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The vertebrate fauna of the upper Permian of Niger—XI. Cranial material of a juvenile

Moradisaurus grandis (Reptilia: Captorhinidae)

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RH: Sidor et al.—Juvenile *Moradisaurus* from Niger

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ABSTRACT—We describe the skull of a juvenile *Moradisaurus grandis*, a moradisaurine captorhinid from the upper Permian Moradi Formation of northern Niger. The juvenile skull is less than half the length of the largest known skull of *M. grandis*, and differs from the latter in featuring a transversely narrower mandible, only five rows of maxillary teeth, as opposed to 10 in the adult, a relatively larger orbit, a relatively taller skull, and a cultriform process of the parasphenoid angled upwards at 20–30° from the basal plate, as well as reduced ossification of the braincase. Most of these features have been considered characteristic of the less derived members of the family (e.g., *Protocaptorhinus pricei*, *Captorhinus laticeps*). Data from the juvenile *Moradisaurus* allow us to amend a previous statement that the braincase of the holotype and largest known skull of the moradisaurine *Labidosaurikos meachami* is characterized by poor ossification: we infer instead that this skull is not skeletally mature and that the braincase would have fully ossified in larger, ontogenetically older individuals of this moradisaurine. An updated cladistic analysis of captorhinids yields *Moradisaurus* as the sister taxon to *Gansurhinus* + *Rothianiscus*, replicating the results of several previous analyses, but improving slightly the robustness of Moradisaurinae and the clade of *Labidosaurus* + Moradisaurinae with respect to previous works.

INTRODUCTION

Captorhinids are early reptiles that are known from every continent except Antarctica and Australia, ranging from the uppermost Carboniferous of North America (Müller and Reisz, 2005) to the upper Permian of Africa (Taquet, 1969; Gaffney and McKenna, 1979; de Ricqlès and Taquet, 1982; Gow, 2000; Modesto and Smith, 2001; Liebrecht et al., 2016). They are a familiar

component of the classic Red Bed assemblages of Texas, Oklahoma, and the Four Corners region of the U.S.A. (Williston, 1911; Romer, 1958; Olson, 1962; Olson and Barghusen, 1962; Sullivan and Reisz, 1999; Kissel and Lehman, 2002). Captorhinids were particularly diverse during early Permian times, owing in part to ongoing research of collections made from the Richards Spur locality in Oklahoma, U.S.A. (Modesto, 1996, 1998; Kissel et al., 2002; Reisz et al., 2015; Modesto et al., 2018; deBraga et al., 2019). Whereas most early Permian captorhinids were faunivorous or omnivorous reptiles (see Modesto et al., 2018), herbivorous captorhinids, which form a monophyletic group known as moradisaurines, appeared during the Kungurian (the final stage of the early Permian) and survived almost to the end of the Permian (Taquet, 1972; de Ricqlès and Taquet, 1982; Dodick and Modesto, 1995; O’Keefe et al., 2005; Reisz et al., 2011; Liebrecht et al., 2016; Modesto et al., 2019; Cisneros et al., 2020).

The largest and one of the best known moradisaurines is the eponymous *Moradisaurus grandis*, from the upper Permian Moradi Formation of northern Niger. The holotype, a skull with mandible, was collected in the 1960s and its mandible was described briefly by Taquet (1969). The skull was later described in detail by de Ricqlès and Taquet (1982). The Moradi Formation was revisited briefly in 2000 and then again in 2003 and 2006 by international teams who collected additional fossils of moradisaurines, pareiasaurs, and temnospondyls. The resulting research revealed that, in contrast to the therapsid-dominated late Permian faunas known from southern and eastern Africa, the Moradi Formation assemblage is atypical in comprising mostly reptiles and non-stereospondyl temnospondyls (Sidor et al., 2003, 2005; Damiani et al., 2006; Steyer et al., 2006; Sidor, 2013; Tsuji et al., 2013; Turner et al., 2015; but see Smiley et al., 2008). In addition, O’Keefe et al. (2005, 2006) described the first postcranial material of *M.*

grandis. More recently, the mandibles of two subadult individuals of *M. grandis* were described by Modesto et al. (2019).

Most phylogenetic analyses that include *M. grandis* recover this moradisaurine in a clade with the genera *Rothianiscus* and *Gansurhinus*, with *Labidosaurikos* and *Captorhinikos* as successive outgroups within Moradisaurinae (Reisz et al., 2011; Modesto et al., 2014, 2018, 2019; Liebrecht et al., 2016). The analysis of Cisneros et al. (2020) recovered a largely polytomous Moradisaurinae, but this uncertainty is attributable to the inclusion of a South American taxon with large amount of missing data. As of Modesto et al. (2019), *M. grandis* can be coded for ca. 72% of phylogenetic characters that have been used to evaluate captorhinid interrelationships. This figure contrasts with that of 86% for the best known moradisaurine, *Labidosaurikos meachami*, which is known from the holotype, a partial but otherwise highly informative skull and mandible from Crescent, Oklahoma (Dodick and Modesto, 1995), and numerous fragmentary specimens (largely tooth plates) from north-central Texas that have been referred to this species (Seltin, 1959; Jung and Sumida, 2017).

Here we describe the remains of two small individuals of *M. grandis*. The more informative specimen consists of a skull and occluded mandible, which preserves areas and sutures that are poorly preserved in the holotype and the referred mandibular material. Our description of this new material of *M. grandis* allows the opportunity to code this taxon for several cranial characters that were indeterminate in previous phylogenetic analyses of moradisaurine captorhinids, towards a re-evaluation of *M. grandis* within Moradisaurinae.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **FMNH**, Field Museum, Chicago, Illinois, U.S.A.; **MCZ**, Museum of Comparative

Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MNN**, Musée National du Niger, Niamey, Niger; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

MATERIAL

MNN MOR149 was found embedded in a red loessic siltstone (Smith et al., 2015) with its dorsal surface weathering out. It was prepared using pneumatic air scribes and pin vises by XXX (Redpath Museum, McGill University) and B. Crowley (Burke Museum, University of Washington). Adjacent to this skull was a larger block containing the remains of at least two additional individuals (MNN MOR150, MNN MORXX), including two skulls as well as one articulated vertebral column and scattered appendicular material (see Smith et al., 2015:fig. 12C.). MNN MOR150 and MNN MORXX were, however, jumbled together and it is very difficult to discriminate between the individuals present.

The following specimens were studied for comparative purposes: AMNH 4705, isolated supraoccipital referred to *Labidosaurus hamatus*; CM 73370, skull of *L. hamatus*; MNN MOR71, lower jaw and hind limb of *Moradisaurus grandis*; USNM 21275, skull and partial postcranial skeleton of *Captorhinikos chozaensis*.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768

CAPTORHINIDAE Case, 1911

MORADISAURINAE de Ricqlès and Taquet, 1982

MORADISAURUS GRANDIS Taquet, 1969

(Figs. 1–3)

Holotype—MNHN MRD1, skull and mandible. This specimen is housed in the MNHN collections but some bones have been lost (J.-S.S., pers. obs.).

Referred Material—MNN MOR42, nearly complete right mandibular ramus (Modesto et al., 2019); MNN MOR78, right mandibular ramus and partial postcrania of a subadult individual (O’Keefe et al., 2005; Modesto et al., 2019); MNN MOR79, articulated pes with associated limb and cranial fragments (O’Keefe et al., 2006); MNN MOR149, partial juvenile skull (Figs. 1, 3, S1–S4, S6–S8); MNN MOR150, partial skull (Figs. 2, S5); MNN MORXX, add detail here.

Locality and Horizon—MNN MOR149 and MNN MOR150 were collected approximately 60 km southeast of Arlit, Agadez Department, northern Niger (see O’Keefe et al., 2005:fig. 1). The locality lies within the upper strata of the Moradi Formation (see S12 of Smith et al., 2015: fig.3), which is the uppermost unit of the Izéguandane Group (Tabor et al., 2011). The age of the Moradi Formation is poorly constrained, but paleontological evidence indicates a Late Permian age (Taquet, 1972; de Ricqlès and Taquet, 1982; Smiley et al., 2008; Tabor et al., 2011).

Revised Diagnosis—Modified from Modesto et al. (2019): captorhinid distinguished from other species by the presence of prominent tubercle on the exoccipital, lateral to this element’s contribution to occipital condyle; skull reaching a maximum length of ca. 45 cm; skull triangular in dorsal aspect and with heavy ornamentation; occipital region enlarged; jaw articulation

posteriorly placed; pterygoids and parasphenoid edentulous; maxillae and dentaries bearing tooth plates composed of 8–12 rows of conical teeth in the largest individuals, with these batteries partially carried on wide flanges of bone extending lingually from maxilla and dentary; mandible broad mediolaterally in large individuals; mandible with strongly developed coronoid eminence. Distinctive characteristics of mandible include extreme medial extension of the dental plateau, mentomeckelian present, coronoid twisted and with conspicuously thickened posterodorsal process, lack of prominent wear facets on the teeth, and anteroposteriorly elongate articular cotyle; and relatively extensive contribution of splenial to lateral surface of lateral/labial surface of mandible. Distinctive characteristics of hind limb include very robust femur with reduced internal trochanter; hypertrophied intertrochanteric fossa, fourth trochanter, and adductor ridge; horizontally oriented proximal condyle; tibial plateau making acute angle with shaft of tibia; astragalus foreshortened with hypertrophied articulations for tibia, fibula, and calcaneum; tibial articulation large, making relatively shallow angle with body of astragalus, and extended medially by accessory ossification; calcaneum co-ossified with distal tarsal five; astragalus and calcaneum both possess irregular accessory ossifications on their ventral surfaces; notch for perforating artery confined to astragalus only; and metatarsals and phalanges stout and foreshortened.

DESCRIPTION

Preservation and General Morphology

Weathering has affected the external surface of all the skull roofing bones of MNN MOR149 to some degree, so that little of the original dermal ornamentation is preserved (Fig. 1).

The right hemimandible, however, is a notable exception. The specimen is missing some of the nasals, lacrimals, and septomaxillae. Furthermore, the parietals, postfrontals, postparietals, and supratemporals are missing. The skull is also somewhat deformed, with the skull roof pushed slightly right, relative to the palate. What remains of the squamosals shows that the skull was relatively deep in life. This interpretation is reinforced by rearticulating the supraoccipital and the epipterygoids, which were found disarticulated but within the cranial vault of the specimen (Fig. 3). The snout is relatively narrow when compared to non-moradisaurines such as *Captorhinus aguti*, but does not show the extreme elongation of *Labidosaurikos meachami*. In contrast, the temporal region appears anteroposteriorly shorter and not as broad as in *La. meachami*, although the holotype of this taxon is almost a third larger than MNN MOR149 (see Stovall, 1950).

As preserved, the maximum length of MNN MOR149 is 20.5 cm, measured from the tip of the snout to the end of the retroarticular process. Measured across the quadratojugals, the width of skull is 15.4 cm. We estimate the height of skull to have been at least 7 cm, when measured from the articular surface of the quadrate to the top of the parietal.

MNN MOR150 consists of the posterolateral corner of the left temporal region and the posterior half of the left hemimandible (Fig. 2). The remainder of MNN MOR150, including postcranial elements, still requires preparation.

Skull Roof

The following morphological description is based on MNN MOR149 (Figs. 1, 3), with supplementary information from MNN MOR150 (Fig. 2). Photographs of the specimens are collated in Supplemental Data 1.

Premaxilla—As in most other captorhinids, the ventral margin of the premaxilla is oriented anteroventrally from the remainder of the upper tooth row, when observed in lateral view (Fig. 1D). There were probably five premaxillary teeth in each premaxilla, although on neither side is the premaxilla-maxilla suture visible clearly. Whereas poor preservation precludes a detailed description of the tooth morphology, it seems clear on the left side that the premaxillary teeth decrease in size posteriorly, with the first tooth being substantially more robust than the others. The dorsal process of the premaxilla is completely eroded, permitting the anterior portion of the narial passageway to be viewed anteriorly. In palatal view (Fig. 1B), the vomerine process of the premaxilla is narrow and clasped by the vomer laterally.

Septomaxilla—The region of the septomaxilla is eroded and nothing of its morphology can be described.

Maxilla—This bone is best preserved on the right side (Fig. 1D). In lateral view, it is extremely low and confined to the ventral margin of the skull. In less derived captorhinids (e.g., *Rhiodenticulatus heatonii*, *Saurorictus australis*), the maxilla has a distinctly convex upper margin where it sutures to the lacrimal (Berman and Reisz, 1986; Modesto and Smith, 2001). In contrast, the dorsal margin of the maxilla in MNN MOR149 is only slightly deepened about midway along its length. The posterior end of the maxilla bends slightly laterally beneath its contact with the jugal. In right lateral view, there are 17 teeth visible on the horizontal portion of the upper jaw, with gaps for two or three more. Only the lateral-most row of maxillary teeth is visible. However, we suspect that three or four additional rows are present more medially because of the convex profile of the lingual margin of the left maxilla and its proximity to the palatine-pterygoid suture in the palatal view, which is strongly reminiscent of that in *La. meachami* (Dodick and Modesto, 1995:fig. 4). Unfortunately, the tight occlusion of the jaws

precludes a direct count. As with the premaxillary teeth, the tooth crowns are not well preserved. However, it appears clear that there were several moderately enlarged teeth present in the anterior portion of the maxilla.

Lacrimal—The lacrimal is partially preserved on both sides. On the left side, its sutural contacts with the maxilla, the nasal, and the jugal are visible. Generally in captorhinids (e.g., Heaton, 1979), the primitive amniote condition is retained, with the lacrimal interposed between the external naris and orbit. We suspect that this condition was also maintained in MNN MOR149, although the poor preservation of the external naris makes this tenuous. The posterior part of the lacrimal extends approximately one-third of the way under the orbit, forming a well-developed suborbital process. In dorsal aspect, the lacrimal is seen to share a broad contact with the palatine. This suture ends posteriorly at the dorsal egress of a relatively large suborbital foramen, of which the lacrimal forms the anterior end.

Nasal—The left nasal is more complete and shows some of the suture between the nasal and the lacrimal. On both sides, the external surface of the nasal is eroded so that the diplöe is exposed. However, the original shape of the bone is preserved and shows that the nasals combined to form smoothly arched snout (Fig. 1A, D).

Frontal—The right frontal is represented by an isolated island of bone lying between the orbits on the skull roof (Fig. 1A). Nothing can be said about its sutural relationships to the surrounding bones of the skull roof.

Prefrontal—Weathering has reduced both prefrontals to small portions of bone along the anterodorsal margins of the orbits and the sutures with the lacrimals, but little detail can be made out (Fig. 1A, D).

Jugal—The right jugal is better preserved than the left (Fig. 1D). Anteriorly, it forms a wedge of bone that extends anterior to the antorbital margin and contacts the lacrimal dorsally and the maxilla ventrally. Posterior to the maxilla, the jugal forms the ventral margin of skull and can be seen to dip slightly to form the anterior portion of a slightly convex posterior cheek. This is in contrast to the condition depicted for *La. meachami*, where the ventral margin is relatively horizontal in this region. The alary process of the jugal is well developed and, in lieu of an ectopterygoid, makes narrow contacts with the palatine and the pterygoid, as seen in dorsal aspect (Fig. 1A). The posterior end of the jugal is broadly spatulate and contributes to the anapsid temporal morphology. However, the temporal region is weathered to the point that sutures with the postorbital, the squamosal, and the quadratojugal are not discernible with confidence. On the left side, the jugal's contacts with the postorbital, squamosal, and quadratojugal are suggested by differences in bone fiber orientation, and the apparent paths of these sutures are dashed in the interpretive drawing in dorsal aspect. The skull roof fragment of MNN MOR150 shows these sutures clearly as broadly serrate contacts (Fig. 2). In dorsal view, the jugal combines with the quadratojugal to form the lateral margin of a relatively broad cheek region.

Postorbital—The presence of a postorbital can be distinguished only on the left side, where its margins are delineated by changes in fiber orientation on the weathered temporal region. If interpreted correctly, the postorbital is a triangular wedge of bone forming the posterior margin of the orbit. This configuration is more similar to that preserved in small-bodied captorhinids such as *R. heatoni* and *S. australis* and dissimilar to the blunt-ended condition seen in *La. meachami* (Berman and Reisz, 1986; Dodick and Modesto, 1995; Modesto and Smith, 2001).

Squamosal—As in all captorhinids, the squamosal is a large bone forming much of the lateral surface of the temporal region. In MNN MOR149 this element is weathered on both sides, thereby exposing its internal architecture, but its posterior surface is relatively well preserved. In lateral view (Fig. 1D), the squamosal contacts the postorbital and the jugal anteriorly and the quadratojugal along its ventral surface. On the right side, the posterior surface of the squamosal is undamaged and is oriented orthogonal to the broader temporal portion. The squamosal contacts the quadrate medially and the quadratojugal ventrally, although the latter connection is less clear.

Quadratojugal—The quadratojugal is preserved on both sides on MNN MOR149, although on neither is its morphology pristine. The element is quadrangular in left lateral view, with a near-vertical suture forming its anterior contact with the jugal. In all captorhinids, the quadratojugal forms the ventrolateral portion of the skull in posterior view, just lateral to the contact between the squamosal and the quadrate. Dodick and Modesto (1995) state that *La. meachami* lacks a quadrate foramen. In MNN MOR149, the posterior aspect of the quadrate shows a curved depression above the quadrate condyle that might represent the medial margin of a quadrate foramen (Fig. 1C).

Palate

In contrast to the skull roof, the bones of the palate are comparatively well preserved and little affected by weathering (Fig. 1A–C).

Vomer—This element is a long and extremely narrow bone that forms the medial margin of the internal nares (Fig. 1B). It is edentulous and it contacts the palatal process of the premaxilla anteriorly. Posteriorly, it has a short contact with the anterior ramus of the pterygoid

and a transverse contact with the palatine. Dodick and Modesto (1995) suggested that *La. meachami* and *M. grandis* possess an elongate vomer. Although ‘elongate’ was not quantified, compared to the short and broad vomer of *Captorhinus*, MNN MOR149 is clearly characterized by the elongate condition. Despite matrix partially obscuring this region, it appears that the choanae were elongated posteriorly as well, reaching at least to the level of the vomer-palatine suture.

Palatine—The palatine is a narrow bone that contacts the vomer anteriorly and the pterygoid along its medial and posterior margins (Fig. 1A, B). The lateral margin of the palatine abuts the expanded tooth-bearing plate of the maxilla. As in *La. meachami* and *M. grandis*, the palatine is edentulous.

Pterygoid—As in most early amniotes, the pterygoid is the largest and most complex bone of the palate. In contrast to the single line of teeth present in other captorhinids, a small patch of teeth is present just anterolateral to the basiptyergoid articulation (Fig. 1B). A row of small teeth extends anteriorly along the medial border of the pterygoid and another row extends more anterolaterally to the suture with the palatine. The pterygoid displays a long anterior process that passes between the palatines to contact the vomers. A narrow interptyergoid vacuity is present. The transverse flange of the pterygoid has a ridge-like ventral surface that extends laterally and somewhat posteriorly. The quadrate ramus of the pterygoid has a thin ventral edge. In occipital view, this ramus has a slightly concave posteromedial face that deepens caudally as it approaches the quadrate condyles. There is no arcuate flange. The posterior margin of the pterygoid’s quadrate ramus is subvertical where it contacts the quadrate, except for a small prong of bone along its ventral margin. The fossa for the articulation of the eipterygoid is visible along the dorsal margin of the left pterygoid.

Quadrate—The quadrate can be seen in ventral (Fig. 1B) and posterior (Fig. 1C) views. On the right side, both of its articular condyles are preserved. The long axes of the condyles are oriented anteromedially. Dorsally and anteriorly the ascending process of the quadrate overlaps the lateral surface of the quadrate ramus of the pterygoid. On the left side, where the occipital face of the squamosal is eroded, the quadrate can be seen to extend slightly above the quadrate ramus of the pterygoid. Dodick and Modesto (1995) state that *La. meachami* lacks a shallow pit on the medial surface of the quadrate to receive the distal end of the stapes. In contrast, this pit is clearly preserved on the left side of MNN MOR149.

Epipterygoid—Both epipterygoids were found disarticulated within the cranial cavity of MNN MOR149. The left epipterygoid is the more complete of the two, and it retains a complete columella (Fig. 3A). However, compared to the condition figured for *La. meachami* (Dodick and Modesto, 1995:fig. 10), the columella is extremely delicate and arches slightly medially when rearticulated with the pterygoid. The base of the epipterygoid is relatively deep, with the anterior portion becoming shallower as it curves medially. The lateral surface of the epipterygoid is smooth and featureless. There is no evidence that the epipterygoid contributed to the basicranial recess, as in *C. aguti* (Fox and Bowman, 1966:fig. 12), but it is possible that, if such was present, it was not ossified in this individual.

Braincase

The braincase of MNN MOR149 generally resembles that of *La. meachami* in its poor consolidation of the individual elements. The parabasisphenoid, basioccipital, and exoccipitals were preserved in articulation, with the right opisthotic in close association with these elements,

but the left opisthotic and the supraoccipital were disarticulated and found floating in matrix within the cranial vault.

Parabasisphenoid—The fused parasphenoid and basisphenoid, here termed the parabasisphenoid, can be divided into anterior and posterior components. Anteriorly, the dermal cultriform process is directed upwards at an angle of approximately 20–30° to the basal plane. This is similar to the condition in *Captorhinus*, but less than that of *L. hamatus*, *La. meachami*, and the holotype of *M. grandis*, which typically project anterodorsally at an angle of greater than 45° (Dodick and Modesto, 1995). In ventral view, the basiptyergoid processes are directed anterolaterally and articulate with the basicranial recesses of the pterygoids (Fig. 1B). In contrast to the condition seen in captorhinids generally, the basiptyergoid process is not separated from the crista by a deep trough or vidian canal. Posteriorly the lateral margin of the basiptyergoid process merges with the cristae ventrolaterales. Between the cristae there is a shallow median trough, which is not as deep as the median groove present in the genus *Captorhinus* (Price, 1935; Heaton, 1979). Posteriorly, the parabasisphenoid broadens considerably, the cristae ventrolaterales curve posterolaterally and become more spatulate, and the median groove broadens towards the contact with the basioccipital tubera. The parabasisphenoid forms an extensive sigmoidal contact with the stapes posterolateral to the cristae ventrolaterales. In dorsal view, the posterior portion of the sella turcica and the dorsum sellae is clearly visible. The former is an elliptical pit bound laterally by the processi clinoides, which in turn curve dorsally at their posterior ends and merge seamlessly with the processi sellares. Between the processi sellares extends the dorsum sellae, which separates the sella turcica anteriorly from the cavum cranii posteriorly. The floor of the latter is not entirely preserved, but what is present, formed by the dorsal surface of the parasphenoid portion of the bone, is smoothly finished.

Stapes—The right stapes is preserved in articulation, extending from the lateral surface of the braincase to the quadrate (Fig. 1B, C). The disinterred left stapes (Fig. 3B–E) reveals that this element bears a well-developed dorsal process that articulates with the ventral surface of the paraoccipital process of the opisthotic. The expanded footplate of the stapes is wrapped around the lateral surface of the braincase. The isolated left stapes of MNN MOR149 shows the degree of enlargement of the stapedia footplate, which appears substantially larger than that of *L. hamatus* (Modesto et al., 2007:fig. 10) but is on par with that of *C. aguti* (Modesto, 1998:fig. 6). The columella is directed posteroventrolaterally towards the medial aspect of the quadrate’s medial condyle. The stapedia foramen is visible in ventral view (Fig. 3E). It is positioned slightly medial to the midpoint of the stapes, which agrees with the position of this opening in the stapes of *La. meachami* (Dodick and Modesto, 1995:fig. 8), *L. hamatus* (Modesto et al., 2007:fig. 5), and that of the *C. aguti* specimen re-described by Modesto (1998:fig. 6). Dodick and Modesto (1995) stated that the stapedia foramen was positioned closer to the footplate in ‘small captorhinids’ (i.e., species of *Captorhinus*), but they appear to have based their statement on Heaton’s (1979) reconstruction of the stapes of *Captorhinus laticeps*. That work, however, is a composite of three or more specimens, including at least one stapes from the Richards Spur locality. Complicating matters is the fact that *C. laticeps* is not known from Richards Spur, and thus Heaton’s (1979) reconstruction combines information from two captorhinid species and should be treated with caution.

Basioccipital—The basioccipital forms the approximate posterior third of the basicranial plate (Fig. 1B). In ventral aspect, the basioccipital tubera receive the parabasisphenoid along a broadly serrate suture. Immediately posterior to this contact, the lateral margins of the basioccipital are slightly embayed for the reception of the medial ends of the opisthotics. The

posterior end of the basioccipital forms the ventral half of the occipital condyle. In posterior aspect (Fig. 1C), at the center of the occipital condyle the notochordal pit appears as a smoothly rounded dimple. In addition, the ventral margin of the occipital condyle is subtly depressed along the midline, giving it the appearance of a mild bifurcation. Whereas the sutures with the overlying exoccipitals can be traced on the condyle, they are indiscernible laterally, as are the foramina for the hypoglossal nerves (CN XII).

Exoccipital—Both exoccipitals are well ossified and were found in articulation with the basioccipital (Fig. 1C). However, the remainder of the exoccipital's usual connections are less well developed. The right exoccipital is still in contact with the opisthotic, but a relatively thick line of matrix is present between the two. A slight notch in the lateral margin of each exoccipital, slightly ventral to the level of the ventral margin of the foramen magnum, marks the medial border of the vagus foramen. The left opisthotic and supraoccipital articulations are open, because these elements were disarticulated. The exoccipitals formed the lateral and ventral margins of the foramen magnum. A well-developed tubercle is present lateral to the exoccipital's contribution to occipital condyle (Fig. 1C), which we consider an autapomorphy of *M. grandis*. This feature is present in the holotype (de Ricqlès and Taquet, 1982:figs. 12–15), and it does not appear to be present in any other captorhinid, and accordingly we are confident in our assignment of MNN MOR149 to *M. grandis*.

Supraoccipital—The supraoccipital (Fig. 3F–I) was disarticulated from the skull roof and the other braincase elements, but found within cranial cavity. This mode of preservation agrees with the description of the braincase of the larger holotype of *La. meachami* as poorly consolidated; Dodick and Modesto (1995) suggested that the supraoccipital was connected to the rest of the braincase by a cartilaginous connection in that species. The morphology of the

supraoccipital of MNN MOR149 is comparable to that of *C. aguti* (Modesto, 1998:fig.8a–d) in that the main body of the bone is plate-like, from the dorsal margin of which extend three processes. Excluding these dorsal processes, the plate-like body of the supraoccipital is broader than it is tall in posterior view (Fig. 3H). The dorsal margin of the foramen magnum is represented by a deep notch in the ventral margin of the bone. From a sagittal, midline eminence, the left and right sides of the main body of the bone slope anterolaterally. The midline eminence thickens slightly dorsally and then forks to give rise to dorsolaterally directed, roughened ridges that in turn give rise to the dorsolateral processes. Whereas the right dorsolateral process is missing, the left is well preserved as a subcylindrical extension that projects posterolaterally well beyond the main body of the bone in dorsal aspect, an orientation that contrasts with the transversely aligned dorsolateral processes in *La. meachami* (Dodick and Modesto, 1995:fig. 11a) and in *C. aguti* (Modesto, 1998:fig. 8c).

The dorsal surface of the supraoccipital is dominated by the dorsomedial process (Fig. 3F–D). Whereas this process has the profile of a blunt finger of bone in occipital aspect, it exhibits a distinctly hatchet-shaped profile in lateral aspect. In proper articulation with the skull roof, the dorsal surface of the dorsomedial process would have underlain the paired parietals along the posterior part of their midline suture, and the posterior (occipital) surface would have been overlapped by the medial portions of the paired postparietals. The contact surface for the latter pair of bones extends ventrally down the occipital surface of the supraoccipital, to the point where the midline eminence bifurcates at its dorsal end (the topographic center of the bone in occipital aspect).

In anterior aspect the supraoccipital closely resembles that of *C. aguti* (Modesto, 1998:fig. 8b), except that the membranous labyrinth is relatively reduced in extent (Fig. 3I). Whereas in *C.*

aguti the membranous labyrinth extends nearly the entire height of the main body of the element and the posterior surface of the cavum cranii is constricted between the otic regions, in MNN MOR149 the membranous labyrinth occupies the ventrolateral corner of the element and the posterior surface of the cavum cranii is only slightly waisted.

Prootic—Presumably, the prootics are preserved amongst the fragments of bone that were found suspended in the matrix that filled the cranial cavity, but none of these fragments is recognizable as either prootic. It seems that this element was not well ossified at this ontogenetic stage.

Opisthotic—Apart from a relatively narrower paroccipital process, the opisthotic (Fig. 1B–D) of MNN MOR149 resembles very closely that of a large individual of *C. aguti* (Modesto, 1998:fig. 7). As in that species, the opisthotic is characterized by a blocky medial portion that contacts the supraoccipital, the exoccipital, the basioccipital, the prootic, and the stapes, and laterally it narrows greatly to form a rod-like paroccipital process. This organization of the bone is dramatically different in the holotypic skull of *La. meachami*, which has an acute, triangular profile in occipital view (Dodick and Modesto, 1995:fig. 7).

Mandible

The mandibular symphysis is unfused, with the right hemimandible moved slightly posteriorly, thereby exposing the left symphyseal pad in medial view. The morphology of the mandible of MNN MOR149 is intermediate between that of basal captorhinids such as *Captorhinus* spp. (Heaton, 1979; Modesto, 1998) and larger individuals of *Moradisaurus grandis* (Modesto et al., 2019). In ventral view (Fig. 1B), each mandibular ramus is relatively straight and narrow, like that of *Captorhinus aguti* (Modesto, 1998:fig. 2), and lacks the broad, sigmoidal

outline of *Labidosaurikos meachami* and larger individuals of *M. grandis*. However, the mandibular ramus of MNN MOR149 is relatively thicker labiolingually than that of *C. aguti* (Modesto, 1998:fig. 2) and the dentary shelf, although not developed to the same degree as in larger individuals of *M. grandis* (Modesto et al., 2019:figs. 1, 2), accentuates the labiolingual breadth of the ramus. Related to these observations is the fewer number of mandibular tooth rows or smaller overall size of MNN MOR149, and it is interesting that specimens of *Captorhinikos chozaensis* that are smaller and have a similar number of tooth rows are substantially broader in their post-tooth-plate region (e.g., USNM 21275; Vaughn, 1958). The lateral profile of the right hemimandible closely resembles that of *La. meachami*, with its deep post-dental portion that attenuates posteriorly to a relatively acute retroarticular process (Dodick and Modesto, 1995:fig. 12a). In lateral view (Fig. 1D), the dentary and the surangular contribute to a prominent shelf on the lateral aspect of the coronoid process. This shelf likely accommodated the slightly depressed ventral margin of the jugal and the quadratojugal. In contrast to most areas of the skull, dermal ornamentation is preserved on the external surface of the right hemimandible. A foramen intermandibularis caudalis is formed at the confluence of the splenial, the angular, and the prearticular. This anteroposterly elongate opening is the same relative size as in MNN MOR78 (Modesto et al., 2019:fig. 2b, d).

Dentary—In lateral view (Fig. 1D), the remains of 21 teeth are visible in the right dentary, with space for another possible tooth. The first tooth is very small and in lateral aspect is oriented in line with the sloping anterior margin of symphysis. As in *Moradisaurus*, the third dentary tooth is largest of the mandibular tooth row. The number of tooth rows is impossible to determine because of the tight occlusion of the jaws. In lateral view, the dentary deepens posteriorly to a point ventral to the penultimate (labial) tooth, and then extends posteriorly and

slightly dorsally, making contacts with the angular posteroventrally, the surangular directly posteriorly, and the coronoid dorsally. Posterodorsally, the dentary contributes to the base of the coronoid process. Anteriorly, the mandibular symphysis is formed by both the dentary and splenial, although the latter element's contribution appears greater.

Splenial—The splenial forms the medial surface of the mandible's anterior half (Fig. 1B). It is mainly a flat, vertical bone, forming long contacts with the dentary both dorsally and ventrally, and deepening posteriorly from its contribution to the mandibular symphysis. Posteriorly the splenial is notched where it forms the anterior border of the foramen intermandibularis caudalis, suturing to the angular beneath the foramen and to the prearticular and coronoid above it.

Angular—The angular forms the posteroventral aspect of the mandible in lateral view (Fig. 1D), contacting the dentary anteriorly, the surangular dorsally, and the articular posteriorly. In ventral view, the angular has a long, narrow anterior process slotted between the dentary and the splenial. Posteriorly, the angular underlies the articular and extends posteriorly to the base of the retroarticular process. Along the medial surface of the mandible, the angular contacts the splenial anteriorly, forming the posteroventral margin of the foramen intermandibularis caudalis, posterior to which the angular forms a long, weakly curving suture with the prearticular dorsally.

Surangular—The lateral face of the surangular is preserved only on the right side (Fig. 1D, 2). It forms a zigzag suture with the dentary and contributes to the posterior half of the lateral mandibular shelf. Posteriorly, the surangular forms a weakly convex suture with the articular, which terminates ventral to the approximate midpoint of the articulating surface on the articular. This organization is different to that documented in larger individuals of *Moradisaurus* (e.g., MNN MOR78), in which the surangular overlaps the lateral surface of the articular and

extends posteriorly to the tip of the retroarticular process. The difference may be an example of individual variation or, given the much smaller size of MNN MOR149, an ontogenetic difference. In medial view, the surangular can be seen to suture to the coronoid on the wall of the mandible's adductor fossa.

Coronoid—The tight occlusion of the jaws precludes a detailed description of the coronoid. What is visible in lateral view (Fig. 1D) is the coronoid's anterior contribution to the coronoid eminence, which exhibits a slightly greater lateral exposure than in the larger specimen MNN MOR78 (Modesto et al., 2019:fig. 2a). The dorsal margin of the coronoid here is also very slightly convex, whereas the homologous margin in MNN MOR78 is slightly concave (Modesto et al., 2019:fig. 2a). As with the morphological differences seen in the surangular, those noted for the coronoid may represent either individual variation or ontogenetic differences. In palatal aspect, the anterior end of the coronoid manifests as a crescent of bone that forms the greater part of the mandibular lingual shelf (supporting the posterior end of the mandibular tooth plate). The medial surface of the left coronoid is partly exposed (and partly obscured by the left transverse flange of the pterygoid and the right hemimandible) in a ventral oblique view of MNN MOR149 (Fig. S5). What can be seen of the left coronoid here conforms with the description of this element by Modesto et al. (2019).

Prearticular—The prearticular is a long, strap-shaped bone visible mainly in ventral (Fig. 1B) and medial (Fig. S5) views. Anteriorly, it contributes to the posterodorsal border of the foramen intermandibularis caudalis, and contacts the coronoid, the splenial, and the angular. It forms most of the ventral margin of the adductor fossa, and expands medially to underlie and accommodate the breadth of the jaw joint. In all these respects, the prearticular is essentially a smaller version of that documented for MNN MOR78 (Modesto et al., 2019:fig. 2).

Articular—The articular is best preserved on the right side, where its retroarticular process and articular cotyles are complete (Fig. 1). The retroarticular process is broader transversely than it is long and has an acuminate posterior margin in lateral aspect. Posterior to the lateral articular cotyle, the articular forms a distinct swelling, termed the posterolateral boss by Heaton (1979). Apart from its smaller size, it does not differ notably from the articular of MNN MOR78 (Modesto et al., 2019).

DISCUSSION

The excellent preservation of MNN MOR149 allows a confident reconstruction of the skull and mandible of a juvenile of *Moradisaurus grandis* in several views (Fig. 4); we exclude a reconstruction of the skull in dorsal view because the sutures of the skull roof are not discernible. Clear differences with the skull reconstruction based on MNHN MRD1 (de Ricqlès and Taquet, 1982:fig. 8) are (1) the relatively narrow profile of MNN MOR149 in ventral aspect and (2) the relatively taller profile of the posterior end of the skull in lateral and occipital aspects. Whereas skull of MNHN MRD1 is barely (ca. 3%) longer than it is broad, that of MNN MOR149 is ca. 25% longer than it is broad and closely comparable to those of *Labidosaurikos meachami* and *Labidosaurus hamatus* (in which these figures are ca. 25% and 29%, respectively: Dodick and Modesto, 1995:1a; Modesto et al., 2007:fig. 1a). The skull roof of MNN MOR149 is relatively tall, with the height ca. 53% of its greatest breadth, compared to ca. 37% in MNHN MRD1 (de Ricqlès and Taquet, 1982:fig. 11). The latter figure is closely comparable to both *L. hamatus* and *La. meachami* (ca. 37% and ca. 38%, respectively), and is strongly suggestive of: (1) a relatively

taller skull in juveniles of *M. grandis* compared with adults, and/or (2) dorso-ventral compression of MNHN MRD1. A few other conspicuous differences are noted below.

Ontogenetic Status of MNN MOR149

Despite several distinct differences in the morphology of MNN MOR149 and MNN MOR150 compared to larger, previously described remains of *Moradisaurus grandis*, such as fewer tooth rows in each tooth plate and the relatively straight mandibular ramus, the presence of a distinct tubercle on each exoccipital of MNN MOR149 is shared with the holotypic skull, MNHN MRD1. This last feature is not known in other captorhinids for which exoccipital material is available, and we identify it as an autapomorphy of *M. grandis*. Accordingly, we are confident in referring MNN MOR149 to *M. grandis*. The exoccipitals of MNN MOR150 are not preserved, and the skull and mandible are incomplete, but what is preserved is indistinguishable from MNN MOR149, and so we regard this specimen to be referable to *M. grandis* as well.

With a total skull length of ca. 182 mm, MNN MOR149 is less than half the size of the holotype and largest known skull, MNHN MRD1 (410 mm: de Ricqlès and Taquet, 1982). Occlusion of the jaws in MNN MOR149 precludes a confident enumeration of the number of tooth rows on the maxillary and dentary tooth plates. However, judging from the basal-tooth diameter of the posterior maxillary teeth and the breadth of the right maxillary tooth plate, we estimate that maxillary tooth plate in MNN MOR149 exhibited five tooth rows. This figure is half that documented for MNHN MRD1 (10 rows; de Ricqlès and Taquet, 1982) and this difference is quite consonant with the smaller absolute size of MNN MOR149 and with recent

work that indicates tooth rows were added to the tooth plates with increasing size in this moradisaurine (Modesto et al., 2019).

In addition to its smaller absolute skull size and our inference that the tooth row complement in each tooth plate is half that of MNHN MRD1, evidence that MNN MOR149 is a juvenile *M. grandis* is suggested also by the relatively large orbit and the poorly ossified braincase. The anteroposterior dimension of the orbit of MNN MOR149 is ca. 24% the total length of the skull, whereas this figure is ca. 17% in MNHN MRD1, which is comparable to that of the holotype of *Labidosaurikos meachami* (ca. 18%: Dodick and Modesto, 1995:fig. 2). With regards to the braincase of MNN MOR149: the disarticulated opisthotics and supraoccipital and the poorly preserved prootics contrast strongly with the well ossified and integrated braincase of MNHN MRD1 (de Ricqlès and Taquet, 1982). The available evidence suggests that ossification of the braincase in *M. grandis* lagged behind that of the remainder of the skull (skull roof, palate, mandible), but eventually developed into a well ossified and integrated structure, as documented by de Ricqlès and Taquet (1982) in the largest known specimen, MNHN MRD1, which we regard as skeletally mature.

The information provided by MNN MOR149 regarding braincase development in *M. grandis* helps to elucidate what was interpreted to be an unusual feature of the skull of *La. meachami*. Dodick and Modesto (1995) described the braincase of the holotype of *La. meachami* (OMNH 04331) as poorly ossified because the supraoccipital was not integrated with the rest of the braincase and, because OMNH 04331 is a relatively large skull for a captorhinid (ca. 280 mm in total length), those authors concluded that the poor ossification of the braincase was a taxonomically important character. However, our work reveals that the braincase is the last cranial structure to coalesce in *M. grandis*, which in turn allows us to suggest that the poorly

ossified braincase in OMNH 04331 is a reflection of the skeletally immature status of this specimen of *La. meachami*. Whereas Seltin (1959) synonymized *Labidosaurikos barkeri* with *La. meachami* and referred the hypodigm of the former to the latter, the cranial materials are largely tooth plates of individuals that are smaller than OMNH 04331. As such, these specimens are not particularly useful for evaluating ontogeny in *La. meachami*. They do establish, however, that *La. meachami* was present in the middle Clear Fork Formation. A large tooth plate of an indeterminate moradisaurine (FMNH UR 29) was described from this formation by Modesto et al. (2016), who estimated that the individual had a skull length of 350 mm. Although FMNH UR 29 does not preserve apomorphies that would allow assignment to *La. meachami* or any other moradisaurine species, *La. meachami* is the only large moradisaurine known from the middle Clear Fork Formation (the smaller moradisaurines *Captorhinikos valensis* and *Ca. chozaensis* are known from the middle and upper parts, respectively, of this formation: Modesto et al., 2014). FMNH UR 29 may represent a very large individual of *La. meachami* and, if so, would demonstrate that this moradisaurine achieved a skull size that is 25% greater than OMNH 04331. If this is correct, it is likely that the latter specimen is not skeletally mature and that the braincase may have ossified completely in larger, ontogenetically older individuals of *La. meachami*, as we have established for *M. grandis*.

O’Keefe et al. (2006) discussed ossification patterns in captorhinids from the perspective of multiple ossification centers forming the astragalus. In contrast to basal captorhinids like *Captorhinus* and *Labidosaurus*, which have three ossification centers, O’Keefe et al. (2006) suggested that four ossification centers were present in the astragalus in *Captorhinikos* and *Moradisaurus*. Furthermore, they noted reduced braincase fusion in the latter taxa, as well as in *Labidosaurikos*, suggesting that both the ankle and braincase showed delayed ossification among

the largest and most derived captorhinids. *Labidosaurikos* currently lacks any postcranial data, and it is unclear if the postcranial elements of MNN MORXX include an astragalus; either would be useful for testing the relationship between cranial and postcranial ossification in moradisaurines.

Relationships of *Moradisaurus grandis*

Our description of MNN MOR149 allows us to code *Moradisaurus grandis* for seven characters that were indeterminate in previous phylogenetic analyses of captorhinids. We used the phylogenetic characters and data matrix of Modesto et al. (2019), which we re-ordered slightly by renumbering their character 76 ('dentary lingual shelf absent or present') as character 57 and former characters 57–75 as characters 58–76. MNN MOR149 allowed us to code characters 20–25 and 51. Character 63 ('coronoid anterior process short or long') is recoded as '1' based on MNN MOR78 (Modesto et al., 2019). The list of phylogenetic characters forms Appendix S1 in Supplemental Data 1 and the data matrix is available as Supplemental Data 2 and as Project #_____ on Morphobank.org. We ran a branch-and-bound search in PAUP (Swofford, 2002), with multistate characters unordered and parsimony as the optimality criterion. The results of our PAUP analysis are available as Appendix S2 in Supplemental Data 1.

PAUP found 2 most parsimonious trees, which differ only in the interrelationships among the species of *Captorhinus*. A simplified version of the consensus of these trees is shown in Figure 5. Our results position *M. grandis* as the sister of the clade of *Rothianiscus* + *Gansurhinus* within Moradisaurinae, i.e. our phylogenetic results replicate those of Modesto et al. (2019). The interrelationships of moradisaurines, however, collapse with the addition of a single step to the

most parsimonious resolution. The addition of two extra steps results in the collapse of all clades within Captorhinidae with the exception of Moradisaurinae and the clade of *Labidosaurus* + Moradisaurinae. Moradisaurinae collapses with two extra steps, Captorhinidae collapses with four extra steps, and the clade of *Labidosaurus* + Moradisaurinae collapses with five extra steps. Interestingly, our improved character scoring for *M. grandis* has resulted in a slightly more robust Moradisaurinae and *Labidosaurus* + Moradisaurinae clade with respect to the results of our previous analysis (in which these clades were found to have Bremer indices of 1 and 4, respectively: Modesto et al., 2019), but it did not result in changes to the Bremer indices of any of the clades within Moradisaurinae itself.

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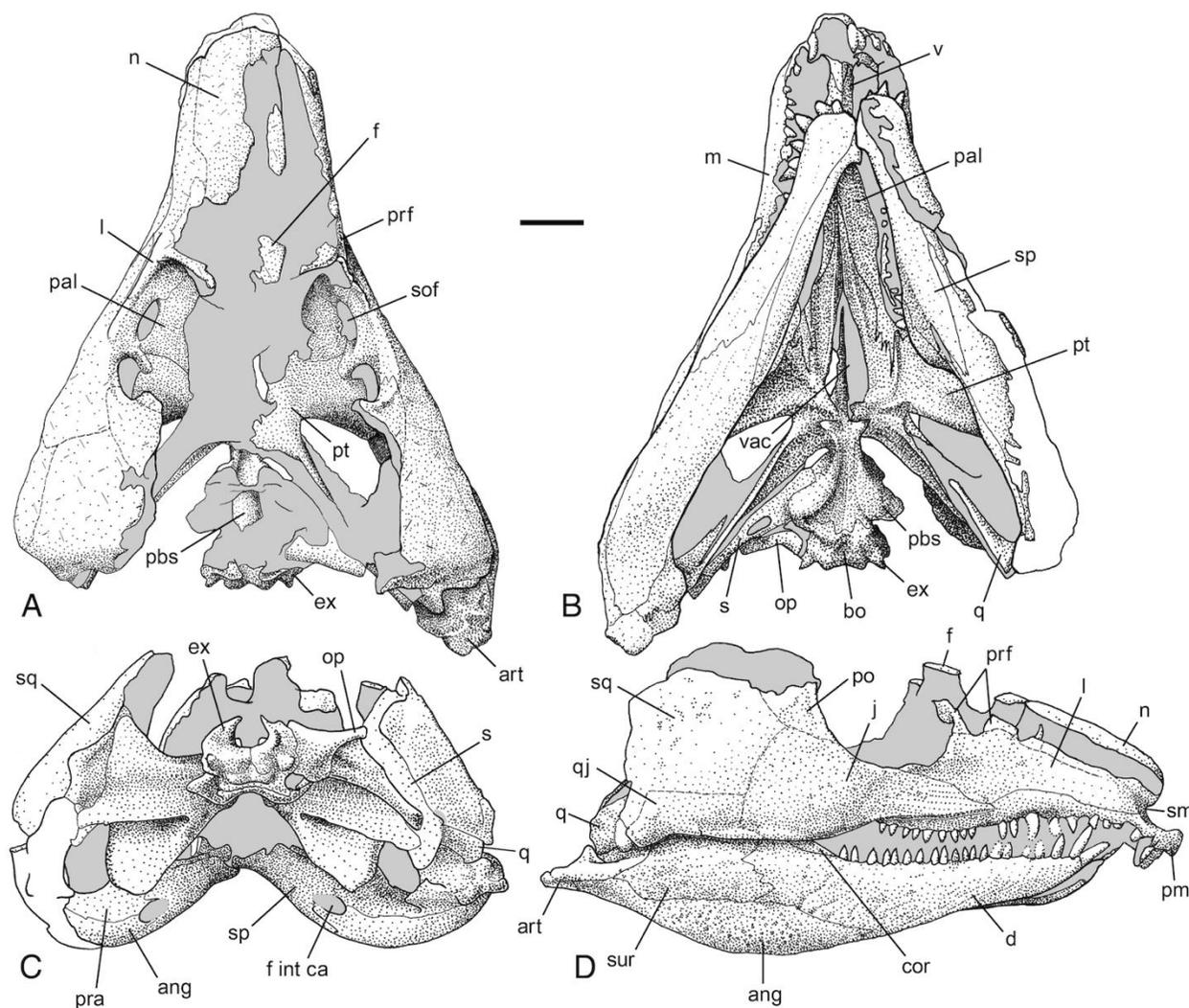


FIGURE 1. *Moradisaurus grandis*, MNN MOR149, interpretive drawings. Skull in **A**, dorsal, **B**, palatal, **C**, occipital, and **D**, right lateral views. **Abbreviations:** **ang**, angular; **art**, articular; **cor**, coronoid; **d**, dentary; **ex**, exoccipital; **f**, frontal; **f int ca**, foramen intermandibularis caudalis; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **pbs**, parabasisphenoid; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process of the opisthotic; **pra**, prearticular; **prf**, prefrontal; **q**, quadrate; **qf**, quadrate foramen; **qj**, quadratejugal; **s**, stapes; **sp**,

splenial; **sq**, squamosal; **sof**, suborbital foramen; **sur**, surangular; **v**, vomer; **vac**, interpterygoid
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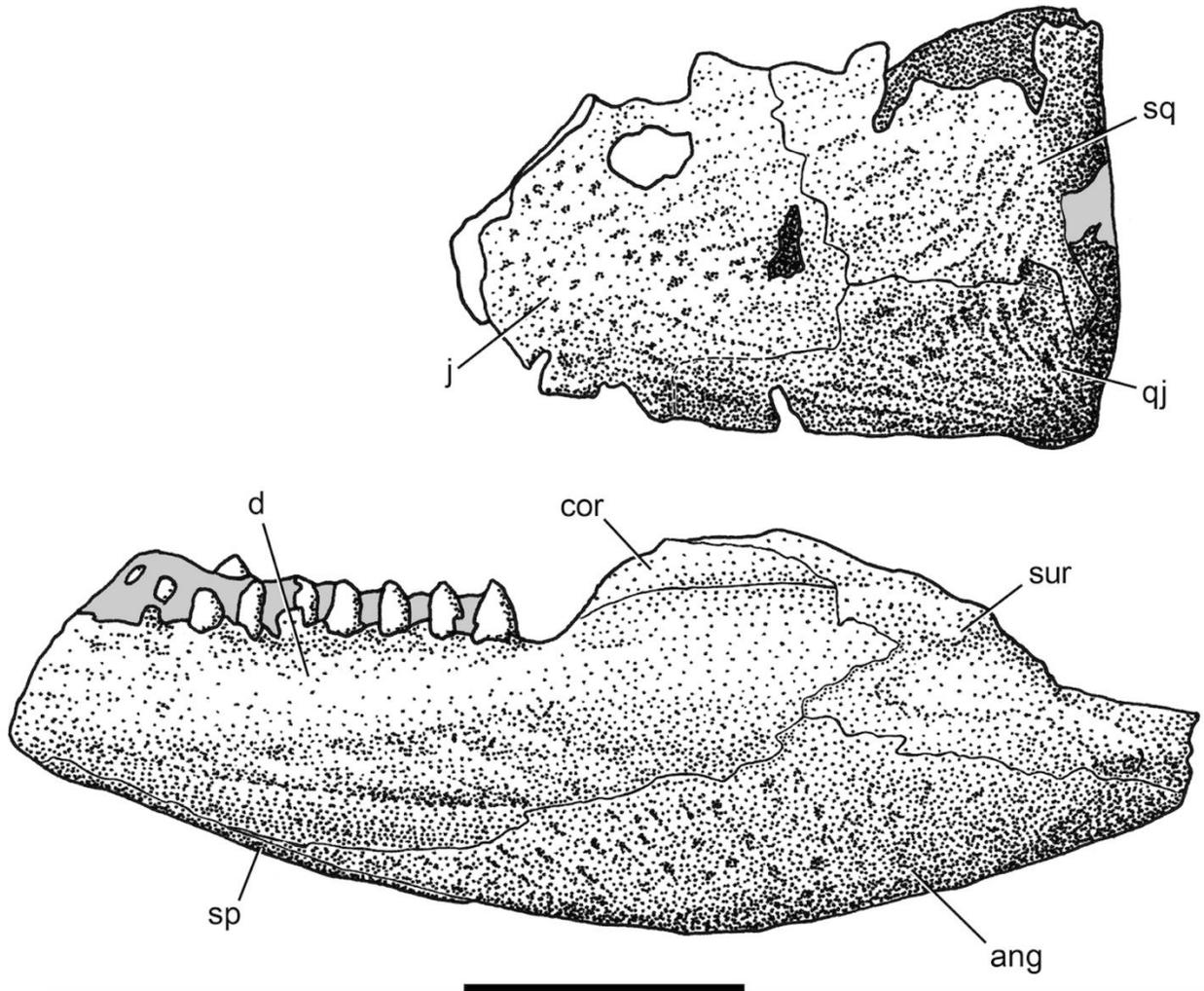


FIGURE 2. *Moradisaurus grandis*, MNN MOR150, interpretive drawing of partial skull roof and right mandibular ramus in left lateral view. **Abbreviations:** **ang**, angular; **cor**, coronoid; **d**, dentary; **j**, jugal; **qj**, quadratojugal; **sp**, splenial; **sq**, squamosal; **sur**, surangular. Scale bar equals 3 cm. [planned for 2/3 page width]

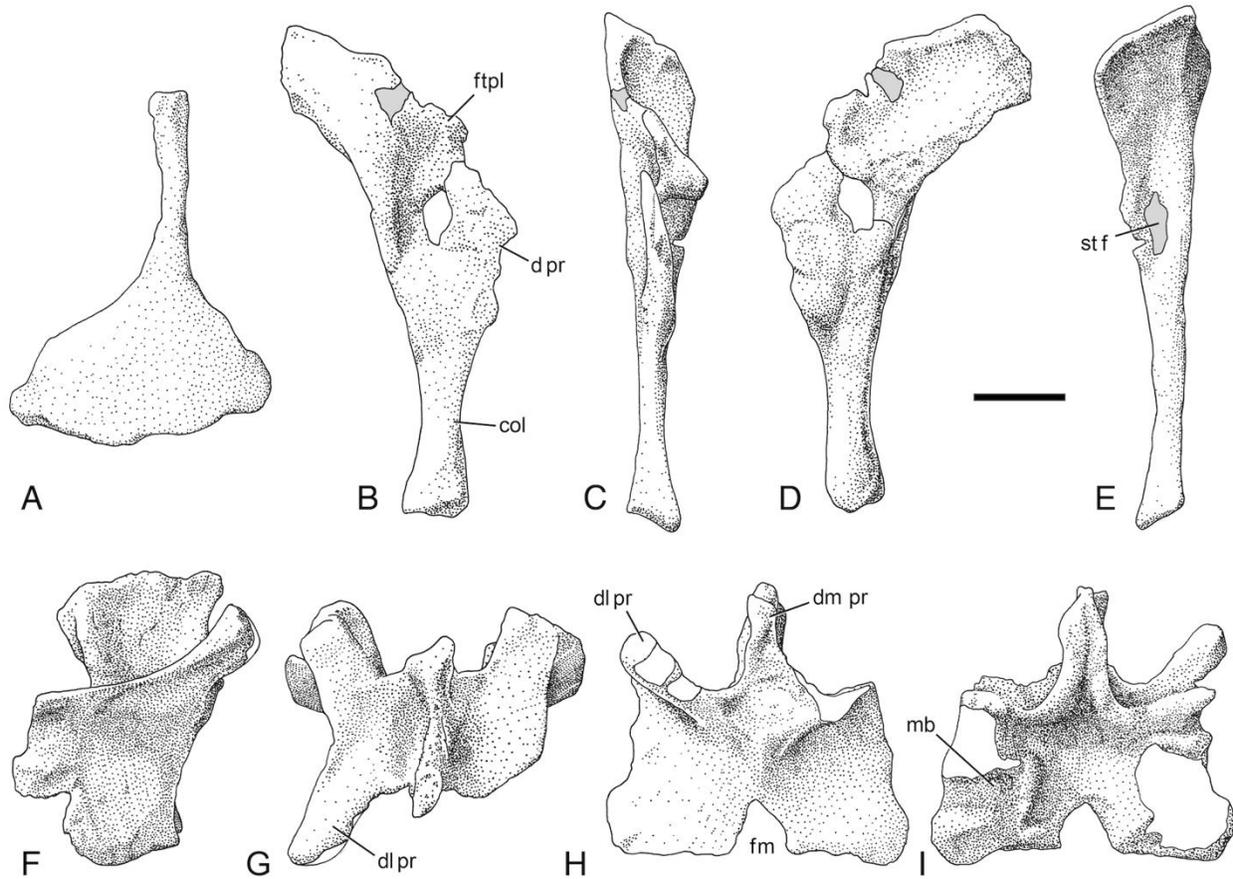


FIGURE 3. *Moradisaurus grandis*, MNN MOR149, interpretive drawings of epipterygoid and braincase elements. **A**, epipterygoid in lateral view. **B–E**, left stapes in **B**, anterior, **C**, dorsal, **D**, posterior, and **E**, ventral views. **F–I**, supraoccipital in **F**, left lateral, **G**, dorsal, **H**, posterior, and **I**, anterior views. **Abbreviations:** **col**, columella; **dl pr**, dorsolateral process; **dm pr**, dorsomedial process; **ftpl**, footplate; **mb**, membranous labyrinth; **st f**, stapedial foramen. Scale bar equals 1 cm. [planned for page width]

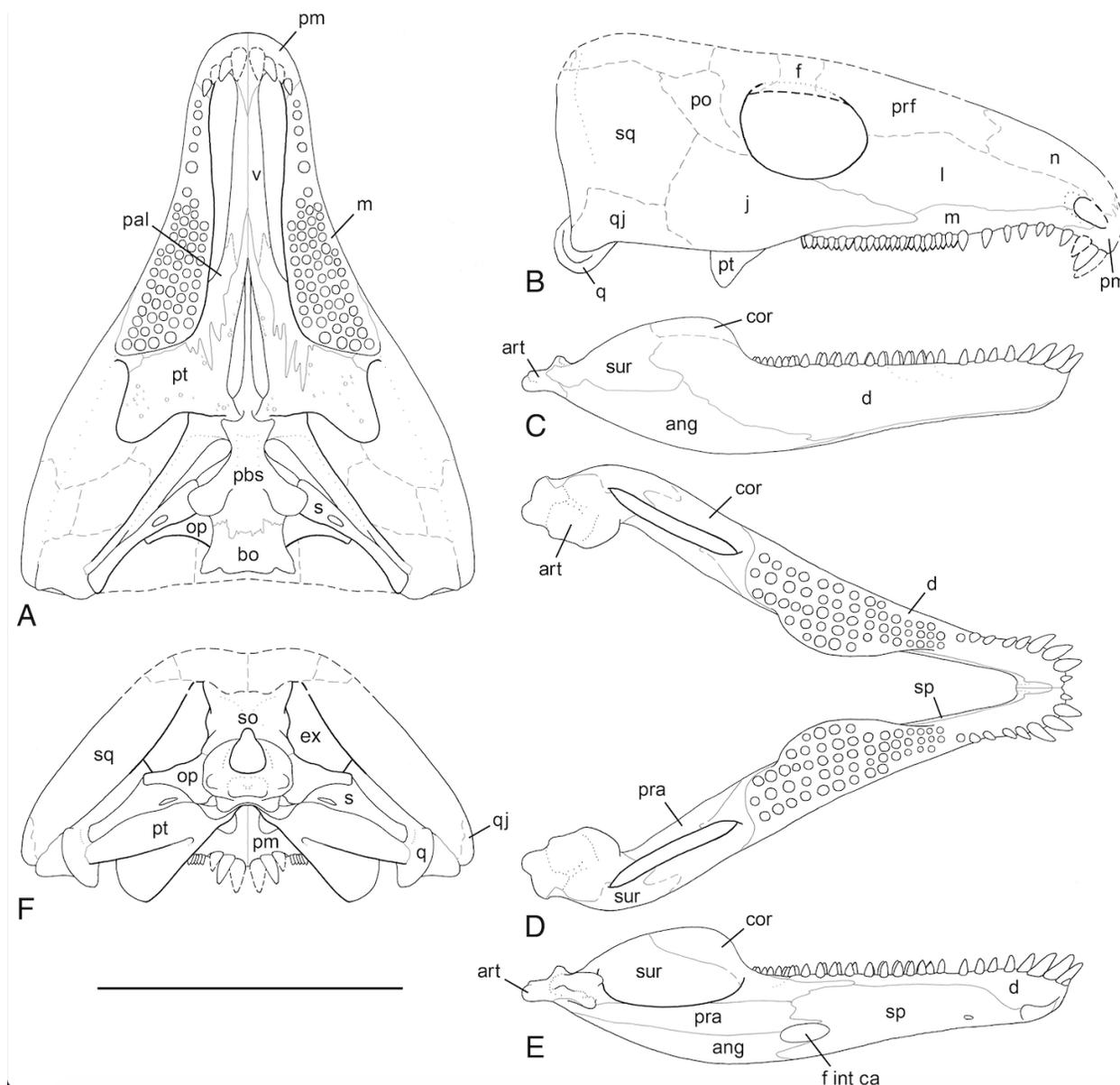


FIGURE 4. *Moradisaurus grandis*, cranial reconstruction based on MNN MOR149 and MOR150. **A**, **B**, skull in **A**, palatal and **B**, left lateral views. **C–E**, mandible in **C**, right lateral, **D**, dorsal, and **E**, medial views. **F**, skull in occipital view. **Abbreviations:** **ang**, angular; **art**, articular; **cor**, coronoid; **d**, dentary; **ex**, exoccipital; **f**, frontal; **f int ca**, foramen intermandibularis caudalis; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **pbs**, parabasisphenoid; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pra**, prearticular; **prf**,

prefrontal; **q**, quadrate; **qj**, quadratojugal; **s**, stapes; **sp**, splenial; **sq**, squamosal; **so**, supraoccipital; **sur**, surangular; **v**, vomer. Scale bar equals 10 cm. [\[planned for page width\]](#)

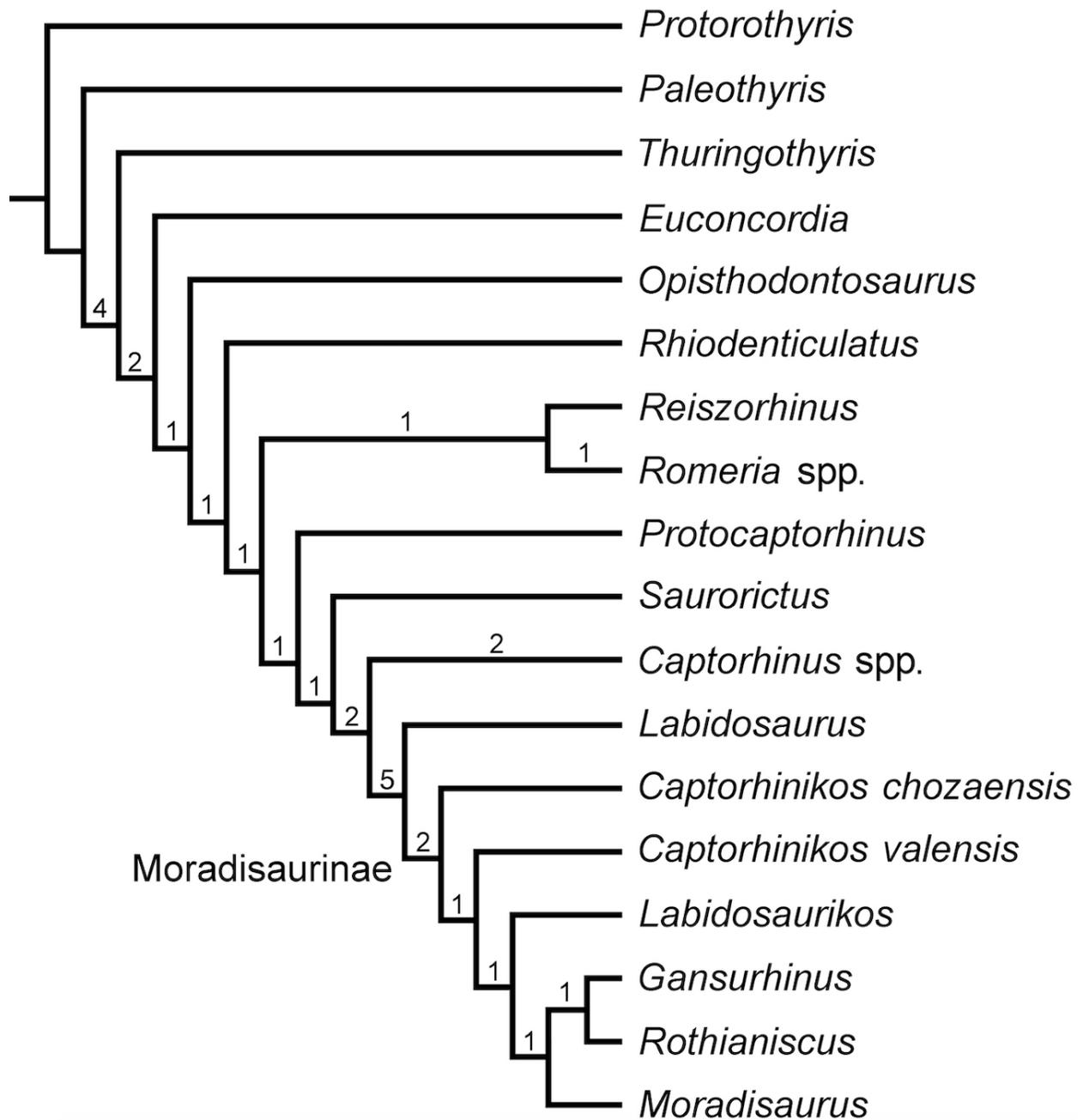


FIGURE 5. A cladogram showing the relationships of *Moradisaurus grandis* based on a PAUP analysis of 21 taxa and 76 characters. For clarity, the clade of the two species of *Romeria* is collapsed into ‘*Romeria* spp.’ and the clade of the three species of *Captorhinus* is collapsed into ‘*Captorhinus* spp.’ [planned for 2/3 width]

