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An overview of the crocodylian fossil record from Sardinia (Italy)

Un aperçu sur les crocodiles fossiles de Sardaigne (Italie)

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ABSTRACT: In the present contribution we focus on an overview of the Cenozoic crocodylians of Sardinia (Italy). Crocodylians from this Italian island have been published since the second half of the 19th Century and a number of papers reported on the presence of these vertebrates in 16 different localities. The remains, some of which apparently lost, are mainly represented by isolated teeth housed in historical collections of different museums (in Italy and The Netherlands) that in most cases have never been figured or described. We illustrate for the first time and provide brief descriptions of all crocodylian teeth collected in the island as well as of the still available holotype of *Tomistoma calaritanum*, the only crocodylian taxon established on material from Sardinia. In addition, we report crocodylian remains from two new localities, one of which testifies the presence of these vertebrates already in the Eocene record of the island.

RÉSUMÉ: Dans la présente contribution, nous nous concentrons sur un aperçu des crocodyliens cénozoïques de Sardaigne (Italie). Les crocodiliens de cette île italienne ont été publiés depuis la seconde moitié du 19e siècle et un certain nombre d'articles ont fait état de la présence de ces vertébrés dans 16 localités différentes. Les restes, dont une partie semble avoir été perdue, sont principalement représentés par des dents isolées, conservés dans des collections historiques de différents musées (en Italie et aux Pays-Bas) qui, dans la plupart des cas, n'ont jamais été figurés ni décrits. Nous illustrons pour la première fois et fournissons une brève description de toutes les dents de crocodiliens collectées sur l'île ainsi que de l'holotype encore disponible de *Tomistoma calaritanum*, le seul taxon de crocodilien établi sur du matériel de Sardaigne. En outre, nous signalons des restes de crocodiliens de deux nouvelles localités, dont l'une témoigne de la présence de ces vertébrés déjà dans les dépôts de l'Éocène de l'île.

Keywords: Crocodylidae, Tomistominae, *Tomistoma calaritanum*, Systematic Palaeontology, Cenozoic, Italy.

Most Clés: Crocodylidae, Tomistominae, *Tomistoma calaritanum*, Paléontologie Systématique, Cénozoïque, Italie.

1. INTRODUCTION

1.1. Palaeogeographic context: The Sardinia-Corsica Massif represents a microplate located in the western Mediterranean basin, between the Liguro-Provençal basin and the Tyrrhenian Sea. It represents a segment of the Alpine orogenic system originally located in continuity with the southern European continental margin. From the early Miocene onwards, the Sardinia-Corsica Massif started to separate from the mainland with anticlockwise rotation (Vardabasso, 1962; Cherchi, 1974). Thus, the Sardinian Neogene fossils represent the oldest known case of endemic insular vertebrate faunas from the Mediterranean Sea (Mennecart et al., 2017). However, the palaeogeographic evolution of this area allowed different few immigration phases of mainland vertebrates during the Neogene (Azzaroli and Guazzone, 1979; Van der Made, 1999; Abbazzi et al., 2004, 2008a, 2008b) and especially during the Quaternary (Azzaroli, 1983; Palombo, 1985, 2009; Van der Made, 1999; Pillola and Zoboli, 2017; Zoboli and Caddeo, 2016; Zoboli and Pillola, 2016a, 2017a; Zoboli et al., 2016, 2018).

1.2. Cenozoic Sardinian Paleoherpétology: The Sardinian fossil record of Cenozoic herpetofaunas is rather interesting, though not abundant and certainly incomplete because many extant species have not been traced yet. However, members of each of the higher taxa currently inhabiting the northern hemisphere have been identified: Squamata (Serpentes, Amphisbaenia, “Lacertilia”), Testudines, and Crocodylia. Squamates were reported from the early Miocene (Oschiri; Venczel and Sanchiz, 2006) to the Holocene (Delfino, 2002). Among snakes, worth mentioning is the “exotic” presence of an extinct aniliid snake, *Eoanilius oligocenicus*, at Oschiri (Venczel and Sanchiz, 2006) and the holotype and only specimen of the booid snake *Palaeopython sardus* Portis, 1901 (Portis, 1901a), that was recently identified as an undetermined fish (Delfino et al., 2014). Booid snakes were in any case present in Sardinia during the late Pliocene as testified by *Eryx* from Capo Mannu (D1 Local Fauna; Delfino et al., 2011). The Pleistocene karst fissures of Monte Tuttavista (Abbazzi et al., 2004) yielded thousands of disarticulated snake remains (mostly isolated vertebrae) belonging to a viperid, a still undescribed new colubrid species, and a grass snake of the genus *Natrix*. The viper of Monte Tuttavista along those of two other sites (Venczel and Sanchiz, 2006; Delfino et al., 2011) represents the only Sardinian evidence for this group of snakes currently extinct on the island (Sindaco et al.,

2006). Colubrid snakes (colubrines and *Natrix*) were also identified at Capo Mannu (D1 Local Fauna; Delfino et al., 2011) and in some Quaternary sites (Delfino, 2002).

Lizards are represented at Monte Tuttavista by the most abundant and informative European remains of agamids (Delfino et al., 2008), by the first evidence in Sardinia of a large-sized lacertid lizard that recently turned out to belong to *Timon* (Tschopp et al., 2018), as well as by smaller lacertid lizards and geckos (Abbazzi et al., 2004). Anguid lizards referred to the genus *Dopasia* have been reported from the early Miocene of Oschiri (Venczel and Sanchiz, 2006) and the Pliocene of Capo Mannu (D1 Local Fauna; Delfino et al., 2011); the latter was recently identified as *Ophisaurus spinari* by Klembara and Rummel (2018). Skinks have been also cited or described from the Miocene of Oschiri (Venczel and Sanchiz, 2006) to the Holocene (Delfino, 2002), but their record is very scarce.

In the Pliocene of Capo Mannu (D1 Local Fauna; Delfino et al., 2011) and Pleistocene of Monte Tuttavista (Abbazzi et al., 2004) amphisbaenians are also present and likely belong to the Blanidae. They were already present in the early Miocene of the island (Oschiri) with *Blanus gracilis* Roček 1984 (Venczel and Sanchiz, 2006).

Fossil turtles are rather common in Sardinia and, with a single exception, are all represented by Neogene and Quaternary cryptodires. One exception consists of a still undescribed pleurodire from the Eocene of Cixerri that was preliminarily referred to *Erymnochelys* (Delfino and Rook, 2008a). Among the cryptodires, softshell turtles are present in a few Eocene and Miocene localities. A revision of *Procyclus orbis sardus* (Portis, 1901b) revealed that the name is a *nomen dubium* and the type is actually an indeterminate pan-trionychine (see Georgalis et al. 2017, and references therein). Testudinids are represented by an extinct species, *Testudo pecorinii* Delfino, 2008 (in Abbazzi et al., 2008a), from the late Pliocene of Capo Mannu D4 local fauna (San Vero Milis) and by *Testudo* cf. *T. hermanni* from the Pleistocene of Monte Tuttavista (Abbazzi et al. 2004). Zoboli (2017) reported a large-size phalanx of a probable testudinid from the Major's Collection of the Naturhistorisches Museum Basel. The fossil was collected in the bone breccias of Monte San Giovanni (southern Sardinia) and could testify for the presence of a giant tortoise in the ?Late Pleistocene of Sardinia. Freshwater turtles have been described in a few localities. Fragmentary remains representing the last Italian evidence of *Mauremys* come from the Late Pleistocene of San Giovanni di Sinis (Chesi et al., 2007), whereas

a well-preserved carapace of *Emys orbicularis* comes from Grotta di Monte Meana, near Santadi (Chesi et al., 2008). Marine turtles, referred to Cheloniidae indet., are present in the early Miocene of Noragugume (Chesi, 2008) and in the late Miocene of Cagliari (Zoboli and Pillola, 2016b). *Trachyaspis lardyi* was identified in the Miocene of Bosa (Chesi, 2008) and *Caretta*, was reported only in Holocene archaeological sites (Wilkins, 2003; Delussu, 2007).

The first fossil crocodylians of Sardinia have been published since the second half of the 19th Century (Gennari, 1868; Capellini, 1890a, 1890b) and since then a number of papers reported on the presence or described remains in localities of different subregions of the Island (Fig. 1). The remains, all Miocene in age, are represented in most of the cases by isolated teeth (see below), but also a nearly complete skull and lower jaw (and associated few postcranial elements such as osteoderms and vertebrae) on the basis of which a new species of tomistomine, *Tomistoma calaritanum* Capellini, 1890, was described (as *Tomistoma calaritanus*, see below; Capellini, 1890b). Due to the number of papers published on the subject (often in old Italian local journals, see references below), the damage and loss suffered by the type material of *T. calaritanum* and its convoluted taxonomic and nomenclatural history, it is here presented an overview on the crocodylian fossil record of Sardinia, with a reassessment of the identifications published in the past.

2. THE CROCODYLIAN FOSSIL RECORD OF SARDINIA

The Sardinian crocodylian fossils herein illustrated are housed in historical collections of different museums. Unpublished materials from two new localities, one of which pushing back to the Eocene the presence of crocodylians in the island, are also described.

Institutional Abbreviations: MDLCA, Museo Sardo di Geologia e Paleontologia Domenico Lovisato, Cagliari, Italy; PARC, Paleo Archeo Centro, Genoni, Italy; MACPL, GeoMuseo Monte Arci “Stefano Incani”, Masullas, Italy; MGPT-PU, Museo di Geologia e Paleontologia dell’Università degli Studi di Torino, Turin, Italy; UU, University of Utrecht, Utrecht, The Netherlands.

2.1. YPRESIAN

2.1.1. Locality: Escalaplano (Sarrabus-Gerrei subregion, southern Sardinia).

Age and geological setting: Monte Cardiga Formation (early Eocene, Ypresian; Cherchi, 1985). The Monte Cardiga Fm. is a lithostratigraphic unit discontinuously cropping out in the south-eastern Sardinia (Salto di Quirra, Sarrabus-Gerrei, Ogliastra). In the Escalaplano and Perdasdefogu areas this formation overlies the Palaeozoic basement and the Mesozoic lithologies (Vardabasso, 1962). At the bottom, the Monte Cardiga Fm. is represented by polygenic conglomerates, sandstones with siliceous cement and marly sandstones with scarce plant remains. In the upper part, marls, calcarenites and bioclastic limestones with a rich foraminiferal fauna are predominant; locally, layers of polygenic conglomerates are present. Furthermore, several levels of calcarenite rich in gastropods (cerithids) and other marine invertebrates are present in the medium-basal portion of the sequence. The crocodile tooth was collected in one of these levels cropping out at the southern periphery of the village of Escalaplano. The Monte Cardiga Fm. is referred to the Ypresian on the basis of the micropalaeontological content (Cherchi, 1985).

Taxon: *Crocodylia* indet.

Material: MACPL 1364, one isolated tooth (Fig. 2A).

Description and remarks: The isolated tooth is still embedded in the calcarenite matrix and only what appears to be a moderately altered lingual surface is visible. The apex is broken off and the root is missing. The preserved portion of the crown is 7.7 mm long. The associated marine fauna suggests the transport of the crocodylian remains from the emerged areas to the seaside.

2.2. ?CHATTIAN - BURDIGALIAN

2.2.1. Locality: “Cava Duidduru” (Genoni, Sarcidano subregion, central Sardinia).

Age and geological setting: Nurallao Formation (?Chattian - early Burdigalian, Funedda et al., 2011). The isolated crocodylian tooth was collected in the “Cava Duidduru”, an abandoned quarry currently reconverted in a geosite. The quarry is opened in the ?Chattian - early Burdigalian marine succession of the Nurallao Fm. (Funedda et al., 2011) belonging to the first Cenozoic sedimentary cycle of Sardinia. The Nurallao Fm. is represented by marine-littoral sediments and is divided in two members: Conglomerato di Duidduru member (at the bottom) and Arenarie di Serra Longa member (at the top). The lower member is constituted by

polygenic and heterometric conglomerates mainly resulting from the erosion of the underlying Palaeozoic basement and subordinately by Cenozoic volcanites. The fossil content is represented especially by fragments of bivalve shells. The lithology changes both laterally and vertically in the sandstone and silicoclastic sands of the Arenarie di Serra Longa member. This latest member is represented by sands and microconglomerates that laterally and vertically change in coarse sandstones with carbonate cement. Furthermore, decimetric-conglomerate levels with elements of quartz, metamorphites and granitoids, and tanatocenosis dominated by bivalves and echinids are present. In the Duidduru quarry is present only this last member of the Nurallao Fm. The crocodylian tooth was found in a poorly-cemented grey sandstone level rich in fragments of carbonized plants, turrilline gastropods and crab-shell fragments. This level seems to testify a proximal depositional environment characterized by fluvial transport and deposition of organic material in a coastal lagoon. To date, the crocodylian remains and a mandible of a small ruminant (Mennecart et al., 2017) are the only continental vertebrates collected in the marine deposits of the latest Oligocene - early Miocene of central Sardinia.

Taxon: Crocodylia indet.

Material: PARC 205626, one isolated tooth (Fig. 2B).

Description and remarks: The tooth is represented by a portion of the crown missing its apex and, probably, its base. The preserved portion, 22.3 mm long, is relatively stout. Mesiodistal carinae are present but weakly developed (Fig. 2B5).

2.2.2. Localities: Srintu de Melonis and Comidiano, between Srintu Argiolu and the train station of Nurri (Nurri, Sarcidano subregion, central Sardinia).

Age and geological setting: Nurallao Formation (?Chattian - early Burdigalian, Funedda et al., 2001, see above).

Taxon: Crocodylia indet. (= ?*Tomistoma* sp. in Lovisato, 1892; *Tomistoma calaritanus* in Del Vecchio, 1921, Spano, 1985; Crocodylia indet. in Kotsakis et al., 2004; *Tomistoma calaritanus* in the original label of MGPT-PU).

Material: MGPT-PU 17336, one isolated tooth (Fig. 2C).

Description and remarks: Two incomplete crocodile teeth, previously referred to ?*Tomistoma* sp. (Lovisato, 1892), were collected by Lovisato in a marly limestone cropping out in the southern suburbs of the village of Nurri, near the cemetery of the village (Strintu de Melonis) (Lovisato, 1892). Del Vecchio (1921) listing the crocodile teeth housed in Cagliari reported a single tooth of *Tomistoma calaritanus* from Comidiano, between Strintu Argiolu and the train station of Nurri. Currently, the teeth from Strintu de Melonis are lost whereas the tooth from Comidiano is housed in Turin and accessioned as MGPT-PU 17336. It is a slender and pointed tooth crown, 21.6 mm long, with sparse, weak longitudinal ridges on the labial and lingual surfaces.

2.2.3. Locality: Laerru (Anglona subregion, northern Sardinia).

Age and geological setting: Perfugas Formation (early-middle Burdigalian, between 18.83 +/- 0.13 and 18.29 +/- 0.13 Ma; Oudet et al., 2010; Sowerbutts, 2000). The fossiliferous site is located on the northern periphery of the village of Laerru. An epiclastic pomiceus-cineritic level underlies silicified lacustrine carbonates of the lower part of the Perfugas Formation (Sowerbutts, 2000). This fossiliferous epiclastic level is divided into three different layers, the majority of the vertebrate remains coming from the top of the lower layer (Zoboli and Pillola, 2017b; Mennecart et al., 2019). In the Anglona subregion, the lower part of the Perfugas Fm. comprises continental lacustrine deposits represented by finely bedded limestones and tuffs (Sowerbutts, 2000).

Taxon: Crocodylia indet. (= cf. *Diplocynodon* sp. in Zoboli and Pillola, 2017b).

Material: MDLCA 14114a-d, four isolated teeth (Fig. 2D-G).

Description and remarks: Zoboli and Pillola (2017b) recently described an interesting early Miocene vertebrate fauna from Laerru. Four tiny (crown length of the biggest tooth = 0.9 cm, bucco-labial diameter = 0.3) and incomplete isolated crocodylian teeth were preliminary referred to cf. *Diplocynodon* sp. However, due to the generalized shape of the teeth and therefore the absence of diagnostic characters, the material is here referred to Crocodylia indet. Noteworthy is that *Diplocynodon* is currently considered a European

endemic and was never reported in insular environments as expected for an alligatoroid that could have shared salt-water intolerance with extant alligatorids (Taplin and Grigg, 1989; Delfino et al., 2007; Delfino and Rossi, 2013).

2.2.4. Locality: Oschiri (Monteacuto subregion; northern Sardinia).

Age and geological setting: “Formazione lacustre” *Auct.* = Perfugas Fm. (Burdigalian, MN3; Van der Made, 2008; Zoboli and Pillola, 2017b). The vertebrate site is represented by a small exposure of lacustrine clay in a road cut near the village of Oschiri (De Bruijn and Rümke, 1974). The age of the mammal assemblage of Oschiri has been discussed by several authors (e.g. De Bruijn and Rümke, 1974; Azzaroli and Guazzone, 1979; Azzaroli, 1983; Van der Made, 2008). The micromammals are quite diverse, with nine taxa including seven endemic species (De Bruijn and Rümke, 1974). The advanced endemism of Ctenodactylidae and the presence of Gliridae, Talpidae and Soricidae are very similar to the mainland taxa, and suggest different phases of colonization of the Corsica Sardinia Massif (Ferrandini et al., 2000; Mennecart et al., 2017, 2019). The Oligo-Miocene palaeogeographical context of the western Mediterranean indicates that the latest additions to the insular association arrived in Sardinia during the European Land Mammal Unit MN3, which is coincident with the early Burdigalian marine regression, around 20 Ma ago (Van der Made, 2008; Zoboli and Pillola, 2017b).

Taxon: *Crocodylia* indet.

Material: UU OS 501, one isolated tooth (Fig. 2H).

Description and remarks: The occurrence of crocodylians at Oschiri is already known in the literature according to Delfino et al. (2011: 379, tab. 1) who reported the presence of “an unpublished isolated tooth stored in the collections of Utrecht University (specimen unnumbered)”. This isolated tooth, now UU OS 501, is rather large because even if devoid of most of the root, is 28.6 mm tall and has a labio-lingual diameter of 11.3 mm (the mesiodistal diameter is slightly smaller but this could be due to preservational reasons). The tooth is conical and slightly bent in lingual direction. The surface is variably damaged,

nevertheless the mesiodisal carina is well visible and smooth. The conical depression that is likely present at the base is still filled with sediment.

2.2.5. Locality: La Crucca (Sassari, Sassarese subregion, northwestern Sardinia).

Age and geological setting: Mores Formation (upper Burdigalian). The crocodylian fossil remains were collected in a compact limestone level of the Mores Fm. (upper Burdigalian) cropping out in the locality of La Crucca, about eight kilometers West of Sassari (Spano, 1985).

Taxon: cf. *Tomistoma* sp. (= *Tomistoma calaritanus* in Spano, 1985; *Crocodylia* indet. in Kotsakis et al., 2004).

Material: two lumbar vertebrae, two sacral vertebrae, two caudal vertebrae, ilium, fragment of left ischium, some rib fragments, right femur, some osteoderms from the caudal region (Fig. 3).

Description and remarks: The material from La Crucca belongs to a single individual briefly described and only partially figured by Spano (1985). Despite the fact that we have not been able to locate this material, thanks to the published illustrations it is possible to refer it to a tomistomine crocodylian on the basis of the broad and anteroposteriorly short osteoderms whose ornamentation is represented by relatively few but large pits (compare Fig. 3A with the type osteoderms of *Tomistoma calaritanum* in Fig. 8; see also Piras et al., 2007; Nojima and Itoigawa, 2017; Shan et al., 2017).

2.2.6. Locality: Monte Orria (between Nulvi and Chiaramonti, Anglona subregion, northern Sardinia).

Age and geological setting: Mores Formation (upper Burdigalian). A middle Miocene age has been attributed by Spano (1985) to the material from Monte Orria, instead Kotsakis et al. (2004) indicated a late Miocene age. However, only the upper Burdigalian littoral carbonatic lithofacies of the Mores Fm. is reported in the Monte Orria area. The original label of MGPT-PU 17337 indicates that the only available tooth from Monte Orria was collected in a breccious limestone.

Taxon: *Crocodylia* indet. (= *Crocodylia* indet. in Del Vecchio, 1921; Spano, 1985; Kotsakis et al., 2004; *Tomistoma calaritanus* in the original label of MGPT-PU).

Material: MGPT-PU 17337, one isolated tooth (Fig. 2I).

Description and remarks: Del Vecchio (1921) listing the material collected in Cagliari reported several small fragments of small teeth from Monte Orria, between Nulvi and Chiaramonti. However, only one isolated tooth from this locality is currently housed in Turin. MGPT-PU 17337 is a small, and poorly preserved crown, 9.5 mm long that is nearly completely enamel-free.

2.3. LANGHIAN - SERRAVALLIAN

2.3.1. Locality: Tresnuraghes (Planargia subregion, western Sardinia).

Age and geological setting: “Crabs-rich” marly limestone (Langhian).

Taxon: *Crocodylia* indet. (= *Tomistoma* sp. in Lovisato, 1892; *Tomistoma calaritanus* and *Crocodylia* indet. in Del Vecchio, 1921; *Crocodylia* indet. in Kotsakis et al., 2004).

Material: not available.

Remarks: Lovisato (1892) reported two isolated teeth from this locality and referred them to *Tomistoma* sp. Del Vecchio (1921) listing the material housed in Cagliari reported two teeth different in size (the smallest referred to *Tomistoma calaritanus* and the largest to *Crocodylia* indet.). These teeth are currently not available and it is therefore impossible to provide a description.

2.3.2. Locality: Bingia Fargeri, Fangario (Cagliari).

Age and geological setting: Argille di Fangario Formation (?middle Langhian - lower Serravallian). The Argille di Fangario Fm. is represented by clayey and/or sandy gray-yellowish marls, developing upward to marly sandstones, with foraminifers, corals, brachiopods, echinoids, molluscs and ichthyolitic fragments,

The micropalaeontological content allows to refer this succession to the ?middle Langhian - lower Serravallian (Cherchi, 1974).

Taxon: *Crocodylia* indet. (= *Tomistoma* cf. *Tomistoma calaritanus* in Capellini, 1890b; *Tomistoma* sp. in Lovisato, 1892; *Tomistoma calaritanus* in Del Vecchio, 1921; *Tomistoma calaritanus* in Spano, 1985; *Crocodylia* indet. in Kotsakis et al., 2004; *Crocodylus calaritanus* in the original label of MGPT-PU).

Material: MGPT-PU 17334, one incomplete isolated tooth (Fig. 2J). Two isolated teeth figured by Del Vecchio, 1921 (Fig. 2K-L).

Description and remarks: Capellini (1890b) reported an incomplete tooth collected by Lovisato at Bingia Fargerì. The author referred the fossil to *Tomistoma* cf. *calaritanus* but Lovisato (1892) referred the tooth to *Tomistoma* sp. Later on, Del Vecchio (1921) described and figured two elongated teeth attributed to *Tomistoma calaritanus* from Bingia Fargerì (Fig. 2K-L). In addition, the author mentioned a third elongated tooth from the same locality. The only available tooth from Bingia Fargerì is now MGPT-PU 17334. It is not possible to correlate the sample housed in Turin with the material mentioned but not figured by Capellini (1890b) and Lovisato (1892). Furthermore, MGPT-PU 17334 is too different from those illustrated by Del Vecchio (1921). MGPT-PU 17334 is a massive crown, 21.5 mm tall, with a worn apex and the surface of the base only partly preserved. However, most of both the labial and lingual surface is preserved and distinctly smooth.

2.3.3. Locality: Florinas (Sassarese subregion, northwestern Sardinia).

Age and geological setting: Florinas Formation (Serravallian). The teeth were found in a sand quarry about two kilometers South of the village of Florinas.

Taxon: *Crocodylia* indet. (= ?*Tomistoma lusitanica* in Marras and Ventura, 1985; *Crocodylia* indet. in Kotsakis et al., 2004).

Material: four isolated teeth. According to Marras and Ventura, 1985 (pp. 25), these teeth were hosted in a private collection: "Si ringrazia il sig. Alberto Piga per averci gentilmente prestato il materiale [Mr. Alberto Piga is thanked for having kindly loaned us the material]". We have not been able to locate the material.

Remarks: The teeth were previously described and figured by Marras and Ventura (1985). The authors doubtfully ascribed the fossils to *Tomistoma lusitanica* (Vianna and Moraes, 1945).

2.4. TORTONIAN - MESSINIAN

2.4.1. Locality: Fiume Santo (Porto Torres, Nurra subregion, northwestern Sardinia).

Age and geological setting: Alluvial deposit (Tortonian - early Messinian). Several isolated crocodylian teeth were collected in the site of Fiume Santo, in upper Miocene alluvial sediments of the third Miocene sedimentary cycle recognized in Sardinia. The detailed stratigraphic data and the geological context of the site of Fiume Santo are not satisfactorily known, however, a late Tortonian - early Messinian age is suggested by the associated Turolian mammal fauna (Abbazzi et al., 2008b; Casanovas-Vilar et al., 2011).

Taxon: *Crocodylia* indet. (= *Crocodylia* indet. in Kotsakis et al., 2004; Abbazzi et al. 2008b).

Material: 49 isolated teeth (unnumbered) hosted in the collections of the Soprintendenza Archeologia, belle arti e paesaggio per le province di Sassari e Nuoro (Fig. 5M-N).

Description and remarks: The general morphology of the crocodylian teeth from Fiume Santo was already described in Abbazzi et al. (2008b) and the two isolated teeth figured here for the first time fit well with that description. The smallest (Fig. 5M; 22.10.1996, Area Ingresso Nord; Zona B), 11.0 mm tall, comes from the posterior section of a maxillary or dentary tooth row; it has well-marked mesiodistal carinae that are even more highlighted by a groove that runs parallel to them on both the lingual and labial surfaces. The largest (Fig. 5N; 23.10.1996, Area Ingresso Nord; A1/BD IV; terra di setacciatura) is massive and 22.1 mm tall, it was probably located in one of the largest alveoli of the tooth row.

2.4.2. Locality: Capo Frasca (Arbus, Monreale subregion, western Sardinia).

Age and geological setting: Capo San Marco Formation (early Messinian). The fossil was collected by Lovisato in a compact limestone.

Taxon: *Crocodylia* indet. (= *Tomistoma* sp. in Lovisato 1892; *Crocodylia* indet. in Del Vecchio 1921; *Tomistoma calaritanus* in Spano 1985; *Crocodylia* indet. in Kotsakis et al. 2004; *Tomistoma calaritanus* in the original label of MGPT-PU).

Material: MGPT-PU 17335, one isolated tooth (Fig. 5L).

Description and remarks: This small, conical fragment can tentatively be considered a portion of the crown of a crocodylian tooth missing both the tip and the base.

2.4.3. Locality: Tuvumannu = Monte San Giuseppe or Monte della Pace (Cagliari).

Age and geological setting: Calcari di Cagliari Formation (late Tortonian - early Messinian). The type material of *Tomistoma calaritanum* and several isolated crocodylian teeth were found in the carbonate succession of the Calcari di Cagliari Fm. (Gandolfi and Porcu, 1967; Cherchi, 1974), cropping out only in the Cagliari area. This succession is represented by three main lithofacies which are, from the bottom to top: “Pietra Cantone”, “Tramezzario” and “Pietra Forte”. Note that the names, informally adopted in the most recent official geological map (Barca et al., 2005), are derived from the names used by quarrymen (Georgalis et al., 2017). The bottom lithofacies (“Pietra Cantone”) is represented by yellow marly-arenaceous limestone with common intense bioturbation. The “Tramezzario” (or “Tramezzara”) is represented by calcarenites and marls with abundant bioclastic components. This lithofacies shows widespread phenomena of syndimentary breccias, slumpings, erosional surfaces and faulting. The uppermost lithofacies (“Pietra Forte” or “Pietra di Bonaria”) consists of massive coarse biostromal limestones (Barca et al., 2005). The carbonate succession of Cagliari is considered to be late Miocene in age (Kotsakis, 1985; Zoboli and Pillola, 2016b). The Tortonian-Messinian boundary is tentatively placed within the upper part of the “Pietra Cantone” (Georgalis et al., 2017).

Crocodylian remains were collected in different localities of Cagliari since the beginning of the 19th Century: Tuvumannu, Piazza d’Armi, Is Mirrionis (= Mirioni in Gennari, 1868; Is Meriones in Capellini

1890b; Is Miriones in Kotsakis et al., 2004), Bonaria, Cimitero Monumentale di Bonaria, Cava Timon - Montixeddu di Bonaria (Gennari, 1868; Capellini, 1890a, 1890b; Lovisato, 1892; Del Vecchio, 1921). The type of *Tomistoma calaritanum* was collected in the “Tramezzario” lithofacies cropping out in the Is Mirrionis neighbourhood (Piazza d’Armi). The associated reptile fauna from Is Mirrionis consists of the type material of the turtle *Procyclus sardus* Portis, 1901, currently referred to an indeterminate pan-trionychine (Georgalis et al., 2017), and of other few isolated pan-trionychine remains (Comaschi Caria, 1958).

Taxon: *Crocodylia* indet. (= *Crocodylia* indet. in Capellini, 1890b, Lovisato, 1892; Del Vecchio, 1921; *Crocodylus* sp. in the original label of MGPT-PU).

Material: MGPT-PU 17333/2, from the “Tramezzario” lithofacies (Fig. 4K); MGPT-PU 17333/1, one isolated tooth from the “Pietra Forte” lithofacies (Fig. 5A).

Description and remarks: Lovisato (1892) reported a large size tooth from the “Tramezzario” of Monte San Giuseppe (= Tuvumannu) and referred it to a “true crocodile”. Lovisato (1829) and Del Vecchio (1921) did not provide the figures of the material from Tuvumannu, therefore a sure correlation with the teeth housed in Turin is not possibile. MGPT-PU 17333/1 (Fig. 5A) is a partial crown, about 26 mm long, still embedded in a block of matrix whereas MGPT-PU 17333/2 (Fig. 4K) is the apex, 14.9 mm long, of a slender and thin tooth with sharp mesiodistal carinae delimiting a broad labial surface and a relatively small lingual surface (Fig. 4K5).

2.4.4. Locality: Bonaria, Montixeddu di Bonaria - Cava Timon (Cagliari).

Age and geologica setting: Calcari di Cagliari Formation (late Tortonian - early Messinian, Gandolfi and Porcu, 1967, see above).

Taxon: *Crocodylia* indet. (= *Crocodylia* indet. in Del Vecchio, 1921 and Kotsakis et al., 2004; *Tomistoma calaritanus* and “*Crocodylus*” sp. in the original label of MGPT-PU).

Material: All teeth are from the “Pietra Forte” lithofacies. MGPT-PU 17330/1, one isolated tooth from Bonaria (Fig. 5J); MGPT-PU 17330/2, two incomplete teeth from Bonaria (Fig. 5H-I); MGPT-PU 17330/3, one isolated tooth from Bonaria (Fig. 5F); MGPT-PU 17330/4, one isolated tooth from Montixeddu di Bonaria - Cava Timon (Fig. 5C); MGPT-PU 17330/5, one isolated tooth from Montixeddu di Bonaria - Cava Timon (Fig. 5G); MGPT-PU 17330/6, one isolate tooth from Bonaria (Fig. 5E); MGPT-PU 17330/7, one isolated tooth from Montixeddu di Bonaria - Cava Timon (Fig. 5K). MGPT-PU 17330/8, one isolated tooth from Montixeddu di Bonaria (Fig. 5D).

Description and remarks: These isolated and incomplete teeth have a total length varying from 5.4 mm (MGPT-PU 17330/3) to about 42 mm (MGPT-PU 17330/7) or even to about 45 mm in the case of MGPT-PU 17330/8 whose state of preservation casts some doubt on its identity as crocodylian. As shown in Fig. 5, some of them are still embedded in a small block of matrix. Curiously, the only preserved mesiodistal carina of MGPT-PU 17330/4 bifurcates proximally (Fig. 5C3).

2.4.5. Locality: Cimitero Monumentale di Bonaria (Cagliari).

Age and geological setting: Calcari di Cagliari Formation (late Tortonian - early Messinian, Gandolfi and Porcu, 1967, see above).

Taxon: Crocodylia indet. (= Crocodylia indet. in Del Vecchio, 1921 and Kotsakis et al., 2004; *Tomistoma calaritanus* in the original label of MGPT-PU).

Material: MGPT-PU 17331/4, one isolated tooth from the “Pietra Forte” lithofacies (Fig. 5B).

Description and remarks: the exposed portion of the partly embedded crown MGPT-PU 17331/4 is very well preserved and shows the wrinkles of the enamel surface extending onto the mesiodistal carinae; considering also the basal portion of the crown that is only minimally preserved, the remain is 23 mm long.

2.4.6. Locality: Is Mirrionis – Piazza d’Armi (Cagliari). The original labels of the material housed at MGPT-PU indicate two different localities: "Is Mirrionis" and "Piazza d'Armi". However, Piazza d'Armi is actually

included in the Is Mirrionis neighborhood, therefore, we prefer to group together all of the isolated crocodylian teeth from these toponyms.

Age and geological setting: Calcari di Cagliari Formation (late Tortonian - early Messinian, Gandolfi and Porcu, 1967, see above).

Taxa: *Crocodylia* indet. (= *Crocodylia* indet. in Del Vecchio, 1923 and Kotsakis et al., 2004; *Tomistoma calaritanus* in the original label of MGPT-PU).

Material: all fossils are from the “Tramezzario” lithofacies. MGPT-PU 17332/1, two isolated teeth (Fig. 4 A-B); MGPT-PU 17332/2, one isolated tooth (Fig. 4D); MGPT-PU 17332/3, one isolated tooth (Fig. 4C); MGPT-PU 17332/4, one isolated tooth (Fig. 4E); MGPT-PU 17332/5, two incomplete tooth (Fig. 4F-G). MGPT-PU 17331/1, one isolated tooth (Fig. 4H); MGPT-PU 17331/2, one isolated tooth (Fig. 4I); MGPT-PU 17331/3, one isolated tooth (Fig. 4J).

Description and remarks: Is Mirrionis: the sample of isolated teeth from Is Mirrionis is characterized by a relatively small size, being the smallest (MGPT-PU 17332/2) just 9 mm long and the largest (one of the two teeth accessioned under the number MGPT-PU 17332/5) about 28 mm long (including the portion that is partly hidden). Some of the teeth are still embedded in a whitish matrix. Piazza d’Armi: MGPT-PU 17331/1 (Fig. 4H) is an isolated, fragmentary crown, 27.2 mm long, whereas MGPT-PU 17331/2 (Fig. 4I) is a large, massive crown, about 36 mm long; the latter is still embedded in the matrix and shows prominent mesiodistal carinae. Also MGPT-PU 17331/3 (Fig. 4J) is still embedded in a small block but it is heavily damaged; it is an elongated tooth with a total length of approximately 39 mm. These isolated teeth, despite the absence of diagnostic characters, may belong to the tomistomine crocodylian described below.

2.4.7. Locality: Piazza d’Armi (Cagliari).

Age and geological setting: Calcari di Cagliari Formation (late Tortonian - early Messinian, Gandolfi and Porcu, 1967, see above).

Taxon: *Tomistoma calaritanum* Capellini, 1890.

Material: one incomplete cranium (MDLCA 148) (Fig 9B-C), eight incomplete osteoderms (MDLCA 14401) (Fig. 8A2, E-G, I, L3, M3, N2), casts of the restored cranium (Fig. 9A) and six osteoderms (Fig. 8D, H2, J2, K2, L2, M2) (collection of Dipartimento di Scienze Chimiche e Geologiche of the University of Cagliari; note that these casts are a copy of the original casts housed in the Museo Geologico G. Capellini of Bologna). Part of the cranium (Fig. 7A-B), some osteoderms (Fig. 8B-C), cervical vertebrae (Fig. 7C-D) and cervical ribs (Fig. 7E-F) were lost or destroyed during the Second World War.

The holotype of *Tomistoma calaritanum* Capellini, 1890: The comparison of the descriptions and illustrations provided by Capellini (1890b) with the current state of preservation of MDLCA 148 (Fig. 9B) clearly indicates that most of the skeletal elements and the morphological information they provided is now lost. As emphasized by Capellini (1890b, p. 514), the figures in his publication do not clearly identify what is represented by plaster versus real bones. However, the color of the plaster cast of the original restored skull (Fig. 9A) represents the only way to discriminate the real extent of the restoration work performed by Capellini. The main skeletal elements still preserved are the posterior region of both the maxillae, part of the nasals and quadratojugals (Fig. 10). The lower jaw still preserves the posterior region of the dentaries, part of the surangular and angular (the latter only on the left side). The surface of the block preserves the morphology of the inner surface of part of the elements of the dorsal area (the posterior area of the nasals and maxillae in particular). Moreover, very fragmentary skeletal elements in section are preserved on the anterior, posterodorsal, and posterior surfaces of the block. They do not provide relevant morphological information and in many cases they cannot be identified with certainty.

The currently available eight osteoderms, collectively accessioned as MDLCA 14401 (Fig. 8), are variably incomplete but share the same external ornamentation characterized by relatively few and very large pits. The anterior smooth surface is anteroposteriorly short and the longitudinal keel is rather low. The largest of the osteoderms (plaster cast Fig. 8H2) is 68 mm wide and 92 mm long. Capellini (1890b) reported the presence of about twenty osteoderms, but figured only nine specimens (the original photographs by Capellini are here shown in Fig. 8A1, B, C, H1, J1, K1, L1, M1, N1). Five of these nine osteoderms figured by Capellini (1890b) are currently lost (Fig. 8B, C, H1, J1, K1), but the plaster casts of three specimens are still

available (Fig. 8H2, J2, K2). Moreover, four incomplete osteoderms originally not figured by Capellini (1890b) are currently available (Fig. 8E, F, G, I) and the plaster cast of a lost specimen is available (Fig. 8D).

Capellini (1890b) listed and briefly described several, mostly incomplete vertebrae (fragments of the I-II cervical vertebrae, the III, IV, VI, VIII, IX cervical vertebrae, fragments of the first dorsal vertebrae, one lumbar vertebra and one caudal vertebra) but figured only two of them (tav IV, figs. 10-11 in Capellini 1890b; Fig. 9C, D in this paper). In addition, Capellini (1890b) figured two cervical ribs (tav. IV, figs. 12-13 in Capellini, 1890b; Fig. 7E, F in this paper). All vertebrae and cervical ribs are currently lost.

Remarks and nomenclatural issues: Gennari (1868) conditionally proposed the name *Croc. Caralitanus* (= *Crocodylus caralitanus*) for the taxon from Piazza d'Armi. Since the paper was published before 1961, according to the Article 11.5.1 of ICZN (1999) the name is not to be excluded just because of the conditional context in which it was proposed. It is actually an available name because Gennari (1868: 128-129) provided a brief description focusing on the elongated snout, on its length versus the length of the rest of skull, and on the number ($24/20 = 84$), the disposition, and the shape of the teeth that resemble *Gavialis gangeticus* and *Crocodylus acutus*. Few decades later, Capellini (1890a,b) clarified that the specimen was actually a tomistomine crocodylian.

Regardless of the generic referral, even if the specific epithet *Crocodylus caralitanus* Gennari, 1868 is available, it is here proposed a reversal of precedence in favor of *Tomistoma calaritanus* Capellini, 1890 because: 1) the senior synonym was never used after 1899 (article 23.9.1.1; ICZN, 1999) (apparently it was used only by Gennari in 1868; and then mentioned by Capellini, 1890, as the name written on the tag of the specimen by Gennari himself), and 2) the junior synonym has been used in the last 50 years in at least in 25 works (sometimes as *T. calaritanum*, see below; Kotsakis and Palombo, 1979; Esu and Kotsakis, 1983; Spano, 1985; Comaschi Caria, 1986; Antunes and Ginsburg, 1989; Rossmann et al., 1996; Brochu, 1997, 2001; Crespo, 2001; Kotsakis et al., 2004; Weems, 2006; Piras et al., 2007; Mas and Antunes, 2008; Delfino, 2010; Delfino and Ragazzini, 2010; Fanti, 2010; Gerali, 2012, 2014; Delfino and Rossi, 2013; Delfino and Rook, 2008b; Abate and Fanti, 2014; Delfino et al., 2014; Jouve et al., 2014; Georgalis et al., 2016, 2017; Zoboli and Pillola, 2016b) published by at least 10 authors in a time span encompassing more than 10 years (article 23.9.1.2; ICZN, 1999). Therefore, it is here formally proposed to maintain the prevailing name

Tomistoma calaritanus Capellini, 1890 that becomes a nomen protectum, whereas *Crocodylus caralitanus* Gennari (1868) is a nomen oblitum. However, worth noting is that Kotsakis et al. (2004) and Piras et al. (2007), considering that the gender of the epithet *Tomistoma* is neutral, correctly modified the specific epithet in *Tomistoma calaritanum*. A reassessment of the validity of this species will be the subject of another project that requires a broad comparison of the holotype with several other extinct tomistomes that were diagnosed and named in the past.

2.5. UNKNOWN AGE

2.5.1. Locality: unknown

Age and geological setting: unknown

Taxon: Crocodylia indet. (= *Tomistoma calaritanus* in Del Vecchio, 1921).

Material: one isolated tooth figured by Del Vecchio, 1921 (Fig. 50). The specimen is not present in the collection of MDLCA and MGPT-PU.

3. CONCLUSIONS

The crocodylian remains from most of the Sardinian localities are exclusively represented by isolated teeth that are not diagnostic beyond the ordinal level despite their original referral (in museum labels or published papers) to *Crocodylus*, *Diplocynodon* or *Tomistoma*. The relevant exception is represented by the remains from Piazza d'Armi in Cagliari referred by Gennari (1868) to the new species *Crocodylus caralitanus* and later on by Capellini (1890a, b) to *Tomistoma calaritanus*. Here we provide evidence for the reversal of precedence in favor of the latter name, that, however, being *Tomistoma* neutral, should be *Tomistoma calaritanum*. The holotype was a relatively well-preserved skull (and associated osteoderms and vertebrae) in origin but was damaged during WWII and then partly lost. The only other informative material from Sardinia consists of some osteoderms and other postcranial elements that are now apparently lost; it comes from the late Burdigalian of La Crucca and can be tentatively referred to a tomistomine. Since extinct

tomistomines are generally found in coastal environments and therefore they were likely able to easily disperse, the validity of *Tomistoma calaritanum* should be reassessed in the context of a broad revision of the Tethysean tomistomines.

Disclosure of interest

The authors declare that they have no competing interest.

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FIGURES

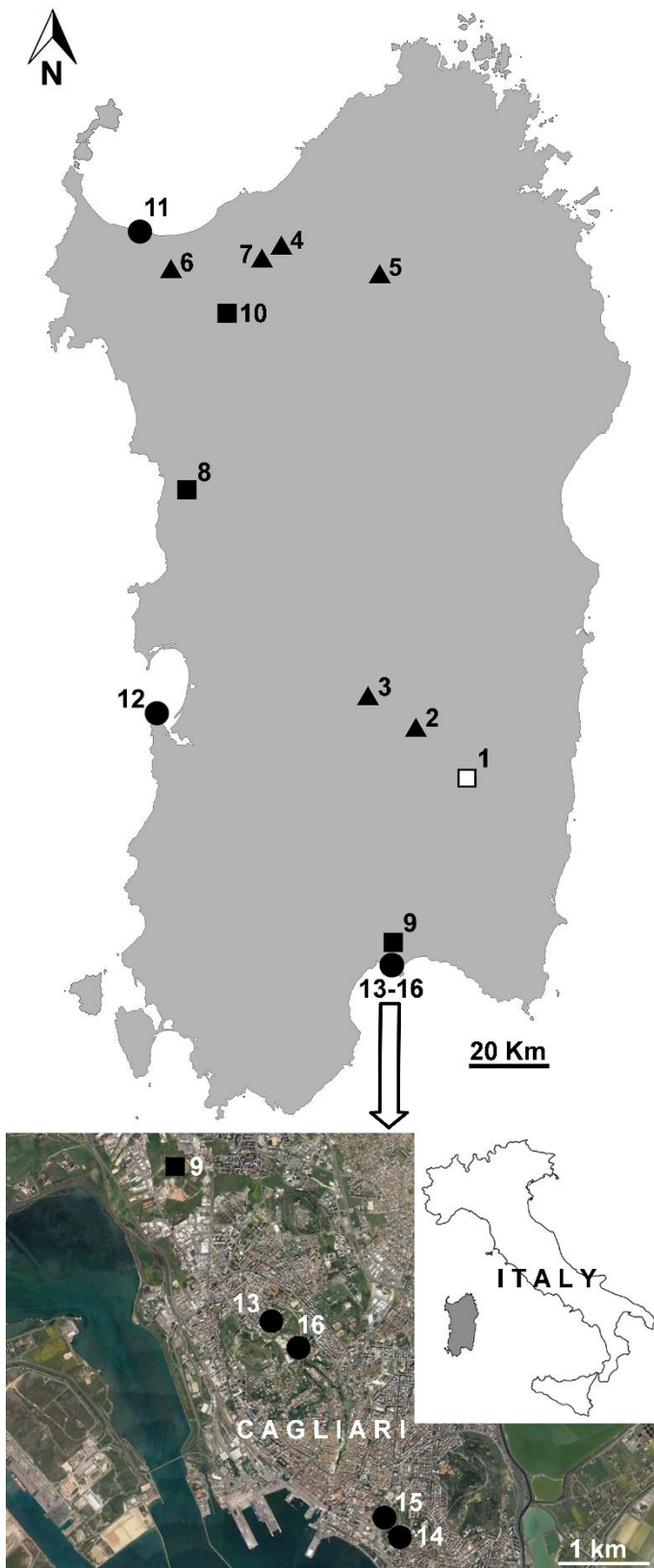


Fig. 1. Sardinian Cenozoic crocodylian-bearing localities: 1, Escalaplano; 2, Cava Duidduru (Genoni); 3, Strintu de Melonis and Comidiano (Nurri); 4, Laerru; 5, Oschiri; 6, La Crucca (Sassari); 7, Monte Orria (Nulvi); 8, Tresnuraghes; 9, Bingia Fargeri (Cagliari); 10, Florinas; 11, Fiume Santo (Porto Torres); 12,

Capo Frasca (Arbus); 13, Tuvumannu; 14, Bonaria and Montixeddu di Bonaria - Cava Timon; 15, Cimitero Monumentale di Bonaria; 16, Is Mirrionis - Piazza d'Armi. White square: Ypresian, triangles: ?Chattian-Burdigalian, black squares: Langhian-Serravallian, circles: Tortonian-Messinian.

Fig. 1. Localités cénozoïques ayant livré de restes des crocodiles: 1, Escalaplano; 2, Cava Duidduru (Genoni); 3, Strintu de Melonis et Comidiano (Nurri); 4, Laerru; 5, Oschiri; 6, La Crucca (Sassari); 7, Monte Orria (Nulvi); 8, Tresnuraghes; 9, Bingia Fargeri (Cagliari); 10, Florinas; 11, Fiume Santo (Porto Torres); 12, Capo Frasca (Arbus); 13, Tuvumannu; 14, Bonaria et Montixeddu di Bonaria - Cava Timon; 15, Cimitero Monumentale di Bonaria; 16, Is Mirrionis - Piazza d'Armi. Carré blanc: Ypresien, triangles: ?Chattian-Burdigalien, carrés noirs: Langhien-Serravallien, cercles: Tortonien-Messinien.

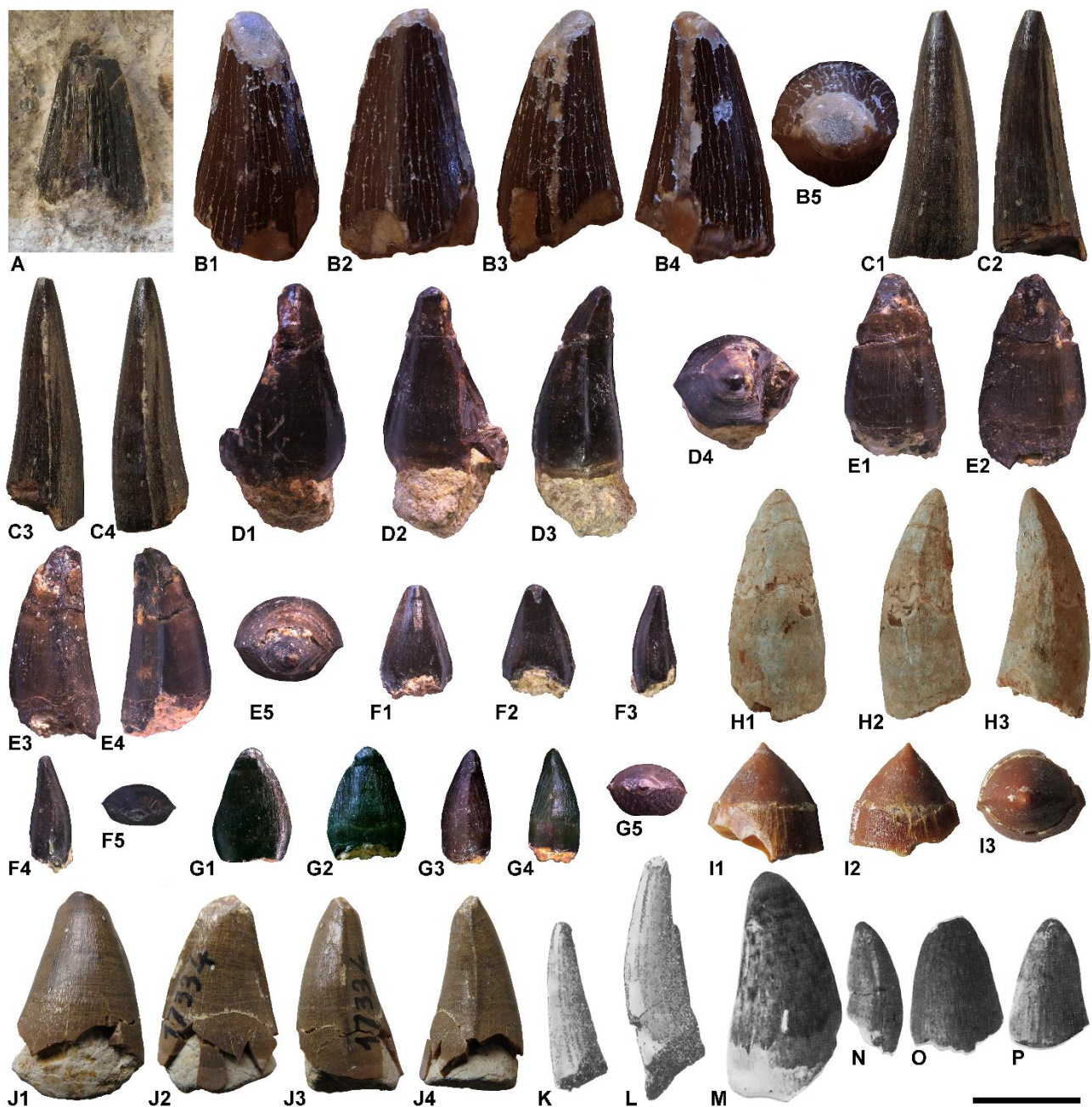


Fig. 2. *Crocodylia* indet., isolated teeth from different localities of Sardinia. A, MACPL 1364 from the Ypresian of Escalaplano (southern Sardinia). B, PARC 205626 from the ?Chattian - early Burdigalian of “Cava Duidduru”, Genoni (central Sardinia); B1, labial view; B2, lingua view; B3-4, lateral view; B5, occlusal view. C, MGPT-PU 17336 from the ?Chattian - early Burdigalian of Comidiano, between Strintu Argiolu and the train station of Nurri (central Sardinia); C1, labial view; C2, lingual view; C3-4, lateral view. D, MDLCA 14114a from the early-middle Burdigalian of Laerru (northern Sardinia); D1, labial view; D2, lingual view; D3, lateral view; D4, occlusal view. E, MDLCA 14114b from the early-middle Burdigalian of

Laerru; E1, labial view; E2, lingual view; E3-4, lateral view; E5, occlusal view. F, MDLCA 14114c from the early-middle Burdigalian of Laerru; F1, labial view; F2, lingual view; F3-4, lateral view; F5, occlusal view. G, MDLCA 14114d from the early-middle Burdigalian of Laerru; G1, labial view; G2, lingual view; G3-4, lateral view; G5, occlusal view. H, UU OS 501 from the Burdigalian of Oschiri (northern Sardinia); H1, labial view; H2-3, lateral view. I, MGPT-PU 17337 from the upper Burdigalian of Monte Orria, between Nulvi and Chiaramonti (northern Sardinia); I1, labial view; I2, lingual view; I3, occlusal view. J, MGPT-PU 17334 from the ?middle Langhian - lower Serravallian of Bingia Fargeri, Cagliari (southern Sardinia); J1, labial view; J2, lingual view; J3-4, lateral view. K-L, from the ?middle Langhian - lower Serravallian of Bingia Fargeri, Cagliari (from Del Vecchio, 1921). M-P, from the Serravallian of Florinas (northwestern Sardinia) (A. Piga private collection, from Marras and Ventura, 1985). Scale bar for A, E, F: 0.5 cm; scale bar for B, C, I, J: 1 cm; scale bar for D: 0.6 cm; scale bar for G: 0.3 cm; scale bar for H: 1.5 cm; scale bar for K-P: 2 cm.

Fig. 2. *Crocodylia* indet., dents isolées provenant de différentes localités de Sardaigne. A, MACPL 1364 de l'Ypresien d'Escalaplano (sud de la Sardaigne). B, PARC 205626 du ?Chattien - Burdigalien inférieur de "Cava Duidduru", Genoni (Sardaigne centrale); B1, vue labiale; B2, vue linguale; B3-4, vue latérale; B5, vue occlusale. C, MGPT-PU 17336 du ?Chattien - Burdigalien inférieur de Comidiano, entre Strintu Argiolu et la gare de Nurri (Sardaigne centrale); C1, vue labiale; C2, vue linguale; C3-4, vue latérale. D, MDLCA 14114a du Burdigalien inférieur-moyen de Laerru (nord de la Sardaigne); D1, vue labiale; D2, vue linguale; D3, vue latérale; D4, vue occlusale. E, MDLCA 14114b du Burdigalien inférieur-moyen de Laerru; E1, vue labiale; E2, vue linguale; E3-4, vue latérale; E5, vue occlusale. F, MDLCA 14114c du Burdigalien inférieur-moyen de Laerru; F1, vue labiale; F2, vue linguale; F3-4, vue latérale; F5, vue occlusale. G, MDLCA 14114d du Burdigalien inférieur-moyen de Laerru; G1, vue labiale; G2, vue linguale; G3-4, vue latérale; G5, vue occlusale. H, UU OS 501 du Burdigalien d'Oschiri (nord de la Sardaigne); H1, vue labiale; H2-3, vue latérale. I, MGPT-PU 17337 du Burdigalien supérieur de Monte Orria, entre Nulvi et Chiaramonti (nord de la Sardaigne); I1, vue labiale; I2, vue linguale; I3, vue occlusale. J, MGPT-PU 17334 du ?Langhien moyen - Serravallien inférieur de Bingia Fargeri, Cagliari (sud de la Sardaigne); J1, vue labiale; J2, vue linguale; J3-

4, vue latérale. K-L, du ?Langhien moyen - Serravallien inférieur de Bingia Fargeri, Cagliari (d'après Del Vecchio, 1921). M-P, du Serravallien de Florinas (Sardaigne du Nord-Ouest) (collection privée A. Piga, de Marras et Ventura, 1985). Barre d'échelle pour A, E, F: 0,5 cm; barre d'échelle pour B, C, I, J: 1 cm; barre d'échelle pour D: 0,6 cm; barre d'échelle pour G: 0,3 cm; barre d'échelle pour H: 1,5 cm; barre d'échelle pour K-P: 2 cm.

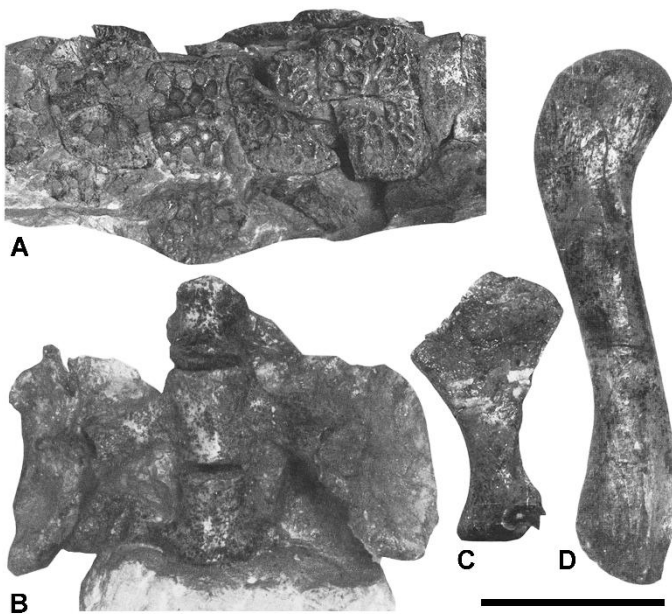


Fig. 3. cf. *Tomistoma* sp. from the late Burdigalian of La Crucca (Sassari), Italy. A, osteoderms from the caudal region. B, articulated vertebrae (two sacral and one lumbar) and iliac bones, ventral view. C, incomplete left ischium. D, right femur. Scale bar: 10 cm. All figures modified from Spano, 1985.

Fig. 3. cf. *Tomistoma* sp., fin du Burdigalien de La Crucca (Sassari), Italie. A, ostéodermes de la région caudale. B, vertèbres articulées (deux sacrales et une lombaire) et os iliaques, vue ventrale. C, ischium gauche incomplet. D, fémur droit. Barre d'échelle: 10 cm. Tous les figures d'après Spano, 1985.

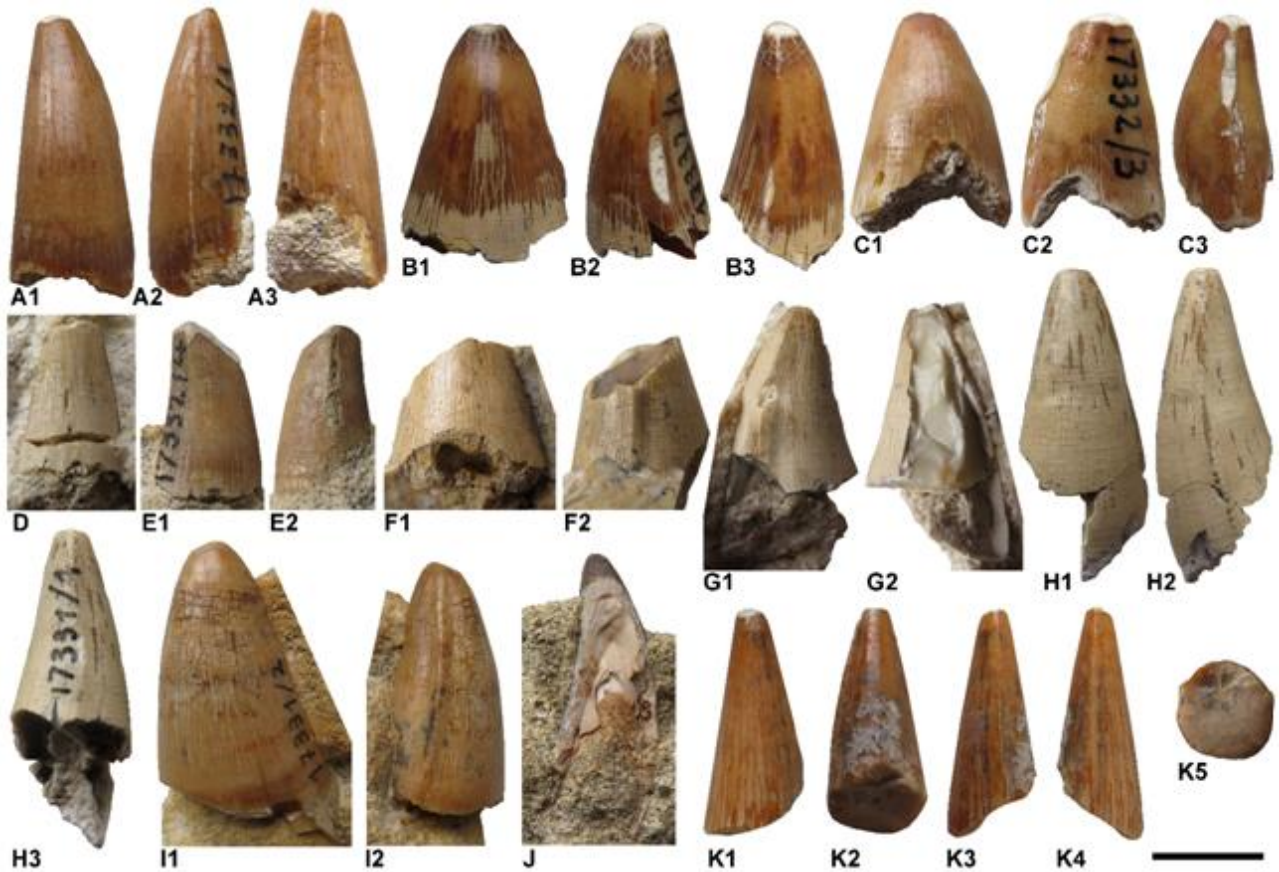


Fig. 4. Crocodylia indet., isolated teeth from the “Tramezzario” lithofacies (early Messinian) of Cagliari (southern Sardinia). A, MGPT-PU 17332/1 from Is Mirrionis; A1, labial view; A2-3, lateral view. B, MGPT-PU 17332/1 from Is Mirrionis; B1, labial view; B2-3, lateral view. C, MGPT-PU 17332/3 from Is Mirrionis; C1, Labial view, C2, lingual view; C3, lateral view. D, MGPT-PU 17332/2 from Is Mirrionis. E, MGPT-PU 17332/4 from Is Mirrionis; E1, labial view; E2, lateral view. F, MGPT-PU 17332/5 from Is Mirrionis (near Piazza d’Armi); F1, labial view; F2, lateral view. G, MGPT-PU 17332/5 from Is Mirrionis (near Piazza d’Armi); G1-2, linguo-lateral view. H, MGPT-PU 17331/1 from Piazza d’Armi; H1, labial view; H2-3, lateral view. I, MGPT-PU 17331/2 from Piazza d’Armi; I1, labial view; I2, lateral view. J, MGPT-PU 17331/3 from Piazza d’Armi, labial view. K, MGPT-PU 17333/2 from Tuvumannu (also called Monte San Giuseppe or Monte della Pace); K1, labial view; K2, lingual view; K3-4, lateral view; K5, cross section. Scale bar for A-C, E, F, H: 1 cm; scale bar for D, K: 0.6 cm; scale bar for G, I, J: 1.5 cm.

Fig. 4. Crocodylia indet., dents isolées issus des lithofaciès «Tramezzario» (début Messinien) de Cagliari (sud de la Sardaigne). A, MGPT-PU 17332/1, Is Mirrionis; A1, vue labiale; A2-3, vue latérale. B, MGPT-PU

17332/1, Is Mirrionis; B1, vue labiale; B2-3, vue latérale. C, MGPT-PU 17332/3, Is Mirrionis; C1, vue labiale, C2, vue linguale; C3, vue latérale. D, MGPT-PU 17332/2, Is Mirrionis. E, MGPT-PU 17332/4, Is Mirrionis; E1, vue labiale; E2, vue latérale. F, MGPT-PU 17332/5, Is Mirrionis (près de la Piazza d'Armi); F1, vue labiale; F2, vue latérale. G, MGPT-PU 17332/5, Is Mirrionis (près de la Piazza d'Armi); G1-2, vue linguo-latérale. H, MGPT-PU 17331/1, Piazza d'Armi; H1, vue labiale; H2-3, vue latérale. I, MGPT-PU 17331/2, Piazza d'Armi; I1, vue labiale; I2, vue latérale. J, MGPT-PU 17331/3, Piazza d'Armi, vue labiale. K, MGPT-PU 17333/2, Tuvumannu (également appelé Monte San Giuseppe ou Monte della Pace); K1, vue labiale; K2, vue linguale; K3-4, vue latérale; K5, coupe transversale. Barre d'échelle pour A-C, E, F, H: 1 cm; barre d'échelle pour D, K: 0,6 cm; barre d'échelle pour G, I, J: 1,5 cm.

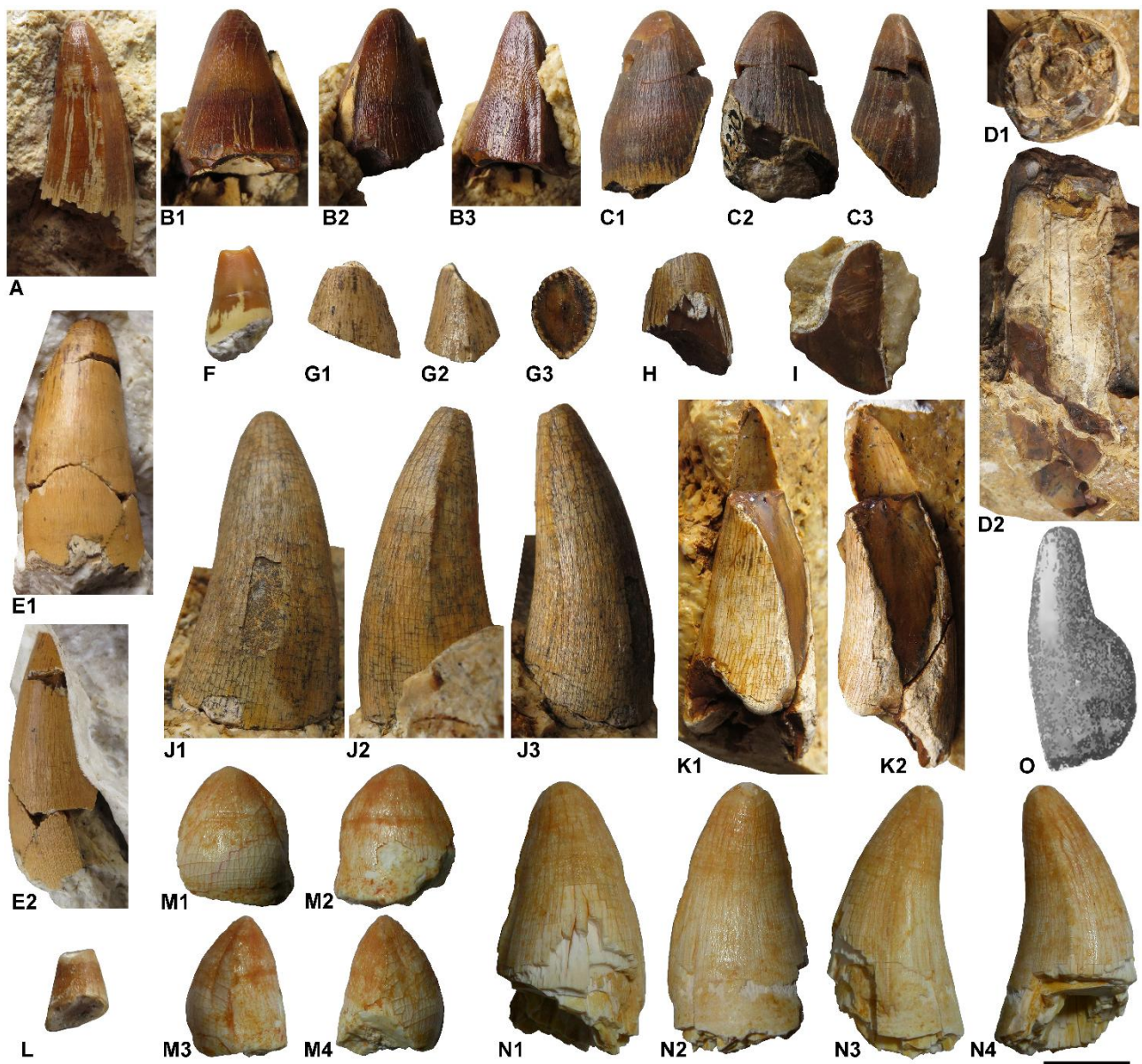


Fig. 5. *Crocodylia* indet., isolated teeth from the late Miocene of different localities of Sardinia. A, MGPT-PU 17333/1 from the “Pietra Forte” lithofacies of Tuvumannu (Cagliari), early Messinian, lateral view. B, MGPT-PU 17331/4 from the “Pietra Forte” lithofacies of Cimitero Monumentale di Bonaria (Cagliari), early Messinian; B1, lingual view; B2-3, linguo-lateral view. C, MGPT-PU 17330/4 from the “Pietra Forte” lithofacies of Montixeddu di Bonaria - Cava Timon (Cagliari), early Messinian; C1, labial view; C2, lingual view; C3, lateral view. D, MGPT-PU 17330/8 from the “Pietra Forte” lithofacies of Montixeddu di Bonaria (Cagliari), early Messinian; D1, cross section; D2, longitudinal section. E, MGPT-PU 17330/6 from the “Pietra Forte” lithofacies of Bonaria (Cagliari), early Messinian; E1, labial view; E2, lateral view. F, MGPT-PU 17330/3 from the “Pietra Forte” lithofacies of Bonaria (Cagliari), early Messinian. G, MGPT-PU

17330/5 from the “Pietra Forte” lithofacies of Montixeddu di Bonaria - Cava Timon (Cagliari), early Messinian; G1, labial view; G2, lateral view; G3, cross section. H-I, MGPT-PU 17330/2 from the “Pietra Forte” lithofacies of Bonaria (Cagliari), early Messinian. J, MGPT-PU 17330/1 from the “Pietra Forte” lithofacies of Bonaria (Cagliari), early Messinian; J1, labial view; J2-3, lateral view. K, MGPT-PU 17330/7 from the “Pietra Forte” lithofacies of Montixeddu di Bonaria - Cava Timon (Cagliari), early Messinian; K1, lingual view; K2, lateral view. L, MGPT-PU 17335 from the early Messinian of Capo Frasca (western Sardinia). M, Unnumbered tooth (22.10.1996, Area Ingresso Nord; Zona B) from the Tortonian - early Messinian of Fiume Santo (northwestern Sardinia); M1, labial view; M2, lingual view; M3-4, lateral view. N, Unnumbered tooth (23.10.1996, Area Ingresso Nord; A1/BD IV; terra di setacciatura) from the Tortonian - early Messinian of Fiume Santo (northwestern Sardinia); N1, labial view; N2, lingual view; N3-4, lateral view. O, from an unknown locality of Sardinia, indeterminate age and geological data (from Del Vecchio, 1921). Scale bar for A-E, G-K, O: 1 cm; scale bar for F: 0.5 cm; scale bar for L: 0.3 cm; scale bar for M, N: 0.7 cm.

Fig. 5. *Crocodylia* indet., dents isolées du Miocène supérieur de différentes localités de Sardaigne. A, MGPT-PU 17333/1, lithofaciès «Pietra Forte» de Tuvumannu (Cagliari), début Messinien, vue latérale. B, MGPT-PU 17331/4, lithofaciès «Pietra Forte» de Cimitero Monumentale di Bonaria (Cagliari), début du Messinien; B1, vue linguale; B2-3, vue linguo-latérale. C, MGPT-PU 17330/4, lithofaciès «Pietra Forte» de Montixeddu di Bonaria - Cava Timon (Cagliari), début Messinien; C1, vue labiale; C2, vue linguale; C3, vue latérale. D, MGPT-PU 17330/8, lithofaciès «Pietra Forte» de Montixeddu di Bonaria (Cagliari), début du Messinien; D1, section transversale; D2, coupe longitudinale. E, MGPT-PU 17330/6, lithofaciès «Pietra Forte» de Bonaria (Cagliari), début du Messinien; E1, vue labiale; E2, vue latérale. F, MGPT-PU 17330/3, lithofaciès «Pietra Forte» de Bonaria (Cagliari), début Messinien. G, MGPT-PU 17330/5, lithofaciès «Pietra Forte» de Montixeddu di Bonaria - Cava Timon (Cagliari), début du Messinien; G1, vue labiale; G2, vue latérale; G3, coupe transversale. H-I, MGPT-PU 17330/2 d'après les lithofaciès «Pietra Forte» de Bonaria (Cagliari), début messinien. J, MGPT-PU 17330/1 d'après les lithofaciès «Pietra Forte» de Bonaria (Cagliari), début messinien; J1, vue labiale; J2-3, vue latérale. K, MGPT-PU 17330/7 des lithofaciès «Pietra Forte» de Montixeddu di Bonaria - Cava Timon (Cagliari), début messinien; K1, vue linguale; K2, vue latérale. L, MGPT-PU 17335 du début du messinien de Capo Frasca (ouest de la Sardaigne). M, Dent non

numérotée (22.10.1996, Zone Ingresso Nord; Zona B) du Tortonien - Premier Messinien de Fiume Santo (Sardaigne Nord-Ouest); M1, vue labiale; M2, vue linguale; M3-4, vue latérale. N, dent non numérotée (23.10.1996, zone Ingresso Nord; A1 / BD IV; terra di setacciatura) du Tortonien - Messinien inférieur de Fiume Santo (nord-ouest de la Sardaigne); N1, vue labiale; N2, vue linguale; N3-4, vue latérale. O, dent provenant d'une localité inconnue de Sardaigne, âge et données géologiques indéterminées (d'après Del Vecchio, 1921). Barre d'échelle pour A-E, G-K, O: 1 cm; barre d'échelle pour F: 0,5 cm; barre d'échelle pour L: 0,3 cm; barre d'échelle pour M, N: 0,7 cm.

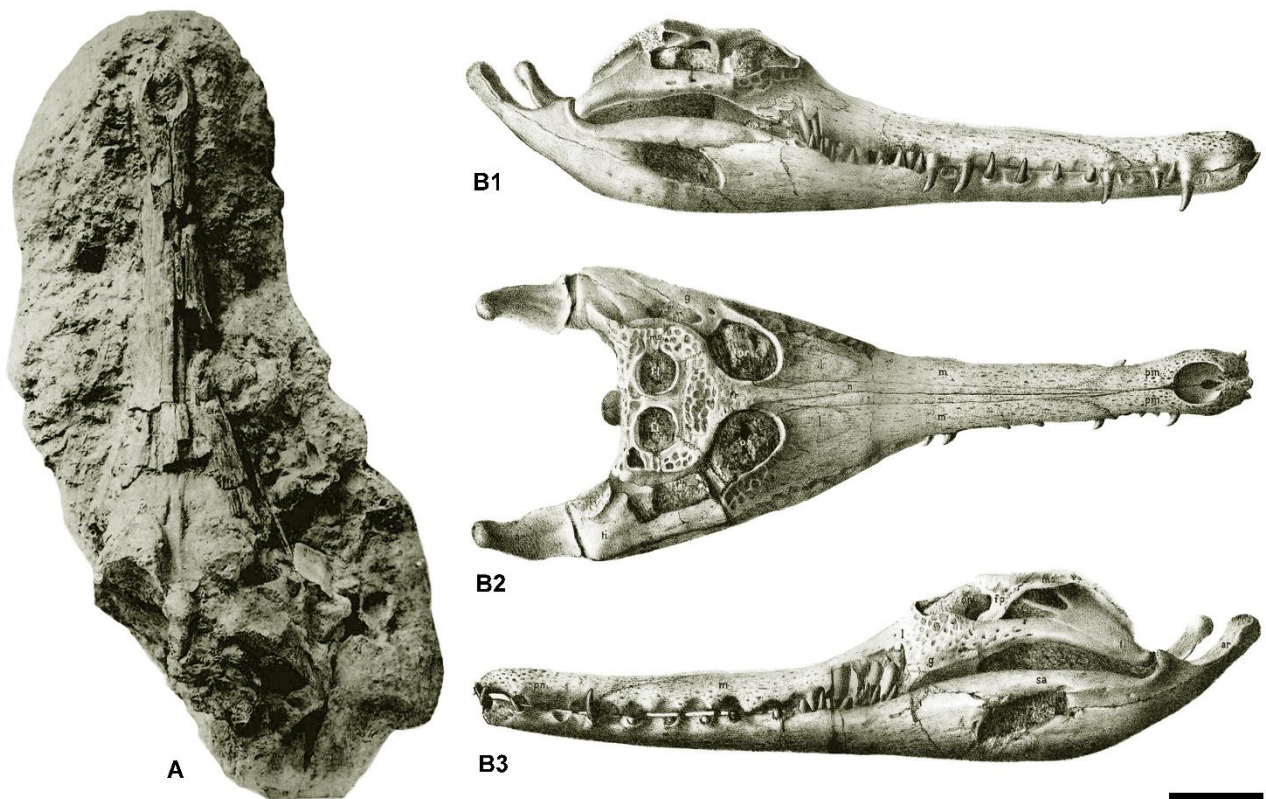


Fig. 6. The holotype skull of *Tomistoma calaritanum* Capellini, 1890 from the late Miocene of Piazza d'Armi, Cagliari (from the original plates of Capellini, 1890b). A, skull before the restoration in dorsal view. B, interpretative drawings of the restored skull; B1, right lateral view; B2, dorsal view; B3, left lateral view. Scale bar: 10 cm.

Fig. 6. Crâne de *Tomistoma calaritanum* Capellini, 1890, holotype, issu du Miocène supérieur de Piazza d'Armi, Cagliari (d'après les planches originales de Capellini, 1890b). A, crâne en vue dorsale avant la restauration. B, dessins d'interprétation du crâne restauré; B1, vue latérale droite; B2, vue dorsale; B3, vue latérale gauche. Barre d'échelle: 10 cm.

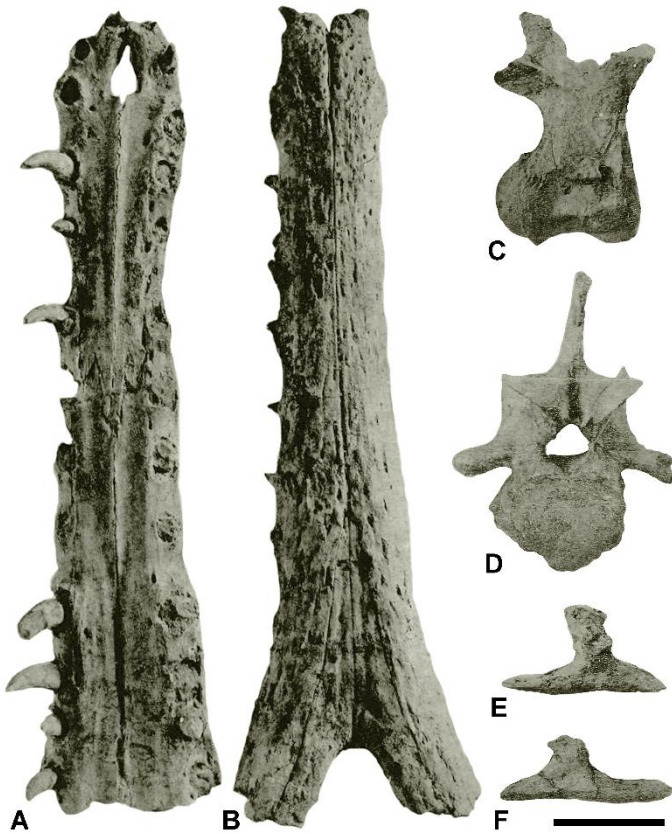


Fig. 7. The lost type material of *Tomistoma calaritanum* Capellini, 1890 from the late Miocene of Piazza d'Armi, Cagliari (from the original plates of Capellini, 1890b). A, premaxillae and maxillae in ventral view. B, dentaries and splenials in ventral view. C, sixth cervical vertebra in lateral view. D, eighth cervical vertebra in posterior view. E-F, cervical ribs. Scale bar: 5 cm.

Fig. 7. Matériel perdu du type de *Tomistoma calaritanum* Capellini, 1890 provenant du Miocène supérieur de Piazza d'Armi, Cagliari (d'après les planches originales de Capellini, 1890b). A, premaxillae et maxillaires en vue ventrale. B, dentaires et spléniales en vue ventrale. C, sixième vertèbre cervicale en vue latérale. D, huitième vertèbre cervicale en vue postérieure. E-F, côtes cervicales. Barre d'échelle: 5 cm.

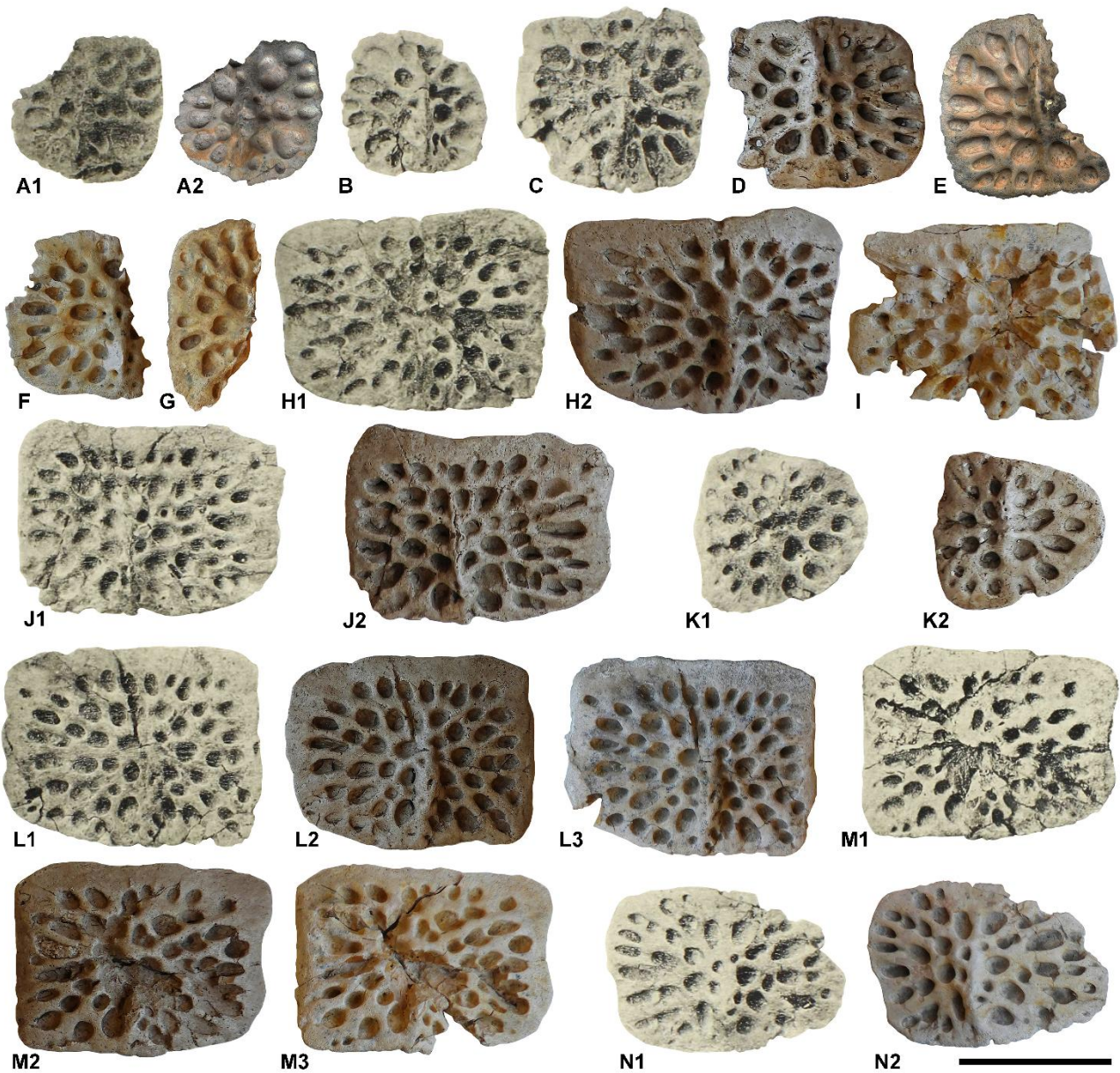


Fig. 8. Type osteoderms of *Tomistoma calaritanum* Capellini, 1890, from the late Miocene of Piazza d'Armi (Cagliari), dorsal view. A, cervical osteoderm; A1, as in Capellini, 1890b (tav. IV, fig. 1); A2, as currently preserved (MDLCA 14401). B, cervical osteoderm (lost element) as in Capellini, 1890b (tav. IV, fig. 2). C, nugal osteoderm (lost element) as in Capellini, 1890b (tav. IV, fig. 3). D, incomplete nugal (?) osteoderm, plaster cast of a lost element. E, incomplete nugal (?) osteoderm (MDLCA 14401). F, incomplete nugal (?) osteoderm (MDLCA 14401). G, fragment of osteoderm (MDLCA 14401). H, dorsal osteoderm of the median series (lost element); H1, as in Capellini, 1890b (tav. IV, fig. 4); H2, plaster cast. I, dorsal osteoderm of the median series (MDLCA 14401). J, dorsal osteoderm of the median series (lost element); J1, as in Capellini, 1890b (tav. IV, fig. 5); J2, plaster cast. K, dorsal osteoderm of the right lateral series (lost

element); K1, as in Capellini, 1890b (tav. IV, fig. 6); K2, plaster cast. L, dorsal osteoderm of the median series; L1, as in Capellini, 1890b (tav. IV, fig. 7); L2, plaster cast; L3, as currently preserved (MDLCA 14401). M, dorsal osteoderm of the median series; M1, as in Capellini, 1890b (tav. IV, fig. 8); M2, plaster cast; M3, as currently preserved (MDLCA 14401). N, dorsal osteoderm of the right lateral series; N1, as in Capellini, 1890b (tav. IV, fig. 9); N2, as currently preserved (MDLCA 14401). Scale bar: 5 cm.

Fig. 8. Ostéodermes du type de *Tomistoma calaritanum* Capellini, 1890, du Miocène supérieur de Piazza d'Armi (Cagliari), vues dorsales. A, ostéoderme cervical; A1, d'après Capellini, 1890b (pl. IV, fig. 1); A2, tel qu'il est conservé actuellement (MDLCA 14401). B, ostéoderme cervical (élément perdu) d'après Capellini, 1890b (pl. IV, fig. 2). C, ostéoderme nucal (élément perdu) d'après Capellini, 1890b (pl. IV, fig. 3). D, ostéoderme nucal (?) incomplet, moulage en plâtre, élément perdu. E, ostéoderme nucal (?) Incomplet (MDLCA 14401). F, ostéoderme nucal (?) Incomplet (MDLCA 14401). G, fragment d'ostéoderme (MDLCA 14401). H, ostéoderme dorsal de la série médiane (élément perdu); H1, comme dans Capellini, 1890b (pl. IV, fig. 4); H2, moule en plâtre. I, ostéoderme dorsal de la série médiane (MDLCA 14401). J, ostéoderme dorsal de la série médiane (élément perdu); J1, comme dans Capellini, 1890b (pl. IV, fig. 5); J2, moule en plâtre. K, ostéoderme dorsal de la série latérale droite (élément perdu); K1, d'après Capellini, 1890b (pl. IV, fig. 6); K2, moule en plâtre. L, ostéoderme dorsal de la série médiane; L1, d'après Capellini, 1890b (pl. IV, fig. 7); L2, moule en plâtre; L3, dans sa forme actuelle (MDLCA 14401). M, ostéoderme dorsal de la série médiane; M1, d'après Capellini, 1890b (pl. IV, fig. 8); M2, moule en plâtre; M3, tel qu'il est actuellement conservé (MDLCA 14401). N, ostéoderme dorsal de la série latérale droite; N1, d'après Capellini, 1890b (pl. IV, fig. 9); N2, tel qu'il est actuellement conservé (MDLCA 14401). Barre d'échelle: 5 cm.

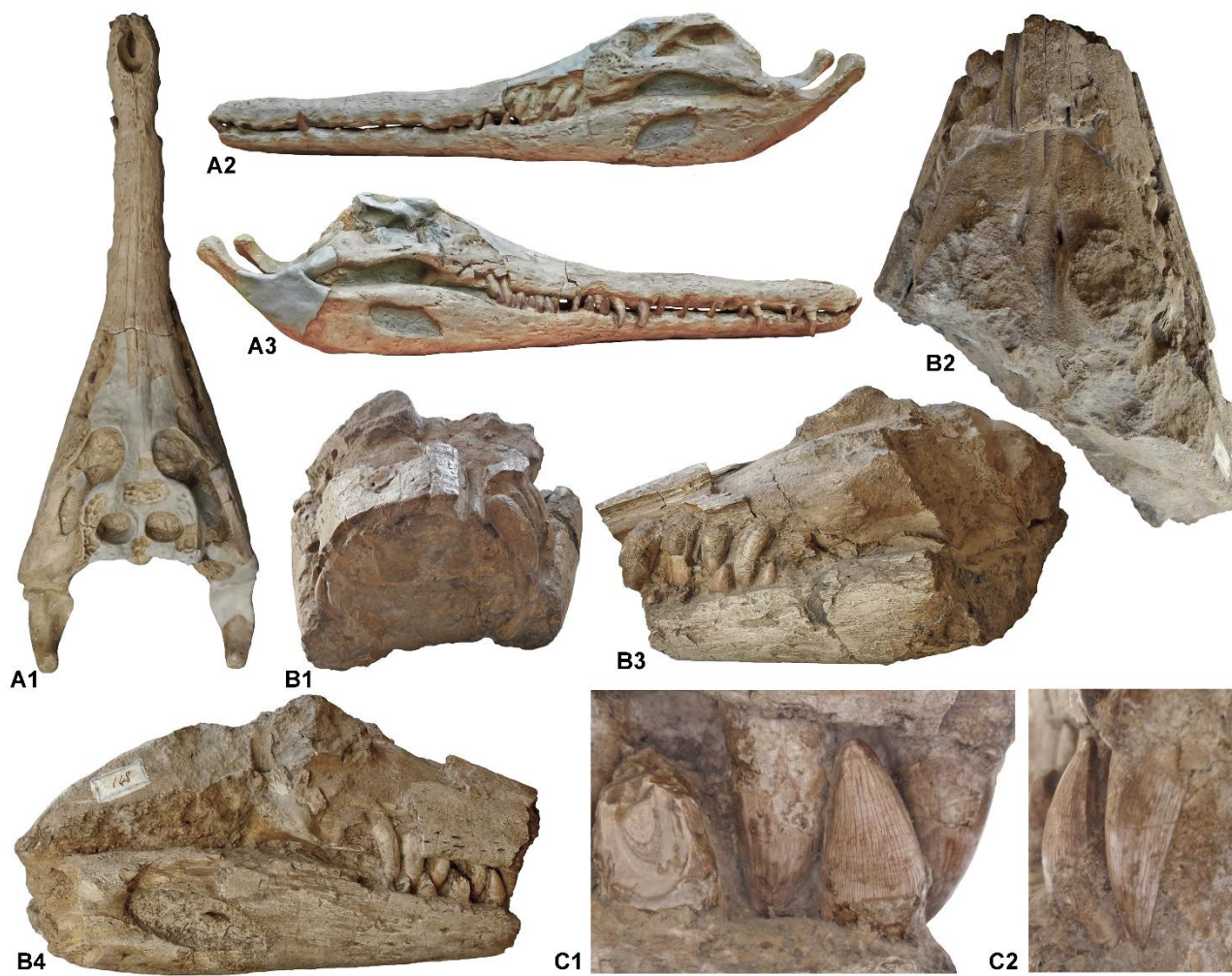


Fig. 9. *Tomistoma calaritanum* Capellini, 1890 (MDLCA 148). A, plaster cast of the restored skull; A1, dorsal view; A2, left lateral view; A3, right lateral view. B, the current state of preservation of the skull; B1, anterior view; B2, dorsal view; B3, lateral left view; B4, lateral right view. C, detail of the right teeth row; C1, buccal view; C2, anterior view. Scale bar for A: 10 cm, scale bar for B: 5 cm, scale bar for C: 1 cm.

Fig. 9. *Tomistoma calaritanum* Capellini, 1890 (MDLCA 148). A, moulage en plâtre du crâne restauré; A1, vue dorsale; A2, vue latérale gauche; A3, vue latérale droite. B, l'état actuel de conservation du crâne; B1, vue antérieure; B2, vue dorsale; B3, vue latérale gauche; B4, vue latérale droite. C, détail de la rangée de dents droite; C1, vue buccale; C2, vue antérieure. Barre d'échelle pour A: 10 cm, barre d'échelle pour B: 5 cm, barre d'échelle pour C: 1 cm.

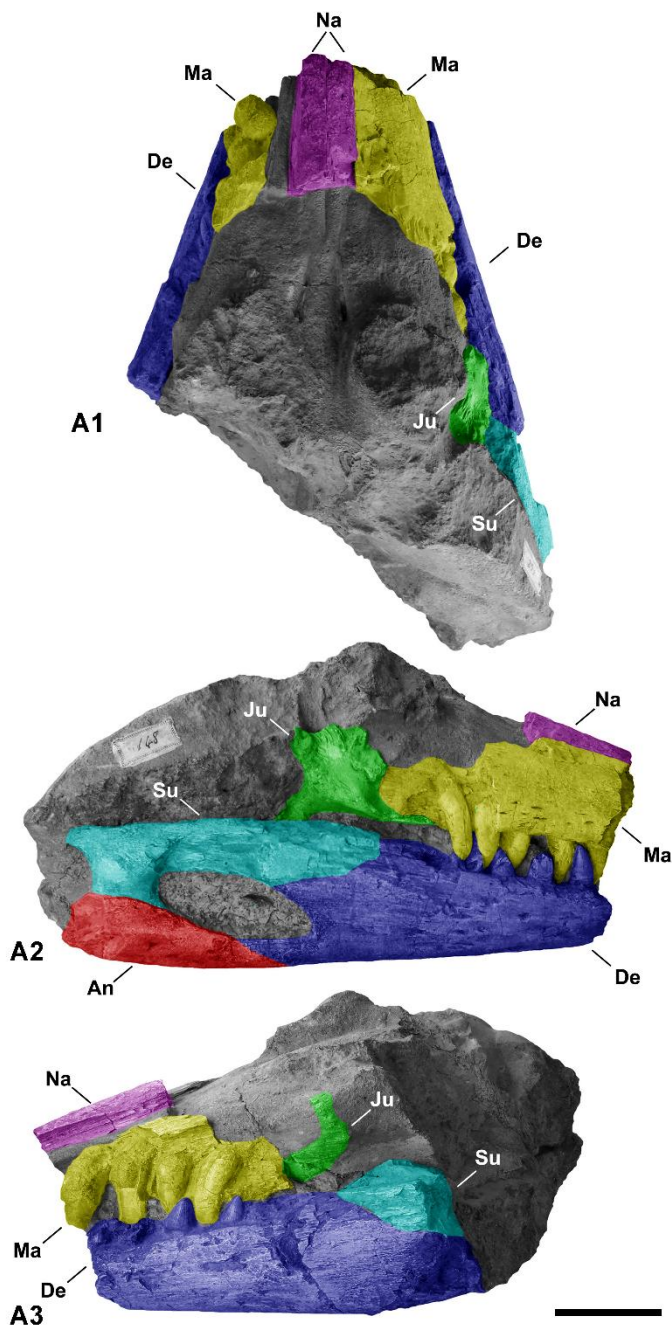


Fig. 10. *Tomistoma calaritanum* Capellini, 1890 (MDLCA 148), preserved skeletal elements of the skull. A1, dorsal view; A2, right lateral view; A3, left lateral view. Abbreviations: An, angular; Su, surangular; De, dentary; Ju, jugal; Ma, maxilla; Na, nasal. Scale bar: 5 cm.

Fig. 10. *Tomistoma calaritanum* Capellini, 1890 (MDLCA 148), éléments squelettiques préservés du crâne. A1, vue dorsale; A2, vue latérale droite; A3, vue latérale gauche. Abréviations: An, angulaire; Su, surangulaire; De, dentaire; Ju, jugal; Ma, maxillaire; Na, nasale. Barre d'échelle: 5 cm.