Journal of Paleontology, 88(3), 2014, p. 444–456

0022-3360/14/0088-444$03.00
DOI: 10.1666/13-106

CRANIAL MORPHOLOGY OF *THERIOSUCHUS SYMPIESTODON* (MESOEUCROCODYLIA, ATOPOSAURIDAE) AND THE WIDESPREAD OCCURRENCE OF *THERIOSUCHUS* IN THE LATE CRETACEOUS OF EUROPE

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Abstract—We present a detailed morphological description of the type-locality cranial material of *Theriosuchus sympiestodon* Martin, Rabi, and Csiki, 2010 from the Maastrichtian Densuş-Ciula Formation of the Haţeg Basin, Romania together with new material of isolated cranial elements and teeth from various sites of the same general area. The recognition of several individuals of distinct sizes allows for an assessment of ontogenetic variation in this taxon. New material, consisting of isolated teeth and an incomplete maxilla with in situ teeth, coming from various late Campanian/early Maastrichtian sites in southern France is referable to ?*Theriosuchus* sp. and hints to a rare but widespread distribution of *Theriosuchus* in the Late Cretaceous European archipelago.

INTRODUCTION

The late Cretaceous continental faunas of Europe are different from those of other continents in that they contain a large number of relictual vertebrate taxa, which can be considered as living fossils of their epoch (e.g., Weishampel et al., 2010). Most of them have Early Cretaceous European ancestors and their survival might be related to the conservational effect of the archipelago paleogeography characterizing this area during the Late Cretaceous. Such an origin has been suggested for turtles including solemydids, dortokids, and *Kallokibotion bajazidi* Nopcsa, 1923 (Nopcsa, 1923; Gaffney and Meylan, 1992; Lapparent de Broin and Murelaga, 1999; Lapparent de Broin et al., 2004; Joyce, 2007; Joyce et al., 2011; Rabi et al., 2013), for nodosaurid (Ősi, 2005) and rhabdodontid (Weishampel et al., 2003; Ősi et al., 2012a) dinosaurs, and for basal eusuchian crocodilians (Ősi et al., 2007; Delfino, 2008; Martin and Delfino, 2010; Rabi and Ősi, 2010). The somewhat unexpected discovery of the atoposaurid *Theriosuchus* Owen, 1879 in the Maastrichtian of Romania adds a new taxon to this list, as the group was formerly restricted to the Upper Jurassic–Lower Cretaceous continental deposits of Eurasia (Martin et al., 2010). Compared to other late-surviving relictual European taxa, little is known of the morphology and distribution of the Late Cretaceous *Theriosuchus sympiestodon* Martin, Rabi and Csiki, 2010. Here, we describe and illustrate the type-locality material of *T. sympiestodon* in detail, together with new cranial elements and isolated teeth from various coeval Romanian localities. An incomplete maxilla and isolated teeth from the upper Campanian/lower Maastrichtian of southern France demonstrates that *Theriosuchus*-like mesoeucrocodylians were a widespread component of the Campanian–Maastrichtian European faunas. The phylogenetic relationships of *Theriosuchus sympiestodon* have been exhaustively explored (Martin et al., 2010); the aim of this contribution is therefore to provide a detailed description and taxonomic assessment of the Late Cretaceous *Theriosuchus* remains and to discuss intraspecific variation in *T. sympiestodon*.

GEOLOGICAL SETTING

Uppermost Cretaceous deposits with continental vertebrates are widespread in Europe, discontinuously covering areas that belonged both to cratonic Europe (the southwestern extremities of the Eurasian Plate), as well as to Alpine Europe (represented by Tethyan and peri-Tethyan areas). Such deposits, formed in continental or marginal marine settings, extend from Portugal to Crimea, and from southern Sweden to northern Italy (e.g., Pereda-Suberbiola, 2009; Weishampel et al., 2010; Le Loeuff, 2012 and references cited therein).

Most of these outcropping areas correspond to former isolated landmasses ('islands') bordered by the east-to-west stretching Tethys Ocean and other seaways connected to it (e.g., Dercourt et al., 2000). Two such areas with continental vertebrate-bearing Upper Cretaceous deposits: the Transylvanian landmass, in northwestern Romania, including the Haţeg Basin area and its surroundings (e.g., Codrea et al., 2010), and the eastern part of the Ibero-Armorican landmass, in southern France (e.g., Le Loeuff, 1991; Buffetaut, 2005), yielded remains referable to *Theriosuchus* or closely related taxa.

The holotype and paratype of *Theriosuchus sympiestodon* come from the middle part of the Densuş-Ciula Formation, from the Tuştea-Oltoane dinosaur nesting site (Grigorescu et al., 2010; Martin et al., 2010) of Maastrichtian age (Bojar et al., 2011). The first specimen referable to *Theriosuchus sympiestodon* (MCDRD 134, a dentary) was recovered, however, in 1981 from the Cioaca Târnovului site, in the southern (middle-upper) part of the Sânpetru section (Groza, 1983; Csiki et al., 2010), belonging to the synchronous Sânpetru Formation (e.g., Grigorescu, 1992; Panaiotu and Panaiotu, 2010). This occurrence is recorded as an isolated bone in a yellowish-gray, medium-to-coarse grained sandstone bed cropping out in the Târnovul Hill, without more precise locality data (Groza, 1983). Another specimen referable to *Theriosuchus*, MCDRD 793, a well-preserved maxilla with in situ teeth originates from a multitaxic, stratiform macrovertebrate bonebed from the lower part of the Sânpetru local section (La Cărare site; Csiki et al., 2010), preserved in coarse-grained fluvial deposits of the Sânpetru Formation. Here, the local succession starts with channel lag conglomerates followed by coarse-to-medium grained gray-greenish channel sandstones and is finally capped by dark brownish, fine-grained silty sandstones. The bonebed yielded, from the mid-1980s through 2009, a large amount of mainly isolated vertebrate remains, but none of this material except MCDRD 793 appears to belong to *Theriosuchus sympiestodon*. Finally, LPB (FGGUB) R.1945, a fragmentary maxilla, was recovered in 2005 while screen-washing the fossiliferous matrix from one of the most important microvertebrate bonebeds (Fântânele, near Vălioara) of the Haţeg Basin, located in the lower part of the Densuş-Ciula Formation (Csiki et al., 2010; Vasile and Csiki, 2010). The microvertebrate accumulation comes from fine-grained, greenish-gray to weakly mottled silty mudstones and siltstones, formed in a poorly drained floodplain setting. Several isolated teeth, reminiscent of those of *Theriosuchus*, were also recovered during screen-washing different microvertebrate bonebeds, including Fântânele, Fântânele 2, and Budurone (Csiki et al., 2010).

Occurrence of specimens reminiscent of *Theriosuchus* is also attested from two localities in southern France. The fragmentary maxilla MHN AIX PV 2011.15.1 was surface collected from red clay sediments in a vineyard from Bendel near Trets (Bouches du Rhône). These deposits belong to a series of fluvial sediments of late Campanian–early Maastrichtian age that crop out in the Aix-en-Provence Basin, south of Montagne Sainte Victoire, a unit known as 'argiles et grès à reptiles' (Buffetaut and Le Loeuff, 1991). The second occurrence of *Theriosuchus*-like mesoeucrocodylians is attested by isolated teeth from the locality of Cruzy (Hérault), which produced a variety of continental vertebrates (Buffetaut, 2005). The outcrop is also dated as late Campanian–early Maastrichtian, and consists of mainly argillaceous fluvial deposits.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations.—NHMUK, Natural History Museum, London, UK; IPFUB, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie of the Freie Universität Berlin, Berlin, Germany; LPB (FGGUB), Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; MCDRD, Muzeul Civilizaţiei Dacice şi Romane, Deva, Romania; MHN AIX, Musée d'Histoire Naturelle, Aix-en-Provence, France.

CROCODILIA Gmelin, 1789
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
ATOPOSAURIDAE Gervais, 1871
THERIOSUCHUS Owen, 1879
THERIOSUCHUS SYMPIESTODON Martin, Rabi and Csiki, 2010
Figures 1–8

Diagnosis.—(After Martin et al., 2010), small-sized non-eusuchian mesoeucrocodylian with slightly laterally compressed skull and longitudinal crest on frontal, sharing the following autapomorphic characters of the genus *Theriosuchus*: presence of transversely directed groove on the anterolateral side of the maxilla; and low-crowned, labio-lingually compressed, pseudoziphodont (sensu Prasad and Lapparent de Broin, 2002) posterior teeth. It differs from other species of *Theriosuchus*, including *T. pusillus* Owen, 1879, *T. ibericus* Brinkmann, 1992, *T. guimarotae* Schwarz and Salisbury, 2005 and *T. grandinaris* Lauprasert et al., 2011, in having only one single enlarged maxillary caniniform tooth and by the anterior teeth lacking striae on both labial and lingual faces.

Description.—*Theriosuchus sympiestodon* is a small crocodilian currently known from a fragmentary skull (Figs. 1, 3), a series of isolated maxillae (Figs. 2, 4, 5, 7), one dentary (Fig. 6), and numerous isolated teeth (Fig. 8). The frontal, postorbital, parietal, squamosal, exoccipital, quadrate, and pterygoid are preserved in a single specimen: the paratype LPB (FGGUB) R.1781. The skull is vertical rather than dorsoventrally compressed and possesses a flat, even dorsal surface of the frontal and skull table.

Maxilla.—The description of the maxilla is based on three specimens of different sizes (LPB (FGGUB) R.1945, LPB (FGGUB) R.1782, and MCDRD 793). The lateral wall of the maxilla is vertical in all three specimens, presenting a sigmoid shape in anterior view. A well-marked anteroventrally directed sulcus runs on the anterolateral surface of the maxilla in FGGUB R.1782 (Fig. 2) and in MCDRD 793 (Fig. 5). This sulcus is barely visible in the smallest specimen (FGGUB R.1945; Fig. 4). A more complex network of sulci or vascular grooves has been reported on the dorsal surface of the maxilla of *Kaprosuchus saharicus* (Sereno and Larsson, 2010) and a single maxillary groove is parallel to the maxillary tooth row in *Terminonaris robusta* (Wu et al., 2001b). In LPB (FGGUB) R.1782 the contact surface for the premaxilla is visible anterodorsally (Fig. 2); despite being broken anteriorly, its configuration is similar to that described in *T. pusillus* (Clark, 1986). A portion of the suture for reception of the nasal is preserved on the highest region of the lateral maxillary wall of LPB (FGGUB) R.1782 and is visible only in medial view. In LPB (FGGUB) R.1945 and MCDRD 793, the sutural contact for the premaxilla is oblique and slopes anteroventrally. The maxillae preserve a rigid and well-developed palatine process, which stands in a very high position relative to the tooth row margin (Figs. 2.3, 4.3, 5.4). The ventral surface of the palatine process is smooth but not planar. The dorsal surface of the palatine process bears an extensive ovoid depression in its posteromedial region as seen in LPB (FGGUB) R.1782 and LPB (FGGUB) R.1945 (Figs. 2.7, 4.3). Two small foramina pierce this depression. On the medial faces of these specimens, above the palatal plate, a ridge extends parallel with the dorsal margin, terminating at the boundary of the first alveolus and the occlusal pit. The palatal suture with the contralateral maxilla is best preserved in LPB (FGGUB) R.1782 and is not parallel to the lateral margin of the bone. The suture for the palatine occurs on the anteromedial corner of the suborbital fenestra. This organization suggests that the palatine sends a very short process anteriorly between the maxillae. In its posterolateral region, the posterior maxillary ramus, which accommodates the posterior toothrow, displays a smooth surface that once received the anterior jugal process.

The lateral margin of the suborbital fenestra is parallel to the posterior part of the toothrow. In the holotype, the anterior margin of the suborbital fenestra extends anteriorly to the level of the sixth alveolus where it draws a narrow and well-marked concavity (Fig. 2.8). The same degree of development of the suborbital fenestra is observed in the Fântânele maxilla (LPB (FGGUB) R.1945; Fig. 4.2) whereas in the larger Deva maxilla (MCDRD 793), the suborbital fenestra extends to the level of the eighth alveolus (Fig. 5.2, 5.6).

The anteriormost margin of the maxilla is more rounded in MCDRD 793 than in LPB (FGGUB) R.1945 and LPB (FGGUB) R.1782 where a circular occlusal pit sits just anterior to the first alveolus aligned with the maxillary tooth row followed by a slightly medially shifted nutritive foramen. In contrast, only half of the occlusal pit is present in the corresponding region of MCDRD 793 suggesting that it further extended onto the premaxilla. LPB (FGGUB) R.1782 preserves at least ten alveoli whereas MCDRD 793 appears to preserve a complete toothrow including eleven alveoli. LPB (FGGUB) R.1945 is less complete, with eight alveoli. The first three alveoli are rather small; the fourth one is the largest and is followed by a smaller but still large alveolus (Figs. 2.5, 2.6, 4.2). Here, medially between the fifth and

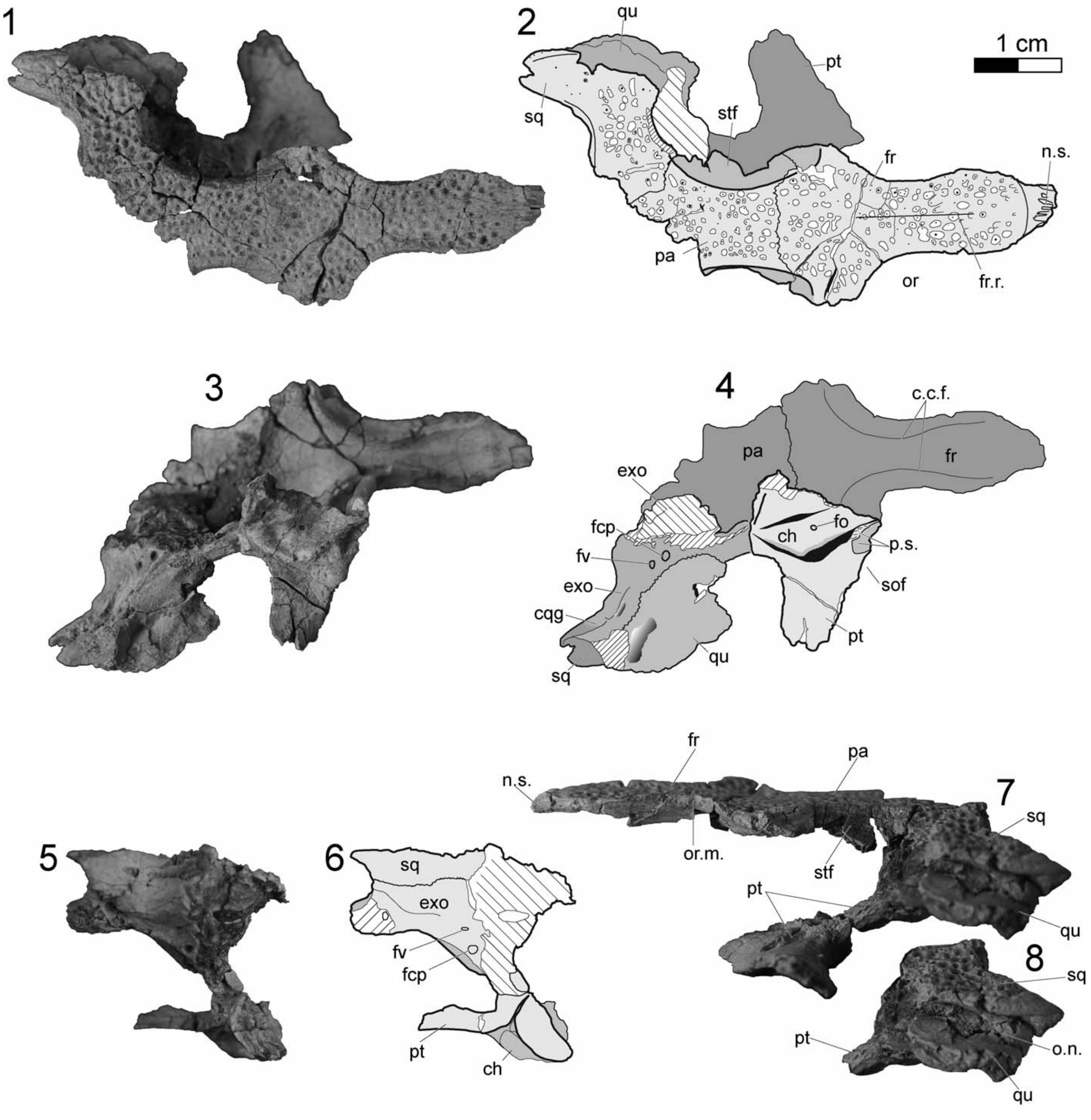

FIGURE *1*—Photographs and line drawings of the paratype partial skull of *Theriosuchus sympiestodon* Martin, Csiki and Rabi, 2010 (LPB (FGGUB) R.1781), associated with the holotype, Maastrichtian of Tuştea, Romania in different views. *1*, *2*, dorsal; *3*, *4*, ventral; *5*, *6*, occipital; *7*, left lateral; *8*, close-up of the otic area from *7*. Abbreviations: c.c.f.=crista craniae frontalis; ch=choana; cqg=cranio-quadrate passage; exo=exoccipital; fcp=foramen caroticum posterius; fo=foramen; fr=frontal; fr.r.=frontal ridge; fv=foramen vagus; n.s.=suture for nasal; o.n.=otic notch; or=orbit; or.m.=orbital margin; pa=parietal; p.s.=suture for palatine; pt=pterygoid; qu=quadrate; sof=suborbital fenestra; sq=squamosal; stf=supratemporal fenestra.

sixth alveoli lies a large ovoid occlusal pit in LPB (FGGUB) R.1782 whereas in the corresponding area this pit is accompanied by a deep notch in MCDRD 793 and by a slight emargination in LPB (FGGUB) R.1945. The anterior part of the toothrow shows separated alveoli but these are replaced in the posterior region by confluent alveoli set in a groove, starting from the sixth tooth position in LPB (FGGUB) R.1782 and from the seventh in MCDRD 793. In LPB (FGGUB) R.1945, the tooth row is broken at the level of the seventh alveolus.

Frontal.—The unpaired frontal is preserved in LPB (FGGUB) R. 1781; it is short and projects horizontally from the skull table but does not significantly extend beyond the anterior level of the orbits (Fig. 1.1, 1.2). The frontal displays a faint but elongate median sagittal crest on its dorsal surface as in the genus *Araripesuchus* (Sereno and Larsson, 2010), in *Shamosuchus djadochtaensis* (Pol et al., 2009) and *Rugosuchus nonganensis* (Wu et al., 2001a), or in *Sunosuchus junggarensis* (Wu et al., 1996). The interorbital width is 8 mm where a moderate

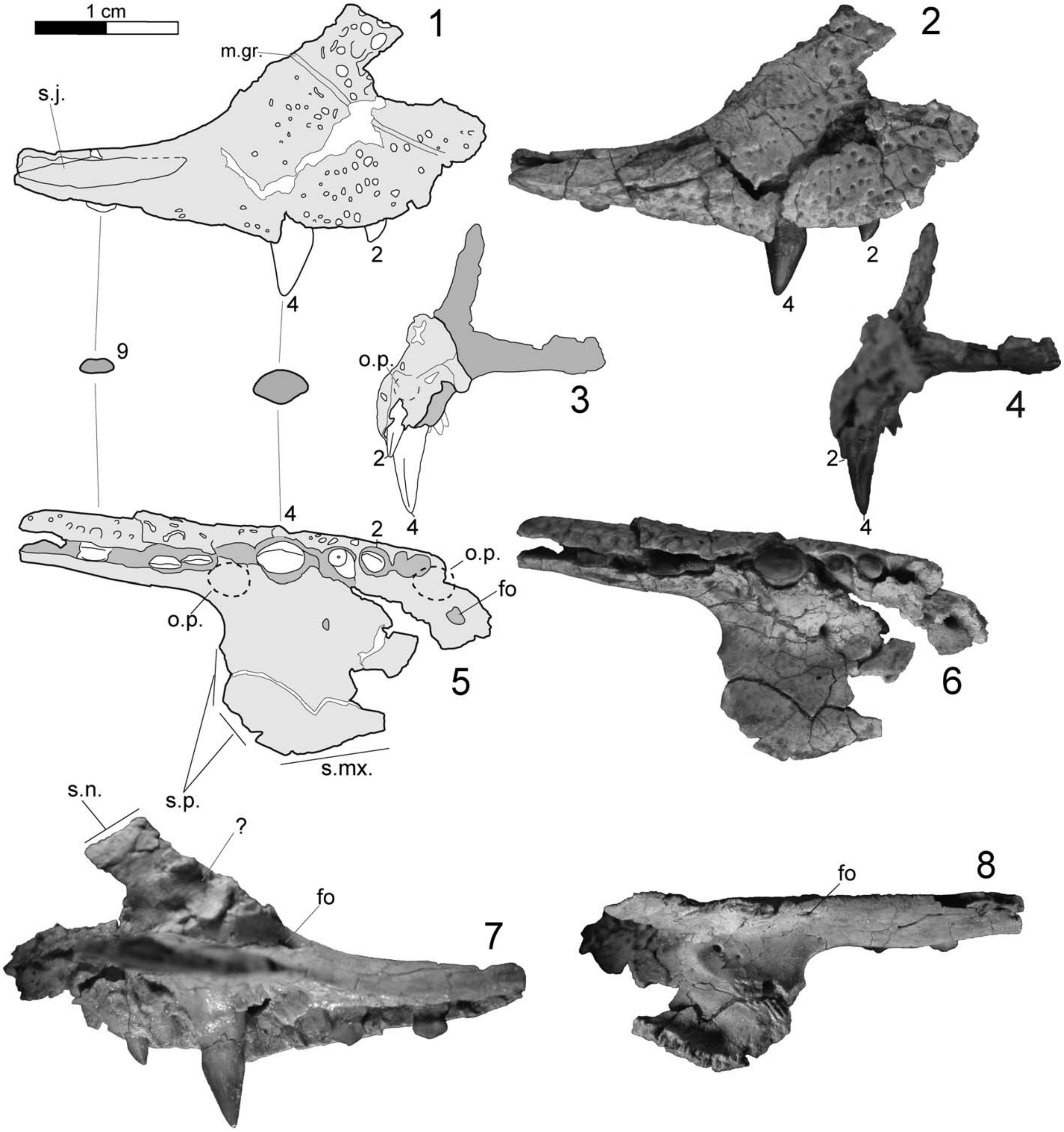

FIGURE 2—Photographs and line drawings of the holotype right maxilla of *Theriosuchus sympiestodon* (LPB (FGGUB) R.1782), Maastrichtian of Tuştea, Romania in different views. *1*, *2*, lateral; *3*, *4*, anterior; *5*, *6*, ventral; *7*, medial; *8*, dorsal. Small numbers correspond to the position of alveoli or teeth. Abbreviations: fo=foramen; m. gr.=maxillary groove; o.p.=occlusal pit; s.j.=suture for jugal; s.n.=suture for nasal; s.mx.=suture for maxilla; s.p.=suture for palatine.

constriction underlined by a rim forms the dorsal orbital margin. The anterior suture for the nasals is transversely straight and marked by fine indentations. Posterior to it, a shallow groove runs parallel to this suture. A short suture for the postorbital is best seen on the right side. It is anteroposteriorly oriented and takes place at the anteriormost level of the supratemporal fenestra. Two shallow depressions are located near the postorbital suture. The frontoparietal suture enters the supratemporal fenestra. This suture is straight on the skull table whereas the parietal sends a pair of short anterior processes in the medial wall of the supratemporal fenestra. The frontal takes part in the anteromedial margin of the supratemporal fenestra, here excluding the postorbital and the parietal from contacting one another. In ventral view, the developed cristae cranii frontales surround the

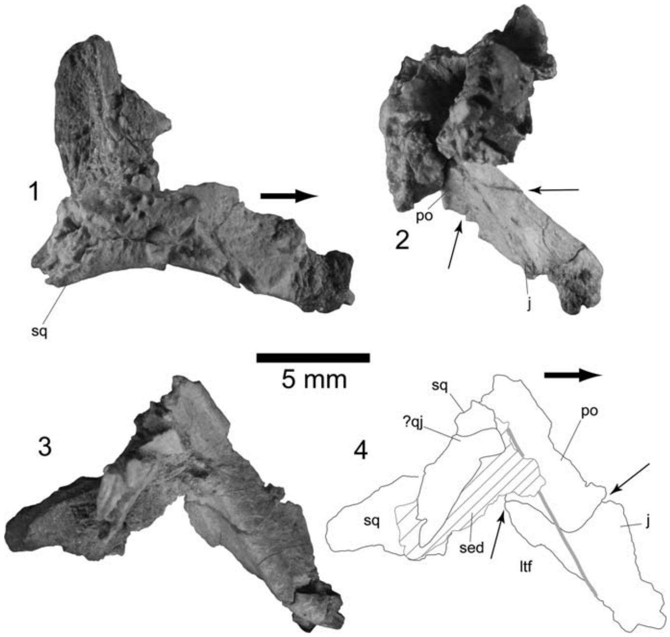

FIGURE 3—Right postorbital of *Theriosuchus sympiestodon* (LPB (FGGUB) R.1781), Maastrichtian of Tuştea, Romania in different views. *1*, dorsal; *2*, posterior; *3*, lateral; *4*, interpretive drawing of lateral view. Abbreviations: ltf=lower temporal fenestra; po=postorbital; sed=sediment; sq=quamosal; qj=quadratojugal. The thick arrows point toward the anterior direction. The thin arrow indicates the postorbital-jugal suture.

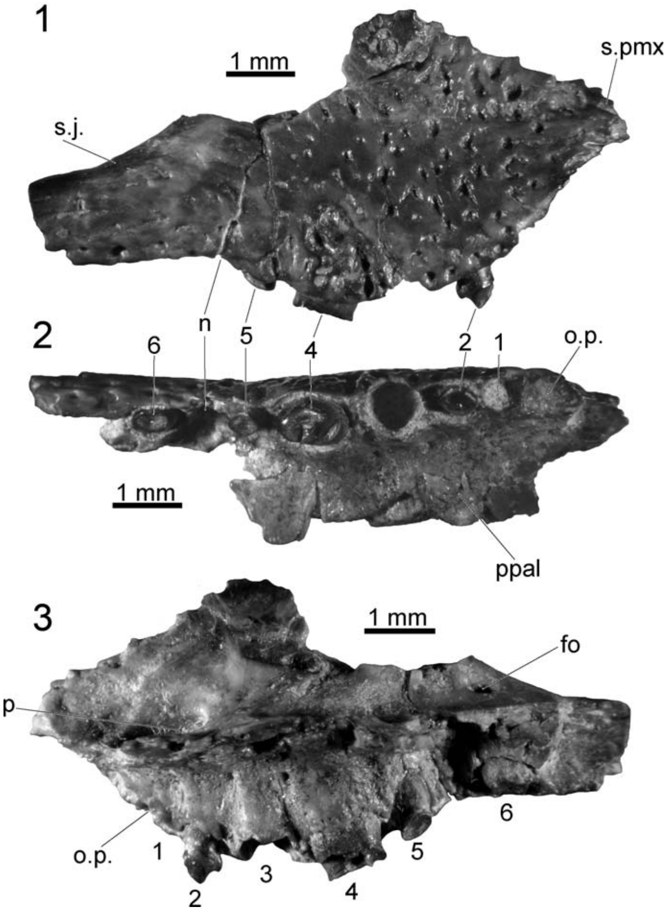

FIGURE 4—Fragmentary right maxilla of juvenile *Theriosuchus sympiestodon* (LPB (FGGUB) R.1945), Maastrichtian of Fântânele, Romania in different views. *1*, lateral; *2*, occlusal; *3*, medial. Small numbers correspond to the position of alveoli or teeth. Abbreviations: fo=foramen; n=notch for reception of mandibular tooth; o.p.=occlusal pit; p=pit on dorsal surface of palatine process; ppal=palatine process; s.j.=suture for jugal; s.pmx=suture for premaxilla.

olfactory tract. Their crests widen in the anterior portion of the frontal and embrace a distinct median ridge (unlike that seen in extant crocodilians), which may have divided the olfactory nerves (Fig. 1.3, 1.4).

Postorbital bar.—In LPB (FGGUB) R.1781, the right postorbital bar is preserved. Below the dorsal surface, the specimen preserves the dorsal wall of the infratemporal fenestra. The anteriormost tip of the squamosal reaches the postorbital bar and seems to send a small pointed process in the infratemporal fenestra, above the quadratojugal but this last feature is unclear and hidden by preservation and sediment (Fig. 3.4). The postorbital bar is well preserved and ventrally it meets the jugal bar and together they form the anterior limit of the infratemporal fenestra. In lateral view, this suture is V-shaped (Fig. 3.2). The postorbital bar is triangular in section and exhibits an acute lateral ridge (Fig. 3.2, 3.3). The medial surface of the bar is flat whereas the anterolateral and posterolateral surfaces are gently concave. The ventralmost tip of the bar is not preserved so it is impossible to assess its configuration at the contact with the dermal part of the jugal.

Parietal.—The incomplete parietal is best preserved in its anterior portion, which is wide, flat and continuous with the supratemporal fenestra (Fig. 1). It divides two large and ovoid supratemporal fenestrae. A faint sagittal crest is visible on the dorsal surface. The margin with the supratemporal fenestra is smooth and does not have an elevated rim. The participation of the parietal to the occipital margin is impossible to assess. The suture with the left squamosal takes place at the posteromedial level of the supratemporal fenestra. The lateral margin of the parietal is not vertical to the supratemporal fenestra but gradually slopes as a flat surface from the skull table. Located on the anteromedial corner of the supratemporal wall, a shallow fossa is present at the level of the frontoparietal suture.

Squamosal.—The left squamosal is missing its anterior region. The bone forms the entire posterior margin of the supratemporal fenestra, and makes an extensive contribution to the posterior margin of the skull table (Fig. 1). The squamosal is flat on the skull table surface and is aligned with the parietal. In dorsal view, the squamosal sends an elongate posterolateral process that prolongs significantly beyond the level of the occipital margin. Unlike bones of the dorsal surface, this prong is devoid of pits in its lateral and posterior portions (the lateral part becomes very thin). The occipital surface of the squamosal is vertical, deeply concave, and builds most of the dorsal surface of the occipital region. In lateral view, the squamosal extensively overhangs the otic region and forms a thin wall for the posterior margin of the otic recess (Fig. 1.7).

Exoccipital.—The dorsomedial region of the exoccipital, above the foramen magnum, is not preserved. The exoccipital forms a significant portion of the occipital surface being mainly located in the ventral region (Fig. 1.5, 1.6). The exoccipital faces posteroventrally unlike in basal eusuchians. The lateral portion of the exoccipital does not prevent the quadrate and squamosal to contact on the lateral margin of the occipital surface (Fig. 1.8). Here, a ventrolateral process of the exoccipital overhangs the medial wall of the cranioquadrate groove, which is bordered dorsolaterally by the squamosal and ventrolaterally by the quadrate. A small perforation for the foramen vagi is visible and sits in the middle of a depressed area. Ventromedially to it, the perforation for the foramen caroticum posterius is larger.

Quadrate.—The left quadrate is incomplete: Both its distal ramus and the anterior portion of the bone at the level of the

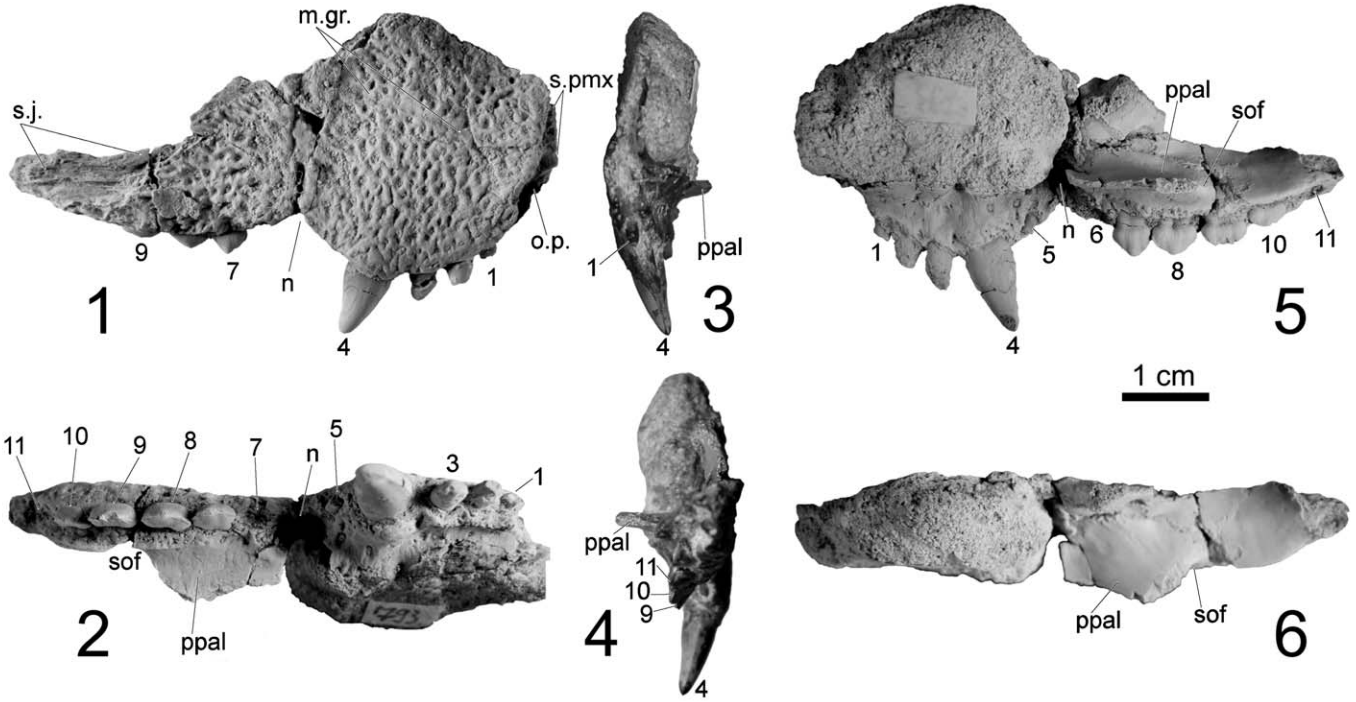

FIGURE 5—Right maxilla of *Theriosuchus sympiestodon* (MCDRD 793), Maastrichtian of Sânpetru, Romania in different views. *1*, lateral; *2*, occlusal; *3*, anterior; *4*, posterior; *5*, medial; *6*, dorsal. Small numbers correspond to the position of alveoli or teeth. Abbreviations: o.p.=occlusal pit; n=notch for reception of dentary tooth; m.gr.=maxillary groove; ppal=palatine process; sof=suborbital fenestra; s.j.=suture for jugal; s.pmx=suture for premaxilla.

supratemporal fenestra are missing. The ventral process of the quadrate stops just below the level of the foramen caroticum posterius and does not send any significant process in the pterygoid (Fig. 1). In cross-section, the quadrate is pneumatized, as evidenced by sediment filled vacuities. The quadrate makes up the posteroventral region of the otic wall. The posterior wall of the siphonium is not inset, but is flush with the quadrate and squamosal walls. The quadratosquamosal suture is horizontal.

Pterygoid.—The pterygoid is fragmented but preserves a large palatal portion, notably a large choanal aperture that occupies all the anteroposterior length of the bone (Fig. 1.4). The secondary choanae are enclosed anteriorly by the posteroventral and posterolateral margins of the palatine, and posteriorly by the pterygoids, unlike in eusuchians. The palatine suture takes place on the anteromedial tip of the pterygoid, along the choanal margin. The choanae are long and large, and in the anterior portion of the pterygoids make a pronounced concavity with a thick lateral wall of the pterygoid that accommodates a posterolateral process of the palatine. This pterygoid wall progressively disappears posteriorly and is continued by a ridge that slightly widens laterally. A marked choanal recess occupies the length of the pterygoid. The ventral plate of the bone displays a diminutive pterygoid wing (only the right side is preserved). The ventral surface of the wing is flat and it has the shape of a small triangle. The dorsal surface is strongly convex and is punctured by a crescentic depression. In ventral view, the pterygoid wing is faintly concave at its posterior margin. Its lateralmost tip is rounded. The anterior margin bears the suture for the ectopterygoid, and indicates absence of a contact between the ectopterygoid and the palatine: The pterygoid participates in the posteromedial corner of the suborbital fenestra. The dorsal process of the pterygoid is partly preserved and ascends between the exoccipital and quadrate. Its relation to the basisphenoid is impossible to assess.

Dentary.—An isolated proximal portion of a small-sized, isolated right dentary (MCDRD 134; Fig. 6) greatly resembles the dentary of *Theriosuchus pusillus* and is here referred to *Theriosuchus sympiestodon* on the basis of its tooth morphology (see below), as well as its occurrence within the same deposits as the other material attributed to this taxon. The lateral side of the dentary is largely convex dorso-ventrally and heavily ornamented, with a coarse, rugose, and pitted surface texture. The symphysis is mesio-distally expanded and extends back to the level of the sixth alveolus. Its ventral surface is flat (Fig. 6.2, 6.3). In the basal eusuchian *Acynodon*, the symphysis is shorter and restricted to the first two or three alveoli (Martin, 2007). The symphysis extension is more similar to that of *Shamosuchus djadochtaensis* (Pol et al., 2009) or the different species of *Araripesuchus* (e.g., Sereno and Larsson, 2010), with an extensive participation of the splenial. The tooth row is probably anteriorly incomplete and appears to preserve the second through the tenth alveoli; it has two waves alternating from the first to the ninth tooth position. The anterior wave supports the largest alveolus (probably the fourth), being followed by a reduction in alveolus size. The second wave presents another enlarged alveolus, the ninth (Fig. 6.2). The ninth tooth likely occluded in the pit or notch between the fifth and sixth maxillary teeth in the upper tooth row. The dorsal surface of the symphyseal area is pierced by two large nutritive foramina, placed just mesial and distal to the fourth tooth position, respectively. Minute foramina are furthermore present medial to the border of the assumed fifth-sixth, and sixth-seventh alveoli, respectively. These small foramina are situated closer to the toothrow and slightly higher (in lingual view) than the more anterior and larger ones. A diastema is present between the supposed seventh and eighth alveoli (Fig. 6.2, 6.3).

Dentition.—The incomplete maxillary dentition is preserved in all three available specimens (LPB [FGGUB] R.1945 and R.1782, as well as MCDRD 793). The teeth of R.1945 are preserved in the second, fourth, fifth, and seventh alveoli, those of R.1782 in the second, fourth, sixth, seventh, and ninth alveoli whereas MCDRD 793 is more complete, only lacking the teeth from the sixth and seventh alveoli; thus, based on these partly overlapping

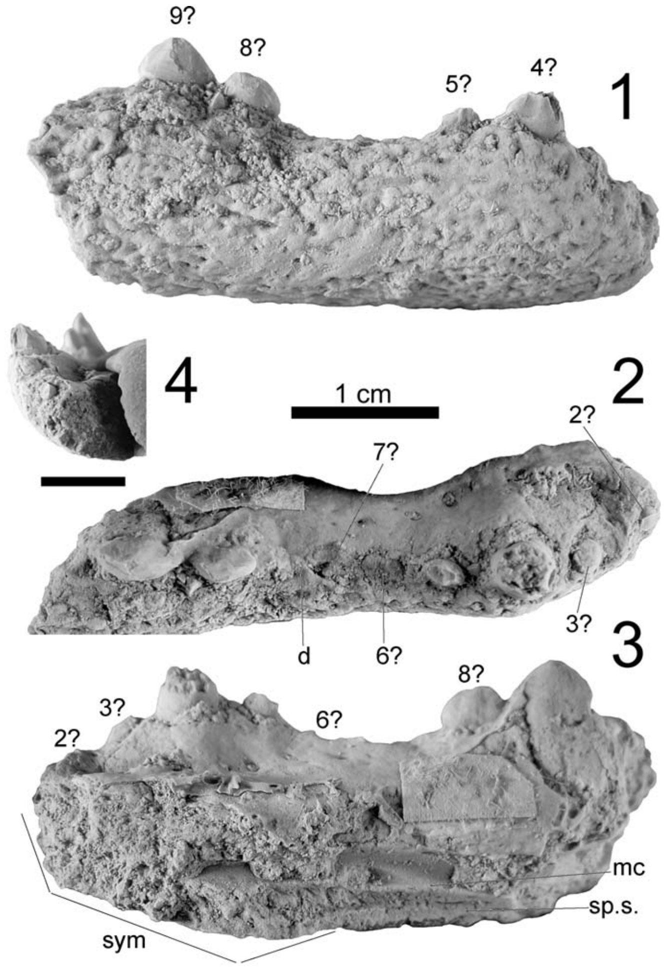

FIGURE 6—Fragmentary right dentary of *Theriosuchus sympiestodon* (MCDRD 134), Maastrichtian of Sânpetru, Romania in different views. *1*, lateral; *2*, dorsal; *3*, medial; *4*, anterior. Small numbers correspond to the position of alveoli or teeth. Abbreviations: d=diastema; mc=Meckelian canal; sp.s.=suture for splenial; sym=symphysis.

specimens, the entire toothrow, consisting of eleven tooth positions, can be reliably reconstructed. It is worth noting that the smallest available specimen (LPB [FGGUB] R.1945) shows a peculiar, unique morphology of the teeth, the detailed description and interpretation of which will be presented elsewhere, and thus only the dental features shared in common with the larger specimens will be noted here.

All the teeth are constricted at the base of the crown. In the anterior maxillary dentition, the teeth have relatively high, slightly labio-lingually flattened conical shapes, with weak mesial and distal carinae that lie lingual to the mesiodistal plane. The labial surface of the crown is convex whereas the lingual side is almost flat to slightly convex. In cross section, all teeth are longer than wide. Teeth in alveoli one to three are small, and show a moderate size increase distally. They have a slightly asymmetrical triangular profile in labial view, with a convex mesial and almost straight distal edge of the crown and, consequently with a slightly backward oriented apex. The fourth sub-conical tooth differs from the more anterior ones in being significantly larger in basal cross-section and in being more than twice as tall, thus standing out very prominently, in a canine-like fashion, from the maxillary toothrow. Moreover, while the more anterior conical teeth are more or less vertically oriented, the fourth (fang) tooth slants slightly distally (Figs. 4, 5). As compared to derived neosuchians, the presence of an enlarged fourth maxillary tooth differs from the confluent and enlarged 4+5 maxillary teeth of Goniopholididae but is recorded in the basal eusuchian *Allodaposuchus* (e.g., Puértolas-Pascual et al., 2013), a character previously considered as an apomorphy of Alligatoroidea (see discussion in Martin, 2010). In other taxa such as the Sebecosuchia, *Hamadasuchus*, *Kaprosuchus*, or *Araripesuchus*, the third maxillary tooth is enlarged, not the fourth.

Following the canine-like fourth tooth, there is an abrupt change in the size and morphology of the maxillary teeth, as seen in both LPB (FGGUB) R.1945 and MCDRD 793: Low-crowned labio-lingually compressed posterior teeth follow the sub-conical (or ovoidal, in occlusal view) anterior teeth. The fifth tooth, comparable in morphology to all the more posterior ones in having a labio-lingually compressed, low, triangular, leaf-like crown and slightly serrated carinae, is already significantly smaller than the fourth. Unlike the more posterior ones, however, the fifth tooth parallels the distally leaning fang-like fourth tooth, has a more acute apical angle and is relatively higher than the more posterior ones.

In the posterior part of the toothrow, the constriction between the crown and root is even better marked; the roots themselves are wide, labio-lingually flattened, plate-like elements with a slight longitudinal depression in the midline of the lingual side. Most teeth appear to be implanted within a continuous, incompletely divided groove, instead of distinct alveoli. From the sixth the posterior teeth are labio-lingually compressed, leaf-shaped, and low-crowned (Fig. 7); they are closely spaced, even slightly overlapping, as happens between the sixth and seventh tooth in LPB (FGGUB) R.1782, or between the eighth and ninth tooth in MCDRD 793. The crowns are becoming relatively lower backwards in the toothrow; whereas crown labio-lingual length and height, respectively, are sub-equal at positions sixth-seventh, crown height equals less than half of its length at positions tenth-eleventh. The labial face of the crown is moderately and continuously convex, while the lingual face has a more complex morphology, with a central raised area leading to the tip and bordered by two slightly depressed apico-basal furrows; lateral to these furrows, the lingual face becomes again swollen, near to the base of the crown. Both the labial and lingual crown surfaces of the posterior maxillary teeth display well-spaced, fine striae. The carinae are pseudoziphodont (sensu Prasad and de Lapparent de Broin, 2002), as the striae running towards the mesial and distal carinae terminate in small denticles (Fig. 7.1, 7.2). Posterior teeth with such morphology have never been reported in eusuchians; their morphology recalls instead that reported in *Araripesuchus* (Sereno and Larsson, 2010, fig. 19).

The dentary dentition is relatively poorly known compared to the maxillary one. More or less complete tooth crowns are preserved in the second to fifth and eighth to ninth alveoli (anatomical positions), but only the posterior ones show enough of the crown to ascertain its morphology. Only the root and basalmost part of the crown is preserved from the anteriormost (second-third) teeth; these seem to have been relatively small, slightly increasing in size backwards. The first preserved tooth appears to have been procumbent. The third preserved tooth position (interpreted as the fourth alveolus) also preserves only the implanted root and the basal part of the crown; based on the roughly circular cross-section of the preserved part, this tooth was, however, significantly larger than the other anterior dentary teeth. The next tooth shows a similar degree of preservation as the fourth, but is again markedly smaller, and appears to have had a moderately labio-lingually compressed cross-section. The last two teeth present in the dentary fragment (eighth-ninth) are the most completely preserved, showing low, triangular crowns with

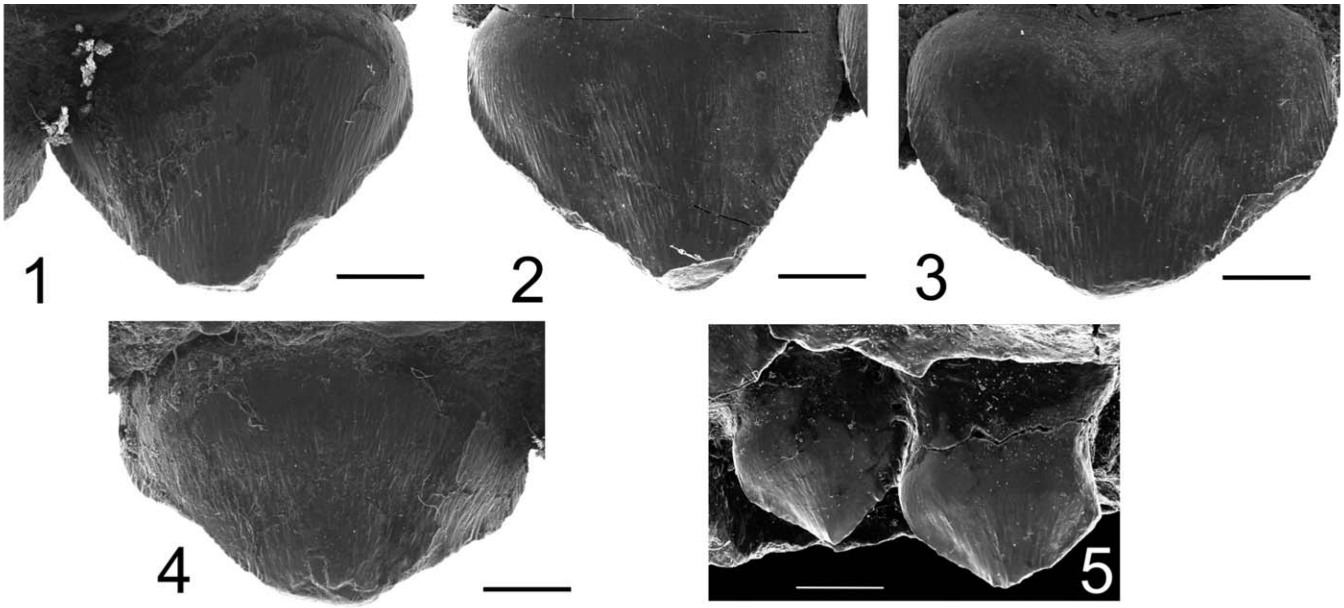

FIGURE *7*—Details (scanning electron microscope microphotographs) of the posterior maxillary dentition of *Theriosuchus sympiestodon*, Maastrichtian of Haţeg Basin, Romania. *1*, *2*, MCDRD 793, seventh tooth in labial and lingual views, respectively; *3*, eighth tooth in lingual view; *4*, tenth tooth in lingual view; *5*, LPB (FGGUB) R.1781, seventh and eighth teeth in lingual view. Scale bar=1 mm.

feeble marginal carinae, separated from the root by a constriction. These are similar to the posterior maxillary teeth in that their labial face is largely and uniformly convex, while the lingual face shows two para-medial furrows bordering a raised area along the midline. The presence or absence of striae or marginal denticulations cannot be ascertained, due to the glue covering the teeth; however, the first of the two posterior teeth shows a hint of marginal denticulation along the distal carine. On the other hand, the dentary teeth seem to differ somewhat from the maxillary ones in that the more distal tooth appears to be both higher and larger than the preceding one, while the height of the tooth crowns decreases gradually in the maxillary tooth row.

Isolated teeth.—A series of isolated teeth (Fig. 8) recovered through screen-washing from the Fântânele, Fântânele 2 and Budurone microvertebrate sites, Vălioara, as well as one isolated tooth from the holotype locality, can be assigned to *Theriosuchus sympiestodon* based on their overall morphology, and, most importantly, on the pseudoziphodont (sensu Prasad and de Lapparent de Broin, 2002) character of their carinae.

Most of the referred isolated teeth are leaf-shaped, basio-apically lower than mesio-distally long, suggesting they were posterior teeth (i.e., more posterior in position than the fourth caniniform tooth). The isolated teeth are labio-lingually compressed, with a convex labial surface, and a generally concave lingual surface, complicated by the presence of two bulges: a basal one, running mesio-distally, and an axial one, extending from the base to the apex of the tooth. Specimen LPB (FGGUB) v.688 shows an even more complicated lingual morphology, with two short additional bulges, placed on each side of the axial one. All isolated teeth have striae extending from the base to the apex of the crown, better developed on the lingual side. Upon reaching the mesial and distal carina, these striae terminate in small denticles, thus giving pseudoziphodont character to the crown margin, as commonly seen in *Theriosuchus* (e.g., Schwarz and Salisbury, 2005; Martin et al., 2010; Lauprasert et al., 2011). All crowns show a strong basal constriction, made even more conspicuous by the presence of the basal bulge. The axial bulge is less developed in the wider and lower-crowned teeth (such as LPB (FGGUB) v.506, v.763b, and v.688; Fig. 8.1, 8.2), which are comparable to the tenth- eleventh tooth position judging from the morphology of the available in situ maxillary teeth. Specimen LPB (FGGUB) v.763c is similar in morphology to the above-mentioned isolated teeth, but is considered to derive from a juvenile, based on its smaller size. Specimens LPB (FGGUB) v.663 and v.763a are more triangular, relatively taller, and have a well-developed axial bulge, visible both lingually and labially (Fig. 8.7, 8.8). Finally, specimens LPB (FGGUB) v.541, v.662, v.763d, v.791, v.845, and v.855 are smaller, taller than wide and their lingual side is less concave, almost flat (Fig. 8.11, 8.12). LPB (FGGUB) v.760 is taller than all the previously mentioned teeth and its shape roughly corresponds to an equilateral triangle.

Holotype.—LPB (FGGUB) R.1782, a right maxilla bearing seven teeth. Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania (referred to as the Tuştea specimen).

Paratype.—LPB (FGGUB) R.1781, a skull roof probably belonging to the same individual as LPB (FGGUB) R.1782 (Martin et al., 2010, supplementary material).

Referred material.—LPB (FGGUB) R.1945, a fragmentary juvenile right maxilla from the Fântânele site, Vălioara (referred to as the Fântânele specimen); MCDRD 134, anterior portion of a right dentary from the Cioaca Târnovului site, Sânpetru; MCDRD 793, a right maxilla from the La Cărare site, Sânpetru (referred to as the Deva specimen); LPB (FGGUB) v.506 and LPB (FGGUB) v.541, isolated teeth from the Fântânele 2 site, Vălioara; LPB (FGGUB) v.662, LPB (FGGUB) v.663, LPB (FGGUB) v.729, LPB (FGGUB) v.760, LPB (FGGUB) v.763a-d, and LPB (FGGUB) v.688, isolated teeth from the Fântânele site, Vălioara; LPB (FGGUB) v.845, isolated tooth from the Budurone site, Vălioara; LPB (FGGUB) v.791, isolated tooth from the Tuştea site.

Occurrence.—Maastrichtian of Haţeg Basin, Romania.

Remarks.—In the original description of *T. sympiestodon* (Martin et al., 2010), the holotype and paratype were referred to using the institutional acronym FGGUB. Subsequently, all fossil vertebrate specimen numbers from the University of Bucharest catalogues were updated by the simple addition of "LPB" acronym; thus, e.g., the holotype of *T. sympiestodon*, a

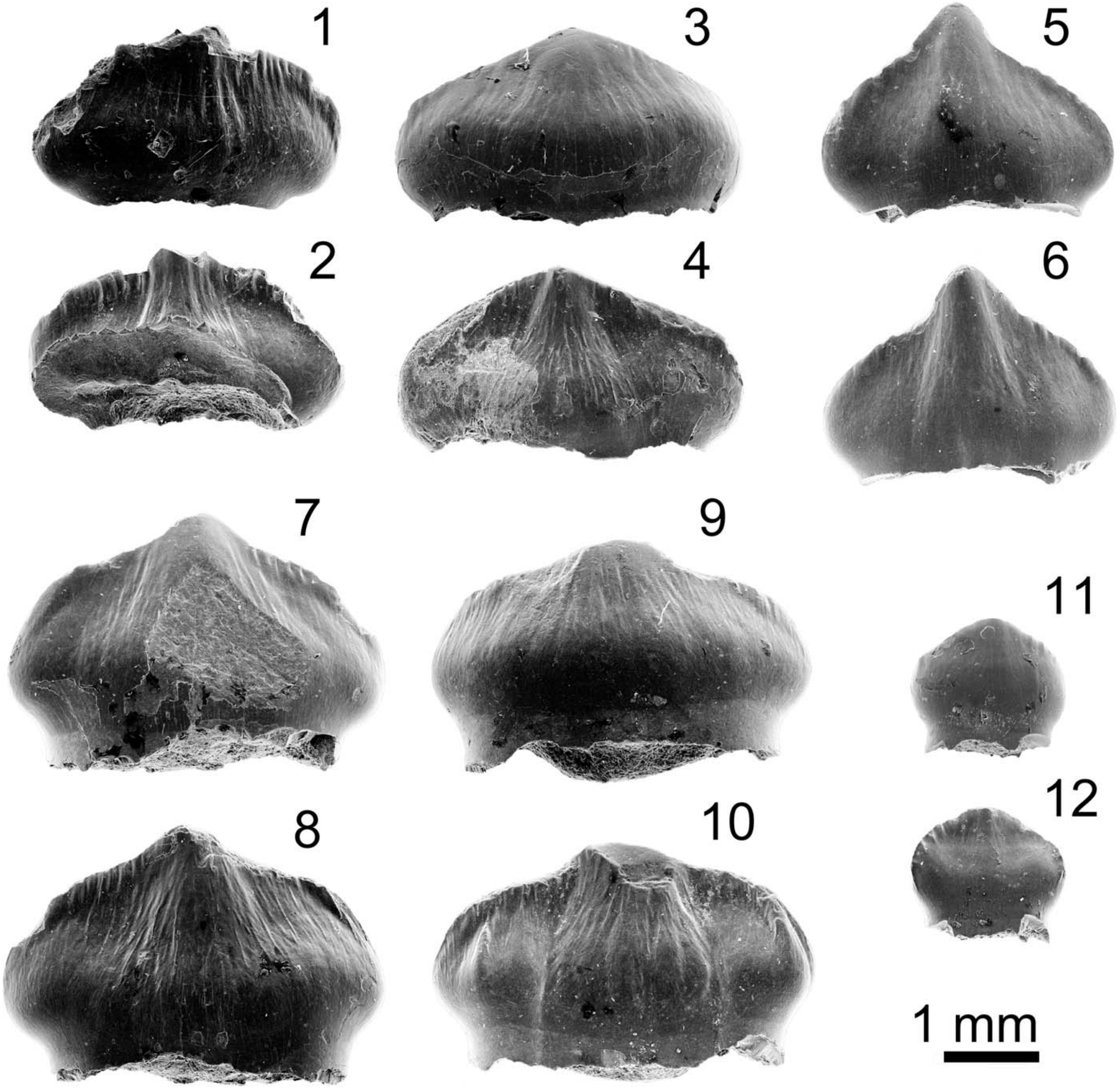

FIGURE *8*—Isolated teeth assigned to *Theriosuchus sympiestodon* from the Maastrichtian of Haţeg Basin, Romania. *1*, *2*, LPB (FGGUB) v.506 in labial and lingual views, respectively; *3*, *4*, LPB (FGGUB) v.763b in labial and lingual views, respectively; *5*, *6*, LPB (FGGUB) v.763a in labial and lingual views, respectively; *7*, *8*, LPB (FGGUB) v.663 in labial and lingual views, respectively; 9, 10, LPB (FGGUB) v.688 in labial and lingual views, respectively; *11*, *12*, LPB (FGGUB) v.845 in labial and lingual views, respectively.

right maxilla known previously as FGGUB R.1782, is now referred to as LPB (FGGUB) R.1782.

MESOEUCROCODYLIA Whetstone and Whybrow, 1983
?THERIOSUCHUS Owen, 1879
?THERIOSUCHUS sp.
Figures 9, 10

Referred material.—MHN AIX PV 2011.15.1, a right posterior maxillary ramus with dentition from the Campanian–Maastrichtian of Trets, Bendel, Bouches du Rhône, France; isolated teeth, Campanian–Maastrichtian of Cruzy, Hérault, France (referred to as Alligatoroidea indet. in Martin and Buffetaut, 2005).

Maxilla.—This specimen consists of the distal portion of a right relatively deep maxilla with six mediolaterally compressed, slightly bulbous teeth (Fig. 9). Bone surface ornamentation is similar to that of the Deva maxilla of *Theriosuchus sympiestodon* (MCDRD 793), consisting of anastomosing pits. Although fragmentary, a similar position of the extent of the suborbital fenestra can also be reconstructed, placed well above the tooth row (reaching to the level of the supposed eighth alveolus in MCDRD 793). Based on comparison with the Romanian material, the preserved teeth possibly correspond to the fifth to tenth teeth positions. All the preserved alveoli form a confluent groove along the tooth row.

Dentition.—The teeth preserved in the Trets maxilla as well as

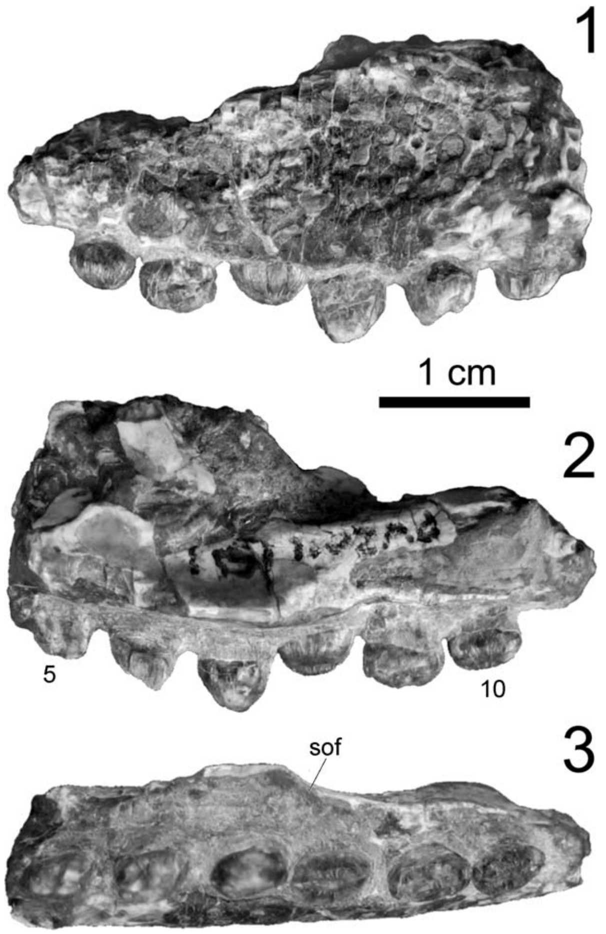

FIGURE *9*—Posterior portion of right maxilla (MHN AIX PV 2001.15.1) attributed to ?*Theriosuchus* sp., Campanian–Maastrichtian of Trets, Provence, France. *1–3*, lateral, medial, occlusal views, respectively. Small numbers correspond to the position of teeth Abbreviation: sof=suborbital fenestra.

the isolated teeth from Cruzy (Fig. 10) are mediolaterally compressed, low-crowned and exhibit a faint ornamentation of the enamel, often slightly more pronounced near the occlusal edge of the crown. The development of the ornamentation is variable and appears to be more obvious in the largest and most blunt/bulbous teeth, both in the Trets maxilla and in some teeth from Cruzy (Fig. 10.13–10.15, 10.22–10.24). Some of the teeth have a triangular outline whereas others are more bulbous. The triangular ones are reminiscent of relatively more anterior position and the latter ones are characteristic of the posteriormost dentition, as interpreted by comparison with the more complete maxillae from Haţeg and the partial one from Trets. The posterior teeth appear to be slightly more bulbous, with more marked vertical striae (almost weak ridges) and are more widely spaced than in the Deva and Tuştea specimens. Denticles are not present along the carinae.

DISCUSSION

Taxonomy and ontogenetic variation.—The MHN AIX PV 2011.15.1 maxilla from France does not show apomorphies of *Theriosuchus* and despite its vertical lateral surface and laterally compressed, low-crowned posterior teeth, a direct referral to *Theriosuchus* can at best be tentative. Indeed, although in the Late Cretaceous of Europe only *Theriosuchus* has pseudoziphodont and mediolaterally compressed teeth, this morphology is widespread among crocodylomorphs (Ősi, 2013). For this reason, we choose to refer this specimen together with the isolated teeth from Cruzy to ?*Theriosuchus* sp.

All the maxillary remains from Romania described above are assigned to *T. sympiestodon* because of the shared presence of a character complex including strongly enlarged, canine-like fourth maxillary tooth, mediolaterally compressed, leaf-like and pseudoziphodont posterior dentition, presence of a constriction between the crown and the root, as well as the presence of a sulcus on the lateral surface of the maxilla (apparently, an autapomorphy of the genus). Therefore, size differences in the studied sample (smallest maxilla length [~26 mm] reconstructed in LPB [FGGUB] R.1945; largest maxilla length [62 mm] in MCDRD 793) are interpreted as ontogenetic variability. This inference is further reinforced by the following features of the holotype (LPB [FGGUB] R.1782) and the likely associated skull roof LPB [FGGUB] R.1781, features interpreted as immature characters according to Mook (1921): relatively smooth lateral surface and shallower pits compared to the larger-sized Deva specimen (MCDRD 793); absence of constriction in the maxillary tooth row between the fifth and sixth alveoli, unlike in MCDRD 793; position of the supratemporal fenestrae, which are relatively widely spaced with their center appearing to be roughly in line with the estimated center of the orbits in dorsal view. The Fântânele specimen (LPB [FGGUB] R.1945) has a weak

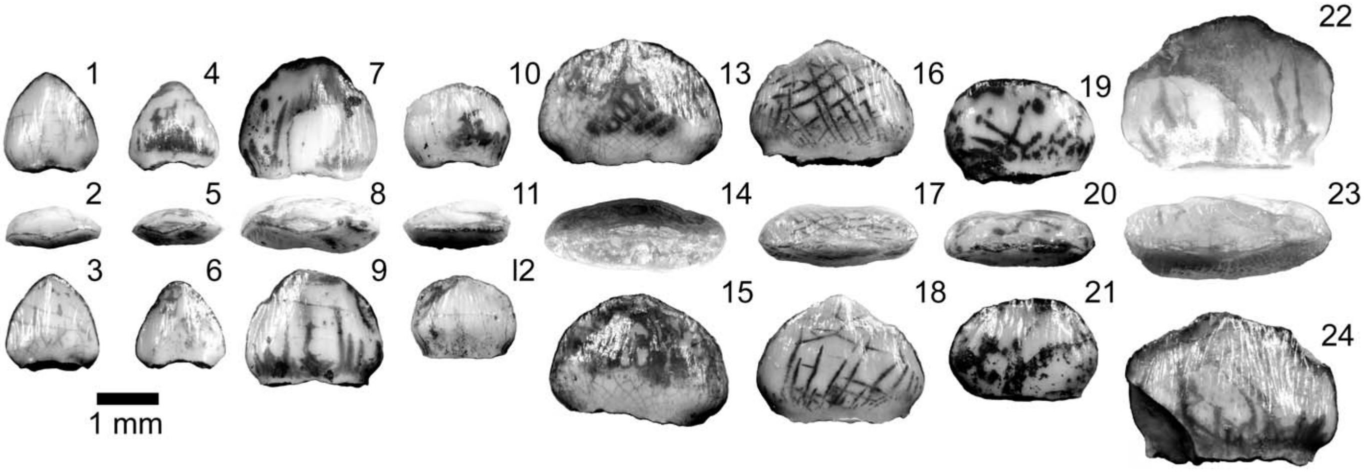

FIGURE *10*—Isolated teeth of ?*Theriosuchus* sp. from the Campanian–Maastrichtian of Cruzy, Hérault, France in different views. *1*, *4*, *7*, *10*, *13*, *16*, *19*, *22*, labial; *2*, *5*, *8*, *11*, *14*, *17*, *20*, *23*, occlusal; *3*, *6*, *9*, *12*, *15*, *18*, *21*, *24*, lingual views.

sculpturing, similar to LPB (FGGUB) R.1782, and based on its diminutive size is interpreted as representing an even earlier ontogenetic stage.

The holotype (LPB [FGGUB] R.1782) and paratype (LPB [FGGUB] R.1781) belong to an individual similar in size to the type specimen of *T. pusillus* (NHMUK 48330), which was attributed to an adult by Clark (1986). However, some characters of NHMUK 48330 can be considered as juvenile, including the large orbits associated with the position of the center of the supratemporal fenestra in line with the center of the orbit (sensu Mook, 1921). On the other hand, the well-developed dermal bone sculpturing and the fact that none of the other Purbeck *T. pusillus* specimens exceed this overall size range might imply an adult age for the holotype of *Theriosuchus pusillus*.

The maxillae MCDRD 793 and LPB (FGGUB) R.1945 have a festooned lateral profile that probably corresponds to the reception pit for an occluding mandibular tooth (likely the tenth as in *T. pusillus*). In contrast, the maxilla LPB (FGGUB) R.1782 is not festooned but exhibits an occlusal pit at the same level. Thus, the presence/absence of a festooned maxilla may be regarded as a variation during ontogenetic development. A modest festooning, although not as developed as in MCDRD 793 and LPB (FGGUB) R.1945, is present in *T. pusillus* (NHMUK 48330, 48240. b. and Owen, 1879, pl. III, figs. 9, 10, 12), *T. guimarotae* (Schwarz and Salisbury, 2005, fig. 2.1, 2.3, 2.4; Fig. 4.3), but is replaced by an occlusal pit in *T. ibericus* (IPFUB 102/21.2). This region is not preserved in the French specimen (MHN AIX PV 2011.15.1), but festooning is furthermore present in two undescribed maxillae of a similar taxon from the Santonian of Hungary (unpublished data). Pending new insights from more complete specimens, we choose to refer all *Theriosuchus* maxillae from Romania to *T. sympiestodon*, with LPB (FGGUB) R.1945 and LPB (FGGUB) R.1782 (together with LPB [FGGUB] R.1781) representing juvenile to subadult individuals, while MCDRD 793 represents an adult.

Another variation, probably also related to ontogeny, occurs in the anterior extension of the suborbital fenestra, reaching the level of the eighth-ninth alveoli in MCDRD 793 whereas it reaches further anteriorly in the smaller specimens, to the level of the sixth alveolus in both LPB (FGGUB) R.1782 and LPB (FGGUB) R.1945. In addition, in MCDRD 793 the occlusal pit anterior to the first alveolus was likely on the premaxilla-maxilla suture whereas in the other specimens it was restricted to the maxilla.

The Deva (MCDRD 793) and Aix (MHN AIX PV 2011.15.1) maxillae belong to individuals roughly twice the size of the holotype of *T. pusillus* (probably an adult) and the type of *T. sympiestodon* (probably a juvenile), and both are very similar in size to *T. ibericus* (IPFUB 102/21.2). Thus, depending on the as yet unresolved phylogenetic position of *T. ibericus*, larger size (~200 mm skull length) was achieved within atoposaurids once during the Barremian and once again during the Campanian–Maastrichtian. Alternatively, these Late Cretaceous forms maintained the size of a larger Early Cretaceous ancestor.

Distribution and abundance.—The newly recognized wider paleogeographic distribution of *Theriosuchus* in the Late Cretaceous allows a refinement of the conclusions of Martin et al. (2010). Besides several sites in Transylvania, ?*Theriosuchus* is now also known from two localities in southern France. In addition, two undescribed maxillae from the Santonian of Hungary and isolated teeth from the same site (Ősi et al., 2012b) as well as tentatively identified atoposaurid teeth reported from the Maastrichtian of Portugal (Galton, 1996) could expand the European distribution of the clade both geographically and stratigraphically. Indeed, it appears that *Theriosuchus*-like small atoposaurids colonized various landmasses, stretching from Portugal to Romania, during the Late Cretaceous (Fig. 11). The survival of atoposaurids was thus not an isolated event, restricted to the Transylvanian island, as suggested previously, but also occurred on different areas of the Ibero-Armorican landmass and possibly in other areas of southern Europe as well. Alternatively, an isolated survival event of *Theriosuchus* was followed by dispersal onto other landmasses, requiring at least limited paleobiogeographic connections between the different islands of the south European archipelago during the Late Cretaceous.

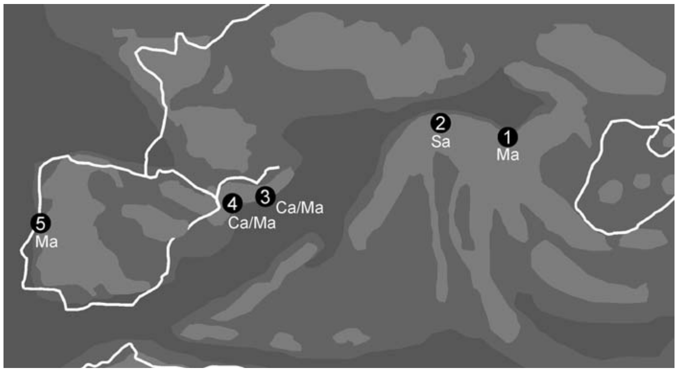

FIGURE *11*—Known distribution of atoposaurid crocodyliforms during the Late Cretaceous of Europe. *1*, *Theriosuchus sympiestodon* Martin, Rabi and Csiki, 2010, Haţeg Basin, Romania (this study, Martin et al., 2010); *2*, Atoposauridae indet., Iharkút, Hungary (Ősi et al., 2012b); *3*, ?*Theriosuchus* Owen, 1879, sp. indet., Trets, France (this study); *4*, ?*Theriosuchus* sp., Cruzy, France (this study, Martin and Buffetaut, 2005); *5*, ?Atoposauridae indet., Taveiro, Portugal (Galton, 1996). Abbreviations: Ca/Ma=late Campanian–early Maastrichtian; Ma=Maastrichtian; Sa=Santonian. Shades: dark gray=deep marine basins, partly floored by oceanic crust; moderate gray=shallow epicontinental seas; light gray=emergent land. Paleo map is modified from Ron Blakey (http://www2.nau.edu/rcb7/globaltext2.html).

Considering their newly recognized widespread distribution, the relative rarity of *Theriosuchus*-like mesoeucrocodylians in uppermost Cretaceous deposits of Europe might be explained by a combination of factors including its ecology and relatively small size (maximum ~200 mm skull length). As suggested by the morphology of the skull bones (forward facing external nares, short snout, straight maxilla, flat frontal continuous on skull table), and by the lower abundance of their remains relative to obvious semi-aquatic crocodilians during the Early Cretaceous (Schwarz and Salisbury, 2005), *Theriosuchus* and other atoposaurids were likely more terrestrial than aquatic, a clearly less favorable precondition for fossilization. Consequently, their occurrence and preservation in Upper Jurassic–Lower Cretaceous lagoonal deposits of France, Germany, and Spain (e.g., Buscalioni and Sanz, 1988) might be viewed as incidental and they more likely inhabited non-marine environments. *Theriosuchus* may have thus spent most of its time in terrestrial habitats; such a habitat preference is supported by the occurrence of all Late Cretaceous atoposaurid (*Theriosuchus* and ?*Theriosuchus*) specimens in purely continental, mainly fluvial deposits. On top of its terrestrial habitat preferences, the small body size of atoposaurids might have represented a further factor impeding the preservation of its remains in fluvial deposits, where transportation and reworking by currents might easily destroy the small and fragile bones.

Several other contemporaneous continental vertebrate taxa shows a trans-European distribution pattern reminiscent of that found in *Theriosuchus*/?*Theriosuchus*. This has been already noted in the case of different genera such as the bothremydid turtle *Foxemys* (Tong et al., 1998; Rabi et al., 2012), the basal eusuchians *Allodaposuchus* (Buscalioni et al., 2001; Delfino et al., 2008a; Martin, 2010; Martin and Delfino, 2010; Puértolas-Pascual et al., 2013) and *Acynodon* (Buscalioni et al., 1997, 1999; Martin et al., 2006; Martin, 2007; Delfino et al., 2008b; Martin and Delfino, 2010), or the basal nodosaurid dinosaur *Struthiosaurus* (Nopcsa, 1929; Pereda-Suberbiola, 1999; Garcia and Pereda-Suberbiola, 2003; Ősi and Prondvai, 2013). Such coherent distributional patterns suggest a similar paleobiogeographic history of these taxa. But whether it was dispersalist or vicariant in nature remains unknown until a better understanding of their taxonomic and phylogenetic affinities, as well as their inter-relationships. Finally, based on its rarity and potential for terrestrial dispersal coupled with a long stratigraphic range, discoveries of Late Cretaceous *Theriosuchus* (or *Theriosuchus* relatives) outside Europe can also be expected. For example, possible isolated atoposaurid teeth were reported, but not described or figured, from the John Henry Member of the Straight Cliffs Formation (Coniacian–Santonian) as well as from the Wahweap Formation (Lower Campanian) of Utah (e.g., Eaton et al., 1999).

ACKNOWLEDGMENTS

For access to specimens, we thank S. Burnaz (Deva), D. Schwartz-Wings (Berlin), and L. Steel (London). Members of the Musée d'Histoire Naturelle (Aix-en-Provence) are acknowledged for their hospitality and helpfulness. Notably, Y. Dutour found the Aix maxilla and E. Turini prepared it; E. Turini also supplied photographs of the specimen. F. Fages and D. Clavel (ACAP, Cruzy) kindly provided access to the isolated teeth from Cruzy. We thank K. Buczkó (Natural History Museum of Hungary) for producing the scanning photos and A. Ősi (MTA-ELTE Lendület Dinosaur Research Group) for providing access to the SEM. Images in Figure 10 were made using a Leica M205C and LAS multifocus image fusion at the 'Institut des Sciences de l'Evolution de Montpellier' (plateforme d'imagerie ANR-PalAsiAfrica). We thank I. Lazăr and M. E. Popa (FGGUB Bucharest) for their help in photographing some of the Romanian specimens. MR was supported by the MTA Lendület Program Project No. 95104, the Doctoral School of Environmental Sciences of the Eötvös Loránd University, the National Bureau of Research and Technology (NKTH TéT:FR-22/2008) and the Hungarian Scientific Research Fund (NF 84193). ZCS-S and SV were supported by CNCSIS project 1930/2008; ZCS-S also acknowledges the support from grant PN-II-ID-PCE-2011-0381 CNCS. A previous version of this manuscript benefited from the constructive comments of C. Brochu and an anonymous reviewer, as well as those of the editor, S. Hageman.

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Accepted 3 October 2013