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TOOTH MORPHOTYPES SHED LIGHT ON THE PALEOBIODIVERSITY OF MIDDLE TRIASSIC TERRESTRIAL VERTEBRATE ECOSYSTEMS FROM NE IBERIAN PENINSULA (SOUTHWESTERN EUROPE)

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Abstract. The Early to Middle Triassic is a key time interval in tetrapod evolution. After the end-Permian biotic crisis, harsh environmental conditions due to global warming and aridity persisted during the Early Triassic. This led to an impoverished biodiversity, especially in equatorial Pangea, until the Middle Triassic, when vertebrate ecosystems re-flourished. The terrestrial European record is characterized by tetrapod communities dominated by temnospondyls and archosauromorphs, followed by a limited presence of lepidosauromorphs, procolophonomorphs and therapsids. Ongoing paleontological sampling at the Anisian Buntsandstein facies of northeastern Iberian Peninsula (southwestern Europe) provides new insights on the vertebrate biodiversity at equatorial paleolatitudes. The Montseny area (Catalan Coastal Ranges) has delivered moderately abundant cranial and postcranial remains in the last decades. Among the known record, dental, mandibular and cranial remains are particularly relevant because they provide information on the dietary habits. In the present work, eight tooth morphotypes have been identified: two correspond to a capitosaur temnospondyl, one to an archosauromorph, one to an indeterminate diapsid and four to a procolophonid, the latter material referred to a single new taxon, *Kapes signus* sp. nov. These finds help to fill a gap in the early Middle Triassic vertebrate biodiversity and distribution in present-day southwestern Europe. Based on dentognathic remains, the oldest Middle Triassic terrestrial tetrapod ecosystems from northeastern Iberia were dominated by capitosaur temnospondyls, followed by much less abundant archosauromorphs, procolophonids and indeterminate diapsids. This contrasts with the ichnotaxonomical composition of the study area, denoting paleoenvironmental and/or taphonomic biases in the dental and osteological record.

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INTRODUCTION

The Triassic represents a period of restructuring and reorganization of the Paleozoic ecosystems. The Permian–Triassic transition was marked by the most severe crisis in the history of life, characterized by extreme global warming and aridity (Benton & Newell 2014; Dal Corso et al. 2022). The first Triassic assemblages after the biotic crisis show impoverished ecosystems, especially in equatorial Pangea, whereas diversity increased in high latitudes because of a poleward migration of faunas (Allen et al. 2020). These migrations allowed a global distribution of the so-called disaster taxa, at least in the immediate aftermath of the end-Permian mass extinction (EPME) (Button et al. 2017; Romano et al. 2020).

Apparent low biodiversity in tetrapod assemblages in equatorial Pangea is supported in Europe by the intensive sampling performed in Lower–Middle Triassic red-bed terrestrial series. These deposits correspond to the Buntsandstein facies, in which direct tetrapod remains are almost absent in the lower part and become more common in the middle and upper sections, dated as late Early to early Middle Triassic (Romano et al. 2020). The Lower to Middle Triassic terrestrial successions of the Buntsandstein facies from central Europe show tetrapod communities characterized by archosauromorph-dominated eureptile assemblages on land and temnospondyls on aquatic and semi-aquatic environments, followed by less abundant terrestrial faunas like lepidosauromorphs, therapsids and procolophonomorphs (Romano et al. 2020). The adaptive radiation of these groups resulted in the appearance of the ancestors of modern tetrapod groups (Chen & Benton 2012; Romano et al. 2020, and references therein).

The Triassic tetrapod record from southwestern Europe, particularly from the Iberian Peninsula and largest Balearic Islands (as they are an extension of the southern Iberian Betic Cordillera to the northeast), has increased in the last decades after multiple paleontological and geological field campaigns (Fortuny et al. 2011a; Mujal et al. 2016, 2017; De Jaime-Soguero et al. 2021; Matamales-Andreu et al. 2021). On the one hand, tetrapod ichnological assemblages reveal that paleobiodiversity, when relying on the osteological record alone, is clearly incomplete (Fortuny et al. 2011a; Mujal et al. 2016, 2017; De Jaime-Soguero et al. 2021; Matamales-Andreu et al. 2021). On the other hand, osteological remains and especially teeth, despite reflecting only part of the biodiversity, are key to understand ecological relations. Thus, considering both osteological and ichnological records, a more complete (and complex) picture of the southwestern European Triassic ecosystems is obtained.

This work is primarily focused on the dentognathic record from the Montseny area (Catalonia, NE Iberian Peninsula; Fig. 1), which forms an exception (Calzada 1987; Valdiserri et al. 2009; Fortuny et al. 2011a, 2011b, 2014; Ezcurra et al. 2017) regarding the overall scarcity of remains of bones and teeth known from Iberian terrestrial successions of the Buntsandstein facies. Particularly, the site of La Mora, discovered in 1989, has provided hundreds of bones collected during different paleontological surveillances. A large number of dentognathic elements (both isolated teeth and teeth associated with cranial/mandibular bones) has been recovered. First interpretations attributed all these specimens to capitosaur temnospondyls (Gaete et al. 1993, 1996), in contrast with the tetrapod ichnofossils from the area, which are mostly referred to small and large archosauromorphs, potential therapsids, procolophonomorphs and lepidosauromorphs (Fortuny et al. 2011a). In similar manner, recent works dealing with dentognathic material from La Mora site showed the presence, even if in lesser proportion, of archosauromorphs (Ezcurra et al. 2017). Finally, in the nearby site of Corral d'en Perera, herein renamed as Corral d'en Pla de Brugues and located around 1.5 km southward from La Mora site, a tooth-bearing mandible was identified as a potential procolophonid parareptile (Fortuny et al. 2014).

The aim of this work is to study the dentognathic record from the lower Middle Triassic (Anisian) Buntsandstein facies of the Montseny area (NE Iberian Peninsula) in order to identify tooth morphotypes that aid in the reconstruction of paleobiodiversity and paleoecological relations of members of the assemblage. For that reason, a database was constructed in order to classify tooth morphologies and attachment types of each morphotype. Potential paleoenvironmental, taphonomic and sampling biases are evaluated by confronting the osteological and ichnological record. Overall, this work aims at filling a gap on the knowledge of the Middle Triassic tetrapod communities of equatorial Pangea.

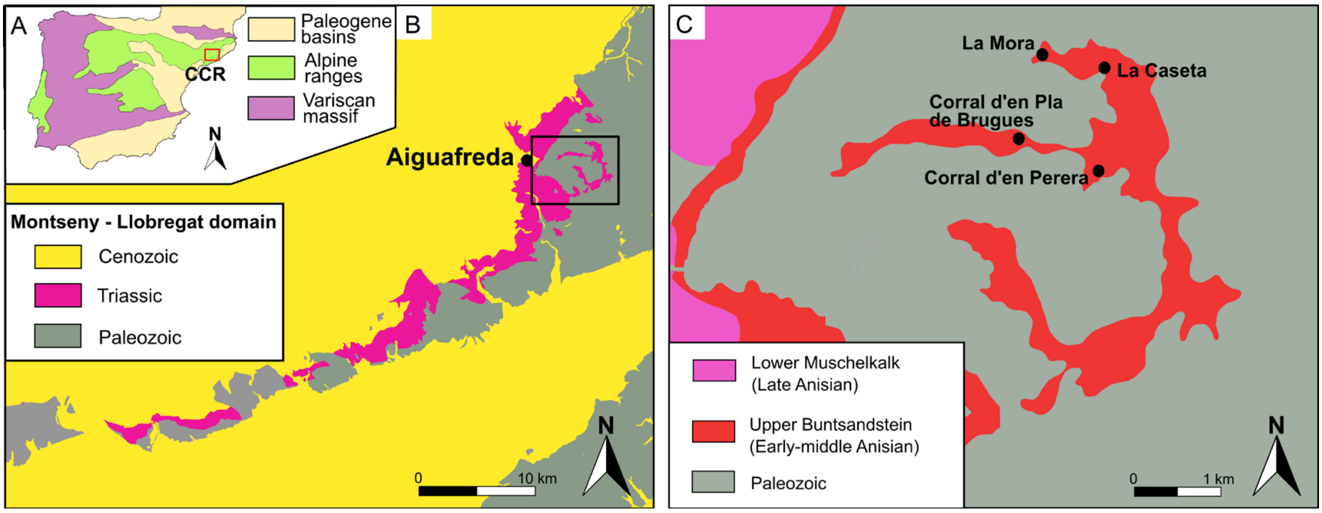

Fig. 1 - Geographical and geological setting. A) Location of the Catalan Coastal Ranges (CCR) in the Iberian Peninsula (Modified from Escudero-Mozo et al. 2015). B) Simplified geological map of the Montseny-Llobregat domain. Aiguafreda refers to nearby town. C) Detailed geological map of the study zone in the Montseny area (square in B) with main fossiliferous sites. Maps in B and C redrawn and adapted from www.icgc.cat.

Geological setting

The sedimentary successions from the Triassic of NE Iberian Peninsula (southwestern Europe) record a shift to an extensional tectonic regime following the compressive tectonics originated during the Variscan orogeny (Galán-Abellán et al. 2013; Gretter et al. 2015). At the end of the Permian and the beginning of the Triassic the Iberian plate was located in the central-eastern side of equatorial Pangea, between Laurasia and Gondwana landmasses, in the Western peri-Tethys domain (Gretter et al. 2015). The Catalan Basin, located in the present-day Catalan Coastal Ranges (Catalonia; Fig. 1A), started its development as a result of the widespread extension of the Iberian plate, creating a NE-SW oriented rift basin with a conjugate NW-SE fault system (Galán-Abellán et al. 2013). In the Catalan Basin, this rifting process created three isolated grabens or domains separated by Paleozoic highs: Prades, Garraf and Montseny-Llobregat, which were infilled with terrestrial sediments during the latest Permian–Middle Triassic (Galán-Abellán et al. 2013). These sub-basins had different subsidence rates, and thus a different evolution and sedimentary record. The facies that build up the Triassic, although diachronic, are equivalent to those observed in most of Europe, the so-called Germanic facies (Buntsandstein, Muschelkalk and Keuper) (Calvet & Marzo 1994). Their age varies due to the non-contemporary sedimentation related to the expansion of the continental rifting, from northern to southern Europe, and the infilling of the different depocenters (Calvet & Marzo 1994). Therefore, the red-beds of the Buntsandstein facies represent the first phase of detrital sedimentation of the Mesozoic rifting, with deposits overlaying the Paleozoic basement in angular unconformity. The nature of the materials is similar everywhere: alluvial fan deposits composed of conglomerates with well-rounded quartz pebbles in the most proximal part, which constitute the base of the Triassic series. The middle and distal parts of the alluvial system are composed of reddish sandstones and mudstones of meandering fluvial systems, and very fine-grained sandstone and mudstone deposits in the floodplain areas (Calvet & Marzo 1994). The Buntsandstein facies are divided in three units in the Catalan Basin (Virgili 1958): a) lower Buntsandstein, mainly composed of oligomictic conglomerates and breccias (dominated by quartz clasts); b) middle Buntsandstein, composed of reddish sandstones, characterized by the presence of cross-bedded stratification; c) upper Buntsandstein, mainly composed of red mudstones with intercalated layers of evaporites (representing the so-called Röt facies, in transition with the Muschelkalk facies).

From the three Triassic grabens or sub-basins that formed the Catalan Basin, Buntsandstein vertebrate remains are mainly known from the Montseny-Llobregat domain (Fortuny et al. 2011a, 2011b, 2014; Ezcurra et al. 2017; Fig. 1B).

The Lower Triassic is almost absent in this domain, likely only represented in the Riera de Sant Jaume section (Dinarès-Turell et al. 2005). In the study area, however, the presence of a sedimentary high has been interpreted (Marzo 1980; Galán-Abellán et al. 2013), and thus sedimentation did not start until the early Anisian (early Middle Triassic) (Calvet & Marzo 1994). The Buntsandstein depositional sequence is overlain by the first marine transgression units, represented by the Muschelkalk facies, deposited during the middle–late Anisian (Calvet & Marzo 1994). The basement is usually overlain by the basal conglomerates of the lower Buntsandstein facies, although when these are absent, the contact is directly with the upper Buntsandstein facies, which correspond to two sequences of sandstones at the base and red mudstones at the top (Marzo 1980). These materials are interpreted as fluvial successions deposited under a semi-arid climate that derived from the erosion of the Iberian Massif, and show a thickness increase from the NE to the SW (Calvet & Marzo 1994; Galán-Abellán et al. 2013).

The studied tetrapod remains come from the upper Buntsandstein, lying only a few meters above the Paleozoic contact, because of the aforementioned sedimentary high of the region (Marzo 1980; Galán-Abellán et al. 2013). The study area includes La Mora site and other neighboring localities (Fig. 1C) that have yielded vertebrate remains (including bones, teeth and traces) corresponding to aquatic, semiaquatic and terrestrial herpetofauna, mainly temnospondyls, but also archosauromorphs and procolophonids; invertebrate trace fossils have also been found (Fortuny et al. 2011a). The paleoenvironment has been interpreted as a large muddy floodplain containing meandering fluvial channels with paleosols developed on top (Fortuny et al. 2011b). This broadly corresponds to an endorheic alluvial system developed in the interdune areas of aeolian dune fields (Galán-Abellán et al. 2013; Borruel-Abadía et al. 2015). The age of the deposits has been constrained to the early–middle Anisian using palynomorph and macroflora assemblages, "conchostracan" (clam shrimp) invertebrates, magnetostratigraphy, and radioisotopic dating methods (Visscher 1967; Marzo & Calvet 1985; Solé de Porta et al. 1987; Gómez-Gras 1993; Calvet & Marzo 1994; Díez et al. 2005; Dinarès-Turell et al. 2005).

MATERIAL AND METHODS

Sampling and data acquisition

In order to collect data, material recovered during different fieldwork campaigns has been examined and prepared when required at the lab facilities of the Institut Català de Paleontologia Miquel Crusafont (ICP). The studied material was mainly recovered in the excavation campaigns in La Mora site from 1990, 2008 and 2010, and the prospecting campaigns in the Montseny area (including La Mora site) from 2009, 2018, 2019 and 2020. All surveillances were performed with the legal permits, issued by the Departament de Cultura of the Generalitat de Catalunya (Catalan Government). In addition, previously recovered material by other teams has also been reviewed. In sum, up to 37 tooth bearing bones and 736 teeth (of which 150 have been measured) have been studied first-hand.

The reexamination of different localities from the Montseny area away from La Mora site has allowed to redefine the formerly named Corral d'en Perera site. The locality of Corral d'en Perera yielded tetrapod footprints and was originally reported by Calzada (1987). However, newly recovered bony fossils (herein studied) from nearby areas (namely, Corral d'en Pla de Brugues and Pedrera de Can Perera) call for a refinement of the toponymy of the fossiliferous beds. The specimen studied by Fortuny et al. (2014), here reviewed, was originally reported as recovered nearby to Corral d'en Perera, whereas this study locates it at Corral d'en Pla de Brugues, a site that has delivered additional specimens in the most recent field campaigns (Fig. 1C, Tab. S1).

Teeth were photographed, counted and described, also accounting additional relevant information (Tab. S1): location in the tooth-bearing bones, side of measurement (most of them have one side still embedded in sedimentary matrix), shape and form, size parameters (apicobasal height of crown, labiolingual and mesiodistal lengths at the crown base), type of attachment, enamel textures, and preservation. The presence of potential macroscopic wear facets was also evaluated in order to complement the morphological descriptions. Only teeth that preserve relevant information were included in the sample. Measurements were taken using an electronic digital caliper with a maximum deviation of 0.02 mm, but the measurements were rounded to the nearest 0.1 mm. When required, specimens were examined and photographed with a Leica M80 microscope, with a camera attached model MC170 HD by using the software Leica Application Suite v.4.10.0. In some specimens, focus stack images were obtained with a Nikon d610 camera, Sigma 105 mm f2.8 EX macro lens, and Kenko extension tubes. The stacking process was performed in Adobe Photoshop CC v.19.1.5. One specimen (IPS124305) was scanned by X-ray µtomography at the CENIEH (Burgos, Spain) to explore the basal section of the teeth; parameters of the µCT-Scan were as follow: 110 mA current and 220 kV voltage, 0.5 mm Cu filter, and a magnification of 8.16. The final reconstructed volumes have an isometric voxel size of 24 µm. Also, photogrammetric three-dimensional (3D) models of selected samples were obtained following the procedures of Falkingham (2012), Mallison & Wings (2014) and Mujal et al. (2020), being produced with Agisoft Metashape (Professional edition, educational version, v.1.8.3) to generate the mesh and the texture, and further edited in MeshLab (v.2020.07). These 3D models are freely available in PLY format in Morphosource repository (see Data Availability section below).

Terminology

Since dental terms are widely used and usually differ between vertebrate groups, this study follows: Smith & Dodson (2003), to describe the general traits of tooth morphology and orientation; Warren & Davey (1992), for the specific features of temnospondyl dentition; Bertin et al. (2018), to describe the different types of tooth implantation of amphibians and reptiles. The terms for tooth macroscopic wear follow those of Mujal et al. (2022) (see Tab. S1).

Institutional abbreviations

IPS, Institut Català de Paleontologia Miquel Crusafont (formerly Institut de Paleontologia de Sabadell), Sabadell, Catalonia, Spain. **MGSB**, Museu Geològic del Seminari Conciliar de Barcelona, Barcelona, Catalonia, Spain.

ZooBank registration of new name

A new taxon name has been registered in ZooBank (http://zoobank.org) in order to comply with the rules of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) for electronic publications (article 8.5.3). The LSID for this publication is: lsid:zoobank.org:act:9D693C78-67EF-476B-9752-4950B554C0BA

RESULTS

Up to eight tooth morphotypes have been identified. Tooth morphotypes do not imply different taxonomical nature as different morphotypes may be linked to a single taxon due to heterodonty (changes in shape along the tooth row) or ontogenetic variation. Considering that isolated teeth are common, individual descriptions grouping them in morphotypes are required.

Temnospondyli Zittel, 1890
(sensu Milner 1990)
Stereospondyli Zittel, 1890
(emend. Fraas, 1889)
Capitosauria Yates & Warren 2000
(sensu Damiani & Yates, 2003)

Calmasuchus acri Fortuny, Galobart & De Santisteban, 2011b

Fig. 2

Material description (Fig. 2):

IPS37401 (LM-83), holotype based on a partial skull.

IPS42407 (LM-4), paratype, a complete hemimandible.

The following slabs correspond to the collection number IPS37401:

G: Small skull fragment exposed in occlusal view.

M1: Posterior end of a hemimandible exposed in lingual view.

O1: Small isolated tooth exposed in lingual view displaying well marked xiphodonty. The tip is missing.

U1: Middle portion of a small hemimandible in labial view.

MB: Slab forming a bone bed containing two partial hemimandibles exposed in lateral view, one partial maxilla in dorsal view and a portion of a premaxilla in palatal view.

MC: An almost complete hemimandible exposed in labial side and an anterior end of a second hemimandible, probably from the same individual.

MA-1: Almost complete hemimandible (only the anterior end is missing) exposed in lingual view.

SAH: Anteriormost part of a small dentary exposed in labial view.

GA: Anterior end of a small dentary exposed in labial view.

GQ: Partial hemimandible in occlusal view.

IPS37401i: Small maxilla embedded in the matrix exposed in palatal view and partially covered by sediment.

IPS37401M slab **SM**: Small anteriormost part of a dentary exposed in labioapical view.

IPS37401N slab **SN**: Antero and middle portion of a medium-size hemimandible in labial view.

IPS44931: Isolated fragment of the anterior part of a hemimandible.

IPS128400: Middle portion of a partial hemimandible exposed in lingual view.

IPS137834: Small fragment of the middle part of a hemimandible mandible.

IPS137870: Isolated middle portion of a hemimandible.

IPS137900: Isolated middle part of a small/medium hemimandible.

IPS137901: Isolated middle portion of a hemimandible.

IPS137902: Isolated middle part of a medium hemimandible.

IPS137912: Two isolated fragments of the anterior part of a hemimandible.

IPS137922: Isolated left vomer.

IPS137928: Almost complete hemimandible.

IPS137929: Anteriormost part of a hemimandible

IPS137931: Isolated anteriormost part of a toothless mandible.

IPS137933: Linked with slab MA-1. Small anterior hemimandible fragment exposed in lingual view.

IPS137934: Fragment of the middle portion of a hemimandible exposed in labial view.

Morphotype T1: Small conical teeth

Fig. 2A–F

Material: A few isolated teeth (IPS124297, IPS37401 slab O1) and, mainly, teeth attached to dentigerous bones (IPS37401: slabs D, G, M1, U1, MB, MC, MA-1, GA, GQ, SN, SAH, SH2-1, SA2-1, IPS37401i: slab SI; IPS42407 (LM-4), IPS137834, IPS137859, IPS137870, IPS137900, IPS137901, IPS137902, IPS137912, IPS137922, IPS137928, IPS137929, IPS137930, IPS44931).

Description. Small (crown heights ranging from 4 to 10 mm), conical and labiolingually gently curved to curved teeth. Cross section at the base round to elliptical, with the long axis of the ellipse oriented perpendicular to the jaw line (Warren & Davey 1992) (Fig. 2). The base of the crown shows an ornamentation consisting of apicobasal (longitudinal) grooves, corresponding to the external expression of the inner plicidentine, as revealed by sectioned teeth. Therefore, the basal cross section reveals that the infolding of the enamel derives from the labyrinthodont condition, while the middle-apical cross section is more massive, showing only the pulp cavity in most cases.

This morphotype shows small variations in shape depending on the location in the oral cavity (Fig. 2A, B), and presumably on the ontogenetic stage (see discussion in "capitosaur taxonomic implications" below). The dentary teeth (e.g., IPS37401n slab SN; Fig. 2C–C") show: elliptical cross section at the base, with the long axis oriented labiolingually; from the middle part of the crown to the tip, the cross section becomes circular; towards the tip, it is elliptical again, aligned with the tooth row. As a result, the apex shows a labiolingually weak compression, and a straight shape, being gently curved lingually (Fig. 2C"). On the contrary, premaxillary teeth (IPS37401 MB; Fig. 2D–D') preserve the circular cross section from the medial part to the tip, resulting in a more conical apex, whereas they are elliptical at the base. The degree of curvature of the tooth crown is also higher in premaxillary series. The palatal teeth (Fig. 2E–E') are mainly located in the vomerine region (IPS124297). Teeth in the parachoanal and interchoanal tooth rows display a pronounced curvature in comparison with the marginal series, and they retain the circular section from the medial part of the crown to the tip. No apical part of teeth belonging to the marginal series of the skull roof are preserved *in situ*, thus their shape is unknown.

Some series of teeth have sharp keels in distal and mesial carinae (indicating xiphodonty *sensu* Warren & Davey 1992; Fig. 2F–F'). This condition is mainly observed in small specimens (IPS37401i, slab SI; IPS44931, IPS37401O1 and IPS137929 This morphotype displays both acrodont and pleurodont implantation types (Warren & Davey 1992).

The mandible and marginal tooth rows of the skull present a pleurodont implantation type, whereas implantation in the palatal tooth rows is acrodont. Implantation correlates with the basal section, circular in the acrodont and more oval to elliptical in the pleurodont condition (although individual variations may occur, thus a general rule should not be assumed, e.g., IPS124297). The marginal teeth are usually anteroposteriorly compressed at the base, as reported for temnospondyls by Warren & Davey (1992). Regarding the general shape, the crowns also show some differences depending on their location on the oral cavity: dentary teeth seem to be less curved labiolingually than those located in the premaxilla. In the palatal dentition, elements are more curved and conical, pointing lingually, with the interchoana row perpendicular to the long axis of the jaws with the teeth pointing anteroposteriorly, and the parachoanal tooth rows situated parallel to the jaw line, being strongly curved lingually.

Xiphodont teeth display sharp carinae in mesial and distal sides, always without denticles. Those teeth are gently compressed labiolingually and present an "eye-shaped" cross section. This variation is observed in small individuals (e.g., IPS37401i slab SI).

Morphotype T2: Large conical teeth (tusks)

Fig. 2A, B, G

Material: Five isolated teeth (IPS124298, IPS124299, IPS124300, IPS124303 and MGSB41387), and several fragmentary teeth still attached to the tooth-bearing bones mainly consisting of the most basal part of the tooth (IPS42407 (LM-4), IPS137922 and IPS37401 in slab MB).

Description. Labyrinthodont teeth, very similar in shape to Morphotype T1, but notably

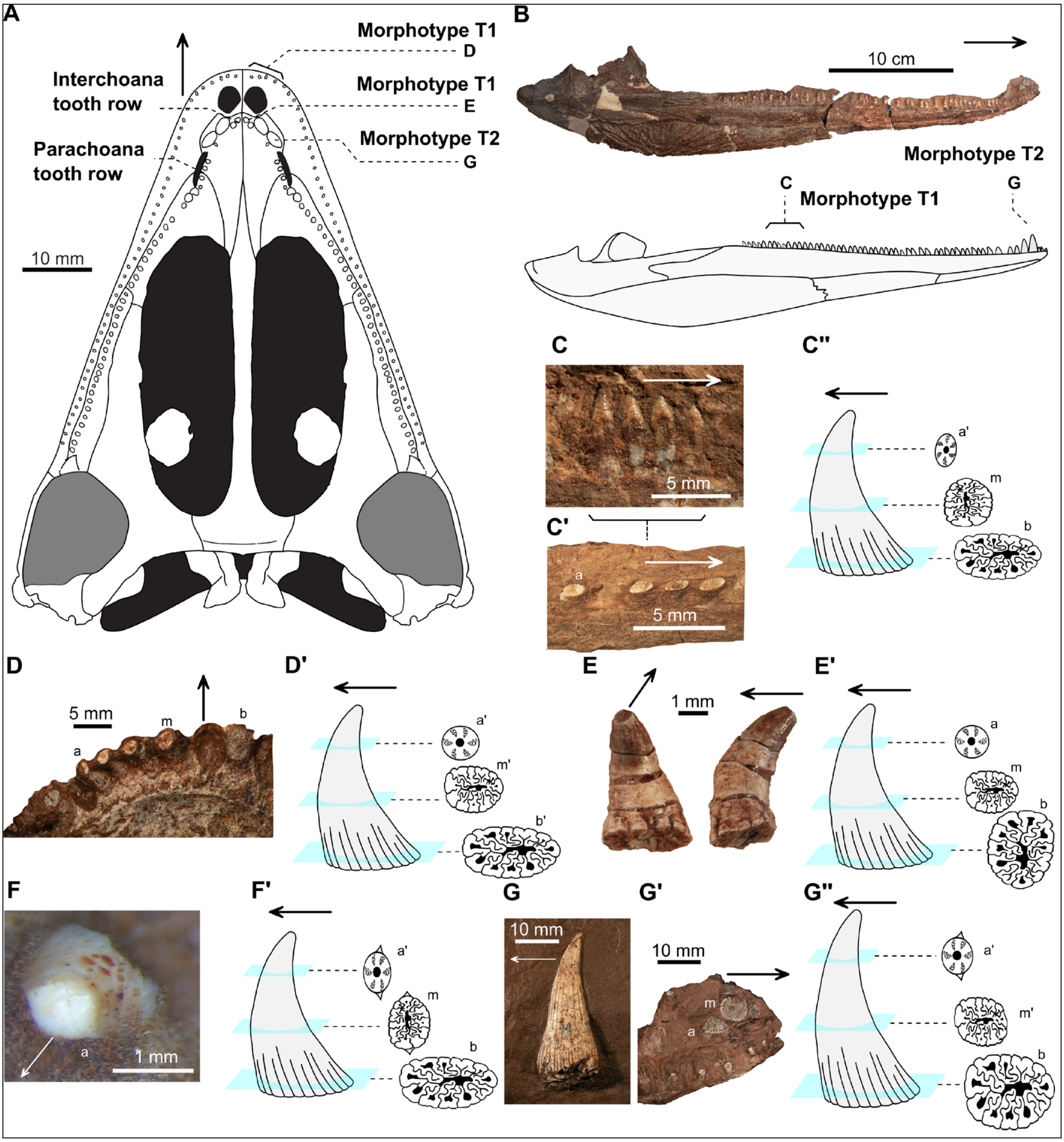

Fig. 2 - Capitosaur temnospondyl teeth, Morphotypes T1 and T2. A) Skull reconstruction of *Calmasuchus acri* in palatal view (modified from Fortuny et al., 2011b). B) IPS42407 (LM-4), paratype, complete hemimandible of *C. acri* (above) and schematic reconstruction of a hemimandible (below) (modified from Fortuny et al., 2011a). C–F'. Small conical teeth, Morphotype T1. C) IPS37401n (slab SN), posterior fragment of a mandible in labial view. C'. Same fragment of mandible as in C, but from more posterior part of the specimen, with teeth sectioned in the apical portion in occlusal view. C". Schematic tooth of Morphotype T1 with apical (a), middle (m) and basal (b) cross sections. D) IPS37401 slab MB, right premaxilla in palatal view, showing different cross sections of broken teeth as in the schematic tooth D'. D'. Schematic tooth as in C". E) IPS124297, isolated palatal tooth in distal (left) and lateral (right) views. E'. Schematic tooth as in C". F) IPS37401 O1, isolated xiphodont tooth in occlusal view; note the sharp carinae in apical (a) cross section. F'. Schematic tooth as in C". G–G". Large conical teeth, Morphotype T2. G) IPS124299, isolated tusk in lateral view. G'. IPS42407 (LM-4), anterior part of a right hemimandible in occlusal view with detail of the pair of tusks in cross section as in the schematic tooth in G"; note the different sizes of the tusks, being cut in different cross sections. G". Schematic tooth of Morphotype T2 with cross sections as in C". In all photos and drawings arrows point anteriorly (except in C", where the arrow points labially). Schematic drawings of teeth modified from Schoch et al. (2018).

larger, reaching up to 2 cm in crown height (Fig. 2G–G'). The cross section of the teeth is angled at the base, which is gently curved, and becomes more circular in the middle part and elliptical towards the apex. Although no complete specimens are found attached to the jaw/skull bones, the curvature direction is assumed to be labiolingually (see Remarks below), like in Morphotype T1. The crown presents apicobasal grooves covering at least two thirds of the total length, reflecting the inner plicidentine. The apex surface is smoothed, lacking ornamentation, and displays xiphodonty. The attachment in the mandibles is not observable due to poor preservation, whereas it is clearly acrodont in the palatal region. In cross section, tusks present a more complex pattern of folded enamel than that of Morphotype T1. However, as in Morphotype T1, the apical part is more massive than the basal portion. All the isolated tusks lack the basalmost portion.

The upper tusks are located in the vomerine region, while lower tusks are located in the symphysis region (Fig. 2B, G') of the mandible. Tusks in the mandible are paired, being the posterior one smaller than the anterior ones (see the paratype of *Calmasuchus acri*: IPS42407 (LM-4); Fig. 2B, G'), although whether this represents an individual variation or a common trait is unclear, because the paratype is the only dentary that preserves both tusks attached. The cross sections correspond to the middle height in the first and a more apical position in the second (Fig. 2G), thus, the angulous shape observed is product of the elongation of sharp longitudinal carinae related to xiphodonty present in this morphotype.

The aforementioned descriptions on the crown morphology of the Morphotype T2 are performed on isolated elements, whereas in all tooth-bearing bone samples, the middle-apical part of the tusk is missing, and the matrix usually covers part of the base. Thus, the real curvature direction is unclear, but in some cases, it can be inferred as labiolingual because of the apicobasal elongation of the xiphodont carinae, less marked towards the mediobasal part, and missing at the base (as in IPS37401 slab MB, IPS137922 and IPS42407 (LM-4)).

Specimens IPS124298 and IPS124303 are incomplete but represent tusks clearly smaller compared to rest of specimens, ranging from 7 to 9 mm in crown height, and consequently both specimens are assigned to juvenile individuals (see "discussion in capitosaur taxonomic implications" below). The base and the tip are missing in both tusks, but in IPS124298 the mesial and distal keels are still visible. IPS124303 does not display sharp carinae and is longer than IPS124298.

Sauropsida Huxley, 1864
Eureptilia Olson, 1947
Diapsida Osborn, 1903
Archosauromorpha Huene, 1946 sensu Dilkes, 1998
Archosauromorpha indet.

Fig. 3A

Morphotype A1: Ziphodont crown

Fig. 3A

Material examined: IPS90631.

Description. Isolated ziphodont tooth with relatively high tooth crown, up to 15 mm in crown height as preserved. The tooth is mesiodistally curved, strongly labiolingually compressed and gently convex in mesial view. As a result of the latter, the tooth apex points lingually (Fig. 3A). The crown is elliptical to "drop-shaped" in cross section. The enamel surface lacks ornamentation, and the root is missing. The mesial carina is rounded and smooth, while the distal carina is serrated. The carina is located more lingually with respect to the midline of the cross section because of the convex condition of the lingual side. The denticles, with a density of 5 denticles/mm (Tab. S1), present some degree of wear, and their complete shape is not recognizable. A notch (*sensu* Mujal et al. 2022) is observed in the basalmost part of the tooth, near the cervix, where the denticles are completely abraded. The apical part is missing.

Remarks. The absence of the root is possibly related to its shed nature (Ezcurra et al. 2017). Despite no root is found, the thecodont implantation type is inferred as the typical condition of archosauromorphs (Ezcurra 2016; Ezcurra et al. 2017).

Diapsida indet.

Fig. 3

Morphotype D1: Blade-like tooth crowns

Fig. 3B, C

Material: IPS90189 and IPS124301.

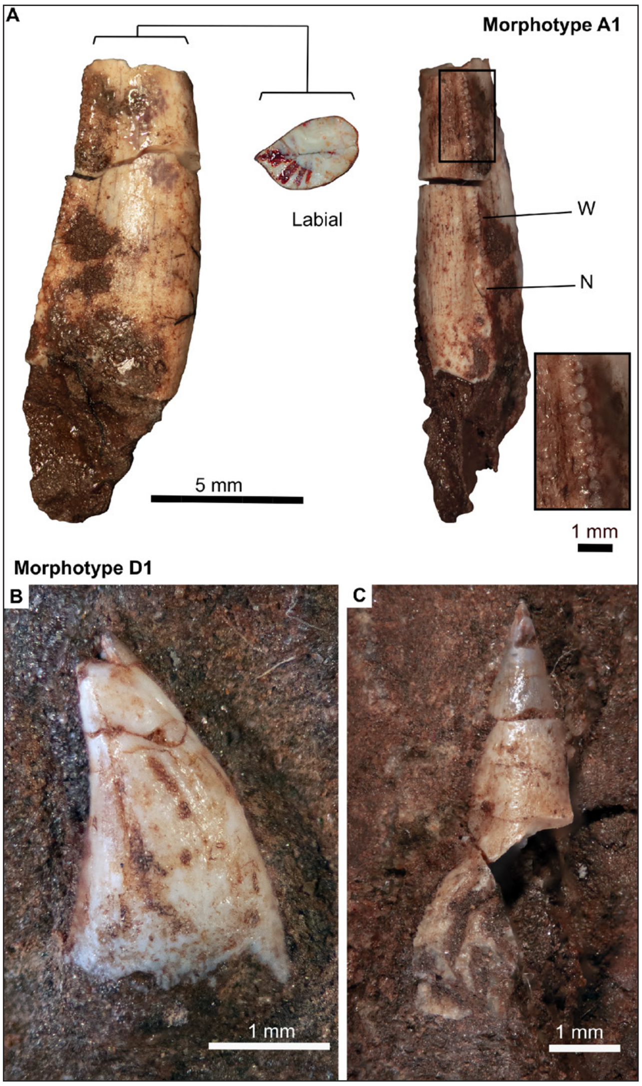

Fig. 3 - Archosauromorph tooth, Morphotype A1. A) IPS90631, partial isolated tooth crown in labial view (left), in apical cross section (middle) and in distal view (right); note the presence of wear facets of abrasion (W) and a notch (N) along the denticles of the distal carina. Indeterminate diapsid teeth. Morphotype D1. B) IPS90189, almost complete small tooth crown; note that most of the enamel is lost, only preserved in the mesioapical part. C) IPS124301, partial tooth crown embedded in the matrix; the enamel is still present, mostly in the apical part.

Description. Isolated laterally compressed blade-like tooth crowns, taller than wider. The specimen IPS90189 (Fig. 3B), embedded in the matrix, is the smallest corresponding to this morphotype, being 3.5 mm in crown height. The overall shape is triangular and is proportionally shorter than the other specimen: it displays a proportionally wider base length (mesiodistally) in comparison with crown height, and presents a straight profile, although the slightly lateral curvature towards the matrix suggests it corresponds to the labial side. The enamel is almost entirely worn away, except in the mesial side of the apex, and the dentine of the distal side lacks denticles. IPS124301 (Fig. 3C) preserves the enamel, although it is damaged in the mediobasal part. Most of the basal part of the tooth is missing, except for the portion of the labial side still embedded in matrix, hampering an assessment of the total length. The medioapical part of the distal carina is exposed showing the lack of denticles. The global shape is straight, with no marked anteroposterior curvature.

Remarks. The reported tooth crowns are not associated to any cranial nor mandibular remains. The different sizes and shapes of this morphotype could belong to different positions of each tooth within the dental series of the same taxon, although in any case it remains unclear whether such differences represent different growth stages or even different taxa.

Parareptilia Olson, 1947
Procolophonidae Lydekker in Nicholson & Lydekker, 1889
Procolophoninae Lydekker in Nicholson & Lydekker, 1890
Kapes Ivakhnenko, 1975

Kapes signus sp. nov.

Figs. 4–6, S1, Suppl 3D models

Origin of the name. From the latin name of the Montseny mountain, *Mount-signus*, which means signal mountain.

Holotype. IPS124305 (Fig.5C), a left partial dentary exposed in lingual view, bearing the posteriormost four molariform teeth.

Paratypes. IPS124295 (Fig. 5B), anteriormost part of a left dentary in labial view, showing four incisiform teeth; IPS60866 (Fig. 5A), a tooth row in occlusal view, displaying nine teeth with the medioapical part of the crowns missing.

Referred specimen. IPS124304 (Fig. 4), left maxilla exposed in lingual side, with five preserved crowns (one incisiform and the rest molariform).

Type locality and horizon. La Mora and Corral d'en Pla de Brugues sites, Catalan Coastal Ranges, Catalonia, Spain; Upper Buntsandstein facies, Montseny-Llobregat domain; early–middle Anisian (Middle Triassic).

Repository*:* Institut Català de Paleontologia Miquel Crusafont (formerly Institut de Paleontologia de Sabadell), Sabadell, Catalonia, Spain

Diagnosis. *Kapes signus* sp. nov. is distinguished from all previously known species of *Kapes* by the following unique combination of morphological characters (asterisks refer to apomorphies): (1) the mandibular tooth row bears nine dental elements. (2) Counting from the anterior, the row displays three different morphotypes: four incisiforms, four angular molariforms and one laterally compressed molariform. (3*) The latter presents ridges in both carinae and a weak basal cingulum in the lingual side. (4*) The crowns of the last three angular molariforms are fused with each other at their basalmost part.

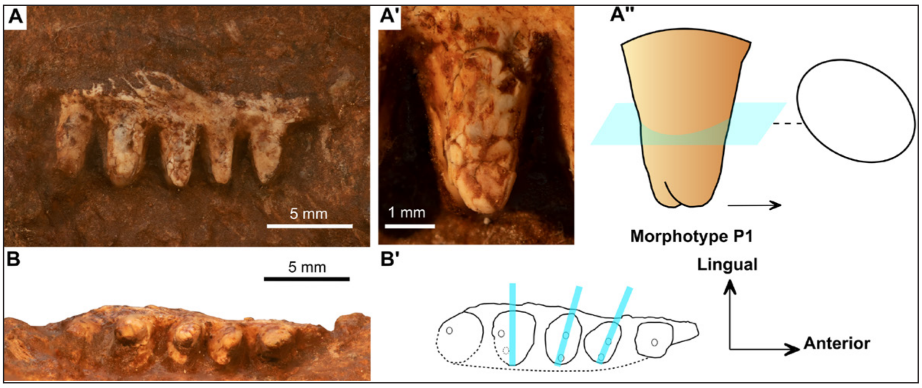

Fig. 4 - Procolophonid teeth, Morphotype P1; *Kapes signus* sp. nov., referred material IPS124304, left maxilla. A) Specimen in lingual view. A'. Detail of the laterally expanded molariform teeth. A". Schematic drawing of Morphotype P1, with oval cross section. B) Occlusal view. B'. Schematic drawing of the apical view showing the long axis of the oval teeth.

Ontogenetic assessment. The available material precludes a confident ontogenetic assessment.

Material description (Figs. 4, 5):

IPS124304 (Fig. 4): Left maxilla, recovered in La Mora site, exposed in its labial side with four laterally expanded bicuspid crowns and at least one incisiform in the anteriormost part of the row, which is in accordance with the upper dentition described for some procolophonines (Spencer & Benton 2000; Spencer & Storrs 2002). The identification of the specimen as a maxilla is also supported by the basal section of the tooth, with the long axis oriented perpendicular to the jaw line, but slightly mesiolingually-distolabially oblique in the first and second teeth, and the increasing size of the tooth row except for the last element. Additionally, IPS124304 presents in the tooth bearing-bone a straight outline and a pair of foramina under the first and one single under the second tooth, and one sulcus, which is present along the bone from the space between the first and the second teeth, towards the most dorsal part of the bone.

IPS60866 (Fig. 5A): Mandible, recovered in Corral d'en Pla de Brugues site, exposed in occlusal view including 9 teeth, of which the 4 anteriormost are incisiform, and the remaining 5 are molariform, being the last element laterally compressed and kidney-like shaped. The crowns are broken exposing the cross section at the middle-basal of the teeth. The surrounding matrix precludes any additional observation on the basal part of the crowns or to the jaw bone.

IPS124295 (Fig. 5B): Anteriormost part of a dentary in labial view, recovered in La Mora site, displaying four laterally compressed incisiform teeth, which are anterolabially to posterolingually oblique oriented respect to the jawline, and with the apices gently pointing posteriorly. The poorly preserved jawbone is curved towards the sedimentary matrix in its anteriormost part, with teeth exposed labially, allowing to observe the symphysis curvature of the dentary.

IPS124305 (Figs. 5C, S1): Posteriormost part of a mandible, recovered from La Mora site, exposed in lingual view and bearing 4 molariform tooth. The three first elements are damaged, lacking the mesiolingual part in the first tooth, and the lingual side in the following two teeth. The last molariform is complete and preserves most of the enamel, its apex is bicuspid and mesiodistal carinae are crested. The anterior-middle part of the dentary, as well as the ramus are lacking, and only the angular and the ventral surface of the mandible is preserved.

Morphotype P1: Laterally expanded molariform teeth

Fig. 4, Suppl 3D models

Material: Left maxilla exposed in lingual view in IPS124304. All teeth from this specimen excluding the anteriormost tooth, which belongs to the morphotype P2 (incisiform) described below.

Description. This morphotype shows an increase in tooth height anteroposteriorly along the tooth row, and labiolingually expanded crowns with a general columnar shape. Teeth are oval in cross section (Fig. 4A), with the long axis of the ellipse transversely oriented (with respect to the jawline) distolabially to mesiolingually in the first and second teeth, and perpendicular on the third one (Fig. 4B). This character cannot be assessed on the last tooth due to poor preservation. Crowns are tall and transversely bicuspid, subequal in size, with heights of 3.0–4.4 mm. IPS124304 is a partial left maxilla (see remarks below), preserving four conical-shaped and laterally expanded teeth in lingual view with two rounded short adjacent cusps (the space between them is equivalent to one cusp, *sensu* Cisneros 2008a) (Fig. 4B). In lateral view, the overall shape is conical, wide at the base. In IPS124304, teeth increase in size from the first to the third. The posteriormost tooth is partially covered, precluding an assessment of its actual size. The last three teeth preserve enamel in the apical part. The enamel presents a smooth texture, with no ornamentation, and is clearly thicker in the apical part, becoming thinner towards the middle part of the crown. The basalmost part seems to be completely fused with the bearing bone. The implantation type seems to be protothecodont/acrodont (acrodont *sensu* Cabreira & Cisneros 2009; see discussion in "in feeding ecology section" below).

Morphotype P2: Incisiform teeth

Fig. 4A, B, 5A, 6, Suppl 3D models

Material: Mandible elements with attached teeth in IPS60866 and IPS124295 and one tooth in the maxilla IPS124304.

Description. IPS60866 only preserves the bases of the crowns, which are surrounded by matrix,

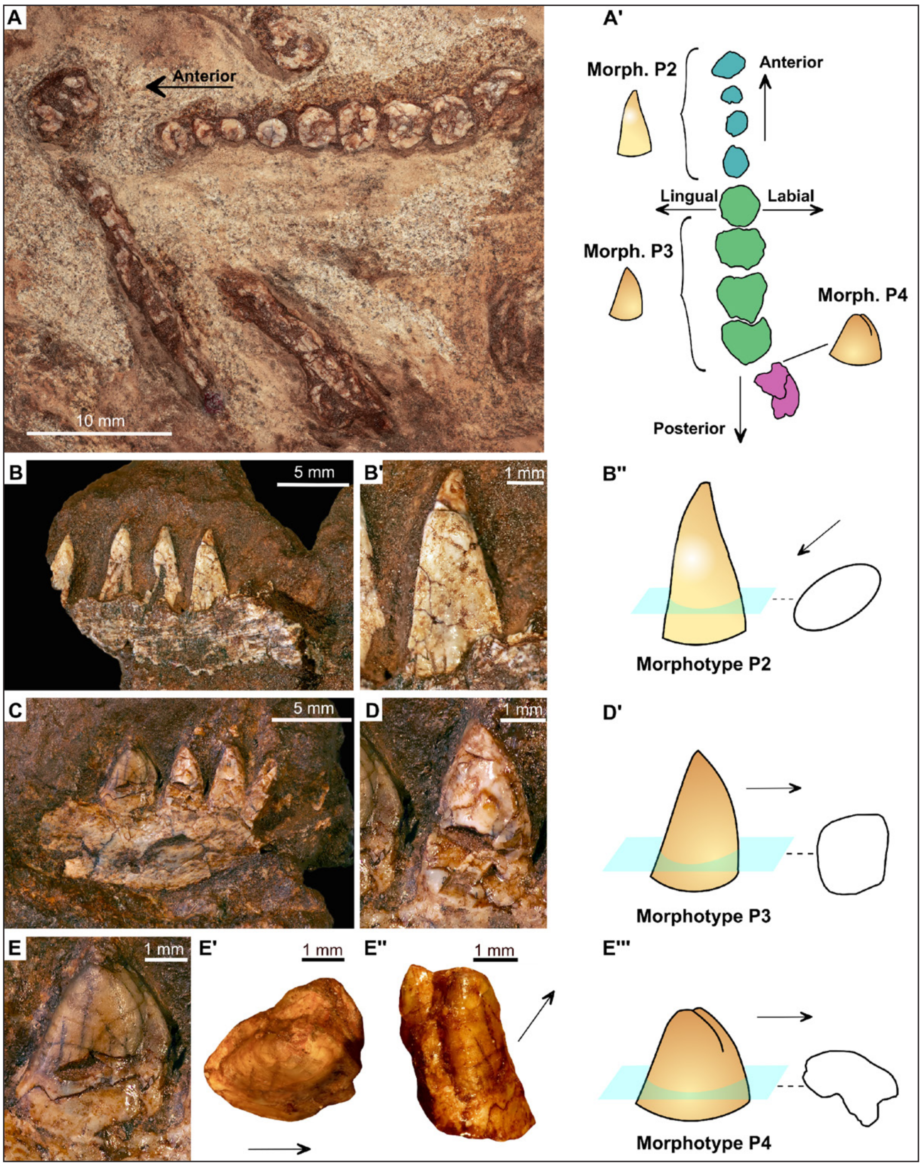

Fig. 5 - Procolophonid teeth, Morphotypes P2, P3 and P4; *Kapes signus* sp. nov. A) Paratype IPS60866, tooth row and several cranial bones in occlusal view; note that most parts of the crowns are missing. A’. Schematic drawing of the tooth row in A, including three morphotypes. B) Morphotype P2, paratype IPS124295, anterior part of a dentary exposed in labial view. B’. Detail of an incisiform tooth from B. B”. Schematic drawing of Morphotype P2, with elliptical cross section. C) Morphotypes P3 and P4, holotype IPS124305, posterior part of a left mandible in lingual view. D) Detail of Morphotype P3, angular molariform tooth from C. D’. Schematic drawing of Morphotype P3, with angular cross section. E) Morphotype P4, IPS124305, detail of a laterally compressed molariform tooth from C. E’. Linguo-apical view of Morphotype P4. E”. Distal view of Morphotype P4. E’”. Schematic drawing of Morphotype P4, with kidney-like cross section.

limiting the observation to the cross section of each tooth (Fig. 5A–A’). IPS124295 is the anterior portion of a tooth row exposed in labial view displaying four complete tooth crowns (Fig. 5B–B”). The crowns present heights of 3.6–5.5 mm (in IPS124295) and 1.1–2.5 mm in diameter (in IPS60866) (Tab. S1). Teeth are ellipsoidal in cross section. The long axis of the ellipse is oriented from mesiolabially to distolingually, thus oblique to the jaw line (Fig. 5A). Tooth bases are gently mesiodistally compressed in the three anteriormost teeth of IPS60866 and in the crowns of all four teeth of IPS124295. These features allow to identify the presence of the same morphotype in both specimens, linking IPS60688 and IPS124295. The crowns are tall and straight, with a tall conical apex, gently curved towards the oral cavity and terminated in a pointed tip. The basalmost part of the crown seems to be set in a socket.

Remarks. Teeth of this morphotype are placed in the anterior part of the mandibular tooth row (Fig. 5A). The series decreases in diameter anteroposteriorly in IPS60866, being the anteriormost tooth more rounded in cross section than the second and the third ones, probably because the section is located in different heights in each tooth. The implantation type is protothecodont/acrodont (acrodont *sensu* Cabreira & Cisneros 2009; see discussion below).

Morphotype P3: Angular molariform teeth

Fig. 5A, C–D, 6, Suppl 3D models

Material: Mandible elements with attached teeth in IPS60866 and a left partial dentary exposed in lingual view, bearing the posteriormost four molariform teeth in IPS124305. The most posterior tooth in both specimens is excluded because it belongs to morphotype P4 described below, as are the four first elements in IPS60866 which belong to the morphotype P2 described above.

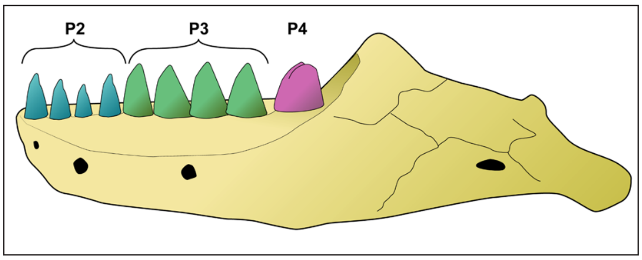

Fig. 6 - Hypothesized reconstruction of the lower jaw of *Kapes signus* sp. nov. based on the holotype, paratypes, as well as the lower jaw of *Kapes bentoni* (modified from Zaher et al. 2019).

Description. The posteriormost portion of specimen IPS60866 (with the exception of the last tooth) has four angular molariform teeth that increase in size anteroposteriorly. All of them are larger than the teeth referred to Morphotype P2, and are rectangular in cross section, with the labiolingual axis (ranging from 2.5 mm to 3.3 mm) longer than the mesiodistal one (Tab. S1). The crowns lack their middle-apical part in IPS60866. The second and third teeth of this morphotype are in tight contact, like the third and fourth, molding the distal face of the third tooth with the mesial face of the fourth tooth, almost suturing each other. Specimen IPS124305 corresponds to a posterior part of a dentary in labial view. It displays four teeth, of which only the three anteriormost ones belong to morphotype P3 (Fig. 5C). They are up to 4.8 mm in crown height and up to 2.7 mm in crown base length. Counting from anterior to posterior, the first tooth lacks the mesial side, and the base of the distal face is fused with the base of the mesial face of the following tooth (Fig. 5C). The second and the third are also poorly preserved in the exposed face but it is possible to observe their overall shape: they are subtriangular with a straight distal face and the mesial face describes a gentle curve from the base to the apex, displacing the tip slightly posteriorly (Fig. 5D). All teeth in IPS124305 display a procumbent orientation (Morphotype P4 included, see description below), tilting slightly anteriorly.

This morphotype corresponds to teeth placed in the posterior portion of the mandible tooth row, with the exception of the last one. Teeth of this morphotype are the widest in the dental row, forming an increasing size series. Although the basal section of the elements in IPS124305 cannot be observed, the exposed surface allows to infer a molariform shape, as it occurs with the basal cross section of IPS60866. The fused bases of the teeth in IPS124305 resemble those in tight contact observed in occlusal view in IPS60866. The general shape of these teeth can be described as molariform, as it is reported for procolophonids (Cisneros 2008a). The implantation type is protothecodont/acrodont (acrodont *sensu* Cabreira & Cisneros 2009; see discussion in "about feeding ecology" below).

Morphotype P4: Laterally compressed molariform teeth

Fig. 5A, C, E, 6, S1, Suppl 3D models

Material: Mandible elements with attached teeth in IPS60866 and a left partial dentary exposed in lingual view, bearing the posteriormost four molariform teeth in IPS124305.

Description. The posteriormost tooth is the mesiodistally longest of the row in IPS124305, being bulbous and laterally compressed. Weakly inclined forward and subtriangular in shape in lateral view. Its distal face is slightly concave, whereas the mesial face is slightly convex. The crown is bicuspid, with closely spaced blunt cusps separated by a shallow groove (Fig. 5E', E"). The presence of a sulcus and a ridge that extends apicobasally in the mesiolingual and distolingual sides is conspicuous, forming blunt, crested carinae. The basalmost part presents a cingulum, at least in the lingual side, which is connected with the mesial and distal ridges (Fig. 5E', E"). The enamel is almost completely preserved, being smooth, without ornamentation or signs of wear. The tooth is clearly set in a socket, and apparently fused with the bone. In IPS60866 (Fig. 5A, A') the crown is not preserved but the kidney-like shape derived from the lateral compression, together with the ridges and the cingulum, can be observed in the cross section.

Remarks. The tooth corresponding to Morphotype P4 is the posteriormost one of the dental rows in both IPS124305 and IPS60866. The characteristic molariform shape and the location in the dental series of this morphotype links both specimens, being the largest tooth mesiodistally in labial view of the tooth row, as is observable in IPS60866 (Tab. S1, Fig. S1). The implantation type of all teeth is protothecodont/acrodont (acrodont *sensu* Cabreira & Cisneros 2009; see discussion in "about feeding ecology" below).

DISCUSSION

Taxonomic implications

Capitosaur temnospondyls. Temnospondyl teeth (Morphotypes T1 and T2; Fig. 2) represent by far the most numerous teeth recovered from the Montseny area (Tab. S1). The identification of those morphotypes as capitosaurs is based on several dental characters, combined with the attachment on the cranial and mandibular elements: palatal arrangement composed by a pair of prechoanal tusks (Morphotype T2). Those are combined with the interchoanal and parachoanal tooth rows (composed by teeth assigned to Morphotype T1) (Fig. 2A), which show the standard pattern in capitosauroid dental series (Shishkin & Sulej 2009). Furthermore, capitosaurs present a high number of marginal and inner teeth that tend to be laterally compressed. Some additional traits are the absence of ectopterygoid tusks, the inner mandibular dentition confined to a symphyseal tooth row and a tooth row present on the posterior coronoid bone (Bystrow 1938; Warren & Davey 1992; Schoch 1999). In addition, the presence of xiphodonty, reported for the first time in *Calmasuchus acri*, has been reported in capitosaurids, such as *Cyclotosaurus* (Rinehart & Lucas 2013) and *Mastodonsaurus* (Schoch 1999; Schoch et al. 2018), and is a common trait in other temnospondyl families (Brachyopidae and Chigutisauridae), as well as in most anthracosaurs (Warren & Davey 1992). Regarding tooth morphology, the specimens here described show the typical labyrinthodont pattern: teeth and tusks are conical, with elliptical or circular basal sections, and a striated base reflecting the infolding involving both plicidentine and enamel, which decreases in complexity from the base to the tip of the tooth (Warren & Davey 1992). This feature is also related to size, being tusks more folded than marginal teeth (Warren & Davey 1992).

The capitosaur remains from the Montseny area mostly come from La Mora site and are attributed to the capitosaur *Calmasuchus acri* (Fortuny et al. 2011b). Mandibular remains of *Calmasuchus* show a remarkable size variability. Furthermore, xiphodonty in Morphotype T1 is only observed in some of the smallest teeth. Otherwise, xiphodonty is observed in all elements of Morphotype T2. Whether these changes are related to interspecific differences (suggesting a second capitosaur taxon) or, more likely, to ontogenetic changes, remains unclear. Unfortunately, the fragmentary preservation of the fossils precludes any statistical analysis to reveal the origin of this variability.

The Lower Triassic Eastern European record – one of the most important areas of the globe regarding Triassic temnospondyls in general, and capitosaurs in particular – shows that each faunal assemblage commonly includes a single, but abundant, capitosaur genus, rarely associated with one or two additional capitosaur taxa (Shishkin & Sulej 2009). This faunal assemblage composition may be comparable to that of the Montseny area, where all temnospondyl remains appear to be related to a single capitosaur taxon. Otherwise, differences among juvenile and adult capitosaur individuals in tooth number and shape were noticed by Bystrow (1938), Warren & Davey (1992) and Shishkin & Sulej (2009). Nonetheless, intraspecific differences in dentition have been reported, for instance, in *Warrenisuchus aliciae* (Warren & Hutchinson 1988) and *Parotosuchus speleus* Shishkin & Sulej 2009, and are presumably associated with ontogenetic variations within the same species. All in all, even if it cannot be ruled out that anatomical changes observed among *Calmasuchus* specimens could be related to interspecific variation, the already recovered Eastern European record suggests that the observed size variability probably mirrors ontogenetic changes of a single taxon.

Archosauromorph eureptiles. The single tooth corresponding to Morphotype A1 (Fig. 3A), presents a laterally compressed ziphodont crown with a serrated distal carina and is apicobasally posteriorly curved with thecodont implantation. These traits allow to refer this tooth to an indeterminate archosauromorph eureptile (e.g., Ezcurra 2016; Ezcurra et al. 2017). Ziphodont teeth are considered homoplasic among hypercarnivorous taxa (Brink et al. 2015; Whitney et al. 2020; Mujal et al. 2022). This convergent morphology of specialized carnivorous teeth seems to lack enough diagnostic characters among different archosauromorph groups, regarding shape and number of distal denticles (Nesbitt 2011; Ezcurra 2016; Ezcurra et al. 2017; see also discussion in Hoffman et al. 2019). This fact is particularly dramatic due to the fact that the taxon from Montseny is represented by a single specimen.

A previous study on IPS90631 concluded that the labiolingually compressed crown, the finely serrated distal carina and the smooth (Fig. 3A), non-serrated mesial carina are synapomorphies of crocopodan archosauromorphs (Ezcurra et al. 2017), because the more derived eucrocopodan clades mainly possess both carinae densely serrated. Moreover, the shape and number of denticles have low taxonomic value (Ezcurra 2016; Ezcurra et al. 2017).

Indeterminate diapsids. Two different teeth (IPS90189 and IPS124301) are attributed to morphotype D1 (Fig. 3B, C). The shape of the crowns is blade-like, laterally compressed with a gently apicobasal posterior curvature and carinae lacking denticles. The specimens herein described are attributed to Diapsida indet. due to the lack of diagnostic traits to differentiate archosauromorphs from other reptile faunas present in the Anisian ecosystems.

The low number of samples precludes the observation of trends in the morphology and, due to the intraspecific variability among diapsids (including archosauromorphs), it is not possible to state if variability correspond intraspecific features, ontogenetic factors, or the presence of different taxa (Ezcurra et al. 2017; Schoch et al. 2018; Hoffman et al. 2019).

Procolophonid parareptiles. Morphotypes P1 to P4 (Figs. 4–6) show a high degree of heterodonty, because a single tooth row contains different tooth morphologies. Of particular interest, different aspects of the preserved dentition imply a complex dental pattern and shape. Even with the limited material from the Montseny area, represented by four partial specimens recovered so far, numerous morphological features are already observed: a high degree of heterodonty displaying both incisiforms and molariforms in the same tooth row, laterally expanded bicuspid crowns in the maxillary molariforms, increase in size from anterior to posterior of the maxillary and dentary molariforms except for the last element, and enlargement of the enamel thickness in the apical part of the teeth (Spencer & Benton 2000; Spencer & Storrs 2002). These dental morphologies enable to identify these specimens as procolophonid parareptiles, more specifically to procolophonines, and clearly different from the coeval clade of trilophosaurs, which present hourglass-shaped laterally expanded teeth with three cusps and an ankylothecodont implantation (Foffa et al. 2023).

During the Triassic, procolophonids experienced a high diversification (Spencer & Benton 2000), presumably linked with the development of different feeding strategies, which include durophagous herbivory, omnivory and insectivory (Cisneros 2008a). Because of the gradual transition of dental series from incisiform to molariform, the variability rate of this transition and the high degree of inter- and intraspecific variation, the establishment of clear morphotypes is still open to debate (Borsuk-Białynicka & Lubka 2009). Therefore, this dental pattern variability is a consequence of the different diet adaptations among procolophonid groups (Cisneros 2008a).

Historically, as mentioned above, two main tooth morphotypes have been distinguished: incisiform and molariform (Spencer & Benton 2000). In order to highlight the differences among the incisiforms and molariforms, two new morphotypes are here proposed, represented by Morphotype P1 (IPS124304; Fig. 4A) and Morphotype P4 (IPS124305 and IPS60866; Fig. 5C, E–E’”), the so-called laterally expanded molariform teeth and laterally compressed molariform teeth, respectively. Criteria to establish these new morphotypes are based on the presence of four distinctive basal sections: ellipsoidal (IPS60866 and IPS124295), angular (IPS60866 and IPS124305), kidney-like (IPS60866 and IPS124305) and oval (IPS124304). The ellipsoidal basal section is best represented in specimen IPS124295 (Fig. 5B”), which displays the incisiform shape, whereas the angular molariform morphotype corresponds to the three first elements in IPS124305 (Fig. 5D’). The kidney-like cross section is found on the posteriormost tooth in IPS60866 (Fig. 5A’, S1), being in accordance with the laterally compressed shape observed in the last tooth of the partial dentary IPS124305 (Fig. 5D’). Thus, the peculiar shape and the relative position in the dental series links both specimens. The laterally expanded bicuspid crowns with oval cross section in IPS124304 (Fig. 4) cannot be correlated with the IPS60866 basal sections, nor with IPS124305 or IPS124295. Therefore, this morphotype is not present in any specimen attributed to a dentary. The overall shape of the laterally expanded molariform teeth is straight, transversally expanded and with a bicuspid apex (Fig. 4). This morphology is in agreement with the maxillary teeth of some procolophonine taxa like *Kapes* (Spencer & Benton 2000; Spencer & Storrs 2002; Novikov & Sues 2004; Zaher et al. 2019).

Derived character states among procolophonids include bicuspid molariform teeth, with closely positioned cusps (e.g., *Kapes*, *Leptopleuron*), or widely separated cusps (e.g., *Tichvinskia*, *Procolophon*), the latter found in much more labiolingually expanded teeth (Cisneros 2008a). Closely positioned cusps are present in the last molariform of IPS124305 but cannot be ascertained in IPS60866 due to the lack of preservation of the crown apices. The cross sections in the latter specimen show non-laterally expanded molariform crowns (Fig. 5A) and seem to be consistent with the observations in lingual view of IPS124305 (Fig. 5C–E). Since leptopleuronines are the most derived procolophonids, the high number of teeth and the lack of the laterally expanded dentary crowns are in agreement with a procolophonine member (Cisneros 2008a), and more specifically with the genus *Kapes*.

Specimen IPS60866 was previously tentatively identified as a potential procolophonine, showing similarities with the genera *Anomoiodon, Tichvinskia* and *Kapes* on the basis of tooth row length, number of teeth, geometry of the dental distribution and absence of transverse expansion of the mandible molariform teeth (Fortuny et al. 2014). Some postcranial remains reported from the same area seem to support this attribution (Fortuny et al. 2014). *Anomoiodon* has been discussed to be a senior synonym of *Kapes*, but recent works support the validity of *Anomoiodon* (e.g., Säilä 2008), both taxa being closely related. *Anomoiodon* displays a clear anteroposterior size increase in the tooth series, and the tallest tooth is not the widest (Säilä 2008), a feature inconsistent with the Montseny specimens here described (IPS60866). IPS60866 differs from *Tichvinskia* in the dentary molariform teeth, which is markedly laterally expanded in the latter (Cisneros 2008a). In addition, *Tichvinskia* is older (Lower Triassic), whereas the taxon herein described is from lower Middle Triassic deposits. Regarding the attributed affinities to *Kapes*, the three first teeth of the series in this genus decrease in size anteroposteriorly (Spencer & Benton 2000; Spencer & Storrs 2002; Novikov & Sues 2004; Zaher et al. 2019), like in IPS60866 (Fortuny et al. 2014) (Fig. 5A), being a trait shared with *Tichvinskia* (Spencer & Benton 2000). This trend is not observed in the incisiforms of IPS124295 (Fig. 5B), which seem to be similar in size, although the surrounding matrix precludes more accurate observations on the basal shape, and the number of elements coincides in both. Nevertheless, in *Kapes bentoni* Spencer & Storrs 2002 differences in the dentary incisiforms shape and size have also been documented (Zaher et al. 2019). The presence of at least one incisiform in the anterior end of the maxilla is also a character present in *Kapes* spp. (Novikov 1991; Spencer & Benton 2000; Spencer & Storrs 2002), and seems to correspond with the first tooth present in the maxilla IPS124304 (Fig.4). Based on the mandible tooth row of IPS60866 the number of teeth is at least nine, being the highest among *Kapes* spp. (Spencer & Benton 2000; Spencer & Storrs 2002; Cisneros 2008a; Zaher et al. 2019), and the bicuspid elements are located close to each other. This number of teeth is similar to that of the potential non-leptopleuronine procolophonids from the Middle Triassic of Nova Scotia, Canada (Sues et al. 2022).

The maxillary and dentary molariforms of *K. amaenus* Ivakhnenko 1975 become larger posteriorly, reaching their maximum size at the fourth element (Spencer & Storrs 2002; Novikov & Sues 2004). This feature is shared with *Kapes* cf. *K. majmesculae* (Ochev 1968) (Novikov & Sues 2004) and is in accordance with the maxilla IPS124304 and with the tooth row IPS60866. In the partial mandible IPS124305, the elements are equal in height and mesiodistal basal length (Tab. S1). The bicuspid crowns of IPS124304 differ in the equal size of the labial and lingual cusps, being the lingual taller than the labial in the upper molariforms of *Kapes* cf. *K. majmesculae* (Novikov & Sues 2004) and *K. bentoni* (Zaher et al. 2019), but resemble *K. komiensis* (Ivakhnenko 1975) in the upper molariforms transverse axes that are oriented distolabially to anterolingually (Spencer & Storrs 2002). The widely spaced teeth of IPS124304 (Fig. 4) and IPS124295 (Fig. 5B) is a trait shared with *Kapes serotinus* Novikov 1991, although this character presents variability within procolophonid taxa, even within the same species (Spencer & Benton 2000). The weak cingulum present in the last molariform (Morphotype P4) of the tooth row in IPS124305 is a trait shared with *K. bentoni* and *K. majmesculae* (Spencer & Storrs 2002). On this regard, *K. bentoni* displays a variable position of a weak cingulum on all lower molariforms, whereas in *K. majmesculae* the cingulum is located at mid-height in all the lower molariforms

(Spencer & Storrs 2002; Zaher et al. 2019). In *Kapes signus* sp. nov., however, the presence and position of a weak cingulum cannot be assessed with confidence in the rest of molariforms due to poor preservation. A weak expansion on the mesiolabial side of the third and, apparently, the fourth molariforms in IPS60866 (Fig. 5A) seems to indicate the presence of a cingulum-like structure, or at least a mesial ridge such as the one observed in the morphotype P4 but in the labial side. This ridge on the mesial and distal carinae, as well as the lateral compression in the last molariform are unique features of the Montseny specimens (Figs. 4E', E", 5A; Suppl 3D models), not observed in any other *Kapes* spp. nor in other procolophonids. Of note, Spencer & Storrs (2002) described a somewhat similar structure in a specimen composed only of the anterior end of a partial jaw bearing three teeth from the Otter Sandstone (Anisian of the UK). The specimen was originally referred as ?Parareptilia *incertae sedis,* but recently re-described as an indeterminate procolophonid (Zaher et al. 2019). Spencer & Storrs (2002) described the aforementioned structure in the indeterminate taxon as a developed lingual cingulum, which continues as a smooth ridge up to the apex of the crown. However, this is different from the new taxon described in this work. The specimen described by Spencer & Storrs (2002) presents cingulum-like structures in the anteriormost teeth of the dentary. The crowns are closely spaced and leaf-shaped, which are broadened at the base and with the long axis oriented distolabially to mesiolingually. Those traits are not observed in IPS124295 nor IPS60866, which display widely separated incisiforms (Fig. 5A, B), clearly thinner than wide, without cingulum-like nor ridge structures, and with the long axis of the ellipse oriented mesiolabially to distolingually. Spencer & Storrs (2002) also noted close similarities between the Otter Sandstone specimen and the leptopleuronine *Sclerosaurus* from the Anisian Upper Buntsandstein of Germany and Switzerland (Sues & Reisz 2008). Nevertheless, the dental patterns of *Sclerosaurus* differ from those of the Montseny specimens. The mandible of *Sclerosaurus* presents blunt conical teeth slightly compressed with an oval cross section that has a long axis oriented mesiolingually to distolabially (Sues & Reisz 2008).

Among the several Russian procolophonids attributed to the genus *Kapes*, Spencer & Storrs (2002) reduced the number of species to three: *K. amaenus*, *K. majmesculae* and *K. komiensis*. Nevertheless, *K. serotinus* is still considered valid by Cisneros (2008a). Besides, an additional species outside Russia (*K. bentoni*) was described from the UK (Spencer & Storrs 2002; Zaher et al. 2019). The wide distribution of the genus *Kapes*, present in several Russian localities (from the Olenekian to the Anisian) (Spencer & Benton, 2000; Novikov & Sues 2004) and the UK (Spencer & Storrs 2002; Coram et al. 2019; Zaher et al. 2019) is particularly interesting, and the presence of *Kapes* in southwestern Europe (this work) is biogeographically relevant, linking the Iberian Peninsula with the Triassic terrestrial deposits of the UK and Russia (Zaher et al. 2019), and providing information about the wide distribution of this genus in the northern hemisphere. All in all, *Kapes signus* sp. nov. extends the paleolatitudinal distribution of this genus at its southernmost limit in equatorial Pangea and provides new biodiversity information in the scarce southwestern European terrestrial record during the Anisian.

Feeding ecology

Labyrinthodont dentition in capitosaurs. The presence of plicidentine, dental row geometry, number of teeth and shape of the snout are of particular interest to understand the dietary habits of the capitosaur temnospondyl from the Montseny area, *Calmasuchus acri*. Plicidentine is convergent among several tetrapod groups and has functional implications (Rinehart & Lucas 2013). Animals with labyrinthodont teeth usually possess slender jaws and flattened skulls, and plicidentine provides an increase of the attachment surface that, together with the arrangement and the high number of teeth, might help to reduce stresses when holding prey (Cohen et al. 2020), compensating the absence of roots.

The anterior palatal teeth in tetrapods are mainly used to hold and manipulate food within the mouth during intraoral transport (Matsumoto & Evans 2017). The distribution of teeth in the palate is useful to grab prey upon puncture, because small teeth are useful to dissipate the stress around the larger tusks (Cohen et al. 2020). Furthermore, xiphodonty has been suggested as a way to increase the penetration of teeth into prey (Rinehart & Lucas 2013). In this sense, the large-sized tusks with sharp carinae may be the main points for prey-holding, being assisted by the marginal and inner rows of smaller teeth. Moreover, the shape of the mouth, the massive tusks and the inferred jaw musculature of capitosaurs have been argued to show that these animals fed on medium-large prey (Damiani 2001; Schoch 1999).

A generalist top-level predator niche has been suggested for capitosaurs, based on its inferred paleobiology (Damiani 2001; Fortuny et al. 2016). This would be the case of *Calmasuchus acri* (Fig. 7), inhabiting a freshwater environment where it would have fed, although semiaquatic feeding capabilities have also been suggested for capitosaurs (Fortuny et al. 2011c). In this aspect, fishes have been traditionally proposed as the main (but not only) prey for capitosaurs (Damiani 2001; Rinehart & Lucas 2013; Schoch et al. 2018). Fishes have been recorded from various temnospondyl assemblages (Shishkin & Sulej 2009; Schoch et al. 2022; Coram et al. 2019), but not in the Montseny area so far. In a similar manner, the presence of juveniles and adults might imply different sizes of prey throughout ontogeny (Schoch & Seegis 2016). All in all, the question of which animals were prey of *Calmasuchus* remains open. Even if it cannot be discarded that this capitosaur occasionally fed on animals roaming shores of water bodies (such as procolophonids and/or small archosauromorphs), it seems more plausible that they fed mostly on other aquatic animals (including smaller conspecifics, see Schoch & Seegis 2016) such as fishes that, even if not recovered, were probably also present in these environments (Fig. 7).

Ziphodont teeth of archosauromorphs. Hypercarnivorous feeding habits have been inferred for several groups of Lower–Middle Triassic archosauromorphs (Ezcurra 2016). It is important to note the apparent absence of herbivorous members of the clade based on dentognathic record from the Montseny area. This fact is in high contrast with the trend during the Middle–early Late Triassic when rhynchosaurs, among other herbivorous archosauromorphs, inhabited all present-day continents except Australia and Antarctica, and became an abundant component of terrestrial ecosystems in the Late Triassic (Benton 2011; Ezcurra et al. 2020).

It should be remarked that the tooth herein referred to a crocopodan archosauromorph represents a medium predator, in contrast with the tetrapod ichnites known from the Montseny area that have been associated to this group (chirotheriids; see Fortuny et al. 2011a), revealing the presence of other larger taxa (see "discussion section about dentognathic and osteological record versus ichnological record" below). The fragmentary nature of the ziphodont tooth puts limits on the value of the information obtained. The isolated nature of the find and the lack of root probably implies a shed tooth (Ezcurra et al. 2017). Nonetheless, the presence of denticles only in the distal carina, and the rounded nature of the mesial carina, both indicate that only the former was used during feeding (cf. D'Amore 2009). Also, the differential distribution of wear on IPS90631 (Fig. 3A, Tab. S1) implies focalized zones where the tooth underwent more stress, like in the base of the distal side, as suggested by the identified notch (*sensu* Mujal et al. 2022). Thus, the feeding method based on "puncture and pull-back" proposed by D'Amore (2009) for theropod dinosaurs is consistent with the denticle distribution, morphology and wear facets present in the specimen here studied (see also discussion in Mujal et al. 2022). In order to make comparisons with extant taxa, ziphodont teeth are restricted nowadays to varanid lizards, some of which (like *Varanus komodoensis* Ouwens 1912) are known to be able to prey on large mammals (D'Amore & Blumenschine 2009). Thus, the ratio among predator/prey size may be the sole limitation on the feeding ecology regarding the archosauromorphs from the Montseny area and it seems plausible to consider that they would have fed on small- to medium-sized taxa such as procolophonids, other archosauromorphs and even adult temnospondyls (Fig. 7).

Blade shaped teeth of diapsids. In spite of the differences among the two teeth recovered, the general shape lacks the complex patterns linked with herbivory as well as the diagnostic traits of hypercarnivory (e.g., serrated carinae), thus the specific trophic specialization remains unclear (see discussion in Schoch et al. 2018; Hoffman et al. 2023). Some studies in archosauromorph isolated teeth found dietary separations between large and small-bodied taxa inferred from minor differences in tooth morphologies (Hoffman et al. 2019). However, considering the small size of the specimens herein reported, and their overall shape, it is plausible that many small to medium diapsids were probably faunivorous (Schoch et al. 2018).

Heterodonty in procolophonids. The high degree of heterodonty among Triassic procolophonids is a product of the diversification and the adaptive radiation of the group (Spencer & Benton 2003; Cisneros 2008a; Pinheiro et al. 2021). This allowed members of the group to use different feeding strategies like non-durophagous omnivory, insectivory and a clear trend towards herbivory combined with durophagous omnivory through time (Pinheiro et al. 2021).

In general terms, laterally expanded molariforms are related with the capability of chewing and processing food, but this does not necessarily imply the capability to process fibrous vegetation. On the one hand, the molariform teeth with cusps and sharp crests, combined with conical anterior teeth, were possibly well adapted to insectivory, because no wear facets derived from the plant processing are found (Cisneros 2008a, b). On the other hand, the presence of bulbous molariform teeth with blunt cusps are probably related with feeding on fibrous items and/or hard-shelled invertebrates (Pinheiro et al. 2021).

The idealized mandible reconstructed from the different specimens from the Montseny area (Fig. 6) shows an intermediate pattern between feeding styles: one the one hand, the presence of incisiform anterior teeth and the absence of the lateral widely expanded molariforms are suggestive of insectivory; on the other hand, the blunt cusps are consistent with an herbivorous or durophagous diet. Another important question is the high number of teeth present in the mandible tooth row IPS60866 (Fig. 5A), in contrast with the general procolophonid trend to reduce number of teeth (Cisneros 2008a). To sum up, the procolophonine present in the Montseny area probably had feeding habits related to insectivory and/or durophagous omnivory (Fig. 7).

Protothecodonthy or ankylosed thecodonthy are traditionally proposed as tooth implantation types for procolophonids. Nevertheless, a histological study on *Soturnia caliodon* Cisneros & Schultz 2003 postulated a general acrodont model, arguing embryological constraints in the development of specific implantation models (Cabreira & Cisneros 2009). However, the definition of acrodonty by these authors differs from the one used by Bertin et al. (2018) as noted by Mueller et al. (2023). Acrodont and protothecodont models occur at the same time in *Scoloparia glyphanodon* Sues & Baird 1998, and different implantation and dental replacement types seems to be present among procolophonid taxa (Jenkins & Bhullar 2022). Of note, the aforementioned taxa belong to the leptopleuronine subfamily and it cannot be discarded that these implantation types are exclusive for that group (Mueller et al. 2023). Considering the lack of studies focused on tooth attachment in procolophonids and specifically in procolophonines, the implantation type of *Kapes signus* sp. nov. remains open.

Dentognathic and osteological record versus ichnological record

In comparison with La Mora site, which has provided hundreds of bones and teeth mainly attributed to *Calmasuchus acri*, temnospondyl occurrences in the rest of the Montseny area are not abundant, even if not rare (Tab. S1). The remains recovered in La Mora site conformed a bonebed, and the sedimentological features suggest a meandering fluvial environment, with channel infilling and an erosional base on a toping plane (Fortuny et al. 2011b). Vertebrate remains were probably deposited postmortem, because the skeletal material is disarticulated. The presence of several disarticulated skeletal remains and their accumulation in a determined area (consistent with sedimentary processes) suggest transportation. In any case, temnospondyls may have inhabited such subaquatic fluvial environments, as it has been generally interpreted for the group (Fortuny et al. 2016).

It is also relevant that besides temnospondyl remains, La Mora site also delivered some disarticulated postcranial elements possibly attributable to procolophonids (herein not described as it is out of the scope of the present study) that were possibly transported from nearby areas. Thus, besides capitosaur temnospondyls, no evidence of other aquatic inhabitants is available, but as discussed above, the presence of fishes in the original ecosystem, even if not documented so far, seems highly probable.

Noteworthy, no tetrapod ichnological record correlated to temnospondyls (nor non-amniotes in general) has been hitherto found in the Montseny area (Fig. 7). This is probably an environmental and/or taphonomic bias on the group (Mujal & Schoch 2020), because the deposits where capitosaur remains are found resulted from erosive water flows that would have erased any potential trace produced

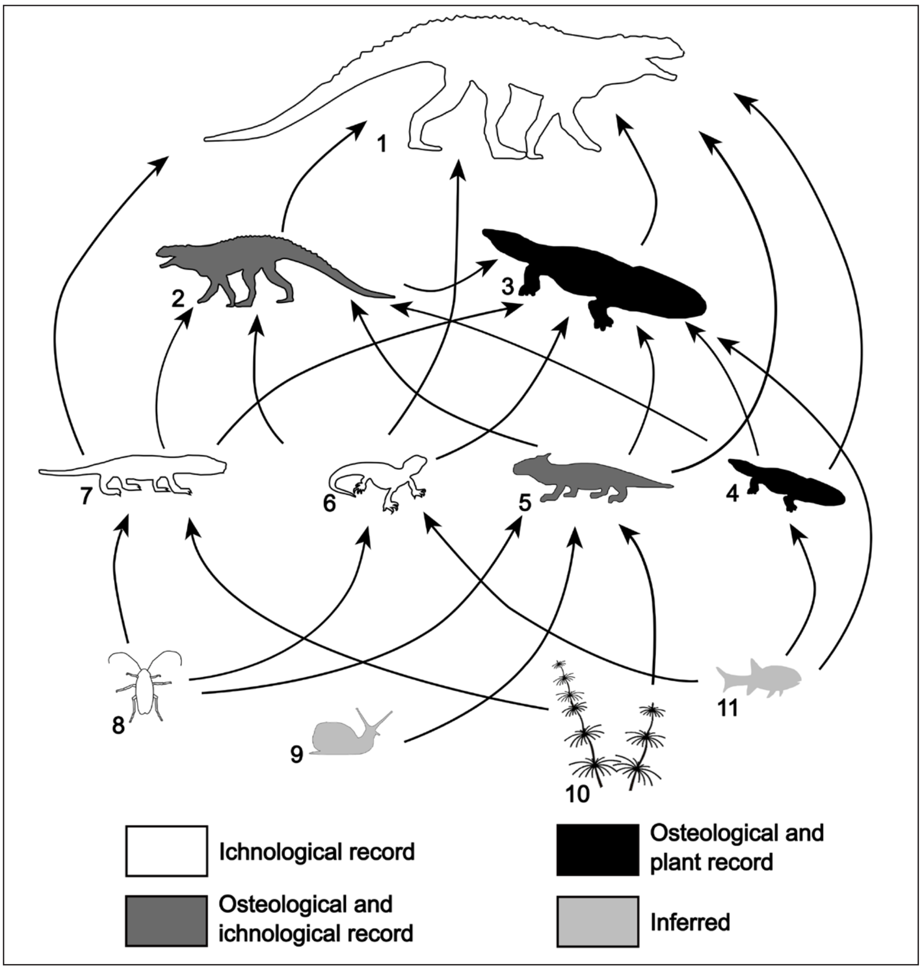

Fig. 7 - Hypothesized trophic web from the Montseny area based on both osteological and ichnological records. 1) Large archosauromorphs; 2) Small archosauromorphs; 3) Adult individuals of the capitosaur *Calmasuchus acri*; 4) Juvenile individuals of *C. acri*; 5) Procolophonids; 6) Lepidosauromorphs; 7) Therapsids; 8) Arthropods; 9) Hard-shelled invertebrates; 10) Plants; 11) Fishes.

by these tetrapods. In this sense, capitosaurs possibly inhabited these streams that had enough energy to disarticulate skeletal elements and transport them for probably short distances (the latter is inferred from the fact that different size elements are found together in La Mora site, i.e., not sorted or selected). They possibly lived on low-energy aquatic environments, like abandoned meandering channels that are not usually preserved due to fluvial dynamics (Miall 1985). Regarding the absence of temnospondyl tracks in other environments, it is plausible to infer an almost aquatic (or semi-aquatic) lifestyle for that group with a low preservation potential of tracks (Mujal & Schoch 2020), in line with the feeding ecology previously discussed for the group.

Several tetrapod ichnotaxa have been documented in the Montseny area (Calzada 1987; Valdiserri et al. 2009; Fortuny et al. 2011a), most of them attributed to purportedly fully terrestrial trackmakers. The ichnological record of terrestrial tetrapods in these fluvial and floodplain environments follows the opposite pattern of temnospondyls: tracks are abundant, revealing a diversity higher than that suggested by the relatively scarce skeletal material (Fig. 7). The semi-arid climate and pedogenesis interpreted for the Buntsandstein facies in the study area (Galán-Abellán et al. 2013; Borruel-Abadía et al. 2015) probably played a role in fossil preservation. Seven different tetrapod ichnogenera have been preliminary identified (*Rynchosauroides* isp., *Chirotherium barthii* Kaup 1835, *Synaptichnium* isp., *Isochirotherium soergeli* Haubold 1967, *Dicynodontipus* isp., *Rotodactylus* isp. and *Procolophonichnium* isp.) (Calzada 1987; Valdiserri et al. 2009). Overall, they show a remarkably different picture from that of body fossils. Therefore, the real faunal paleobiodiversity is skewed by sedimentary and/or taphonomic biases when the tetrapod ichnological record is not considered (e.g., De Jaime-Soguero et al. 2021; Klein & Lucas 2021). Lowermost Triassic faunas had different patterns across the latitudinal distributions based on both ichnological and osteological records, being archosauromorphs the dominant group in present day North America, central Europe and southeastern Asia, with the highest concentrations at mid-low paleolatitudes (Romano et al. 2020).

Lepidosauromorphs are poorly represented in all regions, with present day Europe including the highest number of occurrences (Romano et al. 2020). As for procolophonids, the distribution during the Early Triassic is well known on the southern hemisphere, mainly in present day South America, Antarctica and South Africa, but also on Russian Platform (Ivakhnenko 1975; Spencer & Benton 2000; Novikov & Sues 2004). During the Middle–Late Triassic, procolophonids became globally distributed (Spencer & Benton 2000).

Track-trackmaker correlation is not usually an easy goal, even more when an osteological bias exists, as in the case of the Montseny fossil record. Nonetheless, a general overview of the identified ichnotaxa provides clues about the taxonomical groups that might have been present in the ecosystem, including *Chirotherium*, *Isochirotherium* and *Synaptichnium* (ichnogenera from the chirotheriid group), are traditionally associated with medium- to large archosauromorphs and more derived archosaurs (Klein & Lucas 2021, and references therein). The Middle Triassic coincided with the period of highest diversification of non-archosaur archosauromorphs, which were globally distributed (Ezcurra 2016; Hoffman et al. 2019). Thus, the tetrapod trace fossils from the Montseny area probably represent a higher taxonomic diversity not observed in the dentognathic and skeletal records (Fig. 7). Herbivorous faunas seem to be scarce and large forms are rare in some ecosystems of the Middle Triassic of central Europe (Schoch et al. 2018). This fact seems to be in agreement with the dentognathic record of the Montseny area, because the recovered teeth were from small-sized predatory organisms (see also discussion in Ezcurra et al. 2017). Further sampling is necessary to elucidate the apparent lack of medium- to large archosauromorph direct remains in the Montseny area, so far only represented in the ichnological record.

Procolophonichnium is an ichnogenus with a wide temporal and (paleo-) geographical distribution, ranging from the Lower to the Middle Triassic of the Buntsandstein and Muschelkalk facies of several European basins, North America and Morocco, and even known from the upper Permian–Lower Triassic of South Africa (Klein et al. 2015; Marchetti et al. 2019). It is currently attributed to procolophonid and/or synapsid therapsid trackmakers (Marchetti et al. 2019; De Jaime-Soguero et al. 2021; Klein and Lucas 2021). Thus, there could be a potential correlation between the procolophonid bone remains and this ichnogenus in the Montseny area. However, considering the wide range of potential trackmakers for *Procolophonichnium*, any interpretation is so far tentative.

Rhynchosauroides is correlated to small archosauromorphs and/or lepidosauromorphs (Fig. 7), although the latter are absent in the osteological record of the Montseny area. Regarding this, *Rhynchosauroides* is a waste-basket ichnotaxon, referable to a wide range of amniote (usually diapsid) taxa, in need of a comprehensive revision (Mujal et al. 2018). Thus, it seems plausible that *Rhynchosauroides* could have been produced by other groups, such as procolophonids, especially considering that *Procolophonichnium* could have been produced by therapsids (see above). Regarding procolophonids, it is remarkable the wide distribution of the genus *Kapes*, represented by several well-known species from the Olenekian and Anisian of Russia, and the Anisian of the UK (Zaher et al. 2019), together with the presence of *Anomoiodon* from the Olenekian of Germany (Säilä 2008). All in all, although so far hypothetical, such relatively wide distribution and high diversity of these parareptiles could be reflected by some morphotypes within the ichnogenus *Rhynchosauroides*, which had a virtually global distribution in the Middle Triassic (De Jaime-Soguero et al. 2021).

Dicynodontipus is associated with therapsid synapsid trackmakers (Marchetti et al. 2019). In a similar manner, *Rotodactylus* trackmakers are unclear and open to debate, with dinosauromorph or non-dinosauromorph archosaurs as potential trackmakers (see Brusatte et al. 2011; De Jaime-Soguero et al. 2021; Klein & Lucas 2021 and references therein for discussion). Unfortunately, the lack of postcranial (and particularly appendicular) osteological material of these taxa from the Montseny area precludes any potential trackmaker correlation for all these ichnogenera.

CONCLUSIONS

The aim of the present work is to reappraise the previously known vertebrate biodiversity of the Middle Triassic of the Montseny area (Catalonia, NE Iberian Peninsula) by studying the dentognathic material available, in order to set a background for further studies of the ecosystems of equatorial Pangea. Eight tooth morphotypes have been identified in the upper Buntsandstein (Anisian, Middle Triassic). They are attributed to abundant capitosaur temnospondyls (Morphotypes T1 and T2), and sparser representatives of archosauromorphs (Morphotype A1), indeterminate diapsids (D1) and procolophonids (Morphotypes P1 to P4).

Capitosaur tooth morphotypes display a high degree of variability, however, remains here studied are most probably attributed to a single taxon, *Calmasuchus acri*. Procolophonid specimens, although fragmentary, display a unique set of dental features among the group, indicating the presence of new species, here erected as *Kapes signus* sp. nov. This new species expands the paleogeographic distribution of the European-Russian genus *Kapes* to lower paleolatitudes.

From a paleoecological perspective (Fig. 7), in the Anisian ecosystems of the Montseny area, capitosaurs were probably top predators in freshwater environments, possibly mostly feeding on fishes and, potentially, opportunistically on near-shore animals such as procolophonids and small archosauromorphs. The archosauromorph tooth suggests the presence of medium carnivorous taxa possibly feeding on other archosauromorphs, procolophonids, temnospondyls and other taxa available in the area, although the low number of specimens makes conclusions for the group so far tentative. The representatives of indeterminate diapsids were possibly small reptiles with faunivorous diets. Procolophonid feeding habits probably included insectivory and durophagous-herbivory, as suggested by the similarities with well-known taxa from other paleolatitudes.

The numerous osteological/dentognathic remains of capitosaurs in the study area is in stark contrast with the null tetrapod ichnological record for this group. This may be related with the almost fully aquatic lifestyle proposed for these animals, leading to an environmental/preservation bias as observed elsewhere. Generally, the osteological record of the Montseny area complements the abundant and diverse tetrapod ichnological one, highlighting preservation and taphonomic biases likely related to habitat preferences of the different tetrapod groups.

In summary, the present study highlights the importance of integrating ichnological and osteological data to better understand paleobiodiversity of past ecosystems, in this case from the Middle Triassic low latitudes of Pangea. This work will serve as a platform for future analyses on the still poorly known tetrapod communities in southwestern Europe and their significance at a broader scale.

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Data Availability

Datasets (raw data and 3D models) related to this article can be found at MorphoSource (https://www.morphosource.org/projects/000592824?locale=en), an open-source online 3D data repository hosted by Duke University Research Computing.

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