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ARTICLE

CRYPTOCLIDID PLESIOSAURS (SAUROPTERYGIA, PLESIOSAURIA) FROM THE UPPER JURASSIC OF THE ATACAMA DESERT

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ABSTRACT—This study presents the first plesiosaurs recovered from the Jurassic of the Atacama Desert that are informative at the genus level. One specimen is represented by an articulated axial section that shows distinctive features, such as cervical vertebrae with oval articular facets and gracile neural pedicles. The second specimen preserves similar vertebrae, teeth, propodials, and pectoral elements. Their anatomical characteristics allow us to refer them to *Muraenosaurus*, a genus of cryptoclidid plesiosaur previously reported in Callovian rocks of Europe and Argentina. A third specimen is represented by a fragmentary jaw, which coincides precisely in size and anatomical features with that of *Vinialesaurus caroli*, another cryptoclidid plesiosaur exclusively known from the Oxfordian of Cuba. The material studied represents the first record of *Muraenosaurus* in the Oxfordian of the Profeta-La Ternera Basin in northern Chile, adding to previous regional occurrences of the genus and to the record of *Cryptoclidus*, both also known from the Callovian of Argentina. On the other hand, the specimen referred to *Vinialesaurus* is the first appearance of this genus in the Southern Hemisphere. These new records give strong support to the exchange of marine vertebrates between the northern Tethys and the southern Pacific through the Caribbean Seaway during the Middle and Late Jurassic.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Plesiosauria (Diapsida, Sauropterygia) was a clade of marine reptiles spanning ca. 135 million years of the Mesozoic and documented from all continents. The early history of Plesiosauria goes back to the Triassic of Europe (Wintrich et al., 2017). Early Jurassic plesiosaurians are documented in Australia (Kear, 2012) and Europe, being characterized by a small body size and a low disparity (Benson et al., 2012), becoming more diverse during the Pliensbachian–Toarcian (O'Keefe, 2001; Benson and Druckenmiller, 2014; Sachs and Kear, 2018). During the Aalenian–Bathonian, there is a major gap in the global record of Plesiosauria, with a single taxon (*Maresaurus coccai* Gasparini, 1997) known from the Bajocian of Argentina. From the Callovian and onward through the Upper Jurassic, plesiosaurians became abundant in Europe (Brown, 1981; Benson and Druckenmiler, 2014), with additional records from North America (O'Keefe and Wahl, 2003; O'Keefe and Street, 2009), South America (Gasparini and Spalletti, 1993), Australia (Long and Cruickshank, 1998; Kear, 2012), and even Antarctica (O'Gorman et al., 2018). Despite this abundant Jurassic record, plesiosaurians of Oxfordian age are scarce, being restricted to a few pliosaurid remains from England (Foffa et al., 2018), Poland (Lomax, 2015), Russia (Zherkhov et al., 2017), Italy (Cau and Fanti, 2014), North America (Knight, 1895), and Cuba (Gasparini, 2009), and also a few cryptoclidid records from North America (O'Keefe and Wahl, 2003; O'Keefe and Street, 2009) and Cuba (Gasparini et al., 2001).

Records of Jurassic marine reptiles in northern Chile are frequent (Chong and Gasparini, 1976; Gasparini, 1979; Otero et al., 2015b; Soto-Acuña et al., 2015a). To date, the reports of Thalattosuchia, Ichthyosauria, and Plesiosauria are relatively abundant, but they are mostly represented by fragmentary material, which often hinders more exclusive taxonomic determinations. Thalattosuchians is the most documented, with a diversity of metriorhynchids thus far represented by two species, corresponding to 'Metriorhynchus' casamiquelai Gasparini and Chong, 1977, and 'Metriorhynchus' westermanni Gasparini, 1980, both of Callovian age. These species add to several other indeterminate metriorhynchid records found in Chile with a Bajocian–Oxfordian age (Soto-Acuña et al., 2015a, 2015b, 2018). Remains of ichthyosaurs are also very common; however, the only positive determination corresponds to *Temnodontosaurus* sp. (Otero and Sepúlveda, 2020). Plesiosaur remains have been documented in northern Chile from various localities, showing a chronostratigraphic occurrence of the group throughout the entire Jurassic; however, the material has corresponded only to fragments of little diagnostic value. Burmeister and Giebel

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(1861) described a plesiosaur dorsal vertebra (then considered a thalattosuchian, *Teleosaurus neogaeus*, currently nomen dubium) recovered from levels of probable Bajocian age near Copiapó. Chong and Gasparini (1976) listed several Lower Jurassic–Upper Jurassic localities in the Cordillera de Domeyko, with findings of indeterminate plesiosaurs. Biese (1957, 1961) also recognized the presence of plesiosaur remains in Callovian levels of Cerritos Bayos, west Calama. In the same locality, but from Oxfordian levels, Biese (1961) also mentioned material referable to plesiosaurs. More recently, fragmentary remains referable to indeterminate cryptoclidids, mostly based on isolated teeth and vertebrae, were described in Oxfordian levels of Cerritos Bayos (Otero and Soto-Acuña, 2010; Otero et al., 2015b). Despite this abundant record, no more exclusive taxonomic determinations have been proposed to date.

This work describes three new plesiosaur specimens found in Middle–Upper Jurassic strata exposed in the Atacama Desert. These include the first informative specimens described in northern Chile, and the first local generic identifications of Jurassic plesiosaurs.

Institutional Abbreviations—**MNHNCu**, Museo Nacional de Historia Natural de Cuba; **MUHNCAL**, Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Chile; **NHMUK**, Natural History Museum, London, U.K.

LOCALITIES AND GEOLOGICAL SETTING

The specimens studied were recovered from different Jurassic strata exposed in the locality of Cerritos Bayos, ca. 16 km southwest of Calama, northern Chile, in the central part of the Atacama Desert (Fig. 1A). The fossil-bearing levels are part of the section originally described by Biese (1957, 1961) (Fig. 1B). This mainly marine section seems to be continuous throughout the Jurassic, starting at the base with 50–60 m of *Arietites* shale ('Caliza de *Arietites*' of Biese, 1961), indicating the lower Lias (Sinemurian), extending to the Tithonian with clayey sandstones deposited in a continental or freshwater setting, with gastropods, 'lizard tracks,' and ripple marks (Biese, 1961). The Jurassic section described by Biese (1961) was later formalized as the Cerritos Bayos Formation by Lira (1989). More recently, its former member Campamento was raised and renamed to the Cerro Campamento Formation by Duhart et al. (2018). The vertebrate-bearing levels were recognized in the field based on the original section of Biese (1961), being complemented with new field information added by this investigation. The material was recovered from two sites in the Cerritos Bayos area, west of Calama, described as follows.

Cerro Amarillo—A successive vertebral series, MUHNCAL.20174, was collected from this locality, from calcareous siltstones of yellowish to red color, filled with veins of gypsum, limonite, and other iron oxides. A second specimen, found a few meters south on the same level, is represented by a partial metriorhynchid skull with associated vertebrae (under study by the authors). Isolated ichthyosaur vertebrae were also found in the area, which have not been determined at a more exclusive level. The associated ammonoids are represented mainly by *Subvinialphinctes prophetae* (Parent et al., 2006) and *Euaspidoceras* aff. *tarapacaense* Parent, 2006. *Subvinialesphinctes prophetae* is the most common ammonoid present in the levels studied. This taxon has been previously determined as '*Perisphinctes*' *andium* Steinmann, 1881, and later considered to be Vinialesphinctinae, gen. et sp. indet., by Meléndez and Myczynski (1987). The same ammonoid was later reassigned to *Perisphinctes prophetae* by Gygi and Hillebrandt (1991), and more recently, to *Subvinialesphinctes prophetae* by Parent et al. (2006). This study refers to this taxon following the most updated determination proposed by Parent et al. (2006). The level with plesiosaur remains was first considered by Biese (1961) to be Callovian in age, but the presence of *Euaspidoceras* aff.

tarapacaense indicates that the studied level corresponds to the upper part of the middle Oxfordian.

Biese 3—The name of this informal locality is proposed here, for field identification. Associated skeleton remains were collected from this locality (MUHNCAL.20176). The specimen was preserved in a large concretion of limestone, naturally fragmented. The associated fauna includes fragmentary remains of vertebrates referable to indeterminate ichthyosaurs. Directly associated invertebrates include *S. prophetae*. A phragmocone of the ammonoid genus *Reineckeia* was found a few meters below the concretion horizon. Following the geological map and the section described by Biese (1961), the plesiosaur-bearing level was considered to be of lower Oxfordian age, based on the presence of a '*Perisphinctes* limestone' ('Caliza de *Perisphinctes*' in Biese, 1961). As mentioned earlier, this ammonoid is referred here to *S. prophetae*. The near stratigraphic occurrence of *Reineckeia* at lower levels supports a lower Oxfordian age, close to the Callovian–Oxfordian boundary. Another specimen, MUHNCAL.20205, comprising a fragmentary mandible, was recovered in the same locality from an equivalent level, ca. 200 m north of the site where MUHNCAL.20174 was found.

MATERIALS AND METHODS

MUHNCAL.20174 (vertebral series) was found partially exposed on the surface. The specimen was recovered during 2014 and then prepared by one of the authors (R.A.O.) with mechanical tools (Dremel engraver). In contrast, MUHNCAL.20176 (associated skeleton) was preserved in a single, large concretion that was naturally cracked (Fig. 2). This was found scattered over Recent soil. During sieving, small bony fragments of the skull were recovered, showing that the skull and likely the anterior cervical vertebrae were initially present but went lost through erosion. Thirty blocks were recovered between 2014 and 2018. Most of the bones eroded naturally and are preserved as molds. For its anatomical description, dental silicone (Xantopren) was used to obtain bone casts. The recovered blocks have been numbered, following a craniocaudal axial ordering. The blocks containing appendicular elements were reassembled and labeled with noncontinuous numbers. The complete numbering used here is explained in Figure 2. MUHNCAL.20205 (mandible) was recovered within a concretion fragment. This material was prepared with pneumatic tool (ME-9100 airscribe).

The phylogenetic analysis of MUHNCAL.20176 used the data matrix of Benson and Druckenmiller (2014), plus the characters and states added by Otero et al. (2018b). To this data set we added two recently described plesiosaurians, *Arminisaurus schuberti* Sachs and Kear 2018, and *Lagenanectes richterae* Sachs, Hornung, and Kear 2017, resulting in 88 operational taxonomic units (OTUs) and 270 characters (Supplemental Data 1). TNT version 1.1 (Goloboff et al., 2003) was used to analyze the data set. The IterPCR script (Pol and Escapa, 2009) was used to detect unstable taxa, which were removed from subsequent analyses.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
CRYPTOCLIDIA Ketchum and Benson, 2010
CRYPTOCLIDIDAE Williston, 1925
Genus *MURAENOSAURUS* Seeley, 1874

Type Species—*Muraenosaurus leedsi*, NHMUK PV R.2421 (holotype). Peterborough, England, Callovian.
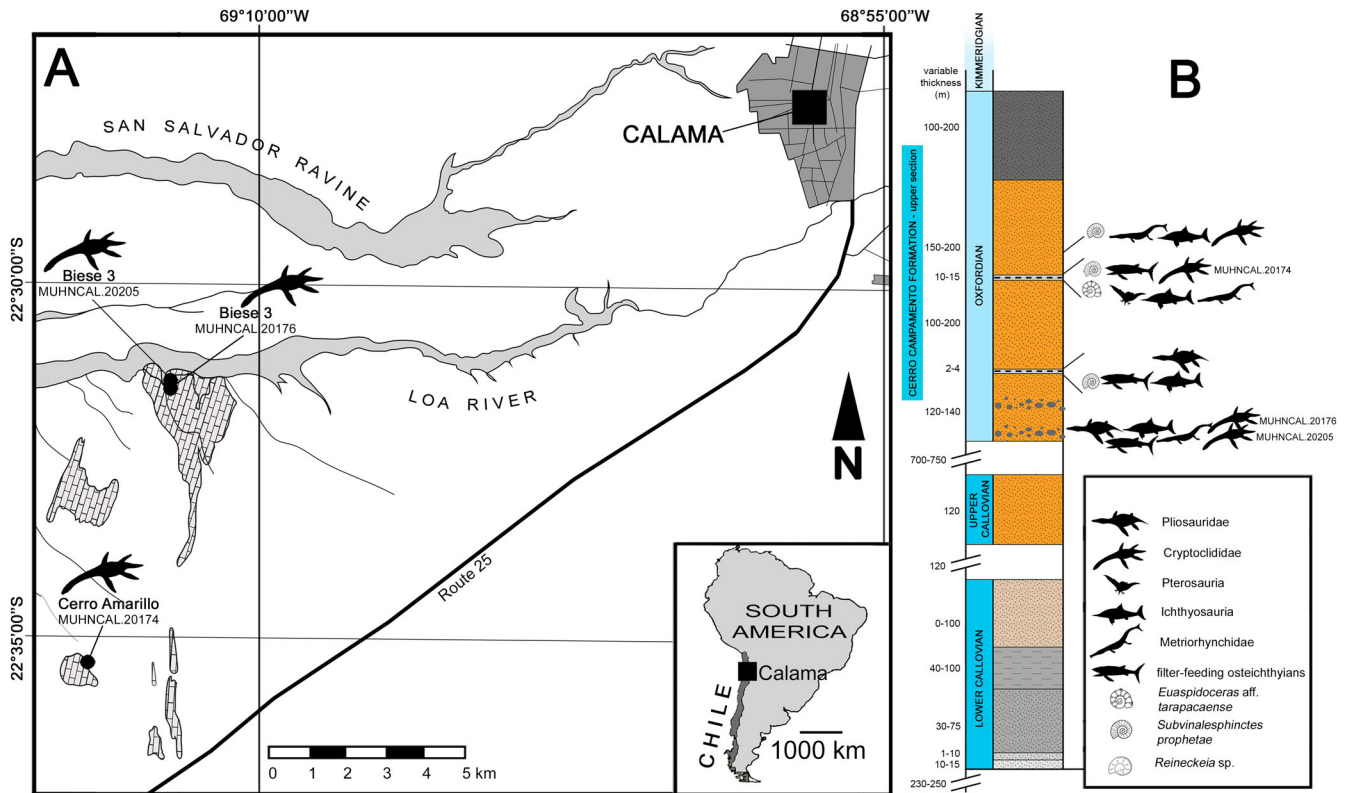
FIGURE 1. **A**, map indicating the Upper Jurassic outcrops at Cerritos Bayos, east Calama, where the studied material was recovered; the provenance of each specimen is indicated. **B**, generalized stratigraphic section of the Cerro Campamento Formation (sensu Duhart et al., 2018), indicating the provenance of the studied specimens.

MURAENOSAURUS sp.
(Figs. 2–4)

Cryptoclididae indet.: Otero, Rojas and J. Rojas, 2018a.

Material—MUHNCAL.20176, a fragmentary skeleton preserving teeth, fragments of the skull, most of the posterior neck, part of the pectoral girdle, gastralia, humerus, and a partial femur (Fig. 2).

Locality and Horizon—Informal locality Biese 3, east Calama, northern Chile. Cerro Campamento Formation, *Subvinialesphinctes prophetae* Zone (= 'Caliza de *Perisphinctes*' of Biese, 1961), lower Oxfordian, Upper Jurassic.

Description of MUHNCAL.20176

Ontogenetic Stage—MUHNCAL.20176 lacks neurocentral suture lines, evident in blocks 01 to 04. In addition, both propodials show prominent articular heads. Complete neurocentral fusion has been considered by Brown (1981) to be a proxy for the adult stage. Also, propodials with well-defined articular heads have been considered to be first appearing in young adults (Otero et al., 2015a). Based in these observations, MUHNCAL.20176 can be considered at least a young adult individual.

Skull Fragments—A few skull fragments were recovered. They were identified based on the presence of highly interdigitated sutures and by the presence of cylindrical matrix filling, indicating the existence of internal ducts or diverticula. Regretfully, the preserved elements are highly fragmentary, making any accurate anatomical identification difficult.

Teeth—Two fragments of functional teeth and one replacement tooth were recovered. The functional teeth are highly eroded, with the enamel damaged. However, the available replacement tooth (Fig. 3A–D) preserves very fine and profuse striations over the labial and lingual surfaces. Two strong opposing axial ridges are present along both sides of the tooth crown, extending from the base to the crown to the tooth apex. The three teeth have an almost circular cross-section.

Axial Skeleton—Remains of at least 17 vertebrae are preserved in blocks 01 to 04, and in block 07, with a few vertebral elements preserved as isolated fragments. The cervical-to-dorsal transition vertebrae are continuously preserved, mostly as molds. Block 01 preserves the two last cervical vertebrae and the first pectoral vertebra (sensu Sachs et al., 2013). The opposite mold of the first pectoral vertebra is preserved in block 02, whereas an isolated small fragment preserves the mold of two pectoral vertebrae that precisely match in length the second and third pectoral centra of block 02. The preserved parts of the cervical vertebrae show centra higher than long, with neural spines almost 150% higher than their centrum. Neural spines have distinctive features, including a cranially recurved angle and very acute pre- and postzygapophyses (Fig. 3E, F). Two isolated neural spine molds are preserved in block 03 (Fig. 3G), being also recurved cranially. They remain in anatomical position with respect to their ribs and the mold of their transverse processes, the latter placed just below the neural spine, indicating that these are dorsal vertebrae. These features allow recognition of the presence of two cervical vertebrae in block 01, three pectoral vertebrae between blocks 01 and 02, and evidence of two dorsal vertebrae (only their upper part with the transverse processes and neural spines) in block 03. Silicone casts were obtained from these blocks, allowing a good anatomical interpretation for
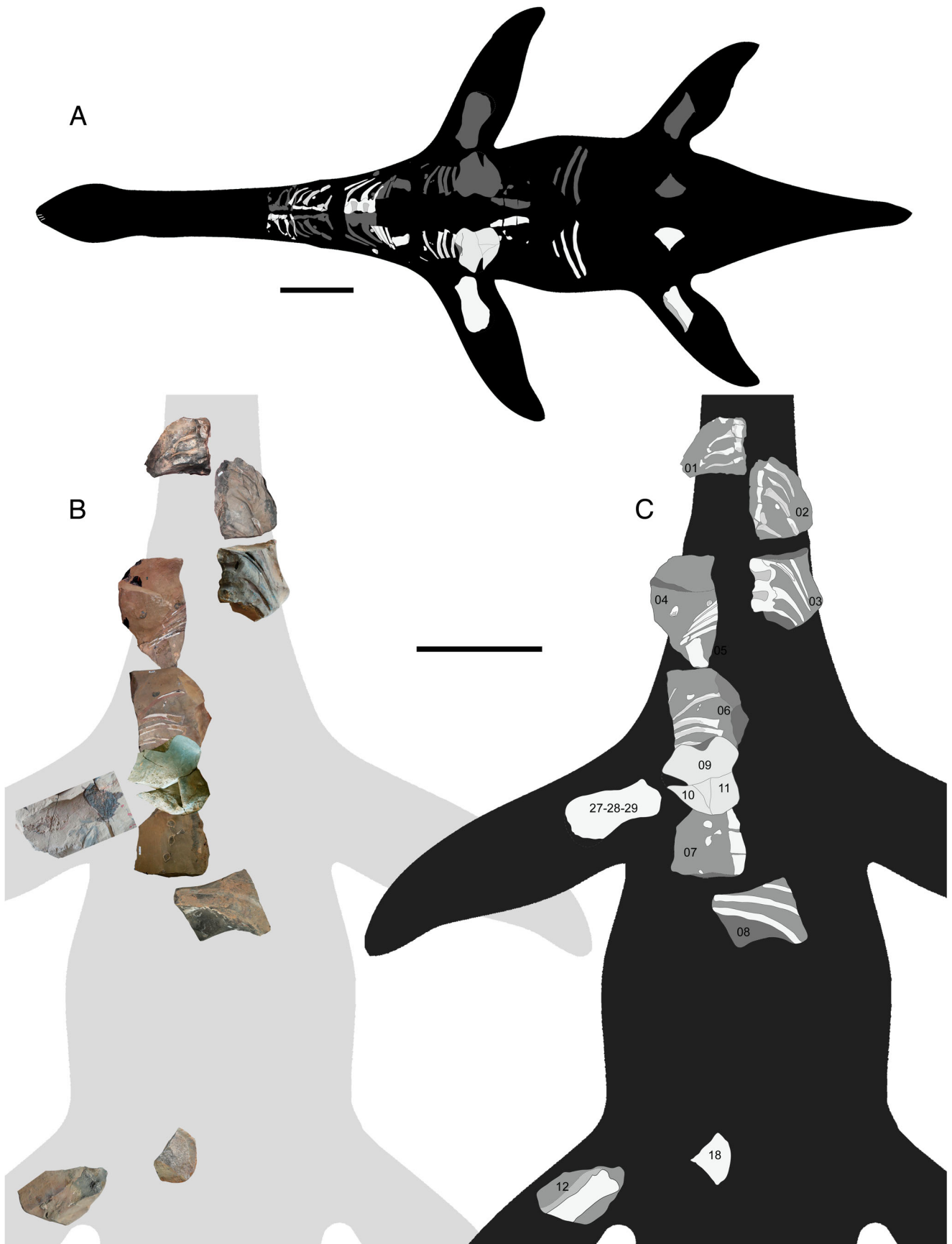
FIGURE 2. *Muraenosaurus* sp., MUHNCAL.20176. **A**, diagram indicating the preserved elements in light gray; mirrored elements are indicated in dark gray. **B**, relative arrangement of the recovered blocks. **C**, line drawing of the blocks, indicating their field numeration, which is used in the description. Scale bars equal 50 cm.
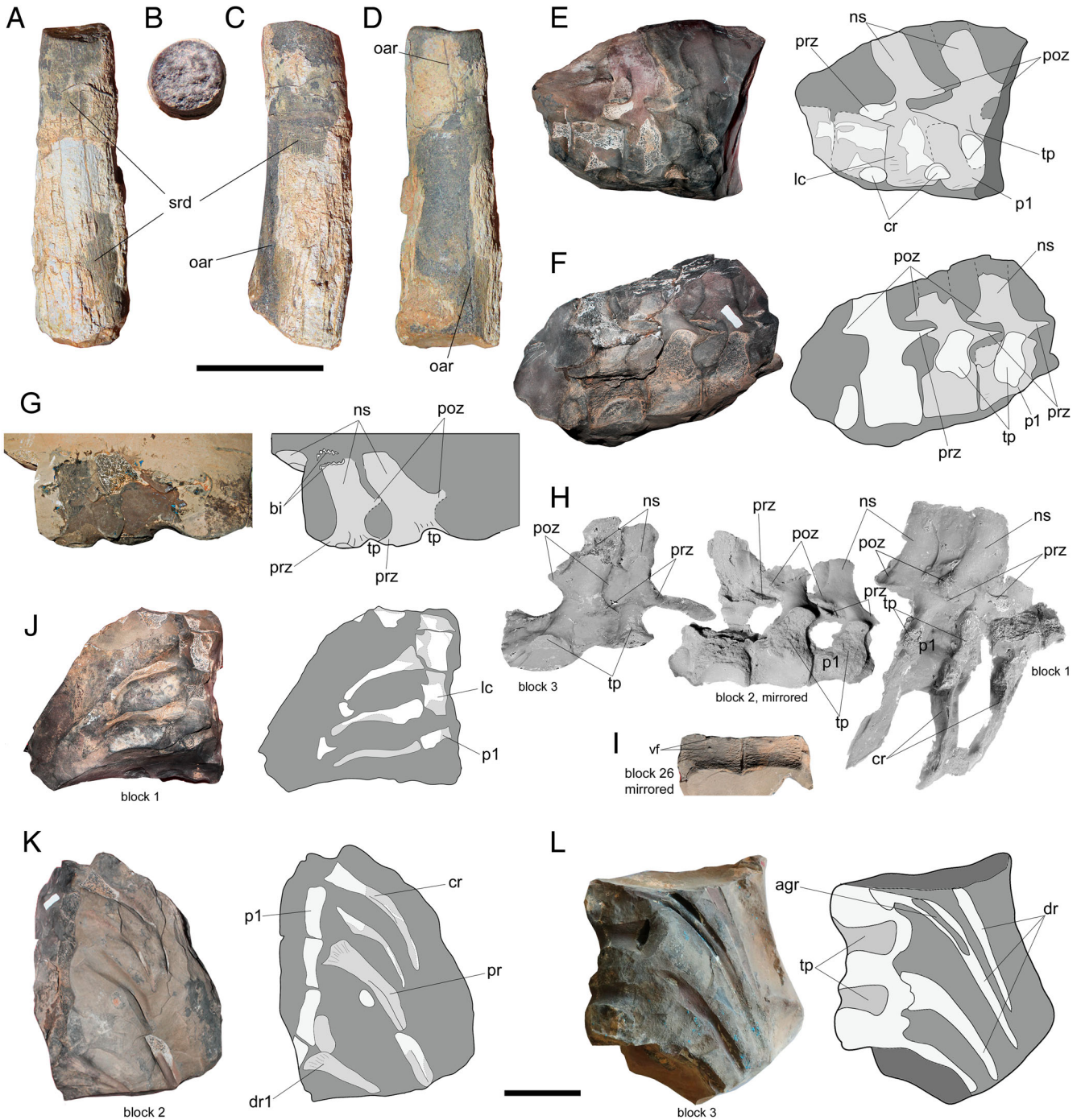
FIGURE 3. *Muraenosaurus* sp., MUHNCAL.20176. **A–D**, best-preserved replacement tooth; **A**, anterior, **B**, cross-section, **C**, profile (craniocaudal), and **D**, opposite profile views. **E**, photograph and line drawing of block 01 preserving part of the three last cervical vertebrae and the first pectoral vertebra. **F**, photograph and line drawing of block 02 showing the opposite mold of the first pectoral vertebra and two successive pectoral vertebrae. **G**, photograph and line drawing of fragments of three neural spines preserved in block 03, with the mold of their transverse processes, indicating that these belong to dorsal vertebrae. **H**, dental silicone casts of blocks 01 to 03. **I**, photograph of block 26 in relative position with equivalent centra from block 03. **J**, photograph and line drawing of cervical-to-dorsal axial section in ventral view of block 01. **K**, block 02 in ventral view. **L**, photograph and line drawing of block 03 in dorsal view. **Abbreviations**: **agr**, anterior groove of the rib; **bi**, bivalve shell; **cr**, cervical rib; **dr**, dorsal rib; **dr1**, first dorsal rib; **lc**, last cervical vertebra; **ns**, neural spine; **oar**, opposite axial ridge; **p1**, first pectoral vertebra; **poz**, postzygapophysis; **pr**, pectoral rib; **prz**, prezygapophysis; **srd**, soft ridges; **tp**, transverse process; **vf**, vertebral foramina. Scale bars equal 10 mm (**A–D**) and 10 cm (**E–L**).

the elements (Fig. 3I, J). Finally, ventral molds of at least three successive vertebrae are present in block 07. They are associated with gastralia, suggesting that these elements are dorsal vertebrae.

Trunk—The cervical-to-dorsal portion is articulated, showing pectoral ribs with a gracile shaft and the first dorsal ribs acquiring a deep anterior medial sulcus that fades
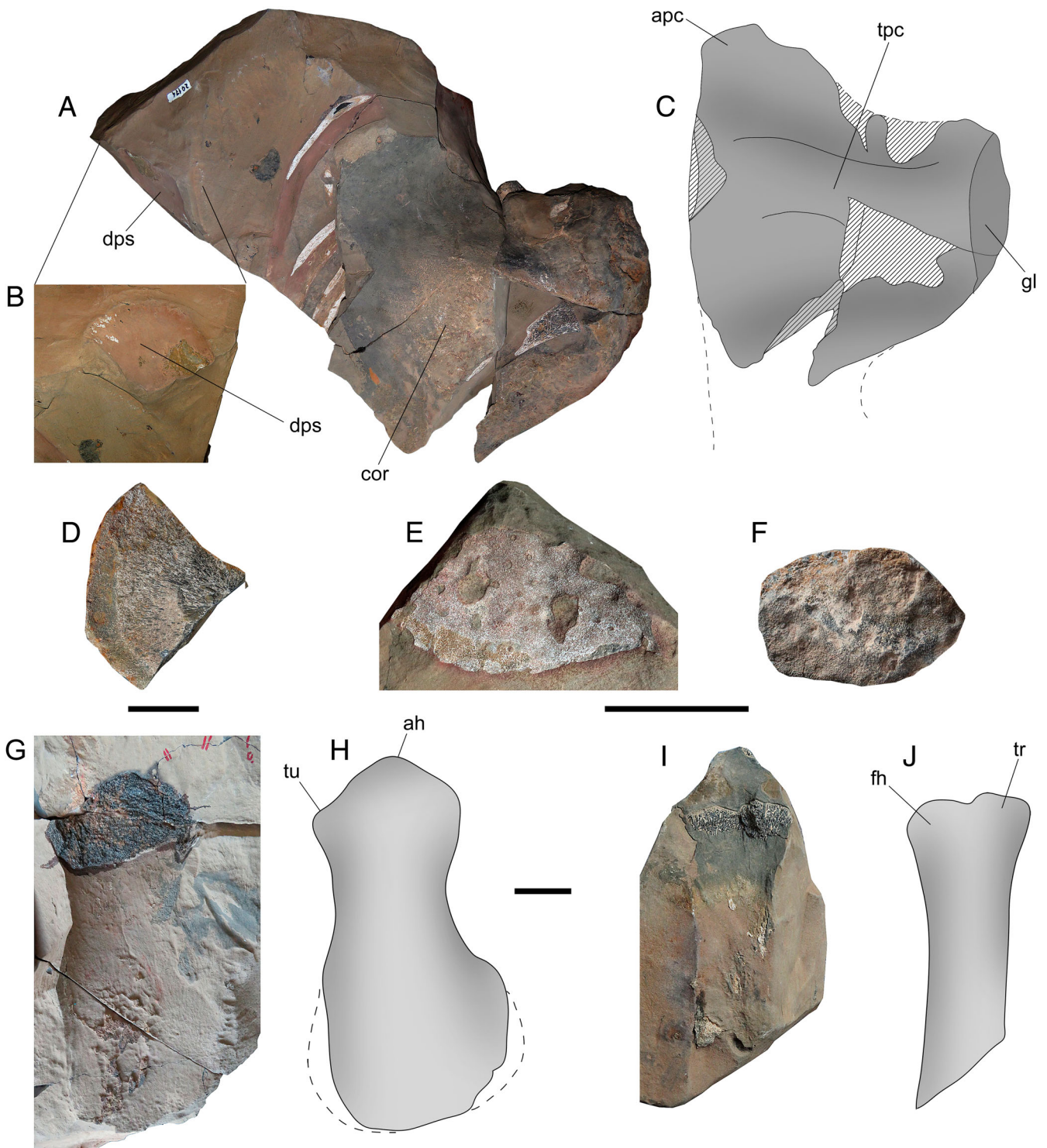
FIGURE 4. *Muraenosaurus* sp., MUHNCAL.20176. **A**, relative position of block 06 and the left coracoid, which is shifted to the right side of the skeleton. **B**, mold of the dorsal process of the right scapula. **C**, line drawing of the left coracoid. **D**, fragment of the right ischium. **E**, **F**, molds of two propodial articular heads, showing evidence of decompression syndrome. **G**, photograph and **H**, line drawing of the right humerus. **I**, photograph and **J**, line drawing of the right femur. **Abbreviations**: **ah**, articular head of the humerus; **apc**, anterior process of the coracoid; **cor**, coracoid; **dps**, dorsal process of the scapula; **fh**, femoral head; **gl**, glenoid of the coracoid; **tpc**, transverse process of the coracoid; **tr**, trochanter; **tu**, tuberosity. Scale bars equal 5 cm.

distally. The cervical-to-dorsal ribs remain in anatomical position (Fig. 3K–L).

Pectoral Girdle—A large anterior part of the left coracoid remains attached to the ribs of block 06 (Fig. 4A, C). This includes

the glenoid and the anterior part of the midline, showing a squared anterior projection that suggests medial contact with the scapula. The coracoid has a dorsal (internal) deep concavity and a prominent ventral transverse process. The glenoid is partially damaged

but allows the scapular and coracoid facets for the humerus to be distinguished. The distal part of the scapular dorsal process is preserved in the lateral part of block 06, placed distally with respect to the rib tips, thus reflecting its anatomical position (Fig. 4B).

Pelvic Girdle—Only the medial part of an ischium is preserved. It has a rounded medial contour (Fig. 4D).

Propodials—Two clearly different propodials were recovered (Fig. 4E–J). The larger and more robust one is interpreted as the humerus, which was recovered in three different blocks (27–29) and later reassembled. The humerus has a low articular head and a slightly prominent tuberosity, which is scarcely separated from the articular head (Fig. 4G, H). The femur (Fig. 4I, J) is comparatively more gracile and slender than the humerus. Its distal part is lost. The femoral head is scarcely convex, and in proximal view the trochanter is medially prominent and squared in contour.

Remarks—MUHNCAL.20176 has cervical vertebrae without ventral depression, as is common in Cryptoclididae (Brown, 1981). The presence of posterior cervical vertebrae with neural spines curved toward the skull is similar to the condition in *Muraenosaurus leedsi* (NHMUK PV R.2861). In addition, the humerus and the femur are very similar to those described for '*Muraenosaurus platyclis*' (= *M. leedsi*) and *Muraenosaurus leedsi* based on NHMUK PV R.2678 and NHMUK PV R.2864, respectively (Andrews, 1910). Based on these observations, we referred MUHNCAL.20176 to Cryptoclididae; furthermore, we refer it to the genus *Muraenosaurus*.

The axially sharp pre- and postzygapophyses in the posterior cervical vertebrae of MUHNCAL.20176 contrast with the axially rounded pre- and postzygapophyses present in *Cryptoclidus* (Brown, 1981:figs. 8, 9), *Muraenosaurus* (Andrews, 1910:figs. 50, 51), *Tricleidus* (Andrews, 1910:pl. VIII), *Djupedalia* (Knutsen et al., 2012a:fig. 8), and *Spitrasaurus* (Knutsen et al., 2012b:fig. 18). The teeth of MUHNCAL.20176 show a combination of features that seems to be unique among cryptoclidids. These include having a rounded cross-section (character 139, state 0 of Benson and Druckenmiller, 2014), being slender (feature 3 of Brown, 1981), and being ornamented with fine and profuse labial and lingual ridges as those of *Tricleidus seeleyi* (Brown, 1981:fig. 24), but also having two strong opposing axial basal-apical ridges as present in *Cryptoclidus eurymerus* (feature 4 of Brown, 1981; character 136, state 0 of Benson and Druckenmiller, 2014). MUHNCAL.20176 teeth differ from those of *Muraenosaurus* species in having opposed axial ridges and by the absence of fine ridges exclusively on their lingual surfaces (Brown, 1981:fig. 19; character 137, state 1 of Benson and Druckenmiller, 2014). This condition also differentiates them from *Kimmerosaurus*, which lacks any tooth ornamentation (Brown, 1981:fig. 39), and from *Spitrasaurus*, which only has lingual ornamentation (Knutsen et al., 2012b). Thus, the vertebral and dental features suggest that this specimen could belong to a new species, but such identification is here precluded because of the fragmentary nature of the specimen.

MURAENOSAURUS sp.
(Fig. 5)

Elasmosauridae indet.: Otero, Soto-Acuña, Alarcón, Ossa-Fuentes, Rojas 2015c.
Cryptoclididae indet.: Otero, Rojas and J. Rojas, 2018a.

Material—MUHNCAL.20174. Eleven vertebrae including the cervical-to-dorsal transition.

Locality and Horizon—Cerro Amarillo, east Calama, northern Chile. Cerro Campamento Formation, *Subvinalesphinctes prophetae* Zone (= Caliza de '*Perisphinctes*' of Biese, 1961), lower Oxfordian, Upper Jurassic.

Description of MUHNCAL.20174

Ontogenetic Stage—All the preserved vertebrae of this specimen (Fig. 5A–E) have strong neurocentral fusion without visible sutures. Following the osteological criteria of Brown (1981), this specimen can be referred to an adult.

Cervical Vertebrae—Measurements of the preserved axial elements are summarized in Table 1. Five cervical vertebrae are preserved. The anterior-most element is represented by a fragmentary centrum, slightly deformed laterally. It has a subtriangular articular contour, with a neural arch breadth less than one-third of the centrum breadth. The ventral surface of the neural canal is preserved, being subcircular in contour. The posterior articular facet of this centrum is lost due to erosion; however, the preserved part indicates that the centrum is longer than high. Part of the respective cervical rib is preserved, being strongly fused, without any visible suture. Four additional cervical vertebrae are fairly complete. Three of them preserve their neural spines as well as the pre- and postzygapophyses. The prezygapophyses are cranially extended and overlap ca. one-third of the preceding centrum. The neural pedicles are cranially shifted, leaving a short gap in the posterodorsal surface of the centrum. One of the available neural spines shows that these are dorsoventrally higher than the centra. Each centrum is longer than high and broader than long, with an average Vertebral Length Index (VLI sensu Welles, 1952) of 98.8 (based on the four complete centra preserved). The ventral surface of the cervical centra is slightly convex, with a pair of subcentral foramina separated by a bony bridge instead of a ventral keel. The neural arches are less than half of the centrum breadth. They have prezygapophyses laterally narrower than the neural pedicles. The prezygapophyses are recurved dorsally and have a medial septum that separates them. The neural canal is subtriangular with rounded edges. The neural pedicles are very thin, nearly one-quarter the ventral breadth of the neural canal.

Pectoral Vertebrae—Four pectoral vertebrae are preserved. The anterior-most pectoral centrum is fragmentary, but it is still attached to the last cervical centrum. From the latter, the rib facet joins to the transverse process, forming a facet between the neural spine and the centrum. This facet is dorsally circular and becomes sharp and ventroposteriorly recurved. The dorsal margin of the pectoral facets has an anterodorsal ridge that rises from the anterior margin of the facet into the dorsal part of the neural spine. The pectoral centra are comparatively shorter than the cervicals. They also acquire a more oval articular contour. The neural canal is narrower than in the cervical vertebrae, whereas the neural pedicles are as thin as those of the cervicals.

Dorsal Vertebrae—Two dorsal vertebrae are preserved. They have nearly circular articular facets. Their transverse processes are oriented almost horizontally, being gracile and not expanded distally. Their centra are as high as broad and longer than broad. In their anterior articular facets, both dorsal vertebrae have a central scar.

Remarks—The material was found partially exposed and keeping its anatomical position (Otero et al., 2018a). Fragments of the neural spines were recovered by sieving. MUHNCAL.20174 has cervical centra without ventral notch; additionally, their neural arches have slender pedicles as those of *Muraenosaurus* (Andrews, 1910:fig. 50), differing from the robust pedicles in the cervical vertebrae of *Cryptoclidus* (Brown, 1981:fig. 8). The posterior cervical centra have oval articular facets as those of *Muraenosaurus* (Phillips, 1871). Based on these observations, MUHNCAL.20174 is here referred to the genus *Muraenosaurus*. Species determination is precluded due to the fragmentary condition of the specimen.

Genus *VINIALESAURUS* Gasparini, Bardet, and Iturralde-Vinent 2001

Type Species—*Cryptocleidus*? [sic] *cuervoi caroli* De La Torre and Rojas, 1949. Redescribed and assigned to the genus and species *Vinialesaurus caroli* by Gasparini et al. (2001). Sierra de Los Órganos, western Cuba. Jagua Formation, middle–late Oxfordian.
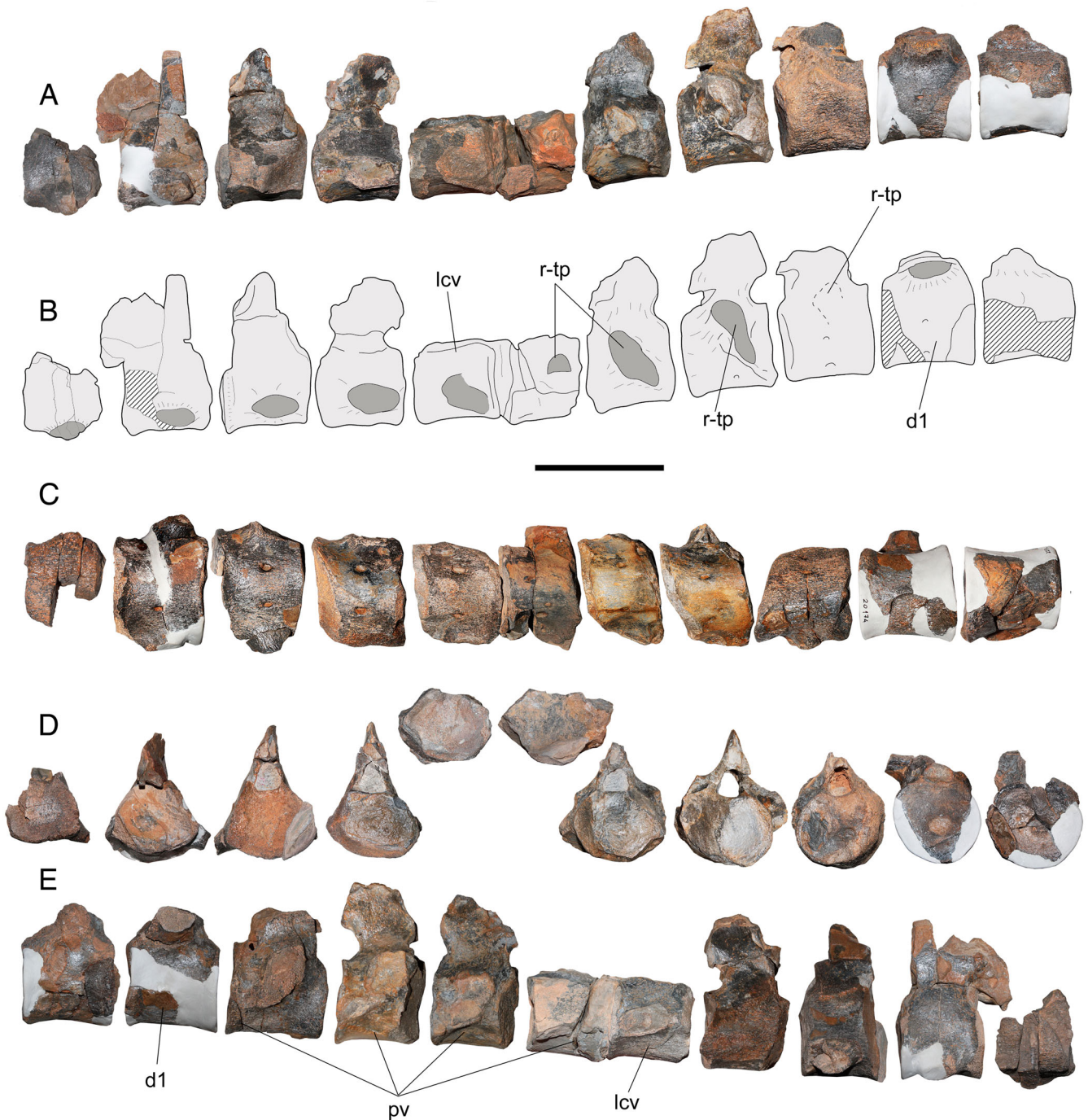
FIGURE 5. *Muraenosaurus* sp., MUHNCAL.20174, cervical-to-dorsal axial section. **A**, photograph and **B**, line drawing in left lateral view. **C**, ventral view. **D**, anterior articular view. **E**, right lateral view. **Abbreviations**: **d1**, first dorsal vertebra; **lcv**, last cervical vertebra; **pv**, pectoral vertebrae; **r-tp**, rib-transverse process. Scale bar equals 10 cm.

VINIALESAURUS sp.
(Fig. 6)

Material—MUHNCAL.20205, a fragmentary mandible.

Locality and Horizon—Informal locality Biese 3, east Calama, northern Chile, 200 m north from the MUHNCAL.20176 site. Cerro Campamento Formation, *Subvinialesphinctes prophetae* Zone (= 'Caliza de *Perisphinctes*' of Biese, 1961), lower Oxfordian, Upper Jurassic.

Description of MUHNCAL.20205

Ontogenetic Stage—The splenial reaches the symphysis, but its contact with the dentaries is obscured, without any visible suture. This suggests that MUHNCAL.20205 was a young adult or a mature individual.

Dentaries—The anterior portion of the right dentary is preserved, including the lingual part of the symphysis and an anterior fragment of the left dentary. In occlusal (dorsal) view (Fig. 6A, B), eight alveoli can be seen. The three posterior alveoli have their

TABLE 1. Measurements (in mm) of the cervical vertebrae of the studied specimens. VLI, Bi and HI vertebral indices follow the definitions by Welles (1952).

Specimen	Anatomical identity	Length	Height	Breadth	VLI	HI	BI
MUHNCAL.20174							
1	Cervical	59.15	49.66	78	92.67	83.96	131.87
2	Cervical	67.85	57.47	77.53	100.52	84.70	114.27
3	Cervical	68.01	55.84	75.74	103.37	82.11	111.37
4	Cervical	62.74	56.4	82.21	90.53	89.89	131.03
5	Cervical	65.66	56.04	73.98	100.99	85.35	112.67
6	Pectoral	68.98	55.43	77.37	103.88	80.36	112.16
7	Pectoral	—	58.18	72	—	—	—
8	Pectoral	64.03	58.25	72.51	97.94	90.97	113.24
9	Dorsal	66.67	62.98	71.3	99.29	94.47	106.94
10	Dorsal	66.31	60.13	70.28	101.69	90.68	105.98
11	Cervical	62.76	54.76	74.28	97.27	87.25	118.36
MUHNCAL.20176							
Block 01	Cervical	51.2	—	48.5	—	—	94.73
	Last cervical	—	—	48.7	—	—	—
	Pectoral 1	—	—	—	—	—	—
Block 02	Pectoral 1	—	—	—	—	—	—
	Pectoral 2	57.1	—	51.4	—	—	90.02
	Pectoral 3	59.4	—	56.3	—	—	94.78
Block 03	Pectoral 4	—	—	—	—	—	—
Block 07	Dorsal	62.1	—	—	—	—	—
	Dorsal	76.1	—	—	—	—	—
Block 26	Pectoral 2	58.6	—	—	—	—	—
	Pectoral 3	59.6	—	—	—	—	—

Vertebrae are in cranial-to-caudal order.

septa collapsed, probably due to erosion. In dorsal view, the alveoli are anterolaterally oriented, with the teeth recurved in occlusal direction. In lateral view (Fig. 6C), the anterior tip of the dentary is thicker compared with the medial part of the same element. In dorsal view, the paradental plate shows at least four resorption pits, with the largest one placed close to the symphysis. The dentary conforms the ventral part of the preserved mandible portion, having a ventral keel.

Splenial—This element covers most of the lingual surface of the mandibular ramus, and it likely participates in the symphysis; however, the anterior suture with the dentary is obscured. In dorsal view, the splenial contacts the dentary, delimitating a lingual groove. The splenial does not reach the ventral part of the mandible (Fig. 6D, E).

Teeth—In the broken tip of the symphysis, two large teeth can be seen embedded inside the dentary, indicating that these are replacement teeth (Fig. 6G). A much-damaged tooth is placed between the sixth and seventh alveoli of the right dentary. This represents the only functional tooth preserved. The replacement teeth show fine and profuse longitudinal ridges over their labial surface. They also display longitudinal cracks. No opposite axial ridges are present. The teeth are robust, and their tip is comparatively blunter than those of *Cryptoclidus* and *Muraenosaurus*.

Remarks—MUHNCAL.20205 was part of a concretion, being probably eroded before burial. The tissue of the occlusal surface (paradental plate) is partially eroded, whereas its ventral periosteal tissue is much damaged. The reduced number of alveoli (in comparison with *Cryptoclidus* and especially with *Kimmerosaurus*) and the presence of larger teeth with respect to the size of the mandible are characteristics present in *Vinialesaurus caroli* (Gasparini et al., 2001), from the upper Oxfordian of Cuba. In addition, MUHNCAL.20205 shares with *Vinialesaurus* the presence of very dense fine striae on the dental crowns and a thin splenial that reaches the symphysis. MUHNCAL.20205 also shares with *Vinialesaurus* a symphysis length that reaches the fourth alveolus; it also has a mandibular symphysis axially larger and dorsoventrally thicker than that of *Vinialesaurus*, but it differs from other cryptoclidids such as *Cryptoclidus*,

Kimmerosaurus, *Tricleidus*, *Muraenosaurus*, *Kimmerosaurus*, *Spitrasaurus*, and *Djupedalia* that have a short symphysis (Brown, 1981; Knutsen et al., 2012a, 2012b). In MUHNCAL.20205, the occlusal surface of the symphysis forms a structure similar to a platform that, among cryptoclidids, is only found in *Vinialesaurus*. In addition, MUHNCAL.20205 is remarkably similar to *Vinialesaurus* in its length, general contour, and alveolar distribution, with a coincident number of alveoli in the preserved mandibular fragment.

PHYLOGENETIC ANALYSIS

The fragmentary condition of MUHNCAL.20176 allowed the scoring of 53 characters, which were used for phylogenetic analysis. We removed from the data matrix the same wildcard taxa detected by Benson and Druckenmiller (2014) (i.e., *Eromangasaurus*, *Pliosaurus irginensis*, *Pliosaurus funkei*, *Eurycleidus*, *Macroplata*, and *Pistosaurus* skull). The IterPCR script allowed identification of the following unstable taxa, which collapsed nodes in the strict consensus: *Avalonnectes arturi*, *Alexandronectes zealandiensis*, and *Arminisaurus schuberti*. In addition, GWWU.A3.B2 was removed, because it is considered to be referable to *Brancasaurus brancai* by Sachs et al. (2016). After removing these taxa from the data set, we performed the analysis (see Supplemental Data 2) with Traditional Search (100 replications, keeping 500 trees per replication), obtaining 480 most parsimonious cladograms (MPCs) (1,564 steps; retention index [RI] = 0.65; consistency index [CI] = 0.27). This data set was later tested with Implied Weighting (K = 3; New Technology Search, Ratchet), obtaining a single MPC (1,525 steps; CI = 0.27; RI = 0.65). The topology of Cryptoclididae in the resulting cladogram (Implied Weighting) is shown in Figure 7.

MUHNCAL.20176 was recovered as the sister taxon of *Muraenosaurus leedsi*. A single synapomorphy of *Muraenosaurus* + MUHNCAL.20176 is the common presence of a humerus having long axis curvature that is almost straight in anterior view (Char. 239, state 0). Autapomorphies of MUHNCAL.20176 include cervical zygapophyses horizontally
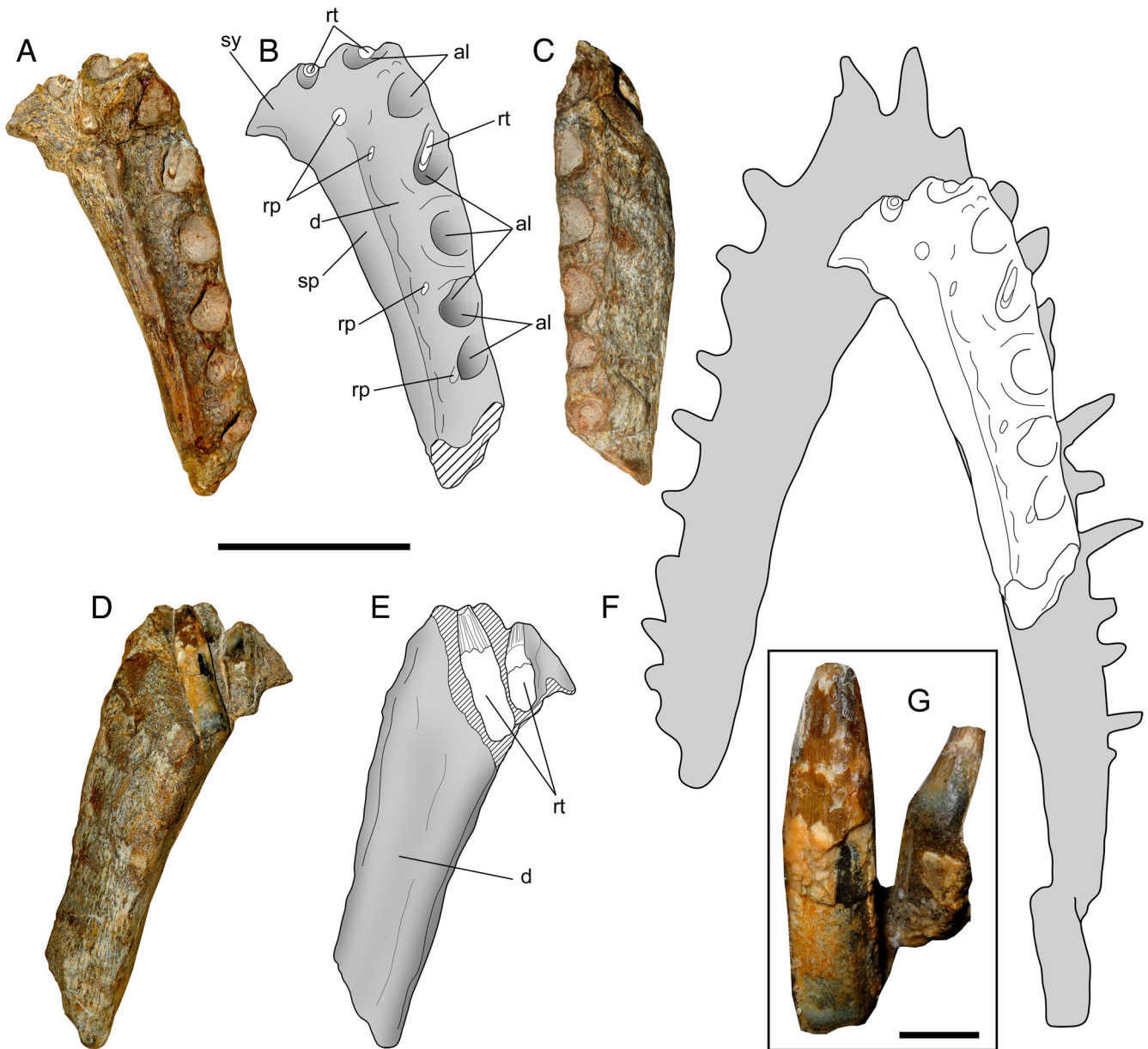
FIGURE 6. *Vinialesaurus* sp., MUHNCAL.20205, incomplete mandible. **A**, photograph and **B**, line drawing of dorsal view. **C**, right lateral view. **D**, photograph and **E**, line drawing of the ventral view. **F**, MUHNCAL.20205 superposed on the outline of the holotype of *Vinialesaurus caroli* (modified from Gasparini et al., 2001). **G**, detail of the replacement teeth with matrix digitally removed. **Abbreviations**: **al**, alveoli; **d**, dentary; **rp**, resorption pit; **rt**, replacement teeth; **sp**, splenial; **sy**, symphysis. Scale bars equal 5 cm (**A–F**) and 1 cm (**G**).

oriented (Char. 167, state 0); the cervical neural spines with apex transversely expanded into prominent spine table (Char. 174, state 1); dorsal transverse processes approximately horizontal (Char. 182, state 1); anterior process of the coracoid dorsoventrally low and thus plate-like (Char, 212, state 0); femur straight or almost straight (Char. 240, state 0); and distal end of propodials uniformly convex (Char. 247, state 0).

DISCUSSION

Hypotheses of Relationships

The topology obtained with the phylogenetic analyses indicates that MUHNCAL.20176 represents a cryptoclidid plesiosaur closely related to *Muraenosaurus leedsi*; however, the lack of the skull makes a more definitive taxonomic determination difficult. The occurrence of material referable to *Vinialesaurus* in the same unit and horizon in the Atacama Desert is also interesting. The postcranial skeleton of *Vinialesaurus caroli* is still unknown. Its holotype (and previously unique known specimen) only comprises an incomplete skull, mandible, and atlas-axis. Due to the lack of overlapping anatomical elements between MUHNCAL.20176 and *Vinialesaurus caroli* holotype, we cannot exclude an eventual taxonomic affinity between both taxa.

Tooth Comparison

The teeth of MUHNCAL.20176 (referred to *Muraenosaurus* sp.) are clearly different from those of MUHNCAL.20205
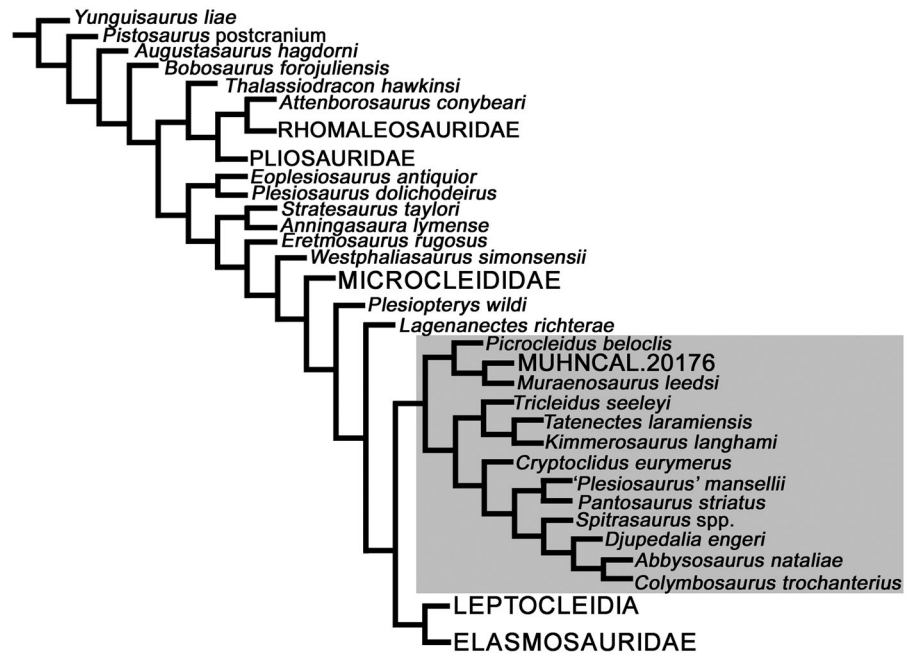
FIGURE 7. Simplified version of the single most parsimonious cladogram (1,525 steps; CI = 0.27; RI = 0.65) obtained with Implied Weighting (K = 3; New Technology Search, Ratchet) showing the topology of the Cryptoclididae (gray field) and including MUHNCAL.20176 (here referred to *Muraenosaurus* sp.).

(referred to *Vinialesaurus* sp.). MUHNCAL.20176 teeth have a rounded cross-section, contrary to those of MUHNCAL.20205, which have an oval cross-section. The general tooth shape is also different, being slender and gracile in the former and robust with a blunter tip in the latter. MUHNCAL.20176 also has profuse labial and lingual ridges and two strong opposing axial ridges along both sides of the tooth crown. Both features are absent in MUHNCAL.20205 (the latter only have soft and profuse lingual ridges). All these differences add support for considering the two specimens to be different taxa.

Comments on the Putative Austral Records of Cryptoclididae

Brown (1981) considered the Maastrichtian genus *Aristonectes* from South America and Antarctica referable to Cryptoclididae, based on the remarkable convergence with the skull of *Kimmerosaurus*. Later, Chatterjee and Small (1989) described a new genus and species, *Morturneria seymourensis*, from the Maastrichtian of Antarctica, also referring it to Cryptoclididae. Additionally, Cruickshank and Fordyce (2002) described a third austral plesiosaur taxon, *Kaiwhekea katiki*, from the early Maastrichtian of New Zealand, which was also considered to be a cryptoclid, reinforcing the hypothesis of a Late Cretaceous austral radiation of the group. A growing body of evidence demonstrates that these three species are indeed endemic, highly derived elasmosaurids (Gasparini et al., 2003; O'Gorman et al., 2013; Otero et al., 2014; O'Keefe et al., 2017). Thus, the known records of cryptoclids in the Southern Hemisphere remain restricted to the Middle–Late Jurassic.

Cryptoclididae are globally absent during the Late Cretaceous, and their records barely exceeded the Jurassic–Cretaceous boundary (Benson and Druckenmiller, 2014). A late radiation of the group is documented in the Tithonian of Norway, with evidence of endemic, derived colymbosaurine cryptoclidids with longer necks that inhabited high latitudes (Knutsen et al., 2012a, 2012b). Only one Early Cretaceous record is known to date, represented by *Abyssosaurus* from the upper Hauterivian of Russia (Berezin, 2011).

Paleobiogeography

Updated records of Cryptoclididae in the Southern Hemisphere are scarce. Material referred to *Muraenosaurus* has been described in the Lajas Formation (Callovian), Chacaico Sur, Argentina (Gasparini and Spaletti, 1993), although initially they were considered to be Elasmosauridae. These authors also described material referred to *Cryptoclidus*, from the same locality and age. The two new records of *Muraenosaurus* and the record of *Vinialesaurus* in the Oxfordian of northern Chile add to an emerging picture regarding the geographic distribution of the group. In the Northern Hemisphere, *Muraenosaurus* has been recorded from the Callovian of England (Seeley, 1874; Andrews, 1910; Brown, 1981; Evans, 1999; Benson and Druckenmiller, 2014) and France (Bardet et al., 1991). The new records from Chile represent the latest known occurrences of *Muraenosaurus*, now extended into the Oxfordian. On the other hand, *Vinialesaurus caroli* was only known by its holotype (MNHNCu P3008) from the Oxfordian of the Jagua Formation, Sierra de los Órganos, Cuba (De la Torre and Rojas, 1949; Gasparini et al., 2001). The new record from the Oxfordian of northern Chile represents its first occurrence outside Cuba and the first coeval occurrence in the Southern Hemisphere. Other Oxfordian cryptoclidids are known in the U.S.A., represented by *Tatenectes laramiensis* (O'Keefe and Wall, 2003; O'Keefe and Street, 2009).

Muraenosaurus had a bihemispheric distribution during the Callovian. Its presence in the Oxfordian of Chile represents a possible relict occurrence for the genus. On the other hand, the presence of *Vinialesaurus* in the Oxfordian of Chile adds solid evidence to the exchange of marine vertebrates through the Caribbean Seaway during the Middle and Late Jurassic. In this sense, a similar Upper Jurassic distribution pattern was previously noted for thalattosuchians (Gasparini, 1996; Gasparini et al., 2000). In addition, Arratia (2008) recognized similar biogeographic patterns for varasichthyid fishes and their sister taxa (*Ascalabos*, *Tharsis*, and Ichthyodectiformes), particularly in their Upper Jurassic distribution between the northern Tethys, the Caribbean, and the Profeta-La Ternera Basin.

Previous Oxfordian Vertebrate Records in the Atacama Desert, Northern Chile

The best-represented vertebrates in Oxfordian rocks of the Atacama Desert are bony fishes, which have been recorded mainly in outcrops of the Cerritos Bayos and El Profeta Formation. In the first unit, Biese (1961) mentioned for the first time the presence of osteichthyans. In particular, this author pointed out the presence of *Lepidotes* and '*Pachycornius*' (misspelling of *Pachycormus*); however, the material was not illustrated, hindering its reassessment. A high diversity of endemic osteichthyans was described from Oxfordian levels of El Profeta Formation, exposed 250 km south from Calama, including ?*Pholidophorus domeykanus* (Arratia et al., 1975c), *Protoclupea chilensis* (Arratia et al., 1975b), *Bobbichthys opercularis* (Arratia et al., 1975a), *Varasichthys ariasi* (Arratia, 1981), *Chongichthys dentatus* (Arratia, 1982), *Domeykos profetaensis* (Arratia and Schultze, 1985), *Protoclupea atacamensis* (Arratia and Schultze, 1985), *Antofagastaichthys mandibularis* (Arratia, 1986), and *Atacamichthys greeni* (Arratia and Schultze, 1987). Also in the Oxfordian of El Profeta Formation, indeterminate Pycnodontiformes as well as indeterminate teleosteans were mentioned by Arratia (1987). The first was later reassigned to *Gyrodus* sp. (Kriwet, 2001). Remains of large filter-feeding osteichthyans from Oxfordian levels of El Profeta Formation and Cerro Campamento Formation were referred to *Leedischthys* (Arratia and Schultze, 1999; Martill et al., 1999; Liston, 2010; Ossa-Fuentes et al., 2015). Later, Ossa-Fuentes et al. (2015) described remains of at least two indeterminate Pachycormiformes different from *Leedsichthys*, including one filter-feeding indeterminate taxon and a second material with affinities to *Eugnathides*. Additionally, Ossa-Fuentes et al. (2015) report remains of fishes that are referred to *Leedischthys* sp., *Lepidotes* sp., *Eughnathides*?, and to the clade Varasichthyidae.

In addition, records of diapsids from the Oxfordian of the Cerro Campamento Formation include metriorhynchid crocodiles (Soto-Acuña et al., 2015a), pterosaur remains (Alarcón et al., 2015, 2018), indeterminate pliosaurids (Otero et al., 2018d), and ophthalmosaurid ichthyosaurs (Otero et al., 2018c).

CONCLUSIONS

Three plesiosaur specimens from the Oxfordian of northern Chile represent the first local material of this age that is informative enough to enable genus-level determination. Two of these specimens, a fragmentary skeleton and an articulated cervical-to-dorsal axial section, are here referred to *Muraenosaurus* sp. A third specimen, represented by a partial mandible, is here referred to *Vinialesaurus* sp. These records show a diversity of cryptoclidids present in southern South America during the Late Jurassic. The two new Oxfordian records of *Muraenosaurus* in northern Chile add to their previous occurrence in the Callovian of Argentina, showing an emerging pattern with continuous presence of the genus throughout the Middle and Upper Jurassic of southern South America, with evidence that suggests the existence of a new taxon. Additionally, the new record of *Vinialesaurus* represents its first occurrence in the Southern Hemisphere, and the second known specimen referred to this genus. The presence of coeval taxa typical of the Tethys, plus the occurrence of a coeval taxon from Cuba, adds support to the fully functional Caribbean Seaway during the Late Jurassic.

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