A three-dimensional skeleton of Goniopholididae from the Late Jurassic of Portugal: implications for the Crocodylomorpha bracing system

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We here describe an articulated partial skeleton of a small neosuchian crocodylomorph from the Lourinhã Formation (Late Jurassic, Portugal). The skeleton corresponds to the posterior region of the trunk and consists of dorsal, ventral and limb osteoderms, dorsal vertebrae, thoracic ribs and part of the left hindlimb. The paravertebral armour is composed of two rows of paired osteoderms with the lateral margins ventrally deflected and an anterior process for a 'peg and groove' articulation. We also compare its dermal armour with that of several Jurassic and Cretaceous neosuchian crocodylomorphs, establishing a detailed description of this type of osteoderms.

These features are present in crocodylomorphs with a closed paravertebral armour bracing system. The exceptional 3D conservation of the specimen, and the performance of a micro-CT scan, allowed us to interpret the bracing system of this organism to assess if previous models were accurate. The characters observed in this specimen are congruent with Goniopholididae, a clade of large neosuchians abundant in most semi-aquatic ecosystems from the Jurassic and Early Cretaceous of Laurasia. However, its small size, contrasted with the sizes observed in goniopholidids, left indeterminate whether it could have been a dwarf or juvenile individual. Future histological analyses could shed light on this.

ADDITIONAL KEYWORDS: crocodiles – Neosuchia – osteoderms – Lourinhã Formation.

INTRODUCTION

Neosuchia was the dominant clade of Crocodylomorpha in Europe since the Jurassic. It is a clade of mesoeucrocodylian crocodylomorphs that appeared at the beginning of the Jurassic and, with the extant representatives of the crown group Crocodylia, remain until the present day. The oldest member of the clade is the goniopholidid *Calsoyasuchus* (Tykoski *et al.*, 2002) from the Kayenta Formation of Arizona, United States (Sinemurian–Pliensbachian, Lower Jurassic). However, the affinity of *Calsoyasuchus* within Neosuchia has recently been challenged and this taxon may be related to Hsisosuchidae instead (Wilberg *et al.*, 2019). Therefore, the appearance of Neosuchia would have occured later during the Middle Jurassic.

Although the crocodylomorph record is scarce in the Middle Jurassic, new discoveries in Europe appear to indicate that it is during this time that many neosuchian lineages appeared and diversified (Young *et al.*, 2016; Yi *et al.*, 2017). Prior to that time, the Mesozoic was dominated by non-mesoucrocodylian crocodylomorphs, such as protosuchians and sphenosuchians (Langston, 1973; Tykoski *et al.*, 2002).

The European representatives of Neosuchia are mainly composed of marine Tethysuchia (Pholidosauridae and Dyrosauridae; e.g. Andrade *et al.*, 2011; Fortier *et al.*, 2011) and terrestrial to semi-aquatic Atoposauridae, Bernissartiidae, Goniopholididae (e.g. Brinkmann, 1989; Buscalioni *et al.*, 2008; Schwarz-Wings *et al.*, 2009b; Gasca *et al.*, 2012; Puértolas-Pascual *et al.*, 2015b; Guillaume *et al.*, this volume), and Eusuchia (Puértolas-Pascual *et al.*, 2016), the latter being the crocodyliform lineage that includes

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living crocodylians and their extinct relatives. Another clade with abundant representatives in the Jurassic and Lower Cretaceous of Europe is Thalattosuchia, a group of exclusively marine crocodylomorphs. Nevertheless, there is no complete consensus on the phylogenetic position of Thalattosuchia within (or outside) Neosuchia, which has been a controversial issue since the first phylogenetic analyses of Crocodylomorpha (e.g. Benton & Clark, 1988; Clark, 1994; Pol & Gasparini, 2009; Wilberg, 2015; Wilberg *et al.*, 2019).

Within terrestrial ecosystems, the typical crocodylomorph fossil assemblage found in Europe from the Middle Jurassic to the Early Cretaceous is mainly composed of Atoposauridae, Bernissartiidae and Goniopholididae (e.g. Brinkmann, 1989; Buscalioni *et al.*, 2008; Schwarz-Wings *et al.*, 2009; Gasca *et al.*, 2012; Puértolas-Pascual *et al.*, 2015b; Tennant *et al.*, 2016a; Guillaume *et al.*, this volume).

Bernissartiidae is a clade of small durophagous neosuchians composed of *Bernissartia fagesi* Dollo, 1883 (Buffetaut, 1975; Buscalioni & Sanz, 1990; Norell & Clark, 1990) and *Koumpiodontosuchus aprosdokiti* Sweetman et al., 2014 from the Barremian of Spain and England. However, isolated teeth assigned to this clade have been recovered in several sites from the Late Jurassic (Brinkmann, 1989; Guillaume *et al.*, this volume) and Early Cretaceous (Buffetaut & Ford, 1979; Buscalioni *et al.*, 2008; Schwarz-Wings *et al.*, 2009b; Gasca *et al.*, 2012; Puértolas-Pascual *et al.*, 2015b) of Europe.

Atoposauridae is a clade of dwarf neosuchian with a record from the Middle Jurassic to the Upper Cretaceous (Young *et al.*, 2016). Recently, its phylogenetic framework has been challenged by Tennant *et al.* (2016b), who removed *Theriosuchus* from Atoposauridae and considered this genus as paraphyletic. In consequence, they created a new genus, *Sabresuchus*, for the taxa *Sabresuchus* (=*Theriosuchus*) *ibericus* (Brinkmann, 1989) and *Sabresuchus* (=*Theriosuchus*) *sympiestodon* (Martin *et al.*, 2010). Subsequently, Schwarz *et al.* (2017) erected the new genus *Knoetschkesuchus* for the German taxon *Knoetschkesuchus langenbergensis* Schwarz *et al.*, 2017, where they also included the Late Jurassic species of Portugal, *Knoetschkesuchus* (=*Theriosuchus*) *guimarotae* (Schwarz & Salisbury, 2005). Therefore, within this new scenario, the genus *Theriosuchus* would be restricted to *Theriosuchus pusillus* Owen, 1879 and *Theriosuchus grandinaris* Lauprasert *et al.*, 2011. However, a small mandible from the Morrison Formation (USA), originally assigned to a juvenile goniopholidid (Foster, 2006), has been recently described as *Theriosuchus morrisonensis* Foster, 2018. In addition, the *Aprosuchus ghirai* Venczel & Codrea, 2019 has recently been described from Maastrichtian

deposits of Romania. *Aprosuchus* could be closely related to the putative atoposaurids *Theriosuchus*, *Sabresuchus* and *Knoetschesuchus* (Venczel & Codrea, 2019). In this work, we follow the traditional phylogenetic framework that includes *Theriosuchus*, *Sabresuchus*, *Knoetschkesuchus* and *Aprosuchus* as members of the clade Atoposauridae, since it is, at the moment, the most used in the literature.

Goniopholididae is a clade of neosuchian crocodylomorphs with a semi-aquatic lifestyle whose record ranges from the Early Jurassic (or Middle Jurassic according to Wilberg *et al.*, 2019) to the Late Cretaceous, with a predominantly Laurasian distribution. Their remains are abundant in the fossil record of the Late Jurassic and Early Cretaceous of Europe (e.g. Salisbury *et al.*, 1999; Schwarz-Wings *et al.*, 2009b; Andrade & Hornung, 2011; Salisbury & Naish, 2011) and the Iberian Peninsula (e.g. Buscalioni & Sanz, 1987; Ortega *et al.*, 1996; Schwarz, 2002; Buscalioni *et al.*, 2013; Puértolas-Pascual, Canudo, & Sender, 2015a; Guillaume *et al.*, this volume). The clade Goniopholididae has also been subjected to a strong review during the last several years. The genus *Goniopholis* has been used as a wastebasket clade for a variety of species based on fragmentary material (Andrade *et al.*, 2011). However, new discoveries and phylogenies show us a much more complex scenario where several new genera and species have been erected (e.g. Andrade *et al.*, 2011; Andrade & Hornung, 2011; Salisbury & Naish, 2011; Buscalioni *et al.*, 2013; Puértolas-Pascual *et al.*, 2015a; Martin *et al.*, 2016; Frederickson *et al.*, 2017; Ristevski *et al.*, 2018). These studies show that Goniopholididae is composed of a variety of basal taxa from Asia and North America and two derived European clades, one of which includes the genus *Goniopholis* and the other comprised of the genera *Anteophthalmosuchus* and *Hulkepholis* (Puértolas-Pascual *et al.*, 2015a).

CROCODYLOMORPHS OF PORTUGAL

The Jurassic of Portugal is rich in fossil dinosaurs (e.g. Antunes & Mateus, 2003; Mateus, 2006), but Crocodylomorpha is one of the most dominant clades in the fossil assemblages from this period (Mateus *et al.*, 2019; Guillaume *et al.*, this volume). The oldest known crocodylomorph in Portugal is the marine thalattosuchian *Pelagosaurus tomarensis* (Ferreira, 1959) from the latest Toarcian or earliest Aalenian (Early or Middle Jurassic) of Tomar (Antunes, 1967; Parrilla-Bel *et al.*, 2013). This taxon was later re-assigned to *Mystriosaurus* cf. *bollensis* by Antunes, (1967). Other remains correspond to isolated teeth assigned to *Machimosaurus* sp. from the Oxfordian of Cesareda, Cesaredas (west-central Portugal) and a partial snout from Malhão (Algarve)
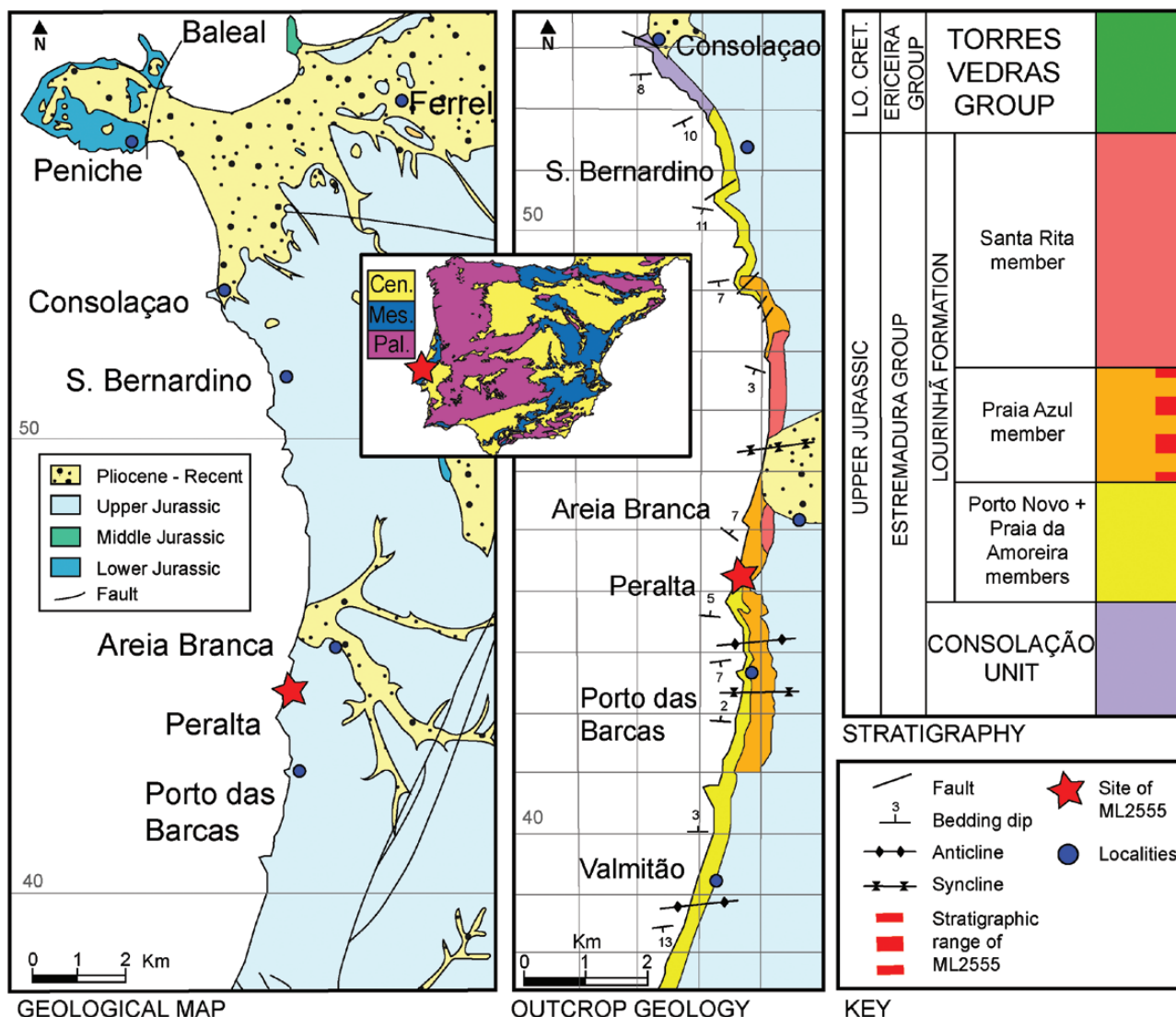
(Sauvage, 1897–98; Young *et al.*, 2014). The Upper Kimmeridgian–Lower Tithonian outcrops have a higher diversity of crocodylomorphs with at least six known taxa coming from the Guimarota mine in Leiria (Alcobaça Formation) and the surroundings of Lourinhã (Lourinhã Formation): the teleosaurid thalattosuchian *Machimosaurus hugii* von Meyer, 1837 (Sauvage, 1897–98; Young *et al.*, 2014), the unplaced *Lisboasaurus* and *Lusitanisuchus* (Seiffert, 1970, 1973; Buscalioni *et al.*, 1996; Krebs & Schwarz, 2000; Schwarz & Fechner, 2004, 2008), the putative atoposaurid *K. guimarotae* (Krebs & Schwarz, 2000; Schwarz & Salisbury, 2005), the goniopholidid *Goniopholis baryglyphaeus* Schwarz, 2002 and *Bernissartia* sp. (Brinkmann, 1989; Guillaume *et al.*, this volume). In addition, two crocodylomorph eggs were also recently described (Russo *et al.*, 2017).

The Early Cretaceous of Portugal is scarce in crocodylomorph fossils (Mateus & Milan, 2010). On the contrary, the Late Cretaceous shows a larger diversity, although it is mostly based on fragmentary material that require an updated review and probably new taxonomic assignments. From the Middle Cenomanian of Viso, near Aveiro, remains assigned to the *nomen dubium* and putative goniopholidid *Oweniasuchus lusitanicus* Sauvage, 1897–98 were recovered. From the Campanian–Maastrichtian of Viso, remains assigned to '*Crocodylus*' *blavieri*? Gray, 1831 were also reported (Sauvage, 1897–98; Jonet, 1981), but the taxonomic assignment and affinities within Mesoeucrocodylia of this taxon remain unclear (Antunes & Pais, 1978). Other remains corresponding to a similar taxon were recovered in the Upper Cretaceous of Taveiro and Cacém (Crespo, 2002). From the Middle Cenomanian of Cacém, jaw fragments and isolated teeth, doubtfully assigned to the goniopholidid *Goniopholis* cf. *crassidens* Owen, 1842, and the putative goniopholidids *Oweniasuchus lusitanicus* Sauvage, 1897, *Oweniasuchus* aff. *lusitanicus* and *Oweniasuchus pulchelus* Jonet, 1981 and the Eusuchia *Thoracosaurus* were also reported (Jonet, 1981; Crespo, 2002; Mateus, 2013; Puértolas-Pascual *et al.*, 2016). Remains assigned to *Oweniasuchus* sp. and *Oweniasuchus pulchelus* have also been recovered in the Middle and Upper Cenomanian of Carenque (Sintra, Lisbon) and Forte Junqueiro (Lisbon) (Jonet, 1981; Crespo, 2002; Puértolas-Pascual *et al.*, 2016). Also, from the Middle Cenomanian of Portugal, Buffetaut & Lauverjat (1978) reported a fragmentary, unidentified, possible dyrosaurid from Nazaré (Leiria). Probably one of the most interesting crocodylomorphs in Portugal corresponds to a partial skull and mandible recently assigned to the new genus and species *Portugalosuchus azenhae* Mateus *et al.*, 2019. *Portugalosuchus* was recovered from the Early Upper Cenomanian of the Tentugal Formation,

in the Baixo Mondego region (west-central Portugal), and corresponds to one of the oldest reliable eusuchian crocodylomorphs in the fossil record and probably the oldest record of Crocodylia (Mateus *et al.*, 2019).

In contrast, Cenozoic crocodylomorphs of Portugal are often known from complete skulls and several individuals. One of the sites where more Crocodylomorpha remains have been recovered was in the Lower Eocene clay pit of Silveirinha (Baixo Mondego). From this fossil site, several cranial and postcranial remains assigned to the crocodylian *Diplocynodon* sp. were recovered (Antunes & Russell, 1981; Crespo, 2001; Antunes, 2003). Other Eocene cranial remains consist of the sebecosuchian *Iberosuchus macrodon* Antunes, 1975 from the Lutetian–Bartonian of the Feligueira Grande Formation (Middle Eocene) located in the Vale Furado (Nazaré, Leiria). From the same fossil site, remains assigned to *Diplocynodon* sp.? have also been reported (Antunes, 2003). The Early Miocene of the lower basin of the Tagus river, Horta das Tripas and other localities around Lisbon, the Middle Miocene of Amôr/Leiria and the Late Miocene of Aveiras de Baixo, also in Lisbon, have yielded several fossil remains doubtfully assigned to *Diplocynodon* sp.? and other undetermined crocodylomorphs (Antunes & Mein, 1981; Antunes, 1994, 2003; Crespo, 2001). One of the most interesting taxa from the Miocene of Portugal is the giant crocodylian *Tomistoma lusitanica* (Vianna & Moraes, 1945), originally described as *Gavialosuchus americanus* (Sellards, 1915). Remains of this taxon, mainly teeth and isolated bones, have been recovered in coastal deposits from the Early–Middle Miocene of the Algarve in Praia Grande (between Lagos and Albufeira), Cerro das Mós (Lagos) and Olhos de Água (Albufeira) (Vianna & Moraes, 1945; Antunes *et al.*, 1981). The most important remains of this taxon come from different Lower–Upper Miocene deposits of the surroundings of the city of Lisbon. The sites of Quinta da Farinheira, near Chelas (Lisbon) and Quinta dos Durões, near Mutela (Almada), stand out, where two huge complete skulls were recovered (Antunes, 1961). Also, during the Middle–Upper Miocene of Lisbon, remains of another crocodylian assigned to *Tomistoma* cf. *calaritanus* Capellini, 1890 has been reported (Zbyszewski, 1949). Although according to Antunes & Ginsburg (1989) this last specimen, and other isolated remains from the lower basin of the Tagus, could actually correspond to *Gavialis* sp. (Antunes & Cahuzac, 1999; Crespo, 2001).

Within this framework, we present a well-preserved crocodylomorph postcranial skeleton from the Lourinhã Formation (Late Jurassic, Portugal). The small fossil ML2555 was found on the beach of Peralta (municipality of Lourinhã, Portugal) (Fig. 1) by Leandro Pereira, a local who donated the specimen (Fig. 2) to the Museu da Lourinhã. The specimen consists of a fragmentary articulated axial skeleton,

Figure 1. Geographical and geological settings of the specimen ML2555 from the Upper Jurassic of Peralta (Lourinhã, Portugal). Modified from Manuppella *et al.* (1996), Taylor *et al.* (2014), Mateus *et al.* (2017) and Gowland, Taylor & Martinius (2018).

dermal armour and hindlimb, from the posterior region of the trunk of a small neosuchian crocodylomorph. By anatomical study of bones, especially osteoderms, we have been able to assign ML2555 to Gonipholididae indet. One of the peculiarities of the specimen is that it was recovered articulated and three-dimensionally preserved volumetrically. This preservation is unusual in the fossil record of Neosuchia from the Late Jurassic, where most skeletons are preserved crushed in two dimensions (e.g. Tennant & Mannion, 2014; Martin *et al.*, 2016). The exceptional preservation of ML2555 has also allowed us to reconstruct and test previous models and hypotheses about the closed paravertebral armour bracing system present in this kind of crocodylomorphs (Salisbury & Frey, 2001).

GEOLOGICAL SETTING

The specimen ML2555 was collected as a loose beach block from Praia da Peralta, and the origin should be from the adjacent sea cliffs, although the exact layer is unknown. The cliffs outcrop Late Jurassic rocks from the Lourinhã Formation, more specifically the Praia Azul Member (Upper Kimmeridgian–Lower Tithonian). This outcrop is also referred to as Sobral Member and Porto das Barcas Member, but those terms refer more to the option of nomenclature rather than different geological units (Ribeiro *et al.*, 2014; Mateus, Dinis & Cunha, 2017). The Praia Azul Member is composed of near-shore continental sedimentary floodplain muds with occasional river channels
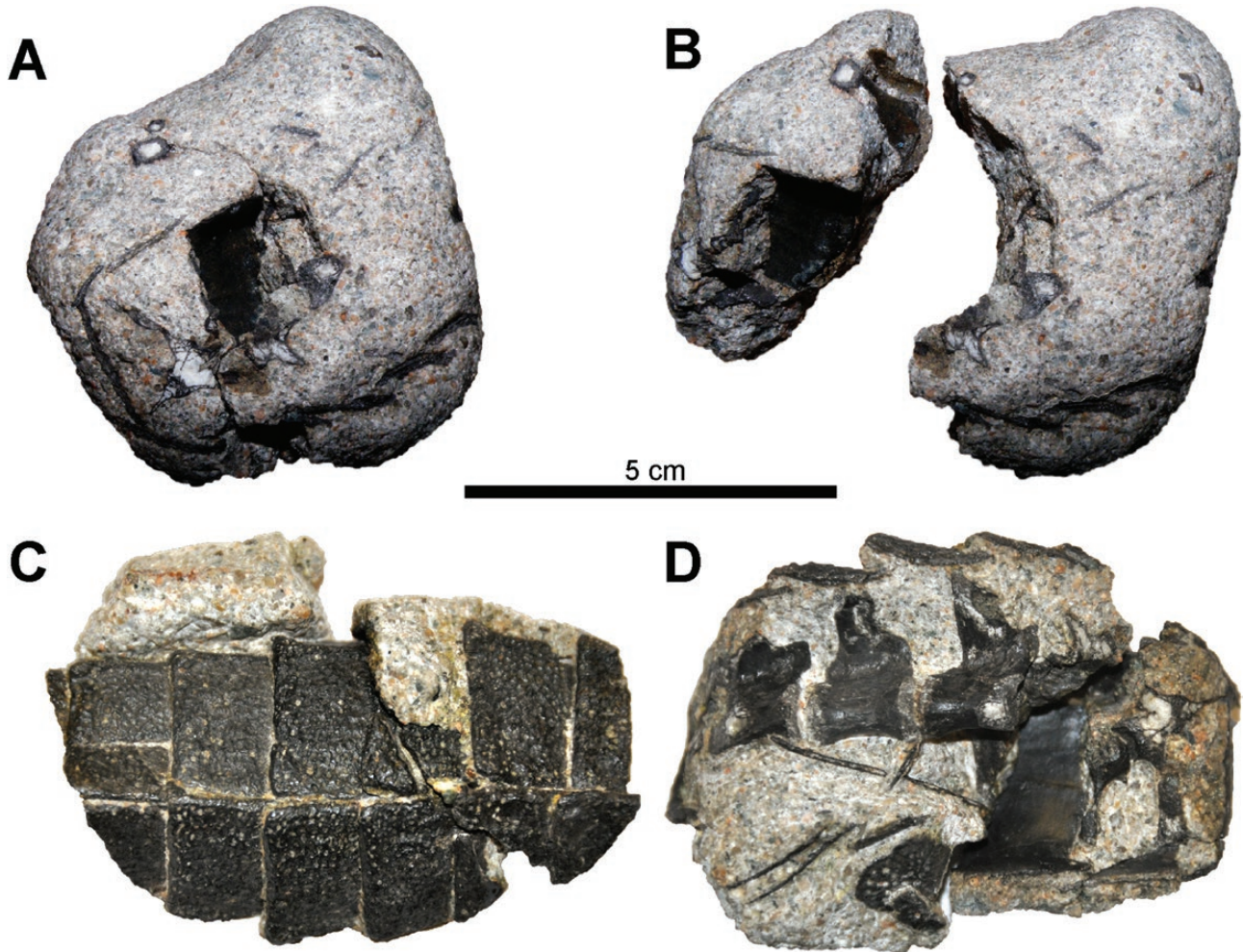
Figure 2. Pictures of ML2555 during the laboratory preparation work. A–B, fossil block as it was found in the field with several bones surfacing. C, dorsal view of the fossil already prepared. D, ventral view of the fossil already prepared.

setting (Taylor *et al.*, 2014). It was part of a seasonal palaeoenvironment with an average temperature around 31 °C (Myers *et al.*, 2012a), with both humid and arid conditions inducing high average soil pCO_2 (Myers *et al.*, 2012b). Multiple indicators suggest continental/freshwater sedimentation: dinosaur nesting grounds, presence of amphibians such anurans and albanerpetontids, freshwater clams such as *Unio alcobacensis* Choffat, 1885 and abundant caliche and palaeosols. Despite it being a terrestrial habitat, there are three short periods of sea transgressions with a wide variety of invertebrates and some marine or brackish water vertebrates, including the thalattosuchian *Machimosaurus hugii*, cryptoclidid plesiosaurs (Ribeiro & Mateus, 2012), plesiochelyid testudines and *Hybodus* sharks (Balbino, 2003). The ephemeral marine transgressions are represented by a bioclastic sandy limestone to calcareous mudstone, less than 50 cm thick. The rock matrix associated with

ML2555 is a medium-sized sandstone similar to the river-channel rocks in the upper layers of Praia Azul Member, but not from transgressive layers.

Peralta is also the type locality of the sauropod *Lusotitan atalaiensis* (de Lapparent & Zbyszewski, 1957), the theropod *Lourinhanosaurus antunesi* Mateus, 1998 (including eggs ML156 and ML771; Ribeiro *et al.*, 2014) and the Cardioidea bivalve *Protocardia peraltaensis* Fürsich & Werner, 1985, which was named for the locality. Other vertebrate occurrences in these layers include the turtle *Selenemys lusitanica* Pérez-García & Ortega, 2011, a *Torvosaurus gurneyi* Hendrickx & Mateus, 2014 nesting site (Araújo *et al.*, 2013) and stegosaur and pterosaur tracks (Mateus & Milàn, 2010). Concerning crocodylomorphs, a few unstudied, incomplete specimens were collected in Peralta, including common *Goniopholis* sp. teeth and the already mentioned *Machimosaurus hugii*.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History (New York, USA); BMNH, British Museum of Natural History, (London, UK); FCT-UNL, Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa (Caparica, Portugal); IPMNHNP, Institut de Paléontologie, Museum National d'Histoire Naturelle (Paris, France); IPFUB, Institut für Paläontologie der Freie Universität (Berlin, Germany); IRSNB, Institut Royal des Sciences Naturelles de Bruxelles (Brussels, Belgium); MG/LNEG, Museu Geológico, Laboratório Nacional de Energia e Geologia (Lisbon, Portugal); ML, Museu da Lourinhã (Lourinhã, Portugal); MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza (Zaragoza, España); USNM, National Museum of Natural History, Smithsonian Institution (Washington DC, USA).

MATERIAL AND METHODS

The specimen ML2555 was mechanically prepared by air scribe in the laboratories of the Museu da Lourinhã (where ML2555 is housed) and in the Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa (Portugal). Due to its small size and fragility, a full preparation was not possible (Fig. 2), therefore a micro-CT scan was carried out to study the bones obscured by the rock matrix.

The micro-CT was performed by V|Tome|X s 240 de GE Sensing & Inspections Technologies at the Centro Nacional de Investigación sobre Evolución Humana (CENIEH) (Burgos, Spain). Two separated acquisitions were necessary to cover the whole specimen. The limb bones yielded 1800 images with 5.33328759 magnification and 0.03750032 mm voxel size; for the axial skeleton and osteoderms we obtained 1800 images with 4.65113026 magnification and 0.04300030 mm voxel size. Raw data from each scan was imported, processed and segmented with a 3D Slicer 4.9.0-2018 (Fedorov *et al.*, 2012) and ImageJ Fiji 1.52i (Schindelin *et al.*, 2012). The 3D models obtained were visualized, analysed, repositioned and rendered with MeshLab v.2016.12 (Cignoni *et al.*, 2008).

OTHER MATERIAL ANALYSED

Knoetschkesuchus guimarotae (Fig. 8A–D): This material presents two institutional abbreviations because the material was returned from IPFUB (Germany) to MG/LNEG (Portugal); IPFUB Gui Croc 8246 (MG/LNEG 26244); IPFUB Gui Croc 7461 (MG/LNEG 26162); IPFUB Gui Croc 8015 (MG/LNEG 26214); IPFUB Gui Croc 73? (MG/LNEG?); IPFUB Gui Croc 7571 (MG/LNEG 259??); IPFUB Gui Croc 8226 (MG/LNEG 26237); IPFUB Gui Croc 8225 (MG/LNEG

25962); IPFUB Gui Croc 7650 (MG/LNEG 26194); IPFUB Gui Croc 7472 (MG/LNEG 26173); IPFUB Gui Croc 8031 (MG/LNEG 26217); IPFUB Gui Croc 7424 (MG/LNEG 26150); IPFUB Gui Croc 7465 (MG/LNEG 26166); IPFUB Gui Croc 7563 (MG/LNEG 26181); IPFUB Gui Croc 7470 (MG/LNEG 26171); IPFUB Gui Croc 8227 (MG/LNEG 26238); IPFUB Gui Croc 8125 (MG/LNEG 26226). *Goniopholis baryglyphaeus* (Fig. 8E): MG/LNEG 26027; IPFUB Gui Croc 1/48 (MG/LNEG 26115); Gui Croc 1/49 (MG/LNEG 26026). *Anteophthalmosuchus escuchae* (Fig. 8F): (MPZ) CCB-1. *Anteophthalmosuchus hooleyi* (Figs 8G, 10B): IRSNB R47. *Bernissartia fagesii* Dollo, 1883 (Fig. 10C): IRSNB R46 / R1538. *Theriosuchus pusillus* (Fig. 9A–B): BMNH 48216. *Pholidosaurus purbeckensis* (Fig. 10E): BMNH R3494. *Amphicotylus lucasii* (Fig. 9C): AMNH 5766. *Eutretauranosuchus delfsi* Mook, 1967 (Fig. 9D): USNM 5836.

RESULTS

SYSTEMATIC PALAEONTOLOGY

ARCHOSAURIA COPE, 1870

CROCODYLOMORPHA HAY, 1930 (*SENSU* WALKER, 1970)

CROCODYLIFORMES HAY, 1930

MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983

NEOSUCHIA GERVAIS, 1871 (*SENSU* BENTON & CLARK, 1988)

GONIOPHOLIDIDAE COPE, 1875

cf. Goniopholididae (unidentified)

Specimen: A partial skeleton, ML2555, that consists of 13 dorsal osteoderms, three ventral osteoderms, four limb osteoderms, six dorsal vertebrae, four thoracic ribs, the distal part of the left femur and proximal parts of the left tibia and fibula. Most of the elements are preserved in articulation, although in some of the bones there is also a slight post-mortem displacement and dorsoventral deformation.

This small size (around 1.2 m long) neosuchian crocodylomorph was assigned to Goniopholididae because of the presence of amphicoelous vertebrae, polygonal ventral osteoderms and two rows of paravertebral osteoderms that are twice as wide as they are long, with an internal angle of around 150° between each pair, 'peg and groove' articulations, dorsal surfaces without ornamentation in the area of overlap with the anterior osteoderm, lateral parts ventrally deflected between 58° to 68°, anteroposterior dorsal bulge (rather than a crest) and shallow ventral

crest with projection in the anterior margin of the osteoderm.

Age and horizon: Lourinhã Formation, Portugal. Kimmeridgian–Tithonian (Late Jurassic, about 150 Mya).

Description

Vertebrae: Six dorsal vertebrae in anatomical articulation were preserved. Three of them are mostly complete (Fig. 3A–C) and the other three are fragmentary (Fig. 3D, E). From the posteriormost vertebra, only part of the left prezygapophysis and a small fragment of the neural spine were preserved, being so fragmentary that it was not included in Figure 3. These vertebrae have been identified as part of the posterior thoracic and lumbar region of the skeleton (see Remarks).

Only the centra of three vertebrae were preserved (Fig. 3A–C), with one of them fully complete (Fig. 3B). All centra are amphicoelous with a shallow, central depression. In anterior view, the articular surface of the centrum is subcircular and gently concave, and is almost as tall (7.1 mm) as it is wide (8.5 mm) (Fig. 4C). The posterior articular surface is also subcircular in outline, gently concave, with almost identical dimensions as the anterior surface but just slightly taller (7.3 mm) (Fig. 4D). The anteriormost preserved centrum seems to have a slightly different contour to its posterior surface (Fig. 3C), being a little wider in the dorsal region than in the ventral one, although its proportions are practically identical to other vertebrae, with a maximum height of 7.4 mm and a width of 8.3 mm. The anteroposterior length in the complete centrum is 14.6 mm, making the centrum almost twice as long as it is wide. The ventral and lateral surfaces of the centra are concave, giving them the typical hourglass shape (Fig. 4F, G). There are no kinds of structures on the ventral and lateral surfaces of the centra, such as crests, grooves, hypapophysis or parapophysis, making the centra smooth.

The neurocentral suture cannot be distinguished clearly in the external surface, but the micro-CT images allow us to see that the vertebrae are not totally fused. In addition, it can also be observed how all the vertebrae are strongly vascularized, with a thin cortex (Fig. 5A–C). The neural canal is relatively large, its diameter one-third smaller than the centrum. In anterior view, the neural canal is subelliptical, being wider (6.3 mm) than it is tall (4.1 mm). In posterior view, the shape and proportions are almost the same, although the neural canal is slightly bigger, measuring 4.5 mm high by 6.9 mm wide. Within the ventral surface of the neural canal (or the dorsal surface of the centrum) there is a deep longitudinal groove that fades until it disappears near the anterior and posterior canal openings. This groove gives the mid-cross-section of the neural canal an inverted teardrop morphology. This groove has also been observed in other goniopholidids, such as *Dakotasuchus* (Frederickson *et al.*, 2018).

The dimensions and orientation of the zygapophyses are practically the same in all preserved vertebrae. The prezygapophyses are dorsally elevated with respect to the dorsal surface of the transverse processes and supported on stout pedicles. In dorsal view, the articular surfaces of the prezygapophyses are oriented anterolaterally, ovate in outline, completely flat and have approximately the same dimensions and proportions as the postzygapophyses. The anterior margin of the prezygapophyses slightly surpasses and overhangs the articular surface of the centrum. This margin is straight and almost perpendicular to the sagittal plane. The prezygapophyses are separated along the midline by a strongly concave area representing an almost absent intraprezygapophyseal shelf. At the intersection of this reduced shelf, at the base of the anterior margin of the neural spine, there is a well-developed subcircular foramen. In the vertebra with all the zygapophyses preserved (Figs 3B, 4C–G), the intraprezygapophyseal width (between the lateral margins of the prezygapophyses) is 18.5 mm, a distance almost identical to the intrapostzygapophyseal width (18.5 mm) and the intrazygapophyseal length (19 mm). Consequently, all of the zygapophyses form a quadrangular perimeter in dorsal view (Fig. 4E). In anterior view, the angle between the articular surface of the prezygapophysis and the axial plane is about 70° (Fig. 4C), planar and oriented almost in the horizontal plane. The same angle is observed in the postzygapophyses.

The postzygapophyses and prezygapophyses are connected by rounded and well-marked suprazygapophyseal ridges that intersect at the base of the neural spine, exhibiting an x-shaped morphology in dorsal view (Fig. 4E). The postzygapophyses are dorsally raised with respect to the prezygapophyses, so that the articular surface of the prezygapophyses of one vertebra coincide in the same plane with the postzygapophyses of the previous vertebra. The pedicles that connect the postzygapophyses with the centrum are slenderer than those observed in the prezygapophyses. The postzygapophyses are posterolaterally oriented and, in ventral view, the contour of the articular surfaces (Fig. 4F) is similar to that which is present in the prezygapophysis (Fig. 4E), although the articular surfaces of the postzygapophyses are slightly concave rather than flat. The posterior margin of the postzygapophyses is convex, and surpasses and overhangs the articular surface of the centrum, being much more posteriorly displaced than the prezygapophyses are anteriorly. In dorsal
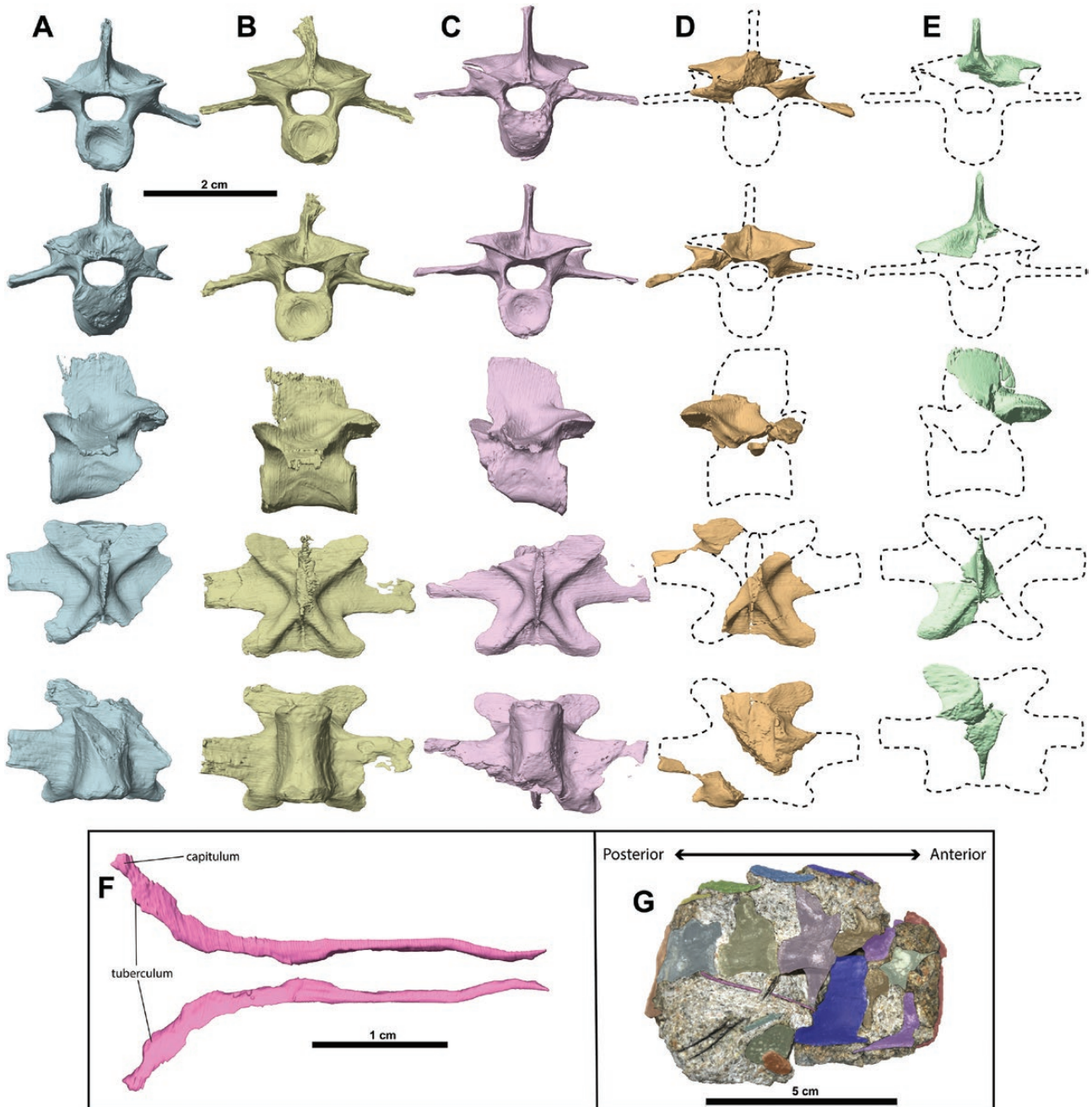
Figure 3. Three-dimensional models of the axial skeleton of ML2555. A–E, vertebrae in anterior, posterior, left lateral (vertebra D in right lateral), dorsal and ventral views (from top to bottom). F, thoracic rib in lateral (top) and medial (bottom) views. G, photograph of the articulated skeleton in ventral view and the position of each axial bone.

view, the area that connects both postzygapophyses is slightly ventrally bent and the posterior concavity is smoother than in the prezygapophyses. Therefore, the intrapostzygapophyseal shelf is much more developed (Fig. 4E–F). On the dorsal surface of this shelf there is a sagittally oriented, longitudinal groove that connects with the postspinal fossa located at the base of the posterior margin of the neural spine. This fossa

is dorsoventrally elongated, teardrop-shaped, and has its lateral margins formed by two rounded ridges with two associated lateral depressions (Fig. 4D).

In cross-section, the transverse processes are subelliptical, horizontal and dorsoventrally flattened, with the ventral margins slightly concave near their lateral ends. In dorsal and ventral views, they are approximately twice as wide (mediolaterally) as they
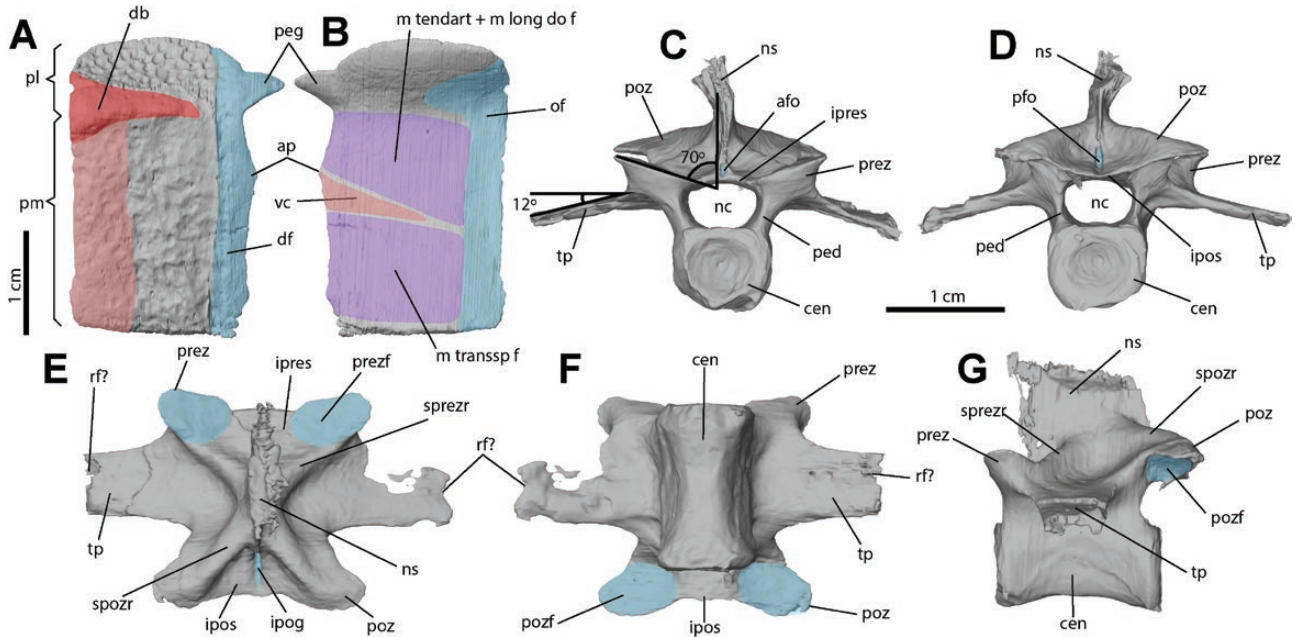
Figure 4. Anatomical details in osteoderms and vertebrae of ML2555. A–B, dorsal osteoderm in dorsal (A) and ventral view (B). C–G, thoracic vertebra in anterior (C), posterior (D), dorsal (E), ventral (F) and lateral (G) views. Anatomical abbreviations: afo., foramen; ap., anterior process; db., dorsal bulge; cen., centrum; df., downlapping facet; ipog., intrapostzygapophyseal groove; ipos., intrapostzygapophyseal shelf; ipres., intraprezygapophyseal shelf; m tendart. + m long do f., M. tendinoarticularis and M. longissimus dorsi insertion facets; m transsp f., M. transversospinalis Group insertion facet; nc., neural canal; ns., neural spine; of., overlapping facet; ped., pedicle; peg., peg articulation; pfo., postspinal fossa; pl., lateral part; pm., medial part; poz., postzygapophysis; pozf., postzygapophysis facet; prez., prezygapophysis; prezr., prezygapophysis ridge; prezf., prezygapophysis facet; rf., rib facet; spozr., suprapostzygapophyseal ridge; sprezr., supraprezygapophyseal ridge; tp., transverse process; vc., ventral crest.

are long (anteroposteriorly). Although all preserved individual transverse processes display a similar length (roughly 5.7 mm), their widths vary from approximately 12 mm in the anteriormost (Fig. 3C) to approximately 10 mm in the posteriormost (Fig. 3A). The ventral inclination of the transverse processes, with respect to the horizontal plane, also varies in the vertebral series, ranging from almost horizontal in the anterior vertebra (Fig. 3C), to becoming progressively inclined in the middle vertebra (12°) (Figs 3B, 4C) and the posterior vertebra (25°) (Fig. 3A). There is no anterior or posterior inclination of the transverse processes, making them almost perpendicular to the sagittal axis. In the best-preserved transverse processes, there are no clear diapophyses or parapophyses for the insertion of the ribs. However, in these transverse processes, a slight concavity in the anterolateral margin is observed (Fig. 4E, F). Nevertheless, whether this concavity was produced by rupture or is a real structure cannot be determined with certainty.

The three most complete vertebrae and the anteriormost vertebra preserve their neural spines, all having the same morphology (Fig. 3A–C, E). They are thin, relatively dorsoventrally short and

anteroposteriorly long, with a maximum length (11.5 mm) similar to their maximum height (9.7 mm). However, although the spines are anteroposteriorly long, they never exceed the anterior or posterior margins of the vertebral centra. In lateral view, the anterior margin of the base of the neural spine is concave (coinciding where the previously mentioned subcircular foramen is located), and then begins to ascend vertically with a slight anterior inclination until it reaches the maximum height. The anterior half of the top of the neural spine is flat and horizontal, forming a right angle with the anterior margin, while the posterior half is more curved and convex. The posterior margin is also curved and convex and becomes abruptly concave towards the base where the postspinal fossa is located. In anteroposterior view, the spines have a relatively constant width, although a slight lateromedial thickening around the anterior half of the top is also visible.

Remarks: Much evidence indicates that these vertebrae correspond to the posteriormost thoracic and lumbar regions. Apart from the evidence provided by the osteoderms, the vertebrae themselves have a series of characters that also point to this hypothesis.
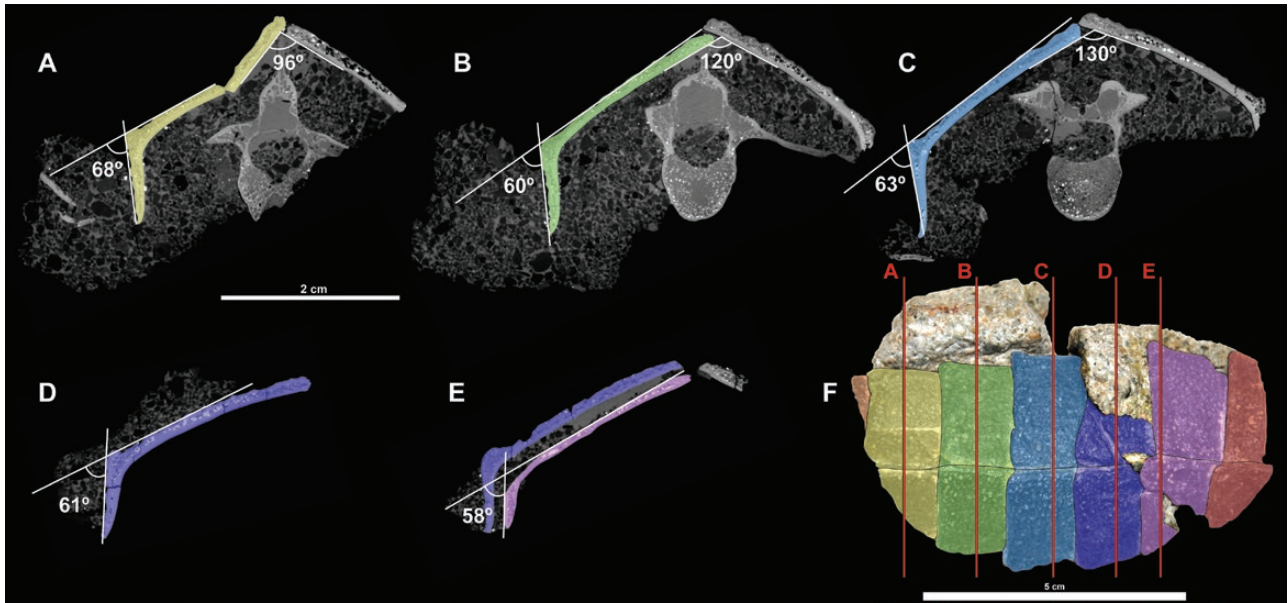
Figure 5. A–E, cross-section images of ML2555 specimen obtained with micro-CT scan. F, location of each cut thorough the skeleton.

The presence of vertebrae with an almost identical distance between the tips of the zygapophyses, longer and wider than in any other cervical or dorsal vertebrae, is typical from the lumbar region (Lauprasert *et al.*, 2007). In addition, the presence of an almost horizontal articular surface of the zygapophyses (angle of about 70° to the median plane) is also typical from the posterior region of the trunk (Schwarz & Salisbury, 2005; Puértolas-Pascual *et al.*, 2015a). Also, the lack of hypapophyses and the presence of anteroposteriorly broad neural spines are typical from these regions.

Relatively short, flat, wide and slightly ventrally inclined transverse processes, without well-marked or no articulation facets, are typical of the last thoracic and lumbar vertebrae (Puértolas-Pascual *et al.*, 2015a). The last thoracic and lumbar vertebrae are similar, the main difference being that lumbar vertebrae do not bear any ribs, resulting in the absence of diapophyses or parapophyses on the transverse processes (Hoffstetter & Gasc, 1969; Gomes de Souza, 2018). Complete transverse processes only have been preserved in two of the vertebrae, and neither of them exhibit clear articulation areas for the ribs. However, it is true that both vertebrae present a slight irregular concavity in the anterior lateral margin of the transverse processes. If this concavity is a real structure, it would be an articulation facet for the ribs, and they would, therefore, be the last vertebrae from the thoracic region. If the concavity is a product of breakage, and there is no articulation surface, they would be the first lumbar vertebrae.

Ribs: Four fragments and one complete rib have been preserved. The only rib informative enough to be described is the complete one (Fig. 3F). This rib could be in anatomical association, since it seems to articulate with the diapophysis of a vertebra. Although it could be articulated, it is clear that it has undergone some displacement and rotation from its original position (see 3D models in Supporting Information, S1 and S2). Part of the rib surface was already exposed to subaerial conditions when it was recovered, so some areas are slightly eroded.

This rib is relatively long (33.5 mm), slender, curved and has a distinct capitular facet. There is a tuberosity in the proximal region that probably corresponds to the tubercular facet, and is reduced (Fig. 3F). The proximal region is flattened in cross-section, while the distal region becomes thinner and cylindrical. The proximal half is curved and irregular due to erosion. The distal half is almost straight, and the distalmost end is tapering into a tip, instead of thickening.

Remarks: The proximal end of the most complete rib (Fig. 3F) almost touches the lateral end of the left transverse process of one of the anterior vertebrae (Fig. 3C), such that they could have been associated. It is obvious that this rib is not exactly in its original position (see 3D model in Supporting Information, S1). Therefore, most probably, the medial part of the overlying osteoderm was pushing the rib ventrally throughout taphonomical deformation, causing it to rotate over its axis, but maintaining its anteroposterior position.

Ribs with reduced or almost non-existent tubercular facets, and with an acute end (rather than thickened), are typical from the most posterior thoracic region. Therefore, the presence of this kind of rib would indicate that its associated vertebra is probably the last or one of the last thoracic vertebrae.

The distal half of the left femur has been preserved (Fig. 6A–E), with a length of 51 mm. The femur was broken approximately around the mid-region of the shaft. The femur is slender, rather than massive. Based on regression equations (Farlow *et al.*, 2005) and comparisons with femora of similar proportions and morphology from other derived neosuchians (e.g. *Sunosuchus junggarensis*, (Wu *et al.*, 1996a); *Anteophthalmosuchus hooleyi*, Martin *et al.*, 2016; *Bernissartia fagesii*, pers. obs.), we estimate a total length of about 90 mm. In anterior/posterior view, it has a maximum distal width at the condyles of 18 mm, and a minimum width of 8 mm in the middle section of the shaft. In lateral/medial view, the maximum length of the condyles is 13 mm. The minimum length of the shaft cannot be determined due to the erosion of the anterior surface of the shaft, although an oval cross-section can

be interpreted as being slightly wider than long. The lateral and posterior margins of the femur are curved, and a typical sigmoidal morphology can be deduced. The posterior surface of the shaft is flat, and a more convex shaft can be inferred from the anterior surface. No structures or muscle insertions, such as the fourth trochanter, have been preserved in the shaft, because these structures are usually placed in the proximal half.

The distal end of the femur bears a lateral and a medial condyle that articulates with the tibia and the fibula. The lateral condyle is larger, and more developed laterally and distally than the medial condyle. In anterior view, the surface between the two condyles is smooth and the intercondylar fossa is shallow and restricted to the distalmost area of the femur. A smooth medial supracondylar crest in the medial condyle can be observed. In posterior view, the two condyles are equally expanded in the posterior direction, although the lateral condyle is slightly enlarged proximodistally and laterally. On the posterior surface, the two condyles are separated by a deep popliteal fossa. The angle formed between the two condyles is 100°. On the lateral margin of the left condyle there is a flattened articular surface for the insertion of the fibula. The
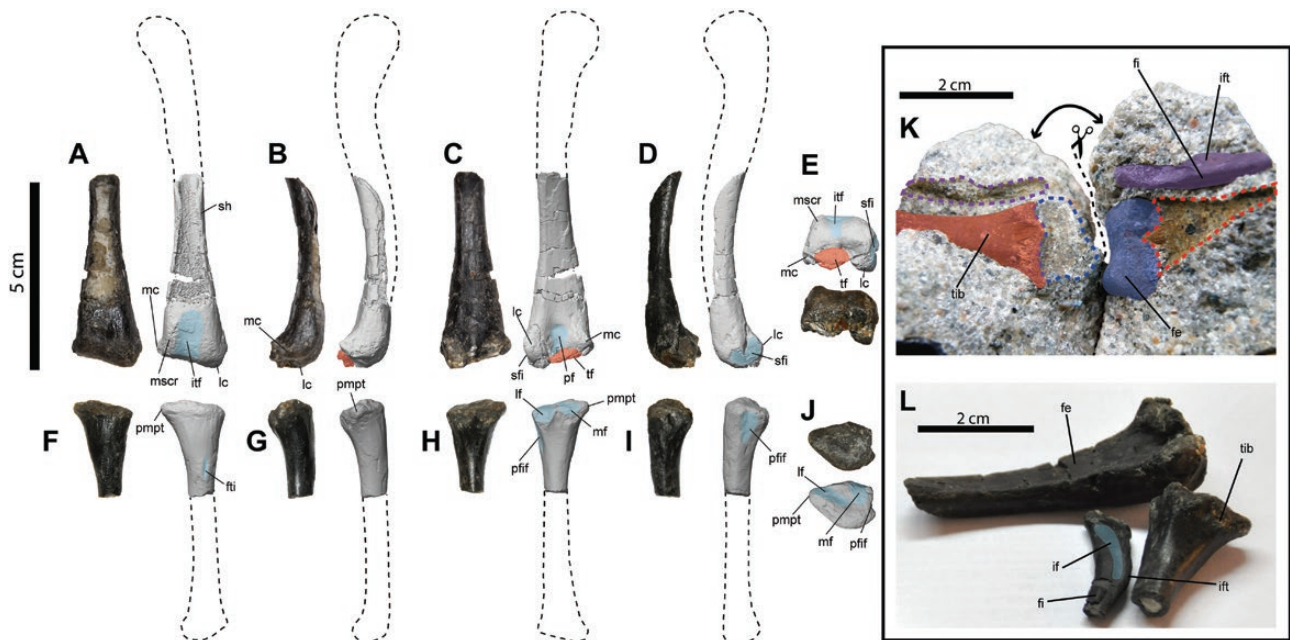

Figure 6. Pictures and 3D models of the hindlimb skeleton of ML2555. A–E, distal end of the left femur in anterior (A), medial (B), posterior (C), lateral (D) and distal (E) views. F–J, proximal end of the left tibia in anterior (F), medial (G), posterior (H), lateral (I) and proximal (J) views. K, view of the divided block containing the hindlimb bones before the preparation (bones are in colour and their respective moulds are in dashed line). L, femur, tibia and fibula after the preparation. Anatomical abbreviations: fe., femur; fi., fibula; fti., M. flexor tibialis internus; if., iliofibularis facet; ift., iliofibularis trochanter; itf., intercondylar fossa; lf., lateral facet; mc., medial condyle; mf., medial facet; mscr., medial supracondylar crest; pf., popliteal fossa; pfif., proximal fibular facet; pmpt., posteromedial proximal process of the tibia; sfi., articular surface for fibula; sh., shaft; tf., tibial fragment; tib., tibia.

entire distal surface is more rugose than the shaft surface. Due to the micro-CT scan, it was possible to observe that the entire shaft is completely hollow, but the internal distal articular area is dominated by the presence of spongy or trabecular bone tissue, making the cortex much thinner than in the shaft.

Tibia: Only the proximal end of the left tibia has been preserved (Fig. 6F–J), with a length of 26 mm. The tibia possesses a straighter shaft than the femur, with an expansion at the proximal end. Following the same methodology as for the femur, we were able to estimate a total tibial length of about 65 mm. It has a maximum proximal width of 16 mm and a maximum proximal length of 12 mm, and is approximately twice as wide and long as the shaft. In cross-section, the shaft is ovate, with its major axis measuring 6.8 mm and its minor axis 5.7 mm. The major axis is not oriented in the same direction as the proximal end of the tibia, making it slightly oblique. The anterior and lateral surfaces of the tibia are straight, while the posterior and medial surfaces are concave, and curved slightly posteriorly from the shaft.

Proximally, the articular surface of the tibia is broad, with a triangular outline, and bears a lateromedially oriented condylar groove. This proximal triangular surface is medially pointed in the posteromedial proximal process of the tibia, posteriorly straight, anteriorly convex and laterally concave. On the lateral surface of the tibial head, a proximodistal shallow groove corresponds to the proximal fibular facet. Near the proximal end, on the anterior surface of the shaft, there is a shallow proximodistal scar that could correspond to the insertion for the flexor tibialis internus muscle. In posterior view, the proximal end of the tibia has two symmetrical breakages that coincide with the area of the facets for attachment with the distal condyles of the femur. Therefore, the femur still has two small fragments from the surface of the tibia stuck to the condyles (see pink fragment in Fig. 6B, C, E). As we already observed in the femur, the whole shaft is completely hollow, with its cortex relatively thick compared to the thin cortex observed in the proximal end, where the spongy bone tissue dominates.

Fibula: Together with the femur and the tibia, the proximal end of the left fibula is also preserved in articulation. Unfortunately, the fibula is now missing. Nevertheless, some characters can be observed from the photographs (Fig. 6K, L) taken during the preparation process before it was lost. The preserved proximal fragment of the fibula has approximately the same length as the fragment of the tibia, and it is much slenderer. The shaft is subcircular in cross-section, while the distal end is flattened mediolaterally. The

proximal end of the fibula is slightly anteroposteriorly expanded, with a concave posterior margin curved posteriorly and slightly laterally away from the shaft. The medial surface of its proximal end is in contact with the proximal fibular facet of the tibia and the lateral facet of the left condyle of the femur. On the anterolateral margin of the proximal end of the fibula, the iliofibularis scar is visible. Posterior to this scar, there is a rounded crest that corresponds to the iliofibularis trochanter.

Dorsal osteoderms: Thirteen dorsal or paravertebral osteoderms from the presacral region of the trunk were preserved, three of them complete (Fig. 7B, C, E), five partially complete (Fig. 7D, F, I–K) and five fragmented (Fig. 7A, G, H, L, M). All osteoderms are articulated, although most of them have undergone slight taphonomic deformation. This deformation consists of a slight ventral displacement of the lateral margin of the osteoderms, so that the ventral angle formed between each pair of osteoderms along the sagittal axis has decreased slightly from the original position (see 'Bracing system reconstruction' section).

The dorsal osteoderms are characterized by having a rectangular shape, approximately twice as wide as they are long. All the osteoderm margins are straight, with the exception of the lateral margin that is slightly rounded and convex. This lateral margin is inclined ventrally, allowing for distinguishing this segment, called lateral part [*parte lateralis* according to Salisbury & Frey (2001)], from the main body of the osteoderm, called medial part [*parte medialis* according to Salisbury & Frey (2001)] (Figs 4A, 7). The lateral part is ventrally deflected around 58° to 68° with respect to the plane formed by the medial part (Fig. 5). The anteroposterior length of each osteoderm is similar along the preserved paravertebral shield, and between 16 and 17 mm. However, their lateromedial width varies slightly, depending on its position along the sagittal axis. This width varies from 19.1 mm in the posteriormost osteoderm (Fig. 7A), to a maximum width of 22.6 mm in one of the osteoderms located in the middle region (Fig. 7E). Anteriorly to this osteoderm, the width decreases again to 22.3 mm in the osteoderm located in the anteriormost position (Fig. 7G). These width measurements refer only to the medial part, so the lateral part was not taken into account due to two reasons: this lateral margin was only fully preserved in four osteoderms (Fig. 7B–E) and the difficulty of taking measurements from photographs of other taxa for comparisons (the real width of the lateral margin is diminished in pictures, because it is not in the same plane as the rest of the osteoderm). In any case, in the four osteoderms where the lateral margin was preserved, their widths were the same (around
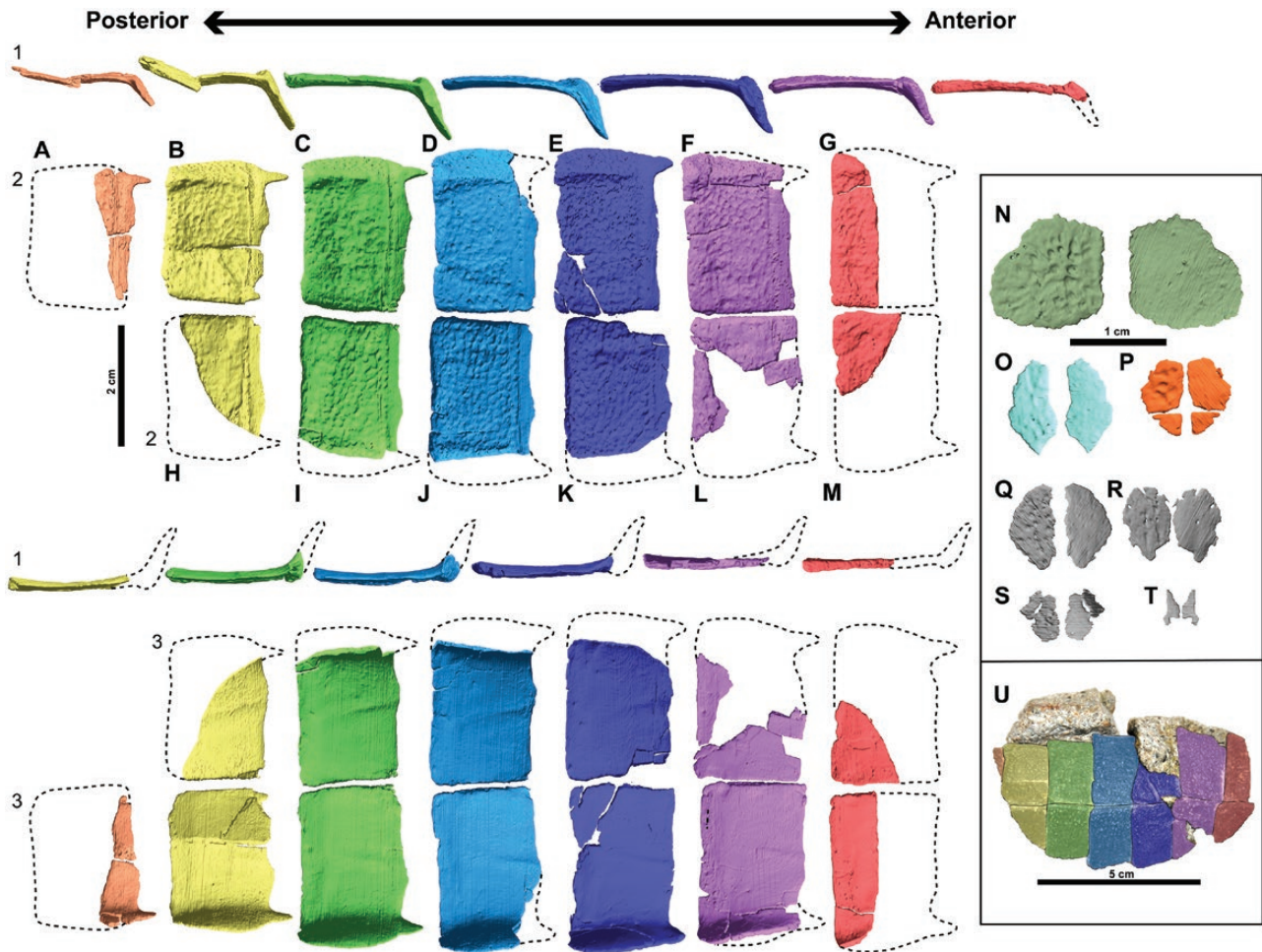
Figure 7. Three-dimensional models of the dermal armour of ML2555. A–M, dorsal osteoderms in anterior view (1), dorsal view (2) and ventral view (3). N–P, ventral osteoderms in dorsal (left) and ventral (right) views. Q–T, limb osteoderms in dorsal (left) and ventral (right) views. U, photograph of the articulated skeleton and the position of each osteoderm.

9.5 mm), so the actual total width of each osteoderm (medial part + lateral part) varies from 30.39 mm (Fig. 7B) to 32 mm (Fig. 7E).

In other taxa with this kind of bracing system, the internal angle between contralateral osteoderms from each transverse row was estimated between 160° and 150° (Fig. 10B) (Salisbury & Frey, 2001). Although this skeleton is three-dimensionally preserved, it has undergone some deformation, and the osteoderms are slightly ventrally inclined from their original position. With this deformation, the angles between contralateral osteoderms from each transverse row vary from 93° in the posterior positions with a greater deformation, to 135°, in the anterior positions, where less deformation is observed. Nevertheless, a repositioned 3D model of the skeleton has been done, in which we tried to restore each osteoderm to its original position. The results obtained show us that these angles were similar to those proposed by Salisbury & Frey (2001)

(see: Fig. 10G; 'Bracing system reconstruction' section; Supporting Information, S2).

Most of the dorsal surface of the osteoderms is irregularly ornamented with deep oval to circular pits ranging from 0.2 mm to 1.9 mm and an average diameter of 0.8 mm. In the dorsal surface, the entire anterior margin of the osteoderms lacks ornamentation. This smooth margin comprises around 20% of the total width of the scute and corresponds to the contact surface with its anterior overlapping osteoderm. In this anterior articulation margin, there is a slight convexity or anterior projection that coincides with the position of a crest on the ventral surface of the osteoderm (Figs 4, 7). This convexity is located approximately in the middle part of the osteoderm or slightly laterally located. Between the medial part and the lateral part there is a flattened conical and non-ornamented spine-like anterior process that articulates in a groove of similar outline located in the ventral surface of

the preceding osteoderm. This type of articulation is usually referred to in the literature as 'peg and groove', 'peg and socket' or 'stylofoveal' articulation (e.g. Wu *et al.*, 1996; Salisbury & Frey, 2001; Lauprasert *et al.*, 2007; Puértolas-Pascual *et al.*, 2015a). In the area where the lateral part is ventrally deflected, an anteroposterior bulge, rather than a crest, is developed. This structure begins just posterior to the anterior, smooth, overlapping margin as a shallow ridge, and begins to expand mediolaterally and dorsally toward the posterior margin of the osteoderm, where it forms a large protuberance (Figs 4, 7). This bulge is more developed in the osteoderms located in a more posterior position. The micro-CT scan shows that this structure is much more vascularized than the main body of the osteoderm (Fig. 5). The entire posterior margin of the osteoderms is slightly elevated, coinciding with the area of overlap with the posterior osteoderm (Fig. 4A). There are smooth suture crenulations in the medial margin of the osteoderms, and the overall contour is interlocking with its medially paired scute.

The ventral surface lacks ornamentation, but some structures can be observed. The entire posterior margin is slightly depressed, coinciding with the area of overlap with the posterior osteoderm (Fig. 4B). The width of this lateromedial depression is coincident with the contact surface between both osteoderms. In addition, a greater depression in the area where the anterior spine-like process of the posterior osteoderm fits, is also observed (Fig. 4A, B). As already noted in the previous paragraph, coinciding with the slight convexity of the anterior margin, an anteroposterior crest on the ventral surface is observed. This ridge manifests as more pronounced in the anterior margin, where is posteromedially directed, until it reaches the middle part of the osteoderm, where it fades. This ventral crest is indicative of the division of two insertion zones for the epaxial musculature.

Remarks: These kinds of osteoderms are present in crocodylomorphs with a closed paravertebral armour (Fig. 10B, G) (Salisbury & Frey, 2001). This bracing-system mechanism consists of only two sagittal rows of rectangular paravertebral osteoderms imbricated along their entire length, with the lateral margins ventrally projected and the presence of 'peg and groove' articulations (e.g. Wu *et al.*, 1996a; Lee, 1997; Salisbury & Frey, 2001; Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2007; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015a; Martin *et al.*, 2016; Frederickson *et al.*, 2017; Ristevski *et al.*, 2018).

In taxa with this kind of bracing system, it has been observed that there is a progressive width reduction of the osteoderms from the mid-region of the trunk towards the posterior region. In addition, the ventral

inclination of the lateral parts also varies between 50° and 60° in the lumbar region, and is around 70° in the sacral region (Salisbury & Frey, 2001). Therefore, the reduction of the width of the osteoderms toward more posterior positions, and the presence of an inclination angle of the lateral parts that varies between 68° and 58° (Fig. 5), allow us to assign the partial skeleton ML2555 to the posterior and lumbar region of the trunk.

Ventral osteoderms: At least one complete ventral or gastral osteoderm (Fig. 7N) is identified in the lateroventral region of the skeleton. Close to this osteoderm, there are two partial scutes (Fig. 7O–P) that may correspond to broken fragments of the ventral armour. Apart from their closeness and similar position to the complete ventral osteoderm, their fragmentary nature makes their anatomical assignation difficult. The description will thus mainly focus on the most complete osteoderm (Fig. 7N).

The osteoderm is flat, equidimensional and slightly quadrangular to pentagonal, with overall dimensions of 11.3 mm by 11.2 mm. It has three fairly straight margins that form right angles between them, and other edges that are more rounded and convex. In the straight margins, there are crenulations that could correspond to suture areas with other osteoderms. Unlike the paravertebral armour, where the ornamented surface is on the dorsal face, all of these osteoderms have their ventral area ornamented with pits and grooves, with a totally flat and smooth dorsal surface. The diameter of these pits varies from 0.3 mm to 1.6 mm with an average diameter of 0.87 mm, similar to the dorsal scutes. The ornamentation is more concentrated in the central area of the osteoderm, with the margins being much smoother. Osteoderms are totally flat, none have ridges or bulges.

Remarks: It has been observed that this morphology differs totally from the osteoderms observed in the dorsal region of the trunk, therefore other possible locations for these scutes are in the ventral armour, the dorsal region of the neck and tail, or the limbs. In crocodylomorphs with this kind of bracing system, the osteoderms from the dorsal region of the tail have morphologies not observed in the preserved scutes of this specimen. The osteoderms from the tail tend to be rectangular, triangular to oval and mediolaterally narrower than those observed in the trunk, with overlapping surfaces in the anterior margin, without 'peg and groove' articulation, and strongly keeled (Wu *et al.*, 1996a; Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2007; Schwarz-Wings *et al.*, 2011). It can also be ruled out that they are osteoderms from the neck region, since these neck scutes tend to be smaller,

ellipsoidal in shape and keeled (Wu *et al.*, 1996a; Lee, 1997; Lauprasert *et al.*, 2007; Puértolas-Pascual *et al.*, 2015a). They also differ from those present in the limbs (see next 'Limb osteoderms' section).

Therefore, several characters suggest that these osteoderms belong to the ventral armour. Most likely, the straighter margins correspond to suture areas with other ventral osteoderms, while the more convex margins would be free of articulation with other scutes. The presence of a more crenulated and irregular margin in the straight edges would also point to this hypothesis. This could indicate that it is an osteoderm from the external margins of the ventral armour, since the osteoderms from internal positions show sutures on all of their margins and are more polygonal, usually hexagonal (e.g. Wu *et al.*, 1996a; Salisbury & Frey, 2001; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015a; Martin *et al.*, 2016). This hypothesis is consistent with its lateroventral position relative to the rest of the skeleton and the ornamented surface facing down. Furthermore, this morphology is similar to that of osteoderms located in the margins of the ventral armour observed in other goniopholidids, such as *Sunosuchus junggarensis* Wu *et al.*, 1996, *Anteophthalmosuchus hooleyi* Salisbury & Naish, 2011 (Martin *et al.*, 2016) and *Anteophthalmosuchus escuchae* Buscalioni *et al.*, 2013 (Puértolas-Pascual *et al.*, 2015a).

Limb osteoderms: Four more osteoderms have been preserved, of which one of them seems to be complete (Fig. 7R), another is split in half (Fig. 7Q) and the other two are fragmentary and small (Fig. 7S, T). All of the osteoderms are totally flat, and from the two that are best-preserved, an elliptical outline is observed. Their dorsal surfaces are covered with subcircular pits, somewhat smaller than those observed in the dorsal and ventral scutes, with a diameter range that varies from 0.1 mm to 0.9 mm and an average diameter of 0.4 mm. These scutes lack any kind of structure such as ridges or sutural margins.

Remarks: These osteoderms probably correspond to appendicular osteoderms. All were found together and located between the preserved hindlimb and the left lateral region of the skeleton. All of this, together with their small size, flat, unkeeled and subelliptical outline, without any sutured or overlapping margins, as well smaller and less marked ornamentation, are characteristic of accessory osteoderms from the limbs that also have been found in other goniopholidids, such as *Sunosuchus junggarensis*, *Siamosuchus phuphokensis* Lauprasert *et al.*, 2007 *Anteophthalmosuchus escuchae* (Wu *et al.*, 1996a; Lauprasert *et al.*, 2007; Puértolas-Pascual *et al.*, 2015a).

DISCUSSION

COMPARISONS

Due to the incompleteness of the specimen, and the lack of bones with highly diagnostic characters, we cannot assign the skeleton ML2555 to a species or genus. The characters observed in the vertebrae, ribs and hindlimb are the typical ones present in most neosuchians, allowing some comparisons, but without great resolution in the taxonomic assignment. However, the morphology of the dermal armour offers a series of characters (Table 1) that allow a more accurate assignment.

The axial bones in ML2555 correspond to a bracing system with a closed paravertebral armour. This kind of bracing system is characterized by: only two imbricated sagittal rows of dorsal osteoderms osteoderms that are wider than they are long and divided in medial and lateral parts, 'peg and groove' articulations between osteoderms and amphicoelous vertebrae (e.g. Wu *et al.*, 1996a; Lee, 1997; Salisbury & Frey, 2001; Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2007; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015a; Martin *et al.*, 2016; Frederickson *et al.*, 2017; Ristevski *et al.*, 2018). This type of bracing system is present in protosuchians, goniopholidids and some notosuchians, sphenosuchians and atoposaurids (Salisbury & Frey, 2001; Martin, 2015). Within Neosuchia, pholidosaurids such as *Pholidosaurus* (Fig. 10B) or *Sarcosuchus* also present two rows of wider than long dorsal osteoderms with 'peg and groove' articulations. However, the dorsal scutes of Pholidosauridae lack the ventral bending in the lateral part and the spine-like anterior processes are more reduced (Fig. 10B). Of all these clades, goniopholidids and atoposaurids are the most common taxa within fossil vertebrate assemblages of the Late Jurassic of Europe. Thus, because the bones of ML2555 closely resemble that of derived neosuchians, the comparisons will mainly focus on these two clades.

Within Neosuchia, the presence of two rows of osteoderms with 'peg and groove' articulation has also been generally attributed to Goniopholididae, *Theriosuchus pusillus* (Pol *et al.*, 2009), *Knoetschkesuchus guimarotae* (Schwarz & Salisbury, 2005) and *Theriosuchus* sp. from China (Wu *et al.*, 1996b). However, the presence of anterolateral articular pegs on the dorsal osteoderms of the paratype specimen of *T. pusillus* (NHMUK PV OR 48216, Fig. 9A, B), or other specimens assigned to *T. pusillus*, is not clear or visible (Joffe, 1967; Salisbury, 2002; Tennant *et al.*, 2016b). Therefore, isolated osteoderms with this feature and assigned to *T. pusillus* most likely belong to small or juvenile individuals of Goniopholididae, such as *Nannosuchus*, which are commonly found alongside specimens of *Theriosuchus* (Clark, 1986;

Table 1. Summary of the different dermal armours among Neosuchia

Taxon / Clade	Ventral armour	Dorsal armour (rows)	Shape dorsal armour	Peg & groove	Bended lateral part	Dorsal crests / bulges	Ventral crest
Goniopholididae	Yes	2	Rectangular	Yes (big / small)	Yes	Yes	Yes / no
Pholidosauridae	Yes	2	Rectangular	Yes (small)	No	Yes	No
Dyrosauridae	Yes	2 + 4 accessory	~ square-shaped	No	No	No	No
Atoposauridae(sensu Tennant *et al*., 2016)	No	2	~ square-shaped	No	No	Yes	No
Bernissartiidae	Yes	2 + 2 accessory	Rectangular	No	No	Yes (2 crests)	No
Eusuchia	No	4 + 2 to 4 accessory	~ square-shaped	No	No	Yes	No
ML2555	Yes	2	Rectangular	Yes (medium)	Yes	Yes	Yes
Vectisuchus	Yes	2	Rectangular	Yes (medium anterior peg & small posterior peg)	Yes	Yes (2 crests)	No
Brillanceausuchus	No	2	Rectangular	No	No	Yes	No

Salisbury, 2001, 2002; Salisbury & Frey, 2001; Schwarz & Salisbury, 2005; Tennant *et al.*, 2016b).

Tennant *et al.* (2016b) also doubted the assignment of isolated osteoderms with anterior articulation pegs to *Knoetschkesuchus guimarotae* (Schwarz & Salisbury, 2005) and *Theriosuchus* sp. (Wu *et al.*, 1996b), and claimed that they probably also belong to small individuals of Goniopholididae. An in-person assessment was made of the osteoderms assigned to *K. guimarotae* (Fig. 8A–D), and whether or not they belong to *K. guimarotae* or Goniopholididae is something that we cannot confirm with certainty since they were isolated elements. Regardless of the taxonomy of these osteoderms, what could be verified is that they are different from the specimen that is the object of this study, ML2555. The main differences between the dorsal osteoderms assigned to *K. guimarotae* and ML2555 are related to the presence of a crest between the medial and lateral parts. In *K. guimarotae*, this structure is a well-marked, thin crest that runs, maintaining its thickness, from the posterior part of the peg articulation to the posterior margin of the osteoderm (Fig. 8A–C). In ML2555 and other goniopholidids, such as *Anteophthalmosuchus epikrator* Ristevski *et al.*, 2018, *A. hooleyi* (Fig. 8G), *Goniopholis baryglyphaeus* (Fig. 8E) or *Amphicotylus lucasii* Cope, 1878 (Fig. 9C), there is a protuberance rather than a thin, longitudinal crest, which is more developed in the posterior region of the osteoderm. This posterior protuberance is sharper and much more developed in *A. hooleyi* than in the aforementioned taxa, especially in the lumbar region (Fig. 8G), which is clearly different from ML2555. In contrast, the

putative goniopholidid *Vectisuchus leptognathus* Buffetaut & Hutt, 1980 has two crests on the dorsal surface (Salisbury & Naish, 2011) and in other goniopholidids, such as *Anteophthalmosuchus escuchae* (Fig. 8F), this ridge or protuberance is smooth or almost nonexistent (Puértolas-Pascual *et al.*, 2015a). Another observable difference between the osteoderms assigned to *K. guimarotae* and Goniopholididae is the degree of development of the articulation peg, which is much longer in most goniopholidids (Fig. 8E–G, 9C, D), small in *K. guimarotae* (Fig. 8A–C) and intermediate in ML2555 (Fig. 3A–M) and some taxa such as the putative goniopholidid *Vectisuchus* (Salisbury & Naish, 2011). The degree of ventral inclination of the lateral part also seems to be somewhat lower in *K. guimarotae* than in ML2555 and in other goniopholidids. The dorsal osteoderms assigned to *K. guimarotae* are also narrower lateromedially than in Goniopholididae (Figs 8, 9). The osteoderms of ML2555 have a similar length/width proportion to the broader osteoderms observed in *K. guimarotae*. However, since the osteoderms of ML2555 are from the posterior region of the trunk, and wider osteoderms would be expected in more anterior positions, the arrangement follows a similar length/width proportion to Goniopholididae. In ML2555, the posterolateral edge of the osteoderms is angled, as in most goniopholidids, and is different from *Dakotasuchus,* whose margin is curved (Frederickson *et al.*, 2017). The presence of a shallow ventral crest for the epaxial musculature in ML2555 has also been reported in the goniopholidid *A. epikrator* (fig. 21B of Ristevski *et al.*, 2018). However, the absence of a crest in other taxa with this type of bracing system
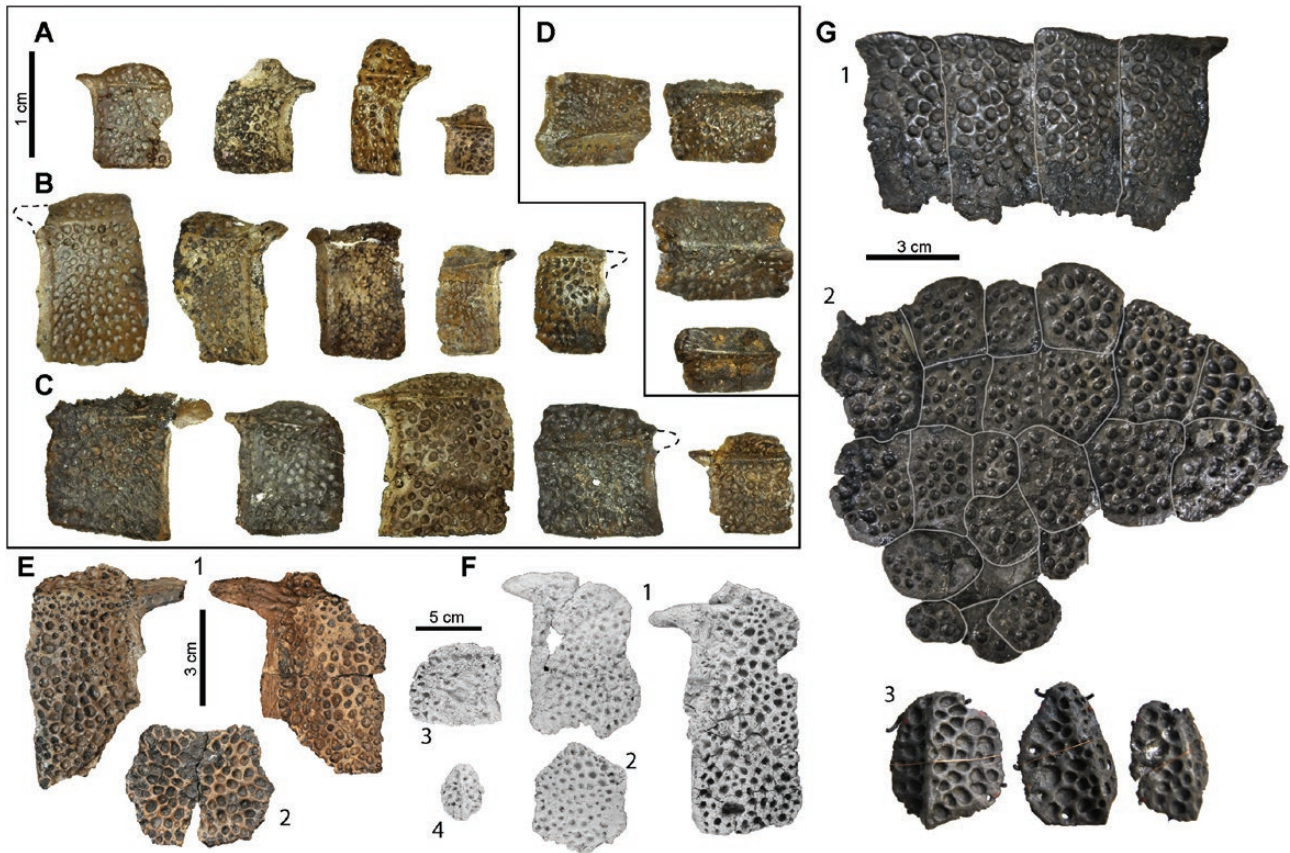
Figure 8. Osteoderms in neosuchian taxa with closed paravertebral armour. A–D, dorsal osteoderms assigned to *Knoetschkesuchus guimarotae* IPFUB Gui Croc 73–82 (MG/LNEG 25–26) (Late Jurassic, Portugal) from the anterior (A), the middle (B) and the posterior (C) regions of the trunk, and the tail (D). E, dorsal (1) and ventral (2) osteoderms of *Goniopholis baryglyphaeus* IPFUB Gui Croc 1 (Late Jurassic, Portugal) in dorsal views. F, dorsal (1), ventral (2–3) and nuchal (4) osteoderms of *Anteophthalmosuchus escuchae* (MPZ) CCB-1 (Early Cretaceous, Spain). G, dorsal (1), ventral (2) and tail (3) osteoderms of *Anteophthalmosuchus hooleyi* IRSNB R47 (Early Cretaceous, Belgium).

is probably a preservation matter, and so we should expect the presence of this structure in osteoderms with a well-preserved ventral surface.

Regarding the osteoderms from other regions of the skeleton, one of the main differences between atoposaurids and goniopholidids is the presence of ventral or gastral osteoderms in Goniopholididae. Gastral osteoderms are also common in protosuchians and sphenosuchians, but they are square or subquadrangular (Salisbury & Frey, 2001). As we already noted in the description, at least one osteoderm of ML2555 has been identified as a gastral scute. Although it does not have the typical hexagonal morphology of most ventral osteoderms in Goniopholididae, it coincides with the shape of the scutes located in the margins of the ventral armour, which is also observed in other goniopholidids, such as *A. hooleyi* (Fig. 8G), *A. escuchae* (Fig. 8F) and *Sunosuchus junggarensis* (Wu *et al.*, 1996a). Several characters allow for ruling out the placement of

this osteoderm in the region of the neck, tail or limbs. In most Neosuchia, the nuchal osteoderms are small, keeled, with oval or leaf-shaped outline (Fig. 8F), or they are similar in shape and size to those of the trunk, as in atoposaurids such as *Alligatorellus*, *Alligatorium* and the putative atoposaurid *Montsecosuchus* (Tennant *et al.*, 2016b). The ventral scute of ML2555 also differs from tail osteoderms, which are also characteristic, being triangular to elliptical in Goniopholididae (Fig. 8G) (Wu *et al.*, 1996a; Lee, 1997) or rectangular in Atoposauridae (Figs 8D, 9B). ML2555 preserves some limb osteoderms (Fig. 3O–T), which are small, elliptical and without keel, and are similar to those of the limbs of most neosuchians (Wu *et al.*, 1996a).

The vertebrae have the typical morphology present in most non-eusuchian neosuchian crocodylomorphs. The vertebral centra of ML2555 are circular in cross-section, gently amphicoelous and with an hourglass profile. The centrum diameter (height/width), in
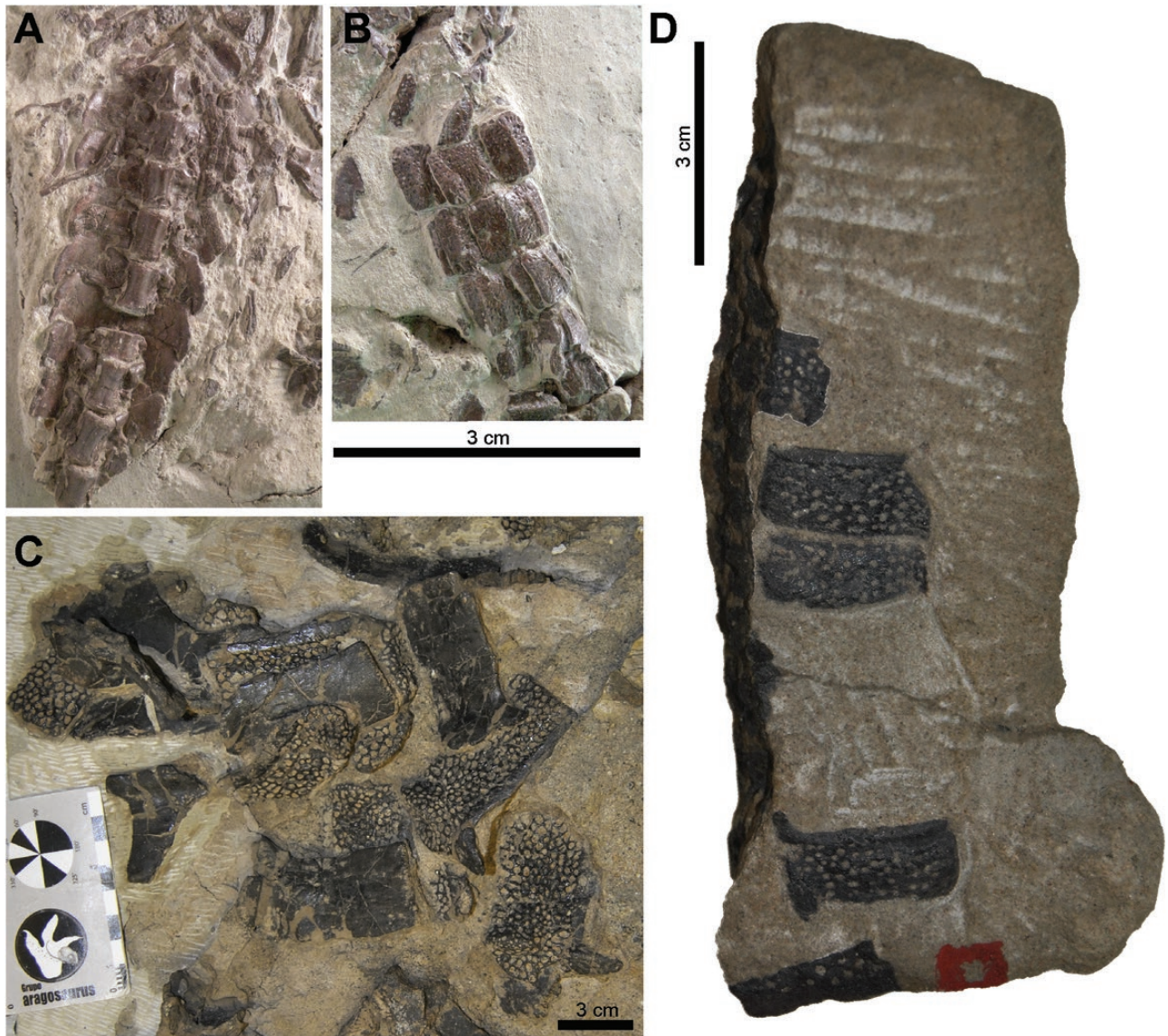
Figure 9. Osteoderms in neosuchian taxa with closed paravertebral armour. A–B, osteoderms and thoracic vertebrae (A) and tail osteoderms (B) of *Theriosuchus pusillus* BMNH 48216 (Early Cretaceous), photograph courtesy of C. A. Brochu. C, dorsal osteoderms of *Amphicotylus lucasii* AMNH 5766 (Late Jurassic, USA). D, dorsal osteoderms of *Eutretauranosuchus delfsi* USNM 5836 (Late Jurassic, USA) in dorsal view.

relation with the neural canal diameter, is smaller than in the centra observed in other goniopholidids, such as *Dakotasuchus* (Frederickson *et al.*, 2017), *A. hooleyi* (Martin *et al.*, 2016), *A. escuchae* (Puértolas-Pascual *et al.*, 2015a), *A. epikrator* (Ristevski *et al.*, 2018) and *Woodbinesuchus* (Lee, 1997). In ML2555, the overall size of the centra is more similar to that which is present in atoposaurids, such as *T. pusillus* and *K. guimarotae* (Schwarz & Salisbury, 2005), and goniopholidids, such as *G. baryglyphaeus* (Schwarz, 2002). However, this comparison should be taken with caution since the size (height/width) of the centra increases with strong

positive allometry during ontogeny, while the diameter of the neural canal does not (Ikejiri, 2015; Iijima & Kubo, 2019). This means that young or small-sized specimens (ML2555, *T. pusillus* and *K. guimarotae*) and medium-sized specimens (*G. baryglyphaeus*) would show proportionally smaller centra than larger specimens (*Dakotasuchus*, *A. hooleyi*, *A. escuchae*, *A. epikrator* and *Woodbinesuchus*). An increase in the cross-sectional area of the centra allows large and heavy crocodylomorph individuals to resist the axial loads on the trunk (Salisbury & Frey, 2001; Iijima & Kubo, 2019). The neural canal is subcircular and can
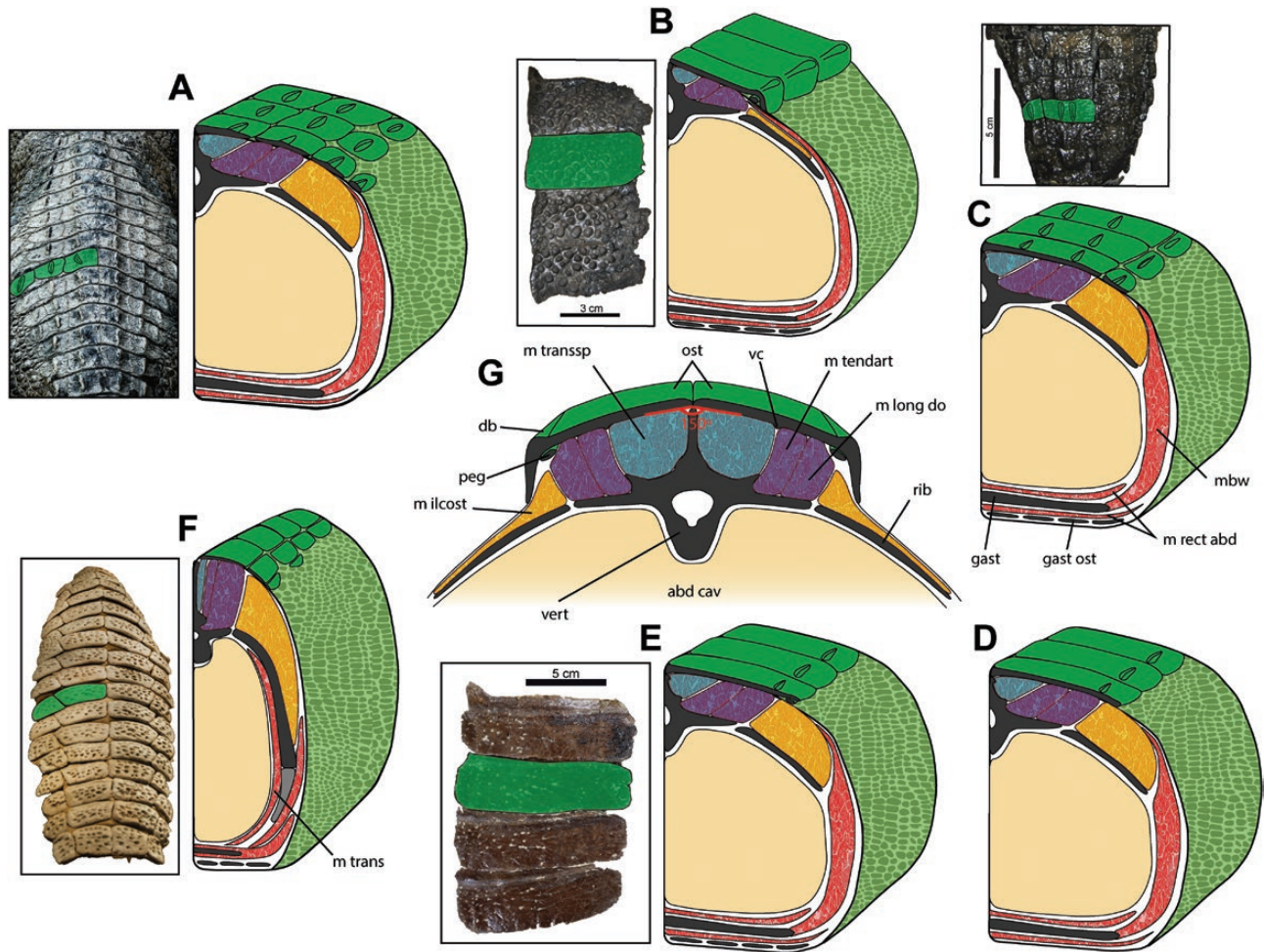
Figure 10. Main bracing systems in Crocodylomorpha including schematic block diagrams of the left-half of the posterior thoracic regions (based on: Salisbury & Frey, 2001; Schwarz-Wings *et al.*, 2009). A, eusuchian bracing system; dorsal osteoderms and corresponding diagram of *Alligator mississippiensis* (Daudin, 1802) (Alligatoridae). B, closed paravertebral armour bracing system; dorsal osteoderms (IRSNB R47) and corresponding diagram of *Anteophthalmosuchus hooleyi* (Goniopholididae). C, open paravertebral armour bracing system with sagittally segmented osteoderms; dorsal osteoderms (IRSNB R46 / R1538) and corresponding diagram of *Bernissartia fagesii* (Bernissartiidae). D, open paravertebral armour bracing system with biserial osteoderms; schematic block diagram based on *Brillanceausuchus babouriensis* (Atoposauridae?). E, open paravertebral armour bracing system with biserial osteoderms with peg articulations, and gastral osteoderms; dorsal osteoderms (BMNH R3494; Scott & Smith, 2014) and corresponding diagram of *Pholidosaurus purbeckensis* (Mansel-Pleydell, 1888) (Pholidosauridae). F, hyposaurinae-type bracing system; dorsal osteoderms of *Dyrosaurus phosphaticus* (Thomas, 1893) (Dyrosauridae), from Shanghai Natural History Museum, and schematic block diagram based on *Congosaurus bequaerti* (Dollo, 1914) (Dyrosauridae). G, closed paravertebral armour bracing system; cross-section diagram based on the specimen object of this study (ML2555). Anatomical abbreviations: abd cav., abdominal cavity; db., dorsal bulge; gast., gastralia; gast ost., gastral osteoderm; mbw., musculature of the lateral body wall; m ilcost., M. iliocostalis; m long do., M. longissimus dorsi; m rect abd., M. rectus abdominis; m tendart., M. tendinoarticularis; m trans., M. transversus; m transsp., M. transversospinalis Group; ost., dorsal osteoderms; rib., rib; peg., peg; vc., ventral crest; vert., vertebra.

be differentiated from other goniopholidids, such as *Dakotasuchus* and *Woodbinesuchus*, where it is heart-shaped (Lee, 1997; Frederickson *et al.*, 2017). ML2555 has vertebrae with a deep groove on the dorsal surface of the centra, a character also observed in the goniopholidid *Dakotasuchus* (Frederickson *et al.*, 2017). The neural spines of ML2555 are low, with a height nearly equal to their length, and their dorsal surface is flat and slightly broader than at their base. This is the typical morphology observed in most neosuchians,

with the exception of Dyrosauridae, which have much higher neural spines (Schwarz-Wings *et al.*, 2009a). The transverse processes of the posterior vertebrae are laterally directed and slightly ventrally inclined. This inclination has also been observed in the lumbar vertebrae of *A. escuchae* (Puértolas-Pascual *et al.*, 2015a).

The hindlimbs appear to be slenderer than in extant crocodylians. The general proportions of the femur are similar to those observed in goniopholidids, such as *Sunosuchus* and *A. hooleyi* (Wu *et al.*, 1996a, Martin *et al.*, 2016), and are more gracile than other goniopholidids, such as *G. baryglyphaeus* and *Siamosuchus* (Schwarz, 2002; Lauprasert *et al.*, 2007). The lateral condyle is bigger than the medial one, more similar to atoposaurids such as *K. guimarotae* (Schwarz & Salisbury, 2002) and goniopholidids such as *Sunosuchus, Siamosuchus* and *Eutretauranosuchus* (Wu *et al.*, 1996a; Lauprasert *et al.*, 2007; Pritchard *et al.*, 2013), and different from *A. hooleyi,* whose condyles have similar dimensions (Martin *et al.*, 2016). A larger and distally projected lateral condyle also contrasts with extant crocodylians, where this projection is less developed (Leardi *et al.*, 2015). The preserved proximal end of the tibia, with its triangular contour and well-developed posteromedial proximal process, is similar to goniopholidids such as *A. hooleyi* (Martin *et al.*, 2015), and differs from atoposaurids such as *K. guimarotae*, where this proximal process is less developed (Schwarz & Salisbury, 2005).

BRACING SYSTEM RECONSTRUCTION

The axial skeleton of most fossil crocodylomorphs seems similar to those of extant taxa, therefore it should implicate the possession of a similar bracing mechanism (Schwarz-Wings *et al.*, 2009a). However, the scenario is more complicated due to a few differences observed in the axial skeleton, which are enough for the development of different kinds of bracing systems along Crocodylomorpha (Fig. 10) (Salisbury & Frey, 2001; Schwarz-Wings *et al.*, 2009a). In addition, enacting biomechanical models of the bracing system in Crocodylomorpha is complicated, because most of the fossils recovered in anatomical association (that are sufficiently complete to perform this kind of reconstruction) have normally been preserved crushed into two dimensions, so that most volumetric information is missing or distorted. According to Salisbury & Frey (2001), there are three main types of bracing systems among crocodylomorphs with amphicoelous vertebrae: taxa without paravertebral osteoderms, taxa with open paravertebral osteoderms (Fig. 10C–E) and taxa with closed paravertebral osteoderms (Fig. 10B). Schwarz-Wings *et al.* (2009a) also proposed the hyposaurine-type bracing system (Fig.

10F) as being different from all other crocodylomorph taxa. The specimen object of this study, ML2555, has closed paravertebral armour (Fig. 10G), so this section will only focus on this bracing-system mechanism.

In order to know how movements could be executed during locomotion for crocodylomorphs with a closed paravertebral bracing system, Salisbury & Frey (2001) tried to reconstruct the force transmission between vertebrae, the geometrical relationships between osteoderms and their epaxial musculature. Epaxial musculature consists of muscles that lie dorsal to the coronal plane of the trunk. Therefore, the reconstruction of this musculature can be estimated by calculating the available space between the dorsal osteoderms and the transverse processes of the vertebrae. To reconstruct the closed paravertebral armour bracing mechanism, Salisbury & Frey (2001) relied mainly on one of the most complete goniopholidid skeletons recovered until now, which is the specimen IRSNB R47 (Figs 8G, 10B), assigned to *Anteophthalmosuchus hooleyi* (Martin *et al.*, 2016). This specimen is currently mounted at the Royal Institute of Natural Sciences in Brussels, Belgium. However, the skeleton was recovered fully articulated but flattened, losing part of the original volumetric relationships between the different bones (see historical drawings in: Martin *et al.*, 2016). Therefore, Salisbury & Frey (2001) reconstructed the epaxial musculature based on the internal angle between contralateral osteoderms from each transverse row. The authors calculated this angle based on the inclination of the medial sutural margin of each osteoderm, estimating an internal angle of 160°–150° between each pair of osteoderms (Fig. 10B). In the ML2555 specimen, we did not observe any inclined facets in the medial margins of the osteoderms that would have allowed us to do this calculation. In order to test the hypothesis of Salisbury & Frey (2001), and since specimen ML2555 was 3D preserved with little deformation, we also estimated this internal angle, restoring the deformation suffered by the osteoderms back to their original position (Fig. 10G; and repositioned 3D model in Supporting Information, S2).

In the specimen ML2555, most of the osteoderms were slightly displaced ventrally and some of their medial margins were overlapped on to their laterally equivalent osteoderms. For restitution, we placed each medial margin of the osteoderms as though aligned with the neural spine of the vertebrae along the sagittal axis. In order to correct for ventral deformation and displacement, we took as a reference the osteoderm that was most horizontal, assuming it to be the one with the least displacement from its original position. We then raised the medial margins of each osteoderm until they were at the same height as the reference osteoderm, with the result reaching slightly above the

transverse processes of the vertebrae, thus facilitating the possible insertion of ribs into their lateral margins. After the reposition of the skeleton (see repositioned 3D model in Supporting Information, S2), the internal angle between each pair of osteoderms was found to be, at least, around 150° (Fig. 10G), so it agrees with the hypothesis proposed by Salisbury & Frey (2001), whose angle they had estimated between 150° and 160°.

Another discussion issue is related to the possible insertions for the epaxial musculature observed in the paravertebral osteoderms of ML2555. Salisbury & Frey (2001) proposed, in their model about crocodylomorphs with closed paravertebral armour, that the three main subsystems of the epaxial musculature (the M. transversospinalis Group, M. tendinoarticularis and M. longissimus dorsi) were attached to the medial part of a single paravertebral osteoderm (Fig. 10B). This hypothesis is based on the preservation of soft tissue in the paravertebral osteoderms of the putative atoposaurid *Brillanceausuchus babouriensis* Michard *et al.*, 1990 (phylogenetically recovered as a paralligatorid by: Tennant *et al.*, 2016b) and the goniopholidid *Goniopholis crassidens* Owen, 1842. In these taxa, a series of lines in the ventral surface of the dorsal osteoderms was interpreted as fossilized collagen fibres for the insertion of the M. tendinoarticularis and M. longissimus dorsi (Salisbury & Frey, 2004). This contrasts with the case in extant crocodilians, where the M. transversospinalis Group is attached to the medial osteoderm, and M. tendinoarticularis and M. longissimus dorsi are attached to the lateral osteoderm (Fig. 10A).

As discussed in the 'Description' section, all the dorsal osteoderms of ML2555 have a posteromedially directed smooth crest on their ventral surface that starts from a slight anterior projection of the anterior margin of the osteoderm (Figs 4B, 7). This crest divides the ventral surface of the medial part into two muscle insertion areas, where the M. transversospinalis Group would probably be inserted on the medial surface, and M. tendinoarticularis and M. longissimus dorsi on the lateral surface (Figs 4B, 10G). Therefore, the presence of this crest on the ventral surface would be consistent with the hypotheses proposed by Salisbury & Frey (2001, 2004). In our specimen, at least in the posterior thoracic and lumbar regions, the M. transversospinalis Group and M. tendinoarticularis + M. longissimus dorsi would have approximately the same insertion surface area (Figs 4B, 10G), contrasting slightly with the model proposed by Salisbury & Frey (2001), where the M. transversospinalis Group is much more reduced (Fig. 10B). Supporting our hypothesis, the presence of an almost identical crest on the ventral surface of paravertebral osteoderms associated with an anterior projection of the anterior margin of the osteoderm has

also been observed in other taxa such as *A. epikrator* (fig. 21 of Ristevski *et al.*, 2018).

The presence of an anterior projection in the anterior margin of the paravertebral osteoderms is also present in several osteoderms from other taxa such as *K. guimarotae* and *A. escuchae* (Fig. 8B, F), although they lack a crest on the ventral surface. If there is a relationship between this anterior projection and the ventral crest in ML2555 (or other taxa such as *A. epikrator*), as we hypothesize, this information could serve to reconstruct the epaxial musculature in crocodylomorphs that do not preserve a ventral crest, but do have projections in the anterior margins of their osteoderms.

BODY SIZE AND ONTOGENY

Due to the small size and fragmentary nature of ML2555, several important questions remain, concerning whether the total size of the specimen can be calculated or its ontogenetic state can be inferred. There are multiple studies that allow for calculating crocodylomorph total body length sizes and age based on cranial proportions (e.g. Sereno *et al.*, 2001; Wu *et al.*, 2006; Platt *et al.*, 2009; Fukuda *et al.*, 2013), but unfortunately the skull of ML2555 has not been preserved. Farlow *et al.* (2005) proposed body size analyses based on femoral lengths, as the femur is a good indicator of body size, at least in semi-aquatic crocodylians. Although the femur of ML2555 is incomplete, Farlow *et al.* (2005) (see also: Godoy *et al.*, 2016) also included regression equations that relate the total body size (TL) and mass (M) with the total width (Fdw) and total height (Fdh) of the distal end of the femur, which are measurements preserved in ML2555 (Fdw = 18 mm; Fdh = 13 mm). According to these equations, [log TL = 2.06 + (log Fdw) 0.82; log TL = 2.24 + (log Fdh) 0.79; log M = −2.78 + (log Fdw) 2.80; log M = −2.23 + (log Fdh) 2.78], the total length (TL) of ML2555 would be between 123 cm (calculated with Fdw) and 132 cm (calculated with Fdh); with a total body mass between 5.43 kg (calculated with Fdw) and 7.36 kg (calculated with Fdh). However, these calculations, mainly based on semi-aquatic extant crocodylians, could give us an overestimated total body length and mass, a point already suggested for cursorial and highly terrestrial crocodylomorphs such as Notosuchia (Pol *et al.*, 2012; Godoy *et al.*, 2016), or on the contrary, an underestimation, as seen in Thalattosuchia (Young *et al.*, 2011). Most goniopholidids have been associated with semi-aquatic palaeoenvironments, having an overall cranial morphology, lifestyle and locomotion similar to that of extant Crocodylians (Salisbury & Frey, 2001; Frederickson *et al.*, 2017; Halliday *et al.*, 2015). Therefore, it is likely that the equations of Farlow

et al. (2005) applied to Goniopholididae would be more accurate than in Notosuchia or Thalattosuchia.

Comparing the estimated total size of ML2555 with other atoposaurids, we can verify that this specimen is much larger than most of the atoposaurids described to date, being even longer than larger taxa, such as the putative atoposaurid *Brillanceausuchus* (80 cm of total length, Tennant *et al.*, 2016b). In addition, the osteoderms of ML2555 are almost twice the size of the largest osteoderms assigned to *K. guimarotae*. This suggests, as we have already commented throughout the text, that it is most likely that ML2555 does not belong to this clade of dwarf crocodylomorphs. Although ML2555 has been assigned to Goniopholididae, its size is too small for what would be expected within this clade of crocodylomorphs of medium/large size, making it most likely a dwarf or a juvenile individual. Dwarf goniopholidids, such as *Nannosuchus*, have been described, but their cranial characters seem to indicate that they are actually juvenile individuals (Joffe, 1967; Salisbury, 2002). The presence of open and partially open neurocentral sutures in the posterior thoracic/lumbar vertebrae of ML2555 should indicate clues toward the ontogeny of this specimen. However, it has been shown that neurocentral suture closure in crocodylians occurs (from tail to neck) in very late ontogenetic states, with the presacral vertebrae remaining unfused even in mature individuals (Brochu, 1996; Ikejiri, 2012). Therefore, the only thing that can be assumed about having neurocentral open sutures in the posterior region of the trunk, is that ML2555 is not a mature individual.

There is an inability to clarify if ML2555 is a dwarf or a juvenile goniopholidid with the current data, although, possibly, further histological studies could shed more light on the ontogeny of this specimen.

CONCLUSIONS

In this work, we describe for the first time a small articulated partial skeleton of a neosuchian crocodylomorph recovered in the Lourinhã Formation (Upper Jurassic, Portugal). The specimen ML2555 is characterized by the presence of amphicoelous vertebrae and two rows of paired dorsal osteoderms, which are rectangular in outline and twice as wide as they are long. Each osteoderm presents its lateral margin ventrally tilted and with an anterior process laterally placed for a 'peg and groove' articulation. In addition, a complete osteoderm from the ventral armour, several limb osteoderms, ribs and a partial hindlimb have been identified. All these features are present in crocodylomorphs with closed paravertebral armour bracing systems, such as protosuchians, goniopholidids and some notosuchians, sphenosuchians

and atoposaurids. Despite the small size of ML2555, which initially appears more consistent with other crocodylomorphs described in the area (such as the atoposaurid *K. guimarotae*), several features, such as the overall morphology of the dorsal osteoderms or the presence of ventral scutes, allow us to assign this specimen to Goniopholididae indet.

Due to a micro-CT scan and the good 3D preservation of ML2555, we were able to test previous hypotheses about the reconstruction of the bracing system and the epaxial musculature in these kinds of crocodylomorphs, obtaining results similar to the previous models (Fig. 10) (Salisbury & Frey, 2001). We were able to verify that in crocodylomorphs with closed paravertebral bracing systems, dorsal armour was more ventrally inclined and that, together with the ventral projection of the lateral part of each osteoderm, the epaxial musculature was much more reduced (Fig. 10B, G) than in crocodylomorphs with open paravertebral bracing systems or eusuchian bracing systems (Fig. 10A, C–F). In addition, the presence of an anteroposterior crest on the ventral surface of the dorsal osteoderms would support the hypothesis that the three main subsystems of the epaxial musculature were attached to the medial part of a single paravertebral osteoderm. This contrasts with extant crocodylians, where the M. transversospinalis Group is attached to the medial osteoderm, and M. tendinoarticularis and M. longissimus dorsi are attached to the lateral osteoderm (Fig. 10A).

Due to regression equations based on the femur dimensions, it was possible to estimate a total body length of about 1.2 m and less than 10 kg of weight. These dimensions contrast with the medium and large sizes observed in most Goniopholididae. However, it was not possible to determine the ontogenetic state of the specimen ML2555, therefore, pending further histological analysis, it is not possible to know if it was a dwarf or juvenile individual.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Information S1 (Supp Info_01_Original Skeleton.ply). Three-dimensional model of the skeleton of ML2555.
Information S2 (Supp Info_02_Repositioned Skeleton.ply). Repositioned three-dimensional model of the skeleton of ML2555.
Information S3 (Supp Info_03_Femur.ply). Three-dimensional model of the femur of ML2555.
Information S4 (Supp Info_04_Tibia.ply). Three-dimensional model of the tibia of ML2555.