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New remains of *Liopleurodon* (Reptilia, Plesiosauria) from the Middle Jurassic of western France and paedomorphosis within pliosaurids

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ABSTRACT

A new specimen of the pliosaurid *Liopleurodon ferox* from the Callovian strata (Middle Jurassic) of France is described. This new specimen represents one of the most-complete post-cranial skeletons known for this species. Remains of *Liopleurodon ferox* were previously reported from central and southern England, Germany, the north of France, and possibly from Poland and Russia. The specimen examined here therefore extends the biogeographical area of the species into central France and represents the southernmost occurrence of this taxon. Based on osteological evidence, the specimen is here identified as an "adult" individual, confirming that the lack of fusion between the cervical neural arches and associated centra is not a reliable indicator of a juvenile condition in pliosaurids. Instead, such a lack of fusion in cervical vertebrae is more likely to be paedomorphic in adult pliosaurids, as noted in previous works. However, this statement does not hold true for dorsal and caudal vertebrae, or cervical ribs, in which the pattern of suture closure may vary according to taxa. Overall, our results indicate that the open or closed conditions of the neurocentral sutures of all the vertebrae of the vertebral column, as well as the suture between ribs and centra, is a poor indicator of ontogenetic stages in pliosaurids.

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INTRODUCTION

Pliosaurids (Sauropterygia, Plesiosauria, Pliosauridae) were among the largest predators of Mesozoic aquatic ecosystems and ranged stratigraphically from the uppermost Triassic (Rhaetian) or lowermost Jurassic (Hettangian), to the early Late Cretaceous (e.g., Benson et al., 2011; Schumacher et al., 2013; Bardet et al., 2014; Benson and Druckenmiller, 2014; Wintrich et al., 2017). They colonized both marine and freshwater environments (e.g., Benson et al., 2013a; O'Gormann et al., 2018) and achieved a cosmopolitan distribution during the Late Jurassic (Barrientos-Lara et al., 2015). In Europe, pliosaurid remains have been mainly reported from England, France, Germany, Poland, Switzerland, and Norway (Bardet et al., 2014). They are particularly abundant in the Upper Jurassic (Callovian) strata of both the Oxford and Kimmeridge Clay formations exposed in England (e.g., Owen, 1869; Tarlo, 1960; Ketchum and Benson, 2011; Benson et al., 2013b; Martill et al., 2023), but are comparatively scarce elsewhere. In France, pliosaurid occurrences have been reported from the Lower, Middle, and Upper Jurassic strata of the north-east of the country: Normandy and Hauts-de-France (Beckary, 1992; Bardet, 1993; Bardet et al., 1993a, 1993b; Maréchal et al., 1999; Vincent et al., 2013), and from Lower Cretaceous strata of eastern France (Buffetaut et al., 2005). However, the preserved material from France consists mostly of isolated teeth and/or partial post-cranial remains, and only a few specimens preserve skull elements (e.g., *Pliosaurus, Liopleurodon;* Bardet, 1993). The main goal of this contribution is to describe a pliosaurid specimen from the Callovian of France preserving an almost complete post-cranial skeleton and to assess its systematic status as well as its phylogenetic affinities. In addition, the geographical occurrence and ontogenetic status of the specimen are discussed. The analysis of neurocentral sutures closure in the cervical vertebrae of pliosaurids, previously addressed by various authors (e.g., Ketchum and Benson, 2022; Araújo and Smith, 2023), has been expanded to encompass the entire vertebral column, as well as the sutures between cervical ribs and centra.

Repositories and Institutional Abbreviations

BEDFM, Bedford Museum, Bedford, UK; **BHN**, Musée d´Histoire Naturelle, Boulogne-sur-Mer, France; **BRSMG**, Bristol City Museum and Art Gallery, Bristol, UK ; **CAMSM**, Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK; **CM**, Carnegie Museum, Pittsburgh, Pennsylvania, USA; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **ComCom Thouarsais**, Community of Communes of Thouarsais, Thouars, France; **FHSM**, The Sternberg Museum of Natural History, Fort Hays, Kansas, USA; **GPIT**, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Tübingen, Germany; **HAUF**, UrweltMuseum Hauff, Holzmaden, Germany; **IGM**, Colección Nacional de Paleontología, Instituto de Geología of the Universidad Nacional Autónoma de México, Mexico city, Mexico; **MAE**, Musée de l'Agglomération d'Elbeuff, Elbeuf-sur-Seine, France; **MANCH**, The Manchester Museum, Manchester, UK; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MJACM**, Museo El Fósil, Vereda Monquirá, Municipio de Villa de Leyva, Departamento de Boyacá, Colombia; **MNA V**, Museum of Northern Arizona, Flagstaff, USA; **MNHNCu**, Museo Nacional de Historia Natural, Havana, Cuba; **MP, VL**, Paleontological collection of the Servicio Geológico Colombiano, Bogotá D.C., Colombia; **MUHNCAL**, Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Chile; **NAMU**, Naturkunde-Museum Bielefeld, Bielefeld, Germany; **NHMUK**, Natural History Museum, London, UK; **OUMNH**, Oxford University Museum of Natural History, Oxford, UK ; **PETMG**, Peterborough City Museum and Art Gallery, Peterborough, UK; **PMO**, University of Oslo Natural History Museum, Oslo, Norway; **QM**, Queensland Museum, Brisbane, Ausralia; **SDSM**, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; **UANL-FCT**, Universidad Autonóma de Nuevo León, Linares N.L., Mexico; **YKM**: Ulyanovskii Oblastnoi Kraevedcheskii Musei I.A. Goncharova, Ulyanovsk, Ulyanovsk Region, Russia.

GEOGRAPHICAL AND STRATIGRAPHICAL SETTING

The specimen described herein was discovered on the municipality of Saint-Laon (Vienne, France), located in the Dive du Nord valley on the southwest margin of the Paris Basin (Dhoste et al., 1987). The deposits correspond to the Jurassic series extending from Poitiers to the region of Thouars (Figure 1A-B). The fossil remains come from a limestone quarry (the Grève Quarry) that was exploited for construction materials. In the 1970s and 1980s, the Grève Quarry was well known among fossil collectors (Saint-Léger, 1987), and provided abundant and diverse ammonites. In the past 30 years, this quarry has been abandoned and inaccessible, preventing the direct observation of the formerly exploited levels.

The sedimentary succession of the Grève Quarry was described by Legendre (1984, p. 98) and Cariou (in Gabilly et al., 1985, p. 45-47). The whole succession was about 4.50 m thick and divided into two formations corresponding to the Bathonian and the Callovian stages, which are separated by a hard and perforated surface, coated with iron oxides (Figure 1C). The Bathonian

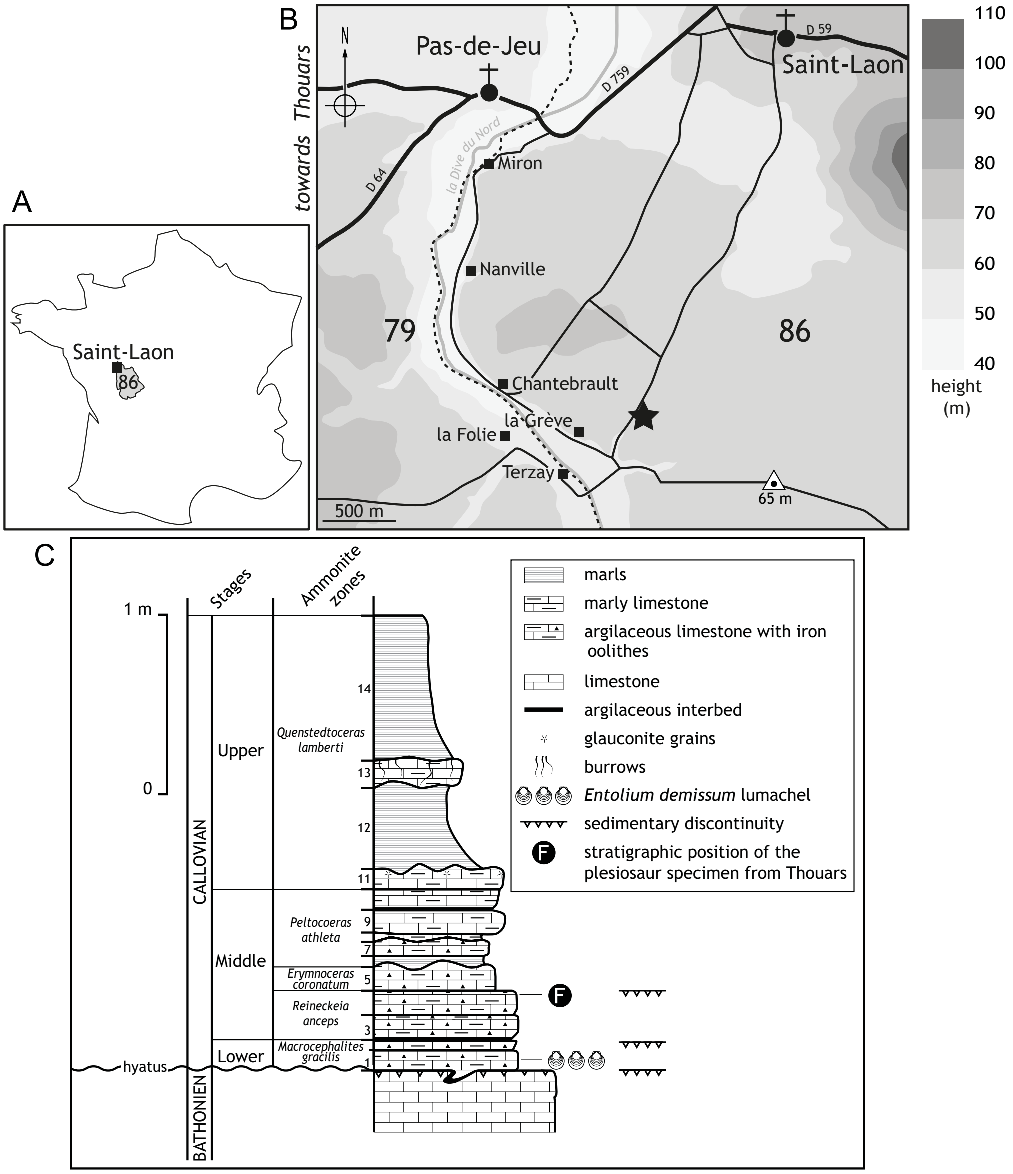

FIGURE 1. A. Geographical location (grey) of the municipality of Saint-Laon in France (86 is the Vienne department number). B. Detailed geographical map showing the locality (star) where the Thouarsais specimen was collected. C. Simplified Callovian succession of the limestone quarry near la Grève, with the stratigraphic position of the ComCom Thouarsais_Geol.0121 specimen.

succession (2 m) corresponds to whitish, nodular, chalky arenaceous limestones and contain sponges, bivalves, and scleractinian corals of the genus *Montlivaltia* (Lamouroux, 1821). The Callovian succession (2.5 m) includes argillaceous limestones with ferruginous ooids and marls, locally known as *"calcaires en platins".* The Callovian succession can be subdivided into three units: (i) a lower unit (beds 1 to 4) consisting of brown to red limestone with abundant and small ferruginous ooids, and characterized by a distinctive *lumachel* (i.e., shell beds containing partial to complete bivalve fossils) of *Entolium demissum* (Phillips, 1829); (ii) a middle unit (beds 5 to 11) corresponding to blue-grey limestones with glauconitic grains, containing less numerous and much larger ferruginous ooids; (iii) an upper unit (beds 12 to 14) corresponding to grey marls that present a discontinuous decimetric level of bioturbated hard limestone ("miches") and contain limited fossil remains of sponges and belemnites.

The stratigraphic level from which the pliosaur specimen came was not accurately located during its extraction. However, the identification of ammonites, i.e., *Hecticoceras (Rossiensiceras) savoiense* Zeiss, 1956, *Rehmannia (Loczyceras) discrepans* (Bourquin, 1968), *Reineckeia (Reineckeia) anceps* (Reinecke, 1818) forme *corroyi*, and *Oecoptychus refractus* (Reinecke, 1818), during the preparation of the material, indicates a possible provenance from bed 4 of the Callovian succession. Such a hypothesis about the stratigraphic position of the specimen is reinforced by the superficial erosion observed on some of the vertebrae, which is like the erosional facies that were visible on the top of the bed 4. The specimen was thus possibly partly embedded in the argillaceous limestones with ferruginous ooids of the *Erymnoceras coronatum* Zone, more precisely at the boundary between the *Leuthardi* sub-zone and the *Rota* sub-zone (Cariou, pers. com. 2006). The abundant pelagic fauna of these Callovian deposits indicates the strata were deposited over an area of shallow waters open to the oceanic domain (Gabilly and Cariou, 1974; Cariou, 1980) in a sublittoral environment (Faugeras, 1985; Legendre et al., 1989).

MATERIAL AND METHODS

The ComCom Thouarsais_Geol.0121 specimen examined here, informally called the 'Thouarsais specimen', is a partial post-cranial skeleton discovered in April 1979 by the fossil enthusiasts Camille Robin and Jean-Pierre Robin. They used a pickaxe and a crowbar to clear the overburden including a Quaternary cover (about 0.8 m thick) over an area of 25 to 30 m². The discoverers were concerned about the conservation of the specimen and donated it to the Community of Communes of the Thouarsais (Communauté de Communes du Thouarsais, Thouars, Deux-Sèvres, France) in 2001. In return, the latter provided the means to extract the skeleton from its limestone matrix and to exhibit it to the public. The preparation was performed out in Thouars in 2006. The removal of the calcareous matrix was first achieved by using a pneumatic micro-hammer and followed by treatment with 10% methanoic acid to precisely finalise the preparation. This was done after embedding the exposed bones with plexigum®, a resin utilized for consolidating, repairing, and reassembling fractured elements such as ribs and vertebrae. The specimen was presented to the public during a temporary exhibition for the "European Heritage Days" in Thouars, and then for the "Science Festival" in 2006. The Thouarsais specimen is currently kept in the paleontological collections of the Community of Communes of the Thouarsais.

To establish the phylogenetic relationships of the specimen within Plesiosauria, a cladistic analysis was performed using the data matrix of Sachs et al. (2023), one of the most recent cladistic data matrix of Plesiosauria including the greatest number of pliosaurid taxa. The data (see Appendix 1) for all plesiosaur taxa were retained except for *Attenborosaurus conybeari* (Sollas, 1881), as we consider that its coding requires revision, given that it is one of the few genera from Toarcian strata whose anatomy has not yet been revised. Data for the Thouarsais specimen were added to the data matrix. The character 172 (the shape of neurocentral suture in anterior–middle cervical vertebrae in lateral view) was not included in the analysis. Indeed, although an open neurocentral suture is considered as a peadomorphic feature in pliosaurid taxa (refer to the *Ontogenetic stage* paragraph), associated changes in the shape of the suture could potentially be linked to their ontogenetic status, as previously reported in some plesiosauroid taxa (Vincent et al., 2017). The data set, including 129 taxa and scored for 269 characters, was analyzed using TNT 1.6 (Goloboff et al., 2008; Goloboff and Morales, 2023). A Traditional Search (1000 replicates) using tree bisection–reconnection (TBR) branch-swapping with all characters unordered and unweighted was performed. Bremer support values were calculated by using the bremer.run script in TNT (Goloboff et al., 2008).

SYSTEMATIC PALAEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Family PLIOSAURIDAE Seeley, 1874
Clade THALASSOPHONEA Benson and Druckenmiller, 2014
Genus *LIOPLEURODON* Sauvage, 1873

Type species. *Liopleurodon ferox* Sauvage, 1873.

Liopleurodon ferox Sauvage, 1873
Figures 2–8

Type material. BHN 3R 197, a single tooth now kept in the Musée d'histoire naturelle de Lille (Lille, France).

Referred material. See Noè, 2001; ComCom Thouarsais_Geol.0121 (described herein).

Type locality and horizon. Le Wast, near Boulogne-sur-Mer (northern France), *Quenstedtoceras lamberti* Zone, Oxford Clay Formation, Upper Callovian (Sauvage, 1873; Noè, 2001).

Other localities. Bathonian-Callovian boundary to Lower Oxfordian of North and Central France, England, Switzerland and Germany. Possibly from the Lower Bathonian of France, Callovian of Poland, Callovian and Oxfordian of Russia, and Lower Tithonian of Germany (see Noè (2001) for details; Zverkov et al., 2024).

Diagnosis. Andrews, 1913; Tarlo, 1960 (in part); for the cranial diagnostic characters see Noè (2001). Pliosaurid possessing short cervical centra (length less than half width or height); cervical centra with a ventral lip and no ventral keel; two cervical rib facets.

Description

Preservation. The Thouarsais specimen measures around 320 cm in length and consists of a sub-complete post-cranial skeleton of a pliosaurid plesiosaur (Figure 2), including 45 vertebrae (10 cervicals, 4 pectorals, 22 dorsals, 4 sacrals, and 4 caudals), remains of ribs and gastralia, partial pectoral and pelvic girdles, as well as partial front- and hind-limbs. For convenience, the vertebrae will be described by using a letter (i.e., C: cervical, P: pectoral, D: dorsal, S: sacral and CA: caudal) followed by an Arabic number (e.g., C1 for the first cervical vertebra). This system does not correspond to the anatomical positions of the vertebrae.

Cervical vertebrae. Ten cervical centra represent middle to posterior elements of the neck (Figure 3). They exhibit gently concave articular surfaces with a central depressed notochordal pit, as in *Peloneustes* and NHMUK R. 3536, a large specimen of *Liopleurodon* (Andrews, 1913; Tarlo, 1960; Ketchum, 2007). In anterior view, the centra are subcircular in outline, slightly heart-shaped with a slight ventral lip in the cervicals C1 to C8 (Figure 3A, C, H). The presence of a ventral lip is reported in *Marmornectes, Liopleurodon, Peloneustes, 'Pliosaurus' andrewsi, Eardasaurus,* and *Simolestes* (Andrews, 1913; Tarlo, 1960; Ketchum and Benson, 2011, 2022) and may be a synapomorphy of a derived clade within Pliosauridae (Ketchum and Benson, 2011). The cervical centra are wider than they are high and long (W>H>L), as in other pliosaurids (e.g., Andrews, 1913; Tarlo, 1960; O'Keefe, 2001; Ketchum and Benson, 2011). Centrum length represents approximately 1/2 to 3/5 of both the width and height of the vertebrae; similar proportions (length being less than half the vertical diameter of the articular faces) are given by Andrews (1913) for *Liopleurodon ferox*. The ventral surfaces of the centra are pierced by two small subcentral foramina (Figure 3I). Similar to the pliosaurids *Marmornectes, Pliosaurus westburyensis, Pliosaurus carpenter,* and *Liopleurodon ferox*, these foramina are not separated from one another by a ridge and differ from the condition reported in *Peloneustes, Pliosaurus brachydeirus,* and the pliosaurid OUMNH J.02247 (Andrews, 1913; Tarlo, 1960; Ketchum and Benson, 2011; Benson et al., 2013b). The cervical rib facets are large and located on the ventral to ventrolateral surfaces of the centra (Figure 3B-E). The centra of cervicals C1 to C8 bear two rib facets (diapophysis and parapophysis) subequal in size (Figure 3B, E, F). The diapophysis is triangular with the apex pointing dorsally whereas the parapophysis exhibits a bowl shape with a rounded ventral margin. The two facets, taken together, are pear-shaped like those described by Andrews (1913) for *Liopleurodon ferox*. The cervical centra C9 and C10 bear a single oval, dorsoventrally elongated rib facet (Figure 3G), similar to *Liopleurodon ferox* (Andrews, 1913). Four cervical neural arches are sub-complete and still attached to their centra showing a V-shaped neurocentral suture (C3-C6; Figure 3D-E). In anterior view, the neural canals exhibit an ovoid keyhole-shape due to a bony bulge located at mid-height on the medial surface of the neural arches, as in *Marmornectes* (Ketchum and Benson, 2011) and *Liopleurodon ferox* (Andrews, 1913). The neural canals represent approximately 50% of the centra height (Figure 3C). The preserved neural spines are straight and sub-rectangular. The neural spines are longer antero-posteriorly than they are wide, as in *Liopleurodon* but unlike the condition

FIGURE 2. General view of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox).* Abbreviations: C, Cervical, CA, caudal, D, dorsal, S, sacral vertebrae. Scale bar equals 10 cm.

observed in *Marmornectes* (Andrews, 1913; Ketchum and Benson, 2011), and measure approximately half of the centra length. The tips of the neural arches widen as in *Liopleurodon ferox* (Andrews, 1913), showing a teardrop to oval outline in dorsal view and appearing sub-rectangular in lateral view. The zygapophyses are narrower than the centra. They are angled at approximately 45 degrees from the horizontal and are separated from one another, the right and left pre- and postzygapophyses being not fused medially. The sutures between cervical centra and associated neural arches, as well as the sutures between cervical centra and the corresponding ribs, are visible on the surface of the bones.

Pectoral vertebrae. Four pectoral vertebrae were identified based on rib facets that are present on both the centrum and the neural arch (Figure 4A-D). The pectoral centra are higher than long, but longer than the cervical centra. On the two first pectorals (P1 and P2), the rib facets show an open neurocentral suture (Figure 4B, D) and appear elongated dorsoventrally (Figure 4B, D). This differs from the last pectoral (P4), in which the rib facet is more rounded (Figure 4E). The subcentral foramen on the right side of the P4 centrum is situated more laterally than in other pectorals, and a larger supplementary foramen is present ventrally.

Dorsal vertebrae. Centra of the 22 dorsal vertebrae are as high as wide, shorter than high, and bear a central notochordal pit (Figure 4F-H). Both the lateral and ventral surfaces of the centra are concave. The articular surfaces of the centra are sub-oval and weakly concave. The centrum width is approximately half of the transverse process width. The rib facets are situated on short and robust transverse processes. Only one complete neural arch and neural spine is preserved in association with the centrum (Figure 4G, H). The zygapophyses are relatively short and proportionally smaller than those on the cervical neural arches. The neural spines extend antero-posteriorly, almost as long as the centrum length (around 70%), and higher than the associated centrum. The thin neural spines are inclined postero-dorsally and present a slightly curved anterior margin in lateral view (Figure 4H). The apices of the neural spines are convex in their centra and rectangular in

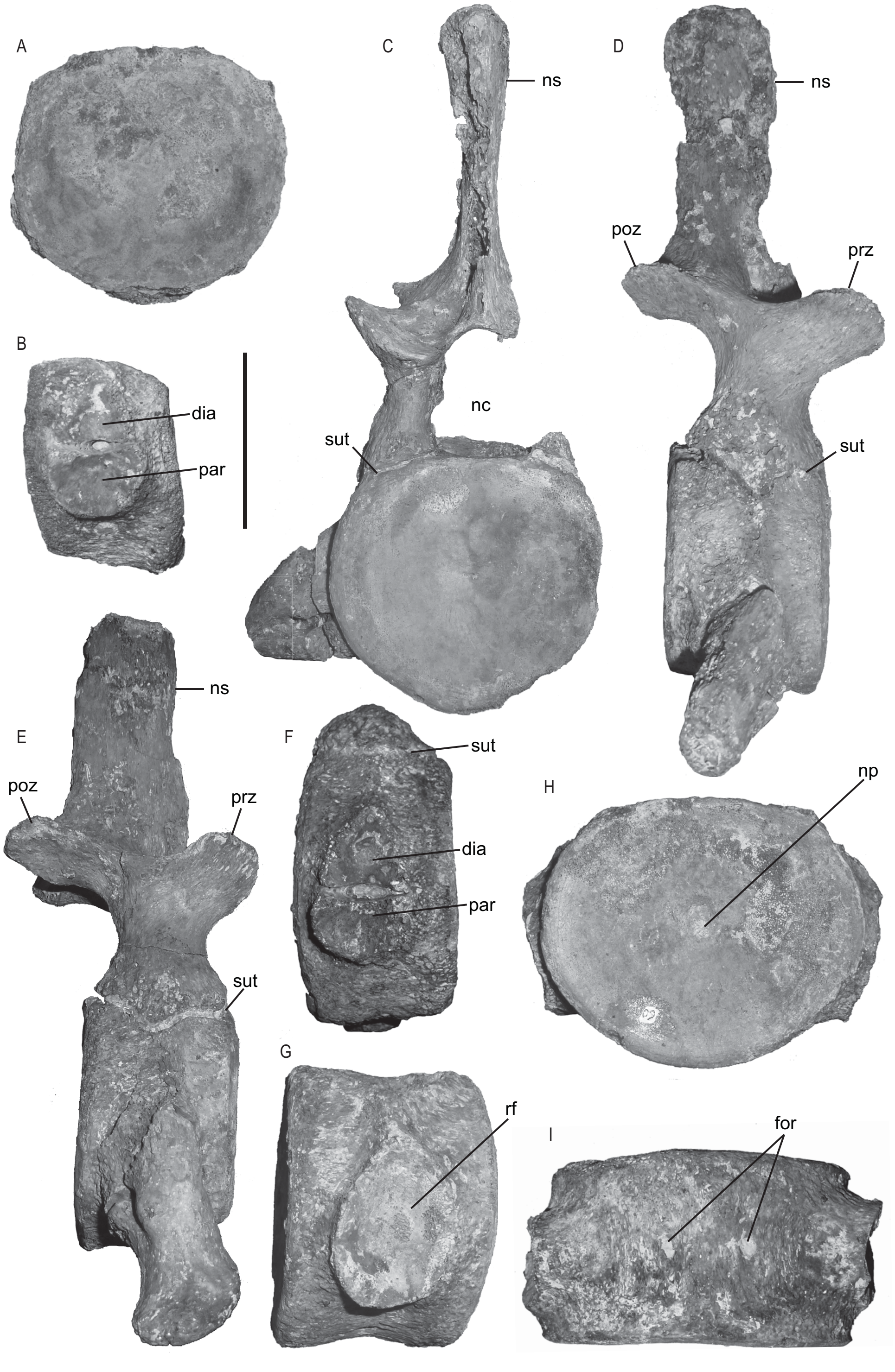

FIGURE 3. Cervical vertebrae of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox):* A. C1 in anterior view; B. C2 in right? lateral view; C. C5 in anterior view; D. C4 in right lateral view; E. C6 in right lateral view; F. C7 in left? lateral view; G-I. C10 in right lateral (G), anterior (H) and ventral (I) views. Scale bar equals 5 cm. Abbreviations: dia, diapophysis; for, foramen; nc, neural canal; np, notochordal pit; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis; rf, rib facet; sut, neurocentral suture.

FIGURE 4. A-D, pectoral vertebrae and F-H, dorsal vertebrae of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox):* A. P1 in anterior view; B. P1 in left lateral view; C. P2 in anterior view; D. P2 in right lateral view; E. P4 in anterior view; F-H. D6, close-up of the rear margin of the neural spine (F), in anterior (G) and right lateral (H) views. Scale bar equals 5 cm. Abbreviations: for, foramen; nc, neural canal; ns, neural spine; sut, neurocentral suture.

cross-section. The posterior margin of the neural spine is vertically grooved, and the postzygapophyses are thus separated by deep medial fossae (observable on D6 and D19; Figure 4F).

Sacral vertebrae. The centra of the four sacral vertebrae (Figure 5A-B) show an open neurocentral suture and bear a dorso-ventrally elongated rib facet, which is formed by both the neural arch and the centrum (Figure 5B). The neural spines are inclined postero-dorsally, the apices being strongly expanded and oval in dorsal view.

Caudal vertebrae. Five caudal vertebral centra are preserved. The articular surfaces are nearly circular in outline and are slightly concave with a pronounced median pit (Figure 5C-D). The caudal rib facets are simple. The chevron facets are located ventrally on the posterior edges of the centra. No neural arches have been preserved.

Ribs. The double-headed cervical ribs are short with a convex dorsal surface and separated by a wide aperture (Figure 3E). Proximally, the width of the aperture (Figure 3C) is much greater than that reported for *Marmornectes* (Ketchum and Benson, 2011), but similar to that reported for CAMSM J.46912 (holotype of *Liopleurodon pachydeirus* Seeley, 1869, considered con-specific with *Liopleurodon ferox* by Noè, 2001). The distal end of the complete ribs preserved on cervical vertebrae C3 and C6 (Figure 3E) shows an undeveloped anterior process, the short posterior process being rounded and flattened as in most pliosauroids (e.g., *Peloneustes, Liopleurodon, Simolestes;* Ketchum and Benson, 2011). Numerous fragments of elongated and curved dorsal ribs are preserved (Figure 5E). The ribs have slightly concave articulatory surfaces. Differentiating gastralia from dorsal ribs among the various broken isolated elements has proved difficult. One element is double-forked (Figure 5F) and is identified as a gastralium, a morphology already observed for gastralia in the Triassic sauropterygians *Corosaurus* (Storrs, 1991) and *Nothosaurus* (Koken, 1893), the plesiosauroids *Plesiosaurus* and *Brancasaurus* (Storrs, 1997; Sachs et al., 2016), both juvenile and adult specimens of the elasmosaurids *Mauisaurus, Terminonatator,* and *Fluvionectes* (Hector, 1874; Martin et al., 2007; Campbell et al., 2021), and in a single specimen of *Peloneustes philarchus*, BMNH R3318 (Ketchum, 2007). This character was not observed in the mounted specimen of *Liopleurodon ferox* GPIT-PV-30093 displayed in Tübingen (syn. PV 17998, GPIT/RE/3184, GPIT 1754/2; see Goller (2021) and Krahl et al. (2022)). This character is variously interpreted as an anomalous ossification (Sato, 2003) or a congenital deformity (Storrs, 1991), and considered rare (Martin et al., 2007), but it may be more widespread than initially thought.

Two sacral ribs are preserved (Figure 5G-I). Similar to other pliosaurids (e.g., *Liopleurodon* and *Marmornectes*), the distal end of the rib is dorsoventrally flattened and flared (Andrews, 1913; Ketchum and Benson, 2011). The proximal end has an elongated oval outline (Figure 5I). The rib shaft is twisted as in *Marmornectes* (Ketchum and Benson, 2011), so that the long axis of the proximal rib facet and the long axis of the distal ilium facet are strongly rotated relative to each other (~90°). A ridge extends dorsoventrally from the rib head to the flared distal end as in *Peloneustes* (Ketchum, 2007).

Pectoral girdle. The pectoral girdle is partially preserved, with only remains of the scapulae and coracoids present, whereas the clavicular arch is missing. Other small and fragmentary elements, probably belonging to the pectoral girdle are preserved; however, they could not be identified and are omitted in this description. Only the posterior ramus of the right scapula is preserved, whereas the almost complete left scapula is triradiate, with the ventral, dorsal, and posterior rami visible (Figure 6A-C). The medial surface of the scapula between the posterior and ventral rami, at the level of the pectoral fenestra, is concave. The ventral ramus is incomplete and directed antero-medially, whereas the complete dorsal process extends postero-laterally. The latter shows an approximately subequal antero-posterior width along its entire dorso-ventral height except for the apex that is slightly enlarged. The dorsal process presents a convex and acute anterior edge, as well as a roundly concave posterior margin. The anterior edge is slightly sinusoidal, as in *Marmornectes* and *Peloneustes* (Ketchum and Benson, 2011) and *Liopleurodon ferox* GPIT-PV-30093 mounted specimen (Linder, 1913; pers. obs.). The apex of the dorsal ramus is a rugose concave, elongated, teardrop-shaped facet, indicating that it was probably covered by cartilage in the living individual, and undulates, as in *Marmornectes* (Ketchum and Benson, 2011). The posterior ramus is robust and bears facets for articulation with the coracoid and the humerus. A ridge extends from the tip of the glenoid facet of the scapula along its lateral surface, enhancing the angle between the ventral and lateral surfaces of the scapula.

A crushed portion of the right coracoid is preserved (Figure 6F). It presents two adjacent facets:

FIGURE 5. A-B, sacral vertebra, C-D caudal vertebra, E-I, rib and gastralia of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox):* A, S3 in anterior view; B, S3 in right lateral view; C, CA2 in anterior view; D, CA2 in right lateral view; E, dorsal rib; F, gastralia; G-I, sacral rib in anterior (G), dorsal (H) and distal (I) views. Scale bar equals 5 cm. Abbreviations: ilf, ilium facet; nc, neural canal; rf, rib facet; sut, neurocentral suture.

the anterior one, triangular, corresponds to the scapular facet of the coracoid, while the posterior facet is concave and oval, corresponding to the glenoid facet of the coracoid. An element preserved separately (Figure 6D-E), showing an antero-posterior curvature and a thickening that culminates in the flattened medial margin, is identified as the anterior-most part of the robust right bar of the coracoid. The part of the symphysis where the coracoids meet is curved dorsally. The anterior process of the coracoid is very short with a subrectangular outline in dorsal view as in *Liopleurodon ferox* (Andrews, 1913).

Forelimb. Both humeri are preserved, the left being almost complete (Figure 7A) whereas the right is severely damaged and lacks most of the proximal and distal parts (Figure 7B). The proximoventral part of the left humerus shows the tuberosity but is severely abraded, and the capitulum is not preserved (Figure 7C). The humeral shaft curves dorso-distally as in other pliosaurids (Figure 7D; Ketchum and Benson, 2011). Distally, the pre- and postaxial margins of the shaft are asymmetrical, similar to *Liopleurodon ferox, Pliosaurus almanzaensis,* and *Peloneustes philarchus* (Linder, 1913; Ketchum, 2007; O'Gorman et al., 2018). A prominent postaxial expansion is visible at the distal end and is much wider than in *Pliosaurus funkei*, *Stenorhynchosaurus*, and *Marmornectes* (Andrews, 1913; Ketchum and Benson, 2011; Knutsen et al., 2012; Páramo-Fonseca et al., 2016). The distal surface of the humerus is suboval in outline (Figure 7E). The radial and ulnar facets are distinct as in *Liopleurodon ferox* (Linder, 1913), contrasting with

FIGURE 6. Girdles of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox):* A-C. Left scapula in lateral (A), medial (B), and posterior (C) views; D-F. Right coracoid in medial (D) and dorsal (E-F) views; G. pelvic girdle; H-I. Left ilium in lateral (H), and posterior (I) views; J-K. Right ilium in medial (J) and posterior (K) views. Scale bars equal D-E, H-K: 5 cm, A-C, F-G: 10 cm. Abbreviations: act, acetabulum; cgf, glenoid facet of the coracoid; corf, scapular coracoid facet; csf, scapular facet of the coracoid; drs, dorsal ramus of the scapula; gle, scapular glenoid facet, ilf, iliac articular facet; isc, ischion; prs, posterior ramus of the scapula; pu, pubis; svr, scapular ventral ridge; tfen, thyroid fenestra; vrs, ventral ramus of the scapula.

Marmornectes (although the propodials are abraded distally in the type and sole specimen of this taxon; Ketchum and Benson, 2011), and *Stenorhynchosaurus,* which both lack prominent articular surfaces for the epipodial elements (Páramo-Fonseca et al., 2016). Posterior to the ulna facet, a third facet is presumed to articulate with a postaxial accessory ossicle. This contrasts with *Stenorhynchosaurus* and *Peloneustes* in which the lack of postaxial ossicles in the epipodial row of the forelimb has been reported (Ketchum and Benson, 2011; Páramo-Fonseca et al., 2016).

Both left and right radii (Figure 7A-B) form a compact and robust bone, longer (left radius: 92 mm) than wide (left radius: 87 mm), with concave postaxial borders and a slightly convex preaxial margin. The postaxial margin forms the preaxial margin of a large epipodial foramen that extends for 2/3 of the length of the epipodials. The humerus facet is extensive, being antero-posteriorly long and dorso-ventrally thick. Distally, the radius bears three facets. The middle one, being the largest, corresponds to the radial facet. Postaxially, a small but well-formed oblique facet contacts with the intermedium and appears relatively shorter than the one observed in *Peloneustes philarchus* (Ketchum, 2007). A third, very reduced and oblique facet, located preaxially to the radial facet, may have contacted a preaxial ossicle.

Only the right ulna is preserved (Figure 7B). It forms a pentagonal bone slightly wider (preaxially to postaxially) than long (proximally to distally), similar to the condition reported in other pliosauroids (Ketchum and Benson, 2011). The ulna (77 mm long; 95 mm wide) is shorter and wider than the radius, as in *Simolestes vorax* (Andrews, 1913). The ulna bears a straight proximal facet for the humerus, as observed in *Simolestes vorax* and *Liopleurodon ferox* (Andrews, 1913; Linder, 1913), but not for a postaxial accessory ossicle. The two distal facets articulate with the ulnare and the intermedium. The preaxial margin of the ulna forms the postaxial border of the epipodial foramen and is concave as in *Liopleurodon ferox* (Linder, 1913), but at a higher degree than in *Marmornectes* and *Peloneustes* (Andrews, 1913; Ketchum and Benson, 2011). The postaxial margin is almost straight and differs from the condition reported in *Simolestes* and *Peloneustes* (Andrews, 1913), but is similar to that observed in *Liopleurodon ferox* (Linder, 1913).

The forelimb intermedium (Figure 7A-B) is a large element (right intermedium: 67 mm wide; 47 mm long) and exhibits distinct facets for the radius, ulna, radiale, ulnare, distal carpals 2 and 3, and distal carpal 4. The intermedium participates in the epipodial foramen, but its involvement is minimal.

The left radiale is a dorsoventrally thick, sub-hexagonal element 62 mm wide and 46 mm long. It bears a long and thick proximal facet for union with the radius, and an anterior facet for the preaxial accessory ossicle (not preserved). Distally, the radiale contacts the distal carpal (dc) 1 through a long facet, and both the intermedium and dc2 and dc3 along its postaxial margin.

The right ulnare is the smallest of the three proximal carpals. It is rounded and contacts the ulna proximally as well as the intermedium medially. Its thickness reduces towards its anterior part to form a very thin edge marked by a profound notch on its extremity, as in *Liopleurodon* and *Simolestes* (Andrews, 1913; Linder, 1913).

The distal carpal (dc) 1 is rounded and articulates with the radiale and the dc2 and 3. The dc2 and 3 is sub-hexagonal and larger than dc1. Additional elements partially preserved may be identified as metacarpal and phalange remains. Only one of them is complete and appears proximodistally elongated and hourglass shaped.

Pelvic girdle. Both pubes are fragmentary (Figure 6G). The left pubis presents a gently concave acetabular facet that is longer than the ischial facet. Its posterior border, medial to the ischial facet, is concave, and forms the anterior border of the thyroid fenestra.

A large portion of the left ischium is preserved and forms a blade-like element, antero-posteriorly longer than wide (estimated length 560 mm), as in other pliosauroids (Tarlo, 1960; Ketchum and Benson, 2011) and polycotylids (Williston, 1903; O'Keefe and Carrano, 2005; Albright et al., 2007a), and which become thinner posteriorly. The dorsal surface of the bone is concave, and its anterior margin forms a broad and concave curve. On the anteromedial side, a forward projection comes to a broad point and forms the anterior end of the curved medial border of the element. Posteriorly, the shaft of the left ischium indicates that the two posterior parts of the ischia would probably diverge from one another, as in *Simolestes* but more pronounced than the divergence reported in *Liopleurodon* and *Peloneustes* (Andrews, 1913). The posterior-most part of the ischium is partially preserved. The thyroid fenestra seems to be more rounded than that of *Peloneustes* (Andrews, 1913; Ketchum, 2007).

Both ilia are partially preserved; the dorsal end of the left one as well as the ventral end of the

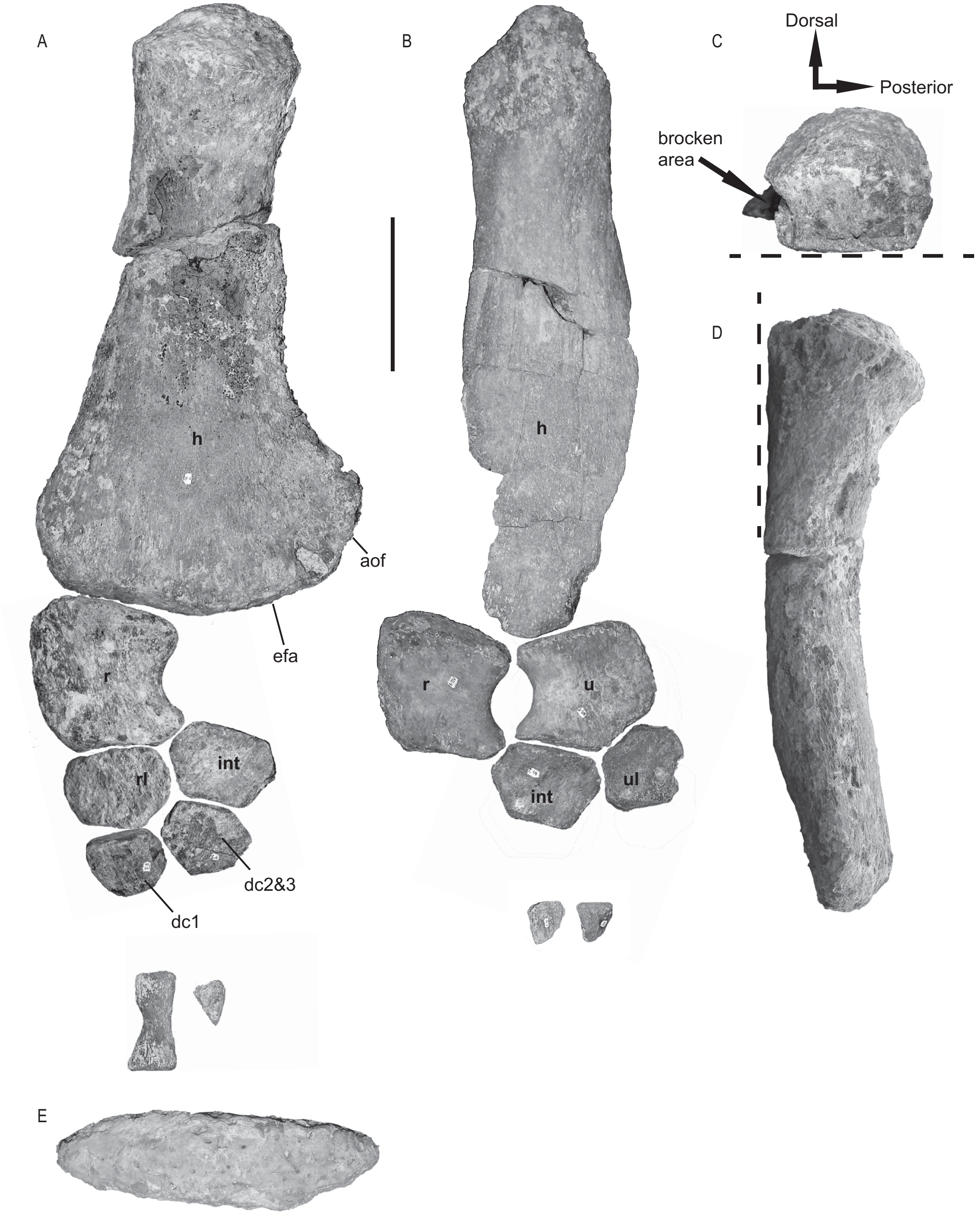

FIGURE 7. Anterior limb elements of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox):* A, left paddle in dorsal view; B right paddle in dorsal view; C, left humerus in proximal view; D, left humerus in anterior view; E, left humerus in distal view. The dotted line indicates the level of bone abrasion. Scale bar equals 10 cm. Abbreviations: aof, accessory ossicle facet; dc, distal carpal; efa, epipodial facet; h, humerus; int, intermedium; r, radius; rl, radial; u, ulna; ul, ulnare.

FIGURE 8. Posterior limb elements of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox):* A-E, right paddle in dorsal (A), distal (B), ventral (C), proximal (D), anterior (E) views; F, left paddle in ventral view. Scale bar equals 10 cm. Abbreviations: cap, capitulum; dt, distal tarsal; f, femur; fi, fibula; fib, fibular; int, intermedium; mt, metatarsal; t, tibia; tib, tibial.

right one are abraded. The ilia are elongate, left, and right measuring 258 mm and 256 mm, respectively. They are expanded at both extremities, the dorsal one (sacral end) more than the ventral (acetabular) one. The mid-shaft of the ilium is sub-oval in outline. The ventral end is approximately rotated about 90 degrees relative to the iliac blade and bears two facets, which are sub-equal in size: a posteromedial ischium facet and a more anterolateral facet contributing in the acetabulum margin. The ilium does not bear any ridge contra that reported for *Peloneustes* (Andrews, 1913; Ketchum, 2007).

Hindlimb. Both femora are preserved (Figure 8) and appear relatively elongate with concave preaxial and postaxial margins. They are slightly longer (right femur: 480 mm long; left femur: 470 mm long) than the humeri, similar to *Pliosaurus rossicus* (Halstead, 1971) and *Liopleurodon ferox* (Linder, 1913), and as robust as the femora observed in other Callovian pliosauroids except *Marmornectes* (Ketchum and Benson, 2011). Both femora are fractured and abraded ventrally (Figure 8D-E). The proximal ends are poorly preserved, preventing the observation, if present, of the postaxial process and the rugosities. The posterodistal end of the right femur is only partially preserved (Figure 8A-B), whereas the distal portion of the left femur is well-preserved (Figure 8C). The latter is expanded and dorsoventrally flattened (Figure 8F) and bears two well-developed, but poorly distinctive, facets for contact with the epipodials. The facet for the tibia is slightly longer than the one for the fibula.

The tibia and fibula are morphologically similar to the radius and ulna, respectively, but longer (left tibia: 120 mm long; right tibia: 117 mm long; left fibula: 93 mm long; right fibula: 96 mm long) as is typical in pliosaurids (e.g., Andrews, 1913; Tarlo, 1960). The overall morphology of the tibia is similar to the one reported in *Liopleurodon, Peloneustes,* and *Marmornectes* (Andrews, 1913; Tarlo, 1960; Ketchum and Benson, 2011). The tibia (Figure 8B-C) is longer than wide, and its proximal facet for the femur is straight as in *Peloneustes philarchus* and *Liopleurodon ferox* (Andrews, 1913). The preaxial border is slightly convex as in *Peloneustes* and *Liopleurodon ferox* (Andrews, 1913; Ketchum, 2007), and the postaxial border is concave, forming the anterior margin of the epipodial foramen. The epipodial foramen is closed distally by contact between the tibia and fibula and is less extensive than that observed in the forelimb. The tibia shows a proximal facet for contact with the fibula, and a short and well-developed distal facet for the intermedium as in *Peloneustes, Liopleurodon,* and other pliosauroids (Andrews, 1913; Tarlo, 1960), but unlike *Marmornectes* (Ketchum and Benson, 2011). A long and concave distal facet for the tibiale is also visible on the tibia, as well as a short and oblique facet, located preaxially, for a preaxial accessory ossicle which is not preserved.

The fibula (Figure 8C, F) has a lunate outline with a concave preaxial margin that forms the posterior border of the epipodial foramen as in *Liopleurodon ferox* (Adrews, 1913; Linder, 1913). A posteriorly oblique proximal facet contacts a postaxial accessory ossicle preserved on the left paddle. The tibiale, intermedium, and ulnare are similar in shape to the elements of the forelimb. Only one distal tarsal (dt) is preserved and identified as the dt2 and 3. One metatarsal (mt) shows a triangular-shaped proximal end and is thus interpreted as the mt2. Only few phalanges are preserved preventing the determination of the phalangeal formula.

Cladistic Analysis

The parsimony analysis of the data matrix yielded 2000 most parsimonious trees of 1937 steps. We do not detail the results within the Rhomaleosauridae, nor the results within the Plesiosauroidea. The topology of the strict consensus (Figure 9) positions the Thouarsais specimen as the sister taxon of *Liopleurodon ferox*, and this clade is supported by four synapomorphies: the presence of transversely concave/convex cervical zygapophyseal facets (character 169, state 1), cervical centrum mediolateral width subequal to height or less (character 171, sate 0), caudal ribs facet located at midheight of centrum or lower in proximal–middle caudal vertebrae (character 188, state 2), and the chevron facets of caudal vertebrae that are located mainly on the posterior edge of the centra (character 192, sate 1). *Thalassiodracon hawkinsii* is sister taxon of the clade grouping Rhomaleosauridae and Pliosauridae. The clade that includes the three species of *Hauffiosaurus* is the sister taxon to all other members of Pliosauridae. The overall relationships among taxa within this latter clade remain largely unresolved, similar to the relationships identified by Sachs et al. (2023) in their analysis using unweighted parsimony.

INTERPRETATION AND DISCUSSION

Comparison and Identification

The Thouarsais specimen displays several typical pliosaurid traits including wide cervical centra related to their length and height, a slightly convex ventral surface on cervical centra, a dorsal tip of the ilium flaring asymmetrically dorsally, and a convex preaxial margin on the tibia (e.g., Andrews, 1913; Tarlo, 1960; O'Keefe, 2001; Ketchum and Benson, 2010, 2011). The specimen also possesses a large antero-posterior expansion of the dorsal part of the ilium, the only unambiguous synapomorphy characterizing the clade Thalassophonea (Benson and Druckenmiller, 2014).

Information regarding the postcranial morphology in pliosaurids are limited, thus comparisons with *Pliosaurus patagonicus* Gasparini and O'Gorman, 2014, *Gallardosaurus iturraldei* Gasparini, 2009, *Pliosaurus westburyensis* Benson et al., 2013b, and *Pliosaurus kevani* Benson et al., 2013b, are not possible as these taxa are only or mostly known through skull remains. However, comparisons with pliosaurids in which postcranial skeletons are known show that (1) the absence of ventral ridge on cervical vertebrae of the Thouarsais specimen, as well as (2) the short size of its cervical centra, (3) the presence of a ventral lip on the latter, and (4) the presence of double-headed cervical rib facets, differ from (1) *Peloneustes, P.*

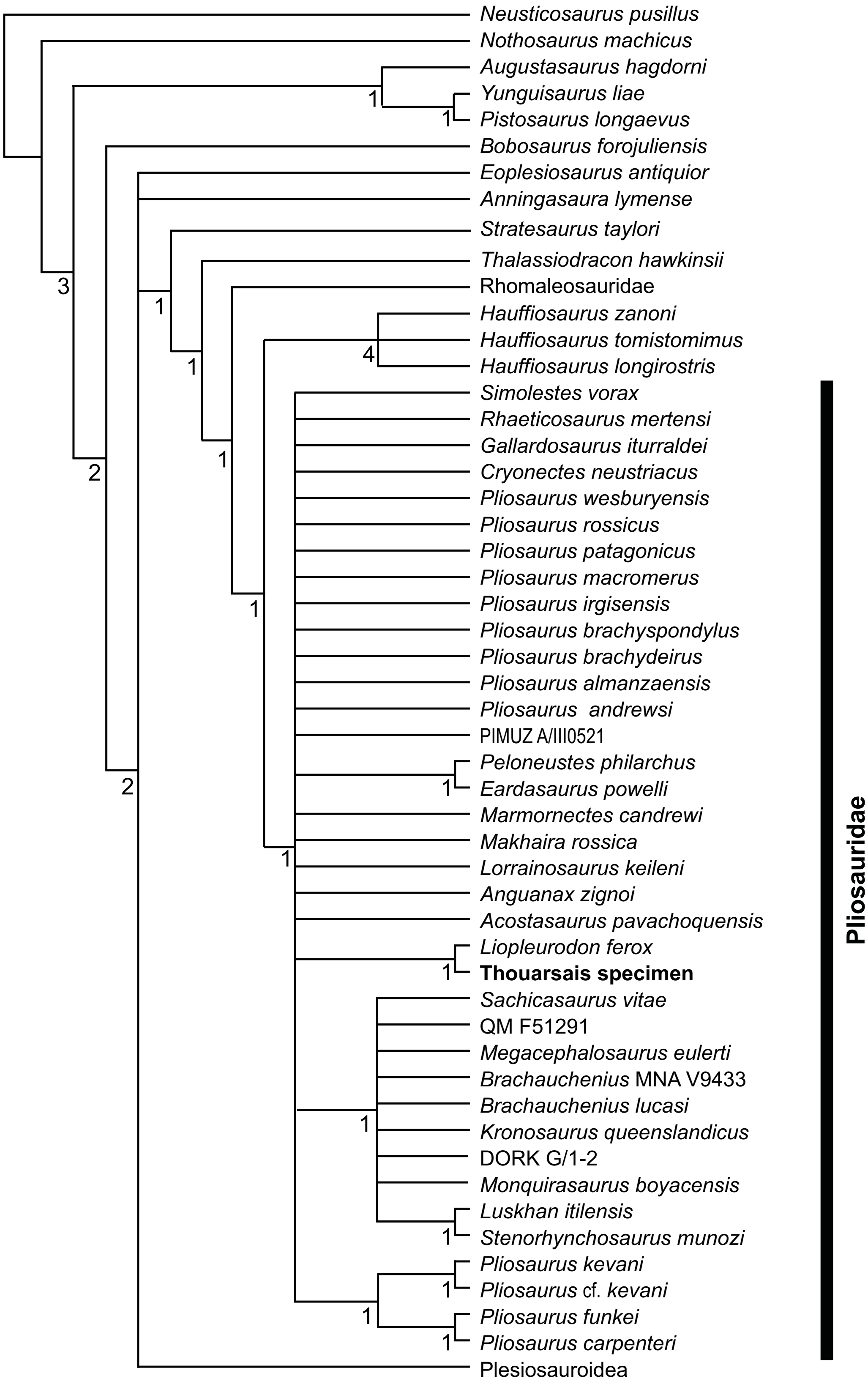

FIGURE 9. Cladogram showing the relationships of the ComCom Thouarsais_Geol.0121 specimen *(Liopleurodon ferox)* within Pliosauridae: strict consensus of the maximum-parsimony analysis. For character matrix, see Appendix 1. CI=0.204, RI=0679. Bremer indices are indicated for each node.

brachydeirus, and *Eardasaurus powelli* Ketchum and Benson, 2022, (2) *Makhaira*, (3) *Stenorhynchosaurus*, BRSMG Cc332 (*Pliosaurus* sp., previously *Pliosaurus brachyspondylus*), as well as *Pliosaurus rossicus,* and (4) *Stenorhynchosaurus, Plesiopleurodon, Brachauchenius,* and *Sachicasaurus,* respectively (Tarlo, 1959; Halstead, 1971; Taylor and Cruickshank, 1993; Carpenter, 1996; Albright et al., 2007a, b; Ketchum and Benson, 2011; Benson et al., 2013b; Fischer et al., 2015; Páramo-Fonseca et al., 2016, 2018). In addition, the presence of ventral foramina on cervical centra in the Thouarsais specimen differs from most brachauchenine pliosaurids, except for *Sachicasaurus* and *Luskhan* (Benson and Druckenmiller, 2014; Fischer et al., 2017; Páramo-Fonseca et al., 2018). The cervical rib facets in the Thouarsais specimen are located ventro-laterally, as is typical in Jurassic pliosaurids (Fischer et al., 2017), and differ from the Cretaceous taxa *Kronosaurus, Luskhan,* and *Brachauchenius* in which the facets are located at mid-height of cervical centra (Fischer et al., 2017). The specimen *'Pliosaurus' andrewsi* (NHMUK R3891) is distinguishable from the Thouarsais specimen by showing cervical neural spines that are transversely expanded dorsally, being wider medio-laterally than long antero-posteriorly (Andrews, 1913).

In the pectoral girdle, the anterior edge of the scapular dorsal process is sinusoidal in the Thouarsais specimen and differs from the one described in *Simolestes, 'Pliosaurus' andrewsi* (NHMUK R3891), *Pliosaurus carpenteri* (BRSMG Cd6172), and *Pliosaurus rossicus* (Tarlo, 1960; Ketchum and Benson, 2011).

Comparisons between propodial elements show that the Thouarsais specimen differs from *Pliosaurus funkei* in which the distal pre- and postaxial margins of the humeral shaft are symmetrical with no prominent postaxial expansion at the distal end (Knutsen et al., 2012). The femur in the Thouarsais specimen presents an expanded distal end that contrasts with the slender femur and the slightly expanded distal end observed in the pliosaurids *Luskhan* and *Stenorhynchosaurus*, as well as in the specimen MUHNCAL.20188 (Páramo-Fonseca et al., 2016; Fischer et al., 2017; Otero et al., 2020).

The epipodials in the Thouarsais specimen, longer proximo-distally than wide antero-posteriorly, differ from those of the pliosaurid specimen CAMSM J.35990 (Tarlo, 1960; Knutsen et al., 2012), previously identified as *Stretosaurus macromerus* Phillips, 1871, but provisionally referred to *Pliosaurus* cf. *kevani* by Benson et al. (2013b), *'Pliosaurus' andrewsi* (NHMUK R3891), and *Pliosaurus brachydeirus* (Tarlo, 1960), as well as *Stenorhynchosaurus, Pliosaurus almanzaensis,* and *Pliosaurus funkei* (Knutsen et al., 2012; Páramo-Fonseca et al., 2016; O'Gorman et al., 2018). In addition, the presence of an epipodial foramen in the Thouarsais specimen allows to distinguish it from *Luskhan* (Fischer et al., 2017). The straight proximal surfaces of both the radius and ulna in the Thouarsais specimen contrast with the highly convex surfaces observed in *Pliosaurus carpenteri* (BRSMG Cd61172; Benson et al., 2013b).

Although the osteological features observed in the Thouarsais specimen contrast with most of pliosaurids, it shares some of the diagnostic characters that were reported from the post-cranial skeleton of *Liopleurodon ferox* (Andrews, 1913; Tarlo, 1960). Indeed, both the Thouarsais specimen and *Liopleurodon ferox* exhibit a ventral lip developed on the anterior surface of the cervical centrum without any ventral keel (Tarlo, 1960), and double-headed rib facets on the cervical vertebrae (Andrews, 1913). In addition, the Thouarsais specimen presents a combination of characters that can be relevant for its assignation to the species *Liopleurodon ferox* following Andrews (1913): short cervical centra (length equal or less than half width or height); cervical centra with a ventral lip and no ventral keel; two cervical rib facets on anterior and middle cervical centra; transversely compressed cervical neural spines longer antero-posteriorly than wide transversely with a teardrop- to oval-shaped dorsal tip; zygapophyses transversely narrower than the cervical centra; dorsal centra as high as wide and shorter than high; thin dorsal neural spine inclined postero-dorsally; sacral rib shaft twisted with a ridge extending dorsoventrally from the rib head to the flared distal end; dorsal process of the scapula with a convex, acute, and slightly sinusoidal anterior edge; humeral shaft that curves dorsodistally; humerus with pre- and postaxial margins of the shaft asymmetrical, distally, and with distinct radial and ulnar facets; radius longer than wide with concave postaxial borders forming the preaxial margin of a large epipodial foramen; ulna with a concave preaxial margin forming the postaxial border of the epipodial foramen, and a nearly straight postaxial margin; a femur longer than the humerus; epipodial foramen enclosed by tibia and fibula; tibia longer than wide.

Differences are also observed between the Thouarsais specimen and specimens previously assigned to *Liopleurodon ferox*. Thus, the length of the cervical centra, represents approximately 2/3 of the width and height of the vertebra in the Thouarsais specimen but less than half of the width and height in *Liopleurodon ferox* specimen NHMUK R.3536 (Tarlo, 1960). In addition, the neurocentral suture between the cervical neural arches and associated centra displays a V-shaped configuration in the Thouarsais specimen differing from the rounded suture observed in mounted specimen of *Liopleuodon ferox* (GPIT-PV-30093; and see character 172 in Sachs et al., 2023). Overall, these comparisons indicate possible intraspecific (including ontogenetic) variation in *Liopleurodon ferox,* and further studies should consider such a variability.

Based on comparisons performed here, the Thouarsais specimen is assigned to *Liopleurodon ferox*. Recently, Madzia et al. (2022) questioned the taxonomic status of the species *L. ferox* and recommended a taxonomic revision of the genus *Liopleurodon*. Pending a possible revision and according to Noè (2001), the genus *Liopleurodon* is monospecific, *Liopleurodon pachydeirus* being con-specific with *Liopleurodon ferox*, and '*Liopleurodon' macromerus* as well as *'Liopleurodon' rossicus* belonging to the genus *Pliosaurus* (Noè et al., 2004; Knutsen, 2012; Benson et al., 2013b). Among the 14 specimens referred to *Liopleurodon ferox* (Noè, 2001), excluding the isolated teeth present in numerous museum collections (Noè, 2001), only four include post-cranial remains: GPIT 2 (Huene, 1934), GPIT-PV-30093 mounted specimen (Linder, 1913), NHMUK R3536 and NHMUK R2446 (Andrews, 1913; Tarlo, 1960). Both specimens GPIT 2 and NHMUK R2446 being less complete, the Thouarsais specimen represents the most complete specimen from France and corresponds to the second or third most-complete post-cranial skeleton of a *Liopleurodon ferox* described so far, depending to what degree the specimen GPIT-PV-30093 is a composite skeleton (Noè, 2001; Martill et al., 2023).

Ontogenetic Stage

Various characters can be used to determine the ontogenetic status of plesiosaur specimens (Araújo and Smith, 2023). Among these characters, the fusion of the vertebral centra with the neural arches is one of the most widely used to determine whether the specimen is mature or not (Brown, 1981; Araújo et al., 2015). Indeed, the neurocentral junction in juvenile vertebrates is an important zone of growth for both the neural arch and the centrum (Vital et al., 1989), which connects these two separately ossified elements by cartilage (Ikejiri, 2012). The neurocentral junction fuses by the ossification of cartilage at or before the time of maturity (Romer, 1956). In plesiosaurs, open neurocentral sutures are present in juvenile and subadult plesiosaur specimens and are probably one of the last juvenile characters to disappear during ontogeny (Vincent, 2010). Here, we follow Brochu (1992, 1996) and Irmis (2007) who have specified certain definitions on this point: "an open suture is one that is visible on the surface of the bone, regardless of whether the two elements are firmly attached to each other. A closed suture has no trace of the suture on the surface of the bone. Whether or not two bony elements have actually 'fused' in the traditional sense cannot be determined without histologically sectioning across the boundary (Brochu, 1996; Cole et al., 2003) or using noninvasive high-resolution imaging such as computed tomography" (Irmis, 2007).

In the vertebral column of the Thouarsais specimen, the neural arches or ribs are attached to their corresponding centra (cervical, pectoral, dorsal, and sacral vertebrae) and show a marked suture on their surface (Figure 3C-E), which is identified as an open suture following Brochu (1992, 1996) and Irmis (2007). The specimen should thus not to be considered as an osteologically mature specimen sensu Araújo et al. (2015), but as a 'juvenile' individual sensu Brown (1981). However, as previously noted by McHenry (2009), Knutsen et al. (2012), and more recently by Ketchum and Benson (2022) as well as Araújo and Smith (2023), the neurocentral sutures between the cervical vertebral centra and associated neural arches remain open (still visible) in all large pliosaurids (see Table 1 and references herein). This differs from the sutures between the neural arches and associated centra of dorsal vertebrae that remain open in all pliosaurids (Table 1) except *Brachauchenius* (adult specimen MNA V9433), in which the suture is open on the cervical vertebrae but closed on the dorsal vertebrae (Albright et al, 2007b). The data available for caudal vertebrae remain rare; however, when observed, the sutures between the neural arches and centra of caudal vertebrae remain open in all pliosaurids (Table 1) except in *Peloneustes* (CAMSM J.46913, holotype), in which closed neural sutures are observed on the posterior caudals (Ketchum, 2007). The sutures between cervical ribs and centra remain open in the Thouarsais specimen. Such a feature is also observed in all pliosaurids in which cervical rib and centra are preserved (Table 1), except for

TABLE 1. Pliosaurid suture conditions, whether closed, open (indicated by the X symbol), or unknown (?), observed between the centra of cervical, dorsal as well as caudal vertebrae, along with their associated neural arches or ribs.

Taxa	Specimen collection numbers	Open sutures between the neural arches and centra of cervical vertebrae	Open sutures between the neural arches and centra of dorsal vertebrae	Open sutures between the neural arches and centra of caudal vertebrae	Open sutures between cervical ribs and centra	References
Arminisaurus schuberti	NAMU ES/jl 36052 (holotype)	x	x	x	x	Sachs and Kear, 2018
Brachauchenius lucasi	MNA V9433	x	closed	?	x	Albright et al., 2007b
Cryonectes neustriacus	MAE2007.1.1(J) (holotype)	x	?	?	x	Vincent et al., 2013
Eardasaurus powelli	OUMNH PAL-J.2247 (holotype)	x	?	?	x	Ketchum and Benson, 2022
Eiectus longmani	MCZ 1285 (holotype)	x	?	x	x/closed	Romer and Lewis, 1935; Noè and Gómez-Pérez, 2022
Gallardasaurus iturraldei	MNHNCu P300 (holotype)	x	?	?	closed	Gasparini, 2009
Hauffiosaurus tomistomimus	MANCH LL8004 (holotype)	x	x	x	x	Benson et al., 2011
Hauffiosaurus zanoni	Hauff uncataloged (holotype)	x	?	x	x	pers. obs; Vincent, 2011
Hauffiosaurus longirostris	MCZ 1033 (holotype)	?	?	?	closed	White, 1940
Kronosaurus queenslandicus	QM F1609 (holotype)	?	?	?	?	Longman, 1924; Noè and Gómez-Pérez, 2022
Liopleurodon ferox	NHMUK R. 3536	x	?	?	x	Andrews, 1913; Tarlo, 1960
Liopleurodon ferox	GPIT-PV-30093 (mounted specimen)	x	x	?	x	Linder, 1913; pers. obs.
Makhaira rossica	YKM 68249/1-10 (holotype)	?	x	?	?	Fischer et al., 2015
Marmornectes candrewi	BEDFM 1999.201 (holotype)	x	x	x	x	Ketchum and Benson, 2011
Megacephalosaurus eulerti	FHSM VP-321 (holotype)	x	?	?	x	Schumacher et al., 2013
Monquirasaurus boyacensis	MJACM 1 (holotype)	x	?	?	?	Noè and Gomez-Perez, 2022
Pachycostasaurus dawni	PETMG R338 (holotype)	x	x	?	x	Cruickshank et al., 1996
Peloneustes philarchus	CAMSM J.46913 (holotype) and refered materiel	x	x	x/closed	closed	Ketchum, 2007
Pliosaurus brachydeirus	OUMNH J.9245 (holotype)	x	?	?	x	Tarlo, 1960; Knutsen et al., 2012
Pliosaurus cf. *kevani*	CAMSM J.35990 (originally referred to as *Stretosaurus macromerus*)	x	x	x	x	Tarlo, 1960; Benson et al., 2013b

Table 1 (continued).

Taxa	Specimen collection numbers	Open sutures between the neural arches and centra of cervical vertebrae	Open sutures between the neural arches and centra of dorsal vertebrae	Open sutures between the neural arches and centra of caudal vertebrae	Open sutures between cervical ribs and centra	References
Pliosaurus funkei	PMO 214.135 (holotype) and PMO 214.136	x	x	?	?	Knutsen et al., 2012
Pliosauridae indet.	NHMUK R2439	x	?	x	x	Ketchum, 2007; Ketchum and Benson, 2011
Pliosauridae indet.	IGM 4546	?	x	?	?	Barrientos-Lara et al., 2015
Pliosauridae indet.	UANL- FCT-R2	x (pectoral vertebrae)	?	?	?	Buchy et al., 2003
Pliosaurus westburyensis	BRSMG Cc332 (holotype)	x	?	?	x	Taylor and Cruickshank, 1993; Knutsen et al., 2012; Benson et al., 2013b
Sachicasaurus vitae	MP111209-1 (holotype)	x	x	?	x	Páramo-Fonseca et al., 2016
Simolestes vorax	NHMUK R. 3319 (holotype)	x	?	?	?	Andrews, 1913
Stenorhynchosaurus munozi	VL17052004-1 (holotype)	x	x	?	x	Hampe, 2005; Páramo-Fonseca et al., 2018
Stenorhynchosaurus munozi	MP050310-1	x	?	?	closed	Páramo-Fonseca et al., 2019
Thalassophonea indet.	CAMSM J.29564 (previously type of *P. brachyspondylus*)	x	?	?	x	Knutsen et al., 2012; Benson et al., 2013b

Gallardosaurus (Gasparini, 2009) and *Peloneustes* (CAMSM J.46913; Ketchum, 2007).

Such a variability makes interpretation of ontogenetic stage from neurocentral sutures difficult in pliosaurids and requires specific attention. Without the observation of pliosaurids exhibiting a closed suture between neural arches and their cervical centra, it is impossible to know whether the neurocentral junctions fused even in old age. Thus, the lack of fusion between cervical neural arches and their centra in pliosaurids does not appear as a reliable indicator of a juvenile condition and could be considered as a paedomorphic feature of adult pliosaurids as already proposed by McHenry (2009), Knutsen et al. (2012), Ketchum and Benson (2022), and Araújo and Smith (2023). However, the lack of fusion between cervical ribs and their centra, as well as dorsal or caudal neural arches and their centra, remains questionable as it is not present in all pliosaurids. The characterization of being an osteologically mature individual of Plesiosauria (sensu Araújo et al., 2015) when the neurocentral suture is closed, should thus not been applied to taxa belonging to pliosaurids. Based on other post-cranial characters, such as the presence of well-defined articular facets on limb bones, the Thouarsais specimen is here interpreted as an ‘adult’ individual (sensu Brown 1981), showing a paedomorphic character of its neurocentral suture closure.

In some extant archosaurs (e.g., *Alligator mississippiensis*), the neurocentral sutures commonly remain open in at least some parts of the vertebral column (e.g., the presacral vertebrae in *A. mississippiensis*) long after sexual maturity (Brochu, 1996; Ikejiri, 2010, 2012). Similarly, the neurocen-

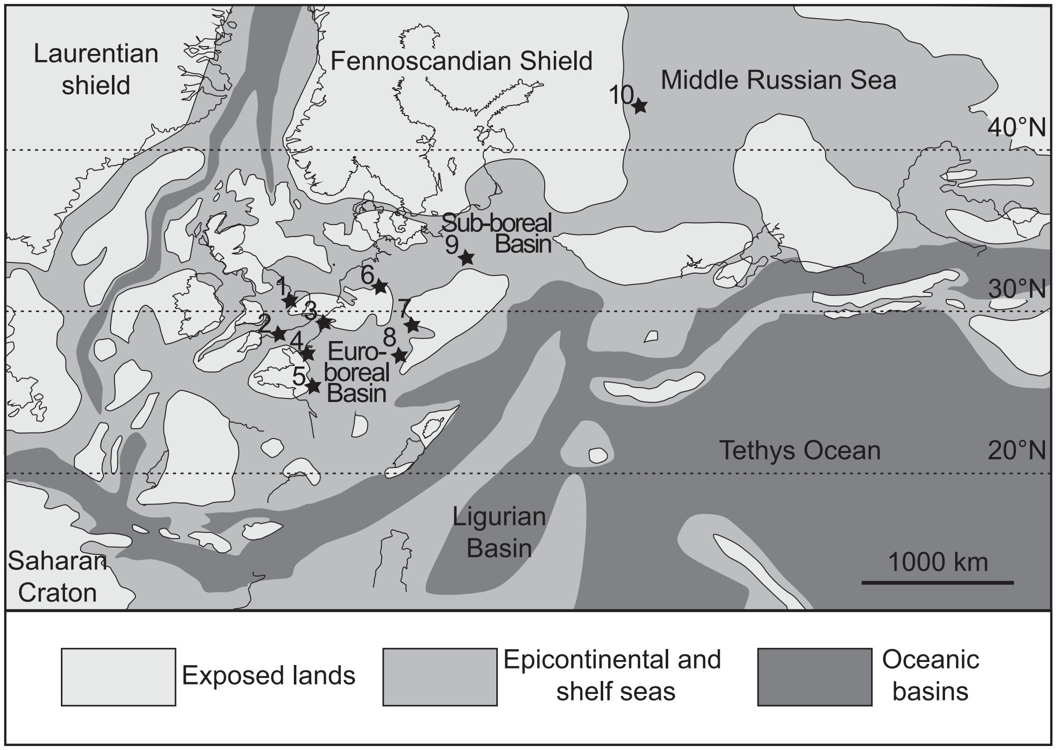

FIGURE 10. Global palaeogeography during the Callovian interval (modified from Wierzbowski and Rogov, 2011) showing the occurrences of *Liopleurodon ferox* specimens worldwide (shown by stars). Localities: 1, east of England (Cambridgeshire, Northamptonshire, Lincolnshire); 2, south west England (Dorset); 3, north France (Hauts-de-France); 4, north-western France (Normandy); 5, western France (Nouvelle-Aquitaine the specimen described here); 6, north-western Germany (Northrhine-Westphalia); 7, south Germany (Bavaria, Swabia and Württemberg); 8, north Switzerland (canton of Aargau); 9, Żnin County (north-central Poland); 10, Moscow basin, Russia (data from Tarlo, 1960; Sachs et al., 1997; Noé, 2001; Rauhut et al., 2016; Zverkov et al., 2017).

tral junctions remain unfused in sauropod dinosaurs even as the animals attained very large body sizes (Fronimos and Wilson, 2017). Such a feature, in archosaurs, is required to delay the closure and thus extends the period of rapid growth at the neurocentral junction that permit large body size (Vital et al., 1989; Ikejiri, 2012; Fronimos and Wilson, 2017). In this context, it is not surprising to observe open neurocentral sutures between neural arches and their centra in pliosaurids, as members of this clade usually achieve a large body size.

Paleogeographic Distribution of *Liopleurodon ferox*

Most of the remains of the pliosaurid *Liopleurodon ferox* have been found in England, but have also been previously reported from France, Germany, Switzerland, Russia and possibly from Poland, although the available remains in this last locality are fragmentary and identified on the basis of teeth only (Lydekker, 1889; Persson, 1963; Bardet, 1993; Bardet et al., 1993b; Noé, 2001; Zverkov et al., 2017, 2024). The Thouarsais specimen extends the biogeographical area of the species *Liopleurodon ferox* into Central France (Figure 10) and represents the southernmost occurrence of this taxon. *Liopleurodon ferox* was thus present in three basins: the Sub-Boreal (i.e., Yorkshire, northern Germany and Poland) and Euro-Boreal basins (i.e., Paris, Central France, Wessex, Swabian basins), and a third one corresponding to the Moscow basin (Persson, 1963; Noé, 2001; Zverkov et al., 2017, 2024).

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APPENDIX 1

Matrix coding for the ComCom Thouarsais_Geol.0121 specimen using data matrix of Sachs et al. (2023).

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Neusticosaurus_pusillus
    0000001000000000???00000000020000?000000?000010??00000001?00?00?00?????????000??
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    0010000000010000000?1000?03000?0000200000110200?00000?0100????00011001000?000001
    200100??20??000000000000?00?0
Nothosaurus_marchicus
    11000021110?00?00??020002100200000001??110000?0??000001?1?0??10?000??1001??001???
    ?????1000100000???1?0??0???101110?10?00010?00???010100121010??????????11000??0??1
    1000000010001000?1000?0?????????[0
    1]00000110100?00000?0100?????00011001000??00001100000??20??000000000000?0???
Augustasaurus_hagdorni
    010100?0010?00000??00100100000000000000100?0010012101000010??????0???0?0000?????
    ?02??000?0110000?0010000????0?1100?10??1001??1???01010002100??00??21??41?01??00
    0000200?0?1000011??0000???????????00?000?102?020000?0?????????????????000??00???
    100000000???0?100?1000???0?00
Bobosaurus_forojuliensis
    ????????????????0???????????????????????????????????????????????????????????????
    ???????????????????????????????????????????????????????02?0?00?00??01?2100000??1
    10?12?000?0??001221100?10?1????????????????????????????????0122010?001??????0???
    1?000????????0???0?0??0??????
Pistosaurus_longaevus
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    ?02??00000??0000?0010020????20????????????????????[1
    2]0100??00?????????????2001110000000000011100101100010????101110?00?001?202100??0?
    ?001????0122210???1??????01?1?00000000???0???0?10????????0
Yunguisaurus_liae
    0001000??10000000??0010010?000010010?000?000110??200??00????01020???????????????
    ?02?10???????0?0?0010020???10011001100?1001?1????13??0??????1??????????41000??00
    ?000000?001?0??01210?0?00[2
    3]??0??????0?000?200?????????????0?00122011?0000002000??11000?000?0?00000001000010
    0000
Abyssosaurus_nataliae
    ????????????????????????????????????????????????????????????????????????????????
    ????????????????????????????????????????????????????????????2???1110??1?1001???3
    201200111??1?01??1011??0???0???????0010000100??2??10?0?001?1?1101110??2?1??1????1
    0???10?22?0?3??110???1001211
Acostasaurus_pavachoquensis
    11?1?0?0211?10210??010110?00210?0100???????00?0103112????201?00?1000012?1?10100??
    ?2?1??0?1101010?0210?3?1?????11101111000111120?00011010000?1110??0??0?0001???1?01
    110000??0?0?????????????????????????????????????????????????????????????????????
    ??????????????????????????
Albertonectes_vanderveldei
    ????????????????????????????????????????????????????????????????????????????????
    ????????????????????????????????????????????????????????????2?1?1101?026311122232
    0220011111001110?1100?01200?11112001110110?[1
    2]1??????10???11?11?01001?0002000??12021010122?12210110[0 1]0110[0 1]1211
Anguanax_zignoi
    ????01?0??????????????????????????1??????????????????????????0??????????????????
    ???????????????????????????????????11????1?????????????1??0????0????1???0?01????
    ?0??10????????????????????00??????????????????????????????????????????????????0?
    ?0???00??1????1?1?0?0????1??0
Anningasaura_lymense
    111000?0120?00??10000100?0010000100000?10000010112001000?10?0?1020?0110111010010?
    00211?100000011?00?000?111??1110?100?1010?110??00010011000?0?00??0?0??10010??3?0
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    ?120100?01?1??????????????????????????????????????????????????????????????
    ???????????????????????????
Archaeonectrus_rostratus
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    ??????????????????????????????11??1????1?????????????11120?0??????????21001001110
    00201???011?0110110110010??????0?????0?20?1??????????????01?2?1100?10001000??1?02
    0?00??11011011010001101100
Aristonectes_parvidens
    00?010??1?0000201??00200200000??00?????11??01010?3212?1?0000?00?1?01212010??????
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    ??200111??1?0????????????????????????????????????????????????????????????????
    ?????????????????????????????
Aristonectes_quiriquinensis
    00??1?0?????0?????????????????????????????????????3???????????00?1????120?0????01
    00??????????????????2?110???????201?10???000???2??0??0?01123?1?10???1?014111122132
    022001111?100?????????????201??01?20?1100111011200?021????????????????100?1000???0
    3201112?1?1?101?00011?01210
Arminisaurus_schuberti
    ?????????????????????????????????????????????????????????????????????????????
    ??????????????????????????????0???010??1011???2?01?????10?0?????????????1001?1?1
    1011[1 2]01001?01[0
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    ??????0????????0
Atychodracon_megacephalus
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    1002111000100011011???00?0002001111?0??20?0?11??0??00001020?0???0???10120001???11
    00?201????0?00111?1012001??20?0?0???????????1?????????????01022110????????00??1?0
    201001?110?1??1010??0?????0
Avalonnectes_arturi
    ??????????01??10????????10?????01??00001000001001100100001010??????????????????
    1??????0?????????????????????????????????????????????????????????????2100?0021
    1001??100?010001101101200?0110?00????1?01201????????????????0102?110??1?????????11
    020?000?110110?101000010?100
Borealonectes_russelli
    11010?1?210?102011100?00?0?0000??010?0010010000????1?000??0?0???20???12000???????
    022?1?0???????0??2???201?????111??00???1?0?110??0??1?01?10?00100??21?120001???2?0
    ??20?????0?0????????1??????????????????????????????????????????????100??00?????
    1101012???2?011?0001???11?1
Brancasaurus_brancai_composite_SHK
    00???0?0?0?????0102???0011??????0??????1?010??02??3?1?1?110?001101?[0
    1]1???1???????0022???????1????????????????????????100?1110???2??1??????????2010???
    10?[1 2]410010[0 1]2320121010110[0 1]0[0 2]1110011[0 1]0000[1 2]011101[0
    1]???1??1??20???????210?0?010121021010??????0111?02001022210???????0????????0
Brachauchenius_lucasi
    00020120211100210??010001000210?111?0001012001000312100012??00??????????????????
    011?0100?1011?0??2100310???211???001?00001?11?????????10?0?0???0?????000002????21
    1?00?????????00??001??????????????????????????????????????????????????????????????
    ??????????????????????11111
Brachauchenius_MNA_V9433
    0102?????1?100210??0100010?0?????????0001???00?002?1210?0?20?0????0??????????????
    ???????00????110??2110210???2111000010?0001?1110000000110000???????????0000211?32
    11100000?20?2?0???01???????????????0?1???????22200002?????11??0011?10?????????????
    ???????????????????????????
Callawayasaurus_colombiensis
    000010?0?10000??10100?0020?000?10????????0101000022010101000111011??02?1010??1?0
    02211001????0?0???2?1100???1?1101??0??20?????2??010000110012??????????52101022320
    22001111?100111211110???????????200100?11001120010?10?01?????????00??0???100?22030
    0102?3101200?10?0111??2?1
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Colymbosaurus_trochanterius
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20?200111??1?01??1011??00?2010101??0???????????2??102?2???????????????201??10111?
22101012210221011102?11101211

Cryptonectes_neustriacus
10???????????1[0
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1?10121?00??000??1?01?10010010?1110?011?01???01????????????1001???1?0??00???0?[0
1]?0??
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Cryptoclidus_eurymerus
00100?0010?101100??001001010000100000201002010010110100000000010?1011101101?111011
111??00101100011?00?0???000?02001100?1000?0021?020000111012111101?01310011123201
1001110000001110110000000010001121011001010201201020200?11002101101 12010?1011130320
1012210130011 0?2??001211

Djupedalia_engeri
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012001110310011 0??1100???????????????11?0???0?0??01??????3??????????????2?0??????1?0
2?0?012?1???101102???1?1211

Dolichorhynchops_bonneri
0012012010000021 0??010000110001?001001010021???223010111010?110??1?0?1?????1????0
013111?10?100011122?020010[0
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2]11

Dolichorhynchops_herschelensis
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2]?110?00?011?100?21110??????2011100201101 11?110?21113????????????????????????????
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Dolichorhynchops_osborni“
00120120110000201110100001 10001?001001010021??22311[0
1]1110100110?01102?201001?011001311111001000111 22?01001010?10000110011010120011 1000
21120?0110100010210001012 32011[1
2]0100000100112011 0?0000???11??10110100000201110020110111011012111321010000010 1200
10221103310110 1011001[1 2]11

Dolichorhynchops_ROM_29010
00?[12]???0????00[1
2]?1110??00???0????????????????????223??01???10???0?0110211010010011001311??1?????
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11?00100???0120101????1?110020??????????1010????????11?210???10???13101022?1?3?10
1?0101?001??1

Dolichorhynchops_tropicensis
00120?20???0002?11101000?1?0001?0010????????1?????2[2
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0??0???111200102?21033101101011 00121?

DORK_G_1_2
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Eardasaurus_powelli
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    ?2211???????????12110300?????1111?110000001111000[1 2]1110102000??00??2??01000[1
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    0?000002100012?0022101110011111111
Edgarosaurus_muddi
    100101?021001020111010001??0?0??001000010?200102220011101000111101?02?2?1?0????10
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Elasmosaurus_platyurus
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    2]????0?????????????????????????????????????????0?????????????????????????????????
    ?????????????100??????????????????0??011??1201?1001?0263111?22320?2101????1???11??
    1110???20011?1??10110?1100??1??102?????01?120?1??01???????????????????????????????
    ?????????
Eoplesiosaurus_antiquior
    ??????????????????????????????????????????????????????????????????????????????????
    ?????????????????????????????????????????????????????????????2??????????4100?0111
    ?0?12?1???0??0??????????01000?11?02??1001002?0?0??00???????0??2?11?00110020000?11
    010100??1?0110?1010000101100
Eopolycotylus_rankini
    00??????????10????????00???[0
    1]?????????????????????????????????????????????????????????????????????????????????
    ????000??????????11?0??1000110?0??????????????0?01?01?2?????1??1?00?01?2?110??????
    ??????0?1100?00202011?1???111110?00?21113210??01??1?12001022210?2???1????11011?1
Eretmosaurus_rugosus
    ??????????????????????????????????????????????????????????????????????????????????
    ???????????????????????????????????????????????????????????????????????????10011?1
    00?1201000000111??11?0???0000?01????1?????????0??0???????0010201200011000000??11
    021?100020011011010000201100
Eromangasaurus_australis
    000000???10000??10200?0020?000??00?000010??0010???????101?0?11????????????????????
    ??2????????????0????????????????1011?????010????????000011001?01?1101??2?2101???3?
    0?????????1?0?????????????????????????????????????????????????????????????????????
    ????????????????????????????
Eurycleidus_arcuatus
    ??????????????????????????????????????????????????????????????????????????????????
    ????????????????????????????????111??????????1?????????01110?????????????100100211
    00020100000100?1?1101???0110100?201101120010201000100?10001020110001??????0101?0
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Futabasaurus_suzukii
    00??000?1?0?00??0??00?0?2?0000?????????????????????0???1??????????????????????????
    ?????????0110000????????????????100??????0?????????10000110????????????????11?22?2
    022001111?10?11110111000??????????????????????????????01301?1??01?0?1100200000220
    300102221122101100011101?10
Gallardosaurus_iturraldei
    ??0?01?022?1??21????????10??????11?0000100200100?3121100020?011021???1???????????
    ?121110???0?010?12110310???211?????1???0???????????????????2???00??2111?0001??1?0
    ?110?0??2?????????????????????????????????????????????????????????????????????????
    ???????????????????????????
Georgiasaurus_penzensis
    0012??2??0??00??11101000???0?0???0???????????????????????????????????????????????1
    00??1????????0?11?????20?1?1??100???????????????????????[1
    2]???0?0???????????0???????????????????????????????????????????????1???????????????
    ????????????????????????????????????????????????????????
Hauffiosaurus_longirostris
    00?20??0?1??12111120??00???2?????????????????????02???????????01001??0???1?0?????1
    110?????????????110?0??0?????1001?100?1100?11?0023010011200???????????????????????
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Hauffiosaurus_tomistomimus
00020?10210?1?110??0100?0?0210100100???????00?00010100?0?101?01011??????1001????
111011?0?0100010?100?010??????1000?100?1100?112002301001120?1100????1231001?11110
?10010000000011101010001??10???0???1??1?0?0????????????00????????00???0?10000120
10000121?01101?1?0?11201?00

Hauffiosaurus_zanoni
00?2??1??1???????????????0?0???????????0?10????????????00?001???010????????????????
11101101?0100010?100?010????20100??100?1100??12002301?01120000?00??????310011?111
00100100?00?00?????????0?0110000201101120??0020000?010?0001020?2?0001001000??110
10?00121??11011010001101100

Hydrotherosaurus_alexandrae
000010?0??0000201?100?002??0000?0011000100111?????2121?111??01???????????????????
?????????????????????????????100010?1?01??112???10000110012???1?????152111222320
2200111?11001110011100002011?11?1001?00001011200?020????120111011000100?000??12031
010123102300110?011101211

Hydralmosaurus_serpentinus
0?0010?0??000???121?020020?0000?0??10??1001????0?3??2?111?0?11???10??12???????0??
?????????????????????????????????1?0???0?????????1???01?0??2???????????6311122232
02200111111001110?11100?02010111??0011???????12????2100?11101100?10?1100??000010?3
1010122103210110??110?1?10

Kaiwhekea_katiki
00001010??000???1020020020?000?????????11????0?0?32?2111000?00??????????????????
?????????????????????????????0101?10??1000??????0300001120?2??????????51011122320
?2?0111?1100?11111?10???2????0???000??00??11?3
2?11??3?12110100?0012?1??0

Kawanectes_lafquenianum
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???21112223
2022?01111?1001??00111000?2001001????1?001?1???????????????01???10??001?0????0???2?
03101112310?3???101??11?1??1

Kimmerosaurus_langhami
??1??0?1??0?0?????????????0?????10??0??????20100000102000000011101010201101?101111
111??????????????200?0????????0200110001000?002??0?00?01220???1?1001?01?00011??3?0
1100111??1?0??
??????????????????????????

Monquirasaurus_boyacensis
??????2????????2???????????0????????11?0??1???0010????2??????????????????????????????
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?1?????????????0??10??1??000??????0
0?110????1??2310????0??0????1

Kronosaurus_queenslandicus
??0?0?20?1??????0???01000?[0
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3]10?????1101000?10011?1120000?1?01010?011?0??2??00000?11?3211?0?000?001??0?20?1?
?0??2?10000?00?10?0?????02??0020????1????????103??????????????????????????????????
??1????

Lagenanectes_richterae
01??????1???00??0??0???0??0???????????????????????????????????????1101??????????????0
1?2211?0?0110000?12?????0???????01???????????11?0??1010011?01?0101101??1?11010??3?
0?210111?00?0?????????????201[0
1]101??????????????????????????10111021???0

Leptocleidus_capensis
010001?1112?1010102002001?0000?10??0000??01001022?201010?0??01??21?????0????????
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Leptocleidus_superstes
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        011001000?00?110?11102???1011001?10110011020??1?100200102??????????????????01???0
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Libonectes_morgani_composite_SK
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Liopleurodon_ferox
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Lorrainosaurus_keileni
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        ???????????????????????????0
Luskhan_itilensis
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Macroplata_tenuiceps
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Makhaira_rossica
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Manemergus_anguirostris
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Maresaurus_coccai
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        ???????????????????????????
Marmornectes_candrewi
        0????????????00??0?????00????????????????????????0????10???0???0??????????????????
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Mauisaurus_haasti
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Mauriciosaurus_fernandezi
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Megacephalosaurus_eulerti
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    ????????????????????????????????????????????????????????????????????????????????
    ??????????????????????????
Meyerasaurus_victor
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    20?00021??11011010001101100
Microcleidus_brachypterygius
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Microcleidus_homalospondylus
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    021?1?00????000??2100100???2001001??00?0???102???10000??0012??????????4210111210
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    1?1001100110110100112011 01
Microcleidus_tournemirensis
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Muraenosaurus_leedsii
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Nakonanectes_bradti
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    0 1]010122?02?101??101?001110
Nichollssaura_borealis
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Pahasapasaurus_haasi
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Palmulasaurus_quadratus
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Pantosaurus_striatus
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Picrocleidus_beloclis
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PIMUZ_AIII0521
    ??????????????????????????????????????????????????????????????????????????????
    ???????????????????????????????0????01??0111???1??0???????????????????????????????
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Plesiopleurodon_wellesi
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Plesiopterys_wildi
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Plesiosaurus_dolichodeirus
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Plesiosaurus_manselii
    ??????????????????????????????????????????????????????????????????????????????
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Pliosaurus_almanzaensis
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Pliosaurus_andrewsi
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Pliosaurus_brachydeirus
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    20??10???0?0?2010??1100?????????????????????????????????????????????????0???00???
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Pliosaurus_brachyspondylus
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Pliosaurus_carpenteri
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Pliosaurus_funkei
    ???????0?????0????????????????????????????????????????????????2?2????????????????
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Pliosaurus_irgisensis
    ???????0??????21?????????????????11?0000100200?0?231?11?002??0???2????1??????????
    ?????????????????????????????????????????????????????????????????????????000??1?1
    ?0?1??000?20????????????????????????????????????????????????????????????001?0????
    ?0???10??1???3???1????1?111??
Pliosaurus_cf_kevani
    ?????????????0???????????????????????????????????????????????????????????????????
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Pliosaurus_kevani
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    ?????????????????????????????????????????????????????????????????????????????????
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Pliosaurus_macromerus
    1101????22??10210??0??011?0????????????????00?0???1??????????0???0??????????????0
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    ?????????????????????????????????????????????????????????????????????????????????
    ????????????????????????????
Pliosaurus_patagonicus
    ?????????????????????????????????????????????????????????????????????????????????
    ???????????0?01???????????????111?0?????0???10?0????????0?1??????????????????????
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Pliosaurus_rossicus
    11?1?1??????10210??01001??????1?11000001??200?0??3111????????????????????????????
    ??????????????????????????????1????????0?????????1?1?01011???????????????????????
    ????????????????????????????????????1000200?2????0?2?????????????????????????????
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Pliosaurus_westburyensis
    110101?0221110210??010011000011?1100000100200100231111000201002020???1????0????0?
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    0?00?????0???00??1100????????????????????????????????????????????????????????????
    ???????????????????????????
Polycotylus_latipinnis
    00120?20?1??1021111010001110001??01?01010021???223210111010?111101????2??0??????0
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QM_F51291
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    ??????????????????????????????????????????????????????????????????????????????
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Rhomaleosaurus_cramptoni
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Rhomaleosaurus_thorntoni
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    0?000100??0??01?21101?00?0110100??01100120210?0?000100?10001220110001??????0111?0
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Rhomaleosaurus_zetlandicus
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    21000121101101101001?????0?
Richmond_pliosaur
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    0?0?1??001??????1???11????10001102 0?11101000?021000100232 0?120100100100100?1100?0
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    1 2]10
Rhaeticosaurus_mertens
    ??????????????????????????????????????????????????????????????????????????????
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    ??0
Sachicasaurus_vitae
    01?2??2121??10210??01010?00?2?0?1?10?0?1?1?00?1??31201??1?0?00?????0???????0????
    ????10?0?01110010?21?03??0002?110001????011?11?0000011010?00001?01?0??10000?1??32
    1?2000?0000?001?10000????1010000????1?0020?00??????????????0?03011?103??????0??1?
    ?110??1?111?????????????????1
Seeleyosaurus_guilelmiimperatoris
    00000?00?10?02?????0???????0?????0??0011001????1?1?01000?0??11?????????????????
    ??????????????????????????????10??100?1010???????10000110 0?2??????????3100?1221
    000???1???0?00?1200110010?1000011011 01001201?10030?1?0???300?02??20001100010 0??11
    020?100?200110110000112011 01
Simolestes_vorax
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Speeton_clay_plesiosaurian
    ??????????????????????????????????????????????????????????????????????????????
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Spitrasaurus_spp
    ??????0?????0???????????????????????????????????????????0???00??1010??????????????1
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Stenorhynchosaurus_munozi
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1210???01?0???2?????????????????20?1???2000??200??2???????????????10???0210000010
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Stratesaurus_taylori
001000?0100100100??0110010000010?0?000010000010001001000010101101012002000010?00
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Styxosaurus_snowii
00001??0?100002?12200?0020?0?0??00??00010011?????3??111110?001???????????????????
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Sulcusuchus_erraini
?0?[1
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2?????????????122?1?01?????100??110??101?1?2011??0?21??0????????????????????????
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Tatenectes_laramiensis
???????0?????????????????0??????0???????1???????????2000?0000???????????????????
???????????????11????????0?1???????????????????????????11??????01001????00011??32
011001?100100?110?110000??????????1011???????01??1020101?10?110021011210??10????0
210101??1?2?001?0211??01??1

Terminonatator_ponteixensis
000010?01?0000201020??002??00?0?001????10??1????0[2 3]21??[0
1]11??001?????????????0010?????????1???0???????????????????100?1011110??12?001010
0110312??????????53111222320?200111110011??????????100???1??????????????????????
????1?12??1??1?100??0000110310101221033101101 0110?1211

Thalassiodracon_hawkinsii
00100001110100111120??0?1000???0000000?10020000001011000010110101010002000011000 1
01011?00011001??100?000????0?11101100010000?1200?001001110010000??2101310010011 10
0120100001000111010000010110000020110110 01?00000001000?000102011100100020000011 01
00000010?11001010000101100

Thalassomedon_haningtoni_composite_SK
00001000??0010211120000020?000010010000100111???0200??011?0?010?10????2????????1?
?221???????????1?2?1??????20??01010???001?1????00010011?302010110210262111022320
2210110110000111011001002000100???01?002020??2??00111001121202021[0
1]11000???010110[2 3]10100220111111012[0 1]1101?210

Thililua_longicollis
000210?0?10000201110000001?2000?001000010??1????2221??111?0?11???????????????????
?????????????????????????????10000?1???1???02????1000110101[1 2]0??1[0
1]0??0?311011013201120100100?00??01??
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Tricleidus_seeleyi
01100???????011010?00?0010?000?100?????????01001?3001000?000010?00?011111????11
1110????????011200?000?1100?0201110001000?0021?01110011001?11?1101?02210011123201
10011100100?11?01100??????????11011000002012010202?13?????????????210??101113021
0101221023001101111101211

Trinacromerum_bentonianum
00020121?1?00021111010001 1?0001??01?01010021???1?31?11110???01??0????12010??????0
01311111??0???11122?13001?00??001?11???10??12???1?000211200?1101000?02?00012??320
1[0
1]201000?0?00???11??????1?000???1101120?0201010020110111?110?211?32????0?????1??
?10?2???33?0??01011001211

Tuarangisaurus_keyesi
000010?0??0000??1020020020?000???0??0001??11???032?2111?00001????????????????????
???11?????????0??2?????????????10??10??1010???2??010000110?1?011111?02?2111??3?02

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    2?0111?11?0??????????????????????????????????????????????????????????????????????
    ?????????????????????????
Umoonasaurus_demoscyllus
    00000100112??1101020??00??00????0??????????0?002222?10???10?11????1??12?11?0??0??
    022?????0?????11122?1211000????????0??1111???????111010?01?????????????1001????20
    ?1??1010?00?11010110200201?00?1???1?01?010?????????????0????????????21????0111?02
    001022210?2???1?0??10?1??1
Vectocleidus_pastorum
    ?????????????????????????????????????????????????????????????????????????????????
    ???????????????????????????????????????????????????????????????????????????01?01?
    ?0?1??1010?00??10??1102??????????????1???1?02???1??01?10?0???????????????????????
    ?????????????????????????????
Vegasaurus_molyi
    ?????????????????????????????????????????????????????????????????????????????????
    ?????????????????????????????????????????????????????????????11?1101?0252111?2232
    02210111?100???10111000?2011101?20?1100111?212001021????010111011000?0???000?1?03
    10111231022???001??1?01???
Wapuskanectes_betsynichollsae
    ?????????????????????????????????????????????????????????????????????????????????
    ?????????????????????????????????????????????????????????????????????????????????
    ????????????????1??1??0???????????2101?2?110?1110110?10??3????????????200???01???
    03000022???????????????????0
Westphaliasaurus_simonsensii
    ?????????????????????????????????????????????????????????????????????????????????
    ??????????????????????????????????????????????????????????????2???????????0011021
    ?0??0010?101000111?1?0010?0000101?211100120??00000001??10000??20?20001?????000110
    021000111001101101000011?1??1
Zarafasaura_oceanis
    0000100011000020102002002000000?001100011021???0020[0
    1]21110000010?010??12?1??0??0??0?????010100010?12?????0?????010101010111000??[1
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    1]?1110???20???01?2?01?01111?11100?0??????11?11?021001?0???00????03101112???[1
    2]???1?0000???????
Thouarsais_specimen
    ?????????????????????????????????????????????????????????????????????????????????
    ?????????????????????????????????????????????????????????????????????????00011121
    20010010100011010?00100?1?2?101?0????1?1000?0?????????1????00?30111??2??????10000
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