or closely related to this genus (Morkovin and Novikov 2000). In the present analysis, *Vladlenosaurus alexeyevi* and the enigmatic *Odenwaldia heidelbergensis* resulted as sister taxa.

On the other hand, the *Watsonisuchus–Edingerella* clade appears as the sister group of the huge clade of Gondwanian forms, plus heylerosaurids and stenotosaurids, being the more primitive forms of the clade. The position of *Edingerella madagascariensis* is controversial. It was initially described as a species of *Benthosuchus* (Lehman 1961) and later to the genus *Parotosuchus*, and then assigned to the capitosaur group (Schoch 2000) and surprisingly to the lydekkerinid group (Damiani 2001). Finally, the genus *Edingerella* was estab-lished for the species *E. madagascariensis* (Schoch and Milner 2000), defined as a stem capitosaur. Recently, a new description of Lehman's (1961) specimens and new excep-tionally well-preserved specimens (Steyer 2003; Maganuco et al. 2009) indicated the basal position of this genus within the capitosaur group and its close relationship with *Watsoni-suchus*, although in a recent revision of the group, Schoch (2008) included *Edingerella madagascariensis* within the trematosaurs. In the case of *Watsonisuchus*, these taxa are studied here at the genus level. Four species (*Watsonisuchus aliciae*, *W. gunganj*, *W. magnus*, and *W. rewanensis*) have been described from the Early Triassic of Australia and South Africa; they are considered as one of the most basal genera within the Capitosauria (Damiani 2001). However, *W. gunjanj* and *W. aliciae* were transferred to the genus *Rewanobatrachus* (Schoch and Milner 2000), another stem-capitosaur. *Watsoni-suchus aliciae* remains the best known species documented by ontogenetical information (Warren 1980; Warren and Schroe-der 1995). Damiani (2001) retained *W. aliciae* within the ge-nus with caution. Recently, the genus *Warrenisuchus* (Mag-anuco et al. 2009) was established for *W. aliciae* (Warren and Hutchinson 1988). This genus is considered basal to *Watsonisuchus*. In the present study, we followed Damiani

(2001), retaining *W. gunganj*, *W. magnus*, *W. rewanensis*, and *W. aliciae* with caution in the genus *Watsonisuchus*. More-over, the analysis reflects the close, sister-taxon relationships between *Edingerella* and *Watsonisuchus*.

Xenotosuchus africanus, *Cherninia denwai*, and *Para-cyclotosaurus crookshanki* form successive sister taxa to the remaining stenotosaurids and heylerosaurids plus *Stanoce-phalosaurus*. Regarding *Stanocephalosaurus*, we consider *S. birdi* as the senior synonym of *P. peabodyi* and separated it from *Wellesaurus*. On the other hand, the South African capitosaur *S. pronus* was included as an *Eryosuchus* member (Damiani 2001). This suggestion was not followed here. In the present analysis, *S. birdi* and *S. pronus* are sister taxa, with two unambiguous synapomorphies, demonstrating that this genus had widespread distribution, being present in South Africa and North America.

The close relationship between the poorly known steno-tosaurids (Paton 1974; e.g., *Procyclotosaurus stantonensis*) and heylerosaurids (e.g., *Eocyclotosaurus* and *Quasicyclo-saurus*) was indicated by Schoch and Milner (2000). Here, stenotosaurids appear as a sister taxon of heylerosaurids, the latter forms being more advanced. On the other hand, the present analysis seems to partially corroborate the hypothesis of the diphyli between *Eocyclotosaurus* and *Cyclotosaurus* (Damiani 2001), which are not closely related forms. Other-wise, the *Eocyclotosaurus–Odenwaldia* relationship is not supported here.

The cosmopolitan genus *Parotosuchus* is known to be from the Early Triassic. Recent published papers clarified the valid species of this genus (e.g., Schoch and Milner 2000; Damiani 2001; Morales and Shishkin 2002; Shishkin and Sulej 2009 and references therein). To date, at least eight spe-cies are considered valid: *Parotosuchus orenburgensis*, *P. nasutus*, *P.helgolandicus*, *P. orientalis*, *P. komiensis*, *P. bog-doanus*, *P. panteleevi*, and *P. speleus*. In the present analysis, *P. orenburgensis* is the sister taxon of *Calmasuchus acri* and their descendants, supported by two unambiguous synapo-morphies. The new capitosaur described here, *Calmasuchus acri*, appears as a more derived form than *Parotosuchus orenburgensis* and the sister taxon of the *Cyclotosaurus–Tatrasuchus* and *Eryosuchus–Mastodonsaurus* clades, re-vealing a more basal position than the tatrasuchines.

Finally, we report a dichotomy between cyclotosaurs and related forms (e.g., *Tatrasuchus*) and the *Eryosuchus–Masto-donsaurus* clade. On one hand, *Cyclotosaurus robustus* and *Tatrasuchus wildi* were found to be sister taxa in previous works (Maryańska and Shishkin 1996; Schoch and Milner 2000; Damiani 2001; Maganuco et al. 2009; present study). On the other hand, the cladistic analysis indicated phylogen-etic affinities between mastodonsaurids and eryosuchids as previously reported by other authors (Maganuco et al. 2009). Further research is needed on related taxa, such as the Anisian *Heptasaurus*, *Komatosuchus*, and the gigantic undescribed skull from Ladinian of Russia referred by Schoch and Milner (2000) to *Eryosuchus* sp., to clarify the relationships within this clade.

Conclusions

The capitosaur remains recovered from the La Mora site (Eastern Iberian Peninsula) allowed us to describe a new form of capitosaur, *Calmasuchus acri*. The remains date to the early-to-middle Anisian (Middle Triassic). Its cranial reconstruction suggests that this capitosaur does not belong to *Parotosuchus*, *Eryosuchus*, or a stenotosaurid indet., as previously suggested (Gaete et al. 1993, 1994, 1996; Shishkin 2000; Damiani 2001). The new capitosaur is characterised by a combination of parotosuchid characters and others such as posterolaterally directed tabular horns, paired anterior palatal vacuities, and unique morphological characters in its lower jaw. The outline of the skull resembles that of tatrasuchines, but several different character polarities demonstrate the basal position of the new form ahead of the tatrasuchines. The phylogenetic analysis suggests that *Parotosuchus orenburgensis* and *Calmasuchus acri* are the sister taxa of the *Cyclotosaurus–Tatrasuchus* and *Eryosuchus–Mastodonsaurus* clades. *Calmasuchus acri* is more derived than *Parotosuchus* sp. As a group, the Capitosauria are supported by seven synapomorphies. *Wetlugasaurus* is the most basal member of the capitosaur clade. We scored the Russian genus *Vladlenosaurus* for the first time. This genus is the sister taxon of *Odenwaldia heidelbergensis*, occupying a basal position in the capitosaur clade, although it is more derived than *Wetlugasaurus*. This latter genus is the most basal member of the Capitosauria. The Madagascarian *Edingerella* is the sister taxon of *Watsonisuchus*.

Acknowledgements

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Appendix 1: Character data

The character data were composed of 53 characters. Of these, 45 correspond to the 47 characters used in the data matrix of Damiani (2001). We excluded characters 22 (posterolateral process of the vomer) and 34 (cheek region of the skull) of Damiani (2001) because these characters were uninformative in the present analysis. We maintained the order of the remaining characters and added eight additional ones at the end of the list. We therefore referred to Damiani (2001) for a detailed description of characters 1–45. The additional characters are from other phylogenetic studies: characters 46–51 from Schoch (2000), character 52 from Maganuco et al. (2009), and character 53 from Schoch (2008). They are described as follows:

46. The parietal longer than the supratemporal and much longer than the postparietal (0); the parietal abbreviated, so that it, the postparietal, and the supratemporal are of similar length (1).

47. The postparietal and tabular are shorter than the parietal and supratemporal (0), or they extend posteriorly to give bones of similar length (1).

48. The interpterygoid vacuities are as wide posteriorly as anteriorly (0), or the basipterygoid ramus of the pterygoid is medially thickened and constricts the interpterygoid vacuities (1).

49. The basal plate of the parasphenoid is quadrangular in outline (0), or it is extends posterolaterally to give a trapezoidal outline (1).

50. The posterior margin of the squamosal is straight or curved in a slightly convex manner (0), or it forms a posteriorly extended plate that roofs the occiput (1).

51. The postglenoid area forms a short, rounded outgrowth with oblique dorsal and ventral margins (0), or it is much elongated and has a straight dorsal margin bilaterally (1).

52. The skull greatest width-to-midline length in adults is 0.8–1.2 (0), <0.8 (1), >1.2 (2) cm.

53. The postorbital and prefrontal are widely separated (0), near each other with thin projections (1), or sutured, excluding the jugal from the orbital margin (2).

Appendix 2: Analysed taxa

The data includes the source literature (cited parenthetically) and actual specimens studied by one author (JF)

Outgroup

1. *Lydekkerina huxleyi* Lydekker, 1889 (Jeannot et al. 2006)
2. *Rhineceps nyasaensis* Haughton, 1927 (Watson 1962; Schoch and Milner 2000; Damiani 2001)
3. *Uranocentrodon senekalensis* Van Hoepen, 1917 (Schoch and Milner 2000; Damiani 2001; Latimer et al. 2002)

Ingroup

1. *Angusaurus* spp. Getmanov, 1989 (Getmanov 1989; Novikov 1990). Specimens: *A. dentatus* (PIN 4196/1), *A. tsylmensis* (PIN 4333/6)
2. *Benthosuchus sushkini* Efremov, 1929 (Bystrow and Efremov 1940). Specimens: PIN 2424/4, PIN 19-2252, PIN 41-2252, PIN 42-2252, PIN 48-2252, PIN 2424/10
3. *Calmasuchus acri* Fortuny, Galobart, and de Santisteban, present study (Gaete et al. 1993, 1994, 1996, present study). Specimens: IPS-37401 (LM-83, LM-63, LM-101, L and M1)
4. *Cherninia denwai* Mukherjee and Sengupta, 1998 (Mukherjee and Sengupta 1998; Damiani 2001)
5. *Cyclotosaurus robustus* Meyer and Plieninger, 1844 (Schoch and Milner 2000; Schoch 2008)
6. *Edingerella madagascarensis* Lehman, 1961 (Lehman 1961; Warren and Hutchinson 1988; Steyer 2003; Maganuco et al. 2009). Specimens: MNHN MAE 3002, MAE 3003, MAE 3009
7. *Eocyclotosaurus* spp. Ortlam, 1970 (Kamphausen and Morales 1981; Kamphausen 1989; Schoch 2000)
8. *Eryosuchus garjainovi* Ochev, 1966 (Ochev 1966). Specimens: PIN 2865/63, PIN 4166/1/2

9. *Mastodonsaurus giganteus* Jaeger, 1828 (Schoch 1999)
10. *Odenwaldia heilderbergensis* Morales and Kamphausen, 1984 (Morales and Kamphausen 1984; Schoch 2008)
11. *Paracyclotosaurus crookshanki* Mukherjee and Sengupta, 1998 (Mukherjee and Sengupta 1998; Damiani 2001)
12. *Parotosuchus orenburgensis* Konzhukova, 1965 (Welles and Crosgriff 1965; Schoch and Milner 2000; Damiani 2001). Specimens: PIN 951/42
13. *Procyclotosaurus stantonensis* Woodward, 1904 (Paton 1974; Damiani 2001)
14. *Quasicyclotosaurus campi* Schoch, 2000 (Schoch and Milner 2001; Liu and Wang 2005; Schoch 2008)
15. *Stanocephalosaurus birdi* Brown, 1933 (Welles and Cosgriff 1965; Damiani 2001)
16. *Stanocephalosaurus pronus* Howie, 1970 (Howie 1970)
17. *Tatrasuchus wildi* Schoch, 1997 (Schoch 1997; Damiani 2001)
18. *Trematosaurus brauni* Burmeister 1849 (Schoch and Milner 2000). Specimens: MB-Am-593, MB-Am-959, MB-Am-961, MB-Am-964, MB-Am-965
19. *Thoosuchus yakovlevi* Riabinin, 1927 (Damiani and Yates 2003)
20. *Vladlenosaurus alexeyevi* Morkovin and Novikov, 2000 (Morkovin and Novikov 2000)
21. *Watsonisuchus* spp. Ochev 1966 (Warren 1980; Warren and Schroeder 1995; Damiani 2001; Maganuco et al. 2009)
22. *Wetlugasaurus angustifrons* Riabinin, 1930 (Bystrow and Efremov 1940; Welles and Crosgriff 1965; Shishkin et al. 2000). Specimens: PIN 4418/1, PIN 524, PIN 3818/1, PIN 3851/115
23. *Xenotosuchus africanus* Morales and Shishkhin, 2002 (Morales and Shishkhin 2002; Damiani 2008)

Appendix 3: Data matrix

Angusaurus spp.	1110011111	0100111011	1111100010	0010011010	1111100000	010
Benthosuchus sushkini	1100101101	0101110011	0100100011	0011011110	0011000000	010
Calmasuchus acri	0101000?00	11?1?1?101	00001?1011	111????111	0011000000	101
Cherninia denwai	0101100200	1112010000	0000111011	111111111?	?????00101	?10

Cyclotosaurus robustus	0102000200	1111001200	1010111111	1111111111	10??10101	000
Edingerella madagascariensis	010010(01)200	1111100000	00001(01)1010	10010?1101	001?011000	000
Eocyclotosaurus spp.	1102101201	0112111001	1110111111	101111111??	????710001	012
Eryosuchus garjainovi	010110020(01)	1111011100	0000111011	1111111111	1011000110	100
Lydekkerina huxleyi	0110000100	0101000000	0000100001	0010001010	0011000000	000
Mastodonsaurus giganteus	0101001201	1101011101	1000111111	1111111111	1111000110	010
Odenwaldia heidelbergensis	110010020?	?1110?0??1	???????1?	??111?11??	?????00???	?10
Paracyclotosaurus crooshkanki	0101100200	111201010?	100?111111	1111111111	00?1011111	?11
Parotosuchus orenburgensis	0100100200	1112010100	0000111011	1111111111	0011000000	110
Procyclotosaurus stantonensis	1102100200	111201100?	0???1??111	?111111??	????01?01	?1(12)
Quasicyclotosaurus campi	0102101201	0102101001	001011?111	10??0111??	????710001	012
Rhineceps nyasaensis	0000000000	0001000000	0000000000	0000000100	0000000000	000
Tatrasuchus wildi	0101?00200	1111000200	0000111011	1111111111	1111010001	100
Thoosuchus yakovlevi	1100011111	0100110011	0111100000	0010011010	1111000000	010
Trematosaurus brauni	1110011111	0100111070?1	1111??010	01100?1010	1111100000	010
Stanocephalosaurus birdi	0101000200	1112011000	0001111111	1111111111	0011011001	111
Stanocephalosaurus pronus	0101000200	1112011000	0001111111	1111?11111	00?1011001	011
Uranocentrodon senekalensis	0000000000	0000000000	0000000001	0?00000100	0000000000	000
Vladlenosaurus alexeyevi	1100100200	0110010010	01001?1011	1???????11	?11?000000	010
Watsonisuchus spp.	0100100200	1112010010	0000111011	1011111111	0011011000	010
Wetlugasaurus angustifrons	010010020(01)	0111010010	0100111011	0101111111	1011000000	010
Xenotosuchus africanus	0101100200	1111011000	0000111011	11?1111111	0011011100	010

Appendix 4: Character-supported nodes

Node 1

Includes *Rhineceps nyasaensis* + *Eocyclotosaurus*

Unambiguous synapomorphies.—2 (1→0), posterolateral skull corners; 8 (1→0), lacrimal flexure of the infraorbital sensory canal; 12 (1→0), the supratemporal; 25 (1→0), crista muscularis of the parasphenoid; 33 (1→0), posttemporal fenestrae; 37 (1→0), the basioccipital; 39 (1→0), postglenoid area; 43 (1→0), coronoid series; 44 (1→0), prearticular

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Node 2

Trematosauria + Capitosauria. Includes *Benthosuchus sushkini* + *Eocyclotosaurus*

Unambiguous synapomorphies.—16 (0→1), prefenestral division of the palate; 19 (0→1), transvomerine tooth rows; 22 (0→1), cultriform process of the parasphenoid; 29 (0→1), marginal teeth; 36 (0→1), crista muscularis of the parasphenoid; 52 (0→1), skull greatest width-to-midline length

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Remarks.—The clade is well supported by six unambiguous synapomorphies. The prefenestral division of the palate (character 16) is shared by all members of the clade, except node 22 (*Cyclotosaurus* + *Tatrasuchus*). In the latter node, the character is reversed. Similarly, transvomerine tooth rows and the cultriform process of the parasphenoid are reversed in node 9 (*Watsonisuchus* + *Eocyclotosaurus*).

Node 3

Trematosauria. Includes *Benthosuchus sushkini* + *Angusaurus*

Unambiguous synapomorphies.—1 (0→1), snout; 7 (0→1), lateral line sensory canals; 10 (0→1), supraorbital sensory canal; 15 (0→1), nares; 20 (0→1), anterior palatal vacuity

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—5 (0→1), orbital margins; 16 (0→1), prefenestral division of the palate; 19 (0→1), transvomerine tooth rows; 22 (0→1), cultriform process of the parasphenoid; 29 (0→1), marginal teeth; 34 (0→1), tabular horns; 36 (0→1), crista muscularis of the parasphenoid; 52 (0→1), skull greatest width-to-midline length

Remarks.—The narrow and wedge-shaped snout (character 1) found in Trematosauria is also present in node 8 (*Odenwaldia* + *Vladlenosaurus*), although this condition was acquired convergently. In addition, the lateral line sensory canals, supraorbital sensory canal, and nares (characters 7, 10, and 15, respectively) also distinguish node 18 (*Quasicyclotosaurus* + *Eocyclotosaurus*), possibly reflecting similar environments of these taxa instead of a direct phylogenetic relationship.

Node 4

Trematosauroidea. Includes *Thoosuchus yakovlevi* + *Angusaurus*

Unambiguous synapomorphies.—6 (0→1), postorbital–prepineal growth zone; 9 (0→1), occipital sensory canal; 14 (1→0), the postorbital; 23 (0→1), cultriform process of the parasphenoid; 24 (0→1), the ectopterygoid; 30 (1→0), ectopterygoid tusks; 38 (1→0), crista falciformis of the squamosal; 41 (0→1), posterior Meckelian foramen; 42 (0→1), labial wall of the adductor fossa; 45 (0→1), glenoid fossa

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—1 (0→1), snout; 7 (0→1), lateral line sensory canals; 10 (0→1), supraorbital sensory canal; 15 (0→1), nares; 20 (0→1), anterior palatal vacuity

Node 5

Includes *Trematosaurus brauni* + *Angusaurus*

Unambiguous synapomorphies.—3 (0→1), otic notch; 17 (0→1), occipital condyles

Ambiguous synapomorphies under DELTRAN.— none

Ambiguous synapomorphies under ACCTRAN.—5 (1→0), orbital margins; 6 (0→1), postorbital–prepineal growth zone; 9 (0→1), occipital sensory canal; 14 (1→0), the postorbital; 23 (0→1), cultriform process of the parasphenoid; 24 (0→1), the ectopterygoid; 30 (1→0), ectopterygoid tusks; 34 (0→1), tabular horns; 38 (1→0), crista falciformis of the squamosal; 41 (0→1), posterior Meckelian foramen; 42 (0→1), labial wall of the adductor fossa; 45 (0→1), glenoid fossa

Node 6

Capitosauria. Includes *Wetlugasaurus angustifrons + Eocyclotosaurus*

Unambiguous synapomorphies.—8 (1→2), lacrimal flexure of the infraorbital sensory canal; 13 (0→1), preorbital projection of the jugal; 26 (0→1), crista muscularis of the parasphenoid; 27 (0→1), "pockets"; 32 (0→1), the quadratojugal; 35 (0→1), oblique ridge of the pterygoid; 40 (0→1), hamate process of the prearticular

Ambiguous synapomorphies under DELTRAN.—5 (0→1), orbital margins; 34 (0→1), tabular horns

Ambiguous synapomorphies under ACCTRAN.—5 (0→1), orbital margins; 16 (0→1), prefenestral division of the palate; 19 (0→1), transvomerine tooth rows; 22 (0→1), cultriform process of the parasphenoid; 29 (0→1), marginal teeth; 34 (0→1), tabular horns; 36 (0→1) crista muscularis of the parasphenoid; 52 (0→1) skull greatest width-to-midline length

Remarks.—Seven unambiguous synapomorphies support the capitosaur clade. The lacrimal flexure of the infraorbital sensory canal (character 8) is absent in most Mesozoic temnospondyls and all Palaeozoic temnospondyls in which sensory canals are present (Damiani 2001). The lacrimal is step-shaped in groups such as lyddekerinds or trematosaurs, in contrast to the typical Z-shaped morphology in most capitosaurs. The quadratojugal relation with the upper jaw condyle is reversed in nodes 11 (*Edingerella + Watsonisuchus*) and 18 (*Quasicyclotosaurus + Eocyclotosaurus*).

Node 7

Includes *Odenwaldia heidelbergensis + Eocyclotosaurus*

Unambiguous synapomorphies.—31 (0→1), denticle field

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Node 8

Includes *Odenwaldia heidelbergensis + Vladlenosaurus alexeyevi*

Unambiguous synapomorphies.—1 (0→1), snout

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—42 (0→1), labial wall of the adductor fossa.

Remarks.—The snout morphology (character 1) is the most similar to nodes 3 (Trematosauria) and 4 (Trematosauroidea), possibly reflecting different ecomorphotypes present in the capitosaur clade.

Node 9

Includes *Watsonisuchus + Eocyclotosaurus*

Unambiguous synapomorphies.—11 (0→1), the frontal; 19 (1→0), transvomerine tooth rows; 22 (1→0), cultriform process of the parasphenoid

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Remarks.—The frontal enters medial to the orbit (character 11) in this node, in clear contrast to node 18 (*Quasicyclotosaurus + Eo-*

cyclotosaurus). In this latter node, the frontal is excluded from the orbital margin. On the other hand, the orientation of the transvomerine tooth rows (character 19) and the polarity of the cultriform process of the parasphenoid (character 22) are reversed in comparison with node 2 (Capitosauria + Trematosauria).

Node 10

Includes *Edingerella madagascarensis + Eocyclotosaurus*

Unambiguous synapomorphies.—46 (0→1) Parietal, supratemporal and postparietal; 47 (0→1) Postparietal, tabular, parietal and supratemporal

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Remarks.—The condition present in the size relation between parietal, supratemporal and postparietal (character 46) is comparable with node 22 (*Cyclotosaurus + Tatrasuchus*).

Node 11

Includes *Edingerella madagascarensis + Watsonisuchus*

Unambiguous synapomorphies.—32 (1→0), the quadratojugal

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Remarks.—The quadratojugal relation with the upper jaw condyle (character 32) is reversed, in contrast to the condition found in node 6.

Node 12

Includes *Xenotosuchus africanus + Eocyclotosaurus*

Unambiguous synapomorphies.—4 (0→1), tabular horns; 48 (0→1), interpterygoid vacuities

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Remarks.—The morphology of the tabular horns (character 4) is considered an ordered character. Tabular horns are laterally directed in all members of the clade, except node 17 (*Procyclotosaurus + Eocyclotosaurus*). In these cases, the character is also considered derived because the tabular sutures with the squamosal. On the other hand, the laterally directed horns were acquired independently in node 20 (*Calmasuchus + Mastodonsaurus*). The derived condition is also found in *Cyclotosaurus*, where the tabular contacts the squamosal.

Node 13

Includes *Cherninia denwai + Eocyclotosaurus*

Unambiguous synapomorphies.—14 (1→2), the postorbital; 50 (0→1), the squamosal

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Remarks.—The postorbital expansion (character 14) is reversed in Trematosauroidea (node 4), and the same morphology of the posterior margin of the squamosal (character 50) is also present in node 22 (*Cyclotosaurus + Tatrasuchus*).

Node 14

Includes *Paracyclotosaurus crookshanki + Eocyclotosaurus*

Unambiguous synapomorphies.—28 (0→1), the exoccipital; 53 (0→1), postorbital and prefrontal location

Ambiguous synapomorphies under DELTRAN.—none

Ambiguous synapomorphies under ACCTRAN.—none

Node 15

Includes *Stanocephalosaurus pronus + Eocyclotosaurus*

Unambiguous synapomorphies.—17 (0→1), occipital condyles; 48 (1→0), interpterygoid vacuities

Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—none
Remarks.—The placement of the occipital condyles in this node is similar to node 4 (Trematosauroidea). The polarity of the interpterygoid vacuities is reversed in contrast to node 12 (*Xenotosuchus + Eocyclotosaurus*).

Node 16

Includes *Stanocephalosaurus pronus + Stanocephalosaurus birdi*
Unambiguous synapomorphies.—5 (1→0), orbital margins; 24 (0→1), the ectopterygoid
Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—none
Remarks.—The condition of the orbital margins (character 5) is reversed in this node. The same polarity is present in node 20 (*Calmasuchus + Mastodonsaurus*). Otherwise, the ectopterygoid is similar to that in node 4 (Trematosauroidea).

Node 17

Includes *Procyclotosaurus stantonensis + Eocyclotosaurus*
Unambiguous synapomorphies.—4 (1→2), tabular horns
Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—1 (0→1), snout; 20 (0→1), anterior palatal vacuity; 23 (0→1), cultriform process of the parasphenoid; 53 (1→2), postorbital and prefrontal location
Remarks.—As previously discussed, the tabular horn in this node contacts the squamosal, resulting in an embayment. This morphology is shared with the genus *Cyclotosaurus*. Our analysis suggests that this morphology was acquired independently in the two nodes.

Node 18

Includes *Quasicyclotosaurus campi + Eocyclotosaurus*
Unambiguous synapomorphies.—7 (0→1), lateral line sensory canals; 10 (0→1), supraorbital sensory canal; 11 (1→0), the frontal; 15 (0→1), nares; 32 (1→0), the quadratojugal; 47 (1→0), the postparietal, tabular, parietal, and supraparietal
Ambiguous synapomorphies under DELTRAN.—20 (0→1), anterior palatal vacuity; 23 (0→1), cultriform process of the parasphenoid; 53 (1→2), postorbital and prefrontal location
Ambiguous synapomorphies under ACCTRAN.—none
Remarks.—The lateral line sensory canals (character 7) are continuous and well impressed in this node. Most capitosaurs show discontinuous and weak-impressed lateral lines. The condition present in this node is similar to that of nodes 3 (Trematosauria) and 4 (Trematosauroidea). On the other hand, the same polarity of the supraorbital sensory canal (character 10) is also shared by nodes 3 (Trematosauria), 4 (Trematosauroidea), 18 (*Quasicyclotosaurus + Eocyclotosaurus*), and 23 (*Eryosuchus + Mastodonsaurus*). Although the phylogenetic analysis revealed the character as significant, the high degree of plasticity of this character is attributable to its intraspecific variation (see Damiani 2001 for further details). The polarity of the frontal, quadratojugal, and postparietal, tabular, parietal, and supraparietal characters (characters 11, 32, and 47, respectively) are reversed. The morphology of the nares (character 15) is similar to that of nodes 3 (Trematosauria) and 4 (Trematosauroidea). The evolution of the frontal bone in relation to the orbit (character 11) needs a comment. Damiani (2001) considered that the frontal bone was excluded from the orbital margin in *Odenwaldia*. This is the same condition present in *Eocyclotosaurus* and *Quasicyclotosaurus*, and was discussed by the author as one of the key characters to infer a relationship between *Odenwaldia* and *Eocyclotosaurus*. Nevertheless, in the re-

cent revised description of *Odenwaldia*, Schoch (2008) codified this character as missing data. He did not find a clear relationship between these taxa. In the present analysis, the addition of *Vladlenosaurus* provides new light to this discussion. In the Russian taxa, the frontal is clearly excluded from the orbital margins. Nevertheless, our cladistic analysis reveals the relationship between *Odenwaldia* and *Vladlenosaurus*. In contrast, any relationship can be assessed with *Eocyclotosaurus* or *Quasicyclotosaurus*.

Node 19

Includes *Parotosuchus orenburgensis + Mastodonsaurus giganteus*
Unambiguous synapomorphies.—18 (0→1), choanal outline; 51 (0→1), postglenoid area outgrowth
Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—none

Node 20

Includes *Calmasuchus acri + Mastodonsaurus giganteus*
Unambiguous synapomorphies.—4 (0→1), tabular horns; 5 (1→0), orbital margins; 52 (0→1), skull greatest width-to-midline length
Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—17 (0→1), occipital condyles
Remarks.—The tabular horns (character 4) are laterally directed in the members of this node, as previously discussed for node 12 (*Xenotosuchus + Eocyclotosaurus*). *Cyclotosaurus* is the unique member of this node displaying the tabular in contact with the squamosal. The condition of the orbital margins (character 5) is reversed.

Node 21

Includes *Cyclotosaurus robustus + Mastodonsaurus giganteus*
Unambiguous synapomorphies.—41 (0→1), posterior Meckelian foramen
Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—48 (0→1), interpterygoid vacuities
Remarks.—The posterior Meckelian foramen is elongated and comparable to that of trematosaurs, possibly reflecting higher adductor musculature in these taxa, instead of a phylogenetic relationship.

Node 22

Includes *Cyclotosaurus robustus + Tatrasuchus wildi*
Unambiguous synapomorphies.—16 (1→0), prefenestral division of the palate; 18 (1→2), choanal outline; 46 (0→1), the parietal, supratemporal, and postparietal; 50 (0→1), the squamosal
Ambiguous synapomorphies under DELTRAN.—none
Ambiguous synapomorphies under ACCTRAN.—none
Remarks.—The prefenestral division of the palate (character 16) is reversed. The choanal outline (character 18) is slit-like in the members of node 19 (*Parotosuchus + Mastodonsaurus*), evolving to circular or subcircular morphology in this node (*Cyclotosaurus + Tatrasuchus*). The condition found at the posterior margin of the squamosal is also present in node 13 (*Cherninia + Eocyclotosaurus*).

Node 23

Includes *Eryosuchus garjainovi + Mastodonsaurus giganteus*
Unambiguous synapomorphies.—49 (0→1), the parasphenoid
Ambiguous synapomorphies under DELTRAN.—17 (0→1), the occipital condyles; 48 (0→1), the interpterygoid vacuities
Ambiguous synapomorphies under ACCTRAN.—10 (0→1), the supraorbital sensory canal