

A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal

Une nouvelle espèce de *Theriosuchus* (Atoposauridae, Crocodylomorpha) du Jurassique supérieur (Kimméridgien) de Guimarota, Portugal

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Abstract

A new species of an atoposaurid crocodylian, *Theriosuchus guimarotae*, is described from the Late Jurassic (Kimmeridgian) of Portugal. *Theriosuchus guimarotae* can be distinguished from other species of *Theriosuchus* by a lateral surface of squamosal bevelled ventrally; a rounded, caudally projecting and dorsally sculptured caudolateral corner of the squamosal; a premaxillomaxillary suture aligned caudomedially in dorsal aspect; a minimum space between the supratemporal foramina that comprises one third of the total width of the cranial table; a minimum width of the frontal between the orbits that comprises one third of the maximum width of the skull at the orbits; a dentition that comprises only pseudocanineiform and lanceolate-shaped teeth; the presence of an external mandibular fenestra and all vertebral bodies amphicoelous. Its osteology also sheds light on the diagnosis of *Theriosuchus* within Atoposauridae. The material additionally includes specimens representative of several ontogenetic stages, each of which is discussed here. With its Late Jurassic age, *T. guimarotae* represents the oldest well-preserved material of *Theriosuchus* and reveals further knowledge about the palaeobiogeography of the genus in western Europe. © 2005 Elsevier SAS. All rights reserved.

Résumé

Une nouvelle espèce de crocodylien atoposauridé, *Theriosuchus guimarotae*, du Jurassique supérieur (Kimméridgien) du Portugal est décrite. *Theriosuchus guimarotae* se distingue des autres espèces de *Theriosuchus* par les caractères de la table crânienne, du rostre maxillaire, les dents et des vertèbres. Son ostéologie apporte une lumière sur la diagnose de *Theriosuchus* au sein des Atoposauridae. Le matériel additionnel comprend des spécimens représentatifs à divers stades ontogénétiques, dont chacun est discuté ici. Datés du Jurassique supérieur, les restes de *T. guimarotae* représentent les plus anciens éléments bien préservés de *Theriosuchus* et apportent des nouveaux éléments dans la connaissance de la paléobiogéographie du genre dans l'Ouest de l'Europe. © 2005 Elsevier SAS. All rights reserved.

Keywords: Crocodylomorpha; Atoposauridae; *Theriosuchus*; Portugal; Late Jurassic; Ontogeny; Palaeobiogeography

Mots clés : Crocodylomorpha ; Atoposauridae ; *Theriosuchus* ; Portugal ; Jurassique supérieur ; Ontogénie ; Paléobiogéographie

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1. Introduction

During long-termed excavations at the Portuguese fossil deposits of Guimarães, numerous crocodylian remains have been unearthed. The first to be described was a large teleosauroid, *Machimosaurus hugii* (Krebs, 1967). The second was the medium-sized neosuchian *Goniopholis baryglyphaeus* (Schwarz, 2002). The majority of crocodylian fossils from Guimarães, however, belong to considerably smaller animals. Some of these remains were preliminary determined as *Theriosuchus*- and *Bernissartia*-like forms by Brinkmann (1989), but after that, the material was not studied any further. Recent investigations on the smaller crocodylian material of Guimarães indicate that at least four taxa of small sized crocodylians not exceeding one meter in length can be distinguished (Krebs and Schwarz, 2000). The majority of these small crocodylian bones can be assigned to the genus *Theriosuchus*. Although they are mainly isolated, the remains are excellently preserved and comprise specimens of several different ontogenetic stages.

Theriosuchus was established by Owen, 1879. Owen erected the genus and type species *T. pusillus* based on a specimen preserved on a single slab of “Beckles residuary marls” from the Purbeck Limestone Group of Dorset, England (Salisbury, 2002). However, as has been pointed out by Clark (1986), Brinkmann (1992) and Salisbury (2002), a slab containing isolated osteoderms was figured and referred to *Theriosuchus* by Owen in an earlier paper (Owen, 1878). Since then, many crocodylian specimens collected from the Purbeck Limestone Group have been referred to *T. pusillus*, the majority of them currently housed in the collections of the Natural History Museum, London. A second species, *T. ibericus*, was reported from the Barremian of Uña, Spain by Brinkmann (1992). *Theriosuchus* material known from other European fossil deposits is rare and of fragmentary nature (Buscalioni and Sanz, 1984, 1987a, 1987b; Cuny et al., 1991; Evans and Milner, 1994; Benton and Spencer, 1995; Thies et al., 1997).

Species of *Theriosuchus* are all small (<1 m in total length) neosuchian crocodylians, with a strongly brevirostrine skull and proportionately large orbits. In addition to the latter features, diagnostic skull characters of *Theriosuchus* include divided nares, and proportionately large supratemporal foramina in relation to length and width of the cranial table.

Theriosuchus has often been thought to share affinities with Eusuchia because it was described as having procoelous vertebrae (Joffe, 1967; Buffetaut, 1982; Benton and Clark, 1988; Buscalioni and Sanz, 1990; Norell and Clark, 1990). At present, *Theriosuchus* is viewed as sister group of a clade comprising of Goniopholidae, *Bernissartia* and Eusuchia (Wu et al., 2001). Most classifications place *Theriosuchus* in Atoosauridae.

Theriosuchus spp. are known from the Late Jurassic (Kimmeridgian) and the Early Cretaceous (Barremian) of Europe. The *Theriosuchus* finds from Guimarães represent some of the oldest known material of *Theriosuchus* yet found. The

exceptional preservation and abundance of the material additionally sheds much needed light on the diagnosis of the genus.

The material is housed in the Department of Palaeontology of the Institute for Geological Sciences at the Freie University Berlin (IPFUB), Germany.

2. Geological setting and the environment of Guimarães

The coal mine of Guimarães/Leiria is positioned at the eastern margin of the Lusitanian Basin (Fig. 1A)—a north–south running sedimentary trough. This basin is part of a rift system that follows the main directions of a late hercynian fracture tectonics and marks the early opening of the north Atlantic. The sediments in the Lusitanian Basin are at the basis clastic and continental strata together with local evaporites, deposited during the Late Triassic and the Early Jurassic. They were replaced in the Middle and Late Jurassic by an inter-fingering of open marine and brackish-lacustrine successions resulting from a transgression. Halokinetic movements from the underlying evaporites beginning in the Middle Jurassic caused additional fracture tectonics and divided the basin into small subbasins (Schmidt, 1986).

The vertebrate-bearing lignite coal layers of Guimarães are known as the “Guimarães-strata” (Fig. 1B). These have recently been considered to belong to the Alcobaça Formation, which is part of the Kimmeridgian Abadia Formation (Manuppella, 1998; Schudack, 2000a). The “Guimarães-strata” comprise a Lower (“Fundflöz”, Schudack, 1993) and an Upper (“Ruafolge”, Schudack, 1993) lignite coal layer separated by marly limestones. Both layers consist of marls, shaley marls and lignite coal marls.

The vertebrate-bearing layers are only locally exposed and do not contain index fossils (Schudack, 2000a). On the basis of charophytes and ostracodes, Helmdach (1971) first determined the age of Guimarães to be Early Kimmeridgian. Based on the floras, Brauckmann (1978) assumed an Oxfordian age for Guimarães. Studies of palynomorphs led Van Erve and Mohr (1988) to also conclude an Oxfordian age. Most recently, Sousa (1998); Schudack (2000a, 2000b) suggested that only the ostracods provide conclusive evidence on the age of the coal mine. These indicate a Kimmeridgian age and a more precise dating of these strata is therefore precluded.

The environment in which the Guimarães-strata were deposited has been interpreted as lagoonal with some freshwater influx and periodically flooded by salt water (Helmdach, 1971; Schudack, 2000a). Palynological investigations (Van Erve and Mohr, 1988) indicate a wooded swamp region, comparable with recent tropical mangrove forests (Gloy, 2000; Martin, 2000a). Systematic excavations and long-termed screen-washing activities in Guimarães were initiated in the hope of finding mammalian remains. These activities were richly rewarded producing abundant vertebrate remains. Non-mammalian vertebrates recovered from Guimarães include chondrichthyans and osteichthyans (Kriwet, 2000), amphib-

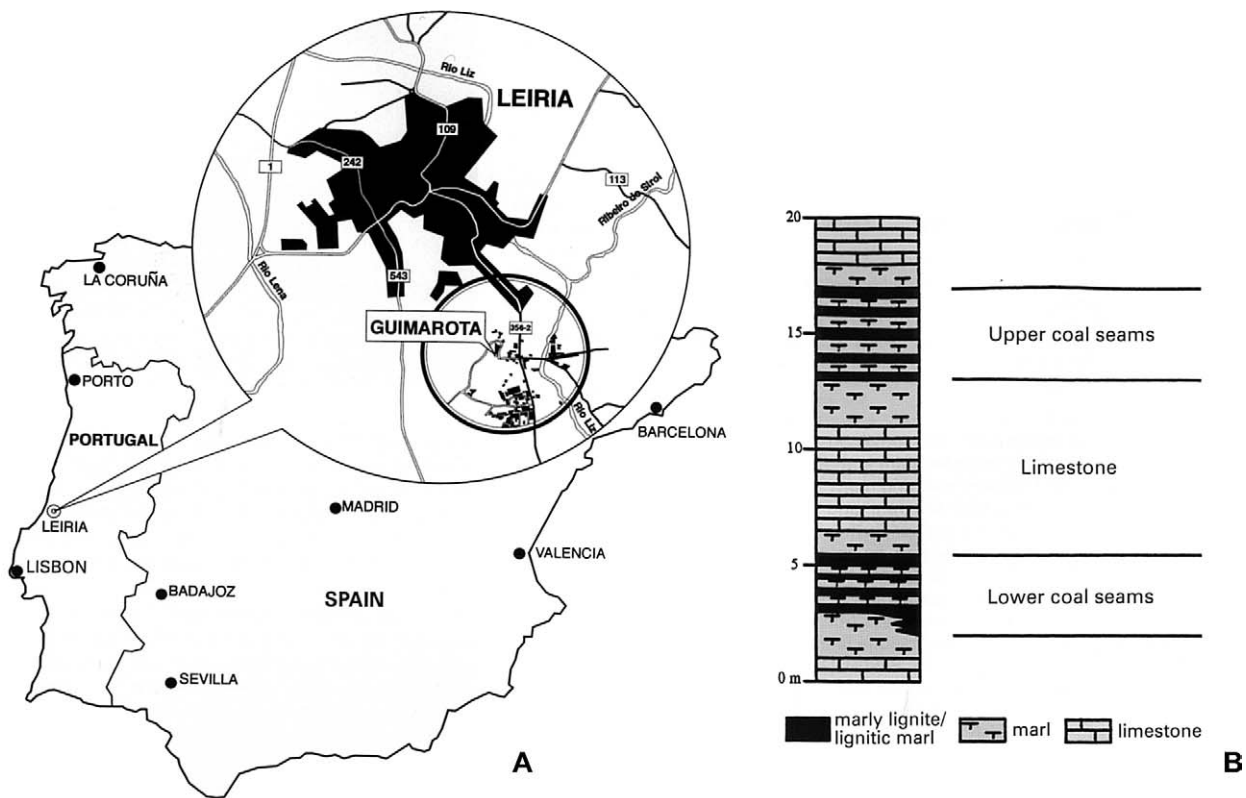


Fig. 1. A. Position of the Guimarota fossil locality within the Iberian Peninsula. B. Simplified stratigraphy of the vertebrate-bearing strata of Guimarota. Both pictures from Martin and Krebs in 2000.

Fig. 1. A. Position de la localit  de Guimarota dans la p ninsule Ib rique. B. Stratigraphie simplifi e des couches avec vert br s fossiles. Images de Martin et Krebs en 2000.

ians (Wiechmann, 2000), turtles (Ga ner, 2000), lizards (Broschinski, 2000), crocodylians (Krebs and Schwarz, 2000), dinosaurs (Rauhut, 2000) and pterosaurs and archaeopterygiformes (Wiechmann and Gloy, 2000). Mammalian finds include docodonts (Martin and Nowotny, 2000), multituberculates (Hahn and Hahn, 2000), dryolestids (Martin, 2000b) and henkeloteriids, including the skeleton of *Henkelotherium guimarotae* (Krebs, 2000). Invertebrates are restricted to ostracods (Schudack, 2000b) and molluscs (Aberhan et al., 2000).

3. Systematic palaeontology

CROCODYLOMORPHA Walker, 1968.

CROCODYLIFORMES Hay, 1930.

MESOEUCROCODYLIA Whetstone and Whybrow, 1983.

NEOSUCHIA Benton and Clark, 1988.

Family ATOPOSAURIDAE Gervais, 1971.

Genus *Theriosuchus* Owen, 1878.

Type species: *Theriosuchus pusillus* Owen, 1879, from the Berriasian of Swanage, Dorset, Southern England.

Theriosuchus guimarotae sp. nov.

Etymology: Referring to its occurrence in the locality of Guimarota/Leiria.

Holotype: IPFUB Gui Croc 7308, partial skull and mandible, part of an isolated surangular, a second sacral vertebra and two partial osteoderms.

Referred material:

- Cranial and mandibular remains: IPFUB Gui Croc 7309, 7403-1, 7709 (partial skulls); IPFUB Gui Croc 73187, 7520, 8240 (premaxillae); IPFUB Gui Croc 7311, 7319, 7320, 7330, 7415-1, 7503, 7528, 75100, 7606, 7608, 7611, 7612, 7701, 7702, 7713, 7719, 8001, 8101, 8102 (maxillae); IPFUB Gui Croc 7333, 7338, 7405, 7591, 75101, 75102, 7708, 7806, 8106 (palpebrals); IPFUB Gui Croc 8008 (lacrimal); IPFUB Gui Croc 7304, 7406, 7414, 7601, 7602, 7630, 7705, 7717, 7807, 8238 (frontals); IPFUB Gui Croc 73120, 7410, 7456, 7506, 7508, 7511, 7613, 7712, 7903, 8004, 8108 (jugals); IPFUB Gui Croc 7326, 7339, 73121, 7519, 7902 (postorbitals); IPFUB Gui Croc 7343, 73103, 73106, 7703, 8043 (squamosals); IPFUB Gui Croc 7510, 7595, 7732, 7802, 7805, 8003, 8239 (parietals); IPFUB Gui Croc 7455, 8202 (supraoccipitals); IPFUB Gui Croc 7340, 7371, 73107, 73108, 73122, 7578 (ectopterygoids); IPFUB Gui Croc 7501, 7593 (pterygoids); IPFUB Gui Croc 7402, 8204, 8207 (basioccipitals); IPFUB Gui Croc 7447, 7539, 7710 (quadrates); IPFUB Gui Croc 7306, 7310, 7316, 73124, 7404, 7411, 7413, 7513, 7518, 7521, 7525, 7530, 7531, 7533, 7534, 7592, 7607, 7704, 7716, 7733, 7737, 7901, 7904, 8005, 8007, 8045, 8105, 8109,

8110 (dentaries); IPFUB Gui Croc 8103, 8201 (splenials); IPFUB Gui Croc 7318, 7331, 7337, 73125, 73186, 7415-2, 7507, 7512, 7524, 7536, 7706, 7707 (angulars); IPFUB Gui Croc 7322, 7328, 73123, 7454, 7587, 7588, 7589, 8042, 8044 (surangulars), IPFUB Gui Croc 7327, 7344 7345, 7347, 7407, 7408, 7412, 7538, 75103, 7605, 7905, 8006, 8046, 8215 (isolated teeth).

- Postcranial remains: IPFUB Gui Croc 7352 (caudal vertebrae, right femur, caudal osteoderms); IPFUB Gui Croc 7441 (caudal osteoderms and left ulna); IPFUB Gui Croc 7545 (three articulated dorsal vertebrae, right and left ischium, paravertebral and caudal osteoderms); Gui Croc 7564 (left femur, left humerus, paravertebral osteoderm); Gui Croc 7634 thoracic and lumbar vertebrae, cervical rib, caudal osteoderms); IPFUB Gui Croc 8037 (cervical and thoracic and lumbar vertebra and osteoderms); IPFUB Gui Croc 7349 (proatlas); IPFUB Gui Croc 7550, 7555 (axis); IPFUB Gui Croc 7381, 7394, 73133 73134, 73135, 7475, 7614, 8138, 8148 (cervical vertebrae); IPFUB Gui Croc 7351, 7360, 7426, 7429, 7560, 75108, 7526, 7743, 7809, 7910, 8033, 8111, 8132 (thoracic and lumbar vertebrae); IPFUB Gui Croc 7472, 8028 (first sacral vertebrae); IPFUB Gui Croc 7423 (second sacral vertebra); IPFUB Gui Croc 7584 (centrum of sacral vertebra); IPFUB Gui Croc 7363, 7388, 7395, 73137, 73138, 73139, 7422, 7478, 7552, 7575, 75109, 75110, 7633, 7654, 7658, 7682, 7725, 7744, 7811, 7906, 7913, 8024, 8047, 8052, 8114, 8133, 8136, 8218, 8248 (caudal vertebrae); IPFUB Gui Croc 7369, 7629, 7727, 7810, 8123 (cervical ribs); IPFUB Gui Croc 7480, 7570, 8017, 8217 (thoracic ribs); IPFUB Gui Croc 7548, 7549, 8116 (coracoids); IPFUB Gui Croc 7420, 7542, 7661, 7674, 7675, 7908, 8142, 8230 (humeri); IPFUB Gui Croc 7391, 7457, 7641, 7668 (ilia); IPFUB Gui Croc 7580, 7678, 7680, 8130 (ischia); IPFUB Gui Croc 7350, 7366, 7389, 7396, 73140, 73141, 73142, 7428, 7839, 7482, 7543, 7544, 7553, 7564, 7568, 7577, 7585, 7599, 75112, 75113, 75127, 7617, 7618, 7621, 7624, 7625, 7643, 7722, 7723, 7728, 7909, 8010, 8016, 8135, 8139, 8210, 8212 (femora); IPFUB Gui Croc 7348, 7397, 7562, 8025, 8039, 8053, 8221, 8231 (tibiae); IPFUB Gui Croc 73125, 7659, 8141, 8232 (metatarsals); IPFUB Gui Croc 75104, 7579, 8245 (phalanges); IPFUB 7301, 7352, 7355, 7357, 7359, 7374, 7375, 7376, 7377, 7379, 7380, 7383, 7385, 7392, 73101, 73128, 73129, 73130, 73131, 73132, 7415-3, 7416, 7417, 7419, 7421, 7424, 7425, 7430, 7431, 7432, 7434, 7437, 7438, 7441-1-6, 7442, 7458, 7459, 7461, 7462, 7463, 7464, 7465, 7466, 7467, 7468, 7469, 7470, 7471, 7472, 7473, 7474, 7496, 74108, 7563, 7565, 7566, 7572, 7583, 75105, 75106, 75107, 75118, 75134, 75135, 7623, 7627, 7650, 7685, 7729, 7730, 7912, 8012, 8014, 8015, 8019, 8026, 8031, 8037, 8041, 8057, 8058, 8113, 8118, 8125, 8137, 8146, 8147, 8159, 8160, 8216, 8226, 8227, 8228, 8236, 8246, 8247 (osteoderms).

Type locality: The coal mine of Guimarães, a suburb of Leiria in north-western Portugal.

Stratigraphical range: Lower (“Fundsichten”) and upper (“Ruafolge”) lignite coal layer of the “Guimarães-

Strata”, within the Alcobaça Formation, Upper Jurassic (Kimmeridgian).

Diagnosis: *T. guimarotae* possesses the following unique combination of features: lateral surface of squamosal bevelled ventrally, with a distinct lateral notch rostrally; caudolateral corner of the squamosal forms a rounded, caudally projecting process with sculpture pitting on its dorsal surface that is similar to that on the rest of the cranial table; premaxillomaxillary suture aligned caudomedially in dorsal aspect; minimum space between supratemporal foramina comprises one third of the total width of the cranial table; dentition that comprises only pseudocanineiform and lanceolate-shaped teeth, all with mesial and distal carinae; minimum width of the frontal between the orbits comprises one third of the maximum width of the skull at the orbits; external mandibular fenestra present; all vertebral bodies amphicoelous.

4. Description

4.1. Preservation

Material referable to *T. guimarotae* currently comprises 159 cranial and 262 postcranial remains, the majority of which are disarticulated. The remains were collected from both the lower and the upper lignite coal layer and show no differences in their preservation. The number of specimens is likely to increase as more crocodylian material from the site is prepared. On those bones that have been removed from the coaly matrix in which they were encased, fractures, foramina and other openings are still filled with matrix. The articular surfaces of the elements are partly resolved by humic acids. Due to the diagenetic pressure of the coal, most of the preserved elements are crossed by fractures, but most of the bones are preserved three-dimensionally with little or no distortion. Some, however, underwent an either lateromedial or dorsoventral compression and are slightly distorted. None of the remains shows traces of rolling from longer transport in fluvial systems. A few of the preserved skeletal parts bear scratch and feeding marks.

The holotype skull and mandible of *T. guimarotae* (IPFUB Gui Croc 7308) is lateromedially compressed. Due to outstanding preparation by Ellen Eggert (FUB), both the right and the left side are visible. The caudal margin of both the cranial table and the mandible are missing. Some of the cranial elements are exposed in dorsal aspect only. Some of the isolated premaxillary, maxillary and dentary remains have teeth preserved in situ. The only articulated postcranial remnants are three thoracic vertebrae. Most of the vertebrae lack their neural spines and the long bones are often broken, such that only the proximal or distal parts are preserved. The repeated occurrence of many fractures and breaks on the bones combined with the presence of so many partial remains indicates that the material was transported a short distance in the lagoon prior to fossilisation. Transportation of the remains is also supported by evidence of palaeocurrents within the Guimarães lagoon (Gloy, 2000).

4.2. Osteology

4.2.1. Skull

4.2.1.1. Form and proportions. The skull of *T. guimarotae* has a rostral length/total skull length index of 0.42 (Fig. 2A, B), making it strongly brevirostrine sensu Busbey (1995). The maximum width of the maxillary rostrum is 22% that of the cranial table. In dorsal aspect the maxillary rostrum is almost triangular in outline, tapering strongly towards the premaxillae (Fig. 2C, D). A shallow notch is present at the premaxillo-maxillary suture for the reception of the fourth dentary tooth. The lateral margin of the rostrum undulates both vertically and horizontally, tracing an outline equivalent to two ventral convexities. The first ventral convexity reaches its maximum curvature at the third and fourth premaxillary teeth, whereas the second ventral convexity is largest at the fourth and fifth maxillary teeth. The antorbital fenestra is positioned directly rostral to the orbit, and has maximum length that is 33% that of the orbit (Fig. 2). The orbit itself comprises 25% of the total skull length. The interorbital region makes up approximately 33% of the total skull width at the orbit. The maximum width of the supratemporal foramen is approximately 66% that of the orbit. The supratemporal foramen and orbit are separated from each other by a narrow bend of the frontal and postorbital. The cranial table widens by about 10% from its cranial to its caudal margin. Its lateral margins are gently convex. In dorsal aspect, the caudal margin of the cranial table is level with the squamososupraoccipital suture.

The dorsal surface of the skull is covered in regularly spaced circular pits. This sculpturing is weakest on the premaxilla, maxilla, nasal and the rostral part of the frontal, and strongest on bones of the cranial table, the palpebrals and the jugal. The region between orbit and supratemporal foramina, the postorbital process, the dorsal process of the jugal and the

quadratojugal are unsculptured. The larger the bones, the greater the degree of sculpture pitting (see Section 5.4 for more details).

4.2.1.2. Naris. The nares are positioned dorsally on the premaxilla and are divided medially by the rostral-most extent of the nasals. The lateral margins of the nares are formed by the premaxillae. Each naris is crescent-shaped in outline (Figs. 2 and 3).

4.2.1.3. Antorbital fenestra. The rostral, rostromedial and lateral margins of the antorbital fenestra are formed by the maxilla. The caudomedial and caudal margins are formed by the lacrimal (Figs. 2 and 3). The fenestra is strongly convex rostrally, widening from rostral to caudal by approximately 25%. The caudolateral corner almost forms a right angle. An antorbital fossa sensu Witmer (1997) is not apparent.

4.2.1.4. Orbit. The oval-shaped orbit is 50% longer than it is wide. It is oriented dorsally, with its rostral margin level with the 12th maxillary tooth. Rostrally, the orbit is bounded by the lacrimal (Fig. 2A, B). Rostrolaterally and caudolaterally its margins are formed by the jugal, whereas the cranial third and the caudal two thirds of the medial margin are formed by the prefrontal and the frontal, respectively. The caudolateral margin of the orbit is formed by the postorbital process (Fig. 3A).

4.2.1.5. Supratemporal foramen. The external margin of the supratemporal foramen is almost rectangular in outline (Fig. 4A). Along the rostral-most third of its medial margin it is bounded by the frontal. The remainder of its medial margin comprises the parietal. Rostrolaterally, it is bounded by the postorbital and caudolaterally by the squamosal. The total width of the foramen decreases internally, and its outline

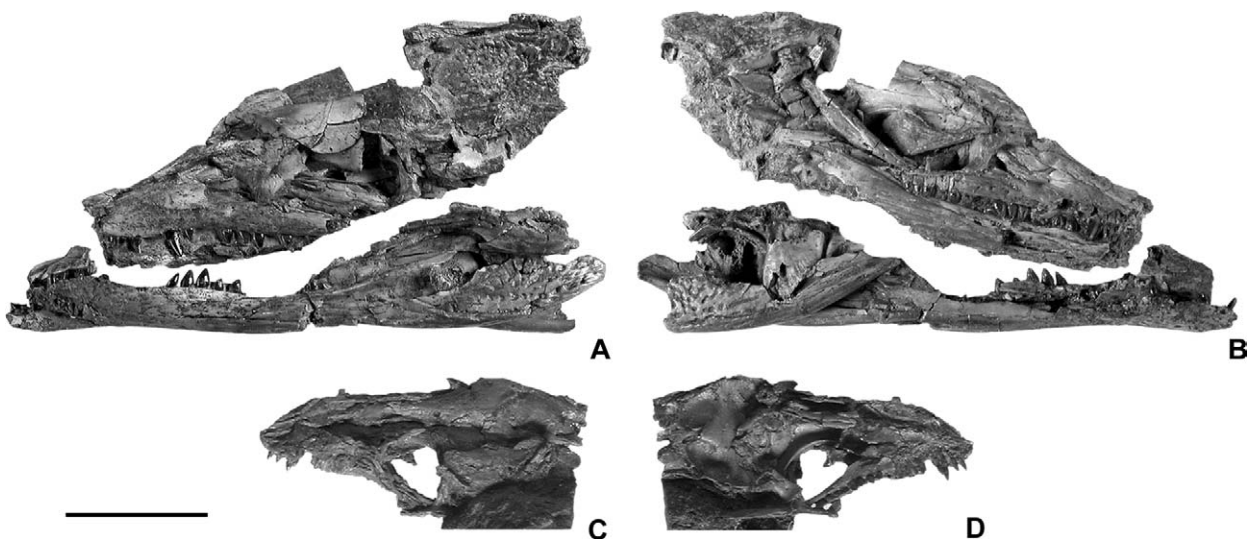


Fig. 2. *T. guimarotae* (IPFUB Gui Croc 7308-1) from the Upper Jurassic (Kimmeridgian) of Guimarota/Portugal, holotype skull and mandible in left (A) and right (B) lateral view; skull (IPFUB Gui Croc 7309) of *T. guimarotae* in dorsal (C) and ventral (D) view. Scale bar represents 10 mm.

Fig. 2. *T. guimarotae* (IPFUB Gui Croc 7308-1) du Jurassique supérieur (Kimmeridgien) du Guimarota/Portugal, holotype du crâne et de la mandibule en vue latérale gauche (A) et droite (B); crâne (IPFUB Gui Croc 7309) de *T. guimarotae* en vue dorsale (C) et ventrale (D). Échelle : 10 mm.

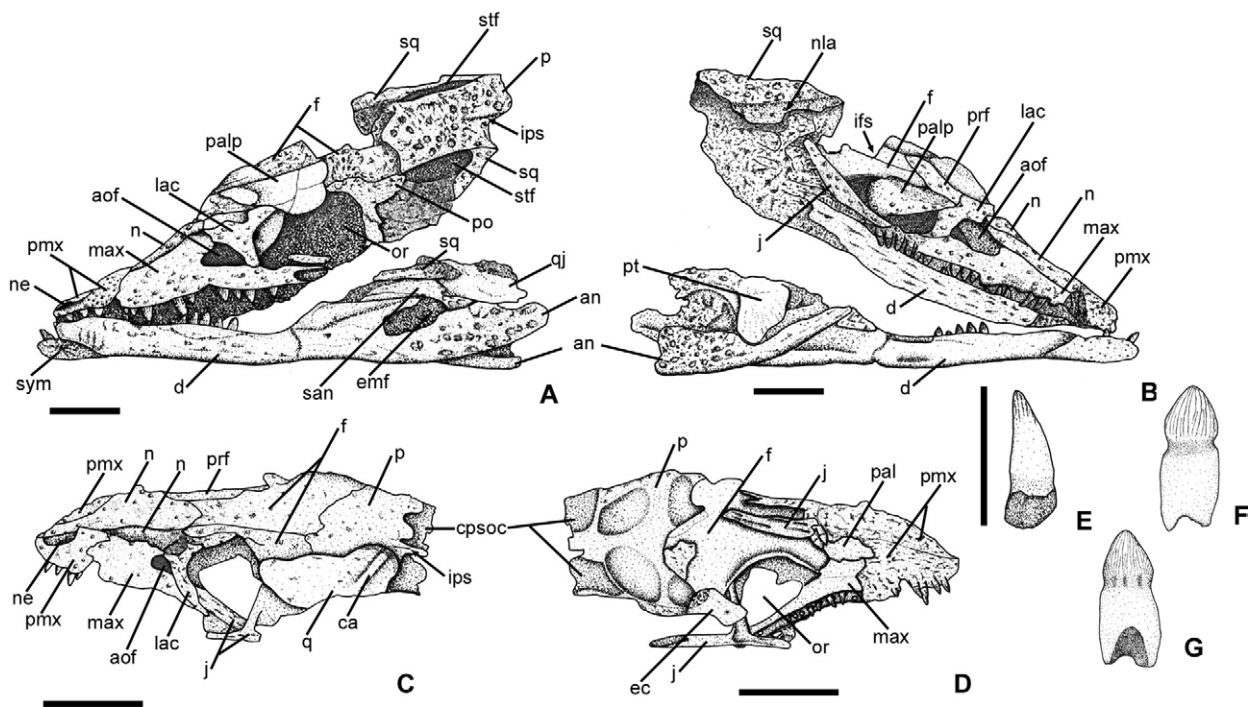


Fig. 3. Interpretational drawings of the holotype skull of *T. guimarotae* (IPFUB Gui Croc 7308-1) from the Upper Jurassic (Kimmeridgian) of Guimarota/Portugal **A**) in left lateral view, **B**) in right lateral view; and of the skull of *T. guimarotae* (IPFUB Gui Croc 7309), **C**) in dorsal view, **D**) in ventral view, **E**) third or fourth maxillary tooth (IPFUB Gui Croc 8006) in lingual view, **F**) 10th maxillary tooth (IPFUB Gui Croc 7345) in labial and **G**) in lingual view. Abbreviations: an, angular, aof, antorbital fenestra, cpsoc, contact between parietal and supraoccipital, d, dentary, ec, ectopterygoid, emf, external mandibular fenestra, f, frontal, ifs, interfrontal suture, ips, interparietal suture, j, jugal, lac, lacrimal, max, maxilla, n, nasal, ne, nares, nla, lateral notch of the squamosal, or, orbit, p, parietal, palp, palpebral, pmx, premaxilla, po, postorbital, prf, prefrontal, pt, pterygoid, qj, quadratojugal, san, surangular, sq, squamosal, stf, supratemporal foramen, sym, mandibular symphysis. Scale bar represent 5 mm.

Fig. 3. Schéma interprétatif de l'holotype de *T. guimarotae* (IPFUB Gui Croc 7308-1) du Jurassique supérieur (Kimmeridgien) du Guimarota/Portugal **A**) en vue latérale gauche, **B**) en vue latérale droite; et crâne de *T. guimarotae* (IPFUB Gui Croc 7309), **C**) en vue dorsale, **D**) en vue ventrale, **E**) 3^e ou 4^e dent maxillaire (8006) en vue linguale, **F**) 10^e dent maxillaire (IPFUB Gui Croc 7345) en vue labiale et **G**) en vue linguale. Abréviations : an, angulaire ; aof, fenêtre antorbitaire ; cpsoc, contact entre pariétal et supraoccipital ; d, dentaire ; ec, ectoptérygoïde ; emf, fenêtre mandibulaire externe ; f, frontal ; ifs, suture interfrontale ; ips, suture interpariétale ; j, jugal ; lac, lacrymal ; max, maxillaire ; n, nasal, ne, nares, nla, intention latérale du squamosal ; or, orbite ; p, pariétal ; palp, palpébral ; pmx, premaxillaire ; po, postorbitaire ; prf, préfrontal ; pt, ptérygoïde ; qj, quadratojugal ; san, surangulaire ; sq, squamosal ; stf, foramen supratemporal ; sym, symphyse mandibulaire. Échelle : 5 mm.

becomes more oval. The medial wall of the supratemporal foramen comprises the frontal in its rostral third, the parietal in its caudal two thirds and the quadrate in its caudolateral third.

4.2.1.6. Infratemporal fenestra. The infratemporal fenestra is two times as long as it is wide (Fig. 5A). The fenestra faces dorsolaterally. It is broadest rostrally, tapering in a caudal direction to a caudolaterally directed tip. It is bounded rostromedially by the postorbital bar, rostrolaterally by the jugal, caudomedially by the squamosal and caudolaterally by the quadratojugal.

4.2.1.7. Suborbital fenestra. The rostral margin of the suborbital fenestra is gently convex (Fig. 5B). Its lateral third of its margin is formed by the maxilla. The rest of it is made up of the palatine. It extends rostrally to the level of the 10th maxillary tooth. The roof of the suborbital fenestra is not preserved.

4.2.1.8. Secondary choanae. The paired choanae are narrow, rostrocaudally oval openings (Figs. 4 and 5). They lie with

their rostral third within the palatines and their caudal two thirds within the pterygoid. The secondary choanae are separated from each other by a median septum and are approximately half as long as the pterygoid.

4.2.1.9. Premaxilla. The premaxillae form the rostral sixth of the skull. In dorsal aspect, the rostral half of each premaxilla is crescent-shaped (Figs. 2A, B and 4A). The caudal part forms a caudomedially directed process that ends at a point level with the third maxillary tooth. Dorsally, the caudal third of the premaxilla contacts the maxilla laterally by means of a strongly serrated, caudomedially running suture. Rostral to the nares both premaxillae meet each other in the median plane. The medial margin of the premaxilla runs caudal to the nares beyond which it is bordered by the nasal. Caudally adjacent to the nares there is a shallow fossa on the dorsal surface of the premaxilla (Fig. 3A).

4.2.1.10. Maxilla. In dorsal aspect, the maxilla is widest in its rostral half, bifurcating into a narrow lateral process and a short medial projection in its caudal half. The caudomedial projection of the maxilla extends for the rostral half of the

antorbital fenestra. Caudomedially, it contacts the prefrontal and ends caudally at the rostral tip of the lacrimal (Fig. 5A). Rostral to the antorbital fenestra the medial margin of the maxilla is straight, contacting the nasal along a sagittally aligned suture. The lateral maxillary process extends caudally to the rostral half of the orbit and interdigitates from the level of the 11th maxillary tooth until its caudal margin with the jugal. Rostral to the jugal the lacrimal is attached to the maxillary process of the maxilla. The dorsal surface of the maxilla is slightly depressed just rostral to the antorbital fenestra (Fig. 4C). Immediately caudal to the junction between the maxilla, premaxilla and nasal, there is a shallow, longitudinally directed sulcus. A sagittally longitudinal oval depression is also visible directly dorsal to the 10th maxillary tooth.

In ventral aspect the maxilla contacts the premaxilla rostrally with a serrated suture that runs obliquely from caudolaterally to rostromedially. The ventral part of the maxilla overlaps its dorsal part rostrally up to a point that is level with the fourth premaxillary tooth. Both maxillae contact each other in the median plane and form the secondary palate. The suture between the palatine and the maxilla starts at a point level with the sixth maxillary tooth and runs caudolaterally to the rostral margin of the suborbital fenestra. The margins of the maxillary alveoli are elevated above the level of the secondary palate to form a distinct alveolar ridge. The fourth and fifth maxillary alveoli are confluent but the first to the third alveolus as well as the sixth to the ninth or 10th are separated from each other by interalveolar septa. In the remains smaller than the holotype, from the 10th maxillary alveolus onwards, and in the holotype as well as in remains larger than the holotype from the 11th maxillary alveolus caudally onwards the maxillary alveoli unite to form a single groove. Caudomedially to each maxillary alveolus is a small nutrient foramen.

4.2.1.11. Nasal. In dorsal aspect, the nasal is narrowest rostrally (Figs. 2A, 3A and 5A). Just caudal to the nares it is constricted laterally by the premaxilla. The rostral tip of the nasal touches the premaxilla at the rostral margin of the nares. At a point that is level with the premaxillomaxillary suture, the nasal widens, but then tapers again in its caudal fourth. Caudally, the nasal wedges out as it contacts the frontal medially and prefrontal laterally, reaching a point that is level with the rostral extent of the orbit. The contact between the two nasals forms a straight median suture in the median line.

4.2.1.12. Lacrimal. In dorsal aspect, the rostral margin of the lacrimal is weakly and the caudal margin is strongly concave (Figs. 2A, 3A and 5). The lateral margin of the lacrimal is rostrocaudally straight. Medially, the lacrimal contacts the prefrontal with a suture bearing a slight medial indentation. A blunt rostral process of the lacrimal separates the antorbital fenestra from the orbit. The caudal margin of the lacrimal is depressed medially where it articulates with the palpebral (Figs. 2A, B and 3A, B).

The ventral part of the lacrimal underlaps its dorsal portion rostrally. In ventral aspect, the caudal opening of the lac-

rimal duct is positioned at the suture between prefrontal and lacrimal. The rostral aperture of the lacrimal duct opens along the lacrimal's rostral margin. The rostral aperture is slightly larger than the caudal aperture. The prefrontal pillar is level with the caudal margin of the lacrimal, situated medioventrally to the caudal third of its ventral surface.

4.2.1.13. Prefrontal. The prefrontal is approximately the same size as the lacrimal, to which it is positioned medially. It is widest in its medial part, and tapering rostrally and caudally. The rostral third of the prefrontal wedges out between the nasal medially and the lacrimal laterally, with its rostralmost tip reaching the maxilla. Caudal to the nasal the prefrontal is bounded medially by the frontal with which it forms a smooth suture. Laterally, the prefrontal contacts the palpebral (Figs. 2 and 3).

4.2.1.14. Palpebral. The dorsal half of the orbit is covered by a large palpebral (Fig. 2A, B). The palpebral is semi-circular in outline, being widest caudally but tapering in rostral direction. The medial margin is strongly convex caudally and slightly concave rostrally. The lateral margin is straight and aligned rostrocaudally. The dorsal surface of the palpebral bears a shallow rostromedial fossa. In medial aspect, the palpebral is slightly concave in its caudal two thirds. In its rostral third it forms an articular surface with the lacrimal that is rostrocaudally oval in shape. The slightly serrated medial margin of the palpebral is parallel to the articular surface.

4.2.1.15. Frontal. The frontal is an elongate bone that forms the medial and mediocaudal margin of the orbit, as well as the rostromedial margin of the supratemporal foramen (Figs. 2, 3 and 5). In dorsal aspect, a rostral process of the frontal projects between the prefrontals, contacting the caudalmost extent of the nasals. The suture between the frontal and the nasals is "w"-shaped in caudal direction. The rostral part of the frontal widens moderately in caudal direction until it reaches the orbit. At the caudomedial margin of the orbit the frontal increases to twice its rostral width. Caudally, it contacts the parietal with a rostrally directed 'w'-shaped suture. Caudal to the orbit, the frontal is bounded laterally by the postorbitals; the contact between the two bones forms a serrated suture. The lateral surface of the frontal is depressed and weakly sculptured, bearing several small crests (Fig. 4E). On the smaller frontals of *T. guimarotae*, a median suture is visible in the caudal half of the bone. On frontals that belong to larger individuals, this suture is replaced by a sagittally aligned crest (see also paragraph in Section 5.4).

The rostral process of the frontals underlaps the nasals ventromedially and the prefrontals ventrolaterally. The ventral surface of the frontal bears laterally a frontal crest that begins at the caudal end of the prefrontofrontal suture and runs parallel to the lateral margin of the frontal, continuing caudally until the caudal margin of the orbit (Fig. 4F). Caudally adjacent to the frontal crest the lateral frontal margin is indented

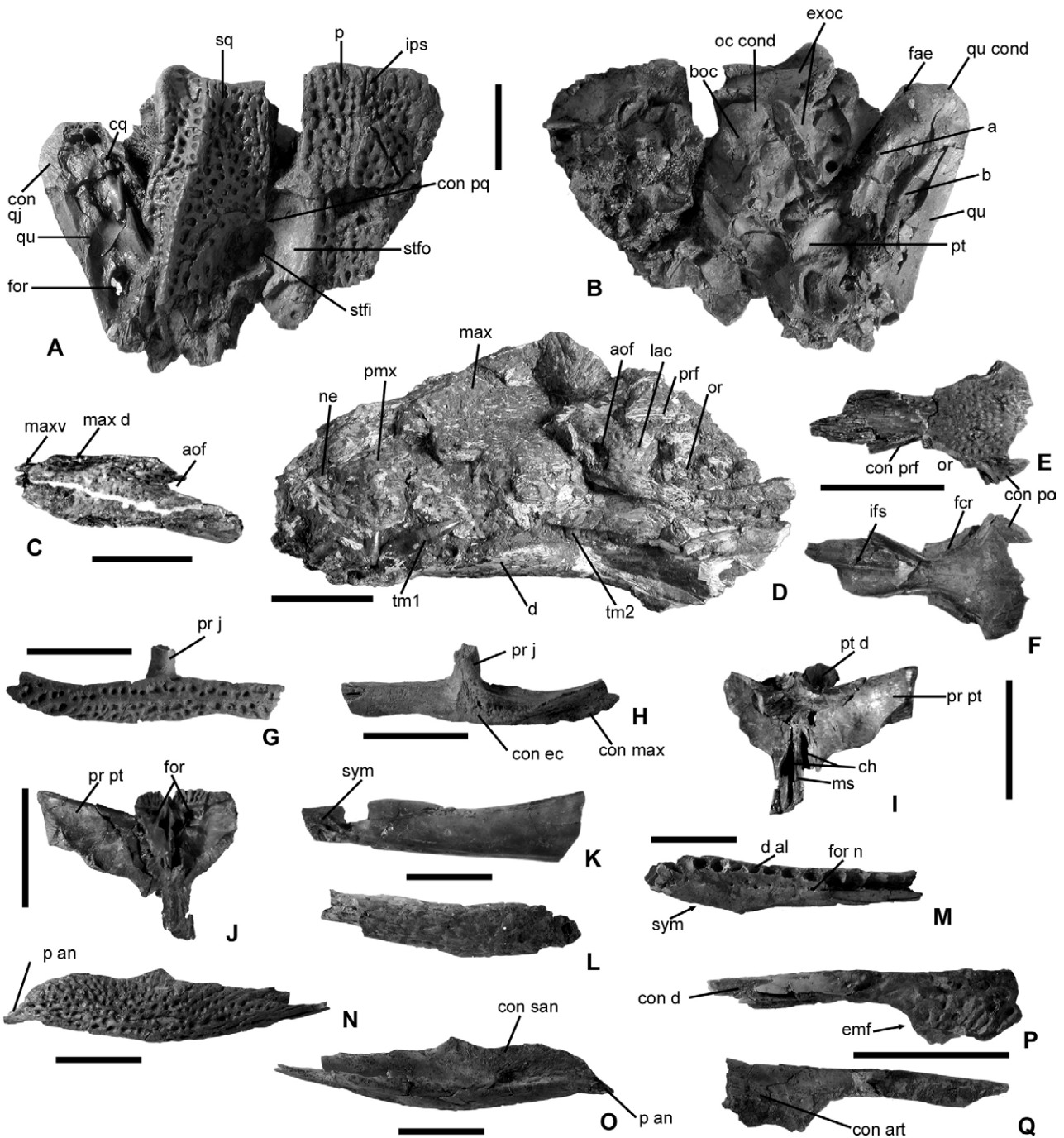


Fig. 4. Cranial elements of *T. guimarotae*: partial cranial table (IPFUB Gui Croc 7709), **A**) in dorsal view, **B**) in ventral view, **C**) left maxilla (IPFUB Gui Croc 7701) in dorsal view, **D**) rostral portion of a skull (IPFUB Gui Croc 7403) in left laterodorsal view; frontal (IPFUB Gui Croc 7601) **E**) in dorsal view, **F**) in ventral view; left jugal (IPFUB Gui Croc 7508) **G**) in lateral view, **H**) in medial view; pterygoid (IPFUB Gui Croc 7501) **I**) in ventral view, **J**) in dorsal view; **K**) right splenial (IPFUB Gui Croc 8103) in medial view; right dentary (IPFUB Gui Croc 8109) **L**) in ventral view, **M**) in dorsal view; right angular (IPFUB Gui Croc 7507) **N**) in lateral view, **O**) in medial view; left surangular (IPFUB Gui Croc 8044) **P**) in lateral view, **Q**) in medial view. Abbreviations additional to those listed in Fig. 3: ch, secondary choanae; con art, contact with the articular; con d, contact with the dentary; con ec, contact with the ectopterygoid; con max, contact with the maxilla; con po, contact with the postorbital; con pq, contact between parietal and quadrate; con prf, contact with the prefrontal; con qj, contact with the quadratojugal; con san, contact with the surangular; cq, cranioquadrate canal; d al, dentary alveolus; fcr, frontal crest; for, foramen; for n, nutritious foramen; max d, rostromedial depression at the maxilla; max v, ventral part of maxilla that rostrally overhangs its dorsal part; ms, median septum; pr j, dorsal process of the jugal; pr pt, lateral process of the pterygoid; pt d, caudal depression at the pterygoid; qu, quadrate; stfi, internal opening of the supratemporal fenestra; stfo, supratemporal fossa; tm1, tooth of the first morphotype; tm2, tooth of the second morphotype. Scale bar represents 10 mm.

Fig. 4. Éléments crâniens de *T. guimarotae* : table crânienne partielle (IPFUB Gui Croc 7709), **A**) en vue dorsale, **B**) en vue ventrale ; **C**) maxillaire gauche (IPFUB Gui Croc 7701) en vue dorsale ; **D**) partie rostrale d'un crâne (IPFUB Gui Croc 7403) en vue latérodorsale gauche ; frontal (IPFUB Gui Croc 7601) **E**) en vue dorsale **F**) en vue ventrale ; jugal gauche (IPFUB Gui Croc 7508) **G**) en vue latérale, **H**) en vue médiale ; ptérygoïde (IPFUB Gui Croc 7501) **I**) en vue ventrale, **J**) en vue dorsale ; **K**) splénial (IPFUB Gui Croc 8103) en vue médiale ; dentaire droit (IPFUB Gui Croc 8109) **L**) en vue ventrale, **M**) en vue dorsale ;

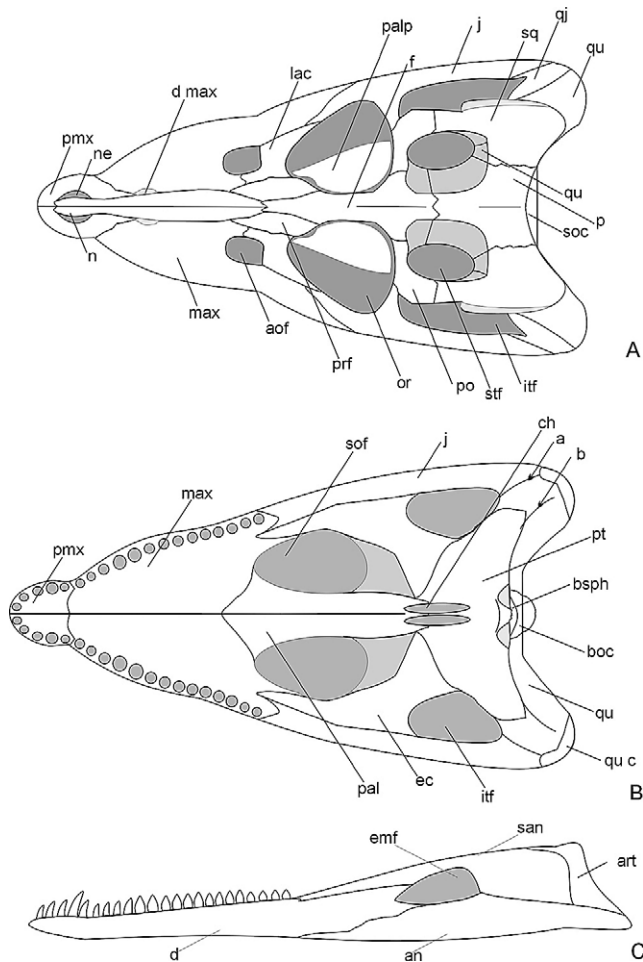


Fig. 5. Schematic reconstruction of the skull of *T. guimarotae* **A**) in dorsal view, **B**) in ventral view, **C**) schematic reconstruction of the left mandibular ramus of *T. guimarotae* in left lateral view. Abbreviations additional to those listed in Figs. 3 and 4: a, crest a of the quadrate; art, articular; b, crest b of the quadrate; boc, basioccipital; bsph, basisphenoid; pal, palatine; qu c, mandibular condyle of the quadrate; sof, suborbital fenestra.

Fig. 5. Reconstitution schématique du crâne de *T. guimarotae* **A**) en vue dorsale ; **B**) en vue ventrale ; **C**) reconstitution schématique de la branche mandibulaire gauche de *T. guimarotae* en vue latérale gauche. Pour abréviations voir figures 3 et 4 et : a, crête a du carré ; art, artulaire ; b, crête b du carré ; boc, basioccipital ; bsph, basisphénoïde ; pal, palatin ; qu c, condyle mandibulaire du carré ; sof, fenêtre suborbitale.

and receives a medial tip of the postorbital. The frontal bears a thin, sagittally aligned crest at its ventral surface. The caudal third of the frontal is vaulted medially and slightly depressed laterally.

4.2.1.16. Parietal. The parietal forms most of the medial and all of the caudomedial margin of the supratemporal foramen (Figs. 2, 4A and 5). In dorsal aspect it is approximately three

times as wide caudally as it is rostrally. Laterally the parietal contacts the squamosal with a straight, rostrocaudally aligned suture, commencing on the cranial table at the caudal margin of the supratemporal foramen. The entrance into the posttemporal canal is positioned within the supratemporal foramen, directly beneath the parietosquamosal suture. The lateral part of the canal is formed by the quadrate, such that the parietal does not contact the squamosal within the supratemporal foramen. The parietal is excluded from the caudal margin of the cranial table by the supraoccipital. The rostrally convex suture between the supraoccipital and the parietal bears a median rostral indentation. The caudal half of the parietal is divided by a faint median suture, but only in individuals smaller than the holotype (Fig. 2C). This suture is overgrown by a sagittally aligned crest on the parietal of the holotype and on parietals that belong to individuals larger than the holotype (Fig. 2A, also see paragraph in Section 5.4).

The ventral surface of the parietal bears four circular depressions. These depressions are positioned in right angles to each other, such that together they resemble a four-leaf clover. Each depression is separated from the other by a sharp crest. Parallel to its caudal margin the contact area between the parietal and the supraoccipital is marked by parallel rostrocaudal striations.

4.2.1.17. Postorbital. In dorsal aspect, the postorbital is an L-shaped bone that forms the rostromedial margin of the supratemporal foramen (Figs. 2 and 3), the caudal margin of the orbit and the rostromedial margin of the infratemporal fenestra. The rostrolateral margin of the postorbital forms the rounded rostrolateral corner of the cranial table. Ventral to the cranial table, the lateral surface of the postorbital is gently bevelled medially. The medial margin of the postorbital is concave. Caudally, the postorbital contacts the squamosal at the rostral third of the supratemporal foramen. The serrated postorbitosquamosal suture is mediolaterally directed for most of its length, inflecting rostrally as it approaches the dorsal margin of the supratemporal foramen. Rostrolaterally, the postorbital descends ventrally and forms the dorsal portion of the postorbital bar. In lateral aspect, the dorsal portion of the postorbital overhangs the postorbital bar cranially, the overhang forming a shallow triangular depression. The lateral surface of the postorbital bar forms a sharp crest that extends ventrally from this depression. The crest opens to a shallow groove that receives the dorsally ascending process of the jugal. The medial surface of the postorbital process bears a slight dorsal depression. Caudal to this depression is a rugose, triangular contact area for the laterosphenoid.

angulaire droit (IPFUB Gui Croc 7507) **N**) en vue latérale, **O**) en vue médiale ; supra-angulaire gauche (IPFUB Gui Croc 8044) **P**) en vue latérale ; **Q**) en vue médiale. Pour abréviations voir figure 3 et : ch, choanes secondaires ; con art, contact avec artulaire ; con d, contact avec dentaire ; con ec, contact avec ectoptérygoïde ; con max, contact avec maxillaire ; con po, contact avec postorbitaire ; con pq, contact entre pariétal et carré ; con prf, contact avec préfrontal ; con qj, contact avec quadratejugal ; con san, contact avec supra-angulaire ; cq, canal craniocarré ; d al, alvéole dentaire ; fcr, crête frontale ; for, foramen ; for n, foramen nutritif ; max d, dépression rostromédiale dans le maxillaire ; max v, partie ventrale du maxillaire qui dépasse rostralement sa partie dorsale ; ms, septum median ; pr j, processus dorsal du jugal ; pr pt, processus latéral du ptérygoïde ; pt d, dépression caudale au ptérygoïde ; qu, carré ; stfi, ouverture interne dans la fosse supratemporale ; stfo, fosse supratemporale ; tm1, dent du premier morphotype ; tm2, dent du second morphotype. Échelle : 10 mm.

4.2.1.18. *Squamosal*. In dorsal aspect, the squamosal is 1.5 times wider caudally than it is rostrally (Figs. 2A, B, 3A, B and 4A). Its lateral margin is weakly convex, forming the caudal two thirds of the lateral margin of the cranial table. The dorsal surface of the squamosal bears a rounded, longitudinally directed crest that separates the dorsal portion from a bevelled lateral portion. This lateral portion of the squamosal extends from the caudolateral corner of the squamosal to a point that, in dorsal aspect, is situated mid-way along the medial margin of the infratemporal fenestra, terminating at a deep notch (Figs. 2B, 4A and 5A). The caudal margin of the squamosal is gently concave. The caudolateral corner of the squamosal forms a short, rounded and strongly sculptured caudolaterally directed process.

The ventral surface of the squamosal is faintly concave in its rostral two thirds. The caudal third of the ventral surface of the squamosal is strongly rugose and serves as contact area with the underlying supraoccipital. Caudomedially, the squamosal roofs the posttemporal canal and contacts the quadrate within the supratemporal foramen. The sutural contact with the quadrate is straight.

4.2.1.19. *Jugal*. The jugal is elongated rostrocaudally with a delicate dorsally ascending process situated mid-way along its medial margin (Figs. 2C, D and 4G, H). This dorsal process is displaced both medially and ventrally from the lateral surface of the jugal. Dorsally, it interdigitates with the postorbital process, but it does not reach the lateral surface of the cranial table. Rostral to the postorbital bar, the jugal broadens dorsoventrally, while caudally it tapers to form a slim, slightly caudomedially aligned rod. The caudal third of the jugal contacts the lateral part of the quadratojugal via a straight, caudolaterally aligned suture.

Four sagittally aligned foramina are present on the medial surface of the jugal, immediately rostral to the dorsal process. The two more rostrally positioned foramina are the largest. In medial aspect the rostral fourth of the jugal is slightly concave and strongly rugose on the surface that contacts the maxilla. The area where the jugal contacts the ectopterygoid is situated immediately ventrally and laterally to the lateral margin of the orbit and the cranial lateral margin of the infratemporal fenestra. This area forms a sagittally oriented groove that is widest rostrally (Figs. 2D and 4H). Medially, the groove ascends the ventral half of the dorsal process. At the dorsal process, it continues dorsally into a narrow sulcus that cuts deep into the process. On jugals that belong to individuals smaller than the holotype, this sulcus is separated from the suture between the jugal and ectopterygoid, whereas on individuals larger than the holotype it is contiguous (see Section 5.4).

4.2.1.20. *Quadratojugal*. In lateral aspect, the quadratojugal is an elongate, rectangular bone that bifurcates rostrally into a lateral and a medial process (Figs. 2A and 3A). The medial process extends rostradorsally, forming the caudal third of the infratemporal fenestra. The lateral process is rostralater-

ally directed and only about half the length of the dorsal process. Laterally, the quadratojugal contacts the caudal portion of the jugal. Medially, the quadratojugal is bounded in its rostral third by the squamosal and in its caudal two thirds by the quadrate. The quadratojugal forms the entire caudolateral angle of the infratemporal fenestra (Fig. 5A).

4.2.1.21. *Quadrate*. In dorsal aspect, the quadrate has a rounded rectangular outline with a slightly convex lateral and a slightly concave medial margin (Fig. 4A). The quadrate overhangs the occiput caudally. The rostral portion of the quadrate forms a mediolaterally directed rod-like process and contacts the parietal medially and the ventral surface of the squamosal dorsally. The lateral margin of the quadrate forms a strongly rugose contact area for the quadratojugal. The contact area for the quadratojugal is widest caudally, narrowing rostrally forming the medial half to a deep sulcus. The quadrate forms the entire mandibular condyle. In occipital aspect, the condyle is kidney-shaped in outline with a convex dorsal and a concave ventral margin (Fig. 4B).

In dorsal aspect, the cranioquadrate canal runs rostrocaudally along the medial third of the quadrate. The canal forms a shallow sulcus, which, in the articulated skull is completely roofed by the squamosal. The foramen æereum is situated rostromedially to the mandibular condyle. Its external opening is visible on the dorsal surface of the quadrate, immediately caudal to the caudal opening of the cranioquadrate canal.

In its rostral half, the dorsal surface of the quadrate is strongly concave. A large, oval-shaped foramen is present in the centre of this depression, its long axis aligned rostralaterally-caudomedially. Directly rostrally to this foramen is a slightly smaller circular foramen. The ventral surface of the quadrate bears a large crest B (sensu Iordansky, 1973) extending from a point level with the medialmost extent of the infratemporal fenestra to just medial of the mandibular foramen (Fig. 4B). This crest is medially convex and well-developed even on those quadrates that belong to hatchling-sized individuals. On the larger quadrates, a faint crest A is present parallel to the medial margin of the ventral quadrate surface (Fig. 4B).

4.2.1.22. *Pterygoid*. In ventral aspect, the pterygoid is triangular in outline, with a straight caudal margin and rostrally directed tip (Fig. 4I). It is approximately twice as long in the mediolateral direction as it is rostrocaudally. The rostralateral margin of each pterygoid wing is straight. Caudally, this margin turns and runs parallel to the sagittal plane. The caudal margin is gently concave, meeting the lateral margin to form a sharp caudolateral corner. The rostralateral part of the pterygoid bears a bevelled lamina covered by lateromedially directed striations where it is sutured with the ectopterygoid.

In ventral aspect, the pterygoid contacts the palatines rostrally and the basisphenoid caudally (Fig. 4I). Cranially adjacent to its caudal margin lie two deeply concave, lateromedially aligned depressions.

The dorsal surface of the pterygoid forms the base of the braincase. Caudally to the pterygoid wings, the dorsal sur-

face is perforated in the median plane by paired circular foramina, each laterally accompanied by a smaller, rostrocaudally oval foramen. The surface around these openings is slightly concave (Fig. 4J).

4.2.1.23. Supraoccipital. The supraoccipital forms the medial third of the caudal margin of the cranial table, excluding the parietal from the occiput (Figs. 2C, 3C and 5A). In dorsal aspect, it is approximately triangular in outline, with a wide caudal margin. The lateral margins converge rostrally and form a strongly obtuse angle. The caudal margin of the supraoccipital is gently concave and at the lateral contact with the squamosals slightly indented. In dorsal aspect, the surface around these lateral incisions is gently concave and rugose. The ventral part of the supraoccipital is twice as long as its dorsal extension. In ventral aspect, the surface of the supraoccipital bears a rostrally convex crest along which it is sutured to the exoccipital. On the ventral surface, rostral to the crest is a pair of circular depressions, separated from each other by a median bulge.

4.2.1.24. Basisoccipital and basisphenoid. The basisoccipital bears the occipital condyle and possesses ventral to the condyle two laterally convex lateral margins. In occipital aspect, the ventral margin of the basisoccipital is strongly convex. The basisoccipital is tilted slightly, such that in lateral aspect its occipital surface faces rostroventrally (Fig. 4B). The occipital condyle is slightly kidney-shaped in caudal aspect and 1.5 times as wide as it is high. The dorsal surface of the condyle bears a median sulcus that runs into the foramen magnum, widening rostrally. The ventral margin of the basisoccipital bears a median incision that represents the central opening of the Eustachian system. Lateral to that opening is a small circular foramen. Dorsal to the median Eustachian foramen, the occipital surface of the basisoccipital bears a rounded tuberosity in the middle of which a sagittally aligned crest arises. Ventral to the occipital condyle, the occipital surface of the basisoccipital is slightly concave and perforated by two nutrient foramina. In rostral aspect a pair of circular depressions are apparent on the ventral surface of the basisoccipital.

A small portion of the basisphenoid is exposed between the caudal margin of the pterygoid and the ventral margin of the basisoccipital. The caudal margin of this exposed area forms the rostral margin of each of the openings of the Eustachian system (Fig. 5).

4.2.1.25. Ectopterygoid. The ectopterygoid is constricted between the infratemporal fenestra and suborbital fenestra (Figs. 2D and 3D) and is approximately hourglass-shaped. Its rostral and its caudal margin are strongly concave. In lateral aspect, the dorsal margin of the ectopterygoid is straight and parallel to the transverse plane. This margin is sutured with the rostral part of the jugal. Medially, the ectopterygoid parallels the medial surface of the dorsal process of the jugal. Rostrally, the ectopterygoid reaches the two caudal-most maxillary teeth (Fig. 5B).

4.2.2. Mandible

4.2.2.1. Form and proportions. In dorsal aspect, caudal to the mandibular symphysis the right and the left mandibular rami diverge from each other at an angle of about 20°. In the caudal third of the mandible the angle between both mandibular rami increases to about 40° (Fig. 4M). Each mandibular ramus is twice as high caudally as it is rostrally. The mandibular symphysis extends to the level of the sixth dentary tooth (Fig. 4M). The splenial is integrated in to the mandibular symphysis, ending rostrally at the third dentary tooth.

The tooth-bearing portion of the dentary is vertically festooned, its dorsal margin tracing two ventral convexities in lateral aspect. The first ventral convexity reaches its maximum at a point level with the third and fourth dentary teeth, whereas the second ventral convexity is highest between the eighth and 10th dentary teeth. The dorsal margin of each ramus is caudal to the tooth row straight, gradually increasing in height towards the articular fossa. In dorsal aspect, the lateral margin of each mandibular ramus is slightly laterally convex at a point level with the third and fourth dentary teeth. Most of the caudal part of each mandibular ramus is incompletely preserved. It is formed in its ventral half by the angular and in its dorsal half by the surangular (Fig. 5C).

Sculpture on the lateral surface of each mandibular ramus is weak rostrally, comprising only a few, intermittently spaced pits. Caudally it is much more distinct, forming longitudinally directed grooves. The lateral surface of the angular and surangular are covered by closely spaced circular and longitudinally oval-shaped pits. The rostral process of the surangular and the caudal-most part of the angular are smooth.

4.2.2.2. External mandibular fenestra. In the caudal fourth of the mandibular ramus an external mandibular fenestra is present (Figs. 2A, B and 3A, B). It is rostrocaudally oval in outline with a slightly pointed rostral end. The rostral and rostradorsal margins of the external mandibular fenestra are formed by the dentary. Ventrally and caudoventrally its margins are formed by the angular, and dorsally by the surangular (Fig. 5C).

4.2.2.3. Dentary. Corresponding to the form of the mandibular ramus, the dentary is approximately one and a half times thicker caudally than it is rostrally, and dorsocaudally inclined caudal to the tooth row. Both dentaries contact each other rostral to the splenial and form the rostral portion of the mandibular symphysis. In lateral aspect, the surface of each side of the mandibular symphysis is convex (Fig. 4L).

In dorsal aspect, the dentary is widest rostrally. It tapers caudally to between the sixth and the 10th dentary alveolus. Medial to the sixth and seventh dentary alveoli there is a longitudinally oval depression. The tooth row is accompanied laterally by a row of circular nutrient foramina. Each foramen is situated between adjacent alveoli. The first and second alveoli are separated from each other by a broad interalveolar septum (Fig. 4L). The third and fourth alveoli, however,

are enlarged and confluent, while the fifth dentary alveolus is contiguous with the fourth. From either the ninth or the 10th alveolus caudally the remaining alveoli are united to a single groove.

Caudal to the tooth row the dentary is bordered dorsally by the surangular (Figs. 2A and 3A). This portion of the dentary forms a bifurcated process that forms the rostral quarter of the external mandibular symphysis. Ventrally, this portion of the dentary is underlapped by the angular. In medial aspect, the dentary is overhung dorsally by the splenial caudal to the mandibular symphysis.

4.2.2.4. Splenial. The splenial increases in height from rostral to caudal. Its ventral margin is straight in lateral aspect. Its dorsal margin is slightly convex in its rostral half, but is straight and caudodorsally inclined in its caudal half (Fig. 4K). Caudal to the mandibular symphysis, a rostrocaudally oval opening is present on the splenial. A nutrient foramen is also present in the middle of the medial surface, situated at point level with the 10th dentary tooth. A low rugose, laterally elevated crest extends caudally along the dorsal margin of the splenial. In lateral aspect, the surface of the splenial is slightly concave in its rostral half. Parallel to the ventral margin is the contact surface for the dentary. This area is covered with rostradorsally and caudoventrally running striations.

4.2.2.5. Angular. The angular extends as a roughly triangular bone with a dorsal tip along the caudal half of the mandibular ramus. Its ventral margin is convex. In lateral aspect, the height of the angular increases from rostrally to caudally in its rostral half, decreasing again in its caudal half (Figs. 2A, B and 4N, O). The dorsal margin of the angular is straight and slightly oblique to the horizontal in lateral aspect. It ends in a distinct, dorsally directed tip. Caudal to the tip, the dorsal margin is slightly convex. Rostrally, a thin process of the angular underlaps the dentary. This process extends rostrally and reaches the level of the caudal-most dentary alveolus. From the dorsal margin of the rostral angular process a thin, rugose ascending lamina of bone is present. The caudal end of the angular forms a tongue-shaped, slightly caudoventrally directed process. In its caudal half the angular contacts the surangular dorsally (Figs. 4O and 5C).

The internal surface of most of the rostral portion of the angular is concave. The medial wall is only one third of the height of the lateral wall (Fig. 4O). Rostromedially, the dorsal margin of the medial wall forms a short, dorsally projecting process with a slightly convex tip. The dorsal half of this wall is also rugose and interdigitates with the surangular. Caudally, the medial wall of the angular diminishes to a rounded crest. This crest runs parallel to the ventral margin to the caudal tip of the angular. On the medial surface of the medial wall there is a longitudinally oval depression rostral to external mandibular fenestra.

4.2.2.6. Surangular. In lateral aspect, the surangular comprises a slender, rod-like rostral process and considerably

higher, rounded rectangular caudal half (Figs. 2A and 4P, Q). Its dorsal margin is straight and rostradorsally oriented. The rostral process of the surangular extends rostrally to contact the caudal end of the tooth row and bears a sagittally elongate ventral groove. The caudal part of the surangular ends ventrally with a rostrocaudally directed, jagged margin and caudally with a dorsoventrally directed smooth margin. Parallel to the ventral margin the lateral surface of the surangular is rugose. On the caudodorsal portion of the medial surface, there is a triangular, rugose contact area for the articular.

4.2.3. Dentition

4.2.3.1. Tooth morphology. The teeth of *T. guimarotae* can be divided into two distinct morphotypes. The teeth of the first morphotype are the premaxillary teeth, the six rostral-most maxillary teeth and the nine rostral-most dentary teeth (Figs. 2A, B and 4D). These teeth are conical and are slightly curved lingually. The base of the tooth crown is circular in cross-section, and the apex is pointed. Mesially and distally a weak carina runs from the base to the apex. The enamel on the labial surface of the tooth crown is smooth, except on the pseudocanines (see below) where there are a few faint, basoapically running striations near the apex. On the lingual surface of the tooth crown, the enamel forms moderately developed but distinct basoapically running striations (Fig. 3E). The size and number of the striations increases with the size of the teeth (Fig. 4D).

The second morphotype comprises teeth from the seventh to the caudal-most maxillary tooth and from the 10th to the caudal-most dentary tooth (Fig. 2A, B). These teeth are lanceolate in either labial or lingual aspect. The tooth crown is wide and slightly swollen at its base, tapering apically to a sharp tip. The teeth are slightly curved and weakly compressed labiolingually. Mesially and distally the enamel forms a faint carina. The enamel on the labial side of the tooth crown is covered with distinct basoapically running striations. These striations run from the apical half of the crown to the apex, some of them terminating on the carinae (Fig. 3F, G). The lingual surface of the crown bears closely spaced striations that fan out from the base to the apical half of the tooth.

From rostral to caudal along the tooth row, the lanceolate teeth become proportionately broader with a slightly rounded apex. On the caudal-most lanceolate-shaped teeth the striations on the lingual side are better developed than those on the more rostrally positioned. The apical margin of the teeth therefore appears to be slightly more jagged. The dentary teeth generally have slightly more distinct striations than the maxillary teeth (Fig. 2A). The larger the lanceolate teeth on both the upper and lower jaw are, the larger they become.

4.2.3.2. Pattern of dentition. The upper jaw in most specimens contains at least 20 teeth, comprising five premaxillary and a minimum of 15 maxillary teeth. Within the rostrum, two peaks of enlarged teeth can be distinguished (Fig. 2A, B). These waves are level with the vertical festooning of the

lateral margins of the rostrum and comprise teeth of the first morphotype (i.e. conical teeth). The first peak reaches its maximum size with the fourth premaxillary tooth, which forms a pseudocanine. The second peak of enlarged teeth reaches maximum size at the fourth and fifth maxillary tooth, which are the largest of the maxillary teeth. The caudally following teeth of the second morphotype are smaller than the teeth of the first morphotype. The size of these teeth decreases moderately in size towards caudally.

In the dentary, the number of teeth is at least 20 in most specimens (Fig. 2A). Similar to the upper jaw, two peaks of enlarged teeth are present. The first peak reaches its maximum at the fourth dentary tooth, which forms a pseudocanine. The second maximum in tooth size comprises teeth of the second morphotype (i.e. lanceolate teeth) and comprises the 10th and eleventh dentary tooth only. The caudally following teeth are of similar size.

4.2.4. Axial skeleton

4.2.4.1. Cervical vertebrae. In dorsal aspect, the proatlas (IPFUB Gui Croc 7349) is subtriangular in shape with a caudally directed tip. Its ventral surface is concave, so that it forms a vaulted roof dorsal to the vertebral canal. The cranial margin of the proatlas is strongly concave. The dorsal surface bears a rounded median crest that overhangs the neural arch of the atlas slightly, both cranially and caudally. The ventral surface of the proatlas is crossed by a median rounded crest. Lateral to this crest is a shallow circular depression at each side.

All the preserved presacral vertebrae have a weakly amphicoelous corpus. Each vertebral corpus is one third as long as it is high and hourglass-shaped in ventral aspect, and a shallow concavity is present on the lateral surface.

The cranial and caudal articular surface of the corpus of the axis (IPFUB Gui Croc 7550, 7555) are trapezium-shaped in cross-section with a dorsal margin that is one fifth wider than the ventral margin (Fig. 6A). The corpus of the axis bears a prominent hypapophysis. The hypapophysis is cranially bifurcated in the vertical plane. On the lateral surface of the corpus is a cranio-caudally directed ridge. On either side of this ridge is a shallow concavity. The neurocentral suture is fused, but still visible as a dorsally convex line. The neural arch of the axis is slightly higher than the vertebral corpus. The vertebral foramen has a rounded rectangular outline in cranial and caudal aspect. The articular surface of the prezygapophysis is situated cranio-laterally to the neural arch and its articular surface is oriented at 25° to the median plane. The postzygapophysis is situated lateral to the caudal margin of the neural arch. Its articular surface is oriented at 45° to the median plane. Extending ventrally from the postzygapophysis is a ventrally rounded ridge. The neural spine of the axis covers the entire length of the neural arch (Fig. 6A) and slightly overhangs the postzygapophyses caudally. Its dorsal margin is convex.

On all the preserved cervical vertebrae, the cranial articular surface of the corpus is semi-oval in outline, with a straight

dorsal margin. The caudal articular surface of the corpus has a rounded triangular in outline, with a ventrally directed narrow end. Ventrally, on the corpus of IPFUB Gui Croc 7381, a short, rounded hypapophysis is preserved, but it is broken on the other cervical vertebrae (Fig. 6B). The hypapophysis is situated in the cranial half of the corpus. In lateral aspect, each hypapophysis bends cranioventrally and has a slightly concave cranial and a slightly convex caudal margin. Each hypapophysis reaches about three quarters of the height of the corpus. The caudal margin of the hypapophysis forms a sharp crest that continues along the ventral margin of the corpus. The neurocentral suture is fused, but visible as an inverted “v” with its apex closer to the caudal end of the corpus. The parapophysis on each cervical vertebra is positioned on the cranial half of the corpus, just ventral to the neurocentral suture. Each parapophysis has an oval articular surface with a lateroventrally directed long axis. A longitudinally oval depression is situated caudoventral to the parapophysis.

The neural arch of each cervical vertebra is as high as the vertebral corpus, but only three quarters as long (Fig. 6B, C). The diapophysis on each corpus is situated centrally on the lateral surface of the neural arch, directly dorsal to the apex of the neurocentral suture. The vertebral foramen is trapezium-shaped in outline in cranial and caudal aspect (Fig. 6C). The prezygapophysis ascends from the cranial margin of the diapophysis. Its articular surface is medio-dorsally oriented. The postzygapophysis arises from the neural arch and has a ventrolaterally directed articular surface. The articular surface of both pre- and the postzygapophysis of IPFUB Gui Croc 7614 and 8138 has an angle of 60 degrees to the median plane. The only preserved neural spine of the caudal cervical vertebrae (IPFUB Gui Croc 7475) occupies the caudal half of the neural arch. The height of the neural spine is up to twice the height of the vertebral corpus. The neural spine is rod-like in lateral aspect, tapering from ventral to dorsal to form a tip (Fig. 6B, C). Its dorsal margin is slightly expanded caudally.

4.2.4.2. Thoracic and lumbar vertebrae. The preserved thoracic and lumbar vertebrae (Fig. 6D) differ from the cervicals in having a caudal articular surface on the vertebral corpus that is rounded square in outline (Fig. 6E). The ventral surface of the corpus of the thoracic and lumbar is narrow. It is either reduced to a ventrally rounded ventral keel (IPFUB Gui Croc 7351, 7360, 75108, 7633, 7743) that bears at IPFUB Gui Croc 7545-2 a weak median groove, or the ventral surface of the corpus is gently convex (IPFUB Gui Croc 7809, 7910, 8111, 8132). The neurocentral suture is fused at IPFUB Gui Croc 7526, 7743, 7809, 8111 and 8132 (Fig. 6D). At IPFUB Gui 7910 the neurocentral suture is visible as a dorsally convex suture.

The neural arch of each dorsal vertebra is two thirds the height of the corpus (Fig. 6D, E). The transverse process is positioned centrally on the lateral surface of the neural arch. It is one third longer than the vertebral corpus is high. Lateromedially, the cranial half of the transverse process is one fifth shorter than its caudal half. The prezygapophyses

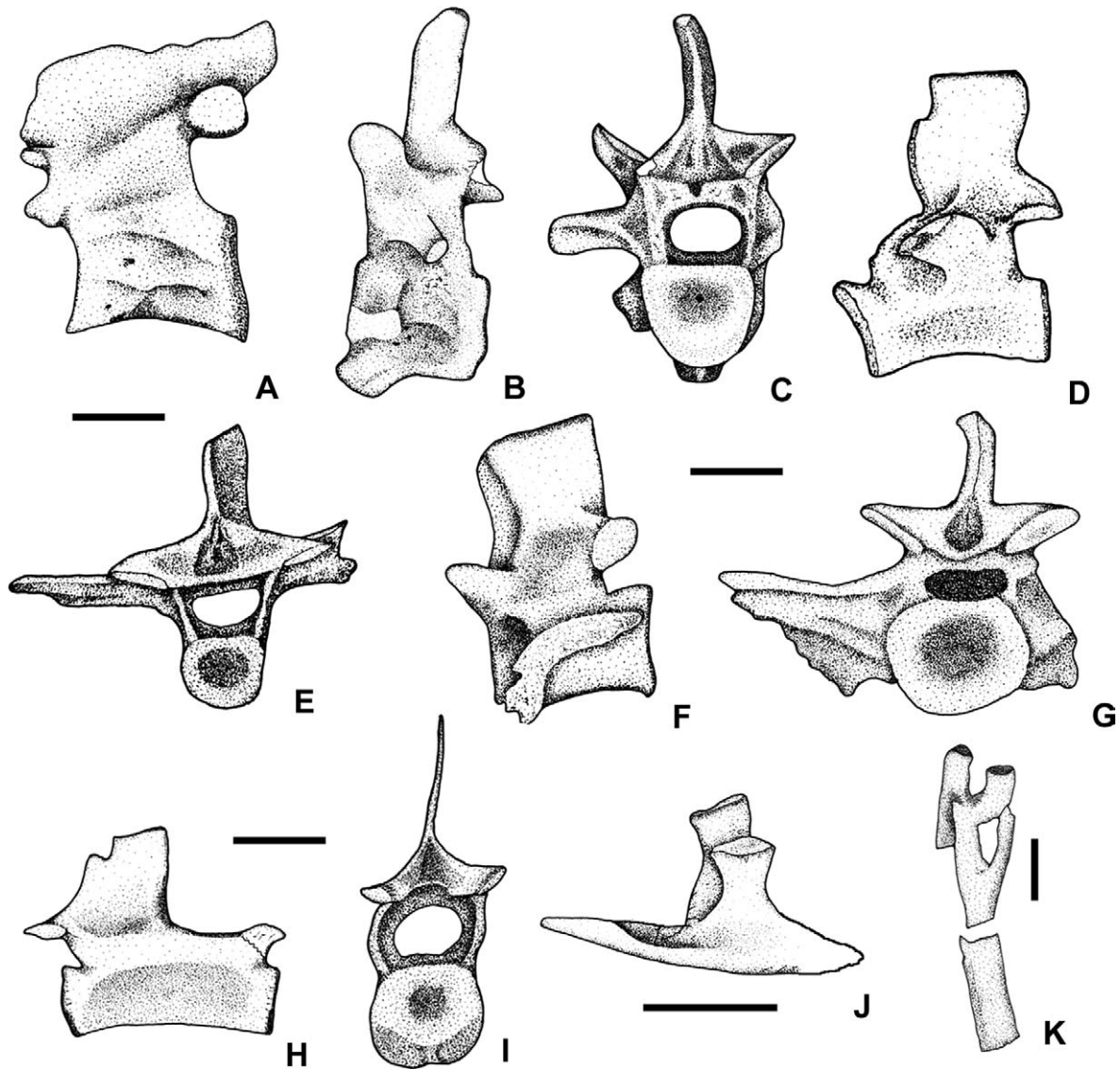


Fig. 6. Postcranial elements of *T. guimarotae*: **A**) axis (IPFUB Gui Croc 7555) in left lateral view; **B**) cervical vertebra (IPFUB Gui Croc 7561) in left lateral view, **C**) in caudal view; **D**) thoracic vertebra (IPFUB Gui Croc 7634) in left lateral view, **E**) in caudal view; **F**) first sacral vertebra (IPFUB Gui Croc 7476) in left lateral view, **G**) in cranial view; **H**) caudal vertebra (IPFUB Gui Croc 7725) in right lateral view, **I**) in caudal view; **J**) left cervical rib (IPFUB Gui Croc 7721) in medial view; **K**) right thoracic rib (IPFUB Gui Croc 8017) in medial view. Scale bar represents 5 mm.

Fig. 6. Éléments postcrâniens de *T. guimarotae*: **A**) axis (IPFUB Gui Croc 7555) en vue latérale gauche; **B**) vertèbre cervicale (IPFUB Gui Croc 7561) en vue latérale gauche, **C**) en vue caudale; **D**) vertèbre thoracique (IPFUB Gui Croc 7634) en vue latérale gauche, **E**) en vue caudale, **F**) première vertèbre sacrée (IPFUB Gui Croc 7476) en vue latérale gauche **G**) en vue crânienne, **H**) vertèbre caudale (IPFUB Gui Croc 7725) en vue latérale droite, **I**) en vue caudale, **J**) côte cervicale gauche (IPFUB Gui Croc 7721) en vue médiale, **K**) côte thoracique droite (IPFUB Gui Croc 8017) en vue médiale. Échelle : 5 mm.

decrease in length from cranially to caudally (Fig. 6E). The postzygapophyses descend from the caudal margin of the neural arch caudoventrally. The articular surface of the pre- and the postzygapophyses of the thoracic and lumbar IPFUB Gui Croc 7526, 7743, 7910 and 8111 are inclined at an angle of 70° to the median plane. The neural spine of the thoracic and lumbar vertebrae IPFUB Gui Croc 7545-2, 7560 and 7910 is positioned in the caudal two thirds of the neural arch and as high as the vertebral corpus (Fig. 6E). Its straight dorsal margin is craniocaudally aligned and slightly expanded.

4.2.4.3. Sacral vertebrae. The corpus of the first sacral vertebra is twice as long as it is high. The corpus of the second

sacral vertebra is three times as long as it is high. The corpus of each sacral vertebrae corpus is hourglass-shaped in ventral aspect, and has a slightly concave ventral surface. The cranial and the caudal articular surface of each corpus is oval in outline, with a lateromedially oriented long axis. In ventral aspect, each corpus bears a craniocaudally aligned median groove on its ventral surface. This groove is wider and deeper in the smaller of the preserved first sacral vertebrae.

The neural arch of each sacral vertebra is twice as high as its corpus (Fig. 6F). The vertebral foramen is slightly rectangular in outline in cranial and caudal aspect, being half as high as it is wide (Fig. 6G). The pre- and postzygapophyses project laterally from the neural arch. The articular surfaces

of the pre- and the postzygapophyses are oriented at an angle of 60° to the median plane. The length of the neural spine on each vertebra is two thirds that of the corpus, and a quarter as high (Fig. 6F). Its dorsal margin is straight.

4.2.4.4. Caudal vertebrae. The corpus of each caudal vertebra is weakly hourglass-shaped in ventral aspect, with a concave ventral surface. The vertebral corpus is about three times longer than it is high in the cranially positioned caudals (Fig. 6H), increasing to approximately four times longer than high in the terminally positioned caudals. The vertebral corpus is compressed lateromedially. In cranial and caudal aspect, the cranial and caudal articular surface of the vertebral corpus is approximately square in outline in the cranially positioned caudals and semi-circular in outline with a straight dorsal margin in the terminal caudals (Fig. 6I). The cranial vertebral fossa extends for the central half of the cranial surface of the vertebra and is only very weakly concave. The terminal vertebral fossa is reduced in size to the central third of the caudal surface of the vertebral corpus. The terminal vertebral fossa is surrounded by an annular rugosity, which forms the lateral third of the diameter of the corpus. The ventral surface of the vertebral corpus bears paired cranial and caudal haemapophysial articular surfaces. Between the cranial and caudal haemapophysial articular surface a shallow median sulcus is developed at the ventral surface of the vertebral corpus. On the terminal-most caudals, the ventral surface of the corpus is only a rounded crest that widens cranially and caudally, but distinct articular surfaces for the haemapophyses are absent. The neurocentral suture is fused on all the caudal vertebrae (Fig. 6H).

The transverse process on each caudal vertebra is positioned laterally on the neural arch at the level of the ventral margin of the vertebral foramen. Each transverse process is caudolaterally directed and tapers laterally to a tip (IPFUB Gui Croc 7395, 7552, 7658 and 7906). The transverse process is reduced to a low tubercle (IPFUB Gui Croc 7811, 8024) and finally disappears in the more terminally positioned caudals (Fig. 6H; IPFUB Gui Croc 7478, 75109, 75110, 7725, 8114 and 8218). The neural arch extends for nearly the entire length of the vertebral corpus. In cranial and caudal aspect, the vertebral foramen is rectangular in outline. The pre- and postzygapophyses decrease in size terminally, and on the terminal-most vertebrae are only short, horizontally aligned processes. The articular surface of the pre- and postzygapophyses (measured in IPFUB Gui Croc 7658, 7682, 7906) is inclined at an angle of 65° to the median plane. The roof of the neural arch of the terminal caudal vertebrae is flattened. Terminally, the neural spine decreases in height, but increases in length (IPFUB Gui Croc 7682, 7744, 7658). On the terminal-most vertebrae (IPFUB Gui Croc 8218), the neural spine forms a dorsally convex projection in the terminal third of the neural arch.

4.2.4.5. Cervical ribs. The corpus of the preserved cervical ribs is perpendicular to the capitulum and tuberculum. The

cranial process forms one quarter of the total length of the rib. The cranial process of IPFUB Gui Croc 7727, 7810, and 8123 ends in a sharp tip, as does the caudal end of the corpus (Fig. 6J). In IPFUB Gui Croc 7369 and 7629, however, the cranial process ends abruptly with a dorsoventrally straight margin. In lateral aspect, the ventral margin of the corpus is slightly concave at the level of the capitulum and cranially and caudally weakly convex. The internal surface of the rib is concave. Caudal to the tuberculum on the external surface there is a weak sulcus parallel to the ventral margin.

The capitulum is two third the length of the tuberculum. The articular surface of the capitulum is craniocaudally oval in outline. Ventral to the articular surface the capitulum is slightly constricted. A delicate crest, better developed on the large specimens (IPFUB Gui Croc 7810 and 7634), extends from the cranial margin of the capitulum. On the larger ribs it continues to the internal margin of the corpus. The tuberculum has a craniocaudally oval-shaped articular surface that is approximately 20% longer than the articular surface of the capitulum.

4.2.4.6. Thoracic ribs. The corpus of the vertebral part of the preserved thoracic ribs is laterally curved, so that its external surface is convex and its internal surface is slightly concave (Gui Croc 8017). The corpus of all the vertebral parts of the thoracic ribs is externointernally flattened. The capitulotubercular incision is v-shaped (Fig. 6K). The external surface of the corpus is depressed slightly between the capitulum and the tuberculum and bears a process that runs from the base of the capitulum to a point halfway along the corpus. The process begins dorsally with a triangular tip and decreases in height in ventral direction to a thin crest. It is highest on the cranial-most thoracic ribs and decreases to a small lamina on the caudal-most thoracic ribs. Both cranial and caudal to the dorsal tip of the cranial process there is a shallow depression on the external surface of the corpus. On the internal surface of the corpus there is a depression between the bases of capitulum and tuberculum. A shallow groove extends ventrally from this depression.

The tuberculum is oriented caudomedially and is approximately 25% longer than the capitulum in IPFUB Gui Croc 8017. The external surface of both the capitulum and the tuberculum bears a thin crest that extends to the articular facets.

4.2.4.7. Sacral ribs and gastralria. The sacral ribs are slightly longer than the corpus on each of the sacral vertebrae. The first sacral rib is caudolaterally directed, the second sacral rib craniolaterally directed. Both ribs are slightly arched dorsally (Fig. 6F). The first sacral rib participates laterally in the cranial articular surface of the corresponding vertebral corpus (Fig. 6F), whereas the second is continuous with the caudal articular surface of its vertebral corpus. The lateral iliac articular surface of the each sacral rib extends for two thirds of the length of the sacral corpus. The iliac articular surface of the first sacral rib is craniocaudally oval in outline, while that of the second sacral rib is craniodorsally convex and cranioventrally to caudodorsally oriented.

One of the two preserved gastralgia (IPFUB Gui Croc 7419-1) is slender and laterally convex. The other (IPFUB Gui Croc 7419-2), however, is straight, widening from medial to lateral. The surface of both gastralgia is rugose.

4.2.5. Appendicular skeleton

4.2.5.1. Coracoid. The dorsal and ventral extensions of the coracoid are 1.5 times wider than the corpus (IPFUB Gui Croc 8116). The cranial and caudal margins are concave, and the corpus is oval in cross-section (Fig. 7A, B). The lateral surface of the coracoid is slightly concave, whereas its medial surface is straight. On the lateral surface of the corpus there is a faint oval depression parallel to the cranial margin. The medioventral extension of the coracoid has a thin, slightly convex ventral margin and lateral and medial surfaces that are slightly rugose. Parallel to the ventral margin, the medial surface of the wing is perforated by three nutrient foramina.

The head of the coracoid projects craniodorsally. Caudally, the head of the coracoid ends with a caudodorsally directed glenoid process bearing a cranially tapering and laterodorsally facing humeral articular surface. The medial surface of the coracoidal head bears a rugose, crescent-shaped ridge that continues cranially along the dorsal margin of the coracoidal head. A depression lies cranioventrally on the lateral surface of the head of the coracoid. The dorsoventrally oval-shaped coracoid foramen is caudally displaced slightly from the coracoidal head (Fig. 7A, B).

4.2.5.2. Humerus. The humerus possesses a straight shaft from which the broad proximal extremity is bent medially. The proximal extremity of the humerus is twisted at about 45° to the long axis of shaft (IPFUB Gui Croc 7661). The shaft is circular in cross-section. The head of the humerus makes up one fifth of the bone's total length.

The head is twice as wide as the shaft and is strongly dorsally convex in either lateral or medial aspect (Fig. 7C, D). The proximal margin of the head forms a caudally directed tip. The articular surface of the humeral head overhangs the medial surface of the proximal extremity (Fig. 7D). The medial surface of the proximal extremity is rugose. The craniomedial (or "deltopectoral") crest extends from the craniomedial edge of the articular surface of the head to the transition between the proximal extremity and the shaft of the humerus, and has a gently triangular outline in lateral aspect. The crest increases in size distally and has a craniomedial tuberosity that is directed medially slightly (Fig. 7D). In lateral view, the cranioventral surface of the humeral head is separated from the caudolateral surface of the humerus by a distinct major cranioventral ridge (Fig. 7C). Directly caudal to that ridge there is a caudolateral rugosity.

The distal extremity of the humerus is at its distal margin as wide as the head. It bears two condyles, separated from each other by a shallow intercondylar sulcus. The medial condyle is slightly larger than the lateral condyle. In medial aspect both condyles terminate in a weak bulge, between

which the medial surface is both strongly concave and rugose (Fig. 7D). On the medial surface there are two to four small foramina. The medial and lateral epicondyles are inset slightly from the margin of their respective condyles. Each is slightly rugose.

4.2.5.3. Ulna. The preserved proximal part of the ulna (IPFUB Gui Croc 7441-7) possesses a slender and dorsoventrally flattened shaft that curves slightly medially in its proximal half. The preserved base of the proximal extremity of the ulna is one and a half times as wide as the shaft and strongly projects medially. At the proximal end of the ulnar shaft there is a distinct rugosity. The dorsocaudally positioned olecranon is weakly developed and weakly rugose. The proximal extremity of the ulna itself is not preserved.

4.2.5.4. Ilium. The ilium (IPFUB Gui Croc 7641) is twice as long as it is high (Fig. 7E, F). It possesses a convex dorsal margin. The dorsal iliac wing is twice as long as the iliac corpus. The craniodorsal process forms a narrow, craniodorsally directed tip (Fig. 7E). The postacetabular process makes up half of the total length of the ilium. The dorsal crest of the iliac wing bears well-developed caudoventrally aligned striations on both its medial and lateral surfaces. The cranial and caudal margins of the iliac body are concave. The iliac margin of the acetabular foramen is dorsocaudally concave (Fig. 7F).

The acetabular fossa occupies most of the ventral half of the lateral surface of the ilium and is craniodorsally and dorsally bounded by a sharp supraacetabular crest. The lateral surface of the iliac wing is concave. The caudal margin of the iliac wing is rugose laterally. In medial aspect, the cranial sacral symphyseal surface is separated from the caudal sacral symphyseal surface by a narrow vertical bulge. The cranial and caudal sacral symphyseal surfaces are semi-circular in outline. Their surface bears a pattern of irregularly spread sharp crests and narrow grooves. The medial surface of the iliac wing is concave.

4.2.5.5. Ischium. The ischium is dorsally narrow and bifurcate, possesses a constricted corpus that widens ventrally to a blade-like expansion. The cranial and caudal margins of the ischiac shaft are gently concave in lateral and medial aspect (Fig. 7G). The acetabular extremity is two and a half times as wide as the shaft. The acetabular concavity is ventrally concave. In lateral aspect, the slender cranial process of the acetabular extremity is slightly higher than the caudal process. It bears a circular articular surface, the ventral half of which is bevelled where it contacts the pubis. The caudal process of the acetabular extremity has a kidney-shaped articular surface with a convex lateral and a concave medial margin. The articular surface is dorsomedially directed and surrounded by fine striations. The lateral surface is situated directly ventral to the acetabular concavity. The blade-like ischiac wing projects caudoventrally (Fig. 7G). Its ventral margin is straight and crossed laterally and medially by well-spaced, dorsocranially aligned striations.

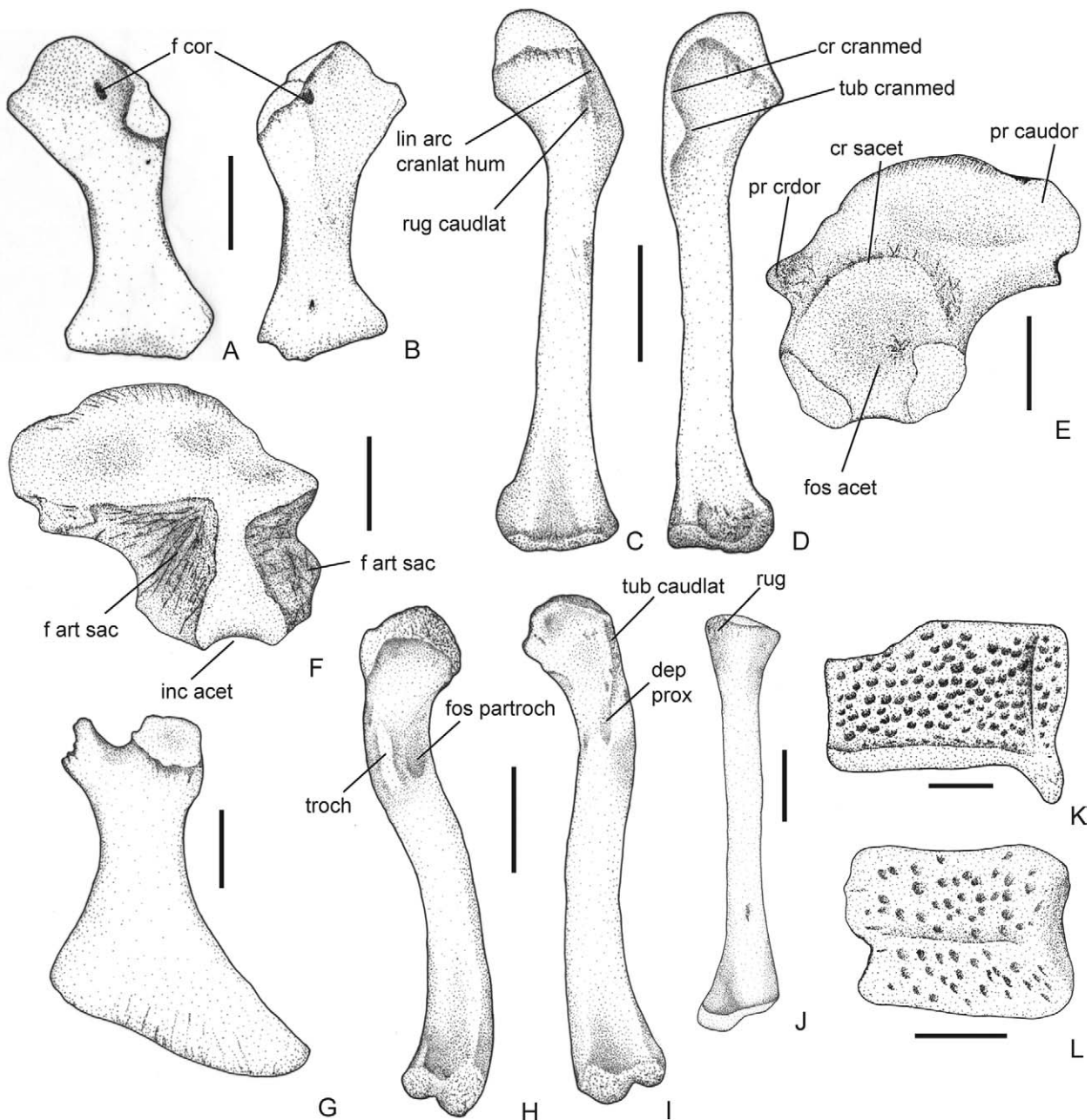


Fig. 7. Postcranial elements of *T. guimarotae*: **A**) left coracoid (IPFUB Gui Croc 7548) in lateral view, **B**) in medial view; **C**) right humerus (IPFUB Gui Croc 7542) in caudolateral view, **D**) in craniomedial view; **E**) left ilium (IPFUB Gui Croc 7641) in lateral view, **F**) in medial view; **G**) partial right ischium (IPFUB Gui Croc 7580) in medial view; left femur (IPFUB Gui Croc 75112) **H**) in medial view, **I**) in lateral view; **J**) right tibia (IPFUB Gui Croc 8053) in lateral view, **K**) left paravertebral osteoderm (IPFUB Gui Croc 8226) in external view, **L**) caudal osteoderm (IPFUB Gui Croc 8227) in external view. Abbreviations: cr cranmed, craniomedial crest; cr sacet, supraacetabular crest; dep prox, proximal depression; f art sac, sacral symphyseal surface; f cor, coracoid foramen; fos acet, acetabular fossa; fos partroch, paratrochanteral fossa; inc acet, acetabular incision; lin arc cranlat hum, major craniolateral ridge; pr caudor, caudodorsal process; pr crdor, craniodorsal process; pr caudor, caudodorsal process; rug, rugosity; rug caudlat, caudolateral rugosity; troch, femoral trochanter; tub caudlat, caudolateral tuberosity; tub cranmed, craniomedial tuberosity. Scale bar represents 5 mm.

Fig. 7. Éléments postcrâniens de *T. guimarotae*: **A**) coracoïde gauche (IPFUB Gui Croc 7548) en vue latérale, **B**) en vue médiale, **C**) humérus droit (IPFUB Gui Croc 7542) en vue caudolatérale, **D**) en vue craniomédiale, **E**) ilion gauche (IPFUB Gui Croc 7641) en vue latérale, **F**) en vue médiale, **G**) ischion droit partiel (IPFUB Gui Croc 7580) en vue médiale, fémur gauche (IPFUB Gui Croc 75112) **H**) en vue médiale, **I**) en vue latérale, **J**) tibia droit (IPFUB Gui Croc 8053) en vue latérale, **K**) ostéoderme paravertébral droit (IPFUB Gui Croc 8226) en vue externe, **L**) ostéoderme caudal (IPFUB Gui Croc 8227) en vue externe. Abréviations : cr cranmed, crête craniomédiale ; cr sacet, crête supraacetabulaire ; dep prox, dépression proximale ; f art sac, contacte area avec les côtes sacrales ; f cor, foramen coracoïde ; fos acet, fosse acetabulaire ; fos partroch, fosse paratrochanterale ; inc acet, incisura acetabulaire ; lin arc cranlat hum, crête craniolaterale majeure ; pr crdor, process craniodorsal ; pr caudor, process caudodorsal ; rug, rugosité ; rug caudlat, rugosité caudolatérale ; troch, trochanter du fémur ; tub caudlat, tubérosité caudolaterale ; tub cranmed, tubérosité craniomédiale. Échelle : 5 mm.

4.2.5.6. Femur. The femur is sigmoidally curved (IPFUB Gui Croc 75127), with the proximal and distal extremities twisted at about 135 degree to each other. The shaft is circular in cross-section proximally, becoming gradually more oval distally. The femoral head is cranially flexed (Fig. 7H, I). The articular surface of the head has a semi-circular margin that is partly continuous with the lateral surface of the femoral shaft. The articular surface overhangs the medial surface of the femoral head. The lateral margin of the head is broadened, whereas the medial margin forms a sharp crest at the level of the femoral trochanter.

The lateral surface of the femoral shaft bears a rugose cranio-laterally aligned ridge that extends along the lateral surface to a point just distal to the femoral trochanter. Craniodistally to this ridge there is a shallow lateral proximal depression (Fig. 7I). The caudal surface of the femoral shaft is broadened and bears a rugose caudolateral tuberosity.

The medial surface of the femoral shaft has a shallow depression proximal to the articular surface of the femoral head. The femoral trochanter is positioned medially in the proximal fourth of the femoral shaft (Fig. 7H). The trochanter itself is a low, proximodistally oriented bulge with a thin central groove. Cranially to the trochanter there is a deep proximodistally oval paratrochanteral fossa, whereas caudal to it there is a shallow, circular impression.

The distal extremity of the femur bears a lateral and a medial condyle. These condyles are separated from each other by a faint intercondylar fossa. The lateral condyle is one third larger than the medial one (Fig. 7H). Caudally, a weak bulge extends proximally from both condyles (Fig. 7H). Between these two bulges the caudal surface of the distal extremity is concave and rugose. Both the caudal and the cranial margin of the distal extremity are strongly rugose.

4.2.5.7. Tibia. The tibia possesses a straight shaft with a broadened head and distal extremity. The tibial shaft is circular in cross-section (IPFUB Gui Croc 8053). The head of the tibia is twice as wide as the shaft and slightly flexed medially (Fig. 7J). The proximal articular surface has a triangular outline and bears a centrally positioned condylar pit. On the lateral surface of the tibial head there is a proximodistally oval tuberosity (Fig. 7J). The distal extremity of the tibia is approximately one third wider than the shaft. The astragalar articular surface is sickle-shaped with a convex lateral and a strongly concave medial margin. The medial surface of the distal extremity is concave and rugose. A rounded crest bounds the distal extremity both cranially and caudally.

4.2.5.8. Metatarsals. Each metatarsal has a straight and flattened shaft that comprises approximately three quarters of its total length (IPFUB Gui Croc 8141). The base of each metatarsal is twice as wide as the shaft and has a straight proximal margin. From its centre, the proximal articular surface tapers distally. The dorsal surface of the base bears a slight proximodistally oriented ridge.

The distal extremity of each metatarsal is slightly wider than the shaft. The distal articular surface bears a lateral and

a medial condylus separated from each other by an intercondylar sulcus. In lateral and medial aspect, the distal extremity is circular in outline. In the centre of each surface there is a shallow depression. The palmar surface of the distal extremity has a shallow semi-circular depression on it.

4.2.5.9. Phalanges. The shaft of each phalanx forms half its total length. The base is slightly wider than the shaft. The proximal metacarpal articular surface is lateromedially oval in outline and deeply concave at its centre. On the palmar surface, a slight median groove is present. The distal extremity is also only slightly wider than the shaft. The lateral and medial surfaces are semi-circular in outline, and bear a central depression. In dorsal aspect the distal extremity is vaulted such that it forms two bulges separated by a proximodistally aligned groove.

4.3. Osteoderms

The paravertebral osteoderms are rectangular in outline and up to twice as wide in a mediolateral direction as they are long. The lateral 25% of each paravertebral osteoderm is tilted lateroventrally and has an angle of about 30 degrees to the medial part of the osteoderm, while the medial part is slightly arched externally. A cranio-caudally oriented keel separates the external surfaces of the lateral and medial parts of the osteoderm. Cranially, this keel merges with a short, pointed articular process (Fig. 7K). The cranial, caudal and medial margins of each paravertebral osteoderm are straight, whereas the lateral margin is gently convex. The medial margin is weakly serrated. The external surface is strongly sculptured with regularly spread circular pits. An unsculptured articular surface extends from the articular process along the cranial margin in a medial direction. This area comprises one tenth of the total width of the osteoderm. The internal surface is crossed by a faint longitudinal groove directly internal to the osteodermal keel. The internal surface is for the most part unsculptured, but does bear a few oblique striations.

Paravertebral osteoderms from the base of the tail have a keel that is twice as high and sharper than those on the osteoderms from the trunk. Isolated tail osteoderms are either rectangular or oval in outline (Fig. 7L). The more cranially positioned tail osteoderms are wider in a mediolateral direction than they are long, whereas the more terminally positioned ones are longer in a cranio-terminal direction than they are wide. The latter osteoderms are additionally vaulted dorsally. All the preserved tail osteoderms possess a cranio-terminally oriented keel on their external surface.

Gular osteoderms are square in outline and only faintly externally arched. The margins of these osteoderms are weakly convex.

5. Discussion

5.1. Assignment to *Theriosuchus*

Of the plethora of material that has been referred *Theriosuchus*, only two specimens are complete enough to serve as

a basis for a genus diagnosis: BMNH 48330, a nearly complete and three-dimensionally preserved skull and BMNH 48216, a partial skeleton. Both these specimens derive from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of Dorset, southern England, and were originally described and figured by Owen (1879) as syntypes (Salisbury, 2002). Following Salisbury (2002), BMNH 48216 is now considered the lectotype and BMNH 48330 the paratype.

A third specimen of *T. pusillus*, BMNH 48328, a left mandibular ramus, also from the Purbeck Limestone Group, displays a number of features not preserved on BMNH 48216 and BMNH 48330. This specimen was originally described as *Brachydictes minor* by Owen (1879), and for reasons of preoccupation renamed as *Oweniasuchus minor* by Woodward (1885). Both Clark (1986) and Salisbury (2002) considered it a synonym of *T. pusillus* – an assignment that is followed here. The remains of *T. ibericus*, though disarticulated, also provide information on the diagnosis of the *Theriosuchus*.

We consider material referred to *Theriosuchus* from other localities, such as that described by Buscalioni and Sanz (1987a), Thies et al. (1997) and Wu et al. (1996b) to be too fragmentary or of uncertain taxonomical status to be of relevance for detailed comparisons.

Ammending the work of Owen (1878, 1879), Joffe (1967), Buffetaut (1981, 1982, 1983), Clark (1986), Buscalioni and Sanz (1990), Norell and Clark (1990), Brinkmann (1992), Wu et al., (1996b), Salisbury (2001, 2002) and Salisbury and Frey (2001), *Theriosuchus* can be diagnosed based on the following combination of diagnostic characters: brevirostrine skull, with the maxillary rostrum forming between 40% and 45% of the total length of the skull; small antorbital fenestra; slit-like, horizontally oriented and rostrally positioned external nares, separated from each other by the rostral-most extent of the nasals; shallow sulcus on the dorsal surface of the maxillary rostrum, immediately caudal to the junction between the maxilla, premaxilla and nasal; proportionately long jugal; medial base of the postorbital process formed by the ectopterygoid median crest on the frontal and the parietal in later ontogenetic stages; frontal and parietal partially unfused in early ontogenetic stages; dorsal margin of the supratemporal foramen smaller than the orbit throughout ontogeny; lateral margin of squamosal bevelled ventrally; proportionately narrow quadrate with a concave mandibular articular surface; secondary choanae bounded by the palatines rostrally and separated by a median septum of the pterygoid; mandibular symphysis does not extend caudally beyond a point level with the sixth dentary tooth; ilium with short praecetabular process and long postacetabular process; biserial dorsal shield comprising parasagittal osteoderms.

All these features are apparent in the material described herein from Guimarota, and we have no hesitation in assigning it to *Theriosuchus*. Differences between the Guimarota material and other material that has been referred to *Theriosuchus* that warrant specific designation are discussed below.

5.2. Further remarks on the diagnosis of *Theriosuchus*

In his diagnosis of *Theriosuchus*, Brinkmann (1992:52) included the character *Orbita groß* [large orbit]. Because this feature is found in all atoposaurids, we are of the opinion that it should be excluded from the genus diagnosis. Proportionately large orbits during the early stages of ontogeny have long been recognised as a feature common to all extant crocodylians (Mook, 1921a, 1921b; Kälin, 1933). In atoposaurids, however, the orbits remain large throughout ontogeny, a characteristic that could be regarded as paedomorphic for the group.

The new *Theriosuchus* material from Guimarota sheds light on a number of additional features that may be diagnostic of the genus. The first relates to the dorsal surface of the maxilla. In *T. guimarotae*, *T. ibericus* and *T. pusillus* (BMNH 48330) there is a shallow sulcus immediately caudal to the triple junction between the maxilla, premaxilla and nasal.

Wu et al. (1996b) considered a “supratemporal foramen separated from the orbit by only a narrow and depressed bend of the frontal and postorbital” as a feature that was diagnostic of *Theriosuchus*. However, this feature is seen in the majority of atoposaurids (Wellnhofer, 1971) and should not be considered diagnostic of the genus.

A retroarticular process formed exclusively by the articular and angular is evident on BMNH 48328, the specimen that was originally designated as the holotype of *Oweniasuchus minor* by Owen (1879), but that is now referred to *T. pusillus* (Salisbury, 2002). As mentioned previously, this is the only complete mandible known from any species of *Theriosuchus*. Isolated surangulars and angulars are known for *T. guimarotae*. All these remains show a similar form of the angular and surangular to that seen in *T. pusillus*, with a slightly caudoventrally directed caudal angular process and a caudal surangular margin that is straight and caudoventrally directed. As to whether this feature is also present in *T. ibericus* is not known. If the collection of additional material referable *T. ibericus* shows that it is, then this feature could be considered diagnostic of the genus.

5.3. Comparison with other *Theriosuchus* species

Theriosuchus pusillus and *T. ibericus*, *T. guimarotae* can be distinguished from each other based on features of the cranial table, maxillary rostrum, teeth and vertebrae.

In *T. pusillus*, the lateral surface of the squamosal is bevelled ventrally. In dorsal aspect, the dorsal part of this surface—that is, the part that contributes to the lateral margin of the cranial table—is convex, extending from the squamoso-postorbital suture caudally to a point two thirds of the way along the dorsal margin of the supratemporal foramen. In *T. guimarotae* and *T. ibericus*, however, the bevelled portion of the squamosal is at the caudal rather than rostral portion of the bone, extending from caudolateral margin of the cranial table to a point level with the caudal third of the dorsal margin of the supratemporal foramen. At the rostral-most extent

of this bevelled surface, there is a distinct lateral notch. In addition, the caudolateral corner of the squamosal of *T. guimarotae* forms a rounded, caudally projecting process. Sculpture pitting on the dorsal surface of this process is similar to that on the cranial table. In contrast, in specimens of *T. pusillus* and *T. ibericus* that are larger than the type material of *T. guimarotae*, the caudolateral corner of the squamosal forms an unsculptured, caudolaterally directed, knob-like process that overhangs the occiput slightly.

In dorsal aspect, the premaxillomaxillary suture in *T. pusillus* and *T. ibericus* is slightly rostromedially oriented, whereas in *T. guimarotae* it is oriented caudomedially.

In *T. guimarotae*, the minimum space between supratemporal foramina comprises one third of the total width of the cranial table. In *T. pusillus* (BMNH 48216, BMNH 48330) this space is only one sixth of the total width of the cranial table. This difference does not appear to be a result of an increase in the size of the supratemporal foramina during ontogeny, as it consistently occurs in different size-classes of both species. Furthermore, in the type material of *T. pusillus*, the medial margin of the supratemporal foramen is slightly elevated above the rest of the cranial table, a feature that is not apparent in *T. guimarotae*. The caudal part of the cranial table is not preserved in *T. ibericus*.

Brinkmann (1992) notes that the teeth of *Theriosuchus* are highly heteromorphic, ranging from pseudocanine-like mesially, to lanceolate-shaped and then to low-crowned mid-way along the tooth row, and strongly labiolingually flattened teeth distally. This type of dentition is present in *T. pusillus* and *T. ibericus*. The dentition of *T. guimarotae* on the other hand, comprises only pseudocanine-like and lanceolate-shaped teeth. None of the specimens collected so far possess labiolingually flattened lanceolate-shaped teeth. The teeth of *T. ibericus* of *T. guimarotae* can also be distinguished from each other by their lack of serrated mesial and distal carinae.

Another feature that may be relevant in distinguishing what are assumed to be mature individuals of each species, is the minimum width of the frontal between the orbits. In the type material of *T. guimarotae*, this space comprises one third of the maximum width of the skull at the orbits. In contrast, on the paratype skull of *T. pusillus* (BMNH 48330) (which is twice as long as *T. guimarotae*), the minimum interorbital space is much narrower, comprising only one fifth of the total skull width at the orbits. Since ontogenetic changes in the skull of recent crocodylomorphs include among other features a decrease in the size of the orbits in proportion to the rest of the skull, and therefore a proportional increase in the width of the interorbital space (Mook, 1921b), a smaller interorbital space in a larger skull is interpreted in this context as a diagnostic (but nonetheless paedomorphic) feature. Other features of the skull of *T. guimarotae*, not visible in *T. pusillus* include dorsal exposure of the supraoccipital on the cranial table. Caudal to the secondary choanae, paired semi-circular depressions are developed in *T. pusillus* and *T. guimarotae*, but not preserved in *T. ibericus*.

Norell and Clark (1990), Brinkmann (1992) and, Wu et al. (1996b) all considered the external mandibular fenestra of *T.*

pusillus to be closed. This condition is apparent on BMNH 48328, the left mandibular ramus of “*Oweniasuchus minor*” (see Salisbury, 2002: Text-fig. 16). However, one of us (DS) is of the opinion that there are two specimens in the Purbeck crocodylian sample that may be referable to *T. pusillus*, where this is not the case. BMNH 48240, a right mandibular ramus labelled as “*Crocodylia* indet.”, possesses the characteristic caudal mandibular margin of *Theriosuchus* (see above). However, unlike other specimens of *T. pusillus* from the Purbeck sample, this mandibular ramus has a small external mandibular fenestra. A similar feature is apparent BMNH 48331, the partly disarticulated mandibular ramus. Although this would be unusual, as has been stressed by Salisbury (2002), it is very likely that these two specimens belong to juvenile individuals of other Purbeck crocodylians. Indeed, the size and position of the external mandibular fenestra on BMNH 48240 is consistent with that seen in *Goniopholis simus* (see Salisbury et al., 1999: Text-fig. 10s).

The caudal mandibular region is destroyed in *T. ibericus*. In *T. guimarotae*, an external mandibular fenestra is well-developed. The presence of this feature is therefore considered diagnostic of the Portuguese species until the collection of additional material proves otherwise.

The morphology of the vertebral bodies in species of *Theriosuchus* has always been matter of debate. A thorough review of all previous accounts is provided in Salisbury and Frey (2001). Their interpretation of all the relevant material is followed here, and is summarised as follows.

T. pusillus: At least one of the preserved cranial cervical vertebrae is procoelous; the caudal surface of the body of the cranial-most thoracic vertebra is gently concave; the remaining thoracic vertebrae and cranial-most lumbar vertebrae are gently amphicoelous; the body of the second sacral vertebra has a flat cranial surface and a gently concave caudal surface; the first caudal vertebra is opisthocoelous, with a shallow, rugose concavity in the centre of the vertebral condyle.

Theriosuchus ibericus: The vertebral morphology of *T. ibericus* is presently unclear, and must await the collection of more complete material. Although it is clear that some of the crocodylians present in the Uña assemblage described by Brinkmann (1992) possess procoelous cervical, thoracic and caudal vertebrae, the taxon or taxa to which these elements belong cannot be proven conclusively (Salisbury and Frey, 2001). Brinkmann (1992) distinguishes *Theriosuchus ibericus* from other species of *Theriosuchus* based only on the possession of procoelous caudal vertebrae, a choana that is narrower than that of *T. pusillus* and a tooth morphology that is slightly different to that of *T. pusillus*. Given the uncertain status of its vertebral morphology, the validity of the species is questionable, particularly if it is based only on tooth morphology and width of the secondary choanae.

T. guimarotae: All the preserved cervical, dorsal, sacral and caudal vertebrae of *T. guimarotae* are amphicoelous. The condition in *T. ibericus* aside, compared with what is seen in *T. pusillus*, the lack of any procoelous or opisthocoelous vertebral bodies in *T. guimarotae* can be considered diagnostic at species level.

5.4. Ontogeny

The proportional and non-proportional changes in the skull of recent crocodylian during ontogeny are well known (Mook, 1921a, 1921b; Kälin, 1933; Iordansky, 1973; Dodson, 1975; Klembara, 1991; Rieppel, 1993). Cranial and postcranial material referable to *T. guimarotae* spans a wide spectrum of sizes representative of different ontogenetic stages.

Ontogenetic differences are apparent on two skulls, from which one (IPFUB Gui Croc 7309) is half as long as the other (IPFUB Gui Croc 7308, holotype). The most obvious difference relates to the ratio between rostral length and total skull length. This ratio changes from 0.39 in the smaller skull (IPFUB Gui Croc 7309) to 0.42 in the medium-sized skull (IPFUB Gui Croc 7308), indicating a lengthening of the rostrum in relation to the total length of the skull. At the quadrate, the crest B sensu Iordansky (1973) is more prominent in larger bones. The density of skull sculpturing increases remarkably from smaller to larger skull fragments. The frontal and the parietal of *T. guimarotae* are only partially fused in the smaller remains. In the larger remains, both these bones are completely fused, but a median crest remains as a trace of the former suture. Paired frontals and parietals during early ontogenetic stages in *Alligator mississippiensis* have been documented by Rieppel (1993). In *Alligator*, the paired frontals and parietals fuse after hatching or remain partly unfused until a young adult stage (Wu et al., 1996a).

Due to its small adult size of about 500 mm and its possession of many osteological features usually only associated with juvenile individuals of extant crocodylian taxa (see Mook, 1921a, 1921; Kälin, 1933; Rieppel, 1993), *Theriosuchus* and other atoposaurids are often considered examples of "dwarf" taxa (Joffe, 1967; Salisbury, 2001). Indeed, Clark (1986) and, Salisbury (2001, 2002) note that a number of specimens referred to *Theriosuchus* actually represent juvenile individuals of other taxa. These include: BMNH 48329 (a right squamosal and paravertebral and gastral osteoderms; labelled *Theriosuchus* but probably a juvenile *Goniopholis simus* or *G. [Nannosuchus] gracilidens*); BMNH 48240 (a left mandibular ramus; labelled *Theriosuchus*, but probably *G. simus*); BMNH 48724 (a right pes, paravertebral osteoderms and left mandibular ramus: labelled *Theriosuchus*, but probably *Goniopholis*). But despite its small size, there are a number of osteological features that clearly identify the majority of *Theriosuchus* specimens as adult individuals. These include dense sculpturing of the dorsal surface of the bones of the skull and the good ossification of the dermal bones. If preserved, the articular surfaces and condyles are all well ossified. Features that seem to indicate a juvenile stage are represented throughout different ontogenetic stages. For instance, Kälin (1933) notes a size-reduction of the orbit during ontogeny in all extant crocodylian taxa, whereas in *T. guimarotae* this opening remains large in proportion to the rest of the skull even in the largest individuals. Kälin (1933) and, Rieppel (1993) both note that juvenile individuals of extant croco-

dilian species possess larger and much more rostrocaudally oval-shaped supratemporal foramina than adults, whereas form and size of the supratemporal foramina in *Theriosuchus* generally do not change during ontogeny.

5.5. Palaeobiogeographic and palaeoecologic implications

The remains of *Theriosuchus* are restricted to European fossil localities (Fig. 8) with the exception of finds in the Early Cretaceous of the Ordos Basin of Inner Mongolia (Wu et al., 1996b). Within the European continent, fossil deposits yielding *Theriosuchus* are concentrated on the Iberian Peninsula (Buscalioni, 1986; Buscalioni and Sanz, 1984, 1987a, 1987b) and southern England (Owen, 1879; Salisbury, 2002). Isolated teeth that may be referable to the genus have also been reported in north-western Germany (Thies et al., 1997) and north-eastern France (Cuny et al., 1991). The remains from



Fig. 8. Distribution of hitherto known European *Theriosuchus* localities. Numbers correspond to the locality numbers of Table 2: 1) Guimarota/Leiria, Portugal; 2a) Langenberg/Oker, 2b) Uppen, north-western Germany; 3) Boulonnais, northern France; 4) Swanage, Dorset; UK; 5) Hastings and Cuckfield, Sussex, UK; 6) Isle of Wight, GB; 7) Morella/Castellón, Spain; 8) Galve/Teruel, Spain; 9) Uña/Cuenca, Spain; 10) Pio Pajarón/Cuenca, Spain. Fig. 8. Répartition des sites à *Theriosuchus* Européens connus jusqu'à présent. Les numéros correspondent à ceux des sites de la planche 2 : 1) Guimarota/Leiria, Portugal ; 2a) Langenberg/Oker, 2b) Uppen, nord-ouest de l'Allemagne ; 3) Boulonnais Nord de la France ; 4) Swanage, Dorset, GB ; 5) Hastings et Cuckfield, Sussex, GB ; 6) Isle de Wight, GB ; 7) Morella/Castellón, Espagne ; 8) Galve/Teruel, Espagne ; 9) Uña/Cuenca, Espagne ; 10) Pio Pajarón/Cuenca, Espagne.

Guimarota described herein add to the record from the Iberian Peninsula.

The age of sites that have yielded *Theriosuchus* remains extend from Late Jurassic (Kimmeridgian) to Early Cretaceous (Barremian). During the late Jurassic, the eastern part of North America and Asia were large landmasses, whereas much of Europe and the eastern part of North America were inundated with shallow epicontinental seas (Ziegler, 1988). As a result of the extensional tectonics accompanying the divergence of parts of Laurasia, lagoonal environments with continental islands, including the Iberian Meseta, formed on the continental margins of most of Laurasia (Ziegler, 1988). Following periodical eustatic sea-level changes and extensive regressions in the Late Jurassic and earliest Cretaceous, freshwater lagoons episodically changed to brackish conditions, and facies such as those represented by the Purbeck Limestone Group were deposited (Allen, 1975).

The *Theriosuchus*-bearing fossil deposit of Guimarota/Leiria in Portugal and Dorset in southern England, and as well those in north-western Germany and north-eastern France are all characterised by changing salinity. In contrast, most of the deposits in Spain such as Galve and Uña, are continental localities. In all the sites that have produced more than isolated skull remains (namely Guimarota, Dorset and Uña/Spain), there is a different species of *Theriosuchus* present. Despite being separated by a considerable amount of time, there is no report of *Theriosuchus* from any other locality in western Europe. This is in contrast to other crocodylian taxa, such as *Goniopholis*, which are commonly encountered at numerous western European sites throughout this time period (Salisbury et al., 1999). It is possible that species of *Theriosuchus* were not as common as other crocodylians during this time or, alternatively, that they were more terrestrially inclined, and thus less common in fossil assemblages than their supposedly semi-aquatic counterparts. The abundance of *Theriosuchus* remains in the Guimarota vertebrate assemblage is comparable with that seen in the Purbeck Limestone Group. Brinkmann (1989) speculated that *Theriosuchus* remains in the Guimarota swamp were transported from afar, presumably from a terrestrial environment. However, the high frequency and ontogenetic variability displayed by this material, as well as the lack of transportation marks on the fossils make it equally likely that most of the carcasses were deposited more or less in situ after death, though some may have been partly transported by currents within the swamp (Gloy, 2000). Based on comparisons with *T. pusillus*, *T. guimarotae* probably reached a maximum length of about 550 mm. Corresponding with its small size, its diet probably consisted of invertebrates and possibly small vertebrates such as amphibians and some mammals, as is the case with juveniles of all extant species (Trutnau, 1994). It therefore seems likely that there was little overlap in diet with adults of larger crocodylians such as species of *Goniopholis*, which may have reached sizes in excess of 3 m. We therefore are of the opinion that these crocodylians could easily have lived sympatrically withing the same habitat.

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