#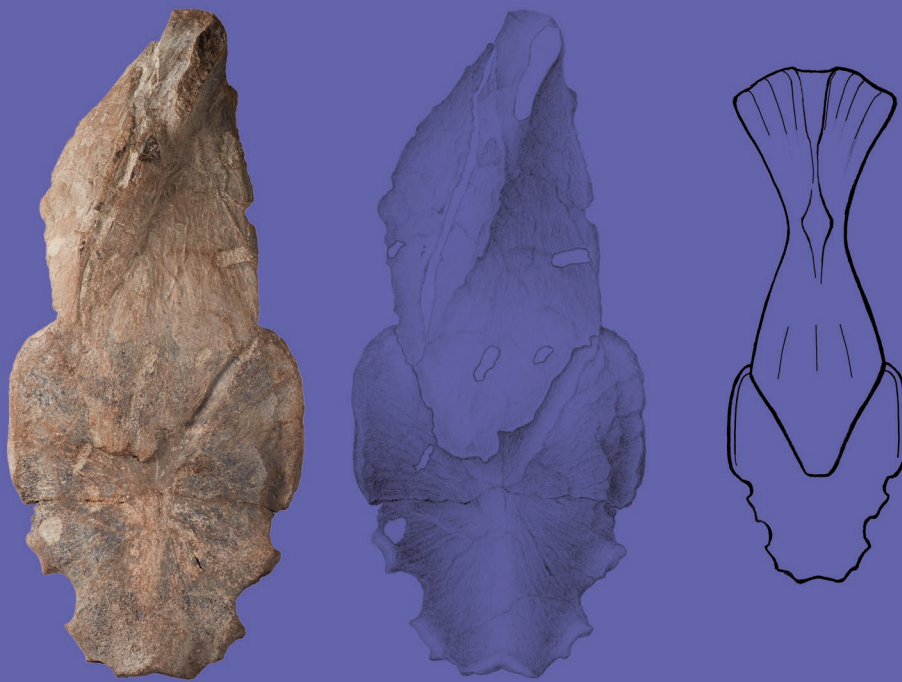 The sternum and interclavicle of *Aelurognathus tigriceps* (Broom & Haughton, 1913) (Therapsida: Gorgonopsia), with comments on sternal evolution in therapsids

Christian A. SIDOR & Arjan MANN

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The sternum and interclavicle of *Aelurognathus tigriceps* (Broom & Haughton, 1913) (Therapsida: Gorgonopsia), with comments on sternal evolution in therapsids

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ABSTRACT

Understanding the origin and evolution of the unique mammalian respiratory system hinges on our knowledge of the osteological changes in the pectoral apparatus (i.e., scapulocoracoid, cleithrum, clavicle, interclavicle, sternum) throughout the synapsid fossil record. Among non-mammalian therapsids, documentation of this anatomy is woefully incomplete, with groups such as dinocephalians and gorgonopsians remaining poorly documented. Here we provide a detailed anatomical description of an articulated sternum and interclavicle of a well-preserved specimen of *Aelurognathus tigriceps* (Broom & Haughton, 1913) from the Lopingian upper Madumabisa Mudstone Formation, Luangwa Basin of Zambia. The sternal morphology reveals new anatomical details on the attachment sites for the ribs, showing three distinct facets, and a previously undescribed depression on the ventral surface for the attachment of the interclavicle. We also provide a preliminary discussion of the morphological variation of these elements both within Gorgonopsia and across Therapsida.

KEY WORDS
Sternum,
Aelurognathus,
Gorgonopsia,
Zambia,
Permian,
Madumabisa Mudstone.

RÉSUMÉ

*Le sternum et l'interclavicule d'*Aelurognathus tigriceps *(Broom & Haughton, 1913) (Therapsida : Gorgonopsia), avec des commentaires sur l'évolution du sternum chez les Thérapsides.*
La compréhension de l'origine et de l'évolution du système respiratoire unique des mammifères dépend de notre connaissance des changements ostéologiques de l'appareil pectoral (scapulocoracoïde, cleithrum, clavicule, interclavicule, sternum) dans le registre fossile des synapsides. Chez les thérapsides non mammaliens, la documentation de cette anatomie est malheureusement incomplète, avec des groupes tels que les dinocéphales et les gorgonopsiens qui restent mal documentés. Nous présentons ici une description anatomique détaillée d'un sternum et d'une interclavicule articulés

d'un spécimen bien préservé d'*Aelurognathus tigriceps* (Broom & Haughton, 1913) provenant de la formation Madumabisa Mudstone supérieure du Lopingien, dans le bassin de Luangwa en Zambie. La morphologie sternale révèle de nouveaux détails anatomiques sur les sites d'attachement des côtes, montrant trois facettes distinctes, et une dépression précédemment non décrite sur la surface ventrale pour l'articulation avec l'interclavicule. Nous fournissons également une discussion préliminaire sur la variation morphologique de ces éléments au sein de Gorgonopsia et des Therapsida.

INTRODUCTION

Bendel *et al.* (2022) recently demonstrated that a specimen referred to the gorgonopsian *Gorgonops torvus* Owen, 1876 possessed a series of three ossified sternebrae posterior to the sternum (synonym of "manubrium" therein). They suggested several interesting evolutionary/functional implications for this multipartite system, including its relationship to the origin of the mammalian diaphragm and overcoming Carrier's constraint, but the lack of prior recognition of this anatomy in the more than 130-year history of gorgonopsian research highlights how little is documented about the group's postcranial morphology. Sigogneau (1970) focused on cranial anatomy in her systematic appraisal of the group, but provided additional examples of postcranial anatomy in a subsequent review (Sigogneau-Russell 1989). Indeed, most work has documented aspects of gorgonopsian postcranial anatomy on a case-by-case basis (e.g. Broom 1930; Colbert 1948; Tatarinov 2004; Sidor 2022), with broader comparisons and documentation of systematic variation seemingly elusive.

Here we describe an articulated sternum and posterior interclavicle for a specimen referable to *Aelurognathus tigriceps* (Broom & Haughton, 1913) from the upper Madumabisa Mudstone Formation of northeastern Zambia. Despite lacking sternebrae, this specimen is remarkably well preserved and was critical for the proper interpretation of the material described by Bendel *et al.* (2022). Furthermore, this specimen can serve as a starting point for a discussion of morphological variation in sternal morphology among gorgonopsians, including a reinterpretation of the sternum of *Cyonosaurus* sp. figured by Bendel *et al.* (2022). We hope that its detailed description, as well as the illustrations provided here, represent a fitting tribute to Diane Scott's exceptional career as a vertebrate morphologist, paleontologist, and scientific illustrator.

MATERIAL AND METHODS

NHCC LB350 was discovered by K. Angielczyk and collected as part of a long-term research project addressing the vertebrate assemblages of the Permian and Triassic of Zambia and Tanzania (Sidor & Nesbitt 2018). It was prepared for study at the Burke Museum by G. Livingston and K. Abrams using airscribes and pin vises. This specimen, as well as the skull roof of a small therocephalian with articulated vertebral column with ribs (NHCC LB1155) that was found in an adjacent exposure of rock, were preserved in a massively-bedded grayish-green siltstone with scattered olive claystone chips. It lacks the hematite-like coating typical of the fossils from the northern portion of the Luangwa Basin (Kitching 1963; Davies 1981), although such an encrustation otherwise occurred on fossils in the general area.

USNM PAL 412381 (*Cyonosaurus* sp.) is represented by a nearly complete skeleton including a sternum that was previously partially obscured by an overlapping right manus. In order to fully study the sternum of USNM PAL 412381, the sternum was further prepared to be free of the overlapping manus by S. Jabo and the second author of this paper at the USNM fossil preparation lab using airscribes and pin vises.

INSTITUTIONAL ABBREVIATIONS
AMNH   American Museum of Natural History, New York;
BP   Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg;
NHCC   National Heritage Conservation Commission, Lusaka;
SAM   Iziko South African Museum, Cape Town;
USNM   National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905
GORGONOPSIA Seeley, 1894
Genus *Aelurognathus* Haughton, 1924

Aelurognathus tigriceps (Broom & Haughton, 1913)

Scymnognathus tigriceps (Broom & Haughton, 1913): 26.

REFERRED MATERIAL. — NHCC LB350, a scattered partial skeleton of a large individual preserving the preorbital portion of the skull and lower jaws, both humeri, the proximal half of the right femur, the posterior portion of the interclavicle, and sternum (Table 1). Referral to *A. tigriceps* is based on the presence of five to six tightly packed maxillary postcanine teeth, a tall and bulbous snout, massive dentary symphysis, and a lower level of pachyostosis around the antorbital and jugal compared to other rubidgeines (Kammerer 2016).

HORIZON AND LOCALITY. — Collected from locality L1, upper Madumabisa Mudstone Formation, Luangwa Basin. This locality is approximately 13 kilometers south-southeast of Mulilo (Muchinga Province) and corresponds to locality 4 of Drysdall & Kitching (1963). Vertebrate fossils from the upper Madumabisa Mudstone Formation generally imply a Lopingian age (Angielczyk *et al.* 2014), but a more precise correlation for this locality will require the systematic review of historical specimens, given the updated biostratigraphic subdivisions recently proposed for the middle of the basin (Peecook *et al.* 2020). Detailed locality information is available from the NHCC or by contacting C.A.S.
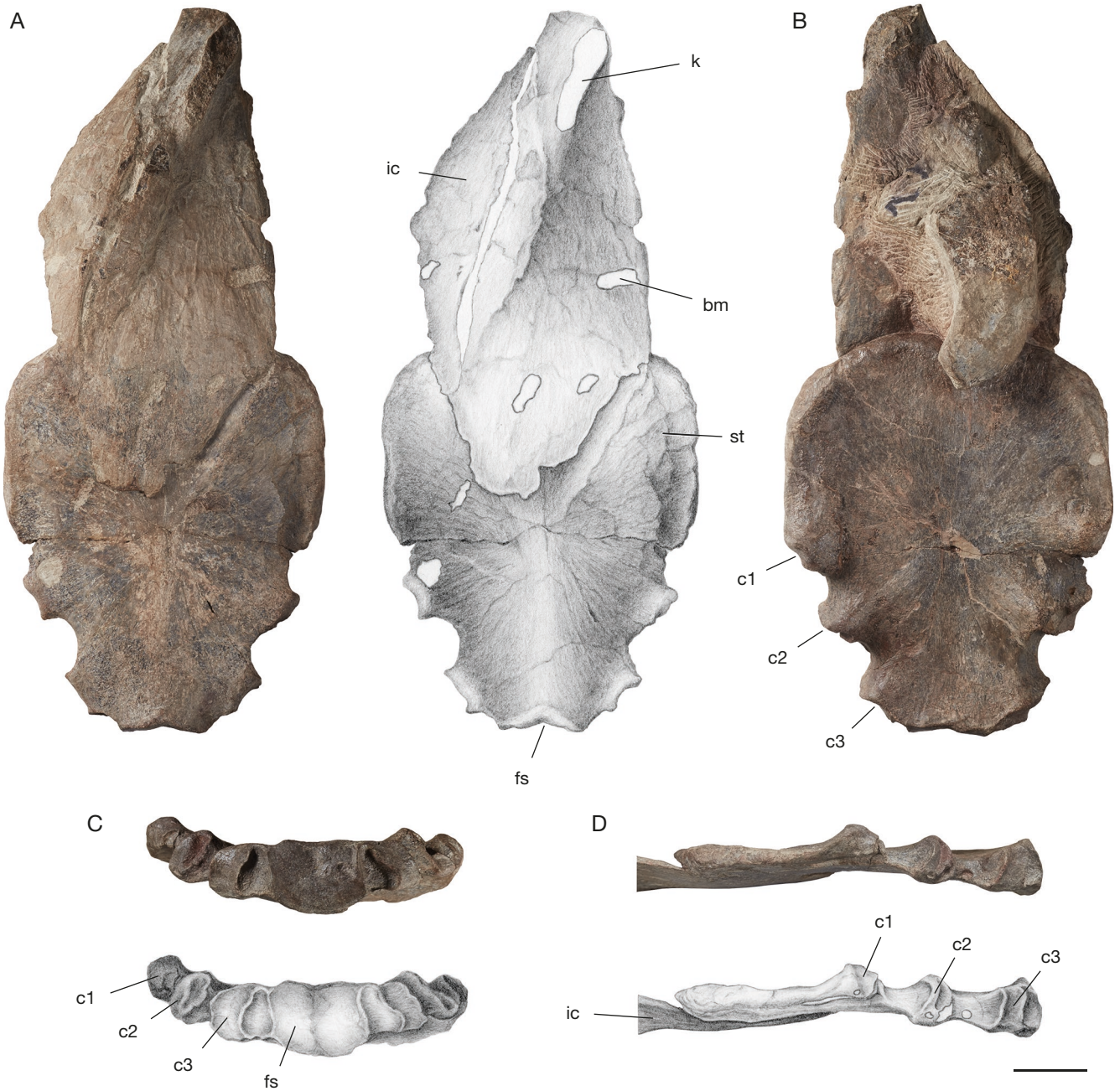
Fig. 1. — The sternum and interclavicle of *Aelurognathus tigriceps* (Broom & Haughton, 1913) (NHCC LB350). Specimen in: **A**, ventral view; **B**, dorsal view; **C**, posterior view; **D**, left lateral view. Anterior is to the top of the page in **A** and **B**, and to the left in **D**. Dorsal is to the top of the page in **C**. Abbreviations: **bm**, possible bite mark; **c1**, facet for articulation of first rib; **c2**, facet for articulation of second rib; **c3**, facet for articulation of third rib; **fs**, facet for articulation of first sternebra; **ic**, interclavicle; **k**, weathered ventral keel; **st**, sternum. Scale bar: 2 cm.

DESCRIPTION

Interclavicle

Figure 1A shows the sternum and interclavicle of NHCC LB350 in ventral view. The interclavicle lies superficial to the sternum, and has been displaced slightly anterolaterally as evidenced by a shallow impression on the ventral surface of the sternum that indicates their contact surface in life. The caudal portion of the interclavicle is relatively flat, with its lateral margins tapering posteriorly to form a blunted V-shape. Interestingly, this shape contrasts the condition depicted for *Aelurognathus*

Haughton, 1924 by Broom (1930: fig. 2), where the posterior margin of the interclavicle was indicated as being broadly curved. Based on the impression on the sternum, we believe the posterior end of the interclavicle would have been more pointed in life, as shown in the reconstruction of this element (Fig. 2A). Anteriorly, the interclavicle in NHCC LB350 tapers towards its "neck", which separates the anterior and posterior portions of the bone and features the base of an elongate ventral keel, unfortunately weathered off to a large extent in the current specimen. However, the outline of the keel shows

Skeleton	Mesurements
Skull preorbital length	167‡
Humerus (left)	
length*	211
width across distal epicondyles	97
minimum midshaft diameter	22
Humerus (right)	
length*	214
width across distal epicondyles	112
minimum midshaft diameter	23
Femur	
midshaft diameter, transverse	37
midshaft diameter, anteroposterior	22
head transverse width	57

that its lateral margins were subparallel and it had a slightly broader anterior end. The right flank of the interclavicle is dislocated and separated from the rest of the interclavicle by a long, matrix-filled longitudinal crack. Other damage includes several oval to irregularly shaped marks scattered across both sides of the interclavicle and sternum that we interpret as bite marks, likely due to scavenging. The ventral surface of the interclavicle shows a pattern of very fine radiating lines that diverge posteriorly. Its dorsal surface (Fig. 1B) is mostly obscured by matrix and a fragmentary right posterior coracoid, but based on what is seen in cf. *Arctops* sp. (NHCC LB396) and other gorgonopsians, one might expect more substantial striations to be present on the interclavicle where it contacted the sternum.

Sternum

The sternum of NHCC LB350 measures 103 mm in maximum anterior-posterior length and 82 mm transversely. Its outline is best observed in dorsal view (Fig. 1B), where it is shield-like, with a broad anterior portion that tapers, albeit irregularly, posteriorly. Most of the dorsal surface of the sternum forms a relatively shallow concave, or dish-shaped, surface. In lateral view (Fig. 1D), the ventral surface of its rib-bearing portion is angled slightly ventrally, which gives the sternum a slightly concave ventral surface when viewed from the side. As preserved, the element is not perfectly symmetrical, with most asymmetry concentrated about the outline of the costal facets. The anterior margin of the sternum is oriented transversely and is slightly thickened at the midline. This thickening continues onto the dorsal surface of the sternum for a short distance, but then flattens out both posteriorly and laterally. Overall, the element is thin dorsoventrally near its center (*c.* 6-8 mm), but is thickened to varying degrees around its perimeter, with the thickest area occurring posteriorly (16 mm). In dorsal view, the anterolateral corners of the sternum are slightly raised and lack finished bone surface. Several authors have suggested that these corners likely contacted the coracoids in life (Broom 1930; Colbert 1948; Sigogneau-Russell 1989).

Three well-defined costal articulations are present on each side of the caudal half of the sternum, with those on the left side being better preserved (Fig. 1D). The first costal facet is the smallest and is positioned at the boundary between the broad anterior portion of the sternum and where it begins to taper. On both sides, the second costal facet has a pocket of unfinished bone adjacent to it, suggesting this is a natural feature. The third costal facet is the best ossified and saddle-shaped, with a parallelogram-like outline. The anatomy preserved suggests that all three were mobile joints, not synarthroses. In dorsal or ventral views (Fig. 1A, B), a semicircular notch is present just posterior to each costal facet, with the anterior two having a sloping surface of finished bone, such that their ventral margin is lateral to their dorsal margin. The third notch is a deep, roughly triangular fossa of unfinished bone with a raised rim (Fig. 1C), unlike the preceding two notches that blend into the dorsal surface of the sternum. Bendel *et al.* (2022) suggested that the third rib articulated on a facet shared between the sternum and the first sternebra in *Gorgonops* Owen, 1876, which is the arrangement seen in modern mammals and would make sense based on developmental studies (Chen 1953). However, a corresponding inference in NHCC LB350 seems difficult given the wide separation of the third costal facet from the relatively narrow and posteriorly-facing sternebral articulation surface. In other words, the first sternebra would need to be very wide in order for it to share the third rib articulation with the sternum.

At the caudal end of the sternum, the articulation for the anteriormost sternebra has a complex shape. In ventral view (Fig. 1A), it can be seen to be formed by two faces that meet at a very high angle. In posterior view (Fig. 1C), the articulation surface as a whole is subrectangular in outline, with a rounded ventral margin, but each face is gently convex. There is no indication of a distinct articular surface for a costal cartilage, as implied by the reconstruction of *Gorgonops* by Bendel *et al.* (2022: fig. 2B). Broom (1930) inferred the presence of an additional element posterior to the sternum in his reconstruction of the pectoral girdle of *Aelurognathus*, and the prominent thickness of this region in NHCC LB350 supports his deduction.

The sternum of non-mammalian therapsids is often shown in ventral view, as it represents the external surface of the element, but this view affords relatively less anatomical detail than the dorsal view because the rib articulation surfaces generally point posterodorsolaterally. However, the semicircular notches posterior to each facet can remain prominent in ventral view. In NHCC LB350, the ventral surface of the sternum bears fine lines that radiate out from the center of the element. In addition, a striking feature is the well-developed anteroventral depression for the articulation of the interclavicle, which seems to have escaped notice in the gorgonopsian literature, if it is indeed a widespread feature. The surface of this depression is smooth, at least in the area where it is not covered by the interclavicle. On the left side, from the first costal articulation to the anterolateral corner, the sternum is fractured and displaced slightly dorsally. A gentle longitudinal ridge connects the depression for the interclavicle to
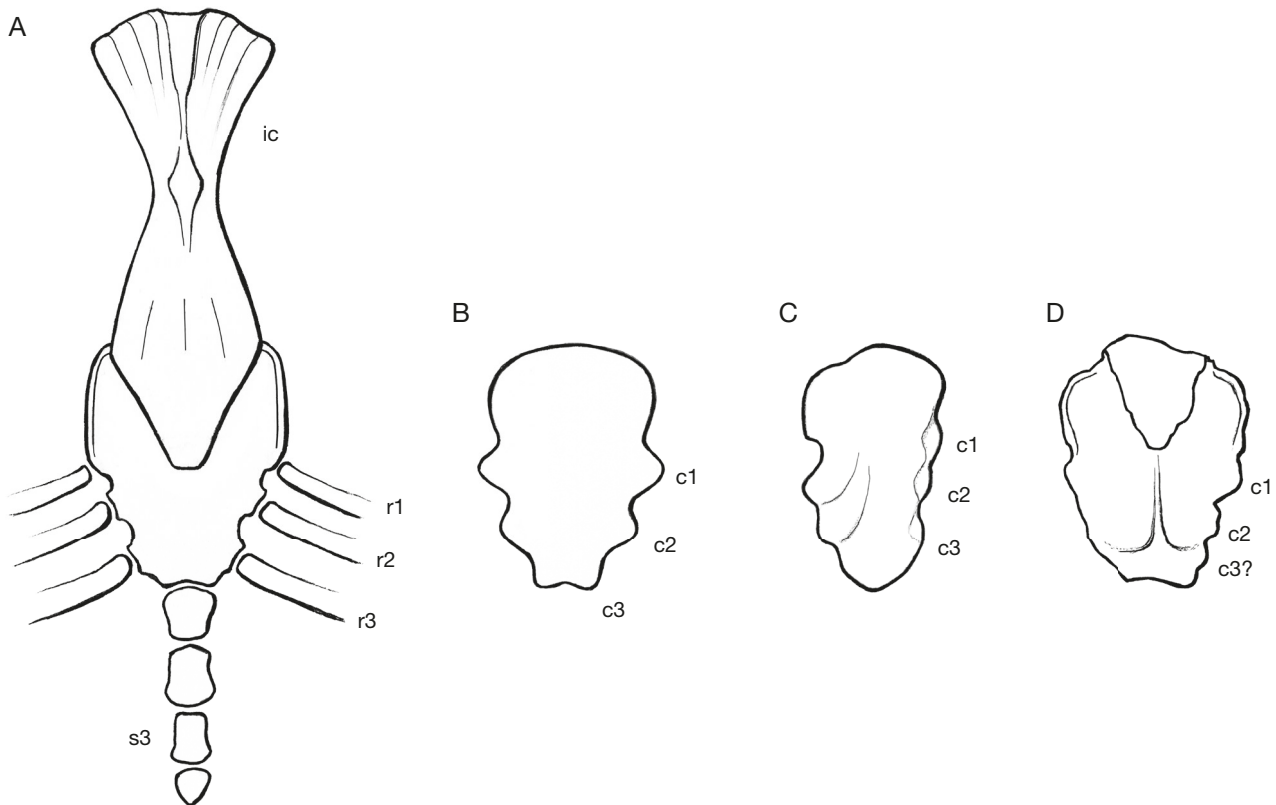
Fig. 2. — Sternal variation in gorgonopsians: **A**, reconstructed sternum and associated elements in *Aelurognathus tigriceps* (Broom & Haughton, 1913) (NHCC LB350) in ventral view. The anterior portion of the interclavicle is reconstructed on the basis of cf. *Arctops* sp. (NHCC LB396) and the sternebrae are based on the reconstruction of *Gorgonops torvus* Owen, 1876 (SAM-PK-K10591) by Bendel *et al.* (2022). Only the ribs articulating with the sternum are shown; **B**, sternum of *Gorgonops torvus* in ventral view; **C**, sternum of *Lycaenops ornatus* Broom, 1925 in dorsal view; **D**, *Cyonosaurus* sp. in ventral view (based on USNM PAL 412381). Abbreviations: **c1**, facet for articulation of first rib; **c2**, facet for articulation of second rib; **c3**, facet for articulation of third rib; **ic**, interclavicle; **r1**, first rib; **r2**, second rib; **r3**, third rib; **s3**, third sternebra. Drawings not to scale. Credits: B, redrawn from Bendel *et al.* 2022; C, redrawn from Broom 1930.

the sternebral articulation along the midline. To either side of this ridge, the ventral surface of the sternum is relatively flat, but forms a thickened rim adjacent to the costal facets.

DISCUSSION

STERNAL MORPHOLOGY IN GORGONOPSIANS

Sternal morphology has not been well documented among gorgonopsians and several discrepancies can be noted between the well-preserved specimen described here and the handful of previous publications (Fig. 2). For context, a single sternum has been documented for "*Aelurognathus*" *microdon* Boonstra, 1934 (SAM-PK-9344; Boonstra 1934), *Cyonosaurus* sp. (USNM PAL 412381; Bendel *et al.* 2022), *Gorgonops torvus* Owen, 1876 (SAM-PK-K10591; Bendel *et al.* 2022), and *Lycaenops ornatus* Broom, 1925 (AMNH FARB 2240; Broom 1930; Colbert 1948) and two examples are now known for *Aelurognathus tigriceps* (current specimen, SAM-PK-2342; Broom 1930). *Aelurognathus tigriceps* thus represents the only rubidgeine gorgonopsian with relevant anatomical data. In most cases, the above-mentioned sterna are visible in only a single view and have not been fully prepared free of matrix, thus leading to ambiguities about their shape and other

characteristics. For example, several of the specimens are markedly asymmetrical as figured (e.g. Fig. 2C), suggesting either deformation of the fossil and/or that the sternum was illustrated from an oblique angle.

In most gorgonopsians, the anterior end is the widest part of the sternum, except for *Gorgonops*, where its reconstruction by Bendel *et al.* (2022) shows the process for the first rib articulation as the widest point (Fig. 2B). In *Aelurognathus* and *Cyonosaurus* Olson, 1937, the lateral margins of the anterior half of the sternum are thickened, but in *Cyonosaurus* this thickening tapers to a thinner edge before the first costal facet (Fig. 3). A more significant difference is the marked "step" that occurs in *Cyonosaurus*: when the anterior and portions of the sternum are held horizontally, they are connected by a sheet of bone angled at roughly 45° when seen in lateral view, with the posterior end dorsal (Fig. 3C). Although there is a gentle angle made between the anterior and posterior portions of the sternum in *Aelurognathus* (Fig. 1D), the "stepped" condition in *Cyonosaurus* is noticeably distinctive, although it remains possible that this feature is the result of taphonomic deformation.

Bendel *et al.* (2022: supplementary fig. 1) showed *Cyonosaurus* (USNM PAL 412381) in what they indicated was a ventral view. However, we disagree with that interpretation.

Additional preparation of this specimen allows us to recognize a thin sheet of bone as the posterior process of the interclavicle articulating on the ventral surface of the sternum (Fig. 3A). The interclavicle is medially thickened and tapers posteriorly indicating the same triangular morphology seen in NHCC LB350. In contrast to the condition in *Aelurognathus*, *Cyonosaurus* has a median keel on the ventral surface of its sternum that grows taller posteriorly. Interestingly, the dorsal surface of the sternum of *Cyonosaurus* (Figs 2D; 3B) also preserves a midline ridge or keel anteriorly that is surrounded by concavities on either side. Additional gorgonopsian sterna will be needed to determine if well-defined dorsal and ventral midline ridges are unique to *Cyonosaurus*, or a common feature among early diverging gorgonopsians. Colbert (1948) described the dorsal surface of the sternum in *Lycaenops* as concave, with no mention of a median keel or ridge.

Another potentially taxonomically variable feature is the number of rib facets present on the sternum. *Aelurognathus* (NHCC LB350), an early diverging rubidgeine, clearly shows three costal facets, and Colbert (1948) and Bendel *et al.* (2022) suggested the same for *Lycaenops ornatus* (AMNH FARB 2240) and *Gorgonops torvus* (SAM-PK-K10591), respectively, although in the latter genus the third rib articulation was thought to be shared between the sternum and first sternebra. Interestingly, the first costal articulation in *Gorgonops*, as reconstructed by Bendel *et al.* (2022: fig. 2B), is located on a lateral projection of the sternum bounded on either side by notches, a condition that contrasts with the anatomy described here for *Aelurognathus* and *Cyonosaurus*, where notches are present only posterior to costal articulations. This, in combination with the lack of an apparent facet for the third rib facet posteriorly near the sternebral surface in *Aelurognathus*, suggests that either the third rib was "shifted" posteriorly in *Gorgonops* relative to *Aelurognathus* (Fig. 2A, B), or that the left side of the sternum in *Gorgonops*, which formed the based of its reconstruction in Bendel *et al.* (2022), misrepresents the anatomy for the taxon. Indeed, a photograph provided during the review process suggests that the right side of the sternum in *Gorgonops* conforms to the anatomy seen in *Aelurognathus* and *Cyonosaurus*, where the first rib facet is followed by a notch in the lateral surface of the sternum. Bendel *et al.* (2023) provided a revised description of sternal anatomy in the specimen of *Gorgonops* in question.

Determining the number of rib articulations in *Cyonosaurus* (USNM PAL 412381) is difficult. Two costal facets are clearly present, with the cranial one located at about mid-length of the sternum, as in *Aelurognathus*. However, the posterior end of the sternum is poorly preserved and difficult to prepare, but preparation suggests that it was likely to feature a third facet. Unfortunately, detailed anatomical comparisons between the sterna of *Cyonosaurus* and *Aelurognathus* are hampered by the preservation of the former. Furthermore, despite resurgent systematic research on gorgonopsians (e.g. Kammerer 2016; Kammerer & Masyutin 2018; Bendel *et al.* 2018), the position of *Cyonosaurus* still remains unclear pending a detailed anatomical and systematic revision. However, the likelihood that this gorgonopsian genus is valid is high with potential

diagnostic traits including a postcanine count of six to seven small, tightly packed, postcanine teeth that are displaced from the canine to the center of the maxilla, alongside a highly elongated, low snout, among other cranial features (Bendel *et al.* 2018). What is clear of *Cyonosaurus* is that it belongs to the non-rubidgeine gorgonopsians like the small-bodied gorgonopsians of South Africa (e.g. *Aelurosaurus* Owen, 1881, *Aloposaurus* Broom, 1910 and *Scylacognathus* Broom, 1913 [Bendel *et al.* 2018]). Given these affinities, the presence of only two well-developed costal rib facets present on the sternum of *Cyonosaurus* remains a possibility and could be representative of the plesiomorphic condition in gorgonopsians and therefore could potentially hold some character significance for phylogenetic analysis of Gorgonopsia. Only further descriptive studies of sternal morphology among early-diverging gorgonopsians can shed light on this hypothesis.

Colbert's (1948) monograph on an articulated skeleton of *Lycaenops ornatus* was a benchmark for understanding gorgonopsian postcranial anatomy. In his description of the sternum, Colbert (1948: 380) noted that "the anterior end of the bone is somewhat expanded laterally" but what he figured in plate 28 seems to show this expansion at the posterior end of the bone. Broom (1930) figured the same specimen in oblique right lateral (plate 27, part 3) and "front" (plate 28, part 17) views. Because the outline of the sternum is reversed between Colbert (1948) and Broom (1930), we suggest that the latter's "front" view corresponds to dorsal view. This specimen is currently on exhibit and so resolving these discrepancies or adding more detail to its description is difficult at this point.

EVOLUTION OF THE STERNUM IN THERAPSIDS

Bendel *et al.* (2022) reviewed the complex evolutionary history of the sternum in Permo-Triassic synapsids. They noted the sporadic appearance of ossified sterna among earlier-diverging therapsids (e.g. in biarmosuchians, derived anomodonts, gorgonopsians, derived therocephalians, and eucynodonts), with unossified sterna likely present in other groups (e.g. dinocephalians, early anomodonts, early therocephalians, early cynodonts). This pattern could either indicate multiple independent evolutions of the sternal ossification, as an unossified sternum is likely the plesiomorphic condition for synapsids (Romer & Price 1940), or a single origin at Therapsida with multiple reversals. Deciding between these options will likely require additional articulated specimens that can help distinguish between taphonomic loss of an ossified sternum or a true lack of ossification. Based on the current evidence, we favor the hypothesis of multiple evolutions of ossified sterna, as Bendel *et al.* (2022) seemed to do as well.

In the earliest amniotes, including pelycosaur-grade synapsids, the interclavicle is the most expansive ventral pectoral element and can be generalized into the presence of an expanded anterior ramus (e.g. diamond or T-shaped) that anchors the clavicles, and a long posterior stalk. This plesiomorphic, early amniote condition is retained in the earliest therapsid clades (e.g. biarmosuchians, dinocephalians, early anomodonts). In more derived therapsids, towards Mammalia, there is a well-established pattern of reduction and loss of the interclavicle
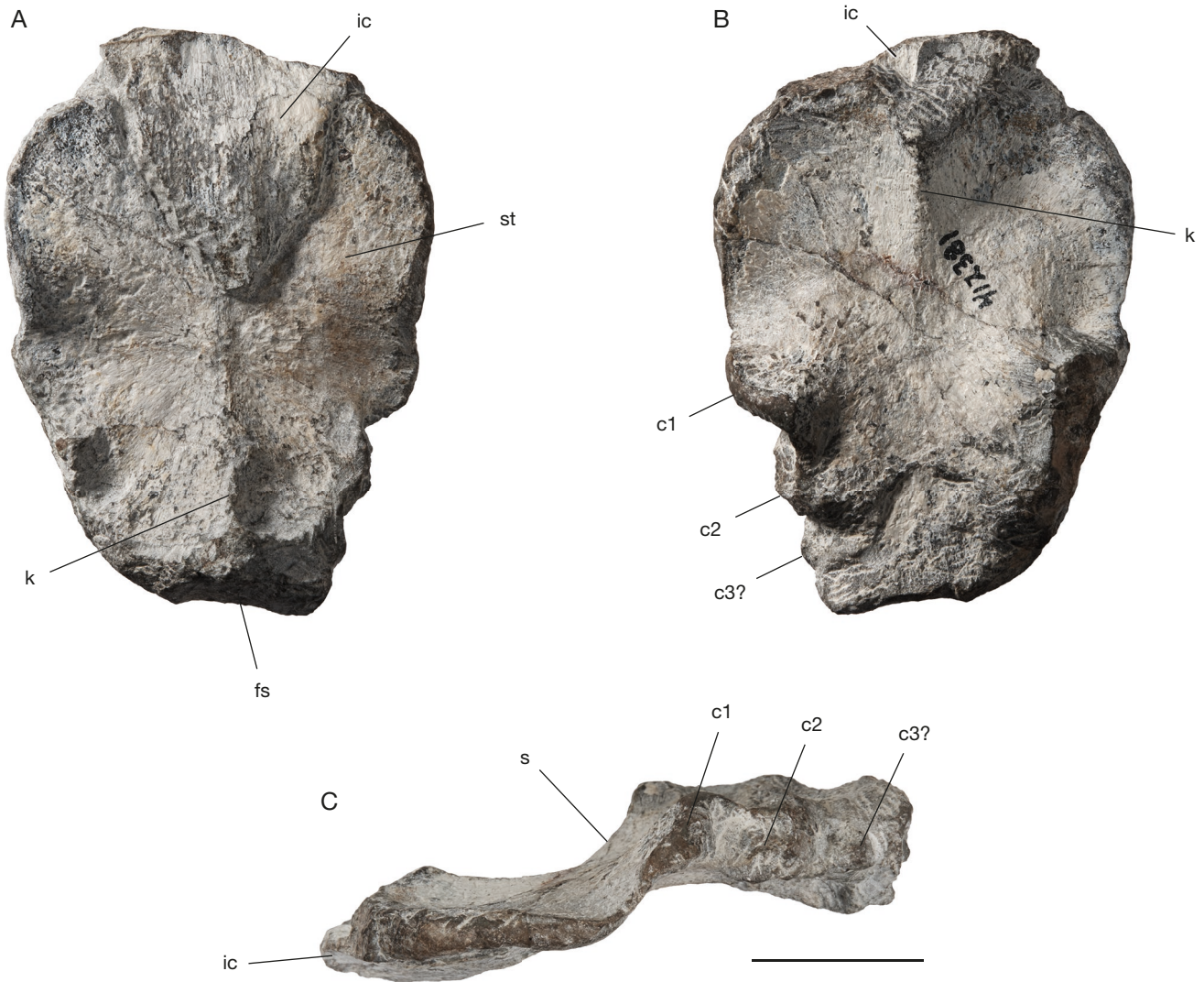
FIG. 3. — The sternum and posterior interclavicle of *Cyonosaurus* sp. (USNM PAL 412381): **A**, ventral view; **B**, dorsal view; **C**, left lateral view. Anterior is to the top of the page in **A** and **B**, and to the left in **C**. Abbreviations: **c1**, facet for articulation of first rib; **c2**, facet for articulation of second rib; **c3?**, possible facet for articulation of third rib; **fs**, facet for articulation of first sternebra; **ic**, interclavicle; **k**, keel; **s**, step between anterior and posterior portions of the sternum; **st**, sternum. Scale bar: 2 cm.

in favor of the sternum as the primary anchor for ribs and musculature, with the interclavicle considered lost in most therians (but see Buchholtz *et al.* 2021; Brent *et al.* 2023). Gorgonopsia appears to represent the earliest departure from the plesiomorphic amniote condition where the sternum and associated sternebrae are nearly as significantly developed as the interclavicle, in a condition perhaps not seen again until mammaliamorphs (Bendel *et al.* 2022). It is likely that this early adaptation was driven in part by their active feeding habits as the dominant macropredators of the late Permian, requiring greater metabolic and respiratory capabilities for pursuit of prey (Bendel *et al.* 2023). Indeed, the smaller size and shape of the interclavicle in comparison to dinocephalians and biarmosuchians seems similar to what is seen in therocephalians and some early-diverging cynodonts. This includes the reduction of the clavicular attachment sites and shortening of the posterior stalk, which in Therocephalia

and Gorgonopsia appear to strongly underlap the ventral surface of the sternum. There appears to be high variability in relative sternum and interclavicle morphology, including size and shape, among therapsids, perhaps rivaling that seen in later mammaliamorphs.

Brent *et al.* (2023) recently provided compelling evidence that the ancestral therian sternum was a composite structure formed by the fusion of the interclavicle and lateral plate mesoderm-derived sternal bands (see also Buchholtz *et al.* 2021), but several questions remain outstanding. For example, Brent *et al.* (2023) proposed that the sternal bands likely differentiated into anterior and posterior components when sternebrae first evolved in eucynodonts (and presumably in gorgonopsians independently). However, if our interpretation of *Aelurognathus* is correct, then it lacked a rib shared between the sternal plate and the first sternebra, which contradicts the proposed mechanism for sternebral formation (Chen 1953;

Brent *et al.* 2023). Unfortunately, the sternum of *Gorgonops* described by Bendel *et al.* (2022) lacks articulated ribs and so the placement of costal facets between adjacent sternebrae was inferred, and no distinct articular facets were described for those elements.

Sidor (2022) noted that assessing systematic variation in gorgonopsian postcrania will be an important goal to supplement the exclusively cranial phylogenetic analyses that are currently available (e.g. Kammerer 2016). The variation reported here among gorgonopsian pectoral morphology supports the importance of continued postcranial studies on Gorgonopsia and presents some potentially important phylogenetic variation. Historically, this type of comprehensive anatomical treatment has not been possible due to the lack of appropriate gorgonopsian postcranial remains (Sigogneau-Russell 1989; Kammerer 2016), however, recent collection efforts from South Africa, Tanzania, and Zambia have produced high quality gorgonopsians skeletons permitting new anatomical descriptions (Kato *et al.* 2020; Sidor 2022; Bendel *et al.* 2022, 2023). Furthermore, new comprehensive postcranial descriptions of Russian gorgonopsians *Viatkogorgon* Tatarinov, 1999, *Sauroctonus* Bystrov, 1955, and *Inostrancevia* Amalitzky, 1922 can add potentially important data to understanding the condition and morphological variations among early diverging gorgonopsians (Tatarinov 2004; Kammerer & Masyutin 2018). Finally, studies on gorgonopsian postcrania can have even greater potential to contribute to our understanding of major evolutionary innovations within Synapsida (Kemp 1982, 2007; Bendel *et al.* 2022).

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