Journal of Vertebrate Paleontology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ujvp20

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**To cite this article:** Bryan M. Gee & Christian A. Sidor (2021) Cold capitosaurs and polar plagiosaurs: new temnospondyl records from the upper Fremouw Formation (Middle Triassic) of Antarctica, Journal of Vertebrate Paleontology, 41:4, e1998086, DOI: 10.1080/02724634.2021.1998086

**To link to this article:** https://doi.org/10.1080/02724634.2021.1998086

Journal of Vertebrate Paleontology e1998086 (13 pages)

DOI: 10.1080/02724634.2021.1998086



ARTICLE

# COLD CAPITOSAURS AND POLAR PLAGIOSAURS: NEW TEMNOSPONDYL RECORDS FROM THE UPPER FREMOUW FORMATION (MIDDLE TRIASSIC) OF ANTARCTICA

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ABSTRACT—The upper Fremouw Formation (Middle Triassic) of Antarctica preserves a diverse record of temnospondyls, with three species currently recognized. To date, all of the described material belongs to a single clade, Capitosauria. Our reanalysis suggests that cursory historical reports suggesting the presence of a benthosuchid (Trematosauria) are in error. Here we report substantial amounts of hemimandibular material of large-bodied temnospondyls from the upper Fremouw Formation. All seven specimens, including the historic material attributed to Trematosauria, exhibit features indicative of capitosaurian affinities. These specimens represent a notable expansion in the physical and conceptual body of temnospondyl material known from the Fremouw Formation, although they cannot be definitively associated with any of the three previously named Antarctic species in the absence of skeletal overlap. In addition, all of the specimens come from large-bodied individuals (i.e., skull lengths exceeding 70 cm), which likely reflects a taphonomic filter created by the high-energy channel lag deposition of the fossiliferous horizon of the upper Fremouw Formation. We also report the first occurrence of a non-capitosaur, an interclavicle belonging to a plagiosaurid. This represents only the third occurrence of Plagiosauridae in southern Pangea during the Triassic, in contrast to a much richer record of this clade in northern parts of the supercontinent and a rich record of the closely related brachyopids in the southern hemisphere. Together with the continued absence of trematosaurs in Antarctica, the plagiosaurid record hints at nuances in the distribution of cosmopolitan clades patterns that are tied to presently unrecognized ecological and physiological differentiators.

Citation for this article: Gee, B. M. and C. A. Sidor. 2022. Cold capitosaurs and polar plagiosaurs: new temnospondyl records from the upper Fremouw Formation (Middle Triassic) of Antarctica. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2021.1998086

## INTRODUCTION

The upper Fremouw Formation of Antarctica preserves one of the highest paleolatitudinal occurrences of Middle Triassic tetrapods. The majority of taxa recorded from this horizon are either capitosaur temnospondyls (Hammer, 1990; Sidor et al., 2007, 2008, 2014a) or therapsid synapsids (Hammer, 1995; Sidor et al., 2014b; Smith et al., 2020), although one archosaur has been noted (Sidor et al., 2014b). There are three documented temnospondyls: *Antarctosuchus polyodon*, *Kryostega collinsoni*, and *Parotosuchus* sp. The holotypes of *A. polyodon* and *K. collinsoni* were collected in the 1985/86 austral summer and were briefly described and figured, but not named, by Hammer (1990). They were subsequently formally named by Sidor et al. (2008, 2014a), following the description of a fragmentary specimen that was referred to *Parotosuchus* by Sidor et al. (2007). All three of these specimens consist either exclusively (*Antarctosuchus*, *Kryostega*) or primarily (*Parotosuchus*) of cranial material without mandibles, and they are all capitosaurs, a cosmopolitan clade with records throughout the Triassic (e.g., Schoch, 2000, 2008; Schoch and Milner, 2000; Damiani, 2001a).

The exclusive occurrence of capitosaurs in the upper Fremouw Formation contrasts with well-sampled coeval deposits at both high and low paleolatitudes. In particular, Middle Triassic capitosaurs frequently co-occur within the same stratigraphic units as brachyopids and trematosaurs, two other large-bodied clades. Examples are globally distributed and include the *Cynognathus* Assemblage Zone of South Africa (CAZ; Damiani and Hancox, 2003; Damiani, 2004b; Hancox et al., 2020); the Denwa Formation of India (Welles, 1993; Muhkerjee and Sengupta, 1998; Bandyopadhyay and Sengupta, 1999; Sengupta, 2003); the Terrigal Formation and the Ashfield Shale of Australia (e.g., Watson, 1958; Cosgriff, 1969, 1973; Warren and Marsicano, 1998; Damiani, 1999); the Holbrook Member of the Moenkopi Formation of the southwestern U.S.A. (Morales, 1987; Lucas and Schoch, 2002; Heckert et al., 2005); the Erfurt Formation in Germany (e.g., Schoch, 2006); and the Donguz Formation in Russia (e.g., Efremov, 1940; Tverdokhlebov et al., 2003). The numerous examples of co-occurrence render the absence of any non-capitosaurian temnospondyls throughout the upper Fremouw Formation as rather unusual, especially given that temnospondyl remains are the most common fossils encountered in the upper Fremouw Formation (Sidor, pers. obs.). Even if all three Antarctic capitosaurs are represented by single specimens (i.e., the record is relatively sparse), there are nonetheless three distinct taxa.

Among the historic cranial specimens noted by Hammer (1990) were a number of hemimandibles, one of which was generically figured by Hammer (1990; also alluded to by Hammer, 1988; Hammer et al., 1990). These hemimandibles have otherwise remained undescribed to date. One specimen (AMNH FARB 24415) was specifically referred to as a benthosuchid (repeated by Sidor et al., 2014b); Benthosuchidae is a subclade of Trematosauria, and this specimen would eliminate the capitosaur exclusivity in the upper Fremouw Formation. However, it is important to note the drastically different taxonomic framework that Hammer operated in – benthosuchids were historically considered to be early diverging capitosaurs (e.g., Yates and Warren, 2000; Damiani, 2001a), and it was not until well after Hammer's

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Published online 14 Feb 2022

cursory identification that benthosuchids were confidently shown to be early diverging trematosaurs (e.g., Schoch, 2008, 2013; Morkovin, 2020). Therefore, Hammer's interpretation may be read as simply another record of a capitosaur. Trematosaurs in their present composition have never been reported from Antarctica despite their otherwise global distribution in the Triassic (e.g., Hammer, 1987). The second abundant clade of the Middle Triassic, brachyopoids, are only represented by highly fragmentary referred material of '*Austrobrachyops jenseni*' from the lower Fremouw Formation (Colbert and Cosgriff, 1974; Warren and Marsicano, 2000). More recent collection of material of large-bodied temnospondyls from the upper Fremouw Formation provides an impetus to review previously unpublished material. Here we formally describe the temnospondyl hemimandibles collected in 1985/6 alongside similar material collected in the 2010/11 austral summer.

**Institutional Abbreviations**—**AMNH FARB**, American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds collection, New York, New York, U.S.A.; **UWBM**, University of Washington Burke Museum, Seattle, Washington, U.S.A.

## MATERIALS AND METHODS

Photographs of the majority of specimens were taken at the Burke Museum by Mike Rich using a Canon EOS 5DS camera with a 50 mm macro lens; the remainder were taken by BMG using a Panasonic Lumix camera using a 24–75 mm lens. Figures were compiled using Adobe Photoshop and Adobe Illustrator.

## SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI von Zittel, 1887–1890 sensu Schoch, 2013
STEREOSPONDYLI von Zittel, 1887–1890 sensu Yates and Warren, 2000
CAPITOSAURIA Yates and Warren, 2000 sensu Schoch, 2008
(Figs. 1–3)

**Referred Material**—A partial right hemimandible including the portions of the dentary, splenial, postsplenial, and angular, AMNH FARB 24401; a partial right hemimandible, AMNH FARB 24418; a partial left dentary, AMNH FARB 24415; postdentary portion of a right hemimandible, UWBM VP 95539; portions of right hemimandible exposed in lingual and labial views, UWBM VP 95541; hemimandibles of a large individual, separated near the symphysis during preparation, UWBM VP 95551; symphyseal region of a right hemimandible, UWBM VP 95554.

**Horizon and Locality**—The AMNH material and UWBM VP 95554 were collected from a large bedding plane of upper Fremouw conglomeratic sandstone exposed at Gordon Valley (~84°21.741′S, 164°3.655′E; Isbell and Macdonald, 1991). UWBM VP 95551 was also collected at Gordon Valley, but 8 meters lower in section on the eastern flank of the main outcrop. The remainder of the UWBM material was collected about 10 km away at Fremouw Peak (~84°16.766′S, 164°17.629′E), but Sidor et al. (2014b) considered that horizon to be likely equivalent to the fossil-bearing horizon at Gordon Valley. The occurrence of *Cynognathus* and *Impidens hancoxi* in upper Fremouw rocks suggest biostratigraphic correlation with the *Cynognathus* Assemblage Zone of South Africa, and thus a possible Anisian age (Hancox et al., 2020; Tolchard et al., 2021), which is also supported by detrital zircon dating (Elliot et al., 2017).

## DESCRIPTION

### Material from Gordon Valley

AMNH FARB 24401 is a large partial right hemimandible, preserved from the symphysis to an indeterminate position anterior to the adductor chamber (Fig. 1A–E). It measures 45 cm along the longitudinal axis and was probably at least twice as long when complete (Table 1). The anteriormost portion of the symphysis is damaged, and the lingual surface of the entire hemimandible is weathered such that the internal trabecular structure is exposed (Fig. 1D). In dorsal view, the specimen is nearly straight except at the symphysis (Fig. 1A). The labial surface is more or less complete, with the sutures having been manually traced onto the surface by a pen (Fig. 1B); our examination reveals no deviations from the previous interpretations of the sutural pattern (Fig. 1C). The fragment thus preserves the dentary, the splenial, the postsplenial, and the angular. Based on the posteriormost extent, which approaches the terminus of the postsplenial, the specimen is likely approximately half-complete, and when complete would have been about a meter in length (Table 1). Conceivably, at least the first and second coronoids (alternatively referred to as the 'precoronoid' and the 'intercoronoid' by some workers) are represented in a fragmentary sense on the lingual surface. Teeth are absent, although the bases of a few marginal teeth broken at the level of the hemimandible are exposed. There are 31 distinctive tooth positions, with room for around another 11 positions. The teeth were markedly longitudinally compressed such that they form transversely elongate ovals in cross-section. Plicidentine can be generally identified but not characterized to the same level as is possible through histology (Warren and Davey, 1992). A pair of lingually positioned sockets is present at the symphysis; it is unclear whether a postsymphyseal tooth row was also present. On the lateral surface, ornamentation is confined to the ventral region, and although weathered, preserves discernible elongate ridges and grooves. There is also a more concentrated region of ornamentation on the symphysis and a deep longitudinal furrow on the dentary. The estimated large size of the specimen suggests either brachyopoid or capitosaur affinities, and the extremely compressed tooth bases align more closely with the anatomy seen in capitosaurs.

AMNH FARB 24415 is a large partial right hemimandible, preserved from the symphysis to an indeterminate position anterior to the adductor chamber (Fig. 1H–L). It measures 41 cm along the long axis and is estimated to have been at least 75 cm long when complete (Table 1). The labial surface consists mostly of the dentary and the splenial, although a small portion of the postsplenial is exposed. The postsplenial is more visible lingually below the coronoid series. The lingual sutures are traced with green ink and appear to be validly interpreted as marked (Fig. 1I, J). The first coronoid ('precoronoid') and the splenial have contributions to the symphysis. The posterior margin of the second coronoid ('intercoronoid') is not apparent, although the relative length to the complete first coronoid suggests that the second coronoid may be essentially complete. There is no anterior Meckelian foramen, but it is usually found at the mid-length and mid-height of the postsplenial, a region not clearly preserved. Hammer (1990) cited the absence of this foramen as the sole rationale for an identification as a benthosuchid, citing Jupp and Warren's (1986) review of Triassic taxa. Contrary to those authors, the absence of an anterior Meckelian foramen is not apomorphic for Benthosuchidae, as it is shared with some capitosaurs (e.g., Schoch, 1997, 1999; Schoch and Milner, 2000), as well as later diverging trematosaurs (e.g., Schoch, 2006; Sues and Schoch, 2013). Additionally, Benthosuchidae historically comprised only species of *Benthosuchus*, all of which lack the foramen, but the more recently described benthosuchid *Qantas samarensis* does have this foramen

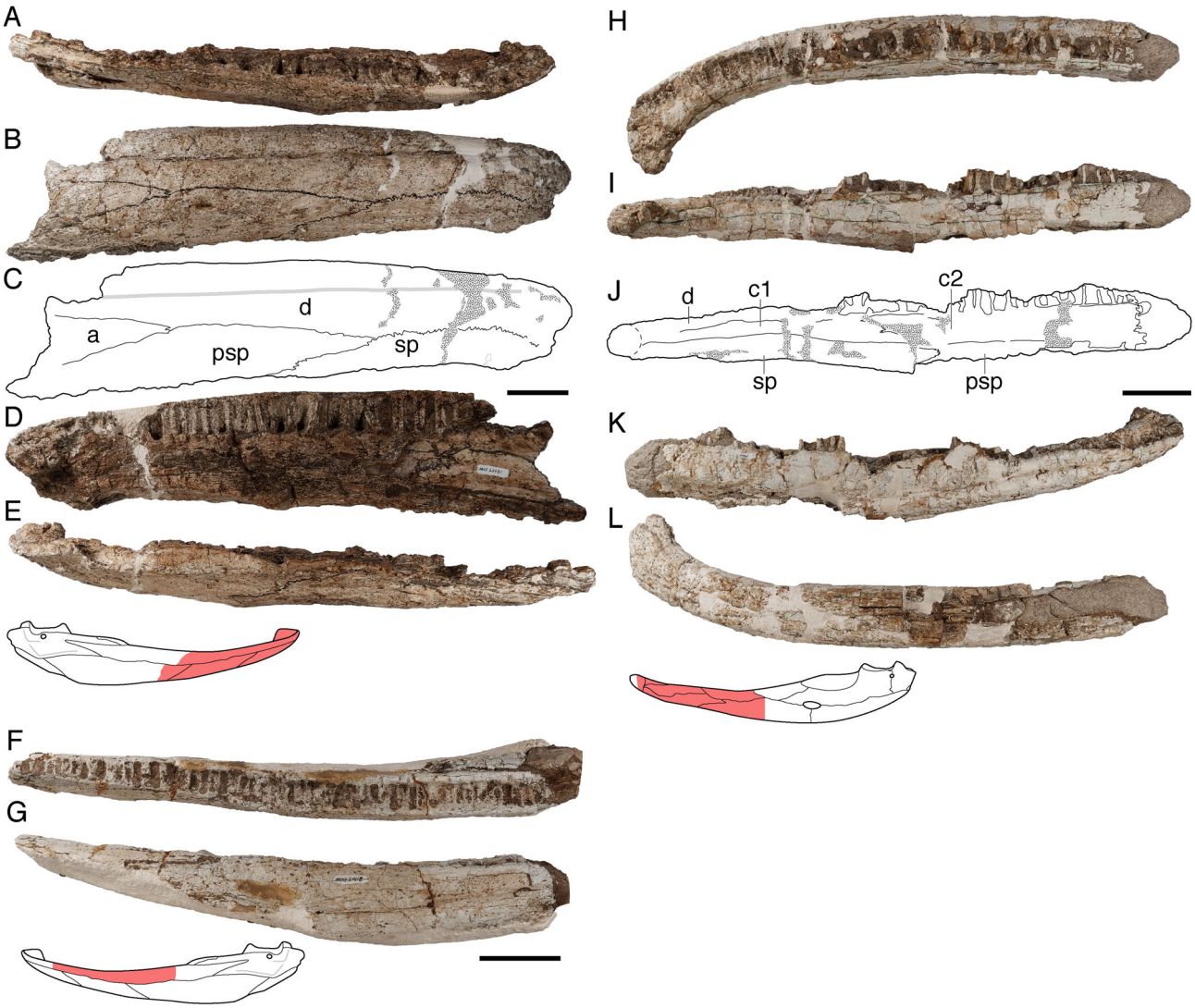


FIGURE 1. Historical hemimandibular material of Capitosauria indet. from Gordon Valley. **A**, photograph of AMNH FARB 24401, partial right hemimandible, in dorsal view; **B**, the same in labial view; **C**, interpretive line drawing; **D**, photograph in lingual view; **E**, the same in ventral view; **F**, photograph of AMNH FARB 24415, partial left hemimandible, in dorsal view; **G**, the same in labial view; **H**, photograph of AMNH FARB 24418, partial right hemimandible, in dorsal view; **I**, the same in lingual view; **J**, interpretative line drawing; **K**, photograph in labial view; **L**, the same in ventral view. A reconstruction of the hemimandible of *Parotosuchus haughtoni* from the *Cynognathus* AZ (Damiani, 2001b) is used to depict which regions are represented by each specimen; the use of this particular taxon should not be interpreted as hypothesized affinities of any specimen. **Abbreviations**: **a**, angular; **c1**, first coronoid (precoronoid); **c2**, second coronoid (intercoronoid); **d**, dentary; **psp**, postsplenial; **sp**, splenial. Scale bars equal 5 cm.

(Novikov, 2012). Therefore, regardless of whether the absence of this foramen is biological or taphonomic, it is not sufficient to refer the specimen to any particular clade. Ornamentation consists of faint grooves and ridges along the ventral margin. There is a longitudinal furrow below the tooth row on the labial surface of the dentary (Fig. 1K).

Teeth are preserved to the posteriormost extent of the specimen, indicating that it is probably no more than 60% complete based on conserved proportions of the dentary in stereospondyls. There are 47 discernible tooth sockets with room for at least another 10 positions. There is no clear symphyseal 'fang' pair or row of symphyseal teeth, but the surface is crushed in the predicted position (Fig. 1H). Most of the teeth are lost or broken at the base, but a few remain embedded in matrix. They are transversely elongate in cross-section, recurved lingually, and bear prominent external striations reflecting the plicidentine throughout their height. Carinae on the anterior and posterior surfaces are not apparent. The large size of the element and the straight profile except in the symphysis restrict candidate clades to Capitosauria and Trematosauria. The absence of carinae suggests capitosaurs affinities (carinae are found in some trematosaurs; e.g., Damiani, 2004a; Milner and Schoch, 2004; Schoch, 2011; Sues and Schoch, 2013), as does the marked anteroposterior compression of the teeth at the base (less pronounced in trematosaurs), but neither feature is formally diagnostic.

AMNH FARB 24418 is a partial left hemimandible preserving a large portion of the tooth row posterior to the symphysis and anterior to the coronoid process (Fig. 1F, G). It measures 36 cm as preserved and was probably twice as large, comparable

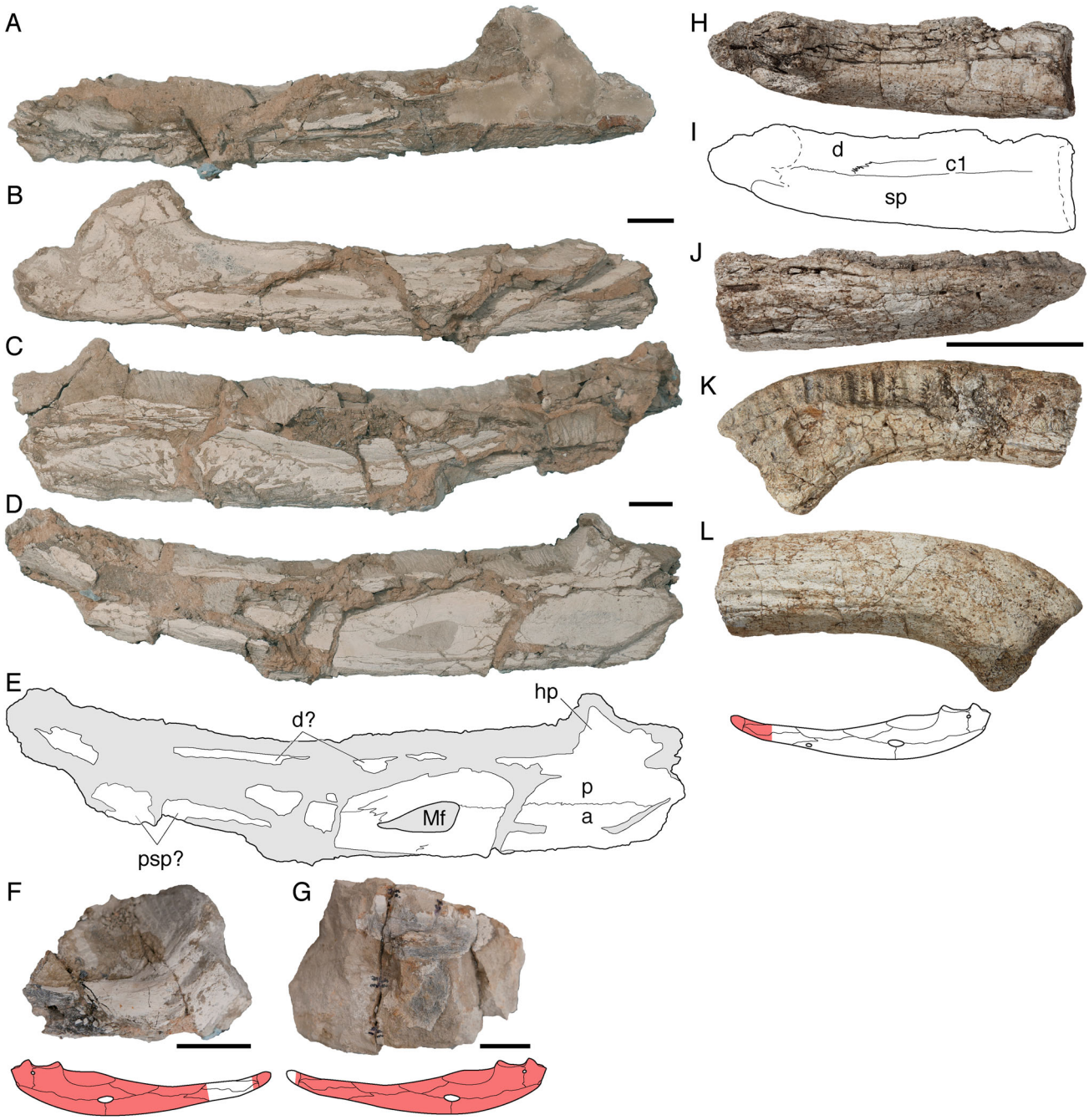


FIGURE 2. Newly collected hemimandibular material of Capitosauria indet. from Gordon Valley. **A**, photograph of the left hemimandible of UWBM VP 95551 in labial view; **B**, the same in lingual view; **C**, photograph of the right hemimandible of UWBM VP 95551 in labial view; **D**, the same in lingual view; **E**, interpretative line drawing; **F**, photograph of the partial left symphysis in ventral view; **G**, photograph of the partial left and right symphysis in broken cross-sectional view; **H**, photograph of UWBM VP 95554, partial right hemimandible in lingual view; **I**, interpretative drawing; **J**, photograph in labial view; **K**, the same in dorsal view; **L**, the same in ventral view. A reconstruction of the hemimandible of *Parotosuchus haughtoni* from the *Cynognathus* AZ (Damiani, 2001b) is used to depict which regions are represented by each specimen; the use of this particular taxon should not be interpreted as hypothesized affinities of any specimen. **Abbreviations**: **a**, angular; **c1**, first coronoid (precoronoid); **d**, dentary; **hp**, hamate process; **Mf**, Meckelian foramen; **p**, prearticular; **psp**, postsplenial; **sp**, splenial. Scale bars equal 5 cm.

to AMNH FARB 24415, although it is not clear whether they belong to the same individual (Table 1). The ventral half of the specimen and much of the lingual surface is either covered in, or composed entirely of, stabilizing plaster, and it is unclear whether substantial portions of any element other than the dentary are present; no sutures are identified. In dorsal view, the specimen is nearly straight and of a consistent width throughout except at the posteriormost end, where it appears to begin expanding slightly on the lingual side (Fig. 1F); this is where the prearticular would be predicted. At least the posteriormost coronoid is probably present as well, though it is not positively identified. Fifty-six tooth positions are confidently identified.

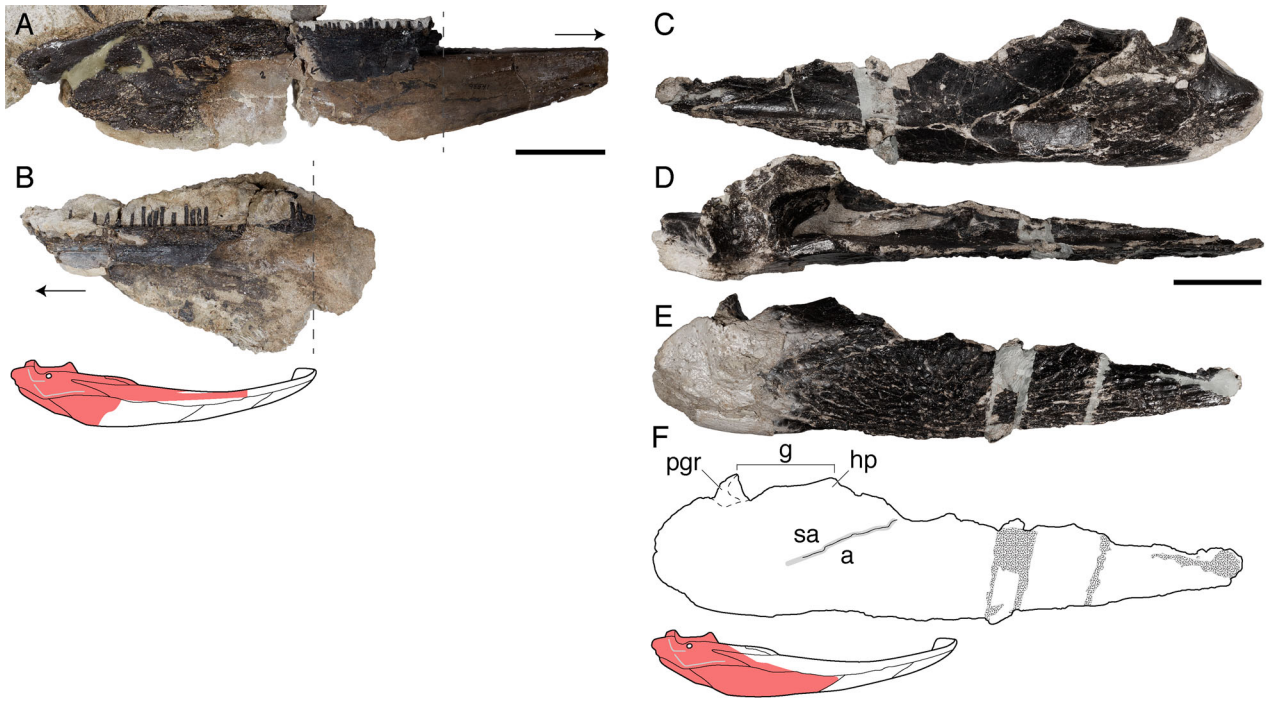


FIGURE 3. Newly collected hemimandibular material of Capitosauria indet. from Fremouw Peak. **A**, photograph of the first fragment of UWBM VP 95339, partial right hemimandible, showing the posterior region in internal view and the middle region in labial view; **B**, photograph of the second fragment of UWBM VP 95539, showing the anterior region in lingual view; **C**, photograph of UWBM VP 95541, partial right hemimandible, in lingual view; **D**, the same in dorsal view; **E**, the same in labial view; **F**, interpretative line drawing. Dashed lines in parts A–B indicate the plane of articulation between fragments; arrows point anteriorly. A reconstruction of the hemimandible of *Parotosuchus haughtoni* from the *Cynognathus* AZ (Damiani, 2001b) is used to depict which regions are represented by each specimen; the use of this particular taxon should not be interpreted as hypothesized affinities of any specimen. **Abbreviations**: **a**, angular; **g**, glenoid; **hp**, hamate process; **pgr**, postglenoid ridge; **sa**, surangular. Scale bars equal 5 cm.

TABLE 1. Summary of preserved length and estimated complete length of all specimens referred to Capitosauria indet.

| Specimen | Preserved length | Estimated length | Taxonomy |
|---|---|---|---|
| AMNH FARB 24401 | 45.3 cm | >90 cm | cf. Capitosauria indet. |
| AMNH FARB 24415 | 40.4 cm | ~75 cm | cf. Capitosauria indet. |
| AMNH FARB 24418 | 36.0 cm | >72 cm | cf. Capitosauria indet. |
| UWBM VP 95339 | 35.0 cm | ~60 cm | cf. Capitosauria indet. |
| UWBM VP 95541 | 40.3 cm | >50 cm | Capitosauria indet. |
| UWBM VP 95551(L) | 69.7 cm | >90 cm | Capitosauria indet. |
| UWBM VP 95551(R) | 84.7 cm | >90 cm | Capitosauria indet. |
| UWBM VP 95554 | 13.3 cm | >60 cm | cf. Capitosauria indet. |

No teeth are preserved, but transversely elongate bases with plicidentine are noted. There is no ornamentation preserved, although a longitudinal furrow is preserved on the labial surface. The marked compression of the teeth suggests capitosaur affinities, but this is the most tentatively identified specimen.

UWBM VP 95551 is a pair of associated hemimandibles, both of which are fractured and too badly weathered to be fully prepared out (Fig. 2A–G). They are complete posteriorly but incomplete anteriorly and are mostly exposed in labial and lingual views. The left hemimandible measures 70 cm as preserved, and the right hemimandible measures 85 cm as preserved; if only the symphysis is missing, then these would have been about 90 cm when complete (Table 1). Both hemimandibles are essentially straight when accounting for post-mortem fracturing and dislodging. The symphyses of both hemimandibles are partially represented by two disarticulated fragments that remain embedded in matrix, one of which preserves the anteriormost part of the left symphysis in ventral view (Fig. 2F) and the other, which preserves indeterminate broken cross-sections of both symphyses (Fig. 2G). The region of the adductor chamber has been compressed transversely such that the greatest width of both hemimandibles is about 5 cm. The left hemimandible may also be dorsoventrally compressed given the notable difference between the Meckelian foramina of both hemimandibles (oblate in the left hemimandible versus triangular in the right hemimandible, which is also taller; Fig. 2B, D) and the ventral margin (straight in the left hemimandible versus convex in the right hemimandible). Sutures are entirely indiscernible on the left hemimandible, which is also largely obscured labially (Fig. 2A). Notable features include the tall hamate process, a short, squared-off retroarticular process, and the Meckelian foramen. A few loose teeth are preserved near the anterior end, but they are mostly obscured without features other than the external striations marking plicidentine. Tooth sockets could not be exposed. The right hemimandible also preserves the tall hamate process and a few sutures around the Meckelian foramen (Fig. 2D, E). The longitudinal articular-prearticular suture extends from the posterior margin of the foramen to an indeterminate point below the glenoid. The postsplenial-middle

coronoid suture extends from the anterodorsal margin of the foramen and extends anteriorly to an indeterminate point. A short portion of the postsplenial-angular suture is identified along the ventral margin of the hemimandible. The only suture identified on the labial surface is a short portion of the angular-surangular suture, although the angular-dentary suture can be estimated to occur along the dorsal edge of the ornamented surface. None of these sutures is particularly informative, although the large lingual exposure of the angular is reminiscent of the type I postglenoid area (PGA; Jupp and Warren, 1986). The prominent hamate process is the primary feature that we identify as evidence for affinities with Capitosauria. The relative length of the Meckelian foramen is often utilized as a binary phylogenetic character among capitosaurs (e.g., Damiani, 2001a; Schoch, 2008), and that of UWBM VP 95551 is relatively large, in contrast to *Parotosuchus haughtoni* from South Africa, for example (Damiani, 2001b). This is a tenuous line of evidence that this specimen does not belong to the Antarctic *Parotosuchus*, although the type species, *P. nasutus*, has a long, oblate Meckelian foramen (Schoch, 2018). Ornamentation on both hemimandibles consists mostly of elongate grooves and pits along the ventral surface. The labial exposure of the right angular preserves a pattern of shallow grooves and striations radiating from the ventral margin.

UWBM VP 95554 is a mandibular fragment preserving the symphysis (Fig. 2H–L). It measures 13 cm as preserved. It is more difficult to estimate the total length due to its fragmentary nature, but an estimate of at least 60 cm seems reasonable (Table 1). There is a pair of large depressions for the symphyseal 'fangs' and 18 identifiable marginal tooth positions, with room for at least six more. While there are a few small depressions posterolingual to the 'fangs,' sockets for a possible postsymphyseal row of teeth are not confidently identified. The marginal tooth sockets are transversely elongate ovals, while those of the 'fangs' are more circular. On the ventrolabial surface, the suture between the dentary and the splenial is visible anteriorly and can also be found on the lingual surface, showing the contribution of the splenial to the ventral margin of the symphysis (Fig. 2H, I). The first coronoid (precoronoid) is also defined anteriorly on the lingual surface where it partially divides the splenial and the dentary. Sutures are untraceable posteriorly on each side. Ornamentation on the labial surface includes foramina aligned in a longitudinal row in the symphyseal region and elongate grooves on the ventral surface of the splenial; smaller foramina are found loosely scattered around the symphyseal region and at the anterior ends of the grooves. The row of foramina may have led to a longitudinal groove posteriorly, but damage and incompleteness preclude definitive identification. The marked compression of the marginal teeth adjacent to a large 'fang' suggest capitosaur affinities.

### Material from Fremouw Peak

UWBM VP 95539 is a partial lower right hemimandible preserved posteriorly and without any portion of the tooth row (Fig. 3C–F). It measures 35 cm as preserved and is probably around 60% complete, giving an estimate of around 60 cm when complete (Table 1). It is most complete ventrally and labially. The sutures are generally not identifiable except for a partial definition of the surangular-angular suture on the labial surface, which is marked by a deep sensory groove (the 'oral groove'). A more posterior longitudinal fracture that has resulted in some shifting of the labially exposed elements is in the approximate position to be the continuation of this suture. Neither the dentary nor the postsplenial are preserved. Only the posterior base of the coronoid process is preserved. On the lingual surface, the angular and the prearticular are represented, although their sutural contact is not preserved (Fig. 3C). The Meckelian foramen is not preserved, but the dental foramen, usually framed between the prearticular and the articular, is present and undistorted. A foramen for the chorda tympani is also not discernible. The postglenoid region is characterized by a well-developed ridge that bounds the glenoid posteriorly and that is as tall as the hamate process. The retroarticular process is short, mostly obscured in labial view, and squared off at the end. When viewed from above, an arcadian process, formed by a short projection of presumably the surangular, is also identified. The glenoid fossa forms a crescentic surface in dorsal view, bounded anteriorly by the hamate process, which projects sharply dorsally when viewed from the side. There are two relatively large foramina at the same height on the posterior face of the fossa. Ornamentation is largely restricted to the angular, with a region of circular pitting near the ventral mid-length of the element. Anteriorly this radiates outward into thin striating grooves, while posteriorly, it transitions to larger, more irregularly arranged oblong pits. The surangular's labial surface is marked by irregularly sized and spaced foramina. An associated fragment is marked by finer radiating grooves and probably pertains to the postsplenial, although it does not articulate with the larger fragment and does not have either sutures or other diagnostic features.

Mesozoic temnospondyls were often divided between clades with a type I postglenoid area (PGA) and a type II PGA, a dichotomy formalized by Jupp and Warren (1986). Most of these features are based on the sutural configurations, which cannot be assessed here. The presence of an arcadian process and a short but distinct retroarticular process are typical type I features, whereas the posteroventral-to-anterodorsal oriented oral sensory groove is a type II feature. While the PGA dichotomy remains employed by many workers (e.g., Datta and Sengupta, 2015), in at least some clades there is intraspecific variation (e.g., Sulej, 2007). Furthermore, some workers have proposed a finer-scale division (e.g., four types for capitosaurs; Maryańska and Shishkin, 1996), and more recent workers have sometimes struggled to situate new material within Jupp and Warren's dichotomy (e.g., Fortuny et al., 2011; Schoch, 2011). The suite of features used to assess the type of PGA is more often divided into individual characters in phylogenetic analyses (e.g., Schoch, 2000, 2008; Warren and Marsicano, 2000; Yates and Warren, 2000; Damiani, 2001a; Steyer, 2002; Damiani and Yates, 2003; Dias-da-Silva and Marsicano, 2011, and derivations thereof), rather than being lumped into a single 'type' character for the entire PGA (as in Schoch, 2011, 2013, and derivations thereof). The work of Jupp and Warren may thus be regarded as an inherently outdated overgeneralization based on what is now a small subset of nominal taxa, and the differences tend to fall along general phenotypic divisions (e.g., relatively long-snouted taxa such as trematosaurs and capitosaurs have typically been characterized as having the type I PGA in contrast to the type II PGA of short-snouted brachyopoids). Here, the dichotomy is only sufficient to indicate that UWBM VP 95541 belongs to a relatively long-snouted taxon. The tall hamate process is a typical capitosaur feature, however (e.g., Jupp and Warren, 1986; Damiani, 2001a; Nakajima and Schoch, 2011), and is specifically an unambiguous synapomorphy in some analyses (e.g., Schoch, 2008; Fortuny et al., 2011), so on this basis, we refer UWBM VP 95539 to Capitosauria.

UWBM VP 95541 is a partial lower right hemimandible divided among several fragments (Fig. 3A, B). Each of them is still embedded in matrix due to their fragility, and thus the various fragments are exposed in different profiles. The posterior portion of the mandible is mostly exposed internally (the internal surface of the lingually facing elements; Fig. 3A), the middle portion is exposed labially (Fig. 3A), and the anterior portion is exposed lingually (Fig. 3B). Collectively, they measure 40 cm in length, and the hemimandible was at

least 50 cm when complete (Table 1); the lack of sutures complicates this estimate. The combination of exposures and lack of sutures result in little informativity of most of the hemimandible; nothing can be discerned about the hemimandible articulation or the coronoid process, for example. The internal space of the mandible is also preserved as a smooth natural cast, and it indicates a relatively narrow and straight profile in dorsal view with a prominent tapering in height anteriorly. Thirty-nine partial to complete teeth are preserved, with room for at least another 29 teeth. The teeth are transversely elongate ovals in cross-section and straight throughout their preserved height. Carinae are not apparent. Based strictly on the teeth, this specimen is tentatively identified as a capitosaur, although the proportions (height, width) of the preserved region suggest it is not the same taxon as the historic AMNH FARB material from Gordon Valley.

TEMNOSPONDYLI von Zittel, 1887–1890 sensu Schoch, 2013
STEREOSPONDYLI von Zittel, 1887–1890 sensu Yates and Warren, 2000
PLAGIOSAURIDAE Jaekel, 1914 sensu Schoch and Milner, 2014
PLAGIOSAURINAE Jaekel, 1914 sensu Schoch and Milner, 2014
(Fig. 4)

**Referred Material**—A partial interclavicle, UWBM VP 95534.

**Horizon and Locality**—Upper Fremouw Formation at Fremouw Peak (UWBM locality C1592; 84°16.804′S, 164° 17.384′E).

**Description**—This specimen is a partial interclavicle (Fig. 4). The primary attribute that associates it with plagiosaurids is the clear presence of pustular ornamentation, although many of the pustules have been partially weathered. There are no pits, and instead the pustules form a similar pattern to that seen in taxa with pitting ornamentation on the interclavicle. Toward the presumed geometric center, the pustules are dense but are not organized in any fashion. Towards the periphery, they form radiating rows, with adjacent pustules being partially connected at their base to form distinct ridges. The ornamentation also permits further referral to the Plagiosaurinae following Schoch and Milner (2014), although it bears noting that differentiation of ornamentation types in plagiosaurids is mostly based on cranial material and may not be as discrete on the ornamented

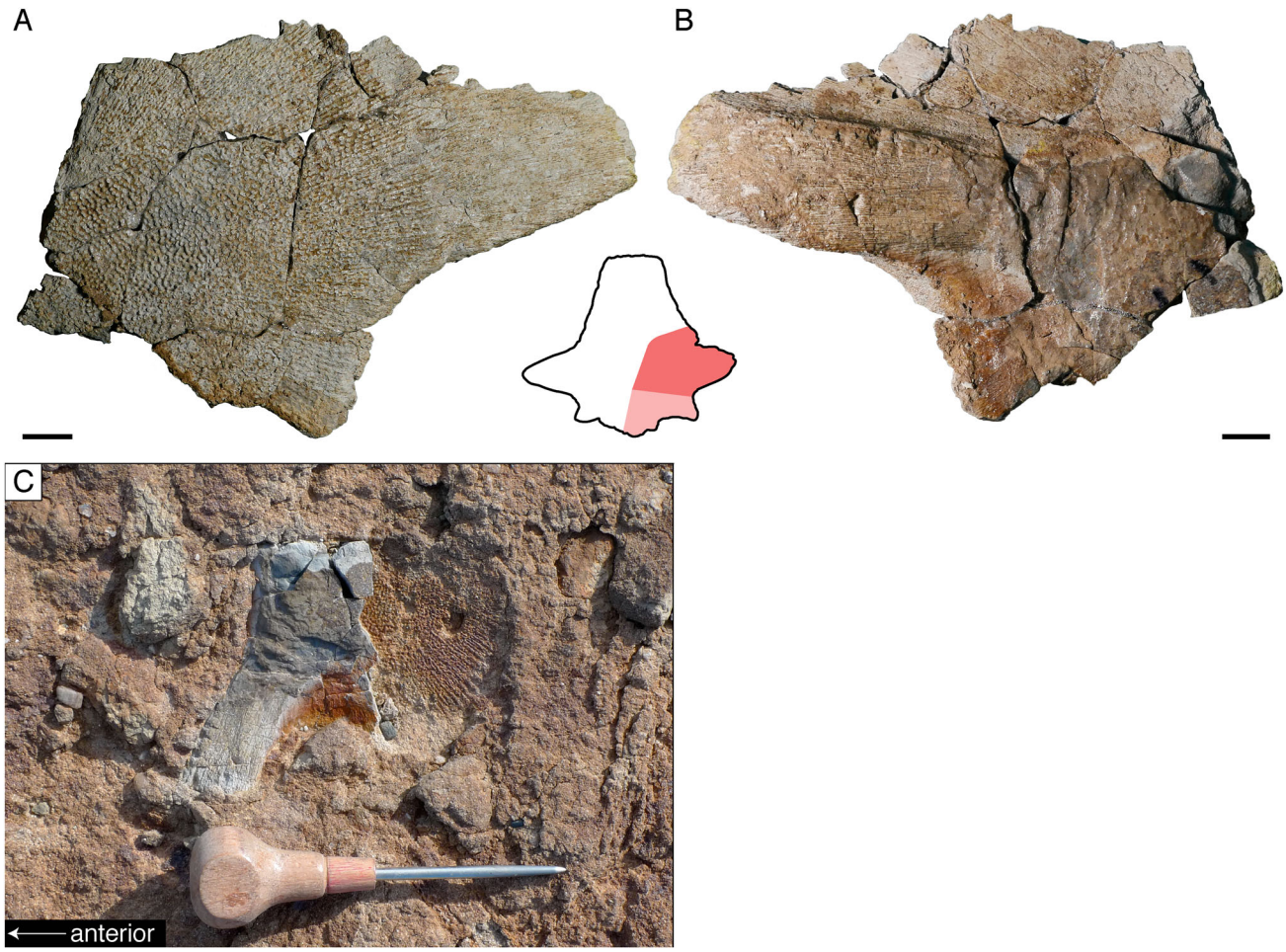


FIGURE 4. Interclavicle of Plagiosaurinae indet. (UWBM VP 95534) from the upper Fremouw Formation. The preserved region of the interclavicle is shown in ventral (**A**) and dorsal (**B**) views. A field photograph of the specimen in dorsal view shows an impression of the eroded posteromedial region (**C**). A reconstruction of the interclavicle of *Plagiosaurus depressus* (Jaekel, 1914) in ventral view is used to depict which region is represented by the specimen (red for the preserved specimen, pink for the impression); the use of this particular taxon should not be interpreted as hypothesized affinities. Scale bar equals 1 cm.

pectoral girdle (e.g., Dias-da-Silva and Milner, 2010). When complete, plagiosaurid interclavicles have a distinctive morphology with prominent laterally projecting processes and no posterior process (e.g., Nilsson, 1946; Shishkin, 1987; Warren and Snell, 1991). One of these processes is preserved here, being formed by a ventrally unornamented surface that is marked by faint striations. On its unornamented dorsal surface, there is a thickened ridge extending along the length of the process (Fig. 4B). One margin of the ridge is straight, and the other is sloped. A portion of the posteromedial region was preserved only as an impression in the field (Fig. 4C); a cast of this region is not figured but is reposited with the physical specimen.

## DISCUSSION

### Taxonomic Identifications

Historically, the temnospondyl assemblage of the upper Fremouw Formation has only comprised capitosaurs (Hammer, 1990; Sidor et al., 2007, 2008, 2014a). Hammer's (1990) cursory identification of a benthosuchid (viz. AMNH FARB 24415) stands out in contemporary literature (e.g., Sidor et al., 2014b) only because the position of Benthosuchidae has shifted in recent years, from the base of Capitosauria (the framework that Hammer operated within) to the base of Trematosauria (the contemporary framework). The mandibular material that we describe here, both the historical material (Hammer, 1990) and more recently collected material, can be provisionally assigned to Capitosauria on the basis of various qualitative differentiators (e.g., marked compression of the marginal tooth bases). However, our assignments must be considered provisional because most specimens are fragmentary or poorly preserved and do not preserve many features that are variable among stereospondyls, let alone recognized apomorphies of Capitosauria; UWBM VP 95539 and UWBM VP 95551, which have a very prominent hamate process, are the only exceptions. Further taxonomic assignment, however tentative, is confounded by the absence of any mandibular material from *Antarctosuchus* and *Kryostega*. Only a sliver of the dentary is known from the single specimen of *Parotosuchus*. All three specimens belong to individuals with skull lengths in excess of 70 cm. It is worth noting that there do appear to be three distinctive morphotypes among the hemimandibles described here – AMNH FARB 24401 has a massive dentary with large tooth sockets when compared with AMNH FARB 24415, AMNH FARB 24418, and UWBM VP 95554, which are in turn larger compared with UWBM VP 95541. Among the previously described Antarctic capitosaurs, the largest marginal teeth are present in the holotype of *K. collinsoni*, while the smallest are found in the holotype of *A. polyodon*. However, we make no formal referrals since there is size disparity between both the cranial and hemimandibular specimens (Table 1), and ontogeny could thus be a partially confounding factor.

### Comparisons with Other Middle Triassic Assemblages

As noted in the Introduction, nearly all Middle Triassic temnospondyls belong to three large-bodied clades: Brachyopoidea (inclusive of Plagiosauridae), Capitosauria, and Trematosauria. All three groups have cosmopolitan distributions such that absence from a certain geographic region is conspicuous and warrants attention, as in the upper Fremouw Formation. Both brachyopids and trematosaurs are found in the equivalent *Cynognathus* Assemblage Zone of South Africa (e.g., Shishkin and Welman, 1994; Damiani, 2001b, 2004a; Damiani and Jeannot, 2002; Damiani and Kitching, 2003) and in Australia (e.g., Warren and Marsicano, 1998; Warren, 2012) but have yet to be identified from any part of the Fremouw Formation. While sampling might be considered for the absence of brachyopids and trematosaurs in the Fremouw Formation, the co-occurrence of these clades with capitosaurs is observed in other historically undersampled regions (e.g., the Zarzaïtine Formation of Algeria and the Ntawere Formation of Zambia; e.g., Jalil, 1999; Damiani, 2001b; Peecook et al., 2018; Steyer et al., 2021). This faunal co-occurrence extends to single sites as well, such as Farm Nooitgedacht in South Africa (Morales and Shishkin, 2002; Damiani and Kitching, 2003), Gosford and St. Peters in New South Wales, Australia (Cosgriff, 1972; Warren and Marsicano, 1998), the Holbrook Quarry in Arizona, U.S.A. (Welles, 1947), and many sites in Baden-Württemberg, Germany (Schoch, 1999, 2006) and Orenburg Oblast, Russia (e.g., Tverdokhlebov et al., 2003). Therefore, it must be considered whether capitosaurs indeed did not co-occur with other large-bodied temnospondyls in Antarctica during the Middle Triassic.

A possible explanation for the absence of trematosaurs is that some species are thought to have been euryhaline (e.g., Hammer, 1987), so it is unlikely that these taxa would be found in the same habitats as other temnospondyls except during possible freshwater excursions. Both capitosaurs and trematosaurs are known from the lower two subzones of the CAZ (Hancox et al., 2020) but not from the same localities. Most of the Middle Triassic sites where capitosaurs and trematosaurs co-occur are in Germany (e.g., Kupferzell, Merkel's Quarry; Haack, 1923; Wagner, 1935; Schoch and Werneburg, 1998; Schoch, 2006, 2018; Schoch and Seegis, 2016). It is more common for capitosaurs to only occur with other capitosaurs or with brachyopoids, including in southern Pangea (e.g., Australia, South Africa). Given the marked undersampling of Antarctica compared with those regions, it is possible that trematosaurs were a main component of other assemblages in Antarctica whose local depositional environments were not preserved or have yet to be found; those assemblages could hypothetically be devoid of capitosaurs. A similar spatial segregation might also explain the peculiar and markedly different distribution of the three clades of brachyopoids, which is addressed in greater detail below.

### Disparity in the Distribution of Brachyopoids

The recognition of a plagiosaurid in the upper Fremouw Formation is somewhat unexpected because it stands in contrast to the global record of the clade. The three brachyopoid clades have markedly different distributions (Fig. 5). Chigutisaurids have no Middle Triassic record but are entirely confined to southern Pangea (Argentina, Australia, Brazil, India, South Africa) throughout their temporal range (Early Triassic to Early Cretaceous; Marsicano, 1999; Warren and Marsicano, 2000; Dias-da-Silva et al., 2012; Fig. 5A, C). Brachyopids have a rich record in southern Pangea, including during the Middle Triassic (Fig. 5A, B). Notably, brachyopids may also occur in the lower Fremouw Formation (Fig. 5A); Schoch and Milner (2014) suggested that some of the material referred to '*Austrobrachyops jenseni*' by Cosgriff and Hammer (1984) could be brachyopid. Plagiosaurids have the richest record of the brachyopoid clades, but almost all of this record is from northern Pangea (Fig. 5). There are only two records of plagiosaurids in southern Pangea throughout the Mesozoic, both from the Early Triassic (Fig. 5A).

Both of these Early Triassic records are quite fragmentary. The first report of a plagiosaurid from southern Pangea was *Plagiobatrachus australis* from Australia (Warren, 1985), which is represented only by vertebral material, and there is some uncertainty about whether it is definitively a plagiosaur or even a temnospondyl (Warren et al., 2009). The second was a plagiosternine cranial fragment from Brazil (Dias-da-Silva and Ilha, 2009; Dias-da-Silva and Milner, 2010). Plagiosaurids are well-

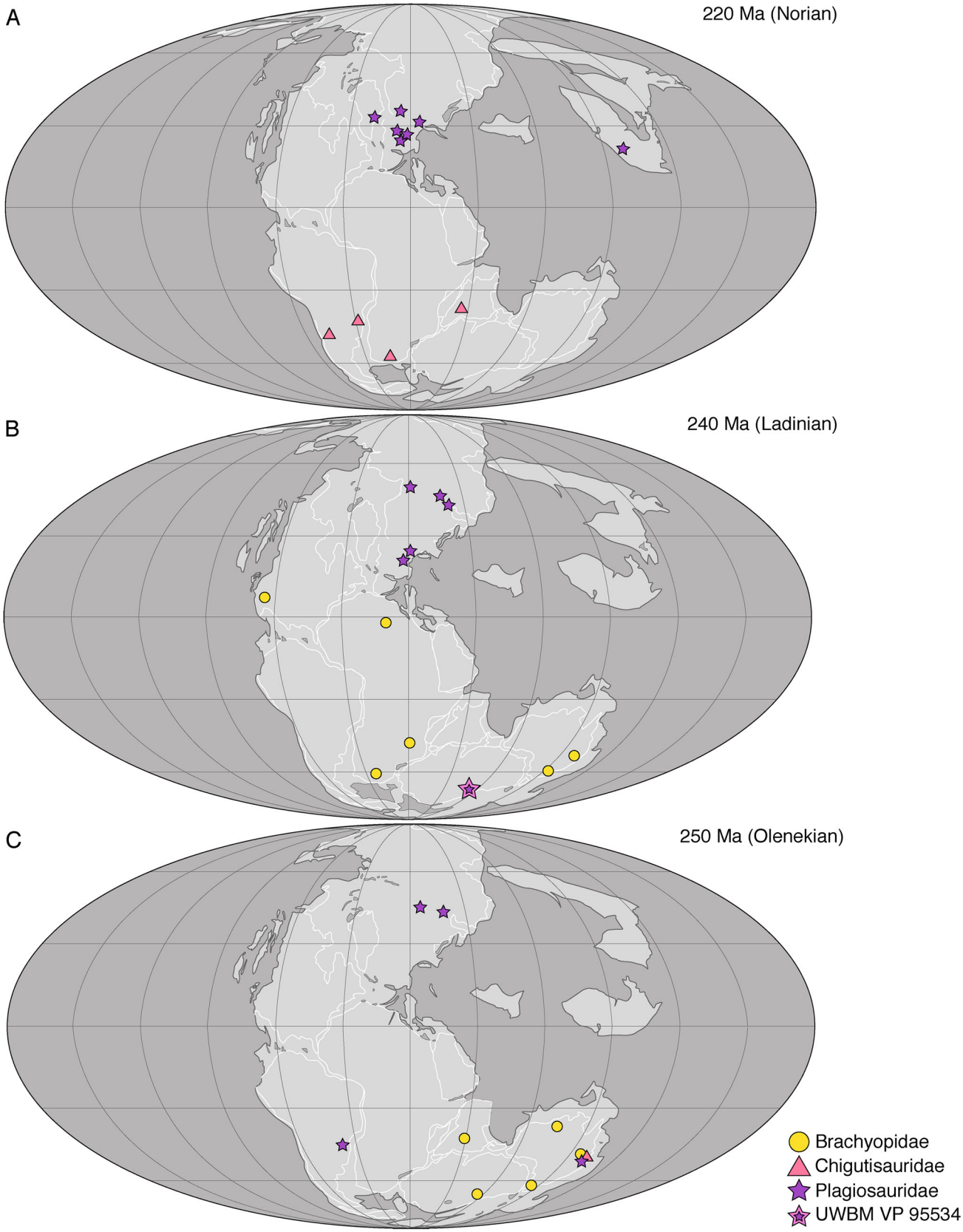


FIGURE 5. Paleomaps comparing the simplified distributions of brachyopids, chigutisaurids, and plagiosaurids (the Brachyopoidea of Schoch and Milner, 2014) throughout the Triassic as plotted on Late Triassic (**A**), Middle Triassic (**B**), and Early Triassic (**C**) paleogeographic reconstructions. The Olenekian reconstruction is from Lawver et al. (2019), and the Ladinian and Norian reconstructions are from Lawver et al. (2021). Plotted occurrences are for localized regions, not single localities, and are primarily derived from Schoch and Milner (2000, 2014) and Warren and Marsicano (2000), with additional data from more recent publications (e.g., Nonsrirach et al., 2021). Co-occurrences of different clades are visually offset for clarity (e.g., the Duckworth Creek locality in the Early Triassic Arcadia Formation of Australia).

documented in western and central Eurasia (e.g., Germany, Greenland, Russia; Warren, 1995; Milner et al., 1996; Damiani et al., 2009; Schoch and Witzmann, 2012; Schoch et al., 2014; Fig. 5), where brachyopids are entirely absent (*Boreosaurus thorslundi* from Svalbard, originally described as a brachyopid, is considered to be an indeterminate temnospondyl by most workers; Schoch and Milner, 2000; Warren and Marsicano, 2000; contra Kear et al., 2016). The Arcadia Formation (Lower Triassic) in southern Queensland is the only instance in which brachyopids (*Xenobrachyops allos*) and plagiosaurids (*P. australis*) occur within the same local region. Most plagiosaurids have distinctive pustular ornamentation on the dermal elements, as in UWBM VP 95534, and a unique vertebral anatomy that should render even fragmentary material readily identifiable. With that said, not all plagiosaurid elements preserve this ornamentation or are otherwise diagnostic, especially when incomplete.

The segregation of brachyopids and plagiosaurids (and perhaps the complete absence of chigutisaurids in the Middle Triassic) hints at an unrecognized ecological or physiological differentiator of these brachycephalic clades. Previous workers have proposed that the iconic Middle–Late Triassic plagiosaurid *Gerrothorax* could tolerate brackish conditions and generally unstable habitats (e.g., Witzmann and Soler-Gijón, 2010; Sanchez and Schoch, 2013; Schoch, 2014; Schoch and Seegis, 2016). This tolerance would not preclude plagiosaurids from living in stable habitats; Late Triassic plagiosaurids frequently co-occur with capitosaurs (among other large stereospondyls) in non-brackish environments of western Europe (e.g., Milner et al., 1996; Seegis, 1997; Milner and Schoch, 2004; Dzik et al., 2008; Schoch and Witzmann, 2012), Greenland (Jenkins et al., 1994; Kear et al., 2016), and Thailand (Suteethorn et al., 1988; Nonsrirach et al., 2021). There is some evidence that fossiliferous horizons rich in *Gerrothorax* material and rare in other tetrapods (Schoch and Wild, 1999; Schoch, 2002; Hellrung, 2003), like at Kupferzell, were relatively unstable habitats (Sanchez and Schoch, 2013). In contrast, deposits with higher taxic richness like Vellberg preserve distinctly lower frequencies of this taxon (Schoch and Seegis, 2016). Therefore, plagiosaurids may have preferred marginal habitats that are not as frequently preserved in southern Pangea (spatially restricted, temporally ephemeral). The most intuitive explanation for a preference of unstable environments is if these habitats were sufficiently unattractive to other taxa and thus resulted in lower competition.

If indeed plagiosaurids preferred marginal habitats, their paucity in southern Pangea could be similar to the absence of trematosaurs in Antarctica (i.e., the preferred habitat differed from that of the more abundant capitosaurs and was either not present or not preserved). The coarse fossiliferous sandstones at Fremouw Peak and Gordon Valley have been interpreted as channel-lag deposits (Isbell and Macdonald, 1991; Sidor et al., 2014b), a high-energy setting that could explain why the temnospondyl record skews towards isolated remains of large-bodied capitosaurs; other taxa might not commonly occur in or adjacent to this depositional setting and smaller taxa might not survive the fossilization process. Plagiosaurids are more commonly found in other paleoenvironments, such as brackish marshes, lakes, or pond deposits (e.g., Suteethorn et al., 1988; Jenkins et al., 1994; Seegis, 1997; Hagdorn and Mutter, 2011; Schoch and Witzmann, 2012; Schoch and Seegis, 2016).

Brachyopids and chigutisaurids are rarely found in deposits with numerous individuals (Warren and Marsicano, 2000; Warren et al., 2011), which has hindered discussion of their ecology. There is no apparent pattern of habitat preference like that of plagiosaurids, but the persistence of these clades beyond the Triassic suggests that they may have had some climatic preference or tolerance that enabled them to survive the Triassic–Jurassic extinction when practically all other temnospondyls went extinct. Warren et al. (1997) suggested tolerance of colder high latitude habitats in Australia for the persistence of chigutisaurids to the Early Cretaceous. The possibly correlated local absence or paucity of aquatic archosauromorphs has also been suggested (e.g., Warren et al., 1997; Maisch and Matzke, 2005), as has the exceptionally large size of post-Triassic taxa (e.g., Steyer and Damiani, 2005). Notably, brachyopids colonized northern Pangea in the Jurassic (China, Kyrgyzstan, Mongolia, Russia, Thailand; Suteethorn et al., 1988; Nessov, 1990; Shishkin, 1991, 2000; Nonsrirach et al., 2021). In fact, brachyopids are only found in the northern hemisphere after the Triassic, and chigutisaurids are the only temnospondyls from the southern hemisphere in the Jurassic and Cretaceous (Warren and Hutchinson, 1983; Warren et al., 1997; Warren and Damiani, 1999). Most of the inferences regarding plagiosaurid ecology are derived from bone histology (e.g., de Ricqlès and de Buffrénil, 2001; Sanchez et al., 2010; Witzmann and Soler-Gijón, 2010; Konietzko-Meier and Schmitt, 2013; Sanchez and Schoch, 2013; Konietzko-Meier et al., 2014; Danto et al., 2016), but brachyopid and chigutisaurid postcranial material is relatively rare (Warren and Marsicano, 2000), so these clades have yet to be histologically characterized to the same degree (see Muhkerjee et al., 2010, for an example). Recovery and sampling of postcrania may be the key to unraveling the spatiotemporal patterns of these clades.

## ACKNOWLEDGMENTS

Fieldwork in the upper Fremouw Formation was supported by NSF ANT-0551163, ANT-0838762, and ANT-1341304, with subsequent research and analysis supported by ANT-1947094. Logistical support in Antarctica was provided by the National Science Foundation through the U.S. Antarctic Program. We thank B. Crowley, S. Egberts, L. Herzog, G. Livingston, R. Masek, and B. Ryan for preparation of the material described here and T. Cully, J. Isbell, A. Huttenlocker, M. Miller, B. Peecook, and R. Smith for their contributions in the field. Additionally, we acknowledge M. Rich for specimen photography and W. Hammer for leading the collection of the AMNH specimens. We thank A. Kufner, one anonymous reviewer, and the editor, A. Huttenlocker, for constructive feedback that improved this manuscript.

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Submitted June 21, 2021; revisions received September 16, 2021;
accepted October 13, 2021.
Handling Editor: Adam Huttenlocker.